

Global invasion patterns and dynamics of disease vector mosquitoes

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The manuscript "Global invasion patterns and dynamics of disease vector mosquitoes" by Pabst et al. describe the global invasion patterns of mosquitoes that are vectors of human diseases and analyze the drivers shaping them.

- I agree with the authors about the importance of creating an updated database of mosquito first records. However, mosquito ecology plays a major role in their invasion and establishment efforts, and their success in colonizing new regions depends on many socioecological factors. Mosquito presence, or in this case, first records is only a small piece of the puzzle. Mosquito community composition, abundance, host availability and diversity, and pathogen circulation must also be considered to assess the risk of mosquito-borne pathogen transmission.

- Another important point is that only selected species can thrive in urban areas and will reach numbers high enough to become a public health threat. Moreover, most invasive species other than known primary mosquito vector species (e.g., *Aedes aegypti*, *Aedes albopictus*, *Culex quinquefasciatus*, *Anopheles gambiae*) have only secondary epidemiological importance, *Culex coronator* is a good example. One could argue that a higher richness of secondary vectors would lead to a dilution effect, thus being beneficial to public health.

- The conclusions of the manuscript are not supported by their results.

"We show that the rates of mosquito introductions into new regions and the emergence of novel non-native species have been increasing in recent centuries, with a particularly pronounced increase observed in recent decades."

"While it is plausible that enhanced surveillance and import controls have contributed to this trend by increasing detection rates (e.g., at ports and airports⁴³), the dramatic rise in first records of newly introduced species strongly matches the substantial expansion and diversification of global trade during the mid-19th century."

Mosquito surveillance has greatly increased over time. Most large cities in the US have large surveillance systems comprised of hundreds of traps, see <https://vectorsurv.org> as an example. Another important point is that there is a major bias in surveillance efforts between low- and high-income countries and even at the jurisdiction level. Different trapping efforts, trap types, lures, etc. also have an impact on the detection of the presence of mosquitoes.

Import controls at ports and airports are just a small part of surveillance systems, and even though they can be effective, such as the detection of *Aedes albopictus* in Amsterdam (DOI: 10.3390/ijerph17103450), many other routes are under the radar and play a much more important role. A good example is the introduction of *Aedes vittatus* to Cuba (DOI: 10.1016/j.actatropica.2020.105739), detected by a surveillance system that's been recently installed considering the scope of this study.

- Another important point is that the environment is key for the proliferation of mosquito species and hotspot analysis at the country level does not provide enough resolution to improve preparedness and guide mosquito control operations.

"Ultimately, our work shows that increased attention should be paid not only to well-known primary vectors such as *Ae. albopictus* and *Ae. aegypti*, but also to other increasingly dispersed mosquito vectors, as they can significantly contribute to the maintenance of pathogens."

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

General

This study examines the invasion patterns of mosquito vectors since their first known introduction, providing quantitative estimates of the invasion process. These findings align with what is generally understood about mosquito invasions. Understanding the dynamics of introductions of non-native disease vector mosquitoes, as well as the patterns and drivers of their spread and establishment, is critical for developing effective surveillance and control measures to prevent future invasions. Hence, the value of this study. The analysis is robust, and the presentation of results is clear. However, I have concerns regarding the database underpinning this analysis. Several points need to be explicitly addressed and discussed: (1) Taxonomic uncertainties and species synonyms: how did the authors handle taxonomic uncertainties and species synonyms? For example, *Culex quinquefasciatus* has many synonyms, with its current description dating back to 1823, but its introduction reported around 1500. Similarly, what is meant by *Culex pipiens* s.l.? Additionally, Table S5 in the Supplementary materials should include the author(s) and year of the species descriptions; (2) Species identification methods: did the authors reassess species identifications, particularly for records predating the era of DNA-based methods now commonly used to validate morphological identifications?; (3) Import pathways: did the authors reassess the import pathways for mosquito introductions, or was the information provided in the original publications deemed sufficient?; (4) Eradicated introductions: How did the authors address cases of successful introductions that were later eradicated, such as *Anopheles gambiae* s.l. in Brazil? How were these accounted for in the database?

Introduction.

- Lines 55-59. The presence of a competent vector is a prerequisite for local transmission to occur, but the authors should also recognize that the introduction of the virus is a key driver as well. Zika is a prime example: the vector was present but only after the introduction of the virus the large outbreak occurred in the Americas. Also, in Europe, the autochthonous transmission of arboviruses so far is linked to index cases with a travel history to endemic countries.
- Lines 63-66. The limited active dispersal ability of mosquitoes is species dependent. *Aedes vexans* for example can disperse actively over long distances. This statement should be made more specific or referring to the fact that passive dispersal is an important driver of global expansion of mosquitoes.
- Lines 70-73. OK but this depends also very much on the larval biology see e.g. the *Anopheles* mosquitoes are unlikely to be transported as larvae except maybe *Anopheles stephensi* which breeds in man-made containers and cisterns.

Results.

- Line 151. What do the authors mean by "unaided secondary spread". Is this active dispersal from an initial point of establishment?
- Figure 3. How did you deal with uncertainties about the species identification e.g. the spread of *Aedes albopictus* in the UK is not in line with what is known (see e.g. the ECDC maps).
- Figure 5 E and F what is your estimate representing. Please specify and use the appropriate term.

Methods

- Line 335. Data compilation. This data compilation is a large effort. The quality of the data is key for the analysis. How did you ensure data quality in terms of content and in terms of data entry (see general comment above)?
- Line 339. Did you exclude the possible detection of a pathogen in blood-fed mosquitoes as the detection in wild caught female mosquitoes is not enough to consider the species as a vector.
- Line 365. Introduction pathways. How did you actually assess the introduction pathways as this is often not very well known or proven. Did you collect this information from the selected literature and if yes, did you reassess the conclusions of the authors?
- Line 427-435. Referring to e.g. the gross domestic product per capita and the total trade openness in US\$, what actual measure was taken: an long-term average, the current 2024 value. Please specify and indicate why this indicator and time period has been chosen.

- Numbering of figures should be according to appearance in the text e.g. figure 1 and 2

(Remarks on code availability)

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The authors have addressed all the points I raised.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

I thank the authors for addressing the different points identified by the reviewers. The Methods section has been expanded and clarification made as per reviewers request. I have no further comments.

(Remarks on code availability)

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Responses to the reviewers

Reviewer #1 - General (Remarks to the Author)

The manuscript “Global invasion patterns and dynamics of disease vector mosquitoes” by Pabst et al. describe the global invasion patterns of mosquitoes that are vectors of human diseases and analyze the drivers shaping them.

Response to Rev#1- General

We thank the reviewer for the overall positive feedback and the suggestions provided, which helped to improve our work.

Comment Rev#1-1: I agree with the authors about the importance of creating an updated database of mosquito first records. However, mosquito ecology plays a major role in their invasion and establishment efforts, and their success in colonizing new regions depends on many socio ecological factors. Mosquito presence, or in this case, first records is only a small piece of the puzzle. Mosquito community composition, abundance, host availability and diversity, and pathogen circulation must also be considered to assess the risk of mosquito-borne pathogen transmission.

Response to Rev#1-1: We fully agree that mosquito-borne pathogen transmission is shaped by a large number of factors, including mosquito community composition, host availability, and pathogen circulation. However, we focus on a critical factor for disease emergence: the global distribution of mosquitoes as disease vectors, and how this is influenced by human activity. While we do not directly assess disease risks - a task that would not be feasible given the high number of species and regions analyzed - we provide a foundation dataset that highlights changes in vector distribution through first introduction records in new regions.

We emphasize that human-driven changes in mosquito vector distributions are fundamentally reshaping global disease patterns, and have therefore added a paragraph with historical examples to undermine the importance of tracking introduction records (lines 343-350):

“In 2007, Europe’s first autochthonous chikungunya outbreak in Italy was enabled by the invasive *Ae. albopictus*, first recorded there in 1990^{60,61}. Similarly, Zika virus, once restricted to Central Africa in the 1950s, reached pandemic levels across tropical regions in the 2010s, driven by the earlier human-mediated dispersal of *Ae. aegypti*¹⁶. The introduction of *Anopheles gambiae* s.l. in Brazil and Mauritius transformed malaria from an endemic to an epidemic threat²⁰. These and many other cases underscore the critical importance of understanding where competent vectors are distributed and how their distributions are changing over time.”

16 Chang, C., Ortiz, K., Ansari, A. & Gershwin, M. E. The Zika outbreak of the 21st century. *Journal of Autoimmunity* 68, 1–13 (2016).

20 Lounibos, L. P. Invasions by Insect Vectors of Human Disease. *Annu. Rev. Entomol.* 47, 233–266 (2002).

60 Dalla Pozza, G. & Majori, G. First record of *Aedes albopictus* establishment in Italy. *J Am Mosq Control Assoc* 8, 318–320 (1992).

61 Rezza, G. et al. Infection with chikungunya virus in Italy: an outbreak in a temperate region. *The Lancet* 370, 1840–1846 (2007).

We agree that in parts of our manuscript the distinction between vector occurrence and risk of disease transmission was not fully clear. Accordingly, we made an effort to improve this

distinction in this new version. Specifically, we have added the sentence (see lines 88-90): “this knowledge serves as a foundation for further risk assessment, mosquito ecology, and disease dynamics research.”

We have also emphasized this distinction in the discussion and added a paragraph arguing on the importance of tracking the first records as vector introduction can serve as precursors of transmission; although in many cases this does not lead to disease outbreaks (see from line 335):

“Ultimately, we emphasize that while the geographical expansion and presence of a mosquito vector does not directly translate to disease outbreaks, it does create the potential for such. Human-driven changes in mosquito vector distributions are fundamentally reshaping global disease patterns²⁹. [...]”

29 Kraemer, M. U. G. *et al.* Past and future spread of the arbovirus vectors *Aedes aegypti* and *Ae. albopictus*. *Nat Microbiol* **4**, 854–863 (2019).

Comment Rev#1-2: Another important point is that only selected species can thrive in urban areas and will reach numbers high enough to become a public health threat. Moreover, most invasive species other than known primary mosquito vector species (e.g., Aedes aegypti, Aedes albopictus, Culex quinquefasciatus, Anopheles gambiae) have only secondary epidemiological importance, Culex coronator is a good example. One could argue that a higher richness of secondary vectors would lead to a dilution effect, thus being beneficial to public health.

Response to Rev#1-2: We thank the reviewer for raising this point. Whether a higher richness of secondary vectors could lead to a dilution effect and thus be beneficial to public health is a compelling question. While a dilution effect is possible, secondary vectors may also sustain pathogen transmission during periods when primary vectors are less active or absent due to their differing ecological requirements/behavior. For example, *Anopheles arabiensis* is adapted to drier conditions and may sustain malaria transmission during the dry season in subtropical areas (Kweyamba et al. 2025). Additionally, one major concern here is that the introduction of secondary vectors may lead to complacency among decision-makers, as their perceived risk is often lower, potentially reducing investment in control measures and allowing pathogens to persist.

Hence, these multiple effects of secondary vectors, regardless of their type of role, illustrates well why it is also important to monitor their distribution, as we do in our work. The distributional information we provide for them can, for instance, help justify anticipatory studies on their potential effects within local epidemiological contexts, facilitating proactive risk assessments.

Comment Rev#1-3: The conclusions of the manuscript are not supported by their results. “We show that the rates of mosquito introductions into new regions and the emergence of novel non-native species have been increasing in recent centuries, with a particularly pronounced increase observed in recent decades.”

“While it is plausible that enhanced surveillance and import controls have contributed to this trend by increasing detection rates (e.g., at ports and airports⁴³), the dramatic rise in first records of newly introduced species strongly matches the substantial expansion and diversification of global trade during the mid-19th century.”

*Mosquito surveillance has greatly increased over time. Most large cities in the US have large surveillance systems comprised of hundreds of traps, see <https://vectorsurv.org> as an example. Another important point is that there is a major bias in surveillance efforts between low- and high-income countries and even at the jurisdiction level. Different trapping efforts, trap types, lures, etc. also have an impact on the detection of the presence of mosquitoes. Import controls at ports and airports are just a small part of surveillance systems, and even though they can be effective, such as the detection of *Aedes albopictus* in Amsterdam (DOI: 10.3390/ijerph17103450), many other routes are under the radar and play a much more important role. A good example is the introduction of *Aedes vittatus* to Cuba (DOI: 10.1016/j.actatropica.2020.105739), detected by a surveillance system that’s been recently installed considering the scope of this study.*

Response to Rev#1-3: We thank the reviewer for the valuable feedback on this point. We fully agree that mosquito surveillance has significantly increased over time, particularly in high-income countries. Thus, we also acknowledge that there are disparities in surveillance efforts between low- and high-income countries, as well as at the jurisdictional level and over time. In this regard, the possibility that the observed temporal trends of recording could, to some extent, reflect improved monitoring efforts is justified. To clarify this point further, we have now revised the text of the manuscript to emphasize that our analysis focuses on ‘first records’ (i.e., the date of the species’ first record reported in a region beyond their native range; pls see e.g., Seebens et al., 2017, Schertler et al. 2024 and Capinha et al., 2023 for key studies defining and using these data) rather than the actual introduction dates (see for example lines 28, 87, 95, 121, 162, 243, 274, 292, 305, 306, 333, 359, 488). Additionally, we now also explicitly mention this issue in the discussion. There, it now reads (line 276 onwards):

“To some extent, the temporal trend of first records we documented likely reflects improvements in global surveillance efforts. Many countries now employ multiple surveillance tools, including citizens science initiatives^{38,39} and have established active surveillance systems^{26,37,40}, particularly at entry points such as ports and airports, as well as urban areas to monitor mosquito presence. For example, first record rates were substantially higher in North America (Fig. 1B), likely because the U.S. and Canada have significant biodiversity monitoring capacities, which enhance the detection of non-native species (e.g., USA <https://vectorsurv.org>).”

²⁶ Wilke, A. B. B. et al. Urbanization creates diverse aquatic habitats for immature mosquitoes in urban areas. *Sci Rep* 9, 15335 (2019).

³⁷ Derrai, J. G. B. Exotic mosquitoes in New Zealand: a review of species intercepted, their pathways and ports of entry. *Aust N Z J Public Health* 28, 433–444 (2004).

³⁸ FLI & ZALF. Mückenatlas. Leibniz-Zentrum für Agrarlandschaftsforschung (ZALF) e.V., Müncheberg (Deutschland) und Friedrich-Loeffler-Institut, Bundesforschungsinstitut für Tiergesundheit (FLI) (2023).

³⁹ IHMT NOVA. MosquitoWeb: A platform for mosquito-related data. <https://mosquitoweb.ihmt.unl.pt/> (no Year).

⁴⁰ Centro de Estudos de Vetores e Doenças Infeciosas Doutor Francisco Camburnac. Relatório REVIVE 2023 - Culicídeos, Ixodídeos e Flebotomos: Rede de Vigilância de Vetores. Instituto Nacional de Saúde Doutor Ricardo Jorge, IP (2024).

We further mention in this section, that it also remains plausible that these first records reflect, to a considerable extent, actual introduction trends. Non-intentional insect introductions are strongly influenced by the volume, diversity, and geographical reach of traded commodities and human travel, factors that have evolved in ways consistent with our findings (Hulme 2021). Furthermore, these trends also align with patterns documented in other unintentionally dispersed taxa (Seebens et al., 2017, Jingjing et al. 2023, Bertelsmeier et al. 2017, Bonnamour et al. 2021, Monteiro et al. 2022). We now added this in the discussion from lines 286-290:

“However, it is also likely that the sharp rise in first records of newly introduced species reflects actual introduction trends to a considerable extent, as it coincides with the substantial expansion and diversification of global trade during the mid-19th century³⁵. Furthermore, these trends also align with patterns documented for many other unintentionally dispersed taxa^{3,6,41–43}.”

3 Seebens, H. et al. No saturation in the accumulation of alien species worldwide. *Nature Communications* 8, 1–9 (2017).

6 Bertelsmeier, C., Ollier, S., Liebhold, A. & Keller, L. Recent human history governs global ant invasion dynamics. *Nat Ecol Evol* 1, 0184 (2017).

35 Hulme, P. E. Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. *One Earth* 4, 666–679 (2021).

41 Bonnamour, A., Gippet, J. M. W. & Bertelsmeier, C. Insect and plant invasions follow two waves of globalisation. *Ecology Letters* 24, 2418–2426 (2021).

42 Jingjing, D., Siming, F., Jiaqiang, Z., Juan, S. & Te, L. Analysis of insect pests identified to species that were intercepted at Chinese ports of entry. *MBI* 14, 641–657 (2023).

43 Monteiro, M. et al. Patterns and drivers of the global diversity of non-native macrofungi. *Diversity and Distributions* 28, 2042–2055 (2022).

Finally, we account for unequal surveillance efforts in our models by examining spatial differences in the number of species recorded. For this, we incorporated a variable that represents expected biases, based on a metric developed by Early et al. (2016) that quantifies countries' proactive and reactive capacity to invasive alien species (please see methods section for a detailed description) For example, this variable identifies Australia, Austria, Canada, New Zealand, the United Kingdom, and the USA as the six countries with the highest detection capacity. Hence, this variable largely accounts for regional disparities in detection effort. Additionally, country size is also included as a variable, as larger countries are more likely to receive a higher number of species simply due to an area effect (MacArthur & Wilson 1963). Then, our models identify hotspots only when the number of introduced mosquitoes is higher than expected according to detection effort and area, indicating a truly higher propensity for introductions rather than merely reflecting surveillance biases or area effects.

Comment Rev#1-4: Another important point is that the environment is key for the proliferation of mosquito species and hotspot analysis at the country level does not provide enough resolution to improve preparedness and guide mosquito control operations.

“Ultimately, our work shows that increased attention should be paid not only to well-known primary vectors such as Ae. albopictus and Ae. aegypti, but also to other increasingly dispersed mosquito vectors, as they can significantly contribute to the maintenance of pathogens.”

Response Rev#1-4: As mentioned above (Rev#1-1, and later in Rev#2-5), while multiple factors contribute to disease emergence, human-mediated vector introductions have arguably been the primary driver of major shifts in the global geography of vector-borne diseases. By identifying global trends and highlighting regions with high rates of mosquito introductions, our work serves as an early warning system to improve surveillance and preparedness at broader

scales. For example, identifying a non-native species within a continent or in a neighboring country can trigger targeted surveillance and preventive measures in high-risk regions. Nevertheless, we agree that in a second step following our comprehensive assessment, future studies should zoom into the regional, environmental context to inform management and control actions. This is however beyond the scope of this manuscript.

By showing that 25% of the 184 mosquito species with known medical significance have already been transported by human activity into regions globally and through the distinction into introduced and established invasion status our database provides important information for prioritization and follow-up assessments on vector-borne disease risk management.

Reviewer #2 (Remarks to the Author):

Rev#2-General

This study examines the invasion patterns of mosquito vectors since their first known introduction, providing quantitative estimates of the invasion process. These findings align with what is generally understood about mosquito invasions. Understanding the dynamics of introductions of non-native disease vector mosquitoes, as well as the patterns and drivers of their spread and establishment, is critical for developing effective surveillance and control measures to prevent future invasions. Hence, the value of this study. The analysis is robust, and the presentation of results is clear.

However, I have concerns regarding the database underpinning this analysis. Several points need to be explicitly addressed and discussed:

Response Rev#2-General

We appreciate the reviewer's time and thoughtful review of our manuscript. We have improved the description regarding taxonomy and the timing of introductions, which were not adequately addressed in the original version of the manuscript.

Our initial plan was to publish the database separately as a data paper, to provide a comprehensive description of its structure and validation processes. With this in mind, we did not elaborate sufficiently on the data recording process in the manuscript, which we now realize left readers with incomplete information. In response to the reviewer's comments, we have made significant improvements to the description of the data collection process and the database in the methods section of the revised manuscript. We further created a supplementary file elaborating all the Suppl. Material files and how they are connected. We hope these changes address the reviewer's concerns and provide the necessary clarity (see detailed descriptions in Response Rev#2-1 to 4, Resp. Rev#2-11).

Comment Rev#2-1: (1) Taxonomic uncertainties and species synonyms: how did the authors handle taxonomic uncertainties and species synonyms? For example, *Culex quinquefasciatus* has many synonyms, with its current description dating back to 1823, but its introduction reported around 1500. Similarly, what is meant by *Culex pipiens* s.l.? Additionally, Table S5 in the Supplementary materials should include the author(s) and year of the species descriptions;

Response Rev#2-1: We thank the reviewer for highlighting these issues. Accordingly, we have now expanded the methods section to provide a more comprehensive explanation of the data collection process, including taxonomy (see three new paragraphs on “Taxonomy”, “Year of first record” and “Potential biases”, lines 391-423):

“Taxonomy

The mosquito taxonomy used is consistent with the Walter Reed Biodiversity Unit WRBU⁶³, <https://wrbu.si.edu>. Where the species may have been recorded under a different name, we have used the currently accepted nomenclature. For example, *Anopheles arabiensis*, although originally identified as *Anopheles gambiae* s.l., was introduced to Brazil in 1930⁶³. Species forms and subspecies within the same species have been combined under a single species name. Therefore, the database includes two columns: “Species”, which denotes the name as cited in the literature, and “SpeciesUsed”, which represents the name used here. Additionally, to address concerns regarding the species identification, we have included a column specifying the certainty of species identification. The identification methods are categorized as follows: Molecular: identification based on DNA analysis; morphological: identification based on optical characteristics; disease outbreak: identification inferred from historical disease outbreak; estimation: presence inferred based on indirect evidence; unknown: source does not specify identification method.

Year of first record

Many records provided only approximate or non-standardized dates for mosquito introductions. To ensure consistency, all dates were converted to a four-digit year format using predefined guidelines (Table 3). For introductions that date back before the 20th century, we used approximations of the date of introduction based on disease descriptions and estimations from other sources (e.g. *Ae. aegypti* introductions inferred from early reports of yellow fever). We applied a standardized approach to approximate dates, ensuring transparency and reproducibility.

Table 3. Guidelines for converting introduction dates.

FirstRecordDatePrecise	YearUsed	Rule
2012	2012	If precise date of introduction was reported, year was used
1870s	Random number between 1870 and 1879	Approximate decade range
After 1879	1879	Earliest possible year used
Before 1960	1960	Latest possible year used

16 th to 18 th century	Random number between 1500 and 1799	Historical estimate
Yellow Fever or Dengue outbreak in the Americas and Europe	Year of outbreak	Proxy for <i>Aedes aegypti</i> introduction
Malaria outbreak in Egypt	Year of outbreak	Proxy for <i>Anopheles arabiensis</i> introduction
First continental introduction in 1495, present today in neighboring countries of the same continent with no specific introduction date	Random number between 1495 and 1900	Spread inferred from contiguous presence

Potential biases

Despite our systematic approach, several biases may influence the dataset. The availability and accuracy of records vary across geographic regions and time periods, potentially leading to underreporting in less-studied areas. Additionally, scientific interest in non-native mosquito species may fluctuate, impacting the completeness of published records. To address geographic bias, we incorporated a proxy variable in our hotspot and coldspot models to account for regional research effort specific to non-native species, as derived from Early et al.⁶⁴. Additionally, language-related bias may have been introduced, as the search terms utilized were restricted to English.

As species continue to be dispersed by human activity, additional introductions may be documented, requiring updates to the database. To facilitate ongoing data refinement, we will publish the dataset in an openly accessible format that allows revision and expansion.”

⁶³ Wilkerson, R. C., Linton, Y.-M. & Strickman, D. *Mosquitoes of the World*. (Johns Hopkins University Press, Baltimore, Maryland, 2021).

⁶⁴ Early, R. et al. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat Commun* **7**, 12485 (2016).

We also added a separate description file (Suppl. Material Read Me) detailing all data files and their columns. See graphical overview here (Figure 1).

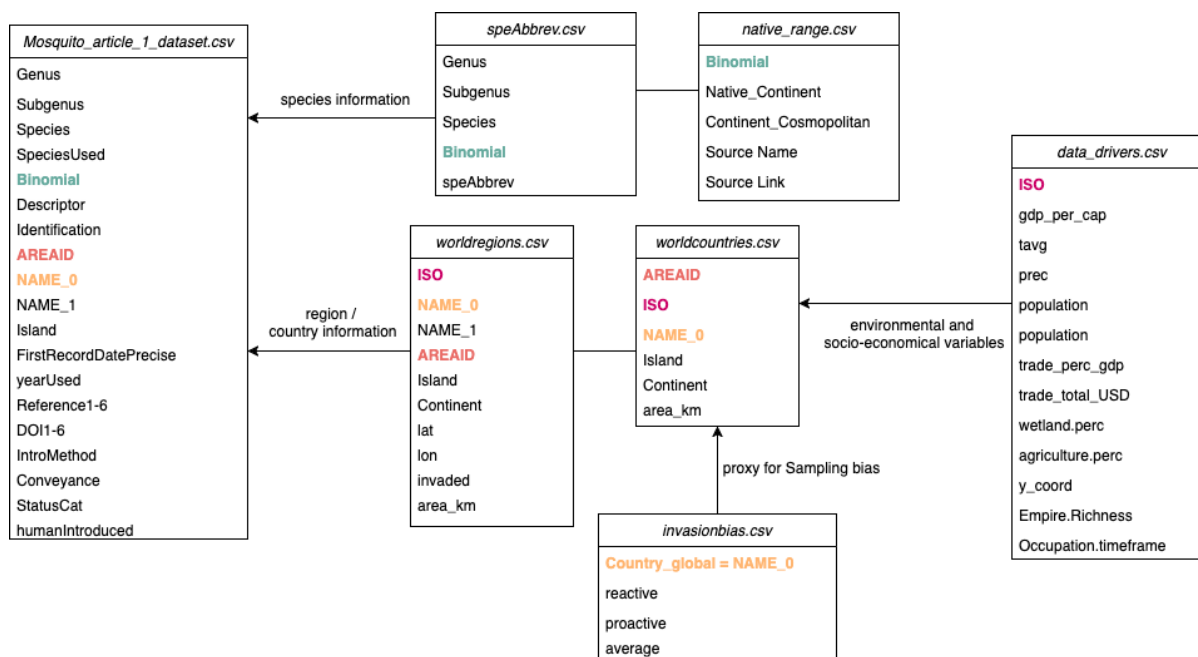


Figure 1. Graphical Overview of the Suppl. Material Read me file. Illustration showing how the CSV files are interconnected. ID variables linking the files are color-coded for clarity. For detailed descriptions of the variables in each file, refer to Tables 1-7.

The reference to *Culex pipiens s.l.* was a typo and has been corrected to *Culex pipiens s.s.*. This taxon includes the two forms, *Culex pipiens f. molestus* and *Culex pipiens f. pipiens*, as well as the subspecies *Culex pipiens pallens* and cases where the specific form was not identified in the source. To ensure accuracy, we have thoroughly revised the manuscript regarding species from the same complex. During this review, we also made some minor adjustments to the database, which reflect newly available information, leading to minor changes of numbers and figures throughout the manuscript.

As requested, the author of species descriptions has now been added to Table S5.

Furthermore, we will publish the dataset in an openly accessible format asap that will allow revision and expansion (i.e., in a so-called ‘living database’) (see lines 421-423):

“As species continue to be dispersed by human activity, additional introductions may be documented, requiring updates to the database. To facilitate ongoing data refinement, we will publish the dataset in an openly accessible format that allows revision and expansion.”

Comment Rev#2-2: (2) Species identification methods: did the authors reassess species identifications, particularly for records predating the era of DNA-based methods now commonly used to validate morphological identifications?;

Response Rev#2-2: To address this, we have included a column in our database that specifies the certainty of species identification, as described now in the Methods section as follows (see Rev#2-1, lines 498-410):

“Additionally, to address concerns regarding the species identification, we have included a column specifying the certainty of species identification. The identification methods include: Molecular: identification based on DNA analysis; morphological: identification based on morphological characteristics; disease outbreak: identification inferred from historical disease outbreak; estimation: presence inferred based on indirect evidence; unknown: source does not specify identification method.”

We acknowledge that species identification may carry some degree of uncertainty in certain studies. However, we have consistently used the most reliable available data and reported it accordingly, in line with the best current standard practices for works of this kind and research in general.

Comment Rev#2-3: (3) Import pathways: did the authors reassess the import pathways for mosquito introductions, or was the information provided in the original publications deemed sufficient?;

Response Rev#2-3: We have relied on the information in the original publications. If no specific introduction route was mentioned in the literature, we categorized the introduction route as “unknown”, hence the large number of entries with “unknown” introduction route. The only exceptions are islands where mosquitoes were introduced before 1900. We have therefore added the following sentence (see lines 432-434):

“For historical introductions to islands (prior to 1900), we assumed that the species were introduced via ships, as this was the most common mode of transportation during that period.”

Comment Rev#2-4: (4) Eradicated introductions: How did the authors address cases of successful introductions that were later eradicated, such as Anopheles gambiae s.l. in Brazil? How were these accounted for in the database?

Response Rev#2-4: We thank the reviewer for raising this point. In our database, species that were successfully introduced but later eradicated are included in the analysis of *introduced but not established* species. For instances where a species was reintroduced after eradication, we did not consider them for our database (focused in first records of introduction). In cases where establishment occurred after several introductions, it was included in the analysis of *established* species, but the date of the first introduction was still used. We clarified this approach in the methods section of the revised manuscript (see lines 370-374):

“In cases where the species was subsequently eradicated or went extinct it was included in the analysis of introduced but not established species. For instances where a species was reintroduced after eradication, we did not consider them unless the species eventually became established. In cases where establishment occurred after several introductions, it was included in the analysis of established species, but the date of the first introduction was still used.”

Comment Rev#2-5: - Lines 55-59. The presence of a competent vector is a prerequisite for local transmission to occurs, but the authors should also recognize that the introduction of the virus is a key driver as well. Zika is a prime example: the vector was present but only after the introduction of the virus the large outbreak occurred in the Americas. Also, in Europe, the autochthonous transmission of arboviruses so far is linked to index cases with a travel history to endemic countries.

Response Rev#2-5: That is correct, and we now acknowledge this in more detail in the discussion. Accordingly, the new version now reads (from line 335):

“Ultimately, we emphasize that while the geographical expansion and presence of a mosquito vector does not directly translate to disease outbreaks, it does create the potential for such. Human-driven changes in mosquito vector distributions are fundamentally reshaping global disease patterns²⁹. However, the autochthonous transmission of vector-borne diseases depends also on the presence of the pathogen. Furthermore, the spatial spread of such diseases is constrained by ecological factors that govern the transmission cycle. Important limiting factors include temperature, precipitation, vegetation and urbanization patterns, which play a critical role in the distribution and bionomics of mosquito vectors, as well as on disease transmission and epidemiology⁵⁷⁻⁵⁹.

Historical examples [...]

29 Kraemer, M. U. G. *et al.* Past and future spread of the arbovirus vectors *Aedes aegypti* and *Ae. albopictus*. *Nat Microbiol* **4**, 854–863 (2019).

57 Ryan, S. J., Carlson, C. J., Mordecai, E. A. & Johnson, L. R. Global expansion and redistribution of Aedes-borne virus transmission risk with climate change. *PLoS Negl Trop Dis* **13**, e0007213 (2019).

58 Lieberthal, B. *et al.* The effects of seasonal human mobility and *Aedes aegypti* habitat suitability on Zika virus epidemic severity in Colombia. *PLOS Neglected Tropical Diseases* **18**, e0012571 (2024).

59 Gubler, D. J. Human Arbovirus Infections Worldwide. *Annals of the New York Academy of Sciences* **951**, 13–24 (2001).

Comment Rev#2-6: Lines 63-66. The limited active dispersal ability of mosquitoes is species dependent. Aedes vexans for example can disperse actively over long distances. This statement should be made more specific or referring to the fact that passive dispersal is an important driver of global expansion of mosquitoes.

Response Rev#2-6: We thank the reviewer for pointing this out and have therefore changed the previous statement: “Due to their limited active dispersal ability, mosquitoes primarily spread regionally through human activities (e.g. trade and transportation).”

It now reads (lines 58-60): “Due to their limited active dispersal ability, when considering long distances (intercontinental), mosquitoes primarily spread through human activities”

Comment Rev#2-7: Lines 70-73. OK but this depends also very much on the larval biology see e.g. the Anopheles mosquitoes are unlikely to be transported as larvae except maybe Anopheles stephensi which breeds in man-made containers and cisterns.

Response Rev#2-7: We thank the reviewer for the comment and agree. We have revised it to a more general statement in which we only mention mosquito transportation (lines 65-66):

“Mosquitoes can now hitch rides on planes, cargo ships, and terrestrial vehicles.”

Results.

Comment Rev#2-8: Line 151. What do the authors mean by “unaided secondary spread”. Is this active dispersal from an initial point of establishment?

Response Rev#2-8: We thank the reviewer for this question. As the reviewer correctly states, by “unaided secondary spread,” we mean the natural dispersal of a species from its initial point of establishment after being introduced to a continent through human activity.

We have revised the sentence to better reflect this definition and clarified it in the methods sections (lines 147-148 and lines 374-376):

“[...], and unaided secondary spread from an initial point of establishment after being introduced to a continent through human activity[...].”

“We only considered records resulting from human mediated introductions or the natural secondary spread of populations that emerged from initial points of establishment (i.e., so-called non-native species²).”

2 IPBES. IPBES Invasive Alien Species Assessment: Full Report. (IPBES secretariat, Bonn, Germany, 2023).

Comment Rev#2-9: Figure 3. How did you deal with uncertainties about the species identification e.g. the spread of Aedes albopictus in the UK is not in line with what is known (see e.g. the ECDC maps).

Response Rev#2-9: We thank the reviewer for their comment regarding uncertainties in species identification and the spread of *Aedes albopictus* in the UK. Figure 3 depicts areas where the four example species have been *introduced*, not necessarily where they have become established. As the reviewer correctly notes, despite *Aedes albopictus* being first

introduced to the UK in 2016 been detected several times since (see Medlock et al., 2017), it has not established a population there. To avoid confusion, we now clarified this distinction in the figure caption as follows (lines 197-198):

“**b-e** Maps show the global distribution of first records independent of establishment (red) for an example species of each of the four groups identified”

Comment Rev#2-10: Figure 5 E and F what is your estimate representing. Please specify and use the appropriate term.

Response Rev#2-10: We have changed that accordingly in the figure as well as better described in the caption (from line 253):

“Regression coefficients with 95% confidence intervals from Generalized Linear Mixed Models (GLMMs) are shown for eight variables tested in relation to **e** species introduction and **f** establishment. [...]”

Methods

Comment Rev#2-11: Line 335. Data compilation. This data compilation is a large effort. The quality of the data is key for the analysis. How did you ensure data quality in terms of content and in terms of data entry (see general comment above)?

Response Rev#2-11: We thank the reviewer for this important comment regarding data quality. As mentioned above (See Response Rev#2-1), we have now expanded the Methods section to provide a more detailed description of the data collection, and validation procedures, as we recognize that the original description was insufficient. (lines 391-423, cited above)

In this regard, we note for example that, to ensure data quality, we built on existing data collections of mosquito introductions (e.g., Lounibos 2002, Wilkerson et al. 2021) and updated them with recent records. Each entry in our database is linked to a supporting source, allowing readers to verify the introduction records. Additionally, we used the Walter Reed Biosystematics Unit (WRBU) as the taxonomic reference to ensure consistency in species identification. Please see more details above in Resp. General, and Resp. Rev#2-1 to 4.

Comment Rev#2-12: Line 339. Did you exclude the possible detection of a pathogen in blood-fed mosquitoes as the detection in wild caught female mosquitoes is not enough to consider the species as a vector.

Response Rev#2-12: Our selection of medically important species relies on the comprehensive review of vector competence by Yee et al. (2022). While we acknowledge the possibility of misclassifications - an inherent challenge in studies of this nature - our work is the most robust and comprehensive compilation available to date. In the text we note that our selection of species is based on this work (lines 365-368):

“Only mosquito species known to be vectors for human diseases in the wild (n=184) were considered (i.e., naturally occurring with a human pathogen). This condition had to be confirmed either by at least two scientific articles as identified by Yee et al. (2022)³² or one source together with an entry in the mosquito catalogue⁶³ that confirmed the link to a disease.”

32 Yee, D. A. et al. Robust network stability of mosquitoes and human pathogens of medical importance. *Parasites Vectors* **15**, 216 (2022).

63 Wilkerson, R. C., Linton, Y.-M. & Strickman, D. *Mosquitoes of the World*. (Johns Hopkins University Press, Baltimore, Maryland, 2021).

Comment Rev#2-13: Line 365. Introduction pathways. How did you actually assess the introduction pathways as this is often not very well known or proven. Did you collect this information from the selected literature and if yes, did you reassess the conclusions of the authors?

Response Rev#2-13: The pathways were collected from literature that explicitly stated how the species was introduced. If no specific pathway was mentioned in the source, we classified the introduction pathway as “unknown.” We did not independently reassess the conclusions of the original authors but relied on the information provided in the literature.

Comment Rev#2-14: Line 427-435. Referring to e.g. the gross domestic product per capita and the total trade openness in US\$, what actual measure was taken: a long-term average, the current 2024 value. Please specify and indicate why this indicator and time period has been chosen.

Response Rev#2-14: We thank the reviewer for their question regarding the socio-economic variables used in our analysis. We selected variables commonly used in this kind of analysis that are globally available and reflect key socio-economic and environmental aspects of the countries studied (see e.g. Dawson et al. 2017, Moser et al. 2018, Monteiro et al. 2022 for studies also applying these variables). We used a 5-year average for variables like GDP per capita and total trade openness (in USD) to ensure data completeness and stability. In some cases, the most recent data were unavailable, making the average a more reliable measure. To keep the methods concise detailed information, including the specific time periods and data sources of each variable, are provided in Supplementary Material Table 4. However, we now added the sources also in the methods section that were before only mentioned in the Supplementary table. In the methods section it reads now as follows (from line 582):

“To explore the factors driving the geography of hot- and coldspots of first records of non-native species introductions, and of those that are now established, we used a GLMM to relate the residual values (log-transformed) to a set of globally available country-level socioeconomic and environmental variables. The variables were (1) gross domestic product per capita (GDP)⁷⁰, (2) total trade openness in US\$⁷¹, (3) time of occupation by one of the eight main European colonial empires⁵ and private communication, (4) number of European empires that had a colonial influence on the country⁵, (5) total human population⁷⁰, (6) long-term average yearly temperature⁷², (7) long-term average yearly sum of precipitation⁷², (8) percentage of land cover⁷³ by wetlands and (9) agriculture, (10) insularity (‘yes’, ‘no’), and (11) the absolute latitude. A detailed list of these variables, along with their measurement units and respective data sources, is available in Suppl. Material Tab. 4.

5 Lenzner, B. et al. Naturalized alien floras still carry the legacy of European colonialism. *Nat Ecol Evol* 6, 1723–1732 (2022).

70 Worldbank. World Development Indicators. <https://databank.worldbank.org> (2024).

71 United Nations. UNCTAD dataset (United Nation Conference on Trade and Development). (2024).

72 Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302–4315 (2017).

73 Copernicus. Land Cover 2015-2019 (raster 100 m), global, annual - version 3. European Commission Directorate-General Joint Research Centre (2020).

Comment Rev#2-15: Numbering of figures should be according to appearance in the text e.g. figure 1 and 2

Response Rev#2-15: We thank the reviewer for this remark, the figure number in line 111 was an error and has been corrected.

Supporting References

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