

Global invasion patterns and dynamics of disease vector mosquitoes

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Mosquitoes are major vectors of human diseases, and their geographic expansion is primarily driven by the unintentional, human mediated introduction beyond their native ranges. Despite the substantial public health implications and rising numbers of disease outbreaks, a global picture of the introduction trends and the resulting range expansions of mosquitoes is missing. Here, we present a comprehensive and up-to-date compilation and analysis of reported first records of human disease vector mosquitoes worldwide. We show that 45 mosquito species (~25% of those known to transmit human pathogens) have been introduced worldwide, with 28 species having established in at least one region. From the 1950's onwards, the introduction of new species has increased sharply, with 12 species recorded for the first time outside their native range since 2000 alone. Initially, most introduced species were native to Africa, but over time, Asian species have become more dominant. North America, Australia and Europe remain the main recipients. Our results highlight the role of global trade and transportation in mosquito spread and emphasizes the need for international cooperation to control their spread and potential threat to public health.

Human activities often lead to the unintentional introduction of species beyond their native ranges^{1,2}. While this phenomenon has existed for millennia, the rate of species introductions, particularly intercontinentally, has accelerated over time³. Especially the European exploration and colonialism in the late 15th century contributed to the large-scale redistribution of biota^{4,5}. This rate has further increased in recent centuries due to the expansion of transportation networks and the globalization of trade and travel⁶⁻⁹. Introduced species can profoundly affect local biodiversity¹⁰, human economic activities¹¹, and pose major threats to human health^{12,13}.

The global distribution and spread dynamics of non-native species have been extensively studied in recent years^{2,3,14}. However, somewhat surprisingly, a significant knowledge gap remains regarding the global invasion patterns and dynamics of disease vector mosquitoes. Non-

native disease vector mosquitoes are currently found worldwide, altering disease transmission patterns and leading to serious consequences for public health¹⁵. Epidemics of diseases, such as Zika and dengue are now common in tropical and subtropical regions due to the high abundances of competent non-native vectors^{15,16}. In temperate regions, these vectors are also causing a rise in the cases of autochthonous transmission (i.e., acquired infection where transmission occurs between individuals through the local mosquito population)^{17,18}. Additionally, due to their substantial impact on public health systems, mosquitoes are among the most costly non-native species worldwide¹⁹. Reported costs to human societies of mosquitoes of the Genus *Aedes*, and the diseases caused by the arboviruses (i.e., arthropod-borne viruses) they transmit rises to an aggregated value of 94.7 US\$ billion (2022) accumulated over the period 1975–2020¹¹.

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The history of non-native mosquito introductions is both long and complex. Due to their limited active dispersal ability, when considering long distances (intercontinental), mosquitoes primarily spread through human activities (e.g., trade and transportation)^{20–22}. The first recorded invasions date back to intercontinental maritime and trading activities as early as 1495, involving species, such as *Aedes aegypti* and those from the *Culex pipiens* complex²⁰, which have been primarily dispersed through water-carrying containers on ships²³. The subsequent intensification of global trade, development of the shipping industry and expansion of aerial and terrestrial transportation networks, coupled with a growing human population, has further exacerbated the opportunities for mosquito spread²⁰. Mosquitoes can now hitch rides on planes²⁴, cargo ships²¹, and terrestrial vehicles²⁵. Additionally, urbanization is also creating artificial breeding sites, such as standing water in discarded containers, facilitating the establishment of some newly arrived species²⁶. One of the most notable examples is *Ae. albopictus*, an Asian-native species that has spread globally through the trade of commodities, such as used tires and lucky bamboo plants, particularly during the 20th century²². Very recently, several emerging non-native mosquito species have been reported worldwide. For instance, *Ae. japonicus*, native to East Asia, has spread to North America and Europe within the last few decades²⁷, while *Anopheles stephensi*, native to South Asia, has recently been detected at the Horn of Africa, posing a new threat for malaria transmission in urban settings²⁸.

The current global invasion patterns and dynamics of mosquito vectors of human diseases remain largely unknown, due to incomplete knowledge about natural and anthropogenic dispersal mechanisms. The spread dynamics of this group have been primarily assessed for single species and only for those causing the most severe impacts^{22,29,30}. Studies that have examined the invasion of mosquito species have focused on mapping species-specific distributions, e.g., ref. 22, are geographically restricted, e.g., ref. 31, or are outdated, e.g., refs. 15,20. Understanding the dynamics of introductions of all non-native disease vector mosquitoes, as well as the patterns and drivers of their spread and establishment, is crucial for developing effective surveillance control measures to prevent future invasions. Moreover, this knowledge serves as a foundation for further risk assessment, improving mosquito ecology, and disease dynamics research.

To fill these gaps and track the introduction of non-native mosquito species that are vectors of human diseases, and to provide a basis for informed predictions about future invasions and their potential impact on human health, we compile a database of the reported regional first records worldwide through a literature search. We then use this database to answer the following research questions: Q1: what are the temporal and biogeographical patterns of invasion from non-native human disease vector mosquitoes? Q2: what are the main introduction pathways and means of transportation for these mosquitoes, and their establishment success? Q3: where did the mosquito species originate and where were they introduced to? Q4: what are the cold- and hotspots of mosquito introductions and establishment, and what is driving these patterns?

Results

Of the 184 mosquito species acting as vectors for human pathogens³², we collected 697 reported first records into new regions. These took place in 288 regions on all continents except for Antarctica. Of these, 612 records (i.e., 87.8% of total) in 283 regions led to species establishment.

High diversity of introduced non-native mosquitoes

45 mosquito species have been introduced to regions where they are non-native, accounting for 24.5% of all mosquito species known to transmit pathogens in the wild. Among these, 28 species have

successfully established. These introduced species belong to five genera: *Aedes*, *Anopheles*, *Armigeres*, *Culex*, and *Mansonia*. Specifically, from the genus *Aedes* 15 species were introduced to a total of 469 regions, of which ten species are established today in 409 regions. From the genus *Anopheles* likewise 15 species were introduced, but only in 33 regions, of which seven species were able to establish in 17 regions. *Armigeres* has one introduced species with a single introduction and establishment record. Twelve species of the genus *Culex* have been introduced in 192 regions, of which nine species have become established in 184 regions. There are two introduced species of the genus *Mansonia* with two regional introduction records, of which one became established (Fig. 1, Supplementary Fig. 1, Supplementary Table 1).

The most widespread non-native vector mosquito species is *Ae. aegypti*, recorded in 192 regions, followed by *Ae. albopictus* (189 regions) and *Cx. quinquefasciatus* (111 regions). *Aedes albopictus* is also the species with the highest number of regions (173) with established occurrences. Both, *Ae. aegypti* and *Ae. albopictus* have been introduced and established on all continents except for Antarctica. However, *Cx. quinquefasciatus* has not yet been introduced to Europe and Antarctica (Table 1).

Many first records and new species since the mid-20th century

The first known records of vector mosquitoes started with the beginning of intercontinental shipping in the 15th century (Fig. 1A). A substantial increase was then observed at the end of the 19th century, with a rise in first records mainly in Australia and Asia (Fig. 1B). This was followed by a further increase in first detections from 1900 onwards, which may be partly due to more attention being paid to mosquitoes as their role as disease vectors was recognized in the same year³³.

Since the mid-20th century, there has been a rapid increase in newly recorded non-native mosquitoes, particularly in Europe, the Americas, and Africa. Nearly half (49%) of all first records occurred after 1950 ($n = 342$). Additionally, 27 of the 45 non-native vector mosquitoes were recorded for the first time after this date, and of these, 12 species were recorded for the first time after the year 2000 (Fig. 1C–E). Concurrently, the volume of trade has increased 30-fold since 1950^{34,35}, likely driving the rapid pace by causing an increased number of accidental introductions of, often small, inconspicuous taxa. This has been observed in ants⁶, plant pests³⁶, earthworms⁹, and individual mosquito taxa²².

Diversification of transport modes and species introduction

Most modes of transport and introduction of the species are unknown, but available data shows a shift in dominance from ship-based transportation to an increasing importance of aircrafts, ground-based transportation, and unaided secondary spread from an initial point of establishment after being introduced to a new region through human activity (Fig. 2A). Known commodities carrying propagules of the species are highly varied (Fig. 2B). The earliest report of mosquito introductions happened through standing water containers (water storage jars) on sailing vessels during slave trades at the end of the 15th century²⁰. Import via dried breeding sites in tyres appeared as an important contaminant in the 1900s. Plants were identified as notable pathways after 1950. Other commodities or objects, such as containers, used machinery, a tent, rubbish bins, plastic foil, cable drums and mining bowls have been observed sporadically since the end of the 20th century³⁷. Relevantly, while the role of aircraft in the introduction of species has become increasingly important, only a small proportion of these introductions establish in the new region (Fig. 2C). Conversely, the relative importance of shipping as a pathway for the introduction of species has decreased since 1900 and the proportion of species that become established after transportation by ship has also decreased (Fig. 2D).

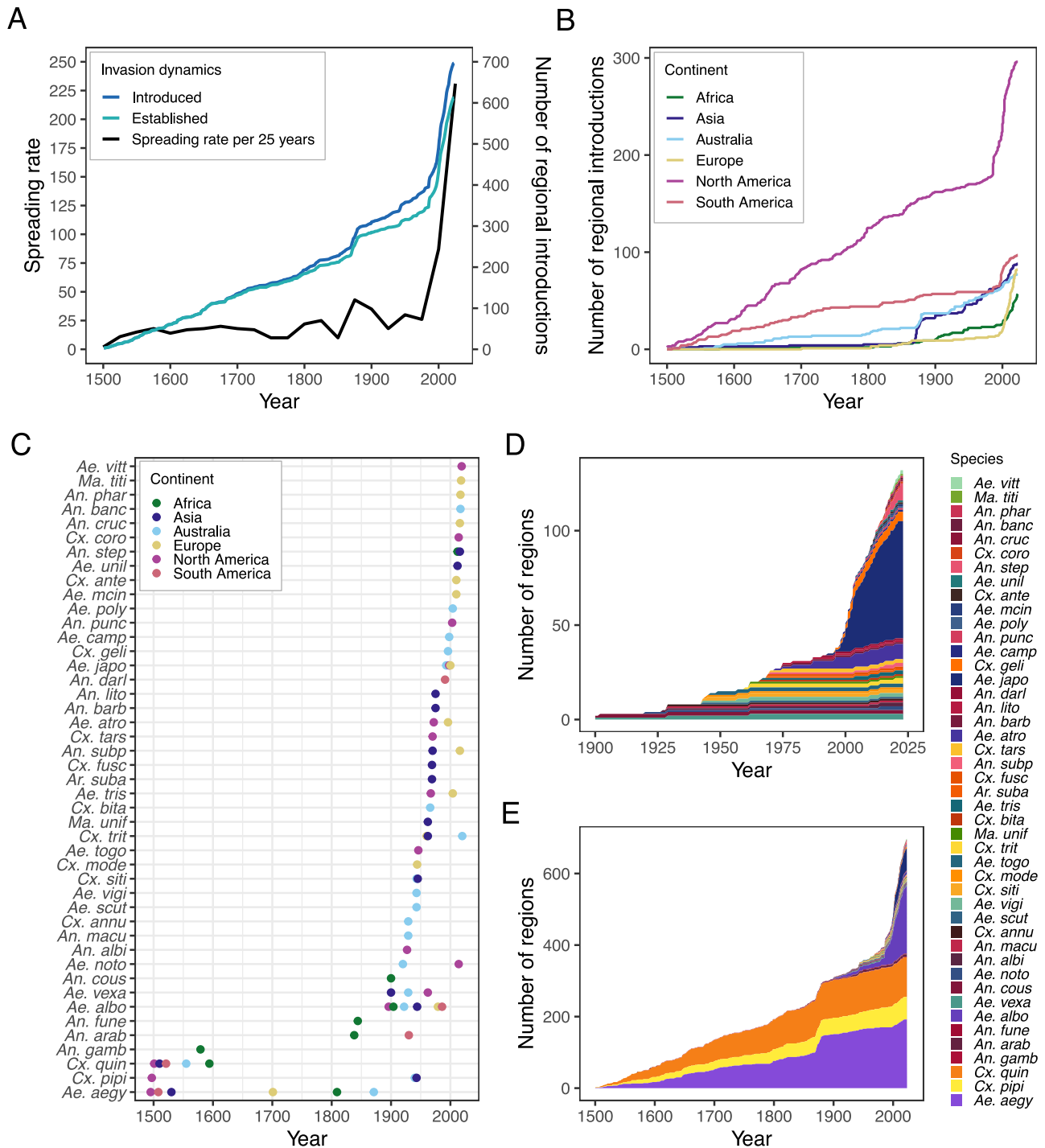


Fig. 1 | Temporal trends in first records of non-native mosquito species.

A The temporal evolution in the cumulative number of first records of non-native mosquito species worldwide and **B** by continent. Spreading rates correspond to the total number of introduced non-native species for a period of 25 years. Cumulative trends of regional first records at the global scale are shown for records regardless of species' establishment in regions of introduction, as well as for records leading to species establishment. **C** Timing of species' first introduction records by continent. **D** Cumulative timeline of the number of first introduction records for species with

global first record after 1900 ($n = 38$) **E** and for all species ($n = 45$). The timelines are shown for each of the 45 species (Names and abbreviations in Supplementary Table 5) with first introduction records in new regions. Figure legend shows species in descending order in terms of global first recording dates (more recently recorded species are showing first). Number of regional introduction records per continent can be found in Supplementary Table 3. Source data are provided as a Source Data file.

Global spread patterns of non-native mosquito species

We found that the number of regions where species have been recorded and the minimum residence time since their first global record are positively correlated (Pearson $r = 0.602$, $p < 0.001$ for records regardless of establishment and $r = 0.593$, $p < 0.001$ for those leading to

establishment), indicating that species have been expanding their ranges over time. However, these correlations do not hold for species first recorded globally after 1900 and 1950 (Supplementary Fig. 5), suggesting that this finding is not true for emerging non-natives species. To further explore this relationship, we characterized the spread

Table 1 | The ten most widely introduced species of the Global Non-Native Mosquito Database, with the total number of regions and continents where a given species was recorded

Rank	Species	Regions introduced	Regions established	Continents introduced	Continents established
1	<i>Aedes aegypti aegypti</i> (Linnaeus, 1762)	192	160	6	6
2	<i>Aedes albopictus</i> (Skuse, 1895)	189	173	6	6
3	<i>Culex quinquefasciatus</i> (Say, 1823)	111	111	5	5
4	<i>Culex pipiens</i> s.s. (Linnaeus, 1758)	63	61	3	3
5	<i>Aedes japonicus japonicus</i> (Theobald, 1901)	62	61	3	2
6	<i>Anopheles stephensi</i> (Liston, 1901)	9	9	2	2
7	<i>Aedes atropalpus</i> (Coquillett, 1902)	8	5	2	2
8	<i>Anopheles arabiensis</i> (Patton 1905)	6	2	2	1
9	<i>Culex gelidus</i> (Theobald, 1901)	5	4	1	1
10	<i>Anopheles gambiae</i> s.s. (Giles, 1902)	2	2	1	1

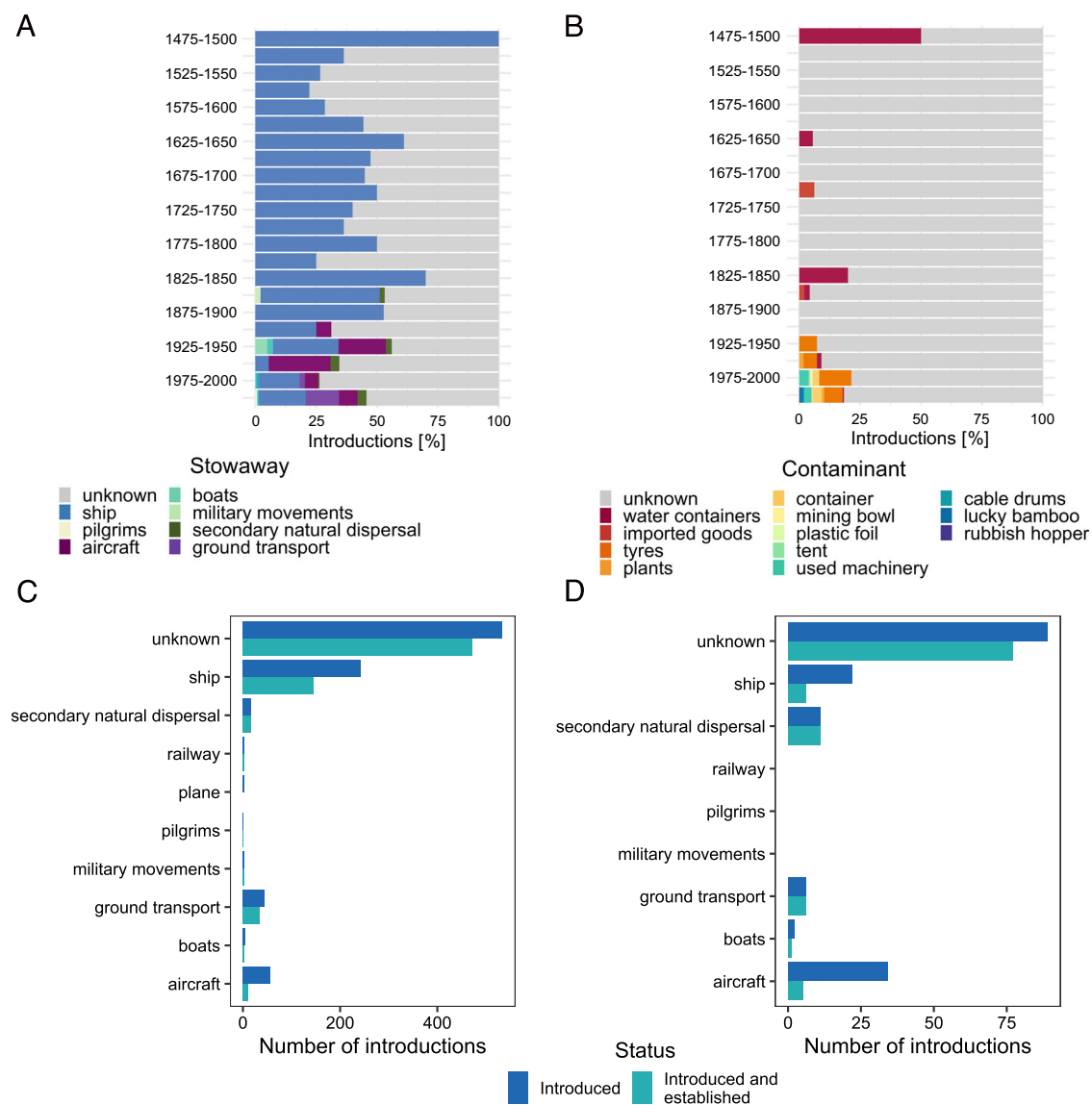


Fig. 2 | Transportation pathways for non-native mosquito species. A Proportion of transportation vectors and **B** transportation contaminants in 25-year intervals of all first records. Establishment success of the species depending on their transportation vector. **C** All species; **D** Species spreading post-1900. Source data are provided as a Source Data file.

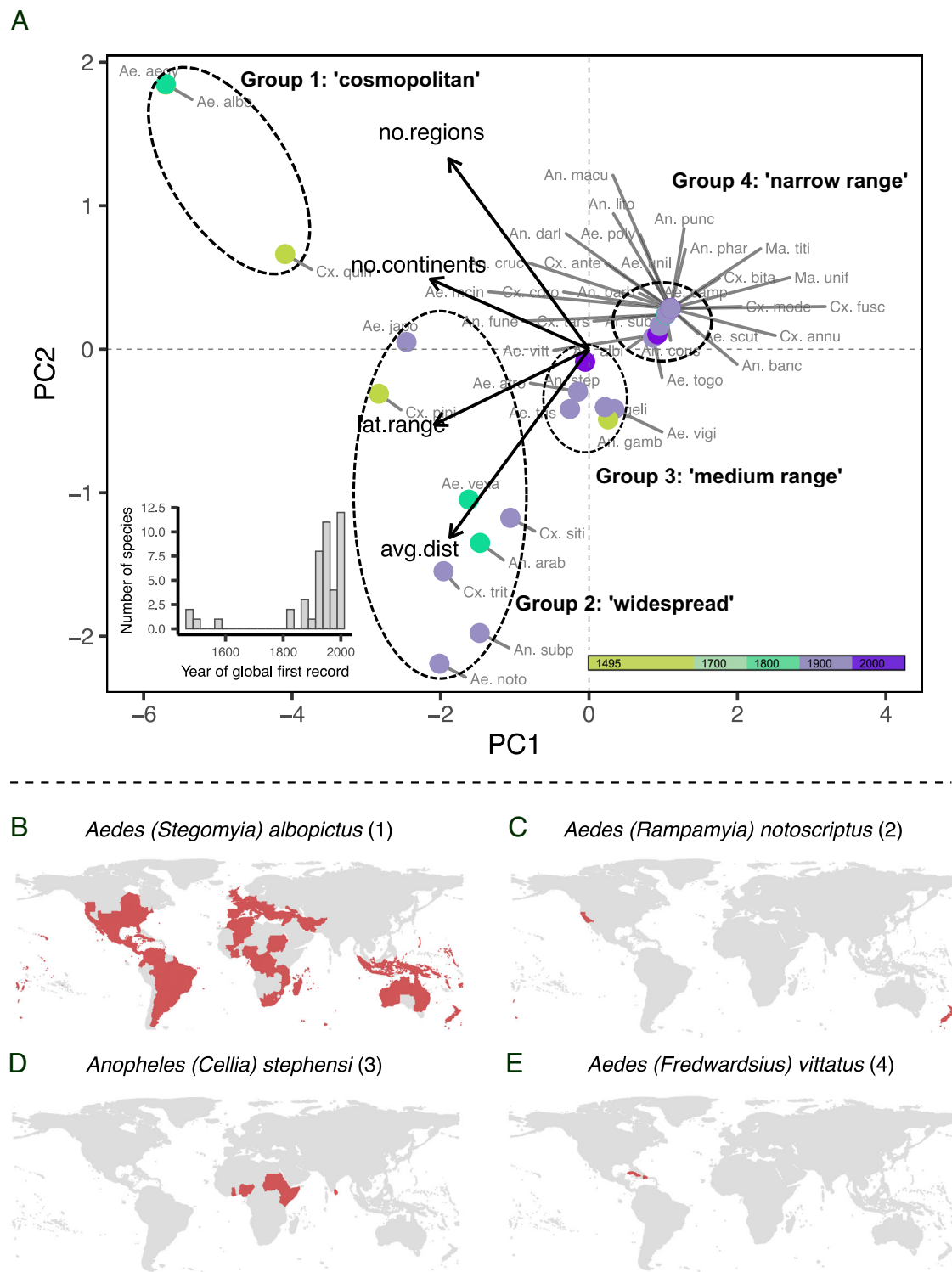


Fig. 3 | Spatial patterns of non-native mosquito introductions. **A** Principal Component Analysis (PCA) of species introduced outside native ranges over time. The axes of the PCA consider the number of regions the species was introduced (no.regions), number of continents (no.continents), latitudinal range between northernmost and southernmost region (lat.range) and average distance between all regions (avg.dist), where the x -axis explains 81.63% and the y -axis explains 14.86% of the total variance. Colors represent the timing of the global first record of each

species. The inset histogram represents the number of global first records of vector mosquitoes per 25-year period. **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. The underlying world map data were obtained from GADM (<https://gadm.org/>), used under their academic-use license. Source data are provided as a Source Data file.

ranges of each species using a set of spatial variables and summarized them through projection into a Principal Component Analysis (PCA; Fig. 3). Following this, k-means clustering was used to broadly classify species into four groups based on similarities of their spread ranges.

The first group includes early cosmopolitan spreaders, comprising three well-known species: *Aedes aegypti*, *Ae. albopictus*, and *Cx. quinquefasciatus* (Group 1). While *Ae. aegypti* and *Cx. quinquefasciatus* began their global spread as early as the 15th century, *Ae. albopictus*

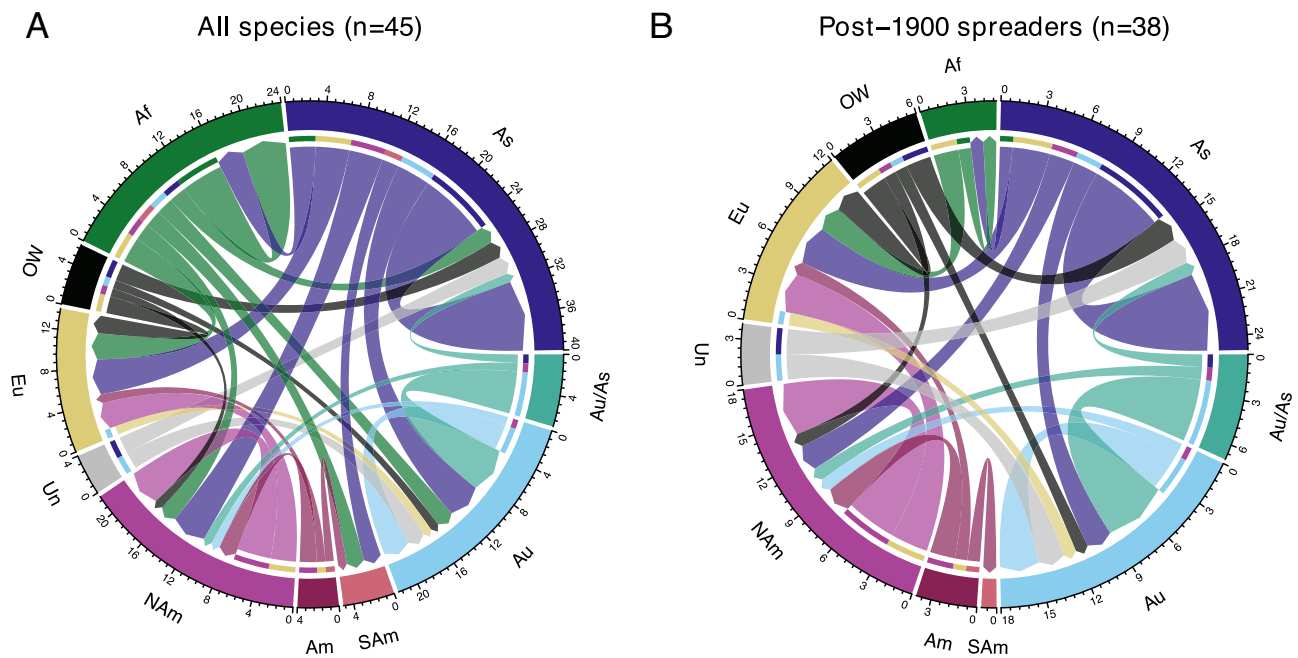


Fig. 4 | Global flows of non-native mosquitoes. Global species flows of non-native mosquitoes, representing the introduced species richness to and from each continent. Each species recorded on a continent was counted only once. **A** Flows for all species, **B** flows for species that started spreading after 1900. Af Africa, Am

America, As Asia, Au/As Australia and Asia, Au Australia, Eu Europe, NAm North America, OW Old World (i.e., Africa, Asian and Europe combined), SAm South America, Un Unknown. Source data are provided as a Source Data file.

only started spreading in 1896. These species are now established in numerous regions across most continents (Table 1). Another group consists of eight widespread species: *Aedes japonicus*, *Ae. notoscriptus*, *Ae. vexans*, *An. arabiensis*, *An. subpictus*, *Cx. pipiens* s.s., *Cx. sitiens*, *Cx. tritaeniorhynchus* (Group 2), which either spread to many regions or overcame very large geographical distances in its spread. The third group contains species with medium-wide non-native range sizes of up to nine regions colonized. Notably, five out of six species in this group began spreading in the 20th century. These species include *Ae. atropalpus*, *Ae. triseriatus*, *Ae. vigilax*, *An. gambiae* s.s., *An. stephensi* and *Cx. gelidus*. Finally, the most numerous group comprises 28 species having narrow non-native ranges. Of these, 22 were introduced only to a single non-native region. The remaining six species (namely: *Aedes togoi*, *Ae. vittatus*, *An. albimanus*, *An. coustani*, *An. funestus* and *Cx. tarsalis*) were introduced to two regions (Group 4). Most of these single-region introductions, representing 18 species (81.8% of the total), occurred after 1965.

Global continental non-native mosquito flows and post-1900 trends

Species flows across continents. The intercontinental flows of species show that Asia and Africa play a dominant role as donor continents of non-native mosquitoes (Fig. 4A). Despite this, we also find a relevant number of species originating from North America ($n = 5$), Australia ($n = 3$), and the Old World ($n = 6$) (i.e., Africa, Asia, and Europe combined). In contrast, Europe and South America primarily are recipients of introduced mosquitoes. In Australia, there is predominantly an intracontinental flow of introduced species, and introductions from Asia. Among continents, Australia, Europe, and North America had the highest number of regional introductions (Table 2, Fig. 4).

Post-1900 colonization trends. When focusing on species that started to spread from 1900 onwards, we found that Africa's role as a donor continent is reduced and that most introduced species come from Asia, Australia, and the Americas. Africa receives only one additional

mosquito species from outside the continent, and only two species are beginning to spread from there. All species native to Australia and the Americas only began to spread after 1900, either within their native continent or to Europe. A single European species (*An. maculipennis*) was introduced to only a single region, New Zealand (Fig. 4B).

Hotspots of non-native mosquito introduction and establishment

Of the 477 assessed regions, 288 have records of the introduction of at least one non-native vector mosquito, representing 63.4% of the world's land area. New Zealand had the highest number of recorded first introductions ($n = 16$), followed by Guam ($n = 12$), the Netherlands ($n = 9$), and three U.S. states (Hawaii, Illinois, Ohio) ($n = 6$) (Table 2, Supplementary Fig. 5). The majority of regions, 62.2%, recorded the introduction of only one or two new species. Guam tops the ranking for established non-native species ($n = 9$), followed by Ohio ($n = 6$), and 15 eastern U.S. states, California, and Cuba ($n = 5$). Despite a strong correlation between the introduction and establishment of species (Pearson $r = 0.76$, $p < 0.001$), some regions exhibit large differences between the species richness of introductions and establishments, such as New Zealand, the Netherlands, France, Guam, Mauritius, Reunion, Pennsylvania, Barbados, Belgium, and the UK.

We identified hot- and coldspots of introduction, defined as countries where the recorded number of introductions is higher or lower than expected, respectively. The hotspots include New Zealand, the Netherlands, USA, France and Mauritius (Fig. 5A), while the Cook Islands, Norway, Poland, Ukraine and Canada were identified as coldspots. Focusing on species that started to spread only after 1900, we identified hotspots of introduction in New Zealand, the Netherlands, USA, France, and Cuba (Fig. 5C). The United Kingdom, Norway, Poland, Portugal, and Austria were identified as coldspots for species spreading after 1900. Compared to hotspots of establishment, the introduction hotspots New Zealand, France, and the Netherlands performed better than expected (Fig. 5B, D). On the contrary Australia is one of the hotspots of species establishment for all species, but this has changed for species that spread after 1900.

Table 2 | Regions with five or more first records of non-native vector mosquito species

No	Region	introduced	established
1	New Zealand	16	2
2	Guam	12	9
3	Netherlands	9	1
4	Ohio (USA)	6	6
5	Hawaii (USA)	6	5
	Illinois (USA)	6	5
6	Cuba	5	5
7	Northern Territory (Australia)	5	4
	Western Australia (Australia)	5	4
8	Arkansas (USA)	5	5
	California (USA)	5	5
	Florida (USA)	5	5
	Georgia (USA)	5	5
	Indiana (USA)	5	5
	Kentucky (USA)	5	5
	Maryland (USA)	5	5
	Mississippi (USA)	5	5
	Nebraska (USA)	5	5
	North Carolina (USA)	5	5
	South Carolina (USA)	5	5
	Tennessee (USA)	5	5
	Virginia (USA)	5	5
9	Michigan (USA)	5	4
	New Jersey (USA)	5	4
10	Pennsylvania (USA)	5	3
11	France	5	2

Drivers of non-native mosquito hotspots and coldspots

The multivariate linear mixed model analysis to identify drivers for the variation in cold- and hotspots of mosquito introduction and establishment, revealed that GDP per capita is significantly positively associated ($p < 0.05$) with the propensity of countries to receive species introductions (Fig. 5E). The total population size of a country had a highly significant effect ($p < 0.01$) on species introductions, and a significant effect ($p < 0.05$) on species establishment (Fig. 5F). Insularity also had a significant effect ($p < 0.05$) on the extent to which species were introduced.

Discussion

We compiled and analyzed a comprehensive global database of first records of mosquito vectors for human diseases across regions and show that a large and increasing number of mosquito species are being dispersed by human activity, following trends in the globalization of trade and transportation. Additionally, we observed substantial shifts in the region of origin of species from Africa to Asia over time and the pathways through which they are introduced, but fairly stable patterns in their recipient regions (i.e., the Americas, Australia, and Europe).

We show that the reported rates of mosquito introductions into new regions and the emergence of novel non-native species have increased in recent centuries, with a particularly pronounced increase observed in recent decades. 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>). 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}. During this period the frequency and volume of commodities transported across continents increased and travel times decreased substantially³⁵. Furthermore, the advent of rapid transportation methods, such as cargo planes, has enabled the unintentional dissemination of short-lived propagules, including adult mosquitoes^{24,44}. Collectively, these factors are increasing the opportunities for the unintentional spread of mosquito vectors and are likely to continue doing so in the coming decades^{21,45,46}.

Most recorded introductions lead to establishment. This very high proportion of established introductions suggests that there may be many casual introductions, which remain unnoticed. On the other hand, many species emerging after 1950 have not become established (yet), with 12 out of 27 species (44.4%) failing to establish in a new region. This low establishment rate may be due to enhanced surveillance and import controls that may detect and intercept these species at the introduction stages or in circumstances that would not typically lead to establishment, such as single adult male mosquitoes²⁰. Additionally, the low establishment rate may reflect lag effects in the reporting of the species or between the introduction of a species and its rapid population growth and spread where detection becomes more likely⁴⁷. This lag phase can vary greatly among species and environments, lasting from a few years to several decades⁴⁸. Therefore, while some detected species are not currently established, they could become so in the future.

A species' establishment success is also influenced by its habitat requirements and adaptability, including the availability of suitable oviposition sites⁴⁹. For example, the genus *Aedes* exhibits approximately 2.5 times more first records than the genus *Culex* and over 13 times more than the genus *Anopheles*. This high number of first records for *Aedes* can be attributed to the ability of their eggs to withstand desiccation, allowing them to be transported over long distances and extended periods (3–6 months) in both artificial and natural carriers that do not require standing water⁵⁰. In contrast, the eggs of other genera, lacking this desiccation resistance, often perish when transported in containers that dry up during transit, leading to unsuccessful colonization in new regions and inherently reducing their potential for further dispersal.

Historical changes in global trade and travel dynamics have led to pronounced shifts in the donor regions of species being transported, most notably a shift from African-origin species to those from Asia. Despite these shifts in geographical provenance, we found that the hotspots of introduction have remained rather stable. These include primarily the USA, several Central European and tropical African countries, and New Zealand, with the European, Australian, and North American continents also consistently having high ratios as destinations.

We also found that socioeconomic variables, in particular per capita GDP and population size, have a significant positive relationship with the invasion and establishment success of mosquitoes, as has been found for other taxa¹⁴. In contrast, colonial relationships, which are a major factor for the introduction of other non-native species, such as plants (including intentionally introduced crops)⁵, were not found to have a significant effect on the introduction of mosquito species, possibly because they were always introduced unintentionally. Insularity also had a significant effect on the extent to which species were introduced, consistent with findings for other taxa¹⁴. These results highlight the necessity of incorporating socio-

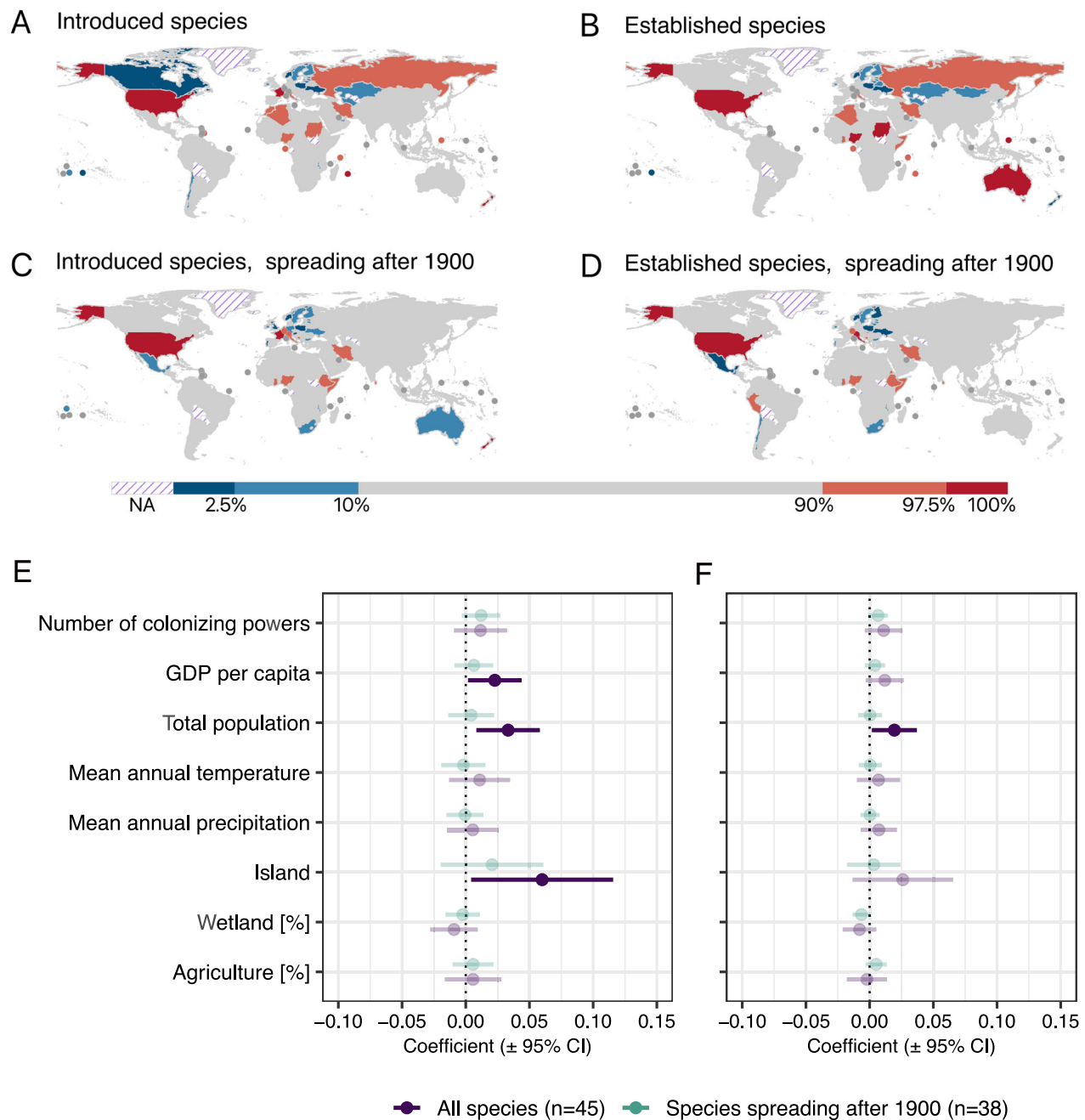


Fig. 5 | Global hotspots and coldspots of non-native mosquito introduction and establishment, and their socio-economic and environmental drivers. Cold- and hotspots of country level first records of non-native mosquito species (left column) and non-native species that are now established (right column). Maps represent **A,B** cold- and hotspots of all species and **C,D** for species spreading post-1900. Colors indicate countries with higher (red) and lower (blue) vector mosquito numbers than expected. Note the non-linear scale of the color legend. For countries in purple stripes no data was available. Countries smaller than 27,106 km² (equivalent to Haiti) are shown as circles. The underlying world map data were obtained from GADM (<https://gadm.org/>), used under their academic-use license. **E,F** show regression coefficients (central dot) and 95% confidence intervals (lines)

from Generalized Linear Mixed Models (GLMMs) assessing the influence of socio-economic and environmental predictors on species introduction (**E**) and establishment (**F**), with continent used as a random effect. Variables were log-transformed and standardized. For species introductions (**E**), significant predictors included GDP per capita ($p = 0.0305$), population size ($p = 0.0077$), and insularity ($p = 0.0314$). For species establishments (**F**), only population size was significant ($p = 0.028$). Statistically significant variables are indicated in darker shades. No adjustments were made for multiple comparisons. Full test details, including model structure and diagnostics, are available in methods and Supplementary Table 4 and Supplementary Table 6. Source data are provided as a Source Data file.

economic relationships into invasion prevention strategies to address the complexities of global flows of commodities and transportation vectors susceptible to carrying mosquito propagules. Research on mosquito spread should expand therefore beyond the widely explored effects of climatic variables and their

changes^{51,52}, and include land-use changes and socio-economic variables, such as poverty, trade and travel⁵³.

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 pathogens⁵⁴. The adaptability of mosquito species⁵⁵ and pathogens⁵⁶, combined with the escalating rate of first records, poses a considerable challenge for global public health.

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 epidemiology^{57–59}.

Historical examples illustrate the interplay between vector expansion and pathogen introduction. 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*⁶. 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.

Once established, mosquito vectors are notoriously difficult to eradicate, as demonstrated by the failed transnational effort to eliminate *Ae. aegypti* in the Americas⁶². Mitigation and prevention efforts should therefore focus on preventing introductions by targeting pathway, prioritizing source and target regions identified as hotspots of non-native mosquitoes, and implementing rapid response protocols following early detection. These strategies are essential to mitigate the public health impacts of non-native mosquito species in an increasingly interconnected world.

Methods

Data compilation

We systematically searched the literature for first records of human-introduced non-native mosquito species. For the standardization of species names, we used the Walter Reed Biosystematics Unit (WRBU) taxonomic reference, which also lists synonyms for each species⁶³. 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.³², or one source together with an entry in the mosquito catalog⁶³ that confirmed the link to a disease. We searched for scientific publications on Google Scholar between March and December 2023, using all combinations of the following search terms: “species name” AND “country name” AND “introduction” OR “invasion” OR “first record”. Additionally, we reviewed existing literature reviews, e.g., refs. 20,30,63, and citing documents. We compiled the results in a database, in which each row represents a single record of the first record of a non-native mosquito species in a new region. 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. 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 species³).

To standardize the record collection, we used regions consisting of countries and added the first-order administrative divisions of the six largest countries (Australia, Brazil, Canada, China, Russia, USA) as obtained from GADM (“<https://gadm.org/>”). Additionally, certain islands, such as Corsica, Sicily, Sardinia, Crete, Madeira, the Azores, the Galapagos Islands, the Balearic Islands, the Canary Islands, and the Torres Strait are considered separately, as water is a barrier to the migration of mosquito species; in total, this approach resulted in a layer of 477 regions.

In a few cases, we could not be certain of the reliability of introduction records. For example, in some situations, it was unclear whether the species' appearance in a region was due to natural dispersal from native populations or human-mediated introduction. Therefore, records for which reliability was uncertain were not included in our database.

The database contains entries on the names of the species, the identification method, the year of first record, the mode of transportation and introduction (when available), the status of establishment and the source of the information. For a more detailed explanation of the data and its structure, please consult the README file available alongside the dataset publicly available on Zenodo⁶⁴.

Taxonomy

The mosquito taxonomy used is consistent with the Walter Reed Biosystematics Unit⁶⁵ (<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 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.

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 under-reporting 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.⁶⁶. Additionally, language-related bias may

Table 3 | Guidelines for converting introduction dates

First Record Date Precise	Year Used	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
16–18th 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

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.

Introduction pathways

The mode of introduction of species is distinguished between two main classes: dispersal vectors (transportation stowaways) and the commodities serving as carriers during dispersal (transportation contaminants). We categorized these two large classes into more specific groups. For transportation stowaways we considered ships, boats, ground transportation (cars), trains, aircraft, secondary natural dispersal (after human introduction to the continent), and unknown sources. For transportation contaminants we considered water containers, plants, tires, lucky bamboo, used machinery, containers, and imported goods and objects. Introduction records were segmented into 25-year intervals, and the proportions of stowaways and contaminants for each period were presented. 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.

Assessing similarities in non-native species ranges

Principal component analysis (PCA) was employed to visually explore (dis)similarities in the non-native ranges of species. The variables describing each species included: 1. The number of regions where the species was recorded. 2. The number of continents where the species was recorded. 3. The average distance (in km) between centroids of the regions where the species was recorded. 4. The latitudinal range, defined as the distance (in km) between the highest and lowest latitude of the centroid of the region where the species was recorded. Following species projection into a bidimensional PCA, whose axes explained 96.48% of total variance in the data, we used the k-means algorithm to group species according to similarities in their spread ranges, and the elbow method to identify the optimal number of clusters (Supplementary Figs. 3 and 4)⁶⁷. To perform the PCA, we used the ‘prcomp()’ function and the k-means was implemented using the ‘kmeans()’ function both from the *base* R package. For visualization and cluster analysis of the PCA results we used the ‘fviz_pca_biplot()’ function from the *factoextra* package (version 1.0.7)⁶⁸.

Continental flows

To visualize the exchange between continental regions, we linked the native region(s) of each species to the continent(s) of its non-native

area of introduction. First, we identified the native continent of each individual species according to the current state of knowledge in the literature (Supplementary Table 4). For a few species, the native ranges were not limited to a single continent. Species mentioned to be native to more than one continent among Europe, Africa, and Asia were grouped under the term “Old World.” Species whose native range was even less precisely defined (e.g., Old World plus Australia) were grouped in the ‘unknown’ category. In some cases, we grouped two continents (i.e., Americas, Australia and Asia). The delineation of continents was made according to the Supplementary Fig. 2. We calculated the number of species introduced to each continent, with each species introduced to a continent counted only once and represented by the arrows pointing to the continents. This included both inter-continental and intracontinental introductions, accounting for instances where a species was introduced to a new region within the same continent. Flow diagrams were created using the *circlize* package (version 0.4.15)⁶⁹.

Assessing patterns and drivers of species distributions

To assess the geographical patterns of species introductions and establishment, we summed the number (richness) of first records per region and the number of species that successfully established. To assess possible temporal shifts in the patterns of introduction and establishment, this was performed considering 1) all species and 2) only those that had their first global record after 1900. To identify hotspots and coldspots of species introduction, we used a general linear mixed model (GLMM)⁷⁰, in which we used the number of first records as dependent variable and as explanatory variables we used country area size and a proxy of country’s recording effort. The first variable was used to account for species-area relationships, wherein regions with larger areas tend to harbor more species⁷¹. The proxy variable for recording effort encompassed both proactive measures (e.g., surveillance initiatives) and reactive responses (e.g., national action plans for invasive species management) as defined by Early et al.⁶⁶. These authors ranked countries based on their capacity to prevent the introduction of Invasive Alien Species (IAS) and their ability to identify and control emerging invasions. This ranking ranged from 0 (lowest capacity) to 3 (highest capacity) and was derived from reports to the Convention on Biological Diversity. Factors considered in the ranking included existing legislation on cargo inspection procedures, public awareness programs, and resources allocated for species identification and reporting. We used the average between proactive and reactive effort. Six countries are at the top of the ranking: Australia, Austria, Canada, New Zealand, the United Kingdom, and the USA. This variable is available at the country level. Consequently, the models were developed at this spatial resolution after aggregating first record data from sub-national divisions. Due to limitations in the spatial coverage of the

recording effort proxy, 47 countries had to be excluded from the analysis. The final models encompassed a total of 181 countries. We fitted the models using the *glmTMB* package (version 1.1.9)⁷⁰, assuming a negative binomial distribution of errors and using continents as a random effect to account for spatial autocorrelation among regions. The residuals of these models were then ranked to calculate the upper and lower quantiles, which serve as boundaries for defining hot- and coldspots for the introduction and establishment of non-native mosquitoes (i.e., upper/lower 10 and 2.5%).

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 socio-economic and environmental variables. The variables were (1) gross domestic product per capita (GDP)⁷², (2) total trade openness in US\$⁷³, (3) time of occupation by one of the eight main European colonial empires, based on published data⁵ and additional data provided by Bernd Lenzner (unpublished data), (4) number of European empires that had a colonial influence on the country⁵, (5) total human population⁷², (6) long-term average yearly temperature⁷⁴, (7) long-term average yearly sum of precipitation⁷⁴, (8) percentage of land cover⁷⁵ 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 Supplementary Table 4.

Of these variables, trade openness and occupation by colonial empires have a more intricate meaning and require a deeper explanation. Trade openness is a measure of a country’s trade globalization. This measure was calculated as an average between 2017 and 2021 of imports and exports of total trade in goods and services as a percentage of the country’s GDP⁷³. To represent colonization patterns, we utilized the Empire Database⁵, which originally had data for the four main colonial empires, but was meanwhile extended to eight empires (unpublished data). This dataset provides information on the duration of occupation by the eight European colonial empires: British, Dutch, Spanish, Portuguese, and extended with Belgian, French, German, and Italian. We calculated the total duration of occupation for each country and the number of colonial powers that occupied each country.

To avoid redundancy between explanatory variables, we only included those with pairwise Pearson correlation coefficients below |0.7| and a variance inflation factor below 3, calculated using the *usdm* package (version 2.1.7)⁷⁶. The variable “total trade openness in US\$” was highly correlated with GDP per capita and population size. Similarly, “absolute latitude” was correlated with temperature, and “colonial occupation time” was correlated with the number of colonial empires. Consequently, these three variables were excluded from the models. Several variables (see Supplementary Table 4) were log transformed to ensure normality and numeric variables were scaled to make them comparable⁷⁷. The correlation matrix for the predictors used in the models to test the drivers can be found in the Supplementary Fig. 6. The model assumed a Gaussian distribution of errors.

All calculations were done using R version 4.3.2 (2023-10-31)⁷⁸ in RStudio⁷⁹. All figures were created using the *ggplot2* package (version 3.4.4)⁸⁰. Data processing and visualization also involved the use of *dplyr*⁸¹ (version 1.1.4), *tidyr*⁸² (version 1.3.0), *GGally*⁸³ (version 2.2.1), *geosphere*⁸⁴ (version 1.5.18), *paletteer*⁸⁵ (version 1.6.0) and *patchwork*⁸⁶ (version 1.2.0). All maps were produced using QGIS (version 3.30.1-‘s-Hertogenbosch’)⁸⁷.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The main dataset containing first records of mosquito species introductions and establishments, along with all post-processed predictor data and R code used in the analyses, is publicly available on Zenodo at <https://zenodo.org/records/15731142>. Raw predictor data can be obtained as follows: invasion sampling bias: <https://doi.org/10.1038/ncomms12485>; trade openness: <https://unctadstat.unctad.org/datacentre/dataviewer/US.GoodsAndServTradeOpennessBpm6>; GDP: <https://data.worldbank.org/indicator/NY.GDP.MKTP.CD>; human population: <https://data.worldbank.org/indicator/SP.POP.TOTL>; land cover: <https://doi.org/10.2909/c6377c6e-76cc-4d03-8330-628a03693042>; climate variables: <https://www.worldclim.org/>. The colonial empire dataset was first used in <https://doi.org/10.1038/s41559-022-01865-1>, and was used in this article with additional extensions of data for four more empires. It is available upon request from Bernd Lenzner. Aggregated predictor data for each country and the analysis code are included and publicly available in the Zenodo repository under the below-mentioned link. Source data are provided with this paper.

Code availability

The R code used for data processing, analysis, and visualization is publicly available on Zenodo at <https://doi.org/10.5281/zenodo.15731142>.

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Author contributions

R.P., C.C., and C.A.S. designed the study. Analyses were performed by R.P. with contributions from C.C. R.P. led the writing with significant input from C.A.S., F.E., A.G.-R., D.L., B.L., A.S., J.L.Z., and C.C. who contributed to preliminary drafts and approved the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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