Why is the tiger mosquito so invasive?

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Where do invasive species come from? How are they introduced? Increased trade has led to an explosion in the frequency of introduction of alien insects on a global scale. However, many factors are decisive for the success of a biological invasion, in particular the ecological and genetic characteristics of introduced populations. Indeed, most species introductions fail. Globalization increases the likelihood of introducing an invasion-prone species at the right time and place. Genetic analysis of invasive populations provides valuable information on how introductions and expansion are taking place, both on a global scale and on a local landscape scale.

1. Biology of the species

An **invasive species** is one whose **populations** have been **transported** from one region to another geographically distant region (introduced populations), and which once introduced are **capable of reproducing** (established populations) and **expanding their geographic distribution** (invasive populations). The mechanisms at work during this invasion process are independent of the notion of impacts, whether ecological, health or economic. Nevertheless, biological invasions are recognized as one of the main causes of **biodiversity change** [1].

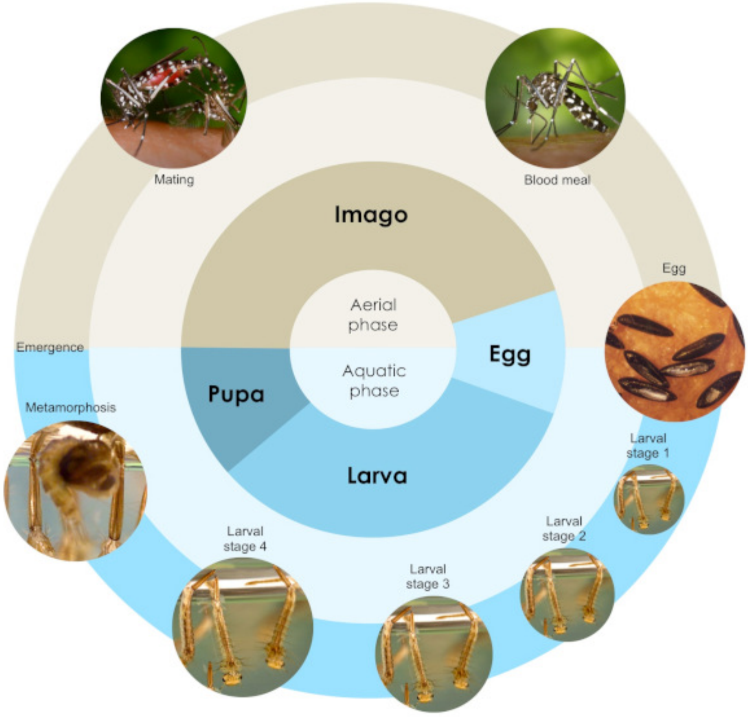

Figure 1: Life cycle of the tiger mosquito. The aquatic phase is shown in blue, the aerial phase in brown. [Source: © Stéphanie Sherpa, from ref 5; Source photos: Centers for Disease Control and Prevention/Henry D. Pratt/James Gathany, via Public Health Image Library]

Among the most invasive species, insects are second after plants, particularly in North America and Europe [2]. Insect invasions can have negative impacts on public health when insects are vectors of infectious diseases (See: Climate change: what effects on our health?). Among them, the **Asian tiger mosquito**, *Aedes albopictus*, can transmit various viruses to humans, such as Dengue, Chikungunya and Zika. Originally from Southeast Asia, it is now one of the **most widespread** mosquito species in the world and is classified as one of the 100 most invasive species [3].

1.1. Life cycle

The tiger mosquito life cycle consists of **four stages**: egg, larva, pupa, and imago (adult), divided into two phases depending on the environment in which the stages occur (Figure 1). The first phase, **aquatic**, consists of the egg, larva, and pupa stages, with the adult stage being **aerial** [4]. Both male and female adult mosquitoes feed on nectar, but the females require a blood meal to provide the nutrients needed for egg development. The eggs are laid on a solid surface close to the water surface, and continue to develop once the surface is covered with water. The eggs are drought resistant.

1.2. Ecology

Figure 2. Tiger mosquito larval habitats. Left: natural sites; right: artificial sites provided by humans. [Source: Images under CC0 license, via Wikimedia Commons & PxHere]

Initially, the tiger mosquito was a forest dwelling species but is now well adapted to **peri-urban and rural** environments. Larvae can develop in a wide range of sites (Figure 2):

natural containers, such as tree stumps, or Bromeliads ;

artificial containers, such as used tires, abandoned containers, flowerpot saucers, or rainwater catchers.

In its Asian native range, the tiger mosquito occurs in a **wide range of environments**: from tropical areas of Southeast Asia (large Indonesian islands, Malay Peninsula) to temperate regions of Northeast China and Japan, and from subtropical areas of the Indochinese Peninsula to India further west (Figure 3). [5]

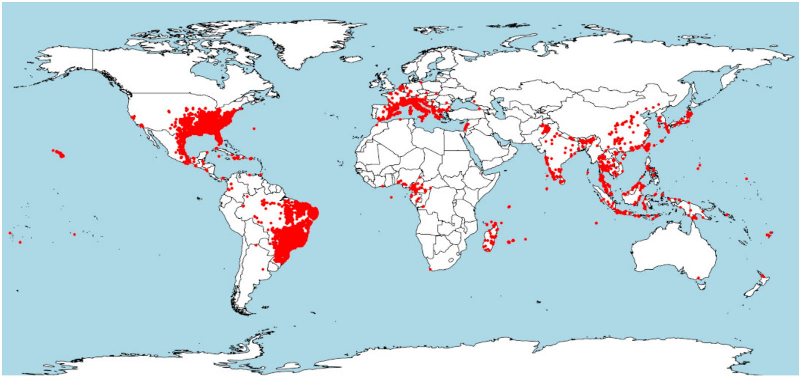

Figure 3. Current geographic distribution of the tiger mosquito. The red dots represent occurrence data [Source: © Stéphanie Sherpa, from ref. 5]

Depending on the geographical origin of the populations, it presents a **seasonal dynamics abundance**. In tropical regions, populations are active throughout the year, whereas climatic conditions in temperate latitudes are unfavourable in winter. Nevertheless, the tiger mosquito has the capacity to lay cold-resistant eggs called **diapausing** eggs [6].

2. Where do invasive populations come from?

The rate of introduction of alien species has increased significantly in recent decades [2], in particular due to increased trade and transport of goods and people (Figure 4).

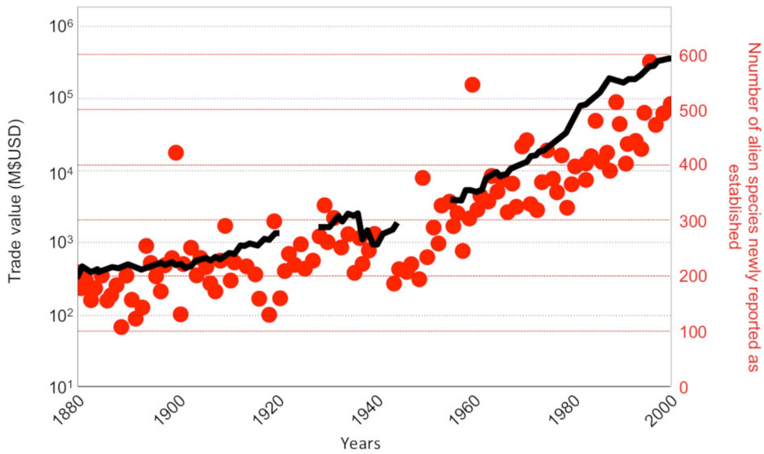

Figure 4. Relationship between invasion and globalization. Changes in the total number of alien species newly reported as established across all groups (red dots) and in the value of trade in commodities (black line) between 1880 and 2000 at the global level. [Source: Author's diagram, based on data from ref. 2]

Although the majority of invasive insects have a **native range** in Asia (See: Climate change and globalisation, drivers of insect invasions), introduced populations are not always directly introduced from their native range, but may originate from other introduced populations, the latter being referred to as 'bridgehead' populations. The reconstruction of **colonisation routes** is based on genetic methods and on spatio-temporal data on species detection (occurrences) to describe the routes used: places of departure and arrival, number of stages, type of transport, frequency and number of introductions [7]. This knowledge of how the species is introduced is necessary to prevent new introductions [8].

The rapid growth in global merchandise trade has increased the number of tiger mosquito introductions. Its spread probably **began in the late 19th century**, but its distribution has rapidly spread to all continents except Antarctica in recent decades, particularly in Europe where the species has been present since the late 1970s [9].

Genetic analysis of European populations shows three **independent introductions**: in Albania from China, in northern Italy from the USA, and in central Italy, where the genetic variability of the populations is the result of a mixture between those initially present in northern Italy and a new introduction from China [10]. Migration patterns at the global scale demonstrate that the source populations at the origin of the introductions correspond to **international trade partners** at the time of the first introductions.

Although each biological invasion has its own history, introductions of other insect species, such as the Asian ladybird [11] and the spotted-wing drosophila [12], have followed a similar geographical pattern. The introduction into Europe has taken place from Asia via bridgehead populations in the United States, suggesting **a predominant role of human transport networks**.

3. Rapid expansion in Europe

3.1. Origin of populations

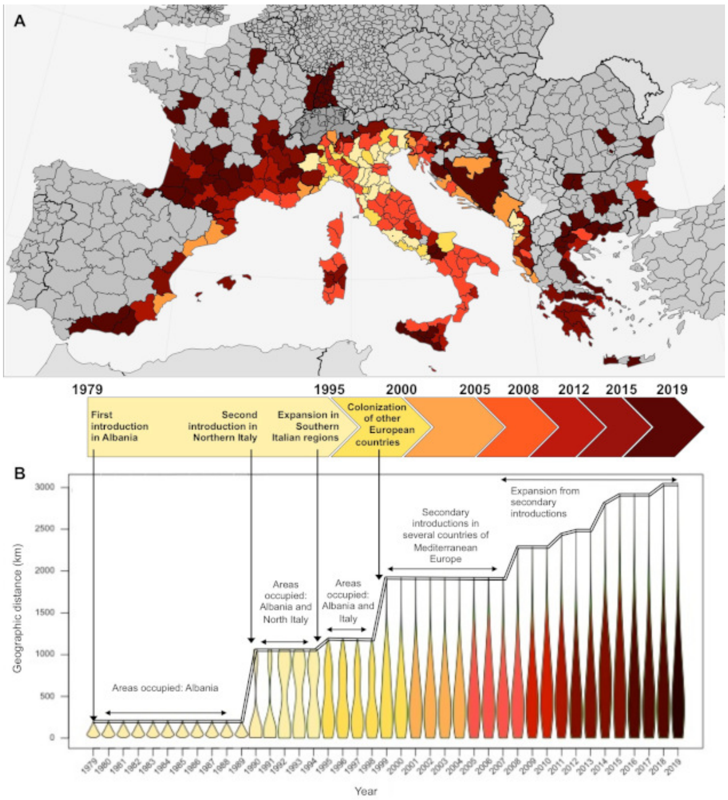

Figure 5: Spatial expansion of the tiger mosquito in Europe. A: Geographical distribution over time. The colour of the units on the map represents the dates of introduction, only for regions where it is recognised as established. Grey: absence of the species or absence of data. B: Evolution of the shortest geographical distance per pair of occurrences per year (accumulation of occurrences since introduction). [Source: © Stéphanie Sherpa, from ref. 5]

Since its first introduction in Albania in 1979, the species was introduced a second time in Northern Italy in the early 1990s [9]. Its geographical distribution remained relatively restricted to these regions until the 2000s, then it gradually invaded all parts of Mediterranean Europe in less than 30 years, colonizing increasingly remote areas each year (Figure 5).

The analysis of a representative sample of the distribution of the species in Europe has made it possible to reconstruct the precise history of the expansion. The three populations initially introduced in Europe (Albania, Northern Italy, Central Italy) constituted centres of dispersal (Figure 6). The migration routes reflect the geography of human transport: **genetic exchanges correlate to**

the geopolitical context in the **Mediterranean basin**.

3.2. Number of introductions

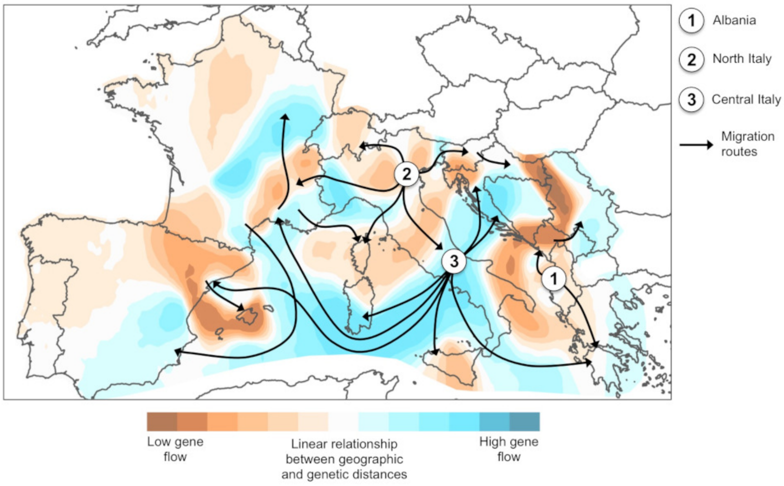

Figure 6. Europe-wide migration routes. The background map represents the results of a population genetics model integrating the geography of populations to identify barriers (brown areas) and corridors (blue areas) for dispersal. The figures represent the location of the first three areas of introduction in Europe in chronological order (1979, 1990, and 2000 respectively). The arrows represent the routes of colonisation. [Source: © Stéphanie Sherpa, modified from ref. 5]

Genetic diversity within a population determines its potential response to environmental changes and its persistence over time [13]. In the context of biological invasions, the genetic diversity of the introduced population is conditioned by the genetic diversity in its source, the number of individuals released and the frequency of introduction events [14]. In general, a small number of individuals are introduced, carrying only a subset of the genes of the source population. This **low diversity** induces high inbreeding among individuals, which increases **the risk of extinction** of the population.

Multiple introductions are one of the main factors increasing population genetic diversity [15]. They can bring two genetically distinct groups of individuals into contact, whose mixing leads to the appearance of new genetic combinations. For example, the tiger mosquito populations established in central Italy, resulting from mixing between two source populations, have higher levels of genetic diversity than those recorded in the native range of the species [10]. Furthermore, the high connectivity between introduced populations has probably favoured the **maintenance of high levels of genetic diversity** within populations on the expansion fronts, **contributing to the rapid expansion in Europe** (Figure 5).

4. A species predisposed to transport and temperate climates

Trade determines the origin of introduced populations and the number of introductions, but cannot explain alone the success of the tiger mosquito. Different elements of its biology and ecology have also played a role in introduction and establishment success.

4.1. Probability of introduction

The adaptation of organisms to human-modified habitats may increase the **likelihood of their introduction** into new regions because populations in areas frequented by humans are more likely to be transported [16]. Among the breeding sites used by tiger mosquitoes, used tires are the preferred egg-laying site. Because they are **drought resistant**, the eggs can survive for several months and can be transported over long distances. Intensified **tire trade** has thus initiated the global expansion of the species through the transport of eggs.

4.2. Probability of establishment

The distribution of tiger mosquitoes in temperate regions corresponds to several thresholds of climatic conditions [17]:

an average temperature in the coldest month **above 0°C** for the winter survival of eggs;

an **average annual** temperature of **11°C** for the maintenance of adult activity;

a **minimum** annual precipitation of **500 mm** for the maintenance of egg-laying sites.

As with many insects, the winter survival of the tiger mosquito in cold environments is primarily determined by the ability of the eggs to enter diapause. This **physiological adaptation** is already present in temperate regions of Asia, where are the sources of the introduction in Albania and central Italy, and in the USA, which is the source of the introduction in northern Italy [5], [18], [19]. Thus, **the tiger mosquito was already pre-adapted to settle in** Europe. Moreover, **the environmental conditions encountered during introduction in Europe were similar to those encountered in the source regions** [20], which may explain the rapid establishment of the populations (Figure 7). These environmental constraints include climatic constraints (temperature, rainfall) but also anthropogenic constraints (urbanisation and artificialisation of habitats).

5. Passive dissemination via road transport

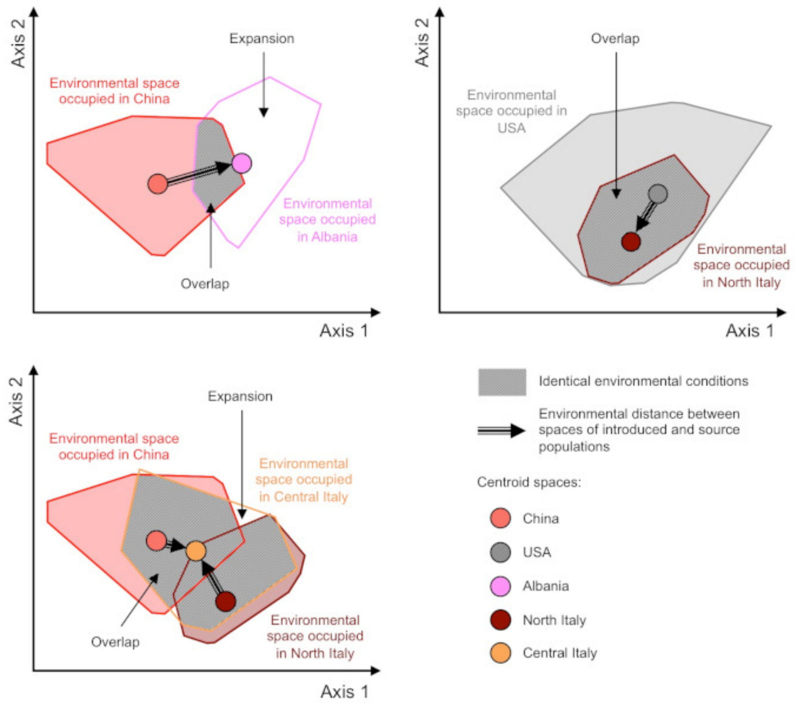

Figure 7. Variation in environmental conditions between introduced populations in Europe and their source populations. Spaces represent the environmental range encountered in each region, determined from occurrence and environmental data (temperature, precipitation, anthropisation). The arrows link space centroids source to visualise environmental change. [Source: © Stéphanie Sherpa, modified from 20]

The intracontinental dispersal of the tiger mosquito after introduction is mainly due to the **passive transport of eggs via road transport**, particularly used tires [21]. Indeed, numerous detections of tiger mosquitoes have been reported in tire storage areas. However, recent research has highlighted the role of daily car travel in the dispersal of adults [22].

There is a direct causal relationship between dispersal [23] and gene flow between populations. Therefore, **landscape genetics** [24] seeks to identify geographic and landscape factors that promote population connectivity. In contrast to colonisation routes, that are reconstructed at a global scale, population connectivity must be studied at a local scale. Although human-assisted long-distance dispersal can be characterized by "jumps", **expansion fronts** provide excellent natural laboratories for studying landscape factors affecting population connectivity.

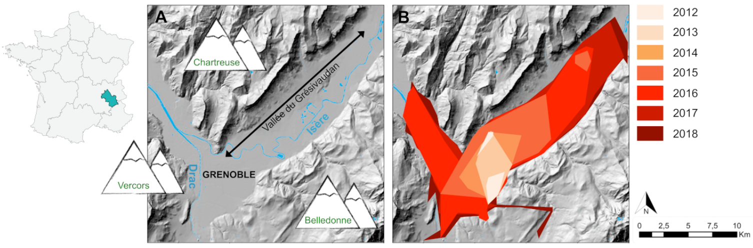

Figure 8. Changes in the geographical distribution of the tiger mosquito over time in the region of Grenoble, France. A: map showing the three valleys on either side of Grenoble and B: limits of distribution per year since introduction in 2012, showing only the expansion front (uninhabited areas within these expanses are not shown). [Source: © Stéphanie Sherpa]

Among the areas recently invaded by the tiger mosquito, the Grenoble region, where it has been present since 2012, is an excellent study area for understanding the expansion dynamics of invasive species. Expansion has only been possible in three directions on either side of Grenoble, corresponding to the three valleys located between the Vercors, Chartreuse and Belledonne massifs (Figure 8).

Modelling the factors structuring the genetic variability of populations at the Grenoble landscape scale, using different types of habitats (open habitats, forests, dense urban areas, residential urban areas, rivers, road networks), revealed that **passive dispersal of tiger mosquitoes along road axes induces strong connectivity between geographically distant populations** on either side of Grenoble [25] (Figure 9).

The tiger mosquito has a **low natural dispersal capacity** of about 200m per generation on average based on estimations from capture-recapture rates [26]. The generation time [27] is about three weeks in the tiger mosquito. Environmental conditions in the Grenoble region being favourable for reproduction from May to October, the species can theoretically complete up to seven generations per year. Thus, the maximum natural dispersal of individuals between 2013 and 2017 is limited to a radius of 6 km. As the geographical distance between genetically close populations on either side of identified roads (Figure 9) can be up to 25 km, this study confirms that **the main factor explaining the connectivity between distant populations in the tiger mosquito is human transport along roads**.

6. Rapid natural expansion due to urbanization of the territories

In the Grenoble area, the **presence of the tiger mosquito is determined by** (Figure 10):

A minimum mean annual temperature of 11°C, correlated to an optimal temperature during the summer months, when the adults are active, and to a winter temperature allowing the survival of the eggs. This temperature threshold corresponds to the 800m isocline.

The presence of diffuse urban habitats, corresponding to residential areas with gardens where egg-laying sites (flowerpot cups, water collectors) and humans (blood meal for females) are abundant, allowing the reproductive cycle to be completed.

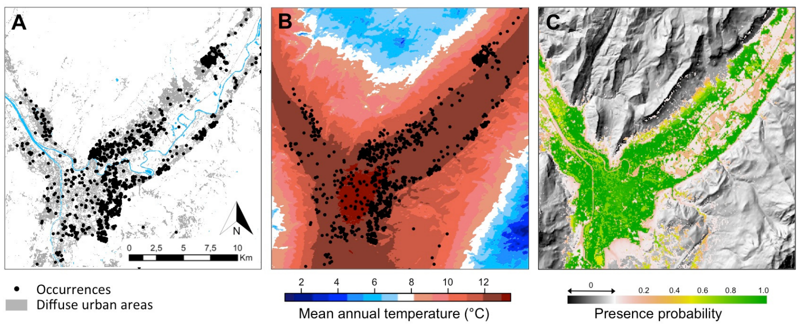

Figure 10. Distribution of suitable habitats for the establishment of the tiger mosquito in the Grenoble region. A: Residential areas are the land-cover category best explaining the mosquito geographic distribution. B: relationship between the presence of the tiger mosquito and temperature, showing a minimum threshold of 11°C. C: probability of presence of the tiger mosquito based on currently occupied areas (black dots on A and B) representing the areas where the species can establish with high certainty (1) and those where it is absent (0). [Source: © Stéphanie Sherpa, modified from 25]

Although often neglected in the context of biological invasions, natural dispersal can also contribute to the expansion of populations at a small spatial scale. A **dispersal model** combining spatio-temporal detections of the species collected by the *Mosquito Control agency in Rhône Alpes* (EID) with suitable habitats identified by ecological modelling (Figure 10) and the biological characteristics of the species (number of generations per year, maximum adult dispersal distance per generation), allows to dissociate dispersal events compatible with natural dispersal from those that are necessarily passive (distance too large). By comparing successive years since introduction, this model reveals that between **70% and 80% of new yearly detections** can be attributed to **natural** dispersal (Figure 11).

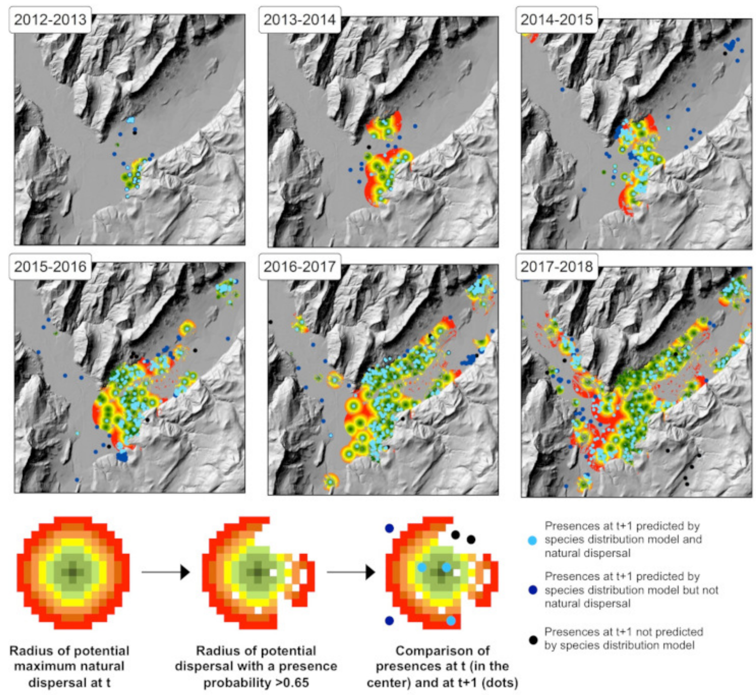

Figure 11. Respective roles of natural and passive dispersal in the expansion of the tiger mosquito since its introduction in the Grenoble region. The maps show the potential natural dispersal area for each comparison of two consecutive years. The theoretical radius represents the number of possible generations of natural dispersal (7 generations per year represented by 7 colours), resulting in a potential dispersal ranging from 0 to 1,500 m (maximum dispersal of 200 m per generation) depending on the date of detection, with a generation time of 3 weeks. The colours of the dots indicate the category of dispersal. Light blue: natural dispersal (the occurrence recorded at t + 1 is within the radius constructed using the occurrences at t), dark blue: human-assisted dispersal (the occurrence recorded at t + 1 is outside the radius constructed using the occurrences at t). [Source: © Stéphanie Sherpa, modified from ref. 25]

This predominance of natural dispersal corroborates the patterns of population genetic differentiation, with **diffuse urban areas** such as parks, private gardens and cemeteries, identified as **barriers to dispersal** (Figure 9). Populations present in diffuse urban areas that are a few hundred metres to two kilometres apart are genetically distant. This low dispersal can be attributed to the fact that diffuse urban areas provide sufficient favourable habitats with a relatively high abundance of egg-laying and host sites (for feeding and breeding) and vegetative areas (for adult resting).

The large proportion of continuous suitable habitats for the tiger mosquito in the Grenoble region **promoted the rapid colonisation** of almost all residential areas a few years after its introduction. Human population growth and the attractiveness of residential areas on the edges of dense urban areas gradually induced an extension of urban residential spaces and a replacement of open habitats, such as meadows or farmland, providing new suitable habitats for the establishment and expansion of the tiger mosquito. **Changes in land use and human pressures on ecosystems promote the establishment and accelerate the expansion of invasive species** (See When invasive plants also walk in the fields).

7. Messages to remember

Genetic analysis of invasive **populations** makes it possible to trace their history (introduction, establishment, expansion) at the global scale, but also at the local landscape scale.

The number of introductions and the origin of introduced populations determining their capacity to establish (genetic diversity and adaptive traits) are conditioned by human **transport networks**.

Human-assisted long-distance dispersal along motorways, leading to **frequent exchanges between populations**, favours their long-term persistence.

The role of **natural dispersal** at the landscape scale in the spatial expansion of populations is often underestimated and depends on the amount of favourable habitats.

The extent and availability of these habitats is directly influenced by **land use change**.

Notes and References

Cover image. Tiger mosquito. [Source: James Gathany, CDC/public domain]

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