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Will the yellow fever mosquito colonise Europe? Assessing the re-introduction of *Aedes aegypti* using a process-based population dynamical model

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ABSTRACT

Aedes aegypti are feared invasive mosquitoes as they transmit pathogens which cause debilitating diseases in humans. Although mainland Europe has not yet witnessed re-establishment and dispersal of *Ae. aegypti* populations, several urban areas along coastlines represent suitable habitats for the species. In addition, European coastal areas are characterised by high exotic species propagule pressure, due to dense international ship traffic.

To assess the likelihood of establishment in order to guide surveillance and control planning, we applied a process-based population dynamical model to simulate both the life cycle and dispersal of *Ae. aegypti* at the local scale after its introduction through ship traffic. We selected five European ports along a latitudinal gradient by considering both environmental conditions and the economical importance of ports: Algeciras and Barcelona in Spain; Venice and Genoa in Italy and Rotterdam in the Netherlands. The model was informed using parameters relevant for *Ae. aegypti* biology, fine-scale temperature time-series, urban structures and road networks.

According to model results, the introduction of small quantities of *Ae. aegypti* eggs (10−1000) has the potential to cause species establishment, high local densities and slow initial dispersal in the two southernmost study areas, Algeciras and Barcelona, whereas Genoa is at the edge of suitability. Barcelona had the highest simulated mosquito densities (584 females/ha), whereas Algeciras densities were never more than 32 females/ha, but were higher during the colder seasons. The median spatial spread of the species varied between a few hundred meters to 2 km/year and was affected by the structure of the road network, topography and urban sprawl along the coast in the surrounding of the port of introduction. The study areas of Genoa, Venice and Rotterdam were found not suitable for establishment of this mosquito species, however, climate change could create conditions for *Ae. aegypti* invasion in these regions in the next decades.

It is commonly accepted that targeted monitoring and early control actions are the most effective methods to hinder the establishment of invasive species in new areas. Our findings and model framework may support surveillance initiatives for those European coastal urban areas which are known to have high propagule pressure and a high modelled probability of *Ae. aegypti* establishment.

1. Introduction

Mosquitoes in the genus *Aedes* (Culicidae: Diptera) are some of the most feared invasive species due to their competence for transmitting debilitating pathogens. Amongst them, *Aedes aegypti* is a global health concern due to its capacity to thrive in urban areas and because it is an unrivalled vector for viruses (Leta et al., 2018). This species evolved in sub-Saharan Africa and was progressively brought outside its original geographical range by human trade. First, the despicable slave trade between the 15th and 19th centuries moved the mosquito from West Africa to Europe and the Americas. Afterwards, intensified trade with Asia during the 18th and 19th centuries and troop movements during World War II caused further expansion of its geographical distribution (Powell et al., 2013).

To date, mainland Europe is the only continent, except Antarctica, where *Ae. aegypti* has no established populations despite having been

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present from Portugal to the Black Sea until the 20th century (Akiner et al., 2016; Cardamatis, 1929; Schaffner and Mathis, 2014). Improvements both in hygiene and in the management of water systems, as well as the widespread application of insecticides to decrease the malaria burden are thought to have led to the extinction of the species on this continent. However, in recent years *Ae. aegypti* has been detected multiple times in mainland Europe or in areas geographically or politically connected with Europe. Multiple introductions of *Ae. aegypti* were detected in the Netherlands from 2010 to 2018 (Brown et al., 2011; Ibáñez-Justicia et al., 2020) and in Germany in 2016 (Kampen et al., 2016). Established populations of *Ae. aegypti* were found along the coast of the Black Sea in 2008 (in Turkey, Georgia and Russian Federation; ECDC, 2019), in the Portuguese island of Madeira, located about 900 km south-west of mainland Portugal, in 2004 and, more recently, from nearby Egypt (Abozeid et al., 2018).

Mainland Europe has not yet witnessed the establishment and dispersal of *Ae. aegypti* populations. However, urban areas distributed along coastlines may represent suitable habitats for the species (Kraemer et al., 2015). European coastlines are also characterised by extremely high exotic species propagule pressure (Blackburn et al., 2020; Dunn and Hatcher, 2015; Lockwood et al., 2005), due to the dense international maritime trade which nowadays accounts for 90% of the exchange of goods in Europe (IMO, 2019). The Mediterranean basin plays a relevant role in global trade and it is expected to become even more important in the next decades since massive investments are planned in coastal and harbour infrastructures (e.g. see for instance the Chinese government's Belt and Roads initiative; Ekman, 2018). Moreover, regions in South, East and Southeast Asia as well as in the Americas where *Ae. aegypti* populations are widespread, represent major sources of goods shipped to Europe. Therefore, in the European context, coastal urban areas and the Mediterranean basin should be considered as focal points when evaluating the potential introduction of invasive mosquitoes. The precedent provided by *Aedes albopictus*, an invasive species related to *Ae. aegypti* could serve as a cautionary tale. This species was detected for the first time in the port of Durazzo, Albania, likely arrived from China (Adhami and Reiter, 1998) and nowadays is distributed along most of south and central Europe. Its introduction, establishment and dispersion in the European continent appear to have been supported by maritime transportation of tires and other goods (Eritja et al., 2005).

Outbreaks caused by *Aedes*-borne pathogens such as chikungunya and dengue have been recorded multiple times in Europe in the last two decades and, more recently, the first cases of Zika infection in humans have been reported in Southern France (Brady and Hay, 2019; Rezza et al., 2007; Venturi et al., 2017). Until now, these outbreaks have been limited in time and space and sustained by *Ae. albopictus*, which is an abundant but more opportunistic feeder and, thus, less competent vector than *Ae. aegypti* (Richards et al., 2006). The establishment of *Ae. aegypti* in Europe would dramatically change the epidemiological landscape by increasing the risk of pathogen transmission among the human population by this species, mimicking the public-health emergency which followed its recent introduction on the West Coast of the USA (Metzger et al., 2017).

Surveillance enabling early detection and rapid control actions is the best tool we have to prevent species invasions, eradicate invading species or manage their populations at low levels (Simberloff, 2014). Here, to support surveillance and early detection of *Ae. aegypti* in Europe, we applied a process-based population model which simulates both life cycle and dispersal of *Ae. aegypti* after its introduction, for example through ship traffic in European ports. To develop the model, we followed the theoretical model structure proposed by Otero et al. (2008) and extended in Montecino et al. (2017). We chose to simulate introductions of *Ae. aegypti* in ports located along a latitudinal gradient to capture the variability of climatic condition along European coastlines. We selected five of the busiest European container ports (Eurostat, 2018) which were also located in areas predicted to be suitable for *Ae. aegypti* (Kraemer et al., 2015, 2019) or where *Ae. aegypti* was detected in the past, namely: Algeciras and Barcelona, Spain; Venice and Genoa, Italy and Rotterdam, the Netherlands.

The main questions we asked in this study were:

- What is the likelihood that *Ae. aegypti* will establish viable populations in major European ports after eggs introduction via ship traffic?
- At what latitude is *Ae. aegypti* establishment more likely to happen?
- What is the minimum propagule pressure required for a successful introduction?
- What is the space-time distribution trend which *Ae. aegypti* populations will follow once established?

2. Methods

To answer these questions we applied a process-based and time-discrete model to simulate *Ae. aegypti* population dynamics after its introduction in five study areas.

2.1. Study areas and road network

To assess the variability of invasion likelihood across latitudinal gradients and environmental conditions, we considered five 100 × 100 km study areas centered on the ports of Algeciras (lat = 36.12, long = −5.43; Spain), Barcelona (41.34, 2.16; Spain), Genoa (44.40, 8.92; Italy), Venice (45.44, 12.25; Italy), and Rotterdam (51.90, 4.50, the Netherlands; Fig. 1). These study areas have very different climatic conditions: Algeciras has a hot-summer Mediterranean climate with an average annual temperature of 18.6 °C and cumulative precipitation of 768 mm; in Algeciras summers are generally hot and dry, whereas winters are mild and wet. Barcelona and Genoa have a hot-summer Mediterranean climate but are surrounded by subtropical areas, reporting annual average temperatures of 21.2 and 16.7 °C and cumulative precipitation of 640 and 1082 mm. Venice is characterised by a humid subtropical climate, with average annual temperature and cumulative precipitation of 14.5 °C and 1101 mm, respectively. Winters in Venice can be cold, with temperatures commonly below 0 °C during December and January. Finally, Rotterdam has a temperate oceanic climate, with average temperature and precipitation of 10.9 °C and 867 mm, respectively. Rotterdam summers are generally cool and winter months rarely record temperature below 0 °C (Fig. 3; Smith et al., 2011; Beck et al., 2018). In addition to variability in the temperature regime, the five study areas show landscape characteristics which may represent natural barriers for active species dispersal. These barriers can be overcome by invasive mosquitoes, nevertheless, through human-aided dispersal, including road-mediated anthropogenic movements (Service, 1997). The road network connecting European cities is amongst the most developed in the world, ensuring fast and easy movements of humans, goods and, unintentionally, introduced mosquito populations (Díaz-Nieto et al., 2016; Nelson et al., 2019). The model included this connection among urban areas and, therefore, the possibility of mosquito dispersal through the road network after introduction (see Section 2.2).

2.2. Description of the population dynamical model

Aedes aegypti life cycle presents four main developmental stages: egg, larva, pupa and adult stage. The model considered a simplified life cycle of *Ae. aegypti*, by merging the larval and pupal stages (which can be assumed to have similar physiological requirements) in a unique compartment which we called "immature". Thus, the model considers three main compartments: egg, immature and adult. Temperature and dispersal capacity can be considered the main environmental drivers of invasive mosquito life cycle ecology (Mordecai et al., 2019), thus development and reproduction events were treated as stochastic processes with probabilities derived from temperature-dependent

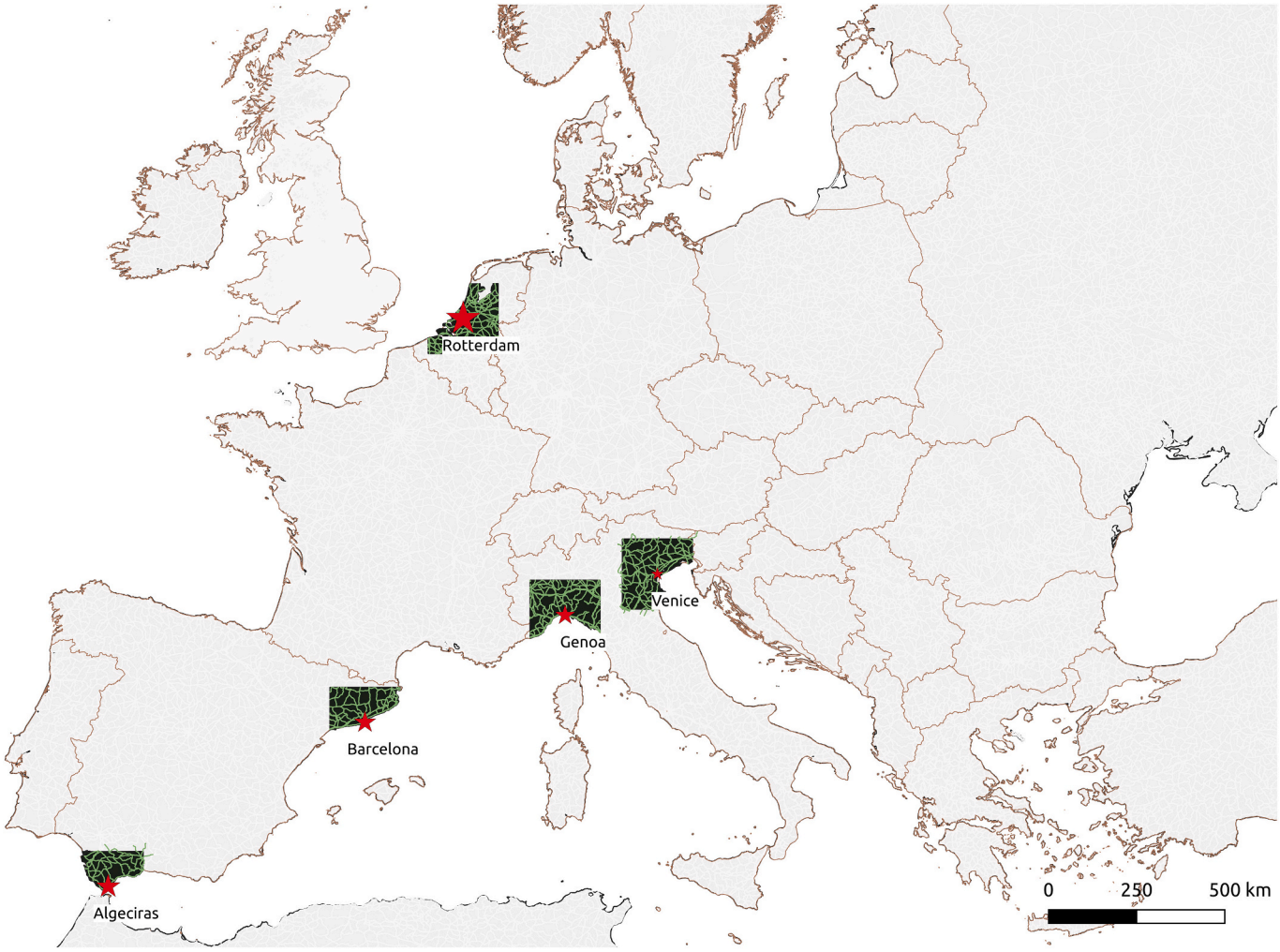

Fig. 1. Locations of the five ports (red stars) investigated along a latitudinal gradient and corresponding study area (black). The network of primary roads is reported in green. The size of the "port" pin is proportional to the quantity of twenty-foot equivalent unit (TEU) received in the corresponding port for the year 2018 (Amsterdam = 13.6, Algeciras = 4.8, Barcelona = 3.4, Genoa = 2.5, Venice = 0.6 TEU; for interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

functions. Similarly, dispersal was determined stochastically by distance-dependent (movement) functions (Fig. 3). Each event in the simulated life cycle occurred once per day always in the same order within grid cells of 250 m spatial resolution, which represented the fundamental spatial units into which *Ae. aegypti* life cycle took place and among which adult mosquitoes dispersed. The 250 m spatial resolution was decided as a trade off between computational effort and the ability to represent temperature variability at the local scale. Indeed, this simplified space-time arena allowed us to reduce dramatically the life cycle of *Ae. aegypti* and, therefore, the computing burden of the model, while retaining temporal, spatial and "biological" resolutions relevant for our questions (Pascoe et al., 2019).

2.2.1. Reproduction and mortality

The number of individuals in each developmental stage dying or surviving day t in cell i is an outcome of binomial draws with probabilities derived from temperature-dependent functions parameterized with data from the appropriate scientific literature. All processes with their associated probability distributions, parameters and references are described in Table 1.

The egg stage (E) is composed by four sub-compartments (SC) which contain eggs of different ages. Eggs enter ESC-1 when laid by ovipositing adult females; the first three sub-compartments contain eggs one, two and three days old that are undergoing embryonation (i.e., incubation time; Christophers, 1960a). The number of eggs (E) in *sc*-1 during day *t-1* that die or move to the next *sc* in day t is defined by a binomial random draw based on mortality and survival probabilities $1 - p_{Es}$ and p_{Es}, respectively:

$$E_{i,t,sc} \sim Binomial\left(E_{i,t-1,sc-1}, p_{E_s}\right) \quad (1)$$

Four days-old eggs can hatch and move to the "immature" (I) compartment. The hatching event occurs with probability p_{Eh}, which is established by a random draw from a Beta distribution. The two shape parameters of this Beta distribution were derived using the average (0.076) and low 95% CI (0.023) proportion of *Ae. aegypti* eggs hatched after being submerged in plastic containers filled with water in field conditions (Soares-Pinheiro et al., 2016).

The immature compartment is composed of six sub-compartments (*ISC*) that contain immatures of different age or immature "sub-stage". Every day immatures in ISC-1 to ISC-5 can die or move to the next ISC based on temperature-dependent probability $1 - p_{Is}$ and p_{Is}, respectively.

$$I_{i,t,sc} \sim Binomial\left(I_{i,t-1,sc-1}, p_{I_s}\right) \quad (2)$$

When immatures reach *ISC-6*, they become ready to emerge as adults and, therefore, can die, survive as *ISC-6* or emerge to move to the "adult" compartment with probability p_{Ie}, which is the outcome of a

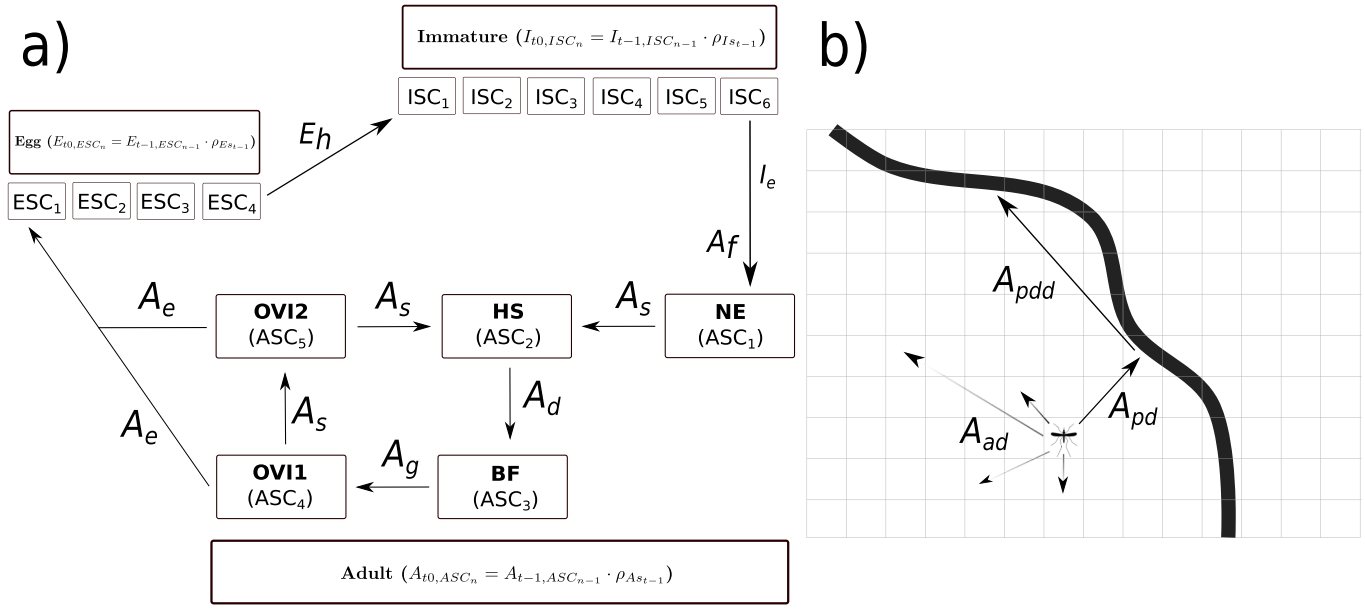

Fig. 2. Graphical representation of model structure: in A) we showed the life cycle of *Ae. aegypti*, and in B) a representation of active and passive dispersal processes. A more detailed description of all model parameters reported in the figure is provided in Table 1. ESC: egg sub-compartment; ISC: immature sub-compartment; ASC: adult sub-compartment; NE: new emergent adults, 1-day old female adults which are developing gonads; HS: host-seeking females; BF: blood-feeding females; OVI1: females in their first ovipositing day; OVI2: females in their second ovipositing day.

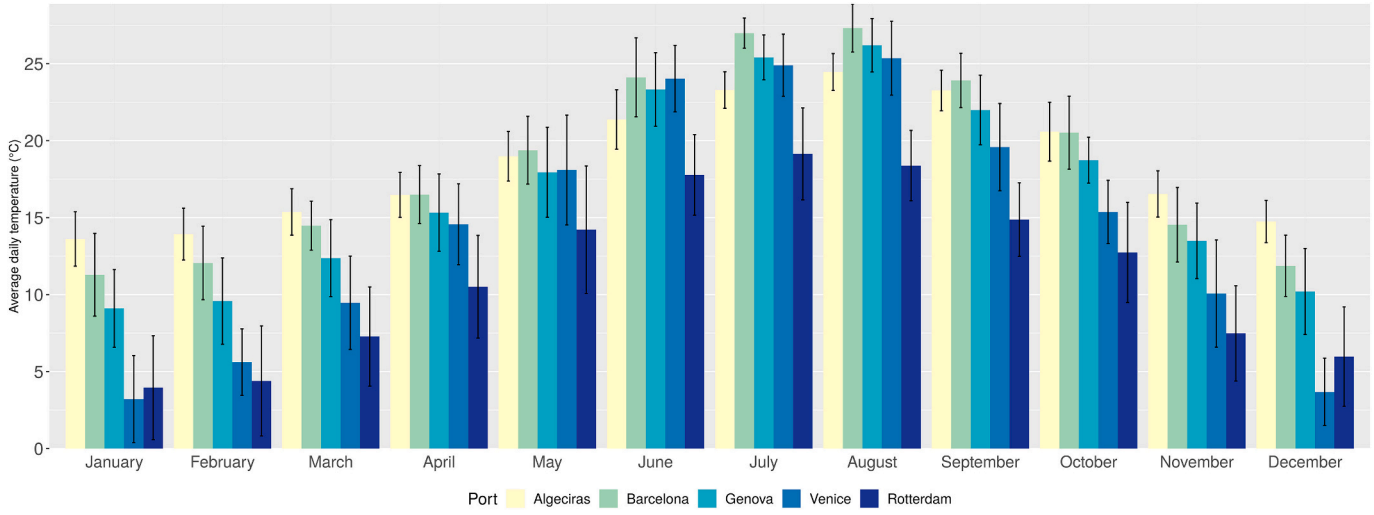

Fig. 3. Monthly average temperature and standard deviation (error bars) for the years 2017–2019 in the five study areas.

temperature-dependent polynomial function as defined in Yang et al., 2009. The pool of immatures moving each day to the adult compartment is subjected to an additional Binomial random draw in order to limit the adult compartment to only female mosquitoes (assuming a 1:1 male/female ratio).

The adult compartment is composed of five sub-compartments that contain adult females in different ages or physiological statuses. *ASC-1* contains 1-day old adults which are developing gonads and, therefore, are not yet sexually mature (Christophers, 1960a). Adults in *ASC-1* can die or move to *ASC-2*, which contains host-seeking adults, following a random draw with a temperature-dependent probability p_{As} (Yang et al., 2009), which also drives the fate of *ASC-2* to *5*. *ASC-2* can die or move to *ASC-3* where they are assumed to have taken a blood meal and entered the gonotrophic cycle. *ASC-3* is, therefore, composed of blood-fed adult females maturing eggs (i.e., completing the gonotrophic cycle). If adult females in *ASC-3* survive day *t-1* they can complete the gonotrophic cycle and move in day *t* to *ASC-4* where they become ovipositing females. The completion of the gonotrophic cycle by *ASC-3* is driven by a binomial random draw based on temperature-dependent probability p_{Ag} (Yang et al., 2009). Females in *ASC-4* in day *t*, first oviposit, then die or move to *ASC-5* which contains females in the second day of oviposition. The number of eggs laid by a female in *ASC-4* or *ASC-5* is the outcome of a Poisson random draw with temperature-dependent probability p_{Ae} (Christophers, 1960a; Yang et al., 2009). Finally, females in *ASC-5* die or move to *ASC-2*, where they will again seek a blood-meal and, if surviving, re-enter the gonotrophic cycle as described above.

2.2.2. *Active and passive dispersal*

In addition to the development and survival cycle of events, host-seeking adult females (*ASC-4*) can also disperse actively (short-range dispersal) or passively (medium-range dispersal). In our model, active dispersal is defined as the probability that an adult mosquito flies at

Table 1
Summary of model processes happening in each day t and cell i, with associated probability density distribution and parameters.

Stage	Process description	Process ppd	Parameters	References
Egg	**Survive**: Probability that an egg survives in day t, cell i.	$E_s \sim Uniform(p_{E_s})$	$p_{E_s} = 0.99$	Otero et al. (2008)
	Hatch: Probability that an embrionated egg hatches in day t, cell i.	$E_h \sim Binomial(p_{E_h})$	$p_{Eh} = Beta(a, b)$; $a = 1.45$, $b = 6.51$	Soares-Pinheiro et al. (2016)
Immature	**Survive**: Probability that an immature survives in day t, cell i.	$I_s \sim Binomial(p_{I_s})$	$p_{I_s} = \mathscr{P}_6(temp)$	Yang et al. (2009)
	Emerge: Probability that an immature >= 6 days old emerges in day t, cell i.	$I_e \sim Binomial(p_{I_e})$	$p_{I_e} = \mathscr{P}_7(temp)$	Yang et al. (2009)
Adult	**Survive**: Probability that an adult survives in day t, cell i.	$A_s \sim Binomial(p_{A_s})$	$p_{A_s} = \mathscr{P}_5(temp)$	Yang et al. (2009)
	Determine sex: Probability that a newly emerged adult is female in day t, cell i.	$A_f \sim Binomial(p_{A_f})$	$p_{A_f} = 0.5$	–
	Mature eggs: Probability that a blood-fed female matures eggs in day t, cell i.	$A_{em} \sim Binomial(p_{A_{em}})$	$p_{A_{em}} = \mathscr{P}_5(temp)$	Yang et al. (2009)
	Oviposit: Number of eggs that an adult female, which underwent eggs maturation, lays in day t, cell i.	$A_{el} \sim Poisson(\lambda_{el})$	$\lambda_{el} = \mathscr{P}_4(temp)$	Yang et al. (2009); Christophers (1960b)
	Disperse a-distance: Probability that a host-seeking adult female disperses in day t from cell i to cell i' at distance d.	$A_{ad} \sim Binomial(p_{A_{ad}})$	$p_{A_{ad}} = LNormal(m, sd)$; $m = 4.95$ $sd = 0.66$.	Marcantonio et al. (2019)
	Disperse p: Probability that a host-seeking adult female in day t in cell ii adjacent to a road intercepts a car.	$A_{pd} \sim Binomial(p_{A_{pd}})$	$p_{A_{pd}} = 0.0051$	Eritja et al. (2017)
	Disperse p-distance: Probability that a passively dispersing adult A_{pd} disperses in day t from cell ii to cell ii' at distance d.	$A_{pdd} \sim Binomial(p_{A_{pdd}})$	$p_{Apdd} = Gamma(\alpha, \beta)$: $\alpha = (c/10000)^2$, $\beta = c/10000^2$, $c = \{18.43, 23.14, 28.14\}$	Alemanno et al. (2012)

distance d_{ad} from the cell of origin and follows a log-normal dispersal kernel (Marcantonio et al., 2019). Thus, in each day t, the number of dispersing *ASC-4* that move to a distance d from the origin cell i is an outcome of a binomial random draw with probability $p_{A_{ad}}$:

$$p_{A_{ad}} \sim LogNormal(meanlog = 4.95, sdlog = 0.66) \quad (3)$$

We assumed that females start dispersing from the center of the cell of origin i, therefore, given a cell side size of 250 m, all mosquitoes dispersing less than 250 m do not leave i. All other dispersing mosquitoes move to a cell i' (landing cell) which is chosen randomly from the set of cells at distance d (i.e. non directional active dispersal).

In addition to active dispersal, the proposed model also considers dispersal aided by car traffic along the main road network. This type of dispersal is thought to be amongst the main drivers of medium-range geographical expansion for *Aedes* mosquitoes (Eritja et al., 2017; Marcantonio et al., 2016). We considered only the network of primary roads in each 100 km^2 study area (Center for International Earth Science Information Network - CIESIN - Columbia University and Information Technology Outreach Services - ITOS - University of Georgia, 2013). Moreover, to consider the eusynantropic ecology of *Ae. aegypti* (ECDC, 2019), we constrained both its life cycle and movements within urban areas, whose boundaries were defined using a spatial GIS layer derived from Schneider et al. (2009).

In the model, adults of all ages greater than 1-day old, that reside in cells intersecting roads may undergo this type of dispersal. We parameterised passive dispersal using the probability of a car transporting *Aedes* mosquitoes p_{Aad} of 0.0051, as reported in Eritja et al. (2017), implying that, on average, only about 5 over 1000 (female) mosquitoes disperse passively every day from each cell of origin. Furthermore, to define the probability of dispersing passively at different distances d, we used data on driving patterns in Europe (Alemanno et al., 2012). We defined p_{Apdd} as the outcome of a Gamma distribution with mean, md, equal to the average driving distance per trip in each of the study areas:

$$p_{pd} \sim Gamma\left(\alpha = (md/(md*sd))^2, \beta = \left(md/(md*sd)^2\right)\right) \quad (4)$$

where md was set to 18.43 km for Italy, 23.14 km for Spain and 28.14 km for the Netherlands (Alemanno et al., 2012). The standard deviation used to parameterize the Gamma distribution was chosen to be very large (100 times the mean) in order to assign a small probability density also to large dispersal distances. The matrix of distances between cells along roads was calculated using the set of *v.net* modules in GRASS GIS 7.6 (Neteler et al., 2012).

Model outputs consisted of a numerical matrix containing the daily number of individuals in each life stage for each 250 m cell of each study area, for each iteration. The model coded in the R statistical language (R Core Team, 2019) together with a comprehensive tutorial is available from the Open Science Framework repository: https://doi.org/10.17605/OSF.IO/537EW.

2.3. Temperature data

Daily temperature estimates at 2 m above-ground for the period 2016–2019 were obtained using the R package *microclima* (Kearney et al., 2020; Maclean et al., 2019) for each study area, considering a region spanning 100 km^2 from the center of each port. *microclima* makes use of 6 h climate and radiation data downloaded from the National Center for Environmental Prediction Reanalysis 2 database at a resolution of 1.8–2.5° (Kanamitsu et al., 2002). The four daily observations are then interpolated hourly with spline interpolation and corrected considering topographic effect using a digital terrain model at 250 m resolution downloaded from EUDEM (Copernicus project, 2019). The *microclima* package allows the user to define a habitat category as defined in MODIS Land use datasets (MODIS product MCD12Q1v006) (Friedl and Sulla-Menashe, 2015), which is used to calibrate a Gaussian curve to estimate hourly vegetation features using an *a priori* established relationship between habitat type and observed vegetation characteristics. We decided to consider the vegetation cover across our study areas according to the MODIS habitat class closer to the ecology of *Ae. aegypti*, which is "Urban and built-up" (MODIS category 14). Coastal effects on temperatures were also considered as described in Maclean et al., 2019. Finally, the temperature times series for each study area derived with *microclima* was further fine-tuned to local weather conditions using the daily average from the National Oceanic and Atmospheric Administration (NOAA) weather station (Smith et al., 2011) closest to the relevant port.

2.4. Experimental design and model validation

We simulated the introduction of 10, 50, 100, 250, 500 or 1000 eggs in a randomly chosen cell within an extended boundary around each introduction port. These boundaries comprised all port infrastructures where goods could have been stored or sorted after arrival and covered 9, 12, 29, 47 and 162 km^2 for Genoa, Algeciras, Venice, Barcelona and Rotterdam, respectively. Eggs were chosen as the introduction propagule as they are the resistant life stage through which *Aedes* mosquitoes overcome periods of adverse climatic conditions, such as cold winters or dry summers (Kramer et al., 2020). Each introduction was iterated 500 times to account for stochastic events in both life cycle and dispersal, as the coefficient of variation of all outcomes of interest stabilised around this number of iterations. The length of each simulated introduction was set to three years in order to allow demographic stabilisation of the simulated populations and integrate inter-annual climatic variability. The introduction year was 2017. In addition, we decided to run preliminary simulations to define the most favourable period of the year for introducing *Ae. aegypti* in order to reduce the chance of false negative results. This set of simulations began with 100 eggs introduced on the 15th of each month of the year 2017 and lasted until the end of the same year. The introduction date in 2017 was thus chosen for each study area as the starting date of the scenario that recorded the highest number of adult mosquitoes in any of the simulated days. In the subsequent full model simulations, successful introductions were defined as those that yielded at least one individual in any life stage on the 20th of June 2018, which represents the end of the spring (and, therefore, the end of adverse climatic conditions for *Aedes aegypti* in Europe) the year after date of introduction (2017). Population demographic and dispersal trends for each introduction scenario were summarised using the interquartile ranges of the distribution of each outcome of interest across iterations for each simulated day.

To assess the credibility of model outputs given the current absence of the species in our study areas, we contrasted the invasion success ratio from simulated introductions against the proportion of the study area below the 10 °C isotherm. As a positive validation criterion, we assumed that the lower the proportion of the study area below the 10 °C isotherm, the higher the invasion success ratio. It is indeed accepted that temperatures around 10 °C represent a theoretical thermal limit for *Ae. aegypti*, below which adult mosquitoes become torpid and unable to move (Christophers, 1960a; Reinhold et al., 2018). The proportion of each study area which experienced days below the 10 °C isotherm for the whole 2017–2018 period was calculated from the European Centre for Medium-Range Weather Forecasts ERA5 reanalysis (1979–2018) dataset (CopernicusClimateChange Service, 2017).

Local sensitivity analysis was performed on model results by varying the values of four model parameters which were considered uncertain, namely: the probability of egg survival (p_{Es}), the probability of egg hatching (p_{Eh}), the number of introduced eggs (E), and the probability of adults dispersing passively (p_{Apd}). We performed the sensitivity analysis by running 200 model iterations over an extensive range of values of each selected model parameter for the study area of Algeciras. The proportion of successful iterations, maximum population dispersal distance, female abundance and invaded area in hectares were plotted against each parameter range in order to assess the sensitivity of model outputs. Results of the local sensitivity analysis are reported and briefly discussed in Appendix 1.

3. Results

3.1. Likelihood of a successful introduction relative to time of the year

Results from the set of preliminary model simulations showed that the month of introduction which resulted in the highest median abundance of adult mosquitoes (relative to the first year of introduction) was March for the port of Rotterdam, April for Barcelona, and May for the ports of Genoa, Venice and Algeciras. Introductions in any month of the year 2017 showed viable populations on the last day of the year (i.e., successful introductions) only in Barcelona, while Algeciras (10 months), Genoa (9), Venice (3) and Rotterdam (1) showed a decreasingly lower number of months suitable for successful introductions (Fig. 4).

3.2. Likelihood and minimum propagule pressure of a successful introduction relative to latitude

The percentage of full model simulations which resulted in established *Ae. aegypti* population was 100% for Barcelona, for a propagule pressure of at least 250 eggs. Algeciras showed somewhat similar results, however, 100% successful introductions were achieved only with a higher minimum propagule pressure of 1000 eggs (Table 2). On the contrary, we did not observe successful introductions for any propagule pressure either in Genoa, Venice or Rotterdam. In Rotterdam, mean daily temperatures during summer were never high enough (>20 °C) to allow the accumulation of an adequate "egg bank" which would have permitted the overwintering of the population (see Fig. 2). Conversely, in Genoa and Venice, although introductions sometimes caused moderate population abundances (>50 adult mosquitoes per ha) during the most favourable months, cold winter temperatures, often under 0 °C, caused extinction for all the introduced populations. The percentage of successful invasions was well associated with the percentage of areas under 10 °C for the period 2017–2018. Interestingly, a relatively small decrease of about 6% of area-days under the 10 °C isotherm between the ports of Barcelona and Genoa represented a climatic divide for *Ae. aegypti* invasion success.

3.3. Space-time trend of established populations

With the exception of Rotterdam, all simulated populations were able to reproduce and spread at local scales during the first summer after introduction. The peak of adult mosquito abundance was reached in autumn in Algeciras, Barcelona and Genoa or in late summer in Venice. Adult female abundances reached maximum overall values of 584 · ha^{-1} in Barcelona, but were considerably lower in the other study areas: Algeciras yielded a maximum of 32 · ha^{-1}, Genoa 28 · ha^{-1}, Venice 20 ·

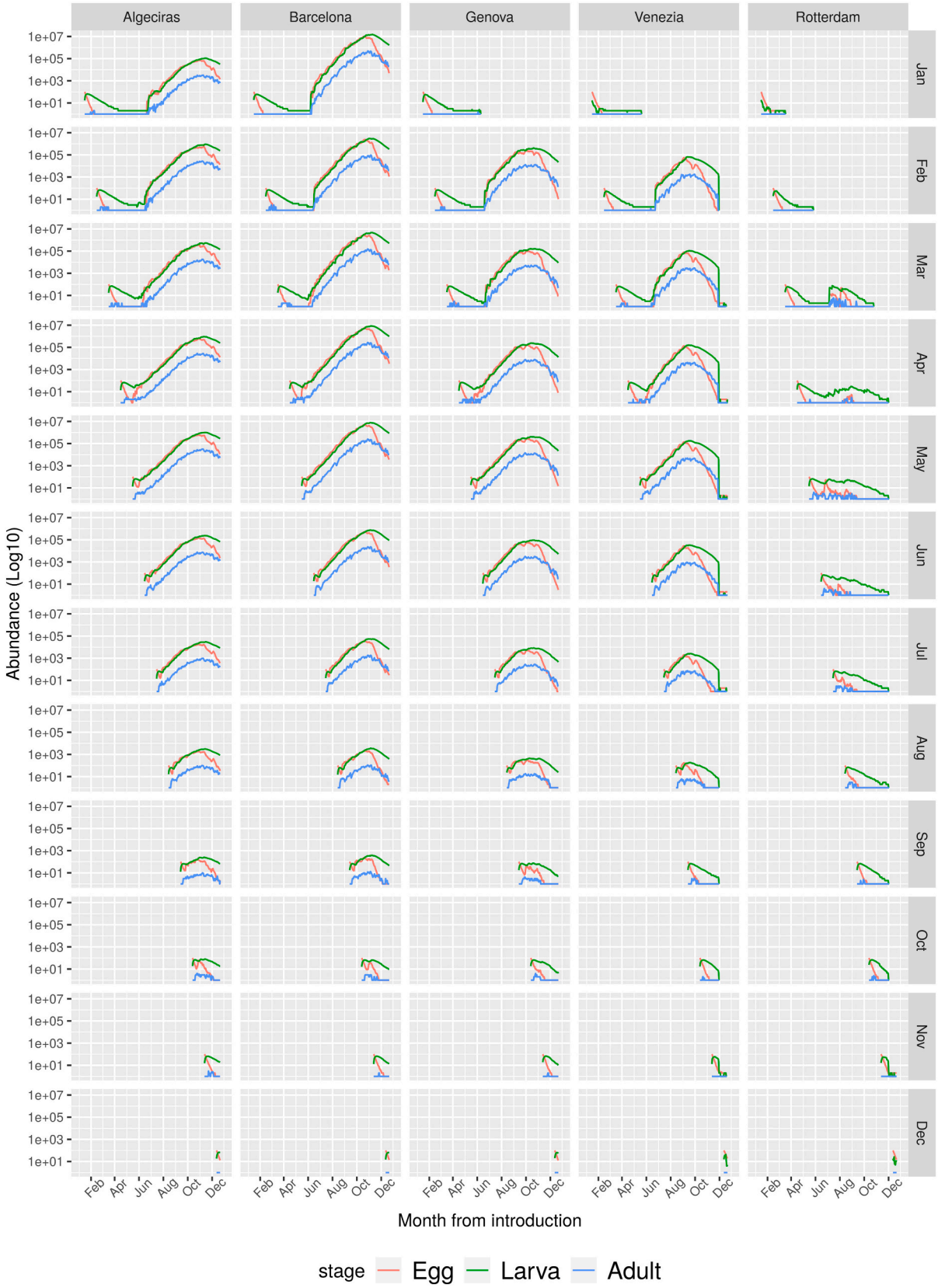

Fig. 4. Time trend of *Ae. aegypti* population abundances from preliminary model iterations simulating the introduction of 100 eggs starting on the 15th of each month of 2017 and ending on the 20th of December 2017 for the five study areas. Blue lines represent adult females, green lines immatures and red lines eggs. Values on the y-axis are transformed using the common logarithm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Number of introduced eggs and corresponding percentage of successful introductions for each of the considered study areas. The last column represent the proportion of each study area that fell below the isotherm of 10 °C for the years 2017–2018 (ERA5 reanalysis (1979–2018)).

Site	Introduced eggs	Introduction success %	Proportion of the study area below 10 °C %
Algeciras	10,50,100,250,500,1000	6,11,16,48,74,100	4.8
Barcelona	10,50,100,250,500,1000	4,26,72,100,100,100	15.3
Genoa	10,50,100,250,500,1000	0	21.7
Venice	10,50,100,250,500,1000	0	24.6
Rotterdam	10,50,100,250,500,1000	0	29.4

ha^{-1} and Rotterdam $2 \cdot ha^{-1}$ (Fig. 5). The pools of eggs and immatures followed trends similar to adult mosquitoes but lagging in time proportionally to differential developmental times, and reaching higher abundances due to the inter-stage survival bottlenecks (Appendix 2 Fig. 8). However, with the onset of colder weather conditions at the end of summer, mosquito populations declined rapidly in all the study areas. The decline was more evident as soon as daily average temperature was constantly under 10 °C, and even in Algeciras and Barcelona, winter densities dropped to a minimum to 1 female/ha during winter months. In these months, the consistent "egg bank" accumulated during the warmer months ensured population overwintering. On the contrary, after the first summer, simulated populations from Genoa, Venice and Rotterdam were not able to overwinter (Fig. 5). The 10 °C isotherm computed for the whole Europe from the 1st of September 2017 to the 31th of May 2018 showed that these three study areas, but not Algeciras and Barcelona, presented mean temperatures values below 10 °C for at least 1 full winter month (Copernicus Climate Change Service, 2017).

The spatial spread of introduced populations was limited during the simulated period, as the median dispersal distance was never higher than 4 km from the port of introduction (Fig. 6). The two study areas which showed viable populations after the first simulated year reported different dispersal trends. *Ae. aegypti* populations in Algeciras showed a more seasonal spatial spread, dispersing more during summer and contracting during winter. The simulated populations in this study area moved further just after introduction, dispersing more than 2 km and invading a maximum of 638 ha, but in the following years the invaded area contracted. On the contrary, Barcelona's populations remained in the area surroundingthe introduction location for more than one year before showing a more marked spread thereafter. During 2019, this simulated population was able to spread to a maximum of 2434 ha, doubling the area invaded in 2018 (Fig. 6).

4. Discussion

The overarching aim of this study was to examine both the likelihood and the subsequent dynamics of a putative re-introduction of *Ae. aegypti* in European ports under current climatic conditions. To do so, we developed a spatially explicit process-based model tailored to the physiological requirements of *Ae. aegypti*. We applied the model to simulate and study the introduction of *Ae. aegypti* in five major European ports with high potential propagule pressure and along a gradient of latitude. Our modelling framework accounted for: i) the effect of spatial and temporal temperature variation on population dynamics, ii) the dispersal at local and regional scales, as well as iii) stochastic events following introduction. The approach we adopted has the advantage of being mechanistically linked to *Ae. aegypti* biology which results in more ecologically-realistic estimates of the likelihood of invasion in already susceptible areas.

According to model results and given current climatic conditions, a relatively low *Ae. aegypti* propagule pressure has the potential to cause species establishment, high local densities and slow initial dispersal in the two southernmost study areas: Algeciras and Barcelona. Overall, mosquitoe densities reported in model outputs are in line with previous observations in areas where *Ae. aegypti* is well established (Focks et al., 1981; Garcia et al., 2016; Ritchie et al., 2013). In the Barcelona study area, we found that the maximum median (over 500 simulations) number of adults was on 2018-09-15 (492 females/ha) and 2019-09-21 (584 females/ha). The dates of the peaks are well in line with observational data for a similar species, *Ae. albopictus*, in Europe (see for example Manica et al., 2016). In fact, until the early 20th century, *Ae. aegypti* was abundant in Southern Europe and in port cities of the Mediterranean Sea, where it was probably re-introduced regularly through trades (Toma et al., 2011). Several outbreaks of yellow fever were recorded in the Andalusia region as well as Barcelona until the late 19th century (Canela Soler et al., 2009; Fontenille et al., 2007; Schaffner and Mathis, 2014) and indeed *Ae. aegypti* was considered a common species in Spain until the 1950's (Rico-Avelló and Rico, 1953).

Model simulations showed that Barcelona was more suitable for *Ae. aegypti* compared to Algeciras, hosting higher abundances and spread velocity of simulated invasive populations. These results are associated with the different layout of urban areas around the two ports as well as local climatic conditions. Algeciras is relatively isolated from other urban areas, therefore, dispersing mosquitoes need to move relatively far to find suitable urban environments, which may have favoured the more "seasonal" dispersal pattern reported in Fig. 6. This pattern may stem from dispersing adult females reaching and colonising new distant areas only rarely, resulting in local extinctions and invaded area contractions with the onset of colder weather during winter months (Roche et al., 2015). On the contrary, the massive urban sprawl of Barcelona seamlessly connects the port area with neighbouring suitable urban areas along the coast either north, west or south (Fig. 5). Consequently, invasive propagules could gradually form new invasion fronts, promoting a longer and more gradual dispersal. Both Algeciras and Barcelona fall in the hot-mediterranean climatic zone, which is characterised by warm summers and mild winters, which are optimal conditions for the *Ae. aegypti* life cycle. The relatively higher invasion success and population densities simulated for Barcelona can be explained considering the warmer temperatures between May and September, which also correspond with the mosquito population growing season. Although we did not consider water availability for breeding sites in our model, it is worth highlighting that this would not represent a limiting condition in either of the suitable study areas, as yearly precipitations are well above the values of 400–500 mm/yr reported to hinder *Aedes* population persistence (Caminade et al., 2012).

Mosquito populations introduced either in the ports of Genoa, Venice and Rotterdam, despite surviving for short-to-longer periods and dispersing in the surrounding areas of each port, were never able to establish overwintering populations. These three areas have longer and harsher cold temperatures during winter months which are at least for one consecutive month below the isotherm of 10 °C, making it impossible for introduced *Ae. aegypti* to overcome the adverse period of the year.

Taken together these results indicate that, regardless of the propagule pressure, the likelihood of *Ae. aegypti* invasion along European coasts is high in the southern Mediterranean basin, is less likely at latitudes between the ports of Barcelona and Venice, and becomes extremely unlikely further up north. However, where the current temperature regime is too cold to allow species survival over winter, either microclimatic refugia under current climatic conditions or climate change in the near future, could still allow *Ae. aegypti* establishment. Microclimatic refugia are widespread in urban areas and can be caused by urban heat-island effects or by urban infrastructures, and have been shown to be exploited by *Ae. aegypti* (Tsunoda et al., 2014). An example of local conditions detached from the regional climatic regime which has allowed *Ae. aegypti* persistence is the city of Washington, DC, USA, where *Ae. aegypti* was able to establish viable populations by overcoming the otherwise unsuitable climatic conditions by sheltering in the myriad of underground refugia of the metropolitan area (Gloria-Soria

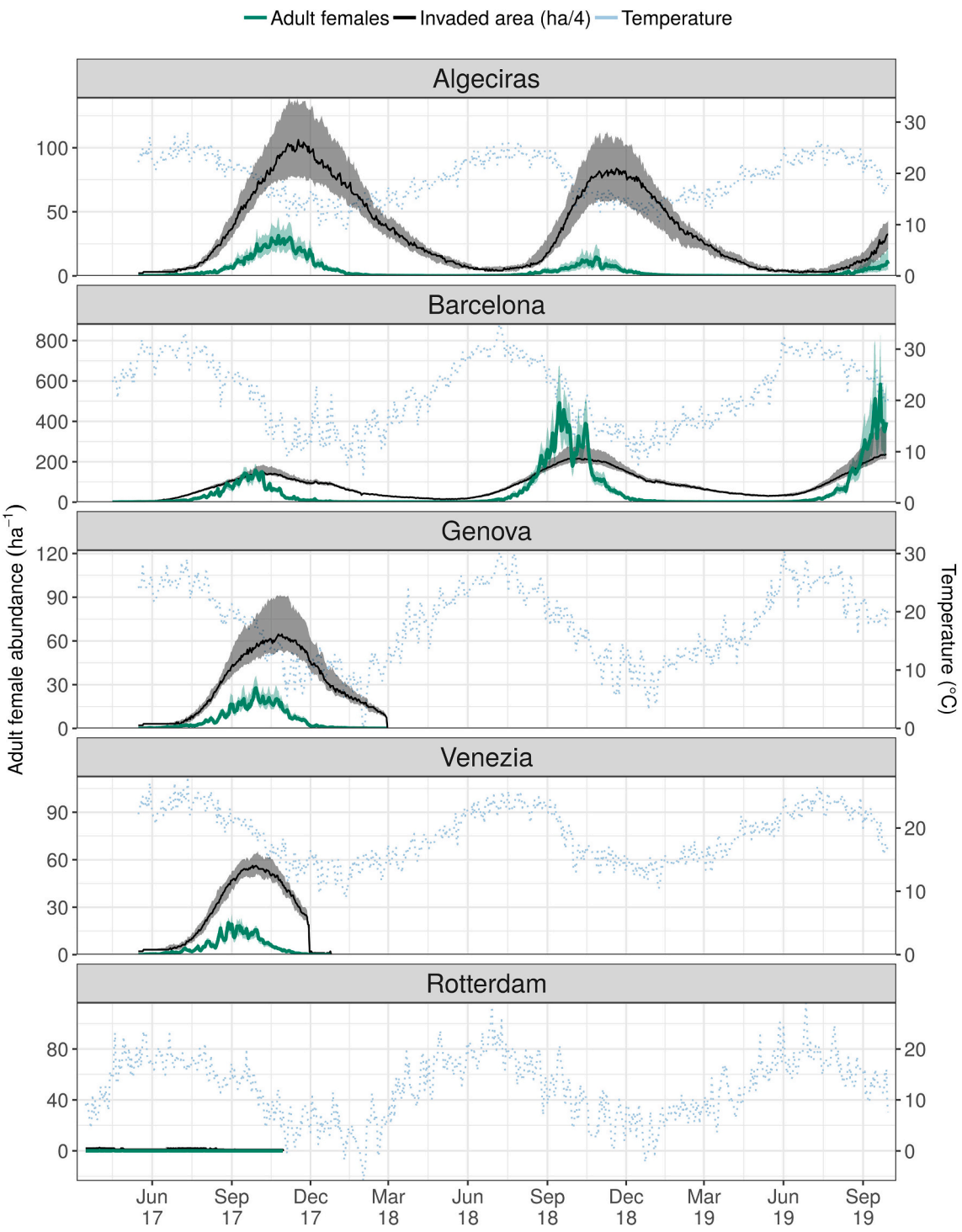

Fig. 5. Temporal trend describing the outputs of model simulations for the five study areas. We reported both median (green lines) and inter-quartile (green ribbons) population densities of adult females per hectare and median (black line) and inter-quartile range (grey ribbons) of the invaded area in hectares (divided by a factor of 4 for scaling reasons), derived from 500 iterated introductions of 100 *Ae. aegypti* eggs in each of the 5 study areas. The light-blue dotted line reports the trend in average daily temperatures and refers to the values in the right y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2018).

Microclimatic urban refugia are by definition limited to small extensions, whereas global change has the potential to expand dramatically the geographical extent suitable for *Ae. aegypti* as well as *Aedes*-borne virus transmission in Europe. Mosquito physiological rates are decreased by increasing environmental temperatures in the range of 10–35 °C (Mordecai et al., 2019), and the 10 °C isotherm of the coldest month is often used as a proxy to assess *Ae. aegypti* geographic suitability. Europe is currently characterised by a 10 °C isotherm of the coldest month extending to most of the south inland areas of Spain, Italy and Greece, which underpins how three out of five coastal areas that we tested were not suitable for *Ae. aegypti* establishment. However, the current direction of global change is predicted to bring warmer temperatures in most of Europe that, coupled with unchanged or increased

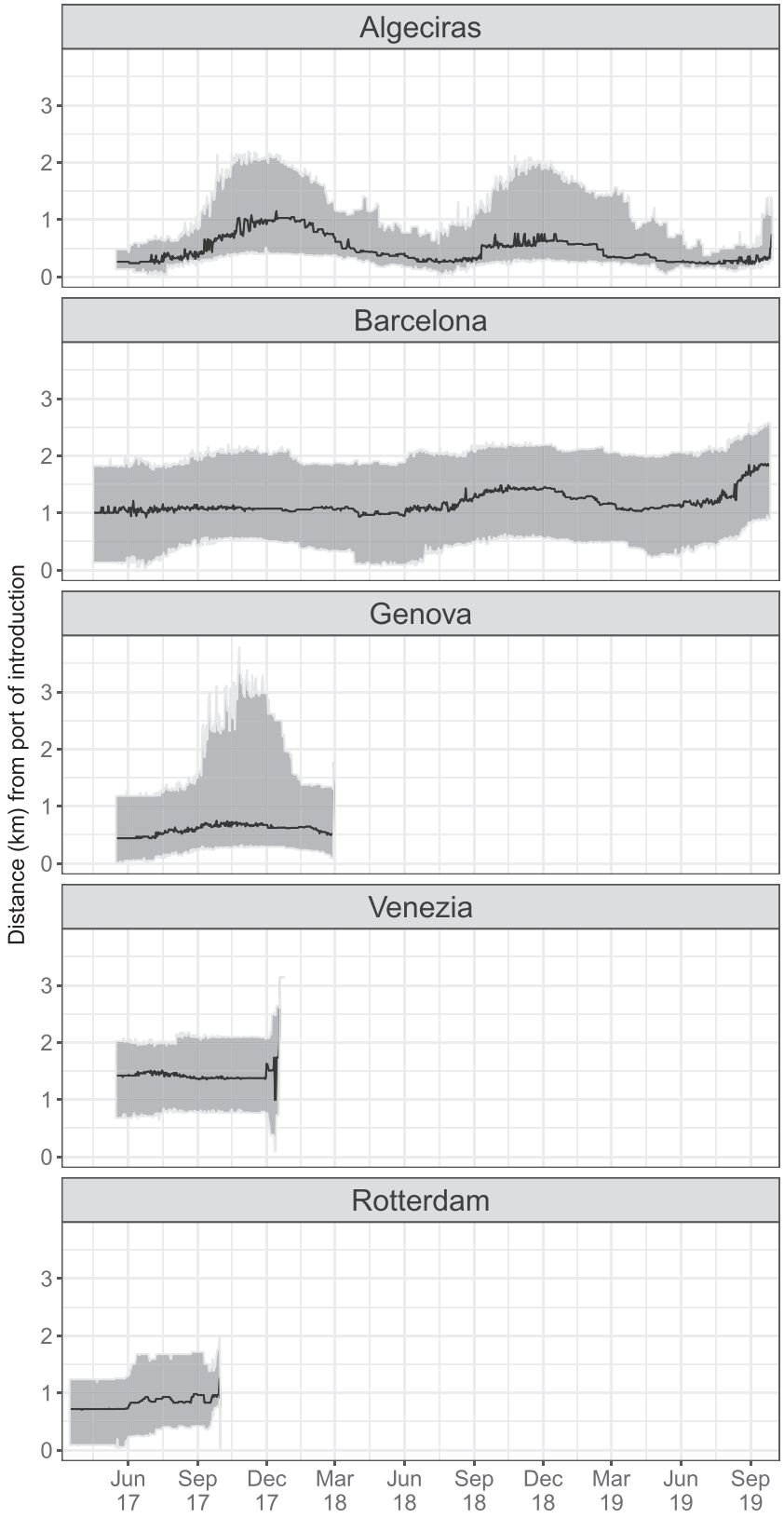

Fig. 6. Median (black line) and inter-quartile (grey ribbons) dispersal distance (km) of simulated mosquito populations derived from 500 iterated introductions of 250 *Ae. aegypti* eggs in each of the 5 study areas. Dispersal distance was calculated as the euclidean distance between the centroid of each port of introduction and centroids of cells with at least one *Ae. aegypti* individual in any developmental stage.

precipitation along coastal areas, will impact the extent of regions where *Ae. aegypti* introduction could cause invasions (Kraemer et al., 2019; Liu et al., 2019; Ryan et al., 2019). That said, our findings suggest that simulated populations introduced in the region of Genoa persisted for most of the winter to become extinct only at the beginning of spring. Some model iterations showed individuals persisting until the month of April 2018. This result may indicate that, according to our model, Genoa is already close to suitability for *Ae. aegypti*. Thus, areas such as the region of Venice and Genoa, which have already acted as ports of introduction for *Ae. albopictus* (Knudsen et al., 1996; Sabatini et al., 1990), another invasive mosquito, may be targeted with preventive surveillance actions for limiting the likelihood of *Ae. aegypti* establishment in the near future.

The potential establishment of populations of *Ae. aegypti* in the southernmost areas considered in this study should be regarded as far from implying outbreaks caused by arboviruses. However, assuming putative introductions of *Aedes*-borne pathogens and the lack of adequate surveillance, the socio-environmental conditions of Algeciras and Barcelona may be suitable to sustain transmission of such introduced pathogens in the human population. In the past twenty years all the chikungunya and dengue autochtonous cases or outbreaks in Europe (Italy, France, Spain, Croatia) were likely the consequence of the establishment of *Ae. albopictus* in densely populated areas, coupled with the introduction of pathogens via infected travellers returning from areas with high incidence rates (Jourdain et al., 2020; Lindh et al., 2019; Liumbruno et al., 2008).

Our modelling exercise is not exempt from caveats. We have parametrised the passive dispersal probability kernel using values based on *Ae. albopictus* and published in Eritja et al. (2017) as, to the best of our knowledge, there are no other studies available that estimate the probability of detecting *Ae. aegypti* in vehicles. We did not consider evolutionary processes which may affect the physiological rates of *Ae. aegypti*, making them more or less adapted to local environmental conditions (Reinhold et al., 2018). For example, variability in the quiescence strategy to prolong embryonic viability, which may favour the fitness of introduced propagules, has been observed in different *Ae. aegypti* populations (Oliva et al., 2018). By contrast, inbreeding events just after introduction could decrease the vigour of *Ae. aegypti* populations, reducing the probability of successful invasions (i.e., strong Allee's effect; McDermott and Finnoff, 2016). In the same way, interspecific larval competition between *Ae. aegypti* and other container-breeding *Aedes* is another potential limiting condition that we did not considered in this study (Carrasquilla and Lounibos, 2015). We also assumed that the availability of both human hosts and breeding sites do not limit introduced populations. However, we relaxed these assumptions by choosing urbanized study areas, which are expected to have a high density of both available human hosts and man-made containers as breeding sites. Finally, we acknowledge that we have considered urban areas as homogeneous land use features, which is far from reality. Urban areas are dynamical landscape features whose heterogeneity in microclimatic and habitat conditions creates emerging interfaces for interaction between humans and other species which has been recognised as key for the establishment of populations of vector species (Vanwambeke et al., 2019).

5. Conclusions

Environmental conditions in Southern European urban areas, such as Algeciras and Barcelona, suggest potential for colonisation by *Ae. aegypti*. We found that the dispersal pattern in time and space following establishment could be a continuous gradual spread or a more seasonal stepping-stone pattern, dictated by the specific characteristics and connectivity of each urban area. Moreover, in case of establishment, simulated *Ae. aegypti* populations in these areas were found to reach abundances similar to regions of the world with active transmission of *Aedes*-borne viruses. European areas located at higher latitudes, such as the port of Genoa, were found not suitable for colonisation by these mosquitoes, but global change could modify conditions for *Ae. aegypti* invasion also in these regions. Finally, colonisation of north European urban areas, aside from the possibility of short-lived and limited space encroachment due to urban refugia, was found to be very unlikely.

It is commonly accepted that targeted monitoring of sensitive areas and early control actions are the most effective methods to prevent the establishment of invasive species in new areas. In the case of a future successful *Ae. aegypti* re-introduction in Europe, maintaining populations at low densities and possibly limiting their spatial spread will be crucial to avoid the risk of pathogen transmission. Our findings and model framework are aimed to inform surveillance initiatives for those European coastal urban areas which have a known high propagule pressure and a high probability of *Ae. aegypti* establishment.

The model we applied for our simulations is freely available as an R function, in the hope to foster reproducibility, further development and application in different scenarios, geographical areas or spatial scales.

Declaration of Competing Interest

None.

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Appendix 1. Sensitivity analysis on uncertain model parameters

In an attempt to assess and report the effect on model results of those model parameters which were judged more uncertain (i.e., lacking experimental or field estimates) we ran a global sensitivity analysis by exploring the parameter space of: the probability of egg survival (p_{Es}), the probability of egg hatching (p_{Eh}), the number of introduced eggs (E), the probability of adult dispersing passively (p_{Apd}; Table 3). We performed the sensitivity analysis iterating 200 times the introduction of 250 eggs (except for E) on the 15th of May on the study area of Algeciras.

Table 3

Model parameter	Parameter space	Value used in the model
Daily probability of egg survival	(0.90,1.00)	0.99
Daily probability of egg hatching	(0.01, 1.00)	0.076
Daily probability of passive dispersal	(0.0018, 0.0180)	0.0051
Number of introduced eggs	(10,1000)	250

Summary statistics of model results were plotted against the range of parameter values to provide a simple and straightforward assessment of model sensitivity (Fig. 7).

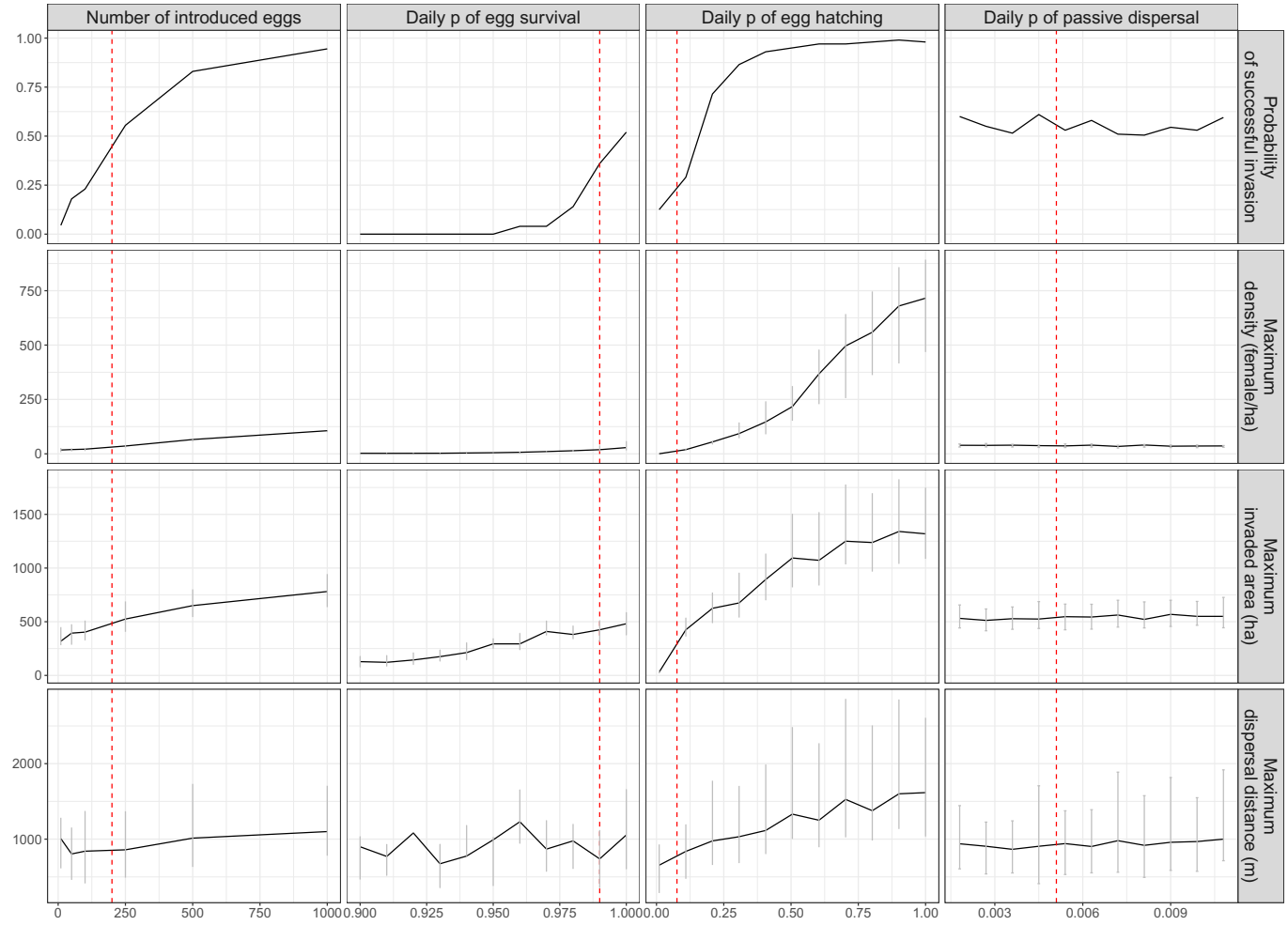

Fig. 7. Matrix of scatterplots showing the effect of the four model parameters (column) selected for sensitivity analysis on different model outputs (rows). The black dots represent median values across the 200 iterations while vertical grey lines the inter-quartile range for each type of output, except for the probability of successful invasion which is cumulative across iterations. The red dashed vertical lines indicate the parameters value used in model simulations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix 2. Temporal and spatial trends of the simulated mosquito populations

Temporal trend for all life stages.

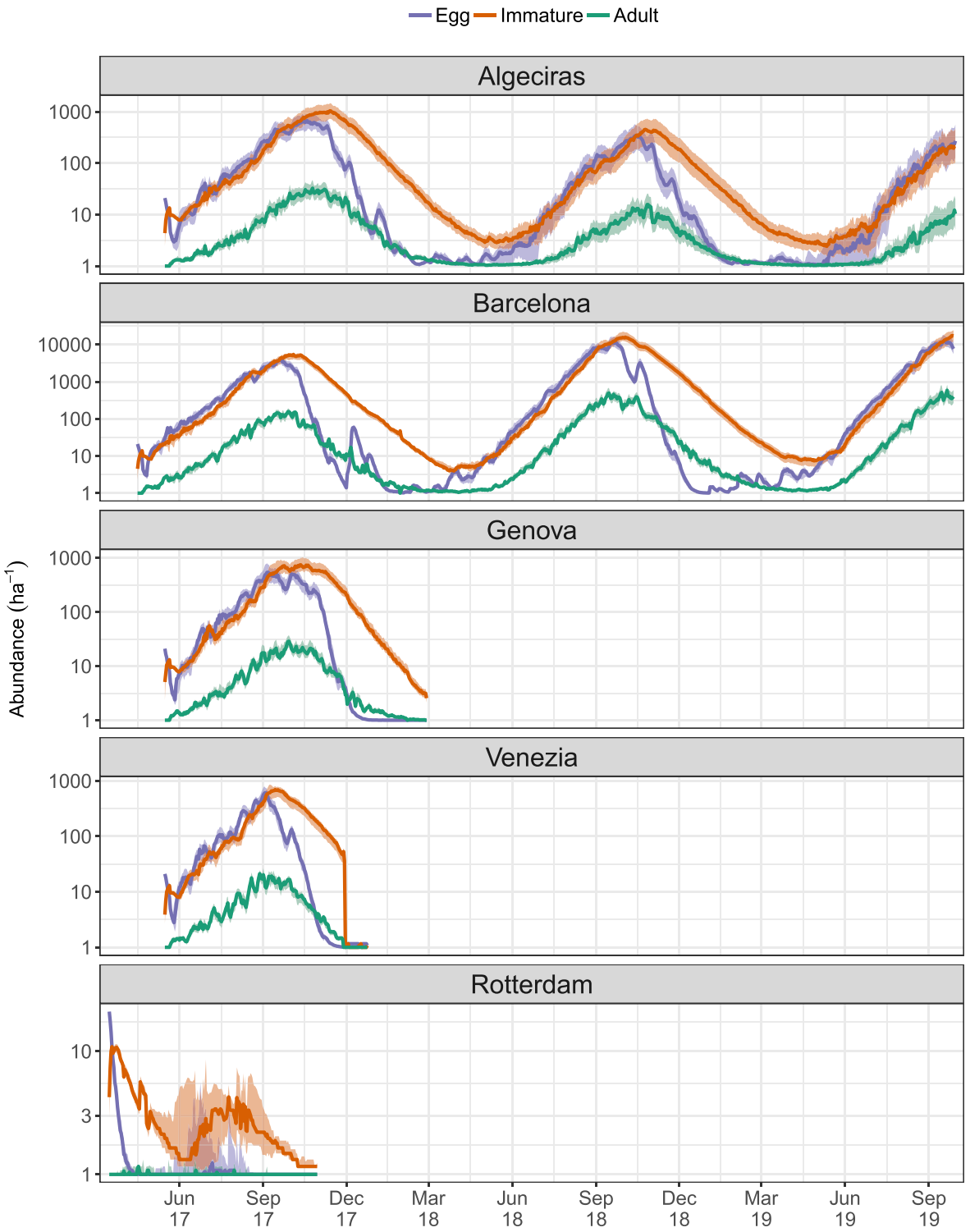

Fig. 8. Temporal trend reporting: i) median (lines) and inter-quartile (ribbons) population abundances for each stage (adults in green, immatures in orange and eggs in purple) for introduced *Ae. aegypti* populations. Values on the y-axis are transformed using the common logarithm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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