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# Biological, ecological and trophic features of invasive mosquitoes and other hematophagous arthropods: What makes them successful?

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1 **Biological, ecological and trophic features of invasive mosquitoes and other**  
2 **hematophagous arthropods: what makes them successful?**

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31 **Highlights**

- 32 ● Genetic and microbiome features of invasive mosquitoes are reviewed
- 33 ● Movement patterns and geographic spread of mosquitoes are explored
- 34 ● A food-web approach to assess the impacts of invasive mosquitoes is presented
- 35 ● Novel perspectives for the management of invasive mosquitoes are considered
- 36

37 **Abstract**

38 Invasive hematophagous arthropods threaten planetary health by vectoring a growing  
39 diversity of pathogens and parasites which cause disease. Efforts to limit human and animal  
40 morbidity and mortality caused by these disease vectors are dependent on understandings of  
41 their biology and ecology — from cellular to ecosystem levels. Here, we review research into  
42 the biology and ecology of invasive hematophagous arthropods globally, with a particular  
43 emphasis on mosquitoes, culminating towards management recommendations. Evolutionary  
44 history, genetics, and environmental filtering contribute to invasion success of these taxa, with  
45 life history trait and ecological niche shifts between native and invaded regions regularly  
46 documented. Pertinent vector species spread readily through active and passive means, via  
47 anthropogenic and natural mechanisms with climate change, although the rate and means of  
48 spread differs among taxa, according to their capacity for entrainment in human vectors and  
49 physiology. It is critical to understand the role of these invaders in novel ecosystems, as biotic  
50 interactions, principally with their resources, competitors, and natural enemies, mediate  
51 patterns of invasion success. We further highlight recent advances in understanding  
52 interactions among arthropod-associated microbiota, and identify future research directions  
53 integrating arthropod microbiota to explain invasion success under changing environments.  
54 These biological and ecological facets provide an integrative perspective on the invasion  
55 history and dynamics of invasive hematophagous arthropods, helping inform on their  
56 management strategies.

57

58 **Key words:** biotic interactions, land-use change, management, microbiota, biological invasion,  
59 vector-borne disease

## 60 1. INTRODUCTION

61 Arthropods contain the largest diversity of taxonomic groups, including insects, crustaceans,  
62 spiders, scorpions, and centipedes. Species from the phylum Arthropoda have been  
63 particularly successful in colonizing almost all types of habitats, across all continents and  
64 realms (Cracraft and Donoghue 2004). This extensive geographic and environmental  
65 distribution has likely been assisted by — and shaped — the mosaic of biological,  
66 morphological, and trophic features arthropods have developed. In particular, a multitude of  
67 feeding phenotypes can be found in arthropods, *e.g.*, carnivory, omnivory, or herbivory, with  
68 some adult insects even being aphagous (Gangwere 2004), and others being opportunistic by  
69 developing on human food subsidies (Oro et al. 2013). For those arthropods feeding on blood,  
70 the so-called hematophagous arthropods, individuals can ingest many blood factors (Pakpour  
71 et al. 2014), and importantly, may vector infectious agents (Wilson et al. 2017).

72 A large number of arthropod species may occasionally become accidental vectors of  
73 pathogens, with minor consequences for transmission (Kalvelage et al. 2022). Yet, a minority  
74 of species of hematophagous arthropods are actually known as vectors of *i.e.* disease-causing  
75 pathogens that play a consistent and epidemiologically-significant role. In most cases, the  
76 host's pathogens are digested together with the blood meal of the hematophagous arthropod,  
77 requiring genetic compatibility between the vector and the pathogen (*i.e.* vector competence)  
78 for transmission to occur (Beerntsen et al. 2000). As a result, populations of a single species  
79 developing in different and/or distant environmental settings may display different genetic  
80 characteristics, and thus, distinct vectorial capacities (*i.e.* abilities to efficiently transmit  
81 pathogens/parasites in a defined setting at a specific period in time). Therefore, the nature of  
82 the host-vector-parasite-environment interactions will determine the vectorial competence  
83 (Fontenille et al. 2020). The arthropod-associated microbiota can further affect host  
84 phenotypes, in turn impacting vectorial capacity (Cansado-Utrilla et al. 2021).

85           The efficacy of a particular genus or species in transmitting pathogens or parasites is  
86 also dynamic through time and space, and can cause changes to host cycles. Humans, for  
87 example, may become competent hosts for West Nile virus, should *Aedes* mosquitoes, which  
88 primarily feed on them become more susceptible to viral infections (Colpitts et al. 2012;  
89 Martinet et al. 2023). Hematophagy may also be specific to some development phase, or occur  
90 across the entire life history. For instance, in mosquitoes, only adult females feed on blood; in  
91 ticks, all developmental stages and sexes do, from the larvae to the nymphs and adults  
92 (Caimano et al. 2016).

93           Hematophagy provides an important, yet context-dependent, route for pathogen  
94 transmission. Each blood meal can transfer a variety of viruses and bacteria, including  
95 rickettsia, protozoa and nematodes, leading to complex co-infections, with some being  
96 pathogenic to the host (Brites-Neto et al. 2015; Murray et al. 2015; Jánová 2019). The burden  
97 of such vector-borne diseases has accelerated with climate change and biological invasions  
98 (Rupasinghe et al. 2022), extending the risks of diseases to populations that were formerly  
99 unaffected (Colón-González et al. 2021). Since the start of the Anthropocene era, biological  
100 invasions have become a burgeoning problem, and represent a major risk to ecosystems,  
101 economies, and public health (Pyšek et al. 2020; Diagne et al. 2021). Several species of  
102 hematophagous arthropod vectors (Lowe et al. 2000) — especially blood-feeding insects and  
103 arachnids — can have massive impacts through nuisance biting and vector-borne diseases  
104 (Obregón Alvarez et al. 2020; Manikandan et al. 2022; Cuthbert et al. 2023). The multiple  
105 threats they pose require significant control efforts and incur substantial costs to healthcare  
106 systems (Juliano and Lounibos 2005; Diagne et al. 2021; Renault et al. 2022a).

107           Understanding invasive hematophagous arthropods as vectors of pathogens presents  
108 an opportunity to draw parallels between invasion and infectious disease sciences, while  
109 reducing impacts (Nuñez et al. 2020). It is therefore imperative to develop a sound  
110 understanding of the underlying biology and ecology of the most impactful vector species to

111 prevent, mitigate, and manage biological invasion, disease emergence and the myriad of  
112 issues around the proliferation of arthropod vectors. Despite several arthropod species (e.g.  
113 mosquitoes, ticks, phlebotomine sand-flies, triatomine bugs, culicoides, body lice, fleas, etc.)  
114 having the potential to carry and transmit infectious pathogens, research efforts into invasive  
115 alien species as vectors of pathogens have insofar mainly focused on mosquitoes, and to a  
116 lesser extent, ticks. These taxa predominantly feed on the blood of terrestrial mammals, birds,  
117 reptiles or amphibians to reproduce. In mosquitoes, sugar, usually acquired from floral or  
118 extrafloral nectar, also represents an important component of their diet (Foster 1995). Some  
119 mosquitoes feed on other semi-aquatic or invertebrate species (Reeves et al. 2020), and a few  
120 are even autogenous (Gulia-Nuss et al. 2015).

121 Here, we examine the genetic, phenotypic, environmental, and behavioral  
122 dimensions of mosquito invasion success (**Fig. 1**). We explore the fundamental biology,  
123 genetics, microbiomics, and ecology of mosquito species in a scoping review of recent  
124 research. We draw inferences from research on phytophagous arthropods, acknowledging  
125 that the two groups are not mutually exclusive (Peach and Gries 2020). Complementary  
126 information on ticks is provided as supplementary material (**Online Resource 1**). We first  
127 unravel the roles of ecological features in supporting invasion success, before considering  
128 biotic interactions. Opportunities to understand responses to environmental changes and  
129 invasion dynamics in light of the arthropod microbiome are also outlined. Finally, we provide  
130 firm management perspectives to more effectively prevent hematophagous vector invasions  
131 and associated disease risk to humans, livestock and wildlife.

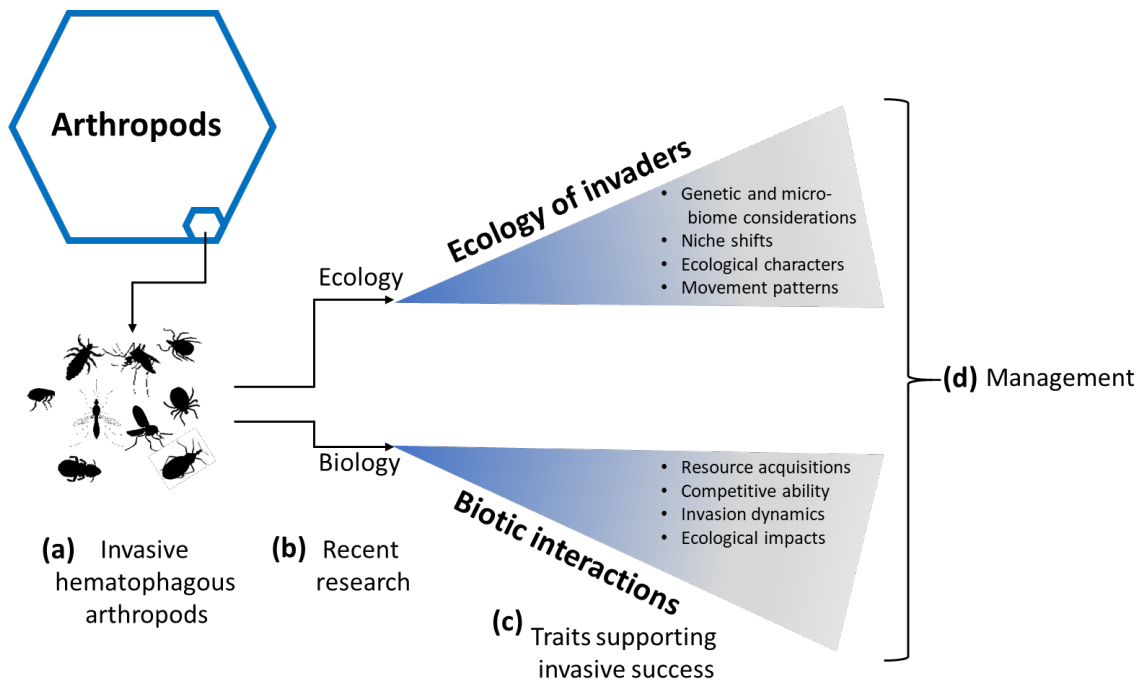
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139 **Fig. 1** Content of this work, highlighting the diversity of invasive hematophagous arthropods  
 140 (a) and how recent research efforts (b) to define the main biological and physiological traits  
 141 supporting invasion success (c) will be relevant for future management efforts (d).

142 Complementary information on ticks is provided as supplementary material (**Online Resource**

## 143 **2).2. GENETIC AND MICROBIOME CONSIDERATIONS**

### 144 **(1) Genetic adaptabilities**

145 The invasion success of non-native organisms is often determined by a mixture of propagule  
 146 and colonization pressures (Lockwood et al., 2009; Briski et al., 2012), and their ability to  
 147 rapidly adapt to novel environments in the initial years after introduction, sometimes starting  
 148 from a low number of founder individuals or a few populations (Allendorf and Lundquist 2003;  
 149 Kaňuch et al. 2020). For example, this is the case for the Asian tiger mosquito, *Aedes albopictus*  
 150 in Europe, historically introduced in three independent southern European sites that  
 151 subsequently acted as dispersal centres (Sherpa et al. 2019b). Being a sub-sample of the  
 152 populations present in the native range, non-native populations within the invaded range are



153 often expected to exhibit lower genetic diversity (Austerlitz et al. 2000; Bock et al. 2015). This  
154 might limit the adaptive response and evolutionary potential of invaders, and make them  
155 more vulnerable to extinction due to the deleterious consequences of demographic  
156 bottlenecks, such as inbreeding or drift load (Simberloff 2009; Briski et al. 2018). Yet, the  
157 genetic paradox of invasion (Estoup et al. 2016) considers the potential role of ‘inbreeding ×  
158 environment’ (I × E) interactions under benign environmental conditions (see Schrieber and  
159 Lachmuth 2017; Mounger et al. 2021), and explains the invasion success of species even when  
160 limited number of specimens successfully established.

161           Spread may be further assisted by genetic admixture, as reported in *Ae. albopictus*  
162 (Sherpa et al. 2019a), whose invasion in Europe was promoted by I × E interactions. Additional  
163 arthropod examples include the marbled crayfish *Procambarus virginalis*, the only decapod  
164 crustacean to reproduce parthenogenetically (Scholtz et al. 2003), and Asian hornet *Vespa*  
165 *velutina nigrithorax* (Jones et al. 2020), which both exhibit invasion success despite low  
166 genetic diversity in invaded areas. Indeed, molecular genetic variation is a poor indicator of  
167 additive genetic variance for any particular biological trait (Lynch and Walsh 1998). We  
168 suggest that this paradox should be explored in more detail for hematophagous arthropods,  
169 and that particular attention should be given towards the importance of epigenetic DNA  
170 modification and consequences for gene expression and transcriptome plasticity. The  
171 epigenome-wide effects, e.g. on the fitness of individuals and descendants, have been  
172 inadequately studied, despite epigenetic changes (DNA methylation, histone modifications)  
173 potentially allowing for rapid adjustments in individuals’ phenotypes and enhanced  
174 responsiveness to novel environmental conditions. The level of DNA methylation has been  
175 reported to be inversely correlated with gene expression in the marbled crayfish, with lower  
176 degrees of body methylation paralleling higher gene expression variability (Gatzmann et al.  
177 2018). Interestingly, a similar association has been reported from very different taxa  
178 (Entrambasaguas et al. 2021), and we thus suggest exploring the role of body methylation as

179 a driver of the plasticity of invasive hematophagous arthropods facing novel conditions, in  
180 turn increasing their abilities to handle environmental constraints and thus invasiveness.

181 Besides the I x E hypothesis, other processes may rapidly select mosquito genotypes  
182 under harsh conditions. Notably, biological invasions have been considered to constitute a  
183 “numbers game” between the number of individuals introduced and the number of  
184 introduction events (propagule pressure) (Simberloff 2009). Indeed, small populations are  
185 more vulnerable to extinction due to instabilities in response to environmental stochasticity  
186 (Simberloff 2009) and demographic effects (e.g. Allee effects; Bock et al. 2015). However, the  
187 invasion process itself can select certain pre-adapted genotypes which enhance invasiveness  
188 of populations beyond this simple “numbers game”. Consistently, preadaptation to  
189 anthropogenic habitats has been suggested to contribute to successful invasion without  
190 genetic depletion (Hufbauer 2012), as exemplified by Rose et al. (2020). These authors  
191 associated *Ae. aegypti* preference for human blood meals with the species’ expansion across  
192 the world as a by-product of adaptation to human settings, in particular to ephemeral  
193 breeding sites under arid conditions. Concomitantly, the recent invasion of the Indian malaria  
194 mosquito *Anopheles stephensi* in Africa is also associated with prior adaptation to urban  
195 habitat conditions (Sinka et al. 2020).

196 Stresses associated with human-mediated movements during the transport stage can  
197 additionally select for individuals with traits increasing the invasiveness of founding  
198 populations (Briski et al. 2018; also see Renault et al. 2018 for a discussion around the role of  
199 environmental filtering). Even attempts at managing pathways of introduction — in particular  
200 those relying on the spraying of chemical insecticides — could select for taxa/genotypes  
201 predisposed to invade given their resistance to treatment pressures. The transport process  
202 could also select for individuals tolerant to environmental stresses associated with long-range

203 transport conditions, on used tires or ships, creating more tolerant and plastic founder  
204 populations for invasion (Powell et al. 2018).

205         So far, the few studies that have assessed and compared the level of genetic diversity  
206 between native and non-native populations of hematophagous arthropods (Goubert et al.  
207 2016; Lounibos 2002) have produced equivocal results in respect to the aforementioned  
208 founder effects. Indeed, a similar genetic diversity has been found in *Ae. japonicus* from the  
209 USA (non-native range) and Japan (native range) (Fonseca et al. 2010). Similarly, *Ae. albopictus*  
210 displayed equal levels of genetic diversity in its native and non-native ranges (Kotsakiozi et al.  
211 2017). Both results would support the scenario of multiple and independent introduction  
212 events, as evidenced for *Ae. japonicus* in North America (Kaufmann and Fonseca 2014,  
213 Baharmand et al. 2020), contributing to increased genetic diversity in established populations.  
214 Indeed, the genetic analysis of mitochondrial markers confirmed successive introduction  
215 events of *Ae. albopictus* in Portugal (Zé-Zé et al. 2020) and in La Reunion island (Delatte et al.  
216 2011). Although invasive *Ae. aegypti aegypti* populations outside Africa are less genetically  
217 diverse than *Ae. aegypti formosus* populations sampled from throughout the ancestral range  
218 in continental Africa (Gloria Soria et al. 2016; Kotsakiozi et al. 2018), a recent population  
219 genomic study revealed multiple and independent introduction events in California (Lee et al.  
220 2019).

221         Overall, the ability of vectors to colonize new environments may involve different  
222 mechanisms depending on the number of independent introduction events and the  
223 environmental conditions within the invaded range, with the 'I × E' hypothesis most likely  
224 relevant under benign environments and the "numbers game" under harsh conditions.

225 **(2) Environmental filtering and genotype selection**

226 During each step of the invasion process, including transport, establishment and geographic  
227 spread, non-native organisms are confronted with a range of ecological filters of biotic, trophic  
228 and/or abiotic origin (Renault et al. 2018), potentially exerting strong selection pressures and  
229 imposing a short- to moderate-term adaptive response in non-native species. For instance,  
230 *Ae. albopictus* rapidly adapted both diapause incidence and timing in response to winter  
231 conditions (Batz et al. 2020). Signatures of such selective processes are traceable at the  
232 genomic level, and include increased frequency of adaptive loci (*de novo* mutations or  
233 standing genetic variation) and reduced overall genetic diversity (Dlugosch et al. 2015).  
234 Recently, a genome scan for transposable element insertions in *Ae. albopictus*, found 92 loci  
235 evidencing a high level of differentiation between populations sampled in their ancestral  
236 tropical range and populations sampled in their recently colonized temperate areas in Europe  
237 (Goubert et al. 2017). In particular, two genes involved in diapause preparation and a third  
238 one whose expression may be associated with diapause maintenance were found to  
239 discriminate against temperate specimens. Consistently, the importance of lipid metabolism  
240 and juvenile hormone signaling as key pathways for diapause in *Ae. albopictus* has been  
241 established (Reynolds et al. 2012; Batz et al. 2019). This body of knowledge supports the  
242 existence of rapid directional selection during the invasion process in *Ae. albopictus*.

243 Another interesting example is the insecticide resistance status of *Ae. aegypti*. This  
244 mosquito exhibited much lower insecticide resistance in its native range in Africa than in the  
245 Americas or Asia, where it established more recently (Moyes et al. 2017). This may be owing  
246 to more feral ecology and a lower level of exposure to insecticides on the origin continent  
247 overall. Therefore, the capacity to develop insecticide resistance in response to higher levels  
248 of exposure may appear to be important for the invasion success of *Ae. aegypti*.

249 High-quality genome sequencing for the mosquitoes *Ae. aegypti* and *Ae. albopictus*,  
250 and the ticks *I. ricinus* and *Ixodes scapularis*, would represent a major step towards identifying

251 adaptive loci responsible for invasion dynamics and support improved population-control  
252 strategies (Celniker et al. 2018; Matthews et al. 2018; Palatini et al. 2020). However, finding  
253 adaptive loci throughout the genomes of *Ae. aegypti* and *Ae. albopictus* is a challenging task  
254 given their very large size — approximately 1.25 Gb and 1.9 Gb, respectively (Matthews et al.  
255 2018; Palatini et al. 2020). Moreover, only major mosquito vectors such as *Ae. aegypti*, *Ae.*  
256 *albopictus* or *An. gambiae* have enough sequenced genomic resources to carry out genome  
257 scan tests. Genomic studies on other invasive mosquitoes, such as *Ae. japonicus* and *Ae.*  
258 *koreicus*, and most other hematophagous arthropods of medical or veterinary importance are  
259 entirely missing, and should be acquired to develop successful strategies to prevent their  
260 spread.

### 261 **(3) Arthropod-associated microbiota**

262 Despite genetic optimization, different traits related to arthropod intrinsic characteristics  
263 appear to be also important factors contributing to the rapid spread and great ecological  
264 plasticity of invasive mosquito species. Importantly, many studies have highlighted the  
265 important roles of non-pathogenic and free-living bacteria in evolutionary and ecological  
266 processes of their insect hosts (Dillon and Dillon 2004; Douglas et al. 2011) (**Fig. 2**). Animals  
267 are now widely known as holobionts, owing to the entire community of interacting organisms  
268 they represent, thus making them a complex symbiotic consortium that constitute their  
269 microbiota (McFall-Ngai et al. 2013). The microbiome is defined as the collective genomes of  
270 the microorganisms — composed of bacteria, fungi, protozoa and viruses — living inside and  
271 on their host (Berg et al. 2020). Whatever the outcome of the interactions (*i.e.* parasitism or  
272 mutualism), microorganisms affect the phenotype of their hosting individual, and the  
273 evolutionary trajectory of interacting partners. As microorganisms can fluctuate in response  
274 to the environment much more rapidly than the host, evolution of the holobiont may be an  
275 important driving force, especially when rapid responses/evolution must take place. In recent

276 years, it has become increasingly clear that many traits of invasive arthropods such as  
277 development, immunity, nutrition, reproduction, protection against pathogens and tolerance  
278 to environmental stress, are affected by these microbial interactions (Guégan et al. 2018a;  
279 Díaz-Sánchez et al. 2019). Importantly, these multi-partner interactions (*e.g.*, host-vector-  
280 pathogens-symbionts), modulated by the environment, have emerged as a major question for  
281 understanding the driving forces of arthropod species adaptation and subsequent  
282 invasiveness (Schapheer et al. 2021).

283         There are now several case studies demonstrating the considerable importance of  
284 individual symbionts or microbial communities in the extraordinary success of insects in  
285 adapting to novel environments and food sources (Tsuchida et al. 2010, Carpenter et al. 2021),  
286 which allow them to expand or constrain their abiotic niche space (Sharon et al. 2010, Waidele  
287 et al. 2019), as well as determine their adaptability to fluctuating environments (Lemoine et  
288 al. 2020). While the contribution of the microbiota in assisting rapid adaptation to local  
289 environments of invasive mosquitoes has received increased attention in recent years, the  
290 role of microbial symbionts in promoting their successful invasiveness is still an open question.

291         It was shown that bacterial and fungal communities associated with invasive  
292 populations of *Ae. albopictus* in France are less diverse, and more homogeneous, than those  
293 associated with autochthonous populations in Vietnam (Minard et al. 2015; Luis et al. 2019).  
294 Moreover, the reduced microbiota diversity was associated with a loss of host genetic  
295 diversity. The authors hypothesized that microbial variations between both populations could  
296 be linked with environmental factors of their habitat, as ecology of breeding sites drives  
297 environmental microbial acquisition in mosquitoes (Guégan et al. 2018b; Girard et al. 2021).  
298 In order to evaluate whether a causal relationship occurs between the structure of bacterial  
299 communities and the genetic diversity of populations, with an emphasis on the role of genetic  
300 determinants involved in the selection of the microbiota, the authors compared the bacterial  
301 diversity of inbred laboratory populations *versus* control lines in which no genetic bottleneck

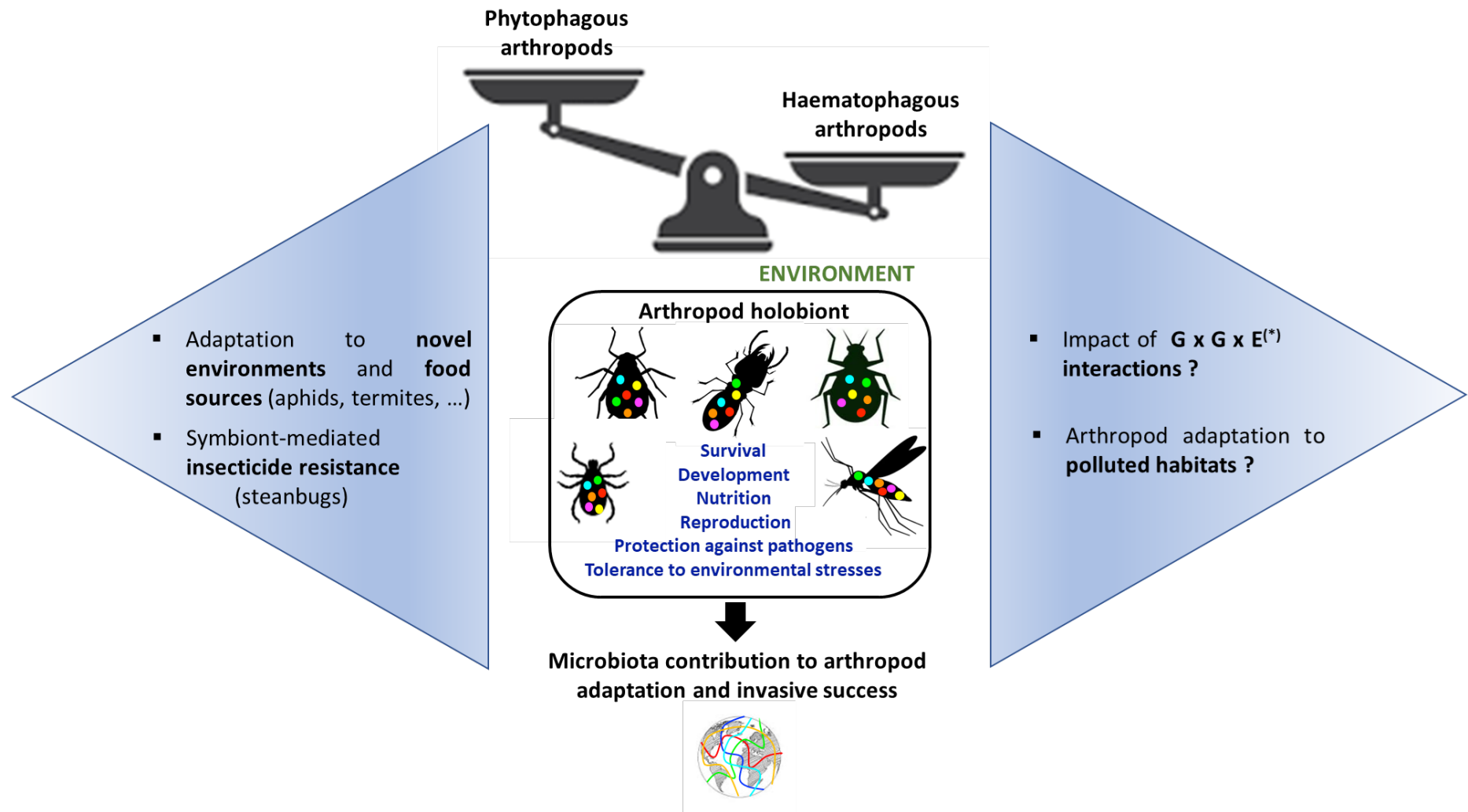
302 was induced (Minard et al. 2018). The results showed that the breeding site, sex, female size  
303 and genetic diversity shaped the composition and diversity of the bacterial microbiota in *Ae.*  
304 *albopictus*. Importantly, reduction in diversity on both the microbiota and host also raised  
305 questions about the possible impact on human pathogen transmission. It is conceivable that  
306 such modifications and their relative immune response could partly explain the efficient  
307 vector competence observed in *Ae. albopictus* populations from metropolitan France  
308 (Zouache et al. 2014; Raquin et al. 2022).

309         Originating from sylvatic habitats, invasive mosquito species are now well established  
310 in peri-urban and urban areas, as demonstrated in several regions around the world (Medlock  
311 et al. 2012; Kolimenakis et al. 2021). Urban environments are characterized by high levels of  
312 anthropic activities and source pollution. How anthropogenic stressor exposure impacts on  
313 the mosquito microbiota structure and whether mosquito-associated microbiota can drive  
314 insect adaptation to polluted habitats are still poorly investigated (Gendrin et al. 2015; Guégan  
315 et al. 2018b; Duval et al. 2023). This could deserve more attention in the future, as previous  
316 studies already demonstrated symbiont-mediated xenobiotic resistance in insects (Kikuchi et  
317 al. 2012; Pang et al. 2018; Antonelli et al. 2022). Following the urbanization process, insects  
318 face numerous anthropogenic stressors and have evolved various detoxification mechanisms  
319 to survive and/or resist these compounds. Stressor exposure can have various impacts on the  
320 composition and structure of insect microbiota that may influence insect biology. In turn,  
321 bacterial communities associated with insects can be involved in detoxification processes,  
322 with the selection of microbes which have xenobiotic-degrading potential. Further studies are  
323 needed to assess the role of invasive arthropod-associated microbiota as important  
324 contributors to the xenobiotic metabolism and thus as a driver for insect adaptation to  
325 polluted habitats.

326         Even though increasing information is now available on the nature of microbiota  
327 harbored by hematophagous arthropod vectors, their contribution on the proven capabilities

328 of invasive arthropod species to rapidly adapt to local environments, and thus prompt their  
329 successful invasiveness, is still largely underexplored. Convincing examples of microbial lability  
330 to environmental fluctuations lack the experimental approaches to demonstrate the effect on  
331 host physiology (**Fig. 2**).





**Fig. 2** Diagram illustrating the contribution of arthropod-associated microbiota in adaptation to local environments. To date, investigations were mainly confined to mutualistic associations in phytophagous insects. Such symbiotic associations allow the hosts to exploit unique or restricted ecological niches that would otherwise be impractical to inhabit. Interestingly, symbiotic microbiota can help termites to deconstruct lignocellulosic biomass with high efficiency. In aphids, the 10 essential amino acids are scarce in the phloem sap diet and are supplied by the obligate bacterial endosymbiont *Buchnera*. Mutualistic gut symbiotic bacteria of the genus

*Burkholderia* establish a specific and beneficial symbiosis with stink bugs and confer resistance of the host against insecticides. By contrast, apart from a few exceptions, few studies have yet investigated if, and how, hematophagous arthropods foster ecologically important traits and therefore facilitate host adaptation to environmental fluctuations leading to successful invasions.

(\*) Gene-by-Gene-by-Environment interactions

### 3. ECOLOGY OF INVADERS

#### (1) Ecological characters of invasive mosquitoes

Often, successful invasive arthropod populations are characterized by certain traits facilitating their establishment in the new environment (Sherpa et al. 2019a; Daly et al. 2023). In mosquitoes, Juliano and Lounibos (2005) reported that desiccation resistance of eggs strongly increases the probability of introduction success. Medley et al. (2019) reported that local adaptation to northern climates by rapid evolution of egg diapause is a key factor in the establishment and invasion success of *Ae. albopictus*. Habitat specialization may also have assisted the success of invasive mosquitoes, as reported in *Aedes* sp. which evolved the capacity of developing in container habitats, a transition accompanied with changes in larval phenotypes (Soghigian et al. 2017). However, there is a complete lack of information on the much broader range of types of life history traits linked with invasiveness, including those pertaining to adult stages, as for other insects (e.g., ants: Fournier et al. 2019).

In the invaded region, genetic diversity along with organism preadaptation likely have a strong effect on the phenotypic expression of key traits inherently linked with vectorial capacity, longevity, anthropophily, biting behavior and vector competence (Bernhardt et al. 2012). While the selection process persists after establishment, the traits that are beneficial during the early stages of colonization will often differ from those favoring continuous range expansion or long-term persistence (Hill et al. 2014). For example, a capacity to produce dormant stages could enhance invasiveness during the early invasion stages, while rapid development, ability for competition (for instance: aggressiveness, anti-predator behavior), capacity for long-range self-dispersal, and adaptability to human-modified environments may be more important at later stages. Broad blood feeding habits (*i.e.* on ectotherms, birds, and mammals) have also been documented in important invasive vector mosquitoes, such as *Ae.*

*aegypti* and *Ae. japonicus*, but strong preference for humans underlies their public health impacts (Cebrián-Camisón et al. 2020).

*Aedes albopictus* is certainly among the most studied invasive hematophagous arthropod vectors (Bonizzoni et al. 2013). Today, all major land masses, except Antarctica, have been colonized by this species (Kraemer et al. 2015), and invasive populations perform particularly well in the urbanized areas of the non-native range (Kraemer et al. 2015). Many studies focusing on the feeding behavior of this species have highlighted strong anthropophilic preferences associated with noticeable plasticity for other mammals and even birds. Such results have been observed both in native and non-native populations of *Ae. albopictus*, suggesting a relative conservation of feeding behaviors during the invasion process, however, anthropophily has been found to be highest in urban habitats. This highly invasive species is especially successful at colonizing artificial environments associated with urban areas (Hawley 1988; Dowling et al. 2013), such as container-style habitats, that are often small and inconspicuous (Dowling et al. 2013).

The comparison of life history traits between native and non-native populations of another mosquito species of the same genus, *Ae. aegypti*, leads to a rather different picture. Native populations are still distributed in Africa, in wooded savanna and across the islands of the South-West Indian Ocean. A morphologically-distinct invasive subspecies arrived in the Americas between the 15<sup>th</sup> and 17<sup>th</sup> centuries, most likely through the slave trade (Powell et al. 2018). Then, it invaded Asia, probably in the middle of the 19<sup>th</sup> century through the Suez Canal. The ancestral form, *Ae. aegypti formosus*, whose larvae preferentially occupy tree-hole habitats outside human settlements, can feed on a large range of mammals and even reptiles. The domestic subspecies, known as *Ae. aegypti aegypti*, strongly associated to human settlements, is mostly anthropophilic for blood feeding and exceptionally well-adapted to

domiciliary and urban environments, which partly explains why it is the most important vector of human arboviruses (Crawford et al. 2017; Rose et al. 2020).

Factors influencing invasion success of mosquitoes still need to be quantified and ongoing evidence of how genetic divergences accumulate over time in new ecological situations (*e.g.*, blood meal availability) need to be compiled for many invasive mosquitoes, and invasive arthropod vectors in general (Lee et al. 2019).

## **(2) Ecological niche shifts during invasion**

In its native range, *Ae. albopictus* is described as a forest edge species and considered to be a rural vector, with larvae developing in various natural micro-habitats, such as tree holes, bamboo stumps, bromeliads and other leaf axils or coconut shells (Hawley 1988; Higa 2011; Li et al. 2014). In contrast, populations in recently colonized areas predominantly use a diversity of artificial and natural larval sites, with clear predominance for artificial containers (Hawley 1988; Simard et al. 2005; Delatte et al. 2008; Bagny et al. 2009).

Rural areas are not exempt from mosquito proliferation, where there are habitats associated with private agricultural lands. One of the most prolific characteristics of agricultural activities boosting mosquito population dynamics is the water surfaces of rice fields and vegetable crops (Darriet et al. 2012; Darriet 2018). On all invaded continents, these activities have the potential to generate swarms of mosquitoes transmitting malaria, Japanese encephalitis, West Nile virus and lymphatic filariasis. In communal farmlands, droughts perversely affect mosquito communities through human alteration of natural enemy-rich pond food webs (Dalu et al. 2017). Deepening of pond systems for water storage disrupts wetting and drying successions that characterize ephemeral hydroperiods, with transitions to permanent aquatic systems favoring stocking of invasive fish species which can, in turn, boost mosquito proliferations through intermediate trophic group enemy release (Pyke 2008;

Cuthbert et al. 2018). To this end, land-use changes stimulated by climate change and agricultural intensification can lead to alterations of the ecological niche placement of invasive hematophagous vector species, lessening biocontrol by natural enemies.

### **(3) Movement patterns and geographic spread**

A range of studies have modeled or measured flight distances and movement patterns in mosquito species (Sota et al. 2015; Marcantonio et al. 2016; Brown et al. 2017; Le Goff et al. 2019). Yet, there is insufficient data to effectively compare the movement patterns of mosquitoes in their native and invaded ranges, and even less information that connects dispersal ecology to spatial genetic structure (but see Schmidt et al. 2021). Meanwhile, the understanding of spatio-temporal dynamics of movements by mosquitoes is instrumental for designing efficient management plans aiming at controlling population outbreaks (Renault et al. 2018; Renault 2020), and for better understanding the patterns of gene flow in invaded areas.

As active movements of eggs and larvae are limited in mosquitoes (although passive movements can span continents *via e.g.*, used tires or standing water on ships), most studies have focused on movements displayed during the adult life stage (Egizi et al. 2015; Webb and Russel 2019). Service (1997) synthesized the different forms (active, passive) of displacement in mosquitoes, including wind-assisted dispersal, airplane, ship, train, or vehicle transportation, and daily flights of the adults. That review highlighted that mosquito movements can be categorized into short and long distance displacements (Service 1997).

Often, short distance movements correspond to intentional displacement of the adult, and these movements include both non-oriented and oriented (host-seeking, breeding site, mate-finding) displacements. Yet, the average maximum displacement distance can differ among genera, as for instance reported for the *Anopheles* and *Culex* genera (e.g. 3490 m

versus 5014 m) (Verdonschot and Besse-Lototskaya 2014). Conversely, mean distances often remain comparable (Verdonschot and Besse-Lototskaya 2014); even if the mean distance travel can reach 1 km (Medeiros et al. 2017), a large proportion (90%) of mosquitoes have frequently been recaptured in a 100 m radius from the initial release point (Marini et al. 2010; Liu et al. 2012). Larger differences in the mean displacement distances were reported when comparisons were performed at the species level. Working with *Cx. pipiens*, Tsuda et al. (2008) found a mean distance traveled by females of ~ 300-500 m. Working with male *Ae. albopictus*, Le Goff et al. (2019) reported a mean distance traveled ranging from 37 to 67 m in La Reunion Island, which varies through the year. In *Ae. aegypti*, even if long displacement distances were measured under controlled conditions in 12-day-old females, which were able to fly for 11.3 km on average (Rowley and Graham 1968), the distance traveled by this insect is very similar to that reported in *Ae. albopictus* — around 50 to 60 m according to a review by Winskill et al. (2015). The distance traveled by non-native mosquitoes is expected to be highly context-dependent, as reported in other insect species (Renault 2020).

The methods employed in experiments can inherently affect the estimation of displacement distances, and several other factors can additionally affect this measure. For instance, displacement distance can vary with the environmental conditions experienced during development, as reported in *Cx. pipiens* complex reared under predation risk. Specifically, the median travel distance of female *Cx. pipiens* originating from larvae grown in fish-free cages was two times lower than their counterparts issued from larvae exposed to predation risk, i.e. ~ 100 m versus ~ 200 m, respectively (Alcalay et al. 2018). The body size and behavior, endophilic for instance, of adult mosquitoes can also determine the dispersal distance they can cover. In *Ae. aegypti*, smaller females can fly over longer distances, with a mean distance of about 79 m as compared with larger ones (about 41 m), and they could spread disease per individual across a greater geographic extent (de Freitas et al. 2007). However, Juliano et al. (2014) also reported that the frequency of infection can be increased

with female size in *Ae. aegypti*. Time to displacement initiation post-blood meal can differ among mosquitoes: Zhang et al. (2006) reported that *An. sinensis* and *Cx. tritaeniorhynchus* rested for a short amount of time after blood-feeding (less than 30 min for 81 % of females in *An. sinensis*, Pan et al., 2012), and then dispersed, while *Cx. p. pipiens* stayed for a significantly longer time.

Long-distance movements can include migration, as well as intentional or unintentional movements, such as wind-assisted long-distance dispersal or transportation (Renault et al. 2018; Huestis et al. 2019; Sanogo et al. 2021; Faiman et al. 2020). For instance, working with aerial kit trap collections, Kay and Farrow (2000) identified several mosquito species, including *Cx. australicus*, *Cx. annulirostris*, and *An. annulipes*. These authors estimated that mosquitoes could cover *ca.* 180 km per day with this non-oriented displacement, a distance further extended to 594 – 648 km *via* backtrack simulations (Eritja et al. 2017; Ritchie and Rochester 2001). Long distance dispersal can have significant implications for invasion processes, as it can contribute to increases in the potential for adaptive evolution of non-native organisms (Prentis et al. 2008), favor multiple population divergence (Suárez et al. 2022), or promote the arrival and potential impacts of non-native/neo-native species that are functionally distinct (Renault et al. 2022b), with all of these phenomena ultimately speeding-up geographic expansion. In metropolitan France however, long-distance “jumps” far from the gradually expanding core colonization area did not result in novel colonization fronts, suggesting that *Ae. albopictus* colonization is mainly following neighborhood dispersal (Roche et al. 2015).

Passive displacements associated with human activities and transportation also exist, yet these events possibly alter the viability of the transported mosquitoes. Aircraft transport of mosquito species has been highlighted by Gratz et al. (2000). Using climatic and air traffic data, principally from Africa, Tatem et al. (2006) highlighted and predicted the occurrence of new airport transport routes. Human-assisted transportation can also greatly assist the



spreading of mosquitoes, but also other hematophagous arthropod vectors, with weak dispersal capabilities, as is the case of *Ae. albopictus* whose displacement distance is enhanced by passive transportation in vehicles (Šebesta et al. 2012; Werner and Kampen 2015; Eritja et al. 2017). Public and private transport, the transport of man-made containers in general, or the transport of lucky bamboo plants, are now recognized as prominent translocation modes to select mosquitoes, and particularly *Ae. albopictus* in some regions (Medlock et al. 2012). When designing efficient management plans against invasive mosquitoes, considering the different spread strategies and potential dispersal distances among invasive species is crucial. For instance, Müller et al. (2020) reported that *Ae. japonicus* primarily dispersed actively from northern Switzerland, while *Ae. albopictus* and *Ae. koreicus* were consistently captured along motorways, revealing a passive dispersal process by vehicle transportation.

A promising approach has been developed by Jansson et al. (2021), whose LIDAR-based protocol revealed the real-time dispersal behaviors of malaria vectors. By applying this forefront technological method to other regions and hematophagous model taxa, we could gain significant information concerning in-field movements (swarming, host-seeking, dispersing) of individuals. Moreover, by providing information on mosquito geolocation and hot spots, such *in-situ* quantifications of movement patterns could revolutionize the ways control strategies are implemented in the field.

#### **4. BIOTIC INTERACTIONS**

##### **(1) Resource acquisition and invasions**

Sugar meals are required for sustenance in both male and female mosquitoes. Furthermore, the nature of plant sugar meals can subsequently affect the fitness of mosquitoes. For instance, females of *An. gambiae* feeding on their preferred plants lay more eggs (Manda et

al. 2007). Moreover, higher quality plant resources, *e.g.*, plant litter and fruit falling in aquatic systems, favor the growth rate of larval *Ae. albopictus* (Reiskind and Zarrabi 2011). Sugar-rich floral nectars may be preferred by mosquitoes, as reported by Gouagna et al. (2010) who showed that the feeding movements of male *An. gambiae* were orientated towards plants offering higher sugar sources (*e.g.*, mango *Mangifera indica* and royal poinciana *Dalmanella regia*). Working with *An. gambiae*, Müller et al. (2010) found that nine plant species, over the 26 species they tested, were significantly attractive, thereby also revealing the large plant spectrum of the insect. Overall, no sugar meal preference has been identified in *Ae. aegypti* (Martinez Ibarra et al. 1997), or *Ae. albopictus*, with these species being opportunistic in terms of sugar-feeding behavior (Qualls et al. 2016). In agricultural pastures, eutrophication via livestock dung inputs into larval habitats can also attract *Culex* and *Anopheles* mosquitoes, increase development rates and potentially increase recruitment into the adult population (Buxton et al. 2020).

Environmental temperatures may additionally interact with nutrition efficiency, so that both factors jointly mediate invasion success, with increased developmental duration when temperature is lower. In particular, the larval developmental time from hatching to pupation increases from 7 days at 32 °C to 28 days at 12 °C in *Ae. albopictus* (Briegel and Timmermann 2001). Temperature and shading also interact in mediating larval *Ae. aegypti* development and mortality, with the number of days from hatching to adult emergence increasing from 7.1 days at 37 °C to 8.3 days at 28 °C in full light conditions, suggesting emergent photosensitivity in this species (Sukiato et al. 2019). Resource acquisition may thus act as an important factor shaping the invasion process in mosquitoes.

Interactions with other invasive species can assist the invasion by hematophagous arthropod vectors, as for *Cx. pipiens* whose population dynamics are enhanced when grown with the leaves and flowers of an invasive plant (Shewhart et al. 2014). In *Ae. albopictus*,

abundance can be promoted by the presence of non-native plants and animals, as reported for the Amur honeysuckle (*Lonicera maackii*) invasion. The rotting leaf litter of this non-native plant, upon which *Ae. albopictus* larvae feed, accelerates pupation and increases imago size, compared to the litter of a commonly co-occurring native plant, whose increasing concentration in the environment alters the same mosquito traits (Russo and Boyd 2018). Similarly, Cuthbert et al. (2020) found leaf inputs from invasive lantana *Lantana camara* and guava *Psidium guajava* to increase mosquito abundances, alongside litter from another native species (*Ficus sycomorus*). While another native plant (*Terminalia sericea*) reduced abundances in that study, this shows that mosquito facilitation rather relates to specific traits pertaining to nutrient inputs and attractants/deterrents.

Other invasive plants favor mosquito proliferation and range expansion through the provisioning of shelter, which can reduce heat stress and provide potential refuge from predators (e.g., Stone et al. 2018). Nevertheless, the presence of non-native species in the recipient community does not systematically facilitate the establishment of arthropod vectors, and opposite effects such as non-native populations regulating hematophagous arthropod populations may be reported.

Last, introduced mosquitoes are potential resources for native predators, altering the organization of local trophic networks (WHO 2003; Juliano et al. 2010; Früh et al. 2019). Predation can thus limit the success of invasion and favor the resilience of native species from interspecific competition (Juliano et al. 2010; Juliano et al. 2019). Certain native predators, such as copepods, have been shown to be more efficient towards invasive (e.g. *Ae. albopictus*) rather than native (e.g. *Cx. pipiens* complex) mosquitoes, owing to prey naivete and behavioural differences (Cuthbert et al. 2019). Classical biological control attempts aimed at mosquito populations with the mosquitofish *Gambusia* sp. have often failed and led to marked non-target impacts on native communities (Pyke 2008).

## (2) Competitive ability and invasion dynamics

Competition for resources and predation at the larval life stage could drive invasion dynamics (Reitz and Trumble 2002), as evidenced in *Ae. aegypti* and *Ae. albopictus*. In urban areas, both of these mosquito species typically share the same artificial larval development sites, often resulting in a competitive displacement of *Ae. aegypti* by *Ae. albopictus* (Bagny-Beilhe et al. 2012; Lounibos et al. 2016). In mosquitoes, competitive reduction may be explained by interspecific larval competition, or asymmetric reproductive interference in the form of satyrization (Tripet et al. 2011; Giatropoulos et al. 2015). Moreover, hatching inhibition has been reported in *Ae. albopictus* over *Ae. aegypti* larvae, as well as infection of *Ae. aegypti* by parasites introduced by *Ae. albopictus* (Lounibos 2002; Juliano and Lounibos 2005). During the adult stage, satyrization between these species has also been found to favour *Ae. albopictus* over *Ae. aegypti*, with sterilization effects unidirectional in inhibiting female *Ae. aegypti* fecundity (Bargielowski and Lounibos, 2016). *Aedes aegypti* can develop resistance to satyrization over generations, but this comes with additional fitness costs relating to reproductive traits (Bargielowski and Lounibos, 2016). Competition for resources during the adult stage may also be a factor influencing invasion dynamics, but has been scarcely assessed (Yang et al. 2021).

The often superior competitive ability of invasive mosquitoes over natives partly results from a quicker larval development due to a greater capacity to exploit food resources, as reported for *Ae. albopictus* larvae (Carrieri et al. 2003; Darriet 2016b). In Europe, the competition between *Ae. albopictus* and *Cx. pipiens* has, however, led to contradictory results, suggesting that the studied ecotype of *Cx. pipiens* and the environmental conditions are important drivers of competitive outcomes in mosquitoes (Carrieri et al. 2003; Marini et al. 2017). For instance, Müller et al. (2018) suggest a competitive superiority of *Cx. pipiens* over *Ae. albopictus* in terms of larval survival in resource-rich microhabitats. In addition to the

availability of resources, the experimental manipulation of the timing of resource enrichment into the larval habitat can alter the competitive interactions among mosquito species. This was reported for larvae of *Ae. albopictus* and *Ae. triseriatus* in an experiment in which resources were added either gradually or in a single pulse, the latter conferring an advantage to the larval development of the invasive species (Bevins 2007).

To sum up, the superior competitive ability of invasive mosquitoes is not necessarily the general rule (Alto 2011), and intraspecific competition may even impede against non-native mosquito species (Hardstone and Andreadis 2012).

### **(3) Ecological network approaches and impacts**

All organisms are embedded in complex interaction networks, which provide a fertile framework to study biodiversity, ecosystem function and ecosystem stability (Montoya et al. 2006; Thomson et al. 2012; Evans et al. 2016; Derocles et al. 2018a). The development of bipartite networks, as commonly applied to mutualist interactions (*e.g.*, plant-pollinator networks, see Geslin et al. 2013 for an example), and trophic interactions (*e.g.*, Tylianakis et al. 2007 for host-parasitoid networks), can overlook the complex description of ecological communities. In these situations, the more complex tri-partite networks (see Macfadyen et al. 2009; Evans et al. 2016 for plant-host-parasitoids) up to multilayer ecological networks including many different types of interactions are better appropriated. To date, the study of Pocock et al. (2012) remains a rare example of these multilayer networks built from the sampling of an actual ecosystem by gathering into a 'network of ecological networks', with seven different types of interactions. Hematophagous arthropods are typically organisms where a multilayer network approach is essential to fully understand their impacts on ecosystems (Bellekom et al. 2021), not only because they can vector diseases, but also because the change of diet between different life stages induce a modification in the interactions mediated by these organisms.

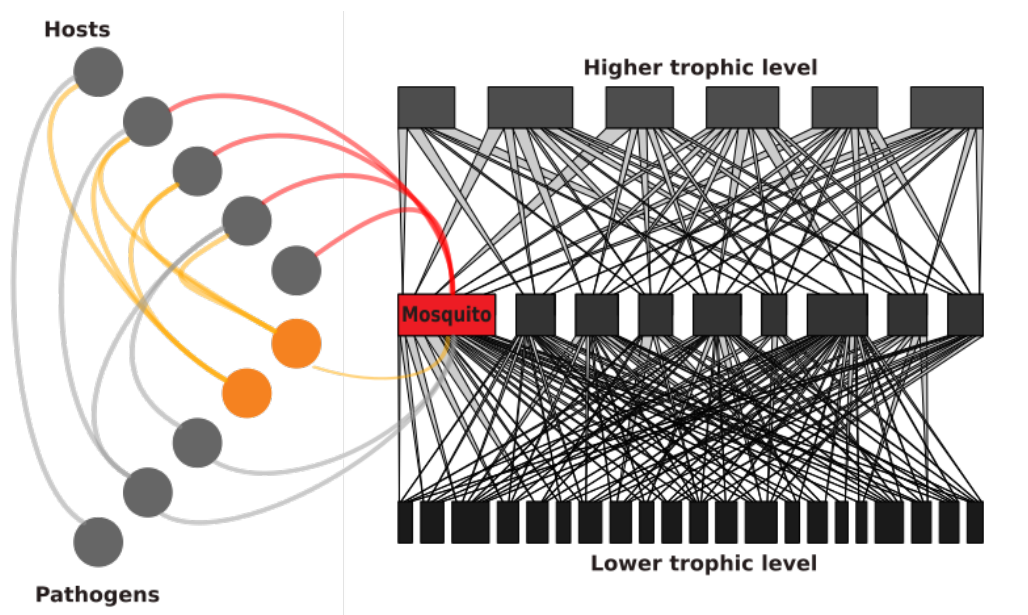
Mosquitoes can have top-down and bottom-up effects in the food webs (Lefèvre et al. 2022). The top-down effects occur most obviously during the adult hematophagous life stages, with the transmission of diseases in particular (**Fig. 3**). The top-down effects can also be mediated in the larval stages: larvae consume a broad range of organisms and therefore can structure the communities of lower trophic levels (Duguma et al. 2017). Regarding the bottom-up effects, since these organisms are a resource for higher predators, a change of their abundance may have cascading effects on the entire food web (Lefèvre et al. 2022) (**Fig. 3**). While the extinction of a species (in the present case through, for example, the management of invasive populations) is a probable cause of secondary extinctions in the ecological networks (Memmott et al. 2004; Evans et al. 2013), even a decrease of abundance may lead to secondary extinctions (Säterberg et al. 2013). However, Derua et al. (2018) showed that a decrease in the density of vector mosquitoes induced by larvicide treatments did not affect higher trophic levels. The consequences of the eradication of certain hematophagous insect species, such *Anopheles* malaria vectors, remain to be established (Lefèvre et al. 2022).

Furthermore, floral visitation has been well-documented in some mosquitoes and pollination is thought to be widespread, while non-pollinating mosquitoes have been classified as “nectar thieves” or “nectar robbers” (Peach and Gries, 2020). However, the context-specific roles of mosquito species in pollination services are sparsely known, such as whether species are co-pollinators with other insects or the degree to which they are specialized towards certain plants (Peach and Gries, 2020). While mosquito per capita pollination is likely low, this may be compensated by their substantial numerical response across ecosystems. The removal of mosquitoes may therefore have unpredictable knock-on effects on plants and other pollinators, and these effects may differ between native and non-native ranges depending on the time since invasion and degree of local adaptation. In this context, we encourage the development of ecological network analyses which can help to

identify the cascading effects of a species eradication on the interactions mediated, and therefore on the network structure. A multilayer network analysis may be particularly informative for mosquito species, since they are embedded in terrestrial and aquatic food webs (Weterings et al. 2018)

While considered as key nodes in food webs and clearly identified as mediators of cascading effects, mosquitoes, and hematophagous arthropods in general, are still rarely studied in an ecological network approach. Recently, DNA-based methods, next-generation sequencing (or high-throughput sequencing; Goodwin et al. 2016) in particular, have nevertheless allowed the construction of ecological networks including hematophagous arthropods (Dumonteil et al. 2018; Hoyos et al. 2021). In *Triatoma dimidiata*, a triatomine able to transmit Chagas disease, Dumonteil et al. (2018) built a network approach by combining the sequencing of several genes to identify the haplotypes of the agent of the disease *Trypanosoma cruzi* (ITS-2 gene), the microbiota (16S gene) and the mammal hosts (12S gene). This network approach identified the key hosts for parasite transmissions to humans. Similarly, Hoyos et al. (2021) demonstrated a high level of specialization and modularity (*i.e.* group of species with a high connection between them but loosely connected to other species) in a mosquito-flavivirus-host system. The integration of the full range of interactions mediated by hematophagous arthropods into an ecological network approach has been performed recently with data from published literature and databases (Bellekom et al. 2021). Surprisingly, this study revealed that many interactions in blood-sucking insects remain to be documented, and for the very well-studied species *Cx pipiens*, the range of known hosts still needs to be completed. Yet, the visualization and the characterization of the networks provided a valuable framework for the detection of the pathways of disease transmission (Bellekom et al. 2021).

The network ecology in invasive hematophagous arthropods is still at its beginning and more network (or food web) approaches are required to assess top-down and bottom-up effects mediated by these taxa, the disease they transmit (Ostfeld et al. 2018), and the structure of their interactions (Selakovic et al. 2014). DNA-based techniques, metabarcoding in particular, provide an interesting opportunity to construct highly-resolved ecological networks (Evans et al. 2016; Derocles et al. 2018; Alberdi et al. 2019).



**Figure 3.** A theoretical simplified multilayer network with hematophagous arthropods, represented in red. Here, a mosquito species is used as an example. In the qualitative network on the left, human diseases and their pathways are represented in orange. In the quantitative network on the right, mosquitoes are predated by top trophic level predators (*e.g.*, birds). The mosquito species (and other species from the middle trophic level) consumes resources from the first trophic level during the larval life stage. Each species is represented by a rectangle proportional to the abundance. The width of each interaction is proportional to the frequency of the interaction.

## 5. INVASION MANAGEMENT AND PERSPECTIVES



Management strategies for biological invasions can be divided coarsely into proactive, pre-invasion approaches and reactive, post-invasion approaches (Cuthbert et al. 2022). In its broadest sense, vector control includes the management and protection against hematophagous arthropods (chiefly mosquitoes and ticks), some being vectors of vertebrate pathogens and parasites. It consists of a variety of methods, including chemical, biological and genetic controls, individual protection, environmental management, health education and social mobilization, which depend on the vector involved in the transmission, and on the epidemiological and socio-economic contexts (e.g., Becker et al. 2010; Nwanade et al. 2022). Most recently, there has principally been a renewed interest in approaches that are non-chemical and eco-friendly, owing to the emergence of insecticide resistance in vector populations (Benelli et al. 2016).

Management strategies are increasingly underpinned by sound understandings of the placement of mosquitoes within wider ecological networks and their interactions. Actual demonstrations on how global changes modify the structure of ecological networks exist, but are infrequent (see Derocles et al. 2018b for an example). Our understanding of biological invasion processes and impacts can also benefit from the ecological network analysis, since invasive species can have cascading effects across multiple trophic levels (Lawson Handley et al. 2011; Doizy et al. 2018). On the other hand, ecological network analysis may also help to determine which ecosystem is more likely to be invaded (David et al. 2017; Hui and Richardson 2019). Nevertheless, how invasive species actually alter the structure of food webs (or their positive counterpart, the mutualist networks) remains rarely investigated (David et al. 2017). This constitutes therefore a priority area for research into mosquito vector ecology in the face of climate change and biological invasion.

Rapid responses to manage invasive hematophagous vectors are far more cost-effective than longer-term control, or the health costs directly induced. Indeed, using

economic costs data for *Aedes* spp., billions of dollars could have been saved annually through timelier prevention and rapid eradication approaches for these vectors (Ahmed et al. 2022). To date, regarding invasive mosquitoes, only certain island countries have managed to meet this type of biosecurity challenge, given their particularly proactive strategies (Holder et al. 2010; Muzari et al. 2017). It is therefore critical for countries to develop improved monitoring infrastructures for these vectors, including the use of citizen science initiatives to report invasive vector sightings (e.g., Mosquito Alert app: Bartumeus et al. 2018). Owing to the difficulties of eradicating established and spreading populations, this can help to improve management efficiencies while raising societal awareness. Improper usage of insecticides can have negative impacts, building up resistance mechanisms among the arthropods targeted, while unintentionally affecting the non-targeted fauna (FAO 2004; Lee et al. 2023). The current strategies are increasingly restricted by regulations and pressures, such as the shrinking range of insecticides allowed by public health bodies, and the increasing pressure from society to use environmentally-friendly substances. A range of natural botanical extracts have, however, shown efficacy in regulating mosquito populations, potentially offering more environmentally friendly solutions (Cuthbert et al. 2020). Today, community strategies seem to be the most efficient, for example, the social mobilization against dengue fever (Andersson et al. 2017) or the use of insecticide-treated nets to reduce malaria transmission (WHO 2017). These especially protect the most vulnerable humans, such as the sick and infants, from bites of aggressive vectors (Andrade and Cabrini 2010; Tsunoda et al. 2013).

Alternative strategies for mosquito control are continuously being developed, including the use of bacterial endosymbiont *Wolbachia* and entomopathogens, the release of sterile males (radiation-induced) or genetically modified mosquitoes, a combination of fertilizers and insecticides, and auto-dissemination of Insect Growth Regulators (IGR) (Gaugler et al. 2011; Hoffmann et al. 2011; Bouyer and Lefrançois 2014; Darriet 2016a; Zheng et al. 2019; Simard 2018). Considerations of competitive relationships between vectors, and risk

assessment for the emergence of new harmful vectors when invasives are under control are crucial and require tight monitoring in native, as well as non-native ranges. Overall, the management of mosquitoes is reliant on a firm understanding of the fundamental biology of these species, from genetics through to trophic interactions within ecosystems, and all of these biological scales should be considered to achieve effective management globally as well as locally.

**Data archiving Statement:**

No data were collected for this study (review). All data and information synthesized in the review are already published and publicly available, and those publications are properly cited in this submission.

**Declaration of interest statement:**

The authors declare that they have no conflict of interest.

**Ethics statement**

This article does not contain any studies with human participants or animals performed by any of the authors.

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**Author contributions**

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