The Role of Environmental and Biotic Drivers in Shaping Mosquito Communities and Distributions

Daniel C. Smith

School of Biological Sciences

University of Reading

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Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Daniel C. Smith
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Acknowledgements

The completion of this thesis marks the end of a challenging yet rewarding journey, one that was interupted in it's early stages by the global COVID-19 pandemic. The disruptions to research and collaboration caused by lockdowns, remote working, and a shifting academic landscape intensified the usual demands of doctoral study. Nevertheless, this thesis is a reflection not only of personal perseverance but also of the invaluable support I received along the way.

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Any errors or omissions in this work are my own.

Abstract

Mosquito-borne diseases (MBDs) pose significant public health risks, driven by environmental changes and species interactions. This thesis takes a community-based approach to understand how multiple drivers—both biotic and abiotic—shape mosquito distributions across local and continental scales, using advanced Joint Species Distribution Models (JSDMs).

In Chapter 2, I analyse mosquito communities in managed UK wetlands, showing how habitat modifications, such as changes in vegetation structure, impact mosquito populations. The study highlights that biotic interactions, including predator-prey dynamics, play a crucial role alongside environmental factors in determining community composition.

Chapter 3 scales up to a European dataset, exploring how environmental factors (e.g., temperature, precipitation) and biotic interactions drive mosquito communities. Importantly, biotic interactions remain influential at large scales, challenging the assumption that environmental variables dominate. This underlines the need to integrate species interactions into disease modelling.

In Chapter 4, I enhance JSDMs by incorporating species traits and phylogenetic data. Traits like thermal tolerance and host preferences improve predictions of mosquito distribution, while phylogenetic relationships provide insights into how evolutionary history shapes community dynamics. These findings offer a deeper understanding of how species traits influence disease risk.

The thesis emphasises that community-based approaches provide a richer understanding of mosquito ecology than single-species models. This is crucial for improving vector surveillance and disease control strategies, particularly in anticipating how community composition impacts disease transmission. Future research should focus on understanding how communities may shape MBD potential, expanding our biological knowledge of lesser studied mosquito species, and interrogating the impact of traits and biotic interactions across different scales in their impact on shaping mosquito communities.

This research advances the field by integrating multiple ecological drivers and species interactions, offering a more comprehensive framework for predicting mosquito distributions and vector-borne disease risks across mixed scales and environmental conditions.

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Chapter 1

Introduction

1.1 Background and Context

1.1.1 The Burden of Mosquitoes

Vector-borne diseases (VBDs) cause substantial morbidity and mortality worldwide, accounting for one-sixth of illness and disability annually (WHO, 2017, 2014). Mosquito-borne diseases (MBDs) are among the most significant contributors to the VBD burden, most notably through the transmission of several diseases such as malaria (approximately 212 million yearly cases), dengue fever (approximately 96 million yearly cases), and lymphatic filariasis (38 million yearly cases) (WHO, 2014). Globally, MBDs are predicted to rise in both incidence and distribution as climatic changes, land use changes, and increased globalization lead to more favourable conditions for transmission and transport of both vectors and disease pathogens to places where they were previously absent (Bakonyi and Haussig, 2020; Bhatt et al., 2013; Bogoch et al., 2016; Zhang et al., 2017).

The impact of MBDs on human health has driven extensive research into the ecology and bionomics of vector species (Becker et al., 2010). Building upon decades of work, we now understand that the distribution of key vector species is critical to comprehending how these diseases spread and persist in various environments (Bhatt et al., 2013; Nanyingi et al., 2015; Nsoesie et al., 2016). In Europe, this knowledge has become increasingly relevant as the continent faces new challenges from both native and invasive mosquito species (Calzolari, 2016; Medlock et al., 2018).

1.1.2 A European Perspective

Europe has a longstanding history with mosquito-borne diseases (MBDs). The successful eradication of malaria in the 1970s was achieved through significant changes in land use, improved sanitation, and modified agricultural practices, including the deliberate drainage of swamps and wetlands, which markedly reduced mosquito breeding sites (Piperaki and Daikos, 2016). Similar transformations in land management, coupled with rapid socioeconomic development during the early 20th century, contributed to the near-elimination of dengue across the continent from the mid-20th century onwards (Moreno-Madriñán and Turell, 2018). Efforts to increase the availability of agricultural land involved extensive drainage projects that diminished mosquito habitats, while urbanization shifted populations from rural to urban areas, reducing direct exposure to mosquito-prone environments. Changes in agricultural practices, such as minimizing standing water, further altered landscapes to make them less conducive to mosquito breeding. Additionally, socioeconomic progress played a crucial role, as higher living standards and increased health awareness helped to lower the risk of exposure.

Despite past achievements in controlling mosquito-borne diseases (MBDs) in Europe, recent decades have witnessed a resurgence of threats, with sporadic cases and localized outbreaks occurring in southern regions. The emergence of chikungunya, outbreaks of West Nile Virus (WNV) and dengue, and even the return of autochthonous malaria transmission in some European countries (Table 1.1) underscore the complex and evolving risk landscape (Angelini et al., 2007; Piperaki and Daikos, 2016; Young et al., 2021). This re-emergence is driven by multiple factors, including climate change influencing vector habitats and increased international travel facilitating disease spread (Johnson et al., 2018; Semenza and Suk, 2018). The situation has been further complicated by the introduction of invasive *Aedes* species from Asia to Western Europe, primarily through human-mediated means such as international trade (Kraemer et al., 2019a). These mosquitoes have not only established themselves in new territories but have also played a critical role in introducing and amplifying the circulation of both endemic and exotic diseases previously rare on the continent.

Among these invasive species, *Aedes albopictus* (Asian tiger mosquito) poses the most significant threat to public health due to its adaptability and widespread presence. Since its first appearance in Albania in 1979, it has spread to over 20 European countries and is now a key vector responsible for most dengue outbreaks in Southern Europe (Ahmed et al., 2020; Schaffner and Mathis, 2014). Its ability to adapt to temperate climates through cold-resistant eggs has facilitated further northward expansion, raising concerns about broader disease risks. *A. albopictus* has been implicated in the transmission of the Zika virus, with local transmission reported in France (Brady and Hay, 2019), and has been linked to outbreaks of the chikungunya virus in Italy and France (Grandadam et al., 2011; Vega-Rua et al., 2013). The species' spread is driven by global trade, particularly the used tyre and lucky bamboo trades, and local dispersal through road networks, suggesting that further expansion across Europe is likely (Benelli et al., 2020). Additionally, its preference for urban environments increases the potential for human contact and transmission of other pathogens such as West Nile Virus and *Dirofilaria*, further underscoring the need for robust surveillance and control measures (ECDC, 2012).

Understanding these intricate relationships between environmental drivers, mosquito ecology, and disease transmission is crucial for predicting and mitigating future MBD risks. As we face ongoing environmental changes, including climate change and increasing land use change, our ability to anticipate and respond to shifts in mosquito communities and associated disease risks becomes increasingly vital for public health and ecosystem management. The added complexity of changing mosquito community compositions further complicates this challenge. These changes, along with potential interactions between species and communities, represent a poorly understood area of mosquito ecology.

Table 1.1 Viruses that appear on the European Centre for Disease Control mosquito-borne diseases. These viruses and their vectors are of importance to European health officials and policymakers. * Symbol indicates the potential implication of the vector in transmission but has not been confirmed in the field/or are not considered to be primary vectors of the disease.

Pathogen	Distribution	Vectors	Recent Impacts EU
Chikungunya virus (CHIKV)	Endemic to Africa, India, and South East Asia. Multiple imported cases present across Central and Western Europe (Powers and Logue, 2007).	*Aedes aegypti* (Gould and Higgs, 2009; Medlock et al., 2012), *Aedes albopictus*	200 confirmed cases in Italy 2007 (Angelini et al., 2008). Autochthonous transmission recorded in Southern France, 2010 (Grandadam et al., 2011).

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Pathogen	Distribution	Vectors	Recent Impacts EU
Dengue virus (DENV)	Endemic lineages in the Americas, Africa, and Asia. Frequently imported cases arising in temperate regions of Europe (Guzman and Harris, 2015; Schaffner and Mathis, 2014).	*Aedes aegypti*, *Aedes albopictus*, *Aedes japonicus** (Schaffner and Mathis, 2014; Schaffner et al., 2013c)	Large epidemic in Greece 1928 (Rosen, 1986). Autochthonous transmission of dengue in France, Nice, 2010 (Ruche et al., 2010), with Croatia experiencing a similar case in the same year (Gjenero-Margan et al., 2011). Further outbreaks in 2012 of 1,891 cases in Madeira (Sousa et al., 2012).

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Pathogen	Distribution	Vectors	Recent Impacts EU
West Nile virus (WNV)	Endemic to the Old World, with high densities of cases across Europe, Africa, and Asia, though distribution decreases with latitude (Rizzoli et al., 2015). Recently introduced into N. America (Kilpatrick et al., 2006).	*Culex pipiens, Culex modestus, Culex perexiguus, Culex theileri, Aedes japonicus*, Aedes aegypti*, Aedes albopictus** (Engler et al., 2013; Muñoz et al., 2012; Sardelis et al., 2002; Schaffner et al., 2011; Turell et al., 2005)	Europe is accustomed to dealing with several cases of the endemic diseases per year. Rapid increases in the number of cases have been reported, up to a 7-fold increase compared to usual (Burki, 2018; Haussig et al., 2018).
Yellow fever virus (YFV)	Originating in Africa and eventually spreading to the Americas and New World.	*Aedes aegypti, Aedes albopictus**(Bryant et al., 2007; Medlock et al., 2012; Monath, 1994)	Imported cases of YFV reported by several EU countries; these cases usually have high mortality rates (Colebunders, 2001; Kiehl, 1999).

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Pathogen	Distribution	Vectors	Recent Impacts EU
Zika virus (ZIKV)	Pacific, Asia, and recently the Americas (Evans et al., 2017; Petersen et al., 2016).	*Aedes aegypti* (Mayton et al., 2020)	Imported cases have been recorded, but local transmission is absent (Tappe et al., 2014; Zammarchi et al., 2015).
Japanese Encephalitis virus (JEV)	Found throughout Asia and the Pacific island regions.	*Culex species, Aedes albopictus*, Aedes japonicus** (Gubler, 2002; Medlock et al., 2012; Schaffner et al., 2011)	No reported cases of JEV in Europe from local transmission, though JEV is suspected to be circulating between birds in Southern Europe (Platonov et al., 2012).
Rift Valley fever (RVF)	Americas and Southern Europe (Kilpatrick and Randolph, 2012).	*Culex species* (Pepin et al., 2010)	Few or no cases reported in Europe, but increasing cases of RVF in Northern Africa prompting concern and subsequent risk analysis for officials (Chevalier et al., 2010).

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Pathogen	Distribution	Vectors	Recent Impacts EU
Sindbis fever (SINV)	Endemic to Northern Europe with occasional outbreaks in Australia, Asia (Lundström et al., 2021). Analysis suggests it was introduced twice from Africa into Europe (Ling et al., 2019).	*Culex species, Culiseta species, Aedes cinereus*, Aedes rossicus** (Bergqvist et al., 2015; Hesson et al., 2015; Lundström et al., 2019)	Clinical cases reported almost exclusively at Northern extremities of Europe (Hesson et al., 2015; Lundström et al., 2019).

Drivers of Mosquito Distributions and Interactions — Consequences for Infection Risk

Environmental drivers profoundly shape mosquito ecology and, consequently, the dynamics of MBDs. These drivers operate across multiple scales, influencing individual mosquito traits, population dynamics, and community compositions (Becker et al., 2010; Lippi et al., 2023a; Wilkerson et al., 2021). At the individual level, abiotic factors such as temperature, humidity, and precipitation directly modulate mosquito development, survival, and behaviour (Agyekum et al., 2021; Reinhold et al., 2018). Higher temperatures typically accelerate larval development and adult mosquito metabolism, potentially ramping up biting rates and shortening pathogen incubation periods (Mordecai et al., 2019). In contrast, extreme temperatures or drought can increase adult mortality rates, reduce breeding site availability, and shrink population sizes (Couret et al., 2014).

At intermediate scales, landscape features and land-use patterns significantly influence mosquito communities (Estrada-Peña et al., 2014; Gleiser and Zalazar, 2010; Roiz et al., 2015). Urban environments, replete with artificial container habitats, tend to favour species like *Aedes albopictus* and *Culex pipiens*, which are adapted to such environments (Kolimenakis et al., 2021; Townroe and Callaghan, 2014), while more natural landscapes often support a greater diversity of species (Ezenwa et al., 2007; LaDeau et al., 2015). Wetlands and areas with persistent standing water serve as ideal breeding grounds for many *Anopheles* and *Culex* species, which also support large populations of hosts for these species (Dale and Knight, 2008; Hawkes et al., 2020). Land-use changes, such as deforestation or urbanization, can reshuffle mosquito species compositions and potentially spark new vector-host interactions (Meyer Steiger et al., 2016).

Across both larger temporal and spatial scales, climate change is increasingly recognized as a major driver of shifts in mosquito distributions and community compositions (Medlock and Leach, 2015; Semenza and Suk, 2018). Warming temperatures are enabling some species to push their ranges into previously inhospitable areas, increasing potential competition with endemic species in traditional habitats (Bartlow et al., 2019; Reiter, 2001; Ryan et al., 2019). These climate-driven changes can trigger novel species interactions and alter disease transmission dynamics (Brass et al., 2024; Ewing et al., 2019). The northward march of *Aedes albopictus* in Europe, for instance, carries implications not only for its potential as a vector but also for its interactions with native mosquito species (Caminade et al., 2019).

A key concept in understanding disease transmission potential is vectorial capacity, which quantifies a mosquito population's ability to transmit pathogens. Vectorial capacity is defined by several parameters: the mosquito biting rate, vector competence (the ability of a mosquito to become infected and transmit a pathogen), mosquito survival rate, and the extrinsic incubation period of the pathogen (Garrett-Jones, 1964; Macdonald. G, 1957). These parameters are influenced by a myriad of factors, including life history traits, species niches, and overall vector competence, which in turn are shaped by complex interactions between species and population-level traits (Cator et al., 2020).

In Europe, for example, *Culex pipiens* s.l. and *Culex torrentium* are competent vectors for flaviviruses like West Nile Virus (WNV), Sindbis, and Usutu (Jansen et al., 2019). The *molestus* form of *Culex pipiens*, with its anthropophilic tendencies, serves as a significant bridge vector, feeding on both humans and birds. In contrast, *Culex pipiens* s.s. tends to prefer avian hosts, lowering the risk of human spillover due to this reduced biting risk, but still contributes to flavivirus persistence in wild bird populations (Bødker et al., 2014).

Mosquito community composition plays a pivotal role in shaping VBD transmission dynamics through a range of mechanisms (Martínez-de la Puente et al., 2018; Roche et al., 2013). The inclusion or exclusion of certain species within a community can either amplify or mitigate the spread of pathogens, with variations in vector and host composition influencing MBD circulation. Patterns in MBD prevalence have been linked to the richness and abundance of these communities, which can both heighten or lessen transmission risks depending on the specific ecological context (Ezenwa et al., 2007; Hermanns et al., 2023; Levine et al., 2017). Moreover, the structure of mosquito and host species communities is affected by shifts in abiotic factors, such as land-use changes, leading to complex interactions that shape overall MBD pressure and risk, thereby impacting zoonotic disease spread and spillover dynamics (Estrada-Peña et al., 2014; Roche et al., 2013).

The intricacy of these ecological relationships often fluctuates across temporal and spatial scales, with shifts in community structure having potentially profound impacts on disease dynamics. Native mosquito species, for example, may be instrumental in maintaining and amplifying disease cycles through overwintering and residual pathogen circulation, as seen in the case of flaviviruses (Folly et al., 2022; M'ghirbi et al., 2023; Sauer et al., 2023). Some mosquito species function as maintenance vectors, perpetuating pathogen transmission among reservoir hosts, while others act as bridge vectors, facilitating the spread of viruses from highly competent hosts to susceptible populations (Muñoz et al., 2012; Rizzoli et al., 2015).

A multitude of mosquito species are known, or suspected, to be involved in the transmission of various MBDs, with several implicated in the spread of more than one pathogen (Figure 1.1). Understanding the intricate interplay between biotic factors (like species interactions) and abiotic factors (such as climate and habitat features) that shape mosquito community composition is vital for assessing disease transmission risks. As we continue to face environmental changes, including climate shifts and intensified land use, anticipating and responding to alterations in mosquito populations and the associated disease threats is increasingly crucial for safeguarding public health and managing ecosystems.

The significance of community composition in understanding VBD ecology is a key gap in our understanding of how wider factors influence MBD risk and transmission. The interactions within and between vector and host species, modulated by environmental influences, fundamentally determine the potential for disease spread and spillover. Thus, a holistic approach that takes into account the dynamics of community composition is essential for the effective prevention and control of disease.

1.1.3 Modelling Mosquito Distributions

Building upon the understanding that ecological and biotic drivers shape mosquito distributions and indeed their vectorial capacity, it is clear that effective management of MBD requires a comprehensive understanding of mosquito distributions. To address the complexities of MBD transmission and risk, researchers and epidemiologists often turn to species distribution models (SDMs) to predict the occurrence of key mosquito vector species. By correlating mosquito occurrence data with environmental variables, such as climate and land use factors, SDMs can generate habitat suitability maps that identify areas at risk for vector presence and subsequent MBD transmission (ECDC, 2021).

Current approaches for managing mosquito-borne diseases in Europe involve extensive mosquito and arbovirus surveillance programmes, which play a critical role in monitoring

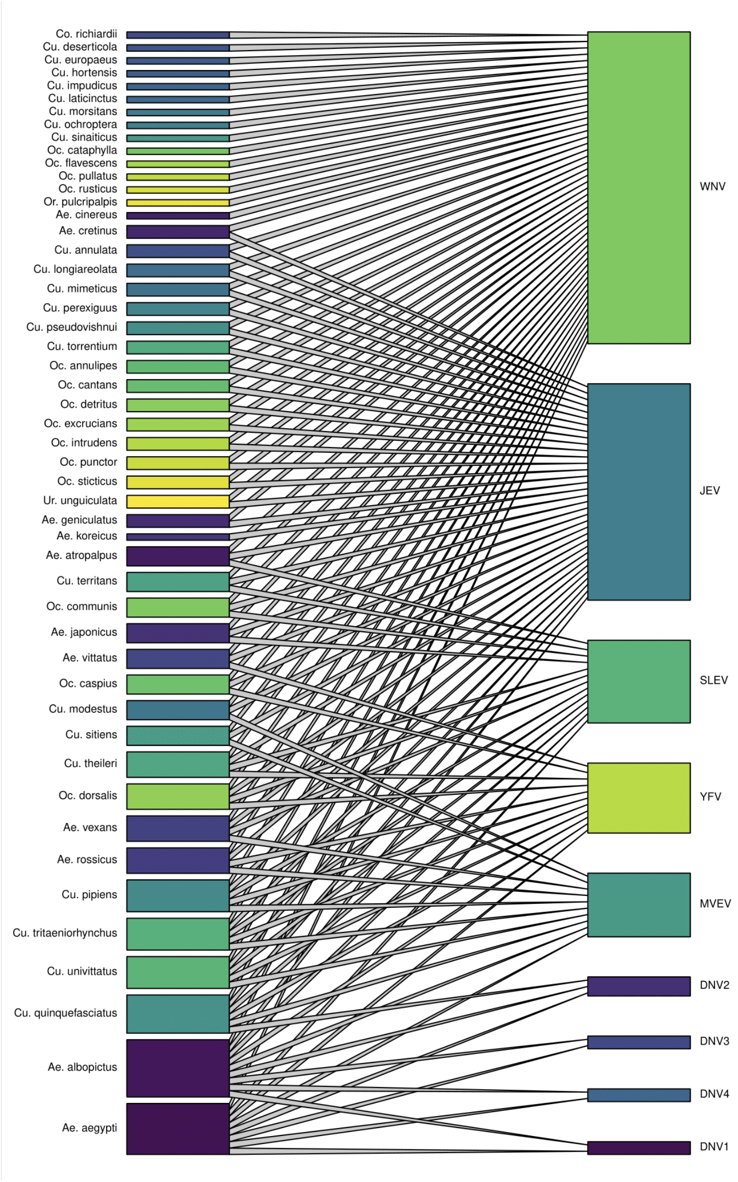

Fig. 1.1 Potential associations between mosquito species and viruses in the western Palearctic region are illustrated, based on data from the EID2 database. The connections indicate that mosquito species may be involved in or linked to the transmission of the associated viruses: West Nile virus (WNV), Japanese encephalitis virus (JEV), St. Louis encephalitis virus (SLEV), yellow fever virus (YFV), Murray Valley encephalitis virus (MVEV), and dengue virus serotypes 1-4 (DENV 1-4). These relationships suggest possible roles for the mosquito species in virus transmission. Details on the methodology used to derive these associations can be found in Wardeh et al. (2015)

vector populations and identifying areas at risk for outbreaks (Petrić et al., 2014; Schaffner et al., 2013a; Zeller et al., 2013). Coupling these surveillance efforts with species distribution modelling (SDM) techniques allows researchers to generate distribution maps for key mosquito vectors, such as *Aedes albopictus*, to inform targeted vector control strategies (ECDC, 2012).

Early Application of SDMs

Hutchinson (1957) provided the initial theoretical framework of SDMs by introducing the ecological niche concept, suggesting that a multidimensional space of environmental conditions was required for adequate species persistence and occurrence in a geographical area (Pulliam, 2000). This idea was crucial for SDMs as it provided a theoretical basis for linking species occurrences to environmental conditions. It laid the groundwork for early interpretations of modelling the relationship between occurrence and environments, and using these models to extrapolate known relationships to larger spatial scales. Hay et al. (1998) presented one of the first SDM applications to mosquito modelling, using remote sensing data to map the distributions of the malaria vector *Anopheles gambiae*. This work showed that rainfall and climate were heavily correlated with *An. gambiae* occurrence and laid the groundwork for the use of SDMs in potential malaria risk mapping across Africa, guiding significant subsequent efforts to better understand the distribution and drivers of MBD burden.

As computational power and data availability increased, a shift occurred in species distribution modelling (SDM) methods. The field moved from simple statistical correlations and generalized linear models towards more advanced techniques capable of handling presence-only data, typically the most abundant and accessible type for mosquito studies. MaxEnt emerged as a particularly useful tool, as highlighted in studies like those of Peterson et al. (2005), who applied the model to project the potential distribution of *Aedes albopictus* in

North America, a vector responsible for dengue and chikungunya transmission. The model's ability to handle complex species-environment relationships contributed to its popularity in vector-borne disease research.

Building on these methodological advancements, researchers began applying SDMs to a wider range of vector-borne disease problems. For instance, Rogers and Randolph (2000) demonstrated how the spread of *Aedes aegypti* and potential suitability maps could help predict vector presence and disease risk. Other studies applied predictions of future climate data to show how changes in climate might affect the future distribution and burden of malaria under shifting environmental baselines. Martens et al. (1999) further advanced the field by combining global climate models with malaria distribution projections, marking early efforts to incorporate climate change scenarios into vector-borne disease risk assessments.

Broad Application of SDM Approaches

The 2010s saw further refinement of SDM techniques, particularly with the integration of machine learning approaches. Studies began using techniques such as Boosted Regression Trees (BRTs) to handle non-linear relationships between environmental variables and mosquito distributions. Messina et al. (2019) applied BRTs to update global distribution maps for *Aedes aegypti* and *Aedes albopictus*, combining occurrence records with environmental and socioeconomic data to identify dengue risk areas. Bhatt et al. (2013) employed a combination of climate models and spatial epidemiological data to estimate the global dengue burden, illustrating the potential of SDMs to quantify not only vector distributions but also disease impacts.

As the decade progressed, researchers developed more dynamic and comprehensive modelling techniques (Lippi et al., 2023a). Recent advancements include the use of ensemble models to improve predictive performance and uncertainty management. Kraemer et al. (2019b) employed an ensemble of SDMs to project future *Aedes* distributions under various climate change scenarios, showcasing SDMs' predictive power for anticipating disease risks. In the same year, Ryan et al. (2019) demonstrated the integration of ensemble approaches with citizen science data for real-time mosquito distribution modelling, addressing challenges posed by climate change and human-induced landscape alterations. These studies highlight the ongoing evolution of SDM techniques in response to the complex and dynamic nature of vector-borne disease systems.

1.1.4 Challenges in Capturing the Complexity in Mosquito Distribution Models

Despite the continual advancement in SDMs, the complexity of mosquito ecology in distribution models remains a significant challenge. A major issue is the paucity and bias in occurrence data for many mosquito species; surveys are often spatially and temporally limited, with efforts concentrated in areas of higher human population density or known disease outbreaks (Kramer-Schadt et al., 2013; Phillips et al., 2009). This can lead to an over-representation of common species or habitats, while others remain under-sampled or undetected (Hughes et al., 2021). These data gaps hinder the development of reliable distribution models, particularly for rare or cryptic species (Jeliazkov et al., 2022; Radomski et al., 2022).

Additionally, many mosquito species, especially those considered non-competent or inefficient vectors of diseases, suffer from scarce data at scales relevant for SDM application (Khatchikian et al., 2011; Rhodes et al., 2023). This scarcity typically prevents us from understanding how communities contribute to disease dynamics, particularly when considering the role of native species (Ferraguti et al., 2021). As such, we may be predisposed to overlook the potentially important ecological roles of less-studied mosquito species and their impact on overall community structure and disease risk.

Moreover, mosquito occurrence data frequently lacks information on sampling effort and detection probability, and is collected using diverse methods with different attractiveness between species and habitats, introducing bias into model outcomes (Giordano et al., 2020). Mosquito populations also exhibit significant spatial and temporal variability, influenced by factors such as climate, breeding site availability, and pesticide control measures (Claflin and Webb, 2017a; Luz et al., 2009; Wilke et al., 2017), and without accounting for this variability, models may inaccurately reflect species distributions.

Multi-Scale Factors Influencing Mosquito Distributions

Another challenge in modelling mosquito distributions is the interplay of environmental factors across different spatial and temporal scales. While broad-scale climatic variables such as temperature and precipitation are influential drivers of mosquito distributions, local-scale factors such as land use, vegetation cover, and host availability can also have a significant influence on overall species prevalence and abundance (Ferraguti et al., 2016; Reiskind et al., 2017; Steiger et al., 2012). Integrating representations of these multi-scale processes into distribution models requires careful selection of predictor variables and modelling approaches that can capture the hierarchical structure of ecological data and how mosquitoes interact with their environment across multiple life stages (Hartemink et al., 2015).

Furthermore, biotic interactions such as competition, predation, and host-vector relationships play a crucial role in shaping mosquito communities (Alto et al., 2005; Juliano, 2009; Saha et al., 2012; Smith et al., 2004). However, incorporating these interactions into distribution models remains challenging, as they often require detailed knowledge of species' ecological relationships and can vary across spatial and temporal scales (Wisz et al., 2013). Traditional SDMs, which focus on individual species' responses to environmental factors, may overlook the importance of these biotic interactions in determining the presence and abundance of mosquito species (Dormann et al., 2018).

The rapid evolution and adaptability of mosquito populations to changing environmental conditions and control measures can also complicate efforts to model their distributions. Mosquitoes have demonstrated the ability to adapt to new habitats, develop insecticide resistance, and shift their biting behaviours in response to interventions (Carrasco et al., 2019; Medley et al., 2019). Traits can provide insights into the mechanisms underlying species co-occurrence and the distribution of mosquito communities.

For example, mosquito traits related to host preferences and biting behaviour are strongly linked to historical phylogenetic relationships between species, and in turn, these traits can strongly influence the role of mosquito species in the transmission of pathogens such as malaria, dengue, or Zika virus (Peach and Gries, 2020; Soghigian et al., 2017). Incorporating these traits into distribution models will require an understanding of the factors driving adaptation and the ability to predict how populations will respond to future environmental changes (Caminade et al., 2019, 2012).

The Current State of Modelling Mosquito Communities

Mosquito ecology and community dynamics are largely understudied at smaller, local, and laboratory scales, especially for species considered not to be primary vectors of MBD. This is despite the fact that interspecific competition between mosquito species is a key driver in both vector competence and the abundance of important mosquito vectors (Alto, 2011; Amatulli et al., 2018; Atwood et al., 2014; Carver et al., 2009). Furthermore, interactions between predators and mosquitoes influence life history parameters such as oviposition site selection, overall fecundity, and larval behaviour (Alto et al., 2012; Bond et al., 2005; Griswold and Lounibos, 2006; Saha et al., 2012). However, a common theme in the current understanding of wider mosquito interactions, particularly biotic ones, is the local nature of these studies and the focus on relatively few mosquito species rather than communities.

When considering intermediate scales, several authors have demonstrated how habitat fragmentation, microclimate variation, vegetation, and land usage can affect overall mosquito community composition (Cardo et al., 2013; Chaves et al., 2011; Ferraguti et al., 2021; Flores Ruiz et al., 2022a). These studies are crucial for understanding the wider impacts that urbanization typically has on mosquito communities, and in some cases, have demonstrated or hypothesized that these changes could result in differential risks of disease prevalence (Brugueras et al., 2020; Roche et al., 2013). These intermediate studies begin to bridge the gap between interactions at local and mesocosm scales and those measurable on the human scale, where, for instance, the urbanization of current land could lead to an increase in potential vectors of MBDs (Burkett-Cadena and Vittor, 2018; Ortiz et al., 2022; Perrin et al., 2023).

Yet, while we have some limited local, and in some cases regional, understanding of the drivers of mosquito communities, scaling up our models to predict community distributions over larger areas requires a more integrated approach that incorporates both local biotic interactions and large-scale abiotic factors. While small-scale models excel at capturing direct interactions like competition and predation, these relationships do not always translate consistently when expanded to larger areas (Araújo and Rozenfeld, 2014; Belmaker et al., 2015). As such, holistic, large-scale mosquito community models remain scarce, and integrating fine-scale ecological interactions with broader landscape processes within a single framework presents significant challenges.

Despite this, large-scale community methods have been successfully applied to other well-studied species groups. For instance, comprehensive community models have been developed for vertebrates (Roberts et al., 2022; Whalen et al., 2023), plants (Briscoe Runquist et al., 2021; Mod et al., 2020), and arthropods (Facon et al., 2021; Planillo et al., 2021). These studies have demonstrated the potential for integrating multiple sources of ecological data and drivers of distributional processes in community ecology across larger spatial extents.

To advance mosquito community modelling, we must utilize community methods to integrate these multiple types of data into a holistic representation of mosquito community responses to various factors and processes. This approach should account for both local interactions (such as species competition and habitat selection) and regional factors (like climate and human land use) within a unified framework. Such an approach would enable more accurate predictions of mosquito species distributions and enhance our understanding of how environmental changes impact disease transmission dynamics across larger areas. While challenging, this integration is essential for comprehensively understanding mosquito ecology and assessing and predicting disease risk at meaningful scales.

1.1.5 Applying Advances in Community Modelling to Mosquitoes

Recent advancements in computational power and statistical methods have allowed for more comprehensive approaches to understanding distributions of communities (Golding and Harris, 2015; Hui, 2016; Niku et al., 2019; Pichler and Hartig, 2021; Pollock et al., 2014; Rahman et al., 2024). These developments aim to address the confounding factors driving mosquito distributions by integrating multiple data types and modelling techniques (Figure 1.2), offering a more ecologically realistic and holistic understanding of these important disease vectors (Wilkinson et al., 2019, 2021).

At the forefront of these advancements are Joint Species Distribution Models (JSDMs), which have emerged as a powerful tool for simultaneously modelling multiple species (Wilkinson et al., 2021). Unlike traditional single-species Species Distribution Models (SDMs), JSDMs aim to capture community-level patterns and provide insights into the factors shaping community patterns and structure, including the potential to infer interactions between species and examine shared species responses to environmental factors (Ovaskainen et al., 2016a; Pollock et al., 2014).

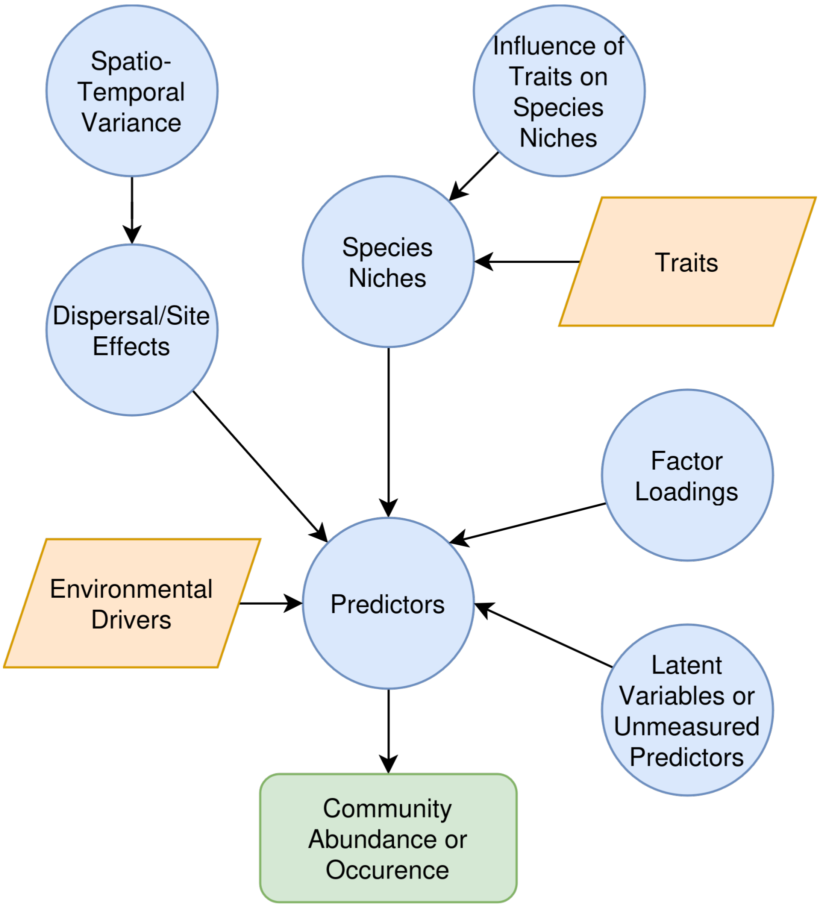

Fig. 1.2 Simplified Directed Acyclic Graph (DAG) of a Joint Species Distribution Model (JSDM) using a latent variable approach. This diagram illustrates the statistical framework used in JSDMs like HMSC and jSDM (Tikhonov et al., 2020b; Vieilledent and Clément, 2023). Orange boxes represent input data, blue circles indicate parameters to be estimated, and arrows depict functional relationships. The model incorporates latent variables (unobserved factors capturing species interactions or unmeasured environmental influences) to account for spatio-temporal variance (variation across locations and time) and dispersal site predictors (e.g., distance to water, elevation). Factor loadings link the predictors to latent variables, indicating their influence.

Integrating Biotic Interactions into Distribution Models

The key distinction between traditional SDMs and JSDMs lies in the latter's ability to model species jointly and capture inter-species covariation across sample sites. While SDMs consider the relationship between species occurrences and environmental variables as independent for each species, JSDMs model these relationships simultaneously for multiple species. This approach means that JSDMs can potentially infer biotic interactions, such as competition or facilitation, through the covariation of species responses to the environment or to one another. This covariation between species is referred to as species residual correlations, representing the nuanced effect that unaccounted-for environmental variables can manifest as covariance between species. As such, more moderate language is needed to describe these relationships with caution when interpreting (Blanchet et al., 2020; Poggiato et al., 2021; Wilkinson et al., 2021; Zurell et al., 2018).

The development of JSDMs was driven by the recognition that biotic interactions play an important role in influencing community abundance and occurrence patterns (Wisz et al., 2013). Early approaches to modelling communities relied on Stacked Species Distribution Models (S-SDMs), where individual species models were combined to predict community composition. However, this "predict first, assemble later" approach often led to oversimplified predictions of species interactions because of the lack of ability to measure how species may show similar responses to environmental variables (Calabrese et al., 2014).

In contrast, JSDMs represent a shift towards an "assemble and predict together" approach, marking a fundamental change in how we model and understand ecological communities (Ovaskainen and Abrego, 2020; Warton et al., 2015). This method allows for a more nuanced understanding of communities, taking into account the interplay between species and their environment. However, it is critical to understand that JSDMs are not thought to be inherently better in raw predictive performance compared to S-SDMs (Zurell et al., 2018), and interpretation of the results from JSDMs requires significant understanding of species drivers and expected associations to draw out biological interpretations (Poggiato et al., 2021; Wilkinson et al., 2021).

However, this “assemble and predict together” paradigm is particularly relevant for mosquito ecology, as it allows us to consider the entire community as an interconnected system rather than a collection of independent species. By representing the entire community structure and using this information to make predictions, there is potential to capture ecological processes such as competitive exclusion and facilitation, thereby helping to understand the different environmental drivers that shape overall community composition. This wider view and utilization of ecological data is crucial for understanding assembly processes and interactions with both biotic and abiotic factors that shape overall mosquito community composition.

Incorporating Traits and Evolutionary Relationships

Additionally, extensions of early versions of JSDM frameworks have been developed to integrate more types of community data typically collected by ecologists, such as traits and phylogenetic relatedness (Ovaskainen et al., 2017b). By incorporating traits such as body size, feeding behaviour, and habitat preferences, there is potential to identify the functional characteristics that determine the spatial distribution and co-occurrence patterns of mosquito species, and these traits can in turn provide information on how species might respond to unmeasured environmental drivers (Niku et al., 2019; Ovaskainen et al., 2016a; Warton et al., 2015). Similarly, phylogenetic information can serve as a proxy for unmeasured traits and shared evolutionary histories, which can influence the responses of mosquito species to environmental factors and these relationships might be leveraged to improve predictions for rare or undersampled mosquito species (Ovaskainen et al., 2017b; Tikhonov et al., 2017; Zhang et al., 2020).

1.1.6 Current Limitations of Applying Community Methods to Mosquito Distribution Modelling

One key challenge is the breadth of data required to generate community-level predictions. Such data are often lacking, particularly for rare or poorly sampled species, and this issue is exacerbated in mosquito sampling data, which often targets medically relevant or invasive species rather than whole communities of mosquitoes. The ability of JSDMs to use shared relationships of phylogeny and traits to help share information across poorly resolved species is an exciting prospect for alleviating some of these challenges, but first requires consideration of how we can best assemble mosquito communities from sparse sampling data across large spatial scales (Poggiato et al., 2021).

Another challenge is dealing with the computational complexity of these models. JSDMs traditionally use Bayesian methods because of their flexibility in model specification, but this flexibility comes at the computational cost of sampling complex posterior distributions (Pichler and Hartig, 2021). This complexity arises from the need for JSDMs to have multiple thousands of parameters, each accounting for different interacting variables influencing the overall distribution of communities of multiple species (Ovaskainen and Abrego, 2020; Wilkinson et al., 2019).

Latent variable models have been utilized in some cases to try to limit the number of parameters needed to fully model a community across all aspects that limit their distribution (Ovaskainen et al., 2016b). Researchers have also explored different approaches to traditional Markov Chain Monte Carlo (MCMC) simulation, including more advanced sampling algorithms to better estimate complex posterior distributions, such as Stan, which uses Hamiltonian Monte Carlo sampling for high-efficiency exploration of these spaces (Carpenter et al., 2017; Hoffman et al., 2014; Vieilledent and Clément, 2023). Additionally, analytical methods for solving and predicting these distributions have been developed, including techniques such as variational approximation, which provides a fast alternative to MCMC sampling for estimating parameters from complex posterior distributions (Hui et al., 2017; Niku et al., 2019).

However, despite these advances, frameworks that can fully explore how environment, traits, biotic factors, and relatedness impact mosquito community composition are only just emerging (Pichler and Hartig, 2021). Even among these emerging approaches, relatively few operate at the spatial scales required for estimating overall community diversity across regions (Pichler et al., 2020; Rahman et al., 2024; Tikhonov et al., 2020a). Leveraging these new methods is key to understanding the drivers of mosquito communities across relevant epidemiological scales, from local breeding sites to regional distributions. Understanding how the importance of these drivers varies across different scales is crucial in developing a comprehensive picture of mosquito ecology. For instance, the factors influencing larval and adult mosquito populations are likely to differ, as these life stages experience environmental resources differently and disperse over different scales in the landscape (Hartemink et al., 2015). Consequently, certain traits might be highly relevant at one scale but less so at another (Gianuca et al., 2017; Krasnov et al., 2011; Suárez-Castro et al., 2018). This scale-dependent variation in the importance of different factors underscores the complexity of mosquito ecology and highlights the need for multi-scale modelling approaches that can capture these nuanced relationships (Fournier et al., 2017; Laporta and Sallum, 2014).

A multi-scale, multi-data approach could provide insights into how both biotic and abiotic factors influence mosquito assembly processes, and ultimately the perceived risk of MBD (Zobel, 1997). As these methods are refined and continue to incorporate more advanced modelling approaches and broader ecological data sources, we must also remember the human dimension of mosquito ecology. The distribution and abundance of mosquito species have profound impacts on human health and well-being, particularly in regions where mosquito-borne diseases are endemic. By improving our ability to predict and understand

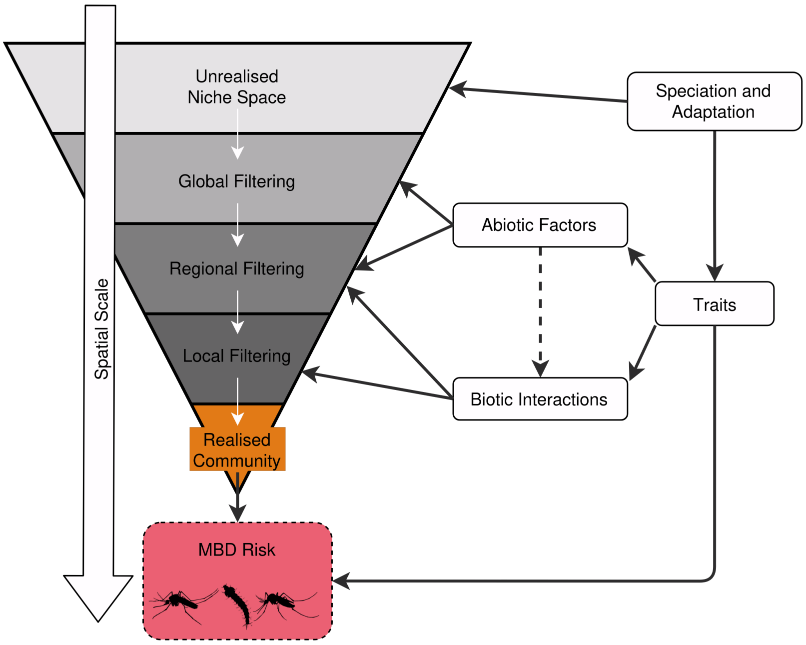

Fig. 1.3 A conceptual model adapted from Zobel (1997) and Ovaskainen et al. (2017b), illustrating the multi-scale filtering of mosquito species from unrealised niche space through global, regional, and local levels to form the realised community. Abiotic factors, biotic interactions, and species traits shape community composition across these scales, with feedbacks from speciation and adaptation. The realised community directly influences mosquito-borne disease (MBD) risk along with traits influencing vectorial capacity, highlighting the importance of integrating multiscale environmental and ecological factors to understand vector dynamics and disease transmission.

mosquito distributions, we can develop more effective and targeted strategies for vector control and disease prevention.

1.2 Overview of the Thesis

This thesis addresses key challenges in understanding mosquito ecology and distributions, focusing on how biotic and abiotic factors impact mosquito community composition across multiple spatial scales. By leveraging advanced Joint Species Distribution Model (JSDM) frameworks and high-performance computing, this research utilizes diverse ecological datasets to provide a multi-scale and multi-data approach to understanding mosquito assemblages across Europe.

The key contributions of this thesis include:

1. Demonstrating the impacts of wetland management on local mosquito populations and their interactions with potential mosquito predators at local scales, highlighting the complex interactions between conservation practices and vector dynamics.
2. Applying JSDMs to large-scale, sparse mosquito occurrence data to understand the impacts of biotic interactions, abiotic drivers, and spatial factors on mosquito communities at continental scales, and across fine to coarse study grains.
3. Integrating species traits and evolutionary relationships into mosquito community models to investigate how mosquitoes interact with environmental drivers and how community composition both explains and is influenced by biological traits and inter-species relationships.
4. Applying high-performance computational methodologies for working with heterogeneous and sparse data to model mosquito distributions at multiple spatial scales, investigating mosquito community interactions at scales not previously explored, and addressing common challenges in vector surveillance.
5. Providing a framework for assessing potential changes in mosquito communities and associated disease risks in response to both environmental and biotic interactions, demonstrating how predictions of species distributions can be improved when leveraging this information.

This research progresses from local-scale studies to continental analyses, culminating in the development of integrated, trait-based community models. The insights and methodologies developed here have implications for vector control strategies, wetland management policies, and public health interventions in the face of ongoing global environmental change.

The following chapters present this research in detail:

Chapter 2: Vegetation Structure Drives Mosquito Community Composition in the UK's Largest Managed Lowland Wetland. This chapter establishes the foundation of the thesis by examining the local-scale impacts of wetland management on mosquito communities, using JSDMs as a basis for modelling biotic and abiotic interactions simultaneously. It focuses on how different management tiers in the Somerset Levels and Moors affect mosquito breeding habitats and community composition. The study reveals that biodiversity-focused management creates conditions favouring certain mosquito species, including shifts from West Nile Virus vectors to other nuisance biting species. This chapter highlights the complex interactions between conservation practices, vegetation structure, and mosquito ecology, setting the stage for broader investigations.

Chapter 3: Environmental and Biotic Drivers of Mosquito Communities Across Europe: A Multi-Scale Joint Species Distribution Modelling Approach. Building on the local insights from Chapter 2, this chapter expands the scope to a continental scale. It introduces the application of JSDMs to predict mosquito communities across Europe using data from the VectorNet consortium of national agencies involved in mosquito surveillance. The study compares JSDMs with Multi-Species Distribution Models (MSDMs) across multiple spatial resolutions, assessing the relative importance of environmental, spatial, and biotic factors in shaping mosquito distributions. This chapter demonstrates the value of community-level modelling approaches in capturing complex ecological interactions at larger scales and with sparse data.

Chapter 4: Integrating Traits and Community Data in Joint Species Distribution Models: Insights into Mosquito Ecology This chapter further refines the modelling approach introduced in Chapter 3 by incorporating species traits, phylogenetic information, and environmental data into the JSDMs. It explores how these additional data types can improve our understanding of mosquito community assembly and distribution. The study assesses the potential of trait-based approaches to predict changes in mosquito communities under various environmental scenarios, and examines how conditional predictions from JSDMs can be used to simulate the impact of invasive species on native communities. Together, these chapters progress from local to continental scales, and from environmental drivers to a more integrated ecological perspective.

Chapter 5: Here I discuss the value of multi-scale, multi-data approaches in understanding mosquito community dynamics and their potential implications for future sampling strategies, changes in disease risk assessment, and vector control. The thesis provides broad recommendations for vector ecologists on the application of community modelling techniques, the integration of diverse data types, and the importance of considering community-level interactions in mosquito research. By showcasing these approaches, this work lays a foundation for a more comprehensive and nuanced understanding of vector ecology, which could inform both public health policies and conservation strategies in the face of changing environments and species invasions.

Chapter 2

Vegetation structure drives mosquito community composition in UK's largest managed lowland wetland

This chapter has been published as an article in Parasites & Vectors:

Smith, D.C., Schäfer, S.M., Golding, N. et al. Vegetation structure drives mosquito community composition in UK's largest managed lowland wetland. Parasites & Vectors, 17, 201 (2024). https://doi.org/10.1186/s13071-024-06280-y

2.1 Abstract

Purpose: The rising burden of mosquito-borne diseases in Europe extends beyond urban areas, encompassing rural and semi-urban regions near managed and natural wetlands, evidenced by recent outbreaks of Usutu and West Nile viruses. While wetland management policies focus on biodiversity and ecosystem services, few studies explore the impact on mosquito vectors.

Methods: Our research addresses this gap, examining juvenile mosquito and aquatic predator communities in 67 ditch sites within a south England coastal marsh, subjected to different wetland management tiers. Using joint distribution models, we analyse how mosquito communities respond to abiotic and biotic factors influenced by wetland management.

Results: Of the 12 mosquito species identified, *Culiseta annulata* (Usutu virus vector) and *Culex pipiens* (Usutu and West Nile virus vector) constitute 47% of 6825 larval mosquitoes. Abundant predators include Coleoptera (water beetles) adults, Corixidae (water boatmen), and Zygoptera (Damselfly) larvae. Models reveal that "Tier 3" management sites (higher winter water levels, lower agricultural intensity) associated with shade and less floating vegetation are preferred by specific mosquito species. All mosquito species, except *Anopheles maculipennis* s.l., are negatively impacted by potential predators. *Culiseta annulata* shows positive associations with shaded and turbid water, contrary to preferences of Corixidae predators.

Conclusion: Tier 3 areas managed for biodiversity, characterized by higher seasonal water levels and reduced livestock grazing intensity, provide favourable habitats for key mosquito species that are known vectors of arboviruses like Usutu and West Nile. Our findings emphasize the impact of biodiversity-focused wetland management, altering mosquito breeding site vegetation to enhance vector suitability. Further exploration of these trade-offs is crucial for comprehending the broader implications of wetland management.

2.2 Background

The burden and risk of mosquito-borne diseases (MBDs) is increasing across Europe, not only in urban areas, driven by invasive *Aedes* mosquitoes (e.g., Dengue, Chikungunya, Zika, Medlock et al. (2012)), but also by native species in more rural or peri-urban areas, at the interfaces between human habitation, agriculture, and natural ecosystems (e.g., West Nile virus, Usutu, Sindbis, Buckley et al. (2003); Cheng et al. (2018)). These changes in risk are attributed to multiple interacting global drivers including climate change (Brugueras et al., 2020), increased trade and travel (Benelli et al., 2020; Kilpatrick, 2011), and land use change, including agricultural intensification and urbanization (Gottdenker et al., 2014; Meyer Steiger et al., 2016; Townroe and Callaghan, 2014). At local scales, human activities in areas with long-standing mosquito presence can be a driver of MBD risk, by increasing potential contact rates between people and competent vectors (Lambin et al., 2010). Man-made habitat modification that leads to shifts in abundance and species composition of mosquito populations can also alter the interaction dynamics between mosquitoes, humans, and animal reservoir hosts, increasing the relative risk of zoonotic disease spillover (Meyer Steiger et al., 2016).

In parallel, there is an increased policy focus on managing natural ecosystems such as wetlands to maximize the provision of ecosystem services and enhance biodiversity (Acreman et al., 2011; DEFRA, 2023a; Gibbs, 2000). Within the UK, for example, government policies and payment schemes to landowners encourage the creation, restoration, and management of existing wetlands to increase biodiversity and foster local and regional flood resilience programs (DEFRA, 2018, 2023a,b). Water is a requirement for mosquito breeding and so there is an urgent need to understand how policy-driven changes in wetlands impact mosquito communities, as well as their interactions with animal and human hosts, and how this trades off with disease transmission risk (Dale and Knight, 2008; Hanford et al., 2020; Martinou et al., 2020; Medlock and Vaux, 2015b).

There is growing evidence globally that wetland management for biodiversity can affect mosquito communities (Rey et al., 2012), not only by changing aquatic breeding site characteristics and vegetation but also via impacts on mosquito predators (Griffin and Knight, 2012; Saha et al., 2012), and that this can lead to public health co-benefits or dis-benefits depending on local context. Some studies have found that mosquito density increases after wetland construction and management (Jiannino and Walton, 2004; Schäfer et al., 2004), but if implemented correctly, wetland management schemes that create diverse and permanent wetland habitats can decrease mosquito populations by simultaneously decreasing habitats suitable for larval mosquitoes while increasing those suitable for known mosquito predators (James-Pirri et al., 2009; Rochlin et al., 2012b).

Altering wetland water levels during the mosquito breeding seasons, including complete drying of water bodies can lead to desiccation of mosquito larvae and prove an adequate control method, but these strategies can negatively impact other aquatic flora and fauna of wetlands (Russell, 1999). In Australia, draining and re-filling of urban wetlands to manage an invasive fish species, led to increased abundance of mosquito species compared to undrained urban wetlands (Hanford et al., 2020). In some contexts, integrated management for biodiversity and reduced public health risks and nuisance biting from mosquitoes has been possible. For example, integrated Marsh Management Schemes employed in salt marshes in the USA, combine tidal flow restoration and vegetation management favouring fish and wildlife biodiversity, with management of open water surfaces (Open Marsh Water Management) to enhance habitats for larvivorous fish predators (Rochlin et al., 2012a).

In Europe and the UK, there is a dearth of data regarding the influence of wetland management on mosquito communities, encompassing both nuisance biters and potential disease vectors (Hawkes et al., 2020). There is some evidence that wetland creation can promote increased populations of various mosquito species, as demonstrated by studies on *Aedes vexans* in river flood plains (Vaux et al., 2021), and on *Aedes detritus* in newly created saltmarshes in England (Clarkson and Enevoldson, 2020). However, existing research is limited in its examination of the potential trade-offs between conservation-oriented management practices aimed at preserving biodiversity and the subsequent implications for public, animal, and wildlife health (Martinou et al., 2020).

This knowledge gap is increasingly pressing for Europe, particularly considering the recent outbreaks of West Nile Virus (WNV). Between 2010 and 2018, there were over 3,500 reported human cases of West Nile fever in Europe, with infections distributed from Turkey to Spain and as far north as Germany, resulting in 379 deaths (Young et al., 2021). Furthermore, the heightened circulation of the Usutu virus across central western and Central Europe, associated with mosquitoes in and around wetlands, adds urgency to the need for a better understanding of the impacts of wetland management on mosquito communities (ECDC, 2021; Ferraguti et al., 2016).

Specifically, recent detection of Usutu virus in Southern England, impacting blackbird populations (Folly et al., 2022), combined with the proximity to ongoing West Nile virus transmission in Germany and the Netherlands (Bakonyi and Haussig, 2020), underscores an increased risk of further mosquito-borne pathogen incursions in the region. This risk is heightened by the high prevalence and overlap of the primary vector, *Culex pipiens* s.l., across Europe (Medlock et al., 2018). Studies conducted in UK fenlands have explored the links between wetland management and mosquito abundance, and revealed that emergent vegetation and sediment build-up can lead to warmer waters and increased densities of Culicine mosquito species, while drainage of water levels can decrease Culicine abundance but create a more suitable habitat for *Anopheles maculipennis* s.l., a species complex known for its nuisance biting behaviour (Medlock and Vaux, 2015a).

Combining empirical mosquito surveys with statistical spatial modelling of abiotic and biotic drivers of mosquito community composition across wetland management gradients may lead to a more detailed understanding of impacts of wetland management on candidate vector species and biting risks. Utilizing such an approach in marshes in the east of England (North Kent Marshes), Golding et al. (2015) found that ditch shrimp and fish predators reduced the prevalence of mosquito larvae, namely of *An. maculipennis* sensu lato (a species complex thought to include minor and historical malaria vectors) and *Culex modestus* (a bridge vector for WNV) and suggested that habitat management for these species could both increase biodiversity and reduce mosquito numbers.

Species distribution models have been applied at national, sub-national and local scales to study the impacts of wetland changes on individual mosquito vector species, but these ignore important species community interactions. However, community modelling approaches such as joint species distribution models (Golding and Harris, 2015; Ovaskainen et al., 2017b; Pichler and Hartig, 2021) may offer great advantages. These models can help identify shared responses to environmental conditions (Poggiato et al., 2021) and account for potential biotic interactions such as competition and predation. Such interactions can strongly influence mosquito population dynamics and persistence (Beketov and Liess, 2007; Braks et al., 2004; Saha et al., 2012) and will likely modulate individual vector species responses to wetland changes (Rey et al., 2012). This study applies community joint modelling methods to sampled larval and adult mosquito population data in a large UK wetland that has been subject to management changes under agri-environmental schemes, where water levels, livestock grazing pressure and mechanical interventions are differentially managed, with the following objectives:

1. To understand the role of abiotic (physico-chemical water parameters, ditch morphology, vegetation structure) and biotic factors (predator communities) in determining larval mosquito community composition.

2. To determine whether wetland management changes under recent agri-environmental schemes are likely to have increased the larval abundance and diversity of key UK mosquito vectors of important mosquito-borne viruses.

2.3 Methods

2.3.1 Study site

The Somerset Levels and Moors (SLM), the largest remaining lowland wet grassland in the UK, spanning 650 km^2 in the southwest of England, holds unique ecological significance.

Designated under the European Commission Habitats Directive and the UK Biodiversity Action Plan, it serves as an exemplary coastal grazing marsh habitat (JNCC, 1994). The SLM's structure consists of interconnected water-filled ditches, locally known as rhynes. This coastal habitat, lying largely below or at sea level forms a large catchment area for Somerset, and this matrix of rhynes drain land that would otherwise be too boggy for farming. The area plays a crucial role in providing essential ecosystem services to local communities and tourists, boasting high biodiversity with a notable presence of wading and migratory birds year-round (Acreman et al., 2011).

The SLM's history is marked by periodic winter inundation over the past 10,000 years, contributing to the development of fertile peat soils and rich biodiversity. However, human activities, such as drainage and ditching for seasonal grazing pastures, began as early as the 9th century and intensified in the mid-20th century, reaching a peak with peat extraction and agricultural practices. Recognizing its environmental sensitivity, the SLM received designation as an Environmentally Sensitive Area (ESA) in 1987. Subsequently, agri-environmental schemes were implemented to support farmers in adopting management practices beneficial to biodiversity and flood management (Morris et al., 2008). This led to the transformation of arable land back into wet grassland.

Operating within a tiered system, these agri-environment schemes prescribe different measures (Table 2.1). The entry-level option, Tier 1, aims to preserve the plant and invertebrate communities in permanent grassland, which are sensitive to disturbance caused by ploughing and arable cropping. In contrast, Tier 3, the most demanding management option, focuses on enhancing plant species diversity and habitat for breeding waders and overwintering wildfowl by promoting wet winter and spring conditions in permanent grassland. This tier encourages lower grazing pressure, minimizes mechanical intervention in fields and surrounding ditches, and maintains higher minimum water levels, particularly during the winter months (Tier 3 versus Tier 1).

We anticipate that these tiered prescriptions will influence various ecological factors, such as shading, vegetation structure, ditch morphology, and the presence of macro-invertebrate predators. Consequently, these conditions are expected to have a significant impact on mosquito species composition and abundance. Our study aims to sample and investigate the key drivers of mosquito community composition in Tier 3 versus Tier 1 sites across the Somerset Levels and Moors (SLM), shedding light on the ecological dynamics influenced by these contrasting wetland management practices. By comparing mosquito communities between the two tiers, we hope to gain valuable insights into how different management approaches affect mosquito populations and their associated ecological interactions.

2.3.2 Ecological Survey

We randomly selected 17 ditch locations across two management regimes, eight in Tier 1 management and nine in Tier 3 of the SLM (Fig 1). At each site, we selected four sampling sites (ditches) within a 500m radius of the location, often part of an interconnected ditch system. We surveyed these sampling sites using a standard dipping protocol across three time points: spring (May), summer (June/July) and autumn (August/September) for three years, from 2009 to 2011. We set up six dip-points, for which we took GPS locations, at each sampling site along the ditch from one to six meters, randomly determined by the throw of a die. During each visit, we took a complete submersion dip sample from both water-body margins and the centre of the ditch using a 1-litre volume mosquito dipper at each of the dip points.

We recorded the abundance of mosquito larvae and pupae, and that of potential mosquito predator groups, at each dip point. Aquatic macroinvertebrate species were identified *in situ* to order and suborder, where possible, using Dobson et al. (2012). Mosquito larvae and pupae were preserved in 70% ethanol and identified to species or species complex level in the laboratory using the morphological keys by Becker et al. (2010); Cranston (1987); Schaffner

Table 2.1 Key differences in management prescriptions for Tier 1 (permanent grassland) and Tier 3 (raised water level areas). For a comprehensive overview, refer to A.1.

Prescription Category	**Tier 1**	**Tier 3**
Fertilizer Application	No more than 75kg nitrogen, 37.5kg phosphate, and 37.5kg potash per hectare. Only home-produced organic fertilizer allowed.	No inorganic fertilizer. Organic manure restricted to home-produced cattle manure (max 25 tonnes/ha per annum). No slurry.
Grazing	Graze with cattle or sheep, avoiding poaching, under- or over-grazing.	Cattle grazing only, not before 20 May. Max density of one animal per 0.75 ha from 20 May to 8 July. Avoid poaching and improper grazing.
Mowing and Hay Making	After cutting grass for hay or silage, graze the aftermath.	No silage. Mow at least one-third of the land (or one year in three), but not before 8 July. No grazing before mowing.
Mechanical Operations	Chain harrowing or rolling allowed. Maintain existing field gutters, ditches, and piping by mechanical means. No additional surface piping allowed.	Same as Tier 1, but no mechanical operations between 31 March and 1 July. Maintain field structures without sprays.
Herbicide Use	Herbicides allowed only for specific weeds (e.g., thistles, docks, ragwort) via spot treatment or weed wiper.	Same as Tier 1, but no herbicides for creeping buttercup.
Water Levels	Maintain at least 15 cm of water in ditches/rhynes at all times.	Maintain water levels not more than 30 cm below field level from May to November, and not less than field level from December to April.

et al. (2001); Snow and Terzi (1990). During each visit, details of bankside, emergent and floating channel vegetation were recorded with reference to Cope et al. (2009); Jermy et al. (1995). Plants within and at the edges of the ditch were identified to genus or species level, and their percentage cover and height estimated. Vegetation height and percentage cover values were averaged across species in three groups based on their functional impact, bank, emergent, and floating vegetation, since these vegetation structures are likely to have differential impacts on habitat suitability across mosquito species (Table 2.2). We measured the physicochemical characteristics of the ditch at each sampling site, assessing ditch width, and area of the ditch shaded (a proxy for habitat openness) as well as pH, temperature, turbidity, and salinity of the water. Average values for the covariates listed in Table 2.2 were summarized across the six dip-points per ditch site in each season.

2.3.3 Statistical Analysis

We used a joint multivariate hierarchical generalized mixed linear model approach, to account for the interdependency of species responses to the environment and species responses to each other in the ecosystem, by modelling all species simultaneously and accounting for each species' response to measured and unmeasured environmental covariates through latent variable factors (Wilkinson et al., 2019). We fitted our model using the R package Hierarchical Modelling of Species Communities (HMSC; Ovaskainen and Abrego (2020); Ovaskainen et al. (2017b)) framework, to explore how biotic and abiotic interactions drive mosquito larval distribution across the SLM.

The multispecies generalized linear latent variable model (with probit link function) was fitted to the presence-absence data for four mosquitoes and eight predator groups obtained from our 320 sampling sites with abiotic covariates on a linear scale (Table 2.2). We excluded any species that occurred fewer than ten times to increase statistical stability (Ovaskainen and Abrego, 2020), leading to the exclusion of one mosquito species and four predator groups

Table 2.2 Effect of Environmental Variables on Mosquito Abundance: Impact and expected ecological implications of key environmental factors on mosquito populations, including vegetation cover, water characteristics, and habitat structure.

Variable	**Description**	**Impact on Mosquito Abundance**
Floating Vegetation Cover (%)	Percentage of water surface covered by floating plants.	Negative impact expected, as dense floating vegetation (e.g., *Lemna spp.*) may inhibit larvae and pupae from accessing air Cuthbert et al. (2020); Eid et al. (1992).
Bank Vegetation Height (cm)	Height of vegetation along ditch margins and banks.	Increases microhabitats for adult mosquitoes and provides sheltered resting places Sauer et al. (2021).
Bank Vegetation Cover (%)	Percentage of banks covered by plant matter.	Similar benefits to height, offering shelter and resting spots.
Emergent Vegetation Height (cm)	Height of vegetation emerging from the water.	Provides shelter for ovipositing females and enhances larval survival by predator avoidance Saha et al. (2009).
Emergent Vegetation Cover (%)	Percentage area of emergent vegetation.	Similar benefits as height, with increased shelter for mosquito development.
Shaded Water (%)	Percentage of water surface shaded.	Positively impacts species preferring vegetated or cool breeding sites Hawkes et al. (2020).
Width (cm)	Width of the waterbody.	Wider waterbodies may support more predators, reducing mosquito density Sunahara et al. (2002). Some species, like *An. maculipennis*, prefer more open habitats.
Water Temp (°C)	Water temperature at sampling.	Warmer temperatures shorten larval development time and improve survival Bayoh and Lindsay (2004).
Dissolved O_2 (ppm)	Concentration of dissolved oxygen.	Impact uncertain as most species tolerate a wide range of oxygen levels.
pH	Water acidity/basicity.	Most mosquitoes prefer neutral pH and are tolerant of moderate changes Emidi et al. (2017).
Turbidity	Water clarity, indication of flow.	Higher turbidity may enhance larval survival by reducing predator efficiency Cano-Rocabayera et al. (2020).
Salinity (ppt)	Salt content in water.	Tolerance varies across species, directly affecting mosquito presence Medlock et al. (2012).

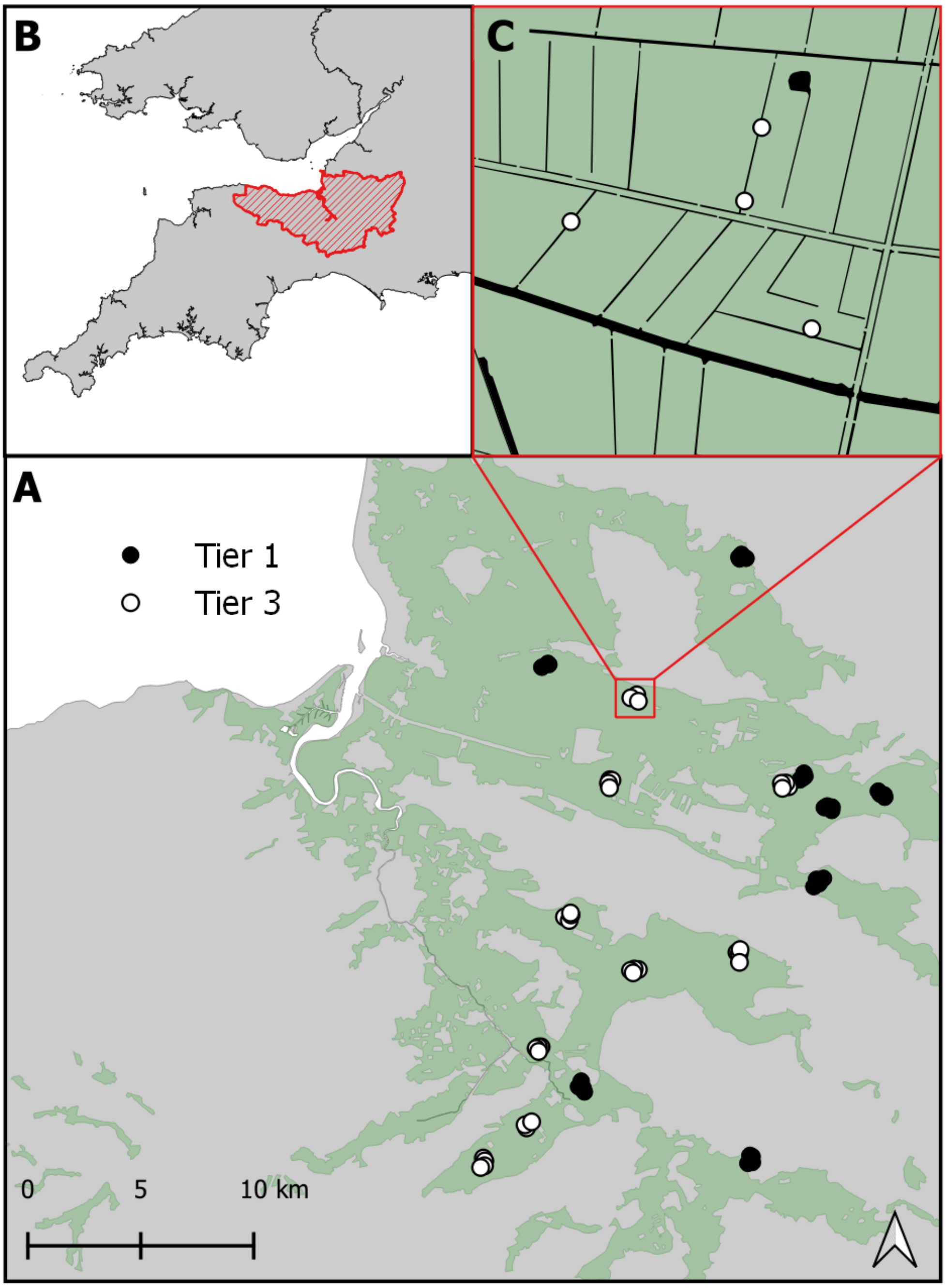

Fig. 2.1 **A** Map of Somerset Levels and Moors study site. Extent of coastal grazing marsh in green with Tier 1 and Tier 3 locations with sampling sites superimposed (black and white circles respectively). **B** Location of the study site (red hatching) in South England. **C** Inset frame showing detailed hierarchical spatial sampling design for each sampling site (circles) in which four ditches were sampled within a 500m square radius for each location.

(see results). To account for potential spatial biases in the sampling data, we generated a distance matrix, calculated from the average coordinates across the six dip points that make up each sampling site, to represent the spatial scales between each sampling unit as a spatially structured random effect (Dormann et al., 2007). We considered the impact of temporal effects on sampling methods by including a nested random effect for both year and time point. In this case we consider the height and cover area of three different plant functional groups, bank, emergent, and floating vegetation, as an abiotic driver as we expect them to function as a regulator of population fitness through shielding of predation or similar processes (Saha et al., 2009).

The model was fitted using four Monte-Carlo Markov Chains (MCMC) with a transient period of 5000 samples and target of 1000 samples per chain using a thinning rate of 1000 for a total of 4 million MCMC post-transient in samples in total. Parameter convergence was measured using Gelman and Rubens potential scale reduction factor (PSRF, Gelman and Rubin (1992)). We used five-fold cross validation to validate model performance, comparing predictive and explanatory values of Tjur's R^2 and the area under curve (AUC) statistic for each species (Lobo et al., 2008; Tjur, 2009). We examined the importance of different sets of covariates in our model by partitioning the variation explained by fitting of partial models (Borcard et al., 1992; Ovaskainen and Abrego, 2020). Furthermore, we originally aimed to construct abundance models that included the same covariates, as we hypothesized that biotic interactions would have a greater impact on species abundance than species presence. However, due to the high complexity of the model, it was deemed computationally infeasible to achieve an acceptable fit and run-times exceeded one month without reasonable convergence for all species (Howard et al., 2014).

To understand if management tiers influence potential abiotic drivers of mosquito populations, we estimated the marginal effect of management tier on each covariate measured in our sampling procedure (Table 2.2). We modelled each covariate separately against management level as a categorical factor, with both a random effect for site and a nested random effect of season within year to account for temporal differences in covariate distribution. Bayesian multivariate models were built in the probabilistic programming language Stan using the BRMS package in R (Bürkner, 2017; Carpenter et al., 2017). Covariates measured on a percentage scale (metrics of vegetation cover and shaded area) used a Zero-One Inflated Beta response distribution. Bank and emergent vegetation height used log-normal hurdle mixed response distributions to account for over-dispersion and the influence of zero values. All other covariates used a student-t distribution for robust estimation of parameter values. Significance was measured across the 95% CI using mean equal tailed intervals of the posterior distribution.

2.4 Results

2.4.1 Differences in environmental conditions between management tiers

Metrics of ditch vegetation structure differed significantly between sites subject to Tier 1 versus Tier 3 management, whilst physicochemical properties of the waterbody and ditch structure parameters did not (Table 2.3). Though water-bodies were on average 8 cm wider in Tier 3 managed areas, this difference was not statistically significant (95% CI [-23.94, 6.31]). There was no measurable difference in turbidity (95% CI [-0.15, 0.18]) or salinity (95% CI [-0.12, 0.15]) between the management tiers, and pH values were on average -0.3 lower in Tier 3 areas, but this was also non-significant (95% CI [0.03, 0.65]).

Bank vegetation was more likely to be present (95% CI [-0.29, -0.10], Table 2.3), and when present it was significantly taller, by 25 cm on average (95% CI[-55.78, -4.24]), in Tier 3 ditches than Tier 1 ditches, but we found no differences in the levels of bank-side vegetation percentage area cover between tiers (Mean = 0.01, 95% CI[-0.05,0.07]). Similarly, we found that emergent channel vegetation was 29% more likely to be present in Tier 3 areas (95% CI [-0.39, -0.18]), and when emergent vegetation was present it was 5 cm taller on average than in Tier 3 areas than Tier 1 areas (95% CI [-12.39, -0.34]). There was no measurable difference in the probability of floating vegetation cover being 0% (95% CI[-0.15, 0.06]) or 100% (95% CI[-0.1, 0.04]) between tiers, but on average there was 10% less floating vegetation cover in Tier 3 areas than in Tier 1 areas and this was significant (95% CI[0.01, 0.19]). The percentage shaded area of the channel did not vary significantly between tiers (Mean = 0.12, 95% CI[-0.01, 0.27]), but the probability of a waterbody being completely shaded was 48% higher in Tier 3 areas than Tier 1 (95% CI[-0.8, -0.2]), and the probability of a waterbody having no shade was 10% more likely in Tier 3 areas (95% CI[0.03, 0.016]).

Table 2.3 Differences in environmental variables between the Tier 1 (T1) and Tier 3 (T3) wetland management regimes. Table shows the marginal effect of Management Tier for each environmental covariate from pairwise posterior distribution contrasts of T1-T3 values. PD (Probability of Direction) estimates above 97.5 are deemed significant and highlighted in bold. MPE (Mean Parameter Estimates) with Lower MPE_{Low} and Upper MPE_{High} estimates represent the equal tailed 95% CI estimate across the model's posterior distribution. Full parameter estimates for each model covariate are given in Table A.1.

Model Covariate	**Effect of Tier 3**	**PD (%)**	**MPE**	$\mathbf{MPE}_{low}$	$\mathbf{MPE}_{High}$
Salinity	–	57.40	0.01	-0.12	0.15
Emergent Vegetation Height (Height_{Emerg})	Taller Emergent Vegetation	**98.41**	-5.30	-12.39	-0.34
Dissolved Oxygen (DO^2)	–	89.17	6.59	-4.10	17.40
pH	–	96.53	0.30	-0.03	0.65
Turbidity	–	59.00	0.02	-0.15	0.18
Floating Vegetation Cover (Cover_{Float})	Less Floating Vegetation Cover	**98.33**	0.09	0.01	0.19
Bankside Vegetation Cover (Cover_{Bank})	–	76.62	0.01	-0.05	0.07
Emergent Vegetation Cover (Cover_{Emerg})	–	70.88	-0.01	-0.04	0.02
Water Temperature	–	88.33	-0.82	-2.24	0.59
Shaded	–	96.37	0.12	-0.01	0.27
Ditch Width	–	87.67	-8.58	-23.94	6.31
Bank Vegetation Height (Height_{Bank})	Taller Bank Vegetation	**99.62**	-25.28	-55.78	-4.24

2.4.2 Abundance and prevalence of sample mosquito and predator taxa

We recorded twelve different aquatic macroinvertebrate taxa in the SLM, of which five were mosquitoes (Table 2.4). We identified 6896 mosquito larvae in total. *Culiseta annulata* (n

= 3250, 47.13%) and *Culex pipiens* (n = 3248, 47.10%) made up the highest proportion of these larvae, followed by *Anopheles claviger* (n = 292, 4.23%) and *Anopheles maculipennis* s.l. (n = 105, 1.52%). *Anopheles maculipennis* s.l. were most prevalent, occurring in 13% of the sample sites, followed by *Cs. annulata* (12%), *An. claviger* (11%), *Cx. pipiens* (10%), and lastly *Aedes (Ochlerotatus) caspius* which was present in just a single sampling site (<0.1%). Because of the low abundance and low prevalence, *Ae. caspius* was omitted from the subsequent analysis.

We identified eight potential predator taxa that were present in at least 10 sites to be included in this statistical analysis (Table 2.4). Of these taxa, adult Coleoptera (water beetles) were most prevalent, being present in the most sampling units (27%, n = 308), followed by Corixidae (water boatmen) which were also the most abundant predator species (26%, n = 647), Zygoptera larvae (damselflies, 25%, n = 349) and Coleoptera larvae (19%, n = 139). The other four taxa had a much lower prevalence and abundance across all sampling units, including Gammaridae (ditch shrimp, 8%, n = 103), Anisoptera larvae (dragonflies, 5%, n = 31), *Ilyocoris cimicoides* (saucer bugs, 3%, n = 19) and *Nepa cinerea* (water scorpions, 3%, n = 11).

Table 2.4 Relative prevalence (rate of occurrence across all sites) and total (and proportional) abundance of mosquito and predator taxa across sampled sites among sampled individuals across study sites.

Taxon	**Prevalence (%)**	**Abundance (Total)**	**Mean Abundance per Sample Site**
Anopheles maculipennis s.l.	13	105	2.44 ± 2.22
Anopheles claviger	11	292	8.11 ± 11.84
Culex pipiens s.l.	10	3248	101.50 ± 244.43
Culiseta annulata	13	3250	81.25 ± 160.62
Corixidae	26	647	7.70 ± 20.89
Coleoptera larvae	19	139	2.24 ± 1.70
Coleoptera adults	27	308	3.58 ± 3.30
Zygoptera larvae	26	349	4.20 ± 5.55
Anisoptera larvae	5	31	1.82 ± 1.42
Ilyocoris cimicoides	3	19	1.90 ± 2.18
Nepa cinerea	3	11	1.10 ± 0.32
Gammaridae	8	103	4.29 ± 4.65

2.4.3 Overall accuracy of community models and partitioning of variance between key sets of drivers

Parameter convergence of the HMSC model was satisfactory, with all chains generating sufficient effective samples and PSRF values (Fig A.1). Explanatory AUC values (for the training dataset) were high for all mosquito species (0.86-0.99) and predictive AUC values (from the cross-validation) were reasonable (0.75-0.89). Explanatory AUC values were similarly high for potential predator taxa (0.78-0.99), but predictive AUC values were much lower for some less abundant taxa (*Nepa cinerea* = 0.4, *Ilyocoris cimicoides*= 0.55, *Anisoptera* larvae = 0.55, *Coleoptera* larvae = 0.57). All other predator taxa had adequate predictive AUC values above 0.69 (Table 2.5).

Metrics of variance explained for the training dataset were higher for Culicine species (*Cx. pipiens s.l.* Tjur's R^2 = 0.47 ; *Cs. annulata* Tjur's R^2 = 0.55) than Anopheline species (*An. maculipennis* s.l. Tjur's R^2 = 0.12; *An. claviger* Tjur's R^2 = 0.23). When examining the importance of different sets of covariates for mosquito species, we found that spatiotemporal effects accounted for on average 43% (SD 29%) of all variation explained by the models (Fig 2.2, Table A.2). Tjur's R^2 values for predator taxa were much lower than for the mosquito species, except for Corixidae (Tjur's R^2 = 0.27) and Zygoptera (Tjur's R^2 = 0.28) larvae.

Random effects accounted for substantial variation in Culicine species and low amounts of variation for Anopheline species (Fig 2.2). For the Anopheline species, a higher proportion of variance was explained by chemical and channel structure covariates than for Culicine species. Temporal effects of year and season explained less variation in presence of mosquito species compared to the predator taxa, and little in Anopheline species (Table A.2)

2.4.4 Larval mosquito responses to environmental drivers

Culex pipiens was significantly positively associated with bank vegetation cover (Mean = 0.03, 90% CI[0.01, 0.04]), negatively associated with bank vegetation height (Mean =

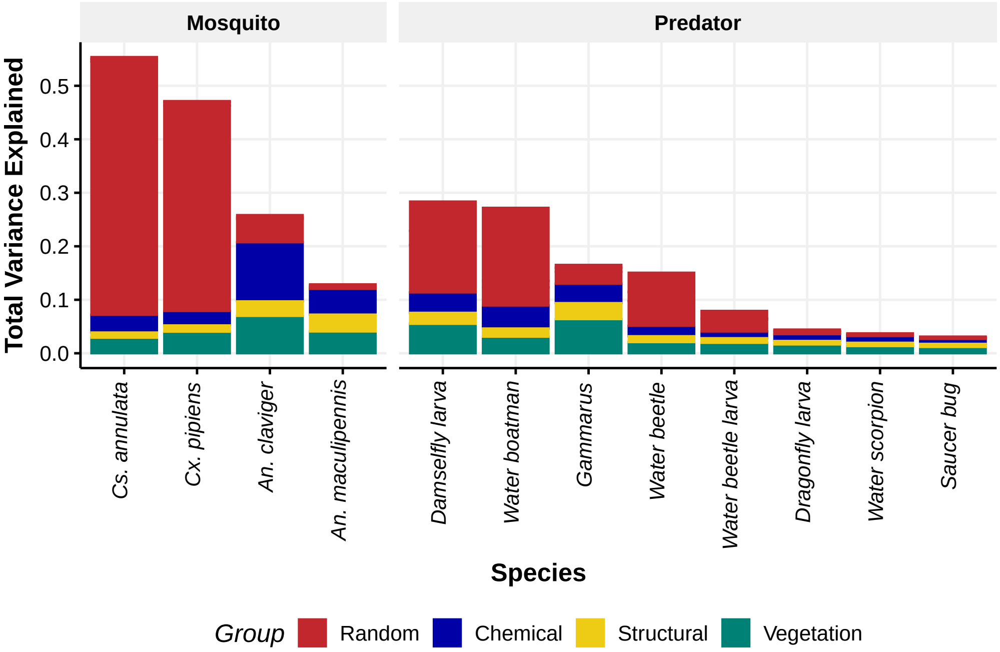

Fig. 2.2 Variance partitioning and total variance explained by each component for larval mosquitoes and predator species prevalent in the study side. Random effects are the variance explained by year season and the spatial component of the model summed for each species. The “chemical” category includes the physicochemical covariates pH, dissolved oxygen, salinity, turbidity and water temperature, the “structural” category includes the width and relative shadiness of the water body, and the “vegetation” category includes all vegetation metrics; floating, emergent and bank, as covariates in the model. Detailed breakdown of the variance explained by the random effects is provided in Table A.2.

Table 2.5 Accuracy with which community models explained and predicted the distributions of mosquito and predator taxa including Area Under the Curve (AUC) and Tjur's R^2 values for explanation and prediction.

Taxa	**Explanatory**		**Predictive**	
	AUC	**R^2**	**AUC**	**R^2**
Anopheles maculipennis s.l.	0.86	0.12	0.75	0.06
Anopheles claviger	0.91	0.23	0.84	0.14
Culex pipiens s.l.	0.98	0.40	0.84	0.22
Culiseta annulata	0.99	0.53	0.89	0.38
Corixidae	0.88	0.27	0.82	0.21
Coleoptera larvae	0.78	0.08	0.57	0.02
Coleoptera	0.81	0.15	0.69	0.08
Zygoptera larvae	0.89	0.27	0.80	0.19
Anisoptera larvae	0.86	0.03	0.55	0.00
Ilyocoris cimicoides	0.87	0.03	0.50	0.00
Nepa cinerea	0.99	0.04	0.40	-0.01
Gammaridae	0.87	0.14	0.76	0.08

-0.006, 90% CI[-0.017, -0.001], and negatively associated with floating vegetation cover (Mean = -0.01, 90% CI[-0.018, -0.001]) (Fig 2.3). *Culiseta annulata* was significantly positively associated with more bankside vegetation cover (Mean = 0.02, 90% CI[0.001, 0.035]) and high turbidity areas (Mean = 1.41, 90% CI[0.28, 2.65]). *Anopheles maculipennis* s.l. showed strong preference for habitats with little shade (Mean = -1.13, 90% CI[-2.20, -0.13]) and higher levels of emergent vegetation (Mean = 0.015 90% CI[0.004, 0.026]) (Fig 2.3). *Anopheles claviger* exhibited a strong preference for shaded habitats (Mean = 1.23, 90% CI[0.34,2.17]), and ditches with little floating vegetation cover (Mean = -0.015, 90% CI[-0.025, -0.006]) (Fig 2.3).

Several potential predator taxa were also significantly correlated with an array of physicochemical and vegetation drivers (Fig 2.3), but we only interpret these further for those predatory taxa for which a larger percentage of variance in occurrence was explained by the model, namely water boatmen and damselfly larvae, (Fig 2.2). The probability of occurrence of water boatmen was significantly negatively associated with lower shading of water bodies

(Mean = -0.96, 90% CI[-1,74, -0.23]). The probability of occurrence of damselfly larvae was significantly positively impacted by higher levels of floating (Mean = 0.009, 90% CI[0.003, 0.015]) and height of bank vegetation (Mean = 0.005, 90% CI[0.001, 0.009], Fig 2.3).

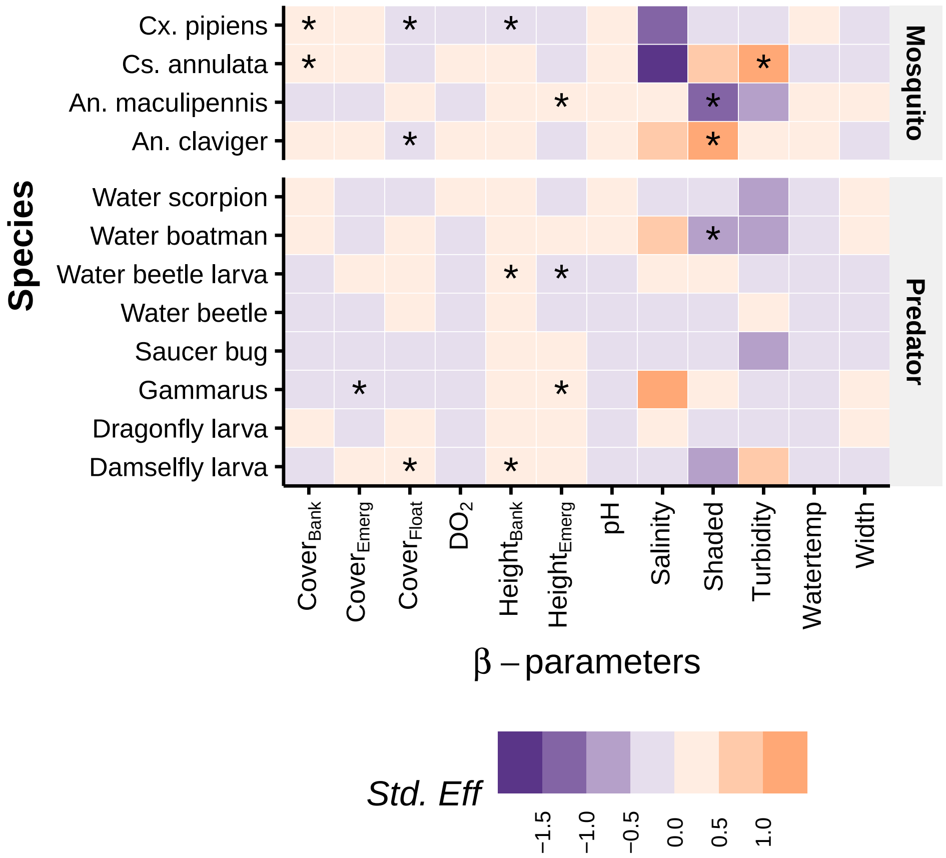

Fig. 2.3 Species responses to covariates by standardised coefficient effect size (Std. Eff). "*" Indicates significance of parameter and cells that are blank indicate where the effect was not significant i.e., the 90% credible interval bridged zero. $Height_{Emerg}$ = Emergent Vegetation height, $Height_{Bank}$ = Bank Vegetation height, $Cover_{Float}$ = Floating Vegetation cover, $Cover_{Bank}$ = Bank Vegetation height, $Cover_{Emerg}$ = Emergent Vegetation cover.

2.4.5 Residual association between species

We found significant positive residual species associations between all mosquito species except *An. maculipennis* s.l. after accounting for environmental responses in the HMSC community model (Fig 2.4). Additionally, we found that all species of mosquito except *An. maculipennis* s.l. show significant negative associations with potential predator taxa including water beetle larvae and adults, and damselfly larvae, water boatmen and *Gammarus* spp. Saucer bugs, dragonfly larvae and water scorpions do not show any significant associations with any other species. All other predator taxa show significant positive associations with one another (Fig 2.4).

2.5 Discussion

2.5.1 Vegetation structure as a key driver of mosquito communities, including potential vectors.

Increased water levels in Tier 3 areas have been previously shown to favour the establishment of wetland meadow plant species, which increase the diversity and quality of vegetation in these areas compared to Tier 1 areas (Acreman et al., 2011). Our study supports this, with Tier 3 areas leading to significant increases in emergent and bankside vegetation height, increasing the structural complexity of vegetation compared to Tier 1 areas (Table 2.3).

Areas such as wetlands and marshes tend to harbour a wide variety of mosquito species, due to the presence of a variety of suitable water bodies for oviposition, and aquatic plants that provide shelter, food, and protection from predators, as well as a diverse set of host species from which to draw bloodmeals (Becker et al., 2010; Medlock et al., 2005). Adult mosquitoes benefit from vegetation that is structurally complex, consisting of plant species communities that create shaded and sheltered micro-habitats that protect the mosquitoes from

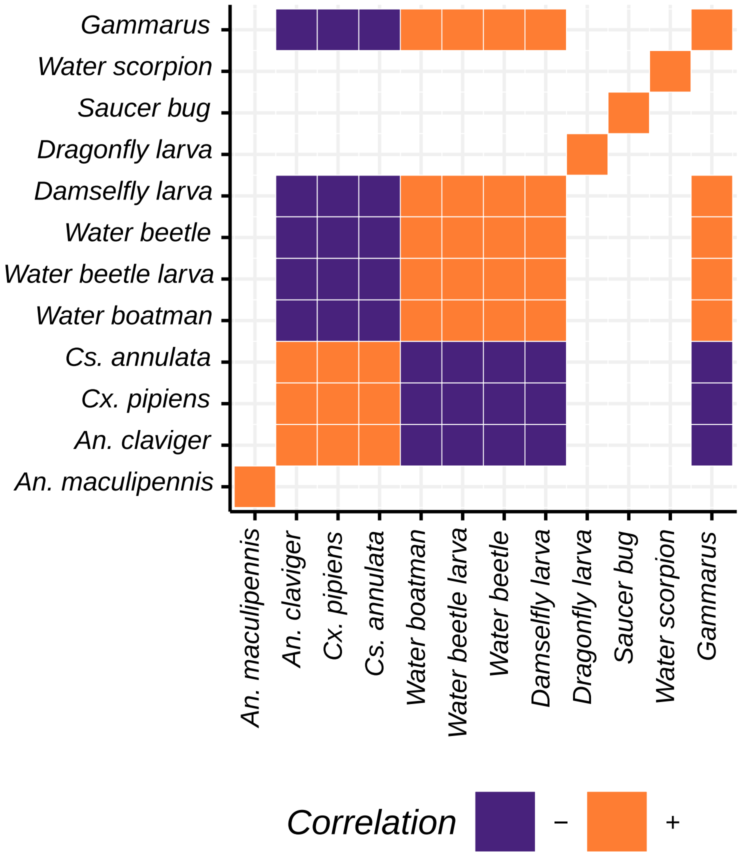

Fig. 2.4 Significant species residual correlations drawn from the Ω model parameter for each species in Hmsc. Coloured regions show which species meet the 95% significance threshold and are expected to be found together more than can be explained by model covariates alone. Correlations that don't meet this significance threshold are blank.

direct sunlight, wind, and other environmental stressors. Such conditions enhance overall habitat suitability for adult mosquitoes (Becker et al., 2010). Juvenile mosquitoes may also perceive similar benefits from the underwater structures of algae and plant roots as refuges from predators (Collins et al., 2019).

A review by Rey et al. (2012) found that wetlands with high vegetative complexity had a greater diversity of mosquito species compared to wetlands with low vegetative complexity. Consistent with these prior studies, we found that the occurrence of three of the key mosquito species in the study area (*An. claviger* and *An. maculipennis* s.l., and to a lesser extent, the *Cx. pipiens* complex) was favoured by more complex ditch vegetation structure characteristic of Tier 3 management (increased height and cover of emergent and bankside vegetation, Table 2.3). Consistent with the associations described by Hawkes et al. (2020), *An. maculipennis* s.l. showed significant preference for less shaded environments, suggesting a preference for open-style habitats, while *An. claviger* showed a preference for heavily shaded habitats (Fig 2.3). For *Cx. pipiens* and *An. claviger*, both of which can cause significant biting nuisances, Tier 3 areas are likely to offer more favourable conditions because of these species' preferences for little floating vegetation cover (Fig 2.3, Table 2.3). Floating vegetation can provide a physical barrier between mosquitoes and oviposition sites, as well as larvae and air, dissuading oviposition in these areas (Eid et al., 1992). Yet, previous studies have found positive associations between floating vegetation cover and mosquito species presence, suggesting the impacts of this factor on mosquito larvae are complex and context-dependent (Cuthbert et al., 2020; Golding et al., 2015).

Except for the association of turbid water with *Cs. annulata* presence, no significant effects of physicochemical characteristics of the water on mosquito occurrence were found (Fig 2.3). This aligns with prior knowledge that Culicine species *Cx. pipiens* and *Cs. annulata*, utilize a breadth of oviposition sites, including drainage ditches, artificial containers, and small stagnant waters that vary widely in water parameters (Hawkes et al., 2020). We found that physicochemical factors had a larger contribution to variance explained for the Anopheline species, *Anopheles maculipennis* s.l. and *An. claviger*, at 11% and 6%, respectively, suggesting more restricted oviposition site preferences. The SLM system is an interconnected network of ditches that covers an area over several hundred square kilometres, leading to relatively homogeneous water chemistry across our study area. This means that the range of conditions experienced by our sampled species might not be large enough to elucidate any meaningful differences in water parameter preferences (and indeed the Tier management regimes did not differ significantly in physico-chemical conditions).

2.5.2 Biotic drivers of larval mosquitoes

Consistent with prior studies of mosquito community composition at the landscape level, we found that biotic interactions may affect the distribution of mosquitos across a wetland environment (Golding et al., 2015). Many of the potential predator taxa, such as dragonfly and damselfly larvae, are frequently observed as effective larval mosquito predators in other contexts, and indeed some, such as dragonfly larvae, have been investigated for biological control of mosquitoes (Medlock and Snow, 2008; Onyeka, 1983; Saha et al., 2012). Water beetles and water boatmen have also been implicated in mosquito larval predation, but their relative predation pressure is thought to be linked to the vulnerability of mosquito larvae (Jeffries, 1988; Medlock and Snow, 2008).

As described above, vegetation structure in and around water bodies modifies the availability of refugia from predators and consequently the effectiveness of predator avoidance strategies of immature mosquitoes (Saha et al., 2009). Environments with complex underwater vegetation limit the space for predators and mosquito larvae to interact and reduce overall predator efficiency (Saha et al., 2009; Sunahara et al., 2002). The higher cover and height of emergent vegetation detected in Tier 3 areas could provide complex vegetation structure both above and below the water level, providing shady refugia that improve predator avoidance in these sites.

It's crucial to recognize that the species interactions deduced from residual correlations in joint occurrence models are not as dependable as direct observations of predator-prey interactions. Instead, these inferred interactions may be indicative of unmeasured factors such as shared or non-shared environmental preferences between species (Poggiato et al., 2021). In essence, while joint occurrence models provide valuable insights, caution should be exercised in attributing the correlations solely to direct predator-prey interactions, as other environmental factors might contribute to the observed patterns (Zurell et al., 2018). For example, though some mosquito species were found to be negatively correlated with *Gammarus* species, we suspect this may reflect different preferences for unmeasured environmental conditions. *Gammarus pulex* and other *Gammarus* species are omnivorous and occupy different depths of the waterbodies compared to mosquito larvae, leading to limited potential predation opportunities (P. Scarlett, *pers. comm.*, June 2023).

The community models exhibited relatively low performance for predator species compared to mosquito species. Therefore, to comprehensively grasp how wetland management may influence predator effects on mosquito populations in this context, additional and more detailed data on predators, with improved taxonomic resolution, could be valuable. Prior studies seem to suggest that management plans targeting biodiversity, like Tier 3, have been suggested to positively impact the abundance of key predator taxa, including fish (Chandra et al., 2008; Griffin and Knight, 2012). Increased predator abundance would provide a potential control agent for mosquito populations, but few studies have shown this in the field, and none in the UK (Griffin and Knight, 2012; Medlock and Snow, 2008; Saha et al., 2012). Our study indicates that water beetle larvae and adults, dragonfly and damselfly nymphs, and water boatmen may be key predator taxa that play a role in regulating mosquito populations within lowland wet grasslands, and that these roles should be investigated further to fully understand trade-offs between biodiversity management and mosquito biting risk.

2.6 Conclusion

We have shown here how management schemes directed at increasing the biodiversity of grazed wetlands could increase the suitability of those habitats for immatures of some key mosquito vectors and nuisance biters, and encouraging diverse vegetation structure in and around water bodies may reduce their vulnerability to predators. However, thinning or removal of vegetation is not a viable strategy to control mosquito populations, being at odds with the targets of wetland management strategies. Vegetation removal impinges upon important wetland ecosystem functions by decreasing biodiversity, lowering water quality and reducing flood resilience of an area (Acreman et al., 2011; Rochlin et al., 2012a).

Furthermore, to interpret disease risk given future incursions of viruses such as West Nile virus, Sindbis virus or Usutu virus into the UK, it would be necessary to understand how these impacts of wetland management on juvenile mosquito populations cascade through into impacts on the ratio of adult vectors to susceptible hosts (a key parameter in disease transmission, see Smith et al. (2004)), by sampling adult vectors, hosts, and their interactions (e.g., via blood meal analysis) across wetland gradients into areas of human habitation (Hanford et al., 2020). This would provide the evidence-base for co-development of integrated mosquito management and risk awareness strategies among cross-sectoral stakeholders that would minimize risk of exposure while aligning with environmental wetland management goals (Martinou et al., 2020). Given the diverse and growing mosquito-borne pathogen threats to people living in and around wetland ecosystems, and the diverse assemblages of potential mosquito vector species involved, the combination of joint models with empirical surveys provides an effective way of inferring the complex ecological interactions that will underpin the trade-offs between disease risk and wetland management.

Chapter 3

Environmental and Biotic Drivers of Mosquito Communities Across Europe: A Multi-Scale Joint Species Distribution Modelling Approach

This manuscript is currently undergoing revision for future submission. While the final published version will be significantly condensed, this thesis presents the full, detailed methodology for the examiners' benefit. The extended version provided here offers a comprehensive overview of the research process and findings.

3.1 Abstract

Mosquito-borne diseases pose a significant threat to public health in Europe, with their risk intrinsically linked to vector distribution. This study presents the first application of joint species distribution models (JSDMs) to predict mosquito communities across Europe. We utilized data from the VectorNet consortium to generate community-level data for mosquitoes at four spatial resolutions (1, 2, 5, and 10 km), comparing JSDMs with Multi-Species Distribution Models (MSDMs) to assess the relative importance of environmental, spatial, and biotic factors in shaping mosquito distributions. Our results demonstrate that JSDMs can effectively predict distributions for nearly half of the analysed species, despite relatively low average community richness. Notably, model performance was not significantly influenced by species prevalence, contrasting with findings from other taxa. JSDMs attributed a large proportion of variance to the biotic component (10%), highlighting the potential of using this community data to generate better predictions. Invasive *Aedes* species displayed consistent negative associations with native species across all spatial scales, potentially indicating niche differentiation or differential environmental responses compared to native species. This study demonstrates the value of JSDMs in leveraging sparse data to explore complex community dynamics, emphasizing the need to integrate potential species interactions and unmeasured environmental variables in mosquito distribution models. Our findings underscore the challenges in accurately reflecting species interactions and environmental responses at appropriate scales, especially given biases in mosquito surveillance data. These insights, coupled with continued refinement of JSDM approaches and improved data collection methods, hold promising potential for enhancing vector surveillance and predicting future disease risks within the context of community ecology.

3.2 Introduction

Mosquitoes are the primary drivers of vector-borne diseases (VBDs) globally, and the rising VBD burden is expected to significantly strain public health finances (Bhatt et al., 2013; Medlock et al., 2012; Stanaway et al., 2016). Land use changes, climate change, biological invasions and globalization are altering the distribution and composition of mosquito vector species across Europe, increasing the risk of disease transmission (Calzolari et al., 2015; Medlock et al., 2018). Several mosquito borne diseases (MBDs) have re-emerged in Europe, such as Dengue (Schaffner and Mathis, 2014), Chikungunya (Delisle et al., 2015; Grandadam et al., 2011; Rezza et al., 2007), West Nile Virus (Bakonyi and Haussig, 2020), Sindbis Virus (Suvanto et al., 2022), and Usutu Virus (Weissenböck et al., 2013). However, significant knowledge gaps remain regarding the complex interactions between environmental factors, vector ecology, and disease transmission dynamics, underscoring the need for continued research and surveillance efforts.

Species distribution models (SDMs) are widely used to assess VBD risks by understanding and predicting mosquito distributions (Fuller et al., 2012; Khatchikian et al., 2011; Wint et al., 2022). These models have evolved from theoretical tools to practical instruments influencing public health strategies and vector control policies (Fouet and Kamdem, 2019; Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). For instance, SDMs have been used to evaluate Rift Valley Fever introduction risk in the UK and Europe (Schaffner et al., 2013a; Simons et al., 2019; Wint et al., 2020), and the European Centre for Disease Prevention and Control has issued technical guidance on vector modelling to enhance surveillance efforts (ECDC, 2021). However, current studies mainly focus on modelling individual species, often neglecting interactions between mosquito species despite criticism that single-species models lack the power to account for biotic interactions (Ovaskainen et al., 2017b; Wilkinson et al., 2021; Zurell et al., 2018, 2020).

Neglecting species interactions can lead to incomplete or inaccurate representations of community assembly processes and species coexistence mechanisms, potentially affecting the accuracy of disease risk assessments and ability to target control measures. For example, McDonough and Holloway (2020) showed for the *Ixodes ricinus* tick in Great Britain and Ireland that models built with only abiotic variables had reduced accuracy and biological realism compared to those that also incorporated host variables. Joint species distribution models (JSDMs) have been developed to address this gap (Golding and Harris, 2015; Pichler and Hartig, 2021; Tikhonov et al., 2022; Wilkinson et al., 2019), and despite challenges in accurately capturing the biotic component (Blanchet et al., 2020; König et al., 2021; Zurell et al., 2018), these models can improve understanding of community assembly processes and underlying drivers (Pollock et al., 2014). The importance of biotic interactions in shaping mosquito distributions has been recognized in local community studies, with Golding et al. (2015) demonstrating significant predator-prey influences on mosquito abundance at the landscape level in the UK (Ferraguti et al., 2016; Golding et al., 2015; Smith et al., 2024).

However, the role of these interactions in driving continental-scale distributions remains less explored. Understanding the interplay of species interactions, interspecific trait variation, and differential environmental responses in shaping mosquito distributions and vector-borne disease dynamics could yield numerous benefits if incorporated into models accounting for these impacts on distribution (Cator et al., 2020; Lefevre et al., 2018; Mordecai et al., 2019). This knowledge may enhance our ability to predict invasive mosquito species spread (Poggiato et al., 2021), identify predator species with regulatory effects on mosquito populations (Golding et al., 2015; Smith et al., 2004), and forecast shifts in community composition under environmental disturbances (Ferraguti et al., 2016; Townroe and Callaghan, 2014).

The sparse distributional data for native and invasive mosquitoes at large geographic scales presents significant challenges for applying community modelling methods, limiting most studies to smaller, local scales (Braks et al., 2004; Ferraguti et al., 2016). The paucity of comprehensive, large-scale mosquito community data has historically constrained the application of community modelling techniques in vector ecology at macro-scales. Recent efforts to centralize, standardize and coordinate sampling data across continents, such as the ECDC VectorNet consortium project (Braks et al., 2022; Wint et al., 2023), have created new opportunities to examine how sparse mosquito data might be leveraged in community modelling contexts at continental scales. The scale dependence of species responses to environmental and biotic factors is a critical consideration in ecological studies, particularly for vector groups and insect taxa. Research has demonstrated that the relative importance of different drivers can shift significantly across spatial scales.

For tick-borne pathogens, Wimberly et al. (2008) showed that climate variables were more influential at broader scales, while land cover factors became increasingly important at finer resolutions. Similarly, de Knegt et al. (2010) found that the strength and even direction of species-environment relationships in butterflies varied with spatial grain and extent. In mosquito ecology, climatic factors often dominate at continental or regional scales (Bhatt et al., 2013), while microhabitat availability, land use, and biotic interactions may play more pronounced roles at local scales (Rochlin et al., 2016). Despite these insights from other taxa, comprehensive multi-scale analyses of mosquito responses to environmental and biotic factors remain limited. To fill these gaps in mosquito community ecology and risk assessment, our study applies joint species distribution modelling and to VectorNet mosquito community data across Europe to address three key questions:

1. How can we effectively leverage sparse, heterogeneous sampling data to construct robust continental-scale vector community models?
2. How do Joint Species Distribution Models (JSDMs), which account for biotic interactions, compare to Multi Species Distribution Models (MSDMs) in terms of ecological insights for mosquito communities?
3. How does the relative importance of biotic interactions, environmental factors, and spatial components in shaping mosquito distributions vary across different spatial scales and species, and what are the implications for vector surveillance and control?

3.3 Methods

3.3.1 Mosquito Data

While single-species SDMs use presence points for individual species, joint species distribution models (JSDMs) require data on occurrence of communities of several species (in a site by species matrix), which are lacking for mosquitoes at broad scales. To enable JSDM application, we generated community data from presence points at 1, 2, 5, and 10 km resolutions across Europe. Resolutions above 10 km were excluded as recent reviews suggest most mosquito flight ranges are below 2-4 km (Verdonschot and Besse-Lototskaya, 2014) and models may have limited ability to capture species-environment responses and reduced utility for management at broader scales (Purse and Golding, 2015).

We used mosquito sampling data from the VectorNet consortium, a network of vector ecologists that collated 38,450 records of mosquito occurrence and abundance for 90 species from 403 studies (Braks et al., 2022). The VectorNet database as accessed in January 2022 covers an area between 23.79° and 66.45° latitude and -17.86° and 56.67° longitude across the palearctic region, spanning Europe (Figure 3.1). As several European mosquito species are morphologically similar and difficult to distinguish to the species level unless genetic methods are used (Chan et al., 2014), these phylogenetically distinct but morphologically similar sets of species were combined into four groups, each modelled together as a single group distribution (Table B.1). The coordinates of all 38,236 records, consisting of 75 individual species and the four species groups from 402 studies, were converted to the EPSG:3035 equal area format. These records were inspected in QGIS and using the CoordinateCleaner R package to identify and remove any duplicate or erroneous records from the dataset (QGIS Development Team, 2009; Zizka et al., 2019).

The sampling data were cleaned, duplicates removed and overlaid onto equal-area grids at 1 km, 2 km, 5 km, and 10 km resolutions across the study region. To mitigate potential

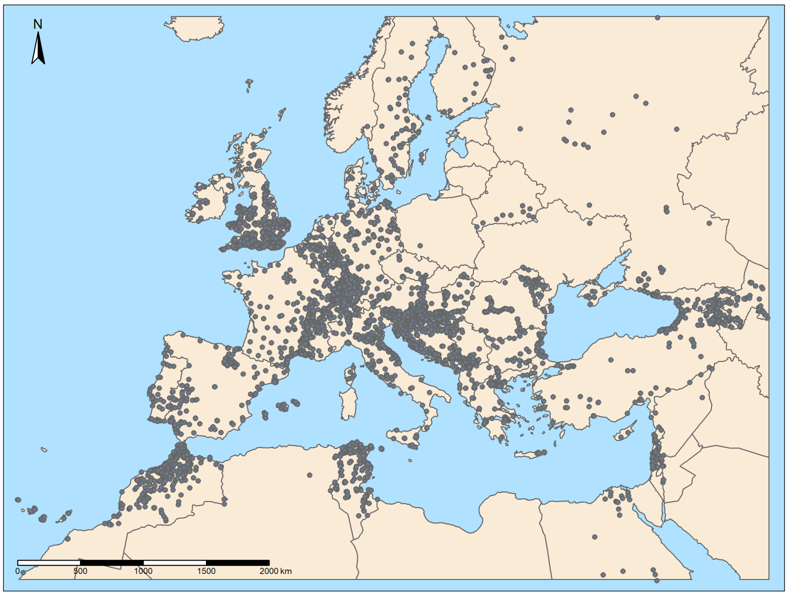

Fig. 3.1 Geographic distribution of mosquito sampling sites included in the study, based on data from the ECDC VectorNet database accessed in January 2022. Each grey dot indicates an individual sampling site where mosquitoes were recorded, visualized in the equal-area EPSG:3035 projection for accurate spatial representation.

biases arising from different sampling methods, we only retained grid cells containing data from both adult and larval sampling methods. Cells with data exclusively from either adult or larval sampling were excluded from the analysis. This selection process resulted in the retention of 402 studies across 7,544 distinct locations, distributed as follows: 4,183 cells at 1 km resolution, 4,148 cells at 2 km resolution, 3,478 cells at 5 km resolution, and 2,759 cells at 10 km resolution. Within each retained grid cell, a species was considered present if it had $\geq$1 occurrence record; otherwise, it was scored as absent. This process generated site-by-species community matrices for each spatial grain. To enhance numerical stability, species occurring in <1% of cells across each resolution's community matrix were removed, leaving 26 species in our dataset (Ovaskainen and Abrego, 2020).

3.3.2 Environmental Predictor Preparation

We adopted a resource-based approach for variable selection, including variables that are known *a priori* to correspond with resource needs for mosquito life stages (Hartemink et al., 2015), or to affect their demographic rates (Barker et al., 2014). We used measures of climate (precipitation and temperature), topography, biting host availability (defined as the travel time to the nearest population centre with at least 50,000 inhabitants), and land use as our environmental predictors (see Table 3.1 for the predictors considered and biological rationale). These predictors were summarised at 1km, 2km, 5km, and 10km grid square resolutions to investigate the scale dependence of species' responses to different environmental factors (Václavík and Meentemeyer, 2012).

We anticipate that climatic effects on mosquito demography may be particularly evident at broader scales (Asigau et al., 2017; Bhatt et al., 2013; Chase and Knight, 2003; Mulatti et al., 2014), while land use, habitat, and host effects may be easier to detect at finer spatial scales (Parham et al., 2015). To address collinearity and singularity, variables with a Pearson's correlation coefficient above 0.7 or exhibiting near-zero variance were candidates for removal. Near-zero variance predictors were identified using the `caret` package in R, with criteria of a frequency ratio exceeding 19 and less than 10% unique values (Kuhn, 2008). Snow and wetland land cover variables met these criteria and were removed, whilst all other variables were retained for analysis.

Table 3.1 Environmental predictors used in the species distribution models, their descriptions, units, and biological rationale for inclusion. The predictors were selected using a resource-based approach, focusing on factors that correlate with resource needs for mosquito life stages. †See Additional File A for the sources and processing methods of these environmental predictors for each spatial resolution.

Predictor Category	**Predictor Name**	**Description / Units**	**Biological Rationale**
Climate	Precipitation of Warmest Quarter	Total precipitation of warmest quarter (mm)	Influences breeding sites and larval development; higher precipitation increases mosquito populations (Brugueras et al., 2020; Ruiz et al., 2010).
Climate	Annual Precipitation	Total precipitation (mm)	Affects moisture availability for breeding; wetter conditions support larger populations (Deichmeister and Telang, 2011; Roiz et al., 2014).
Climate	Mean Temperature of Coldest Quarter	Mean temperature of coldest quarter (°C)	Cold temperatures limit mosquito survival and restrict geographical distribution (Ciota et al., 2014).
Climate	Annual Mean Temperature	Mean temperature (°C)	Influences development rates, survival, and behaviour; warmer temperatures favour populations (Mordecai et al., 2019).
Climate	Growing Degree Days	Cumulative number of days above 10°C	Represents accumulated heat required for mosquito development; higher values indicate faster development and more generations (Mulatti et al., 2014).
Climate	Enhanced Vegetation Index (EVI)	Measure of vegetation greenness and productivity (unitless)	Indicates mosquito habitats such as moist areas with shade and resting sites (Brown et al., 2008).
Climate	EVI Homogeneity	Measure of EVI value change across a year (unitless)	Seasonal consistency of vegetation greenness; heterogeneous landscapes provide various microhabitats for different species.
Topography	Elevation	Elevation above sea level (m)	Limits distribution due to changes in temperature, humidity, and vegetation; specific ranges for some species (Asigau et al., 2017).
Topography	Accessibility	Distance to nearest population centre of 50,000 inhabitants (km)	Influences ease of mosquito sampling and species introduction through human activity (Egizi et al., 2016).
Biting Host Availability	Mammalian and Avian Livestock Densities	Log number of livestock per km^2	Livestock provide blood meals for mosquitoes; higher densities may support larger populations.
Biting Host Availability	Human Population Density	Number of people per km^2	Provides blood meals and alters landscapes through urbanisation and land-use changes (Townroe and Callaghan, 2014).
Land Use	Land Cover (Wetland, Urban, Tree, Shrub, Agricultural)	Categorical land cover types (%)	Different land cover types offer various habitats; wetlands for breeding, urban areas, trees, shrubs, and agriculture for resting and feeding (Fuller et al., 2012).

3.4 Fitting Joint and Multi-Species Distribution Models at Multiple Spatial Scales

3.4.1 Analysis Pipeline

The full analysis pipeline was implemented separately at four focal spatial resolutions (grain sizes): 1 km, 2 km, 5 km, and 10 km, allowing examination of how the determinants of species distributions and communities vary across spatial scales. The 1 km scale matches the most commonly used SDM resolution, while coarser grids allow us to examine how species responses and model accuracy vary across scales. The analysis pipeline applied to each focal resolution is illustrated in a detailed process diagram (Figure 3.2).

3.4.2 Accounting for Spatial Autocorrelation

Spatial predictors based on distance-based Moran's eigenvector maps (dbMEM) were incorporated to account for unmeasured spatially structured environmental factors and to mitigate spatial autocorrelation in model residuals (Dray et al., 2012; Viana et al., 2022). For each study grain (grid cell size), a dbMEM was derived using the centroid coordinates of the community grid cells. The first 10 significant components of the dbMEM were retained and used to generate a spatial matrix to serve as a spatial random effect, controlling for autocorrelation in model fitting. These first 10 eigenvectors were inspected using correlograms and captured spatial autocorrelation peaks between 1 and 60 km across all resolutions. Subsequent eigenvectors represented lower levels of autocorrelation (Moran's I value < 0.3), indicating that the retained components adequately captured the spatial structure in the community data.

3.4.3 Hyperparameter Selection

An elastic net regularized regression approach was employed to tune the hyperparameters, alpha (α, mixing parameter) and lambda (λ, regularization strength), which control the influence of environmental, spatial, and biotic (species-to-species associations) model components (Friedman et al., 2010; Zou and Hastie, 2005). Two hundred randomized combinations of alpha and lambda values were selected and applied to 5-fold cross-validation subsets of the data, partitioned into environmental, spatial, and biotic components (see Additional File A for the distribution used for sampling random hyperparameters). This tuning process identified optimal hyperparameter settings that minimized cross-validation negative log-likelihood for each data component. The negative log-likelihood was used as the loss metric, as it provides a measure of model fit, with lower values indicating better fit.

3.4.4 JSDM and MSDM Fitting

Using the optimal hyperparameters, two types of models were fitted:

1. **Joint Species Distribution Models (JSDMs)** incorporating environmental, spatial, and biotic components. JSDMs model multiple species simultaneously, allowing for residual correlations between species through a covariance matrix. This approach captures species interactions and shared responses to unmeasured environmental factors (Ovaskainen and Abrego, 2020).

2. **Multi-species Distribution Models (MSDMs)** use the same environmental, spatial, and biotic predictors as JSDMs but treat each species independently. MSDMs do not model residual correlations between species, meaning any associations are due to similar responses to measured variables, rather than species interactions or shared responses to unmeasured factors (Pichler and Hartig, 2021).

Both models utilized a probit link function to relate predictors to species presences/absences, enabling comparison of JSDM performance with independent species treatments in MSDMs.

3.4.5 MSDM and JSDM Performance

To evaluate model performance, a randomized hold-out method was used, with 20% of the data randomly reserved for testing and the remaining 80% for training. This process was repeated 10 times to mitigate the risk of excluding rare species from the test sets, which can impact overall assessment of accuracy. The model's ability to discriminate species presence from absence was assessed using the area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS). These metrics were calculated independently for each species.

Model outputs showing species suitability in grid cells were converted to binary predictions using thresholds that minimized the difference between sensitivity and specificity. AUC scores range from 0 to 1, where values ≥ 0.7 are considered good to excellent predictions (Allouche et al., 2006; Araújo et al., 2005). TSS values over 0.4 are considered acceptable, and values ≥ 0.6 are considered useful (Allouche et al., 2006; Elith and Leathwick, 2017; Elith et al., 2008). Models with AUC ≥ 0.7 or TSS ≥ 0.4 were considered accurate for predicting species distributions, and species not meeting these thresholds were discarded from further analysis, using thresholds that minimized the difference between sensitivity and specificity (Lobo et al., 2008).

3.4.6 Factors Influencing Model Performance

To further investigate factors influencing model performance, we implemented three Bayesian models using the `brms` R package (Bürkner et al., 2022).

1. Species-level regression models examined the influence of spatial resolution, model type, and species prevalence on AUC and TSS. A beta distribution was used for AUC, and a Student's t-distribution for TSS.

2. A logistic regression model with a Bernoulli distribution examined how spatial resolution and species prevalence influenced significant associations between mosquito species and environmental parameters.

3. A Gaussian model explored scale-dependent changes in residual species correlation strengths, with spatial resolution as a fixed effect and unique species interaction pairs as random effects.

3.4.7 Variance Partitioning

To quantify the relative importance of environmental, spatial, and biotic factors underlying community structure, we employed variance partitioning of the fitted JSDMs and MSDMs following Leibold et al. (2022). A series of Bayesian regression models was used to investigate the effects of spatial resolution, model type, and species prevalence on responses to risk factors. Fixed effects for spatial resolution and model type, along with a second-order polynomial for prevalence, were incorporated. Random intercepts accounted for variation among species and within-species differences between model types.

3.4.8 Predicting Species and Community Distributions

The JSDM was used to generate predictions of species responses to environmental predictors and residual species correlations, following Pichler and Hartig (2021). Environmental data for mainland Europe and Great Britain were employed to produce continental-scale species occurrence predictions. Habitat suitability predictions were generated for all well-predicted species (based on AUC and TSS values). To estimate model uncertainty, a bootstrap resampling technique with 100 samples was used to retrain the model, calculating 95% confidence intervals for predictions.

3.5 Results

3.5.1 Derived Mosquito Community Patterns

The most prevalent species across all spatial grains included important disease vectors, namely *Culex pipiens*, *Aedes albopictus*, *Aedes japonicus*, and *Anopheles maculipennis*. *Culex pipiens* was particularly ubiquitous, occurring in 36.79% of cells at 1 km resolution and increasing to 39.84% at 10 km resolution (Table 3.2). In contrast, *Anopheles atroparvus*, *Aedes sticticus*, *Aedes annulipennis*, and *Anopheles sacharovi* were consistently the least prevalent across scales. *Anopheles atroparvus*, for instance, was found in only 1.03% of cells at 1 km resolution, increasing slightly to 1.37% at 10 km resolution.

Several moderately prevalent species were found across 25-73% of the cells at each spatial grain. These included *Culex theileri*, present in 6.48% of cells at 1 km and 8.64% at 10 km, *Aedes caspius* (7.84% at 1 km to 7.73% at 10 km), and *Culiseta annulata* (10.61% at 1 km to 10.19% at 10 km). Other species, such as *Aedes annulipes/cantans*, *Culex perexiguus/univittatus*, and *Culex territans*, were found in less than 20% of cells across all spatial grains, with *Aedes annulipes/cantans* showing the lowest prevalence among these (1.22% at 1 km to 1.37% at 10 km). Average species richness of the mosquito community increased as the spatial grain became coarser. At the finest resolution of 1 km, we observed a mean of 1.81 ± 1.55 sampled species per cell, which gradually increased to 2.11 ± 1.84 species per cell at the coarsest 10 km resolution. This trend was accompanied by a decrease in the number of cells containing communities from, 4,518 at 1 km resolution to 2,759 at 10 km resolution. Despite these changes, the maximum species richness remained relatively stable across resolutions, ranging from 16 species at 1 km to 18 species at coarser scales.

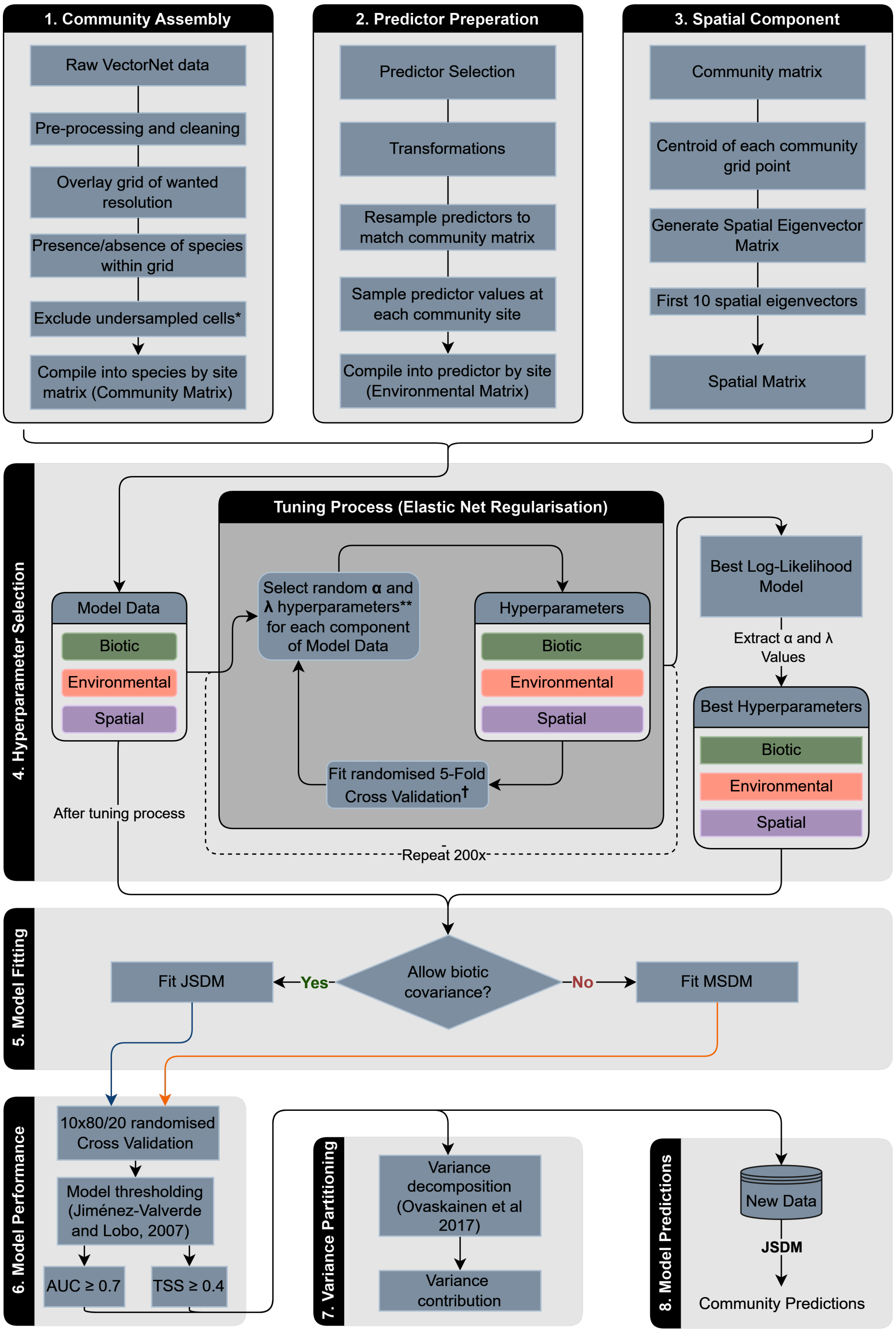

Fig. 3.2 Analytical process diagram for generating Joint/Multi Species Distribution Model outputs. *Undersampled cells contain only juvenile or adult mosquito sample data. **Hyperparameter distributions are provided in Figure B.1. †Cross-validation metrics during hyperparameter tuning assesses model accuracy across all species predictions collectively rather than individually.

Table 3.2 Variation in mosquito community characteristics and species prevalence across different spatial grains created from the VectorNet dataset using grid-based aggregation.

Species	**1 km**	**2 km**	**5 km**	**10 km**
Aedes albopictus	940 (22.47%)	785 (21.63%)	599 (21.77%)	387 (22.15%)
Aedes annulipes/cantans	51 (1.22%)	48 (1.32%)	38 (1.38%)	24 (1.37%)
Aedes caspius	328 (7.84%)	291 (8.02%)	225 (8.18%)	135 (7.73%)
Aedes cinereus/geminus	123 (2.94%)	113 (3.11%)	103 (3.74%)	83 (4.75%)
Aedes detritus/coluzzi	214 (5.12%)	187 (5.15%)	132 (4.80%)	67 (3.84%)
Aedes geniculatus	127 (3.04%)	115 (3.17%)	96 (3.49%)	77 (4.41%)
Aedes japonicus	679 (16.23%)	617 (17.00%)	506 (18.39%)	336 (19.23%)
Aedes sticticus	48 (1.15%)	41 (1.13%)	35 (1.27%)	26 (1.49%)
Aedes vexans	299 (7.15%)	276 (7.60%)	235 (8.54%)	157 (8.99%)
Anopheles atroparvus	43 (1.03%)	40 (1.10%)	31 (1.13%)	24 (1.37%)
Anopheles claviger	373 (8.92%)	342 (9.42%)	281 (10.21%)	194 (11.10%)
Anopheles labranchiae	204 (4.88%)	191 (5.26%)	157 (5.70%)	120 (6.87%)
Anopheles maculipennis	587 (14.03%)	532 (14.66%)	415 (15.08%)	291 (16.66%)
Anopheles messeae	63 (1.51%)	59 (1.63%)	54 (1.96%)	38 (2.18%)
Anopheles plumbeus	197 (4.71%)	180 (4.96%)	150 (5.45%)	113 (6.47%)
Anopheles sacharovi	45 (1.08%)	45 (1.24%)	37 (1.34%)	27 (1.55%)
Coquillettidia richiardii	190 (4.54%)	161 (4.44%)	123 (4.47%)	70 (4.01%)
Culex hortensis hortensis	193 (4.61%)	174 (4.79%)	154 (5.60%)	129 (7.38%)
Culex modestus	104 (2.49%)	96 (2.64%)	82 (2.98%)	60 (3.43%)
Culex perexiguus/univittatus	75 (1.79%)	71 (1.96%)	63 (2.29%)	47 (2.69%)
Culex pipiens	1539 (36.79%)	1358 (37.41%)	1078 (39.17%)	696 (39.84%)
Culex territans	71 (1.70%)	65 (1.79%)	61 (2.22%)	51 (2.92%)
Culex theileri	271 (6.48%)	243 (6.69%)	201 (7.30%)	151 (8.64%)
Culex torrentium	190 (4.54%)	178 (4.90%)	154 (5.60%)	115 (6.58%)
Culiseta annulata	444 (10.61%)	389 (10.72%)	285 (10.36%)	178 (10.19%)
Culiseta longiareolata	193 (4.61%)	172 (4.74%)	146 (5.31%)	105 (6.01%)

3.5.2 Model Performance

Predictive performance was not significantly different between JSDMs and MSDMs (Table 3.3, Figure 3.3), with twelve of the 27 modelled mosquito species classified as "well predicted" by our criteria by either method. The mean AUC values were 0.69 ± 0.11, and the mean TSS values were 0.34 ± 0.2 across all species and methods (Figure 3.3). The JSDM was most accurate at predicting distribution for *Anopheles labranchiae* (AUC 0.95 ± 0.02, TSS 0.86 ± 0.06), followed by *Culex perexiguus/univittatus* (AUC 0.90 ± 0.03, TSS 0.72 ± 0.12) and *Culex torrentium* (AUC 0.80 ± 0.05, TSS 0.48 ± 0.09). In contrast, the JSDM performed poorly at predicting *Culex pipiens* and *Aedes vexans* distributions, with mean AUC values of 0.56 ± 0.03 and 0.58 ± 0.05, respectively, and correspondingly low mean TSS values (0.11 ± 0.04, 0.16 ± 0.07). Several species, such as *Culex theileri* (AUC 0.79 ± 0.05) and *Aedes japonicus* (AUC 0.77 ± 0.05), with mean AUC values above 0.70, were predicted adequately by both JSDM and MSDM models (Figure 3.3).

Across all species, neither model type nor grid cell resolution had a meaningful impact on AUC values of distribution models (Table 3.3). Unlike previous studies for other taxa, AUC was also not associated with species prevalence (posterior median = -1.29, 95% CI [-5.52, 2.82]). The significance of the species level random effect suggests that unmeasured species level factors explained a significant amount of variability in model AUC. The significant random effect interaction between species and model type indicates that whether JSDMs or MSDMs are more accurate depends on the species in question, though this effect is small (Table 3.3). For TSS, model type (posterior median = -0.01, 95% CI [-0.03, 0.00]), spatial resolution (posterior median = 0.00, 95% CI [0.00, 0.00]), and species prevalence (posterior median = -0.61, 95% CI [-1.68, 0.45]) similarly showed minimal impacts on distribution model accuracy (Table 3.3). Again, the species-level random effect (posterior median = 0.18, 95% CI [0.14, 0.25]) and the interaction between species and model type (0.02, 95% CI [0.01, 0.04]) had significant, but small impacts on TSS.

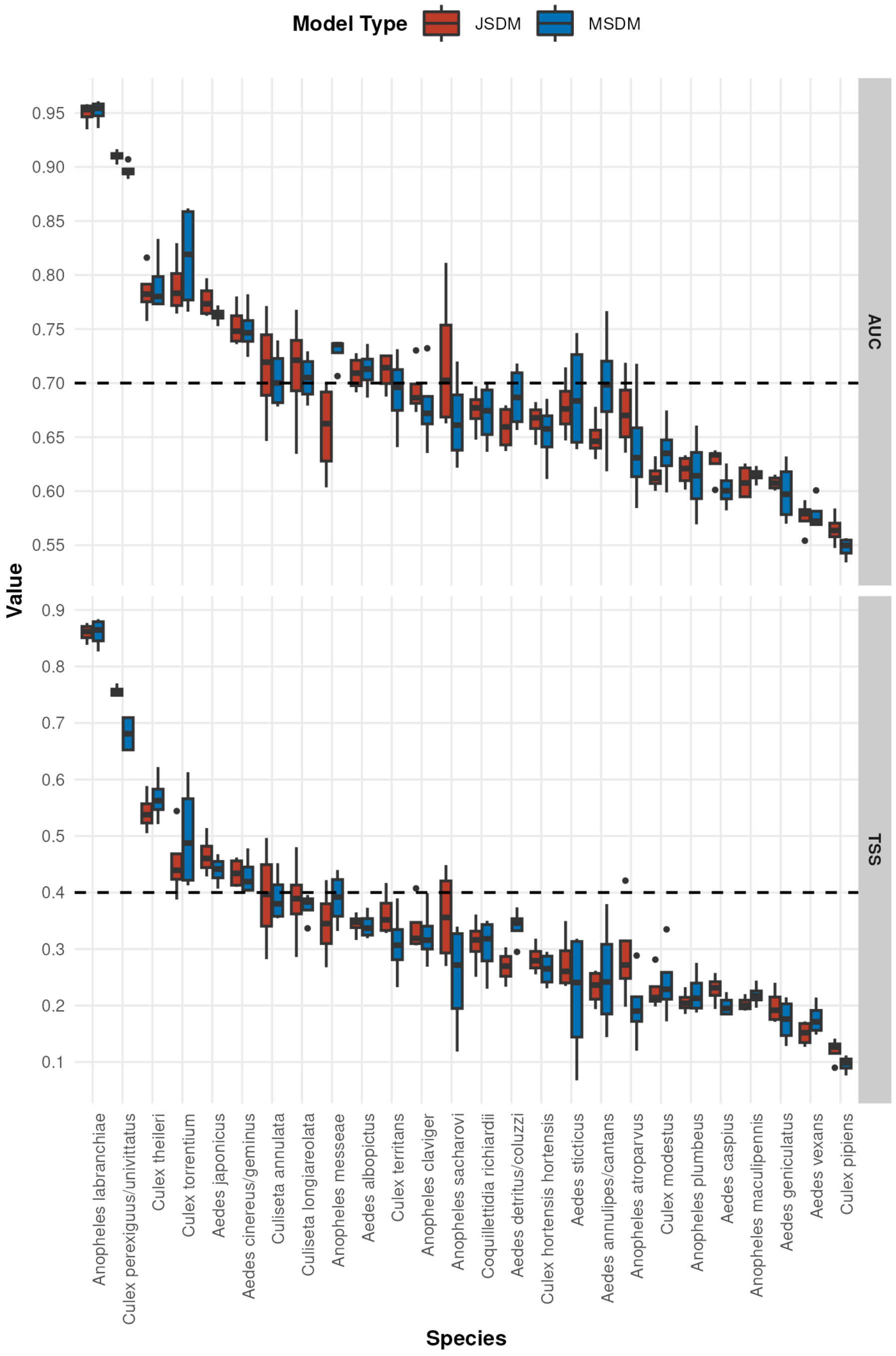

Fig. 3.3 Model performance metrics distribution and mean values of two performance metrics, AUC (Area Under the Curve) and TSS (True Skill Statistic), for different models (JSDM and MSDM) across all resolutions. Boxplots represent the interquartile range and median of the values for each metric. Colours represent different models (JSDM: red, MSDM: blue) and horizontal lines represent thresholds for well-predicted species (AUC ≥ 0.7, TSS ≥ 0.4). Full details on AUC and TSS values for each species can be found in Table B.3 and Table B.4.

Table 3.3 Results of Bayesian regression models predicting Area Under the Curve (AUC) and True Skill Statistic (TSS) for species distribution. The AUC model employed a beta regression, while the TSS model utilised a Student's t-family regression. The table presents parameter estimates along with their 95% credible intervals.

Parameter Type	**Model Term**	**AUC**	**TSS**
Fixed	Intercept	0.91 [0.67, 1.14]	0.34 [0.26, 0.41]
Fixed	Model type (MSDM)	0.01 [-0.04, 0.06]	-0.01 [-0.03, 0.00]
Fixed	Resolution	0.00 [-0.01, 0.00]	0.00 [0.00, 0.00]
Fixed	Species prevalence	-1.29 [-5.52, 2.82]	-0.61 [-1.68, 0.45]
Dispersion	phi (ϕ)	35.66 [33.49, 37.94]	-
Variance	sigma (σ)	-	0.08 [0.07, 0.08]
Random	Species	0.56 [0.43, 0.77]	0.18 [0.14, 0.25]
Random	Species:Model	0.07 [0.03, 0.11]	0.02 [0.01, 0.04]

3.5.3 Variance Decomposition in JSDMs and MSDMs: Environmental, Spatial, and Biotic Components

Across all spatial resolutions, the median total variance explained was marginally higher in the JSDM (65%, 95% CI [64%, 65%]) compared to the MSDM (64%, 95% CI [64%, 65%]), though this difference was not statistically significant (Figure 4). The median variance explained by the environmental component was identical for both methods (JSDM: 45%, 95% CI [43%, 46%]; MSDM: 45%, 95% CI [44%, 46%]) across well-modelled species (Figure 2, Table 3.4). The MSDM attributed 7.2% more variance to the spatial component than the JSDM, with median values of 18% (95% CI [16%, 19%]) and 11% (95% CI [9%, 12%]) across well-modelled species, respectively. Conversely, the JSDM attributed a substantially larger proportion of variance to the biotic component (10%, 95% CI [9%, 11%]) compared to the MSDM (1%, 95% CI [0%, 2%]) (Figure 2, Table 3.4). Species prevalence had no effect on the amount of variance attributed to different variance components (Table 3.4). Spatial scale (resolution) had no significant impact on the variance attributed to the biotic component (-1.1%, 95% CI [-4.4%, 2.2%]). The percentage of variance explained by the environmental component significantly decreased across spatial scales from 1 km to 10 km grid cells (-2.9%, 95% CI [-4.6%, -1.1%]), while the percentage of variance explained by the spatial component significantly increased (4.5%, 95% CI [1.6%, 7.2%]). The total variance explained showed a slight but significant decrease with increasing spatial scale (-0.56%, 95% CI [-0.88%, -0.21%]).

Table 3.4 Parameter estimates, and variance explained from Bayesian hierarchical beta regression models predicting total variance and variance components

Parameter Type	**Model Term**	**Biotic**	**Environmental**	**Spatial**	**Total**
Fixed	Intercept	-2.40 [-3.10, -1.80]	-0.06 [-0.67, 0.47]	-2.50 [-3.20, -1.80]	0.63 [0.33, 0.89]
Fixed	Resolution	-0.01 [-0.04, 0.02]	-0.03 [-0.05, -0.01]	0.05 [0.02, 0.07]	-0.01 [-0.01, -0.00]
Fixed	Model Type (MSDM)	-1.64 [-2.31, -0.99]	-0.01 [-0.35, 0.30]	0.57 [0.06, 1.08]	-0.02 [-0.05, 0.01]
Fixed	Prevalence	-2.30 [-31.70, 28.10]	-5.60 [-30.90, 26.50]	-5.20 [-41.40, 28.80]	2.80 [-7.10, 11.20]
Fixed	Phi (ϕ)	59.00 [40.00, 81.00]	53.00 [37.00, 73.00]	36.00 [25.00, 50.00]	1945.00 [1346.00, 2736.00]
Random	Species	0.44 [0.02, 1.12]	0.72 [0.37, 1.34]	0.80 [0.29, 1.48]	0.43 [0.24, 0.77]
Random	Species:Model	0.71 [0.41, 1.12]	0.34 [0.19, 0.64]	0.51 [0.29, 0.94]	0.03 [0.00, 0.05]

3.5.4 Species-Specific Patterns in Explained Variance Across Model Types and Components

The MSDMs and JSDMs explained the highest proportion of total variance in species distribution for *Anopheles sacharovi*, with both model types showing similar performance across all resolutions (72% of variance explained, 95% CI [71.4%, 73.3%], Figure 3.4). The models also performed well for the *Culex perexiguus/univittatus* group and *Anopheles messeae*, explaining over 71% of the total variance for each across all resolutions (95% CI [70.4%, 72.4%], Figure 3.4). In contrast, the models explained considerably less variance for invasive species across all resolutions. For *Aedes albopictus*, the MSDM and JSDM explained only 43% (95% CI [41.9%, 44.0%]) and 44% (95% CI [43.5%, 45.6%]) of the total variance, respectively across all resolutions. *Aedes japonicus* showed slightly better model performance, with 56% of variance explained by the MSDM (95% CI [55.2%, 57.2%]) and 57% by the JSDM (95% CI [55.9%, 57.9%]). *Anopheles labranchiae* had the highest variance explained by the environmental component of around 62.5% (95% CI [56.1, 68.9]) for both the MSDM and JSDM, followed by the *Culex perexiguus/univittatus* group. *Culex* *torrentium* and *Culiseta annulata* had the lowest variance explained by the environmental component, at 12.6% (95% CI [8.82, 17.0]) and 17.4% (95% CI [12.9, 22.5]). Notably, in addition to having a low total variance explained, the invasive species *Aedes albopictus* had a low variance explained by environmental components, with 19.2% (95% CI [14.4, 24.5]) for the MSDM and 26.6% (95% CI [21.0, 32.5]) for the JSDM (Figure 3.4).

Spatial factors significantly influenced the distributions of several mosquito species, with notable variations across genera (Figure 3.4). The *Culiseta* genus demonstrated the strongest spatial dependencies, with spatial components accounting for up to 44.4% (SD = 11.6%) of the variance in MSDMs for *Culiseta longiareolata*. Other species like *Aedes albopictus* and *Anopheles sacharovi* also showed substantial spatial components, ranging from 8.9% to 23.9% across model types. In contrast, species such as *Culex torrentium* and *Anopheles labranchiae* exhibited relatively low spatial components (less than 3% in both JSDMs and MSDMs).

Within JSDMs, *Culiseta annulata* had the highest proportion of variance explained by biotic interactions (26.8%; 95% CI [21.0, 32.5]), followed by *Anopheles messeae* (14.2%; 95% CI [10.1, 18.8]), *Anopheles sacharovi* (13.6%; 95% CI [9.5, 18.1]), *Culex perexiguus/univittatus* (12.9%; 95% CI [8.9, 17.3]), and *Culex territans* (11.2%; 95% CI [7.5, 15.3]). *Aedes japonicus* and *Anopheles labranchiae* had the lowest proportion of variance explained by biotic interactions, with median values of 4.3% (95% CI [2.3, 6.8]) and 4.5% (95% CI [2.5, 7.2]), respectively, followed by *Aedes cinereus/geminus* (4.8%; 95% CI [2.7, 7.4]) and *Aedes albopictus* (9.0%; 95% CI [5.9, 12.8]) (Figure 3.4).

3.5.5 Species-species residual associations

The analysis revealed both positive and negative correlations between species across different spatial scales, after filtering out very weak correlations ($|r| \leq 0.01$). Positive correlations predominated across all scales examined. At the 1 km scale, 322 correlations were observed

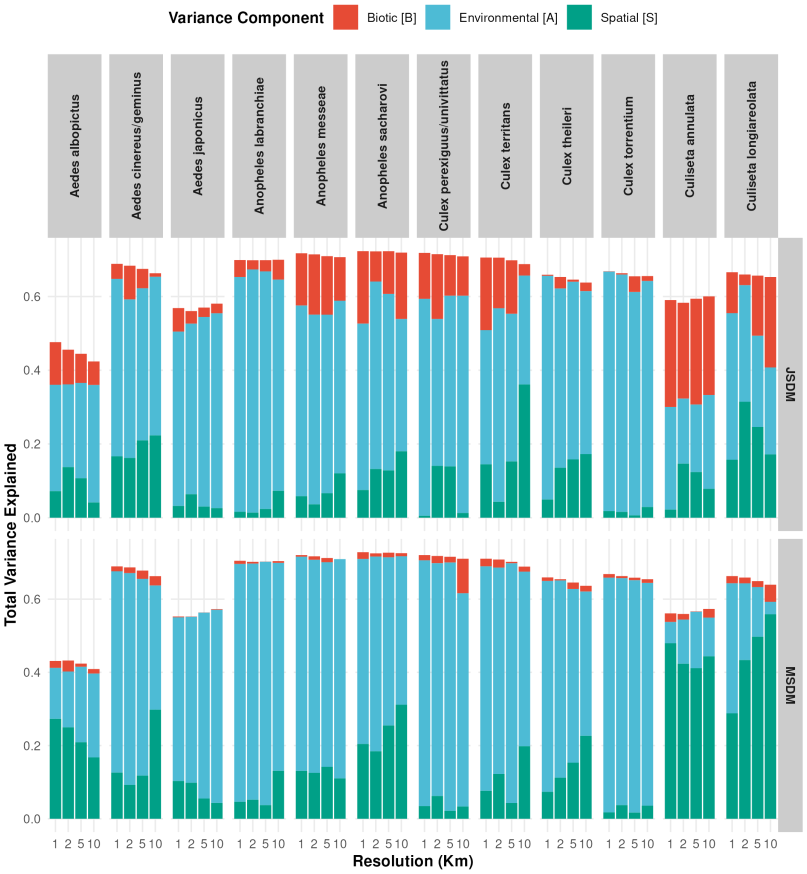

Fig. 3.4 Total variance explained across all resolutions for a set of well-modelled species using Multi-Species (MSDM) and Joint (JSDM) SDM approaches. Variance is decomposed into constituent components: Environmental [A], Biotic [B], and Spatial [S].

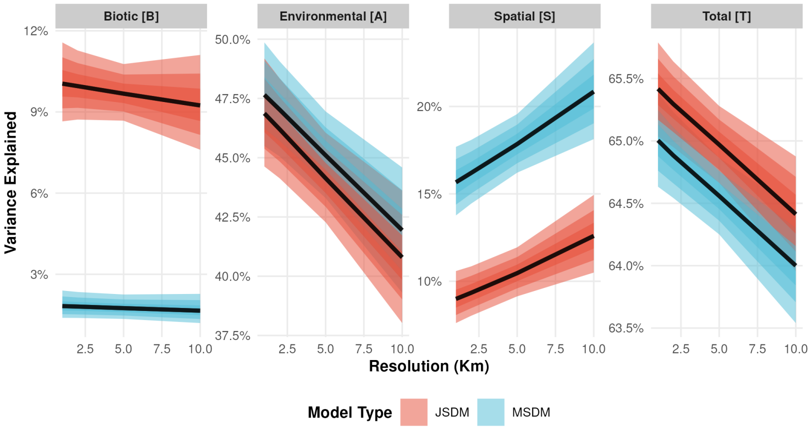

Fig. 3.5 Marginal effects of resolution on median variance explained across all well-predicted species for each variance component and for total variance, also showing the interaction between model type and resolution. For all panels lines and shaded areas indicate median estimates and 95% confidence intervals, respectively.

(77.0% positive), while the 2 km scale showed 280 correlations (80.0% positive). The 5 km scale exhibited 276 correlations (77.9% positive), and the 10 km scale demonstrated the highest number at 326 correlations (84.0% positive). The invasive species *Ae. albopictus* and *Ae. japonicus* displayed divergent residual correlation patterns compared to native mosquito species, exhibiting negative correlations with all other species across all spatial scales. These negative correlations were strongest at 1 km and 10 km scales, and weakest at 2 and 5 km scales (Figure 3.6).

3.5.6 Environmental drivers of mosquito distribution

Environmental drivers of mosquito distribution exhibited scale-dependent effects, with the likelihood of detecting significant environmental predictors decreasing as model resolution increased from 1 km to 10 km (-0.09, 95% CI [-0.15, -0.04], see Figure B.2). For well-modelled species, those with higher prevalence were more likely to show significant effects of environmental variables (median posterior estimate for species prevalence of 16.79, 95% CI [12.22, 22.08]). Notably, the direction of environmental effects remained consistent across spatial scales, though effect magnitudes often increased at coarser resolutions (Figure 3.7).

Among the well-modelled species, climatic factors emerged as significant predictors for 11 out of 12 species, yielding 29 significant species-predictor relationships. Temperature-related variables, particularly mean annual temperature and minimum winter temperature, were the most influential climatic predictors across species. Host availability was a significant predictor for eight out of 12 species, with human population density being the primary host-related factor, followed by mammalian and avian livestock densities. Topographic variables, specifically elevation and accessibility (measured as distance to the nearest population centre of 50,000 or more inhabitants), were significant for seven out of 12 species. Elevation showed particularly widespread significance across scales. While precipitation and vegetation metrics also demonstrated significant associations, these were less frequent. Land use factors

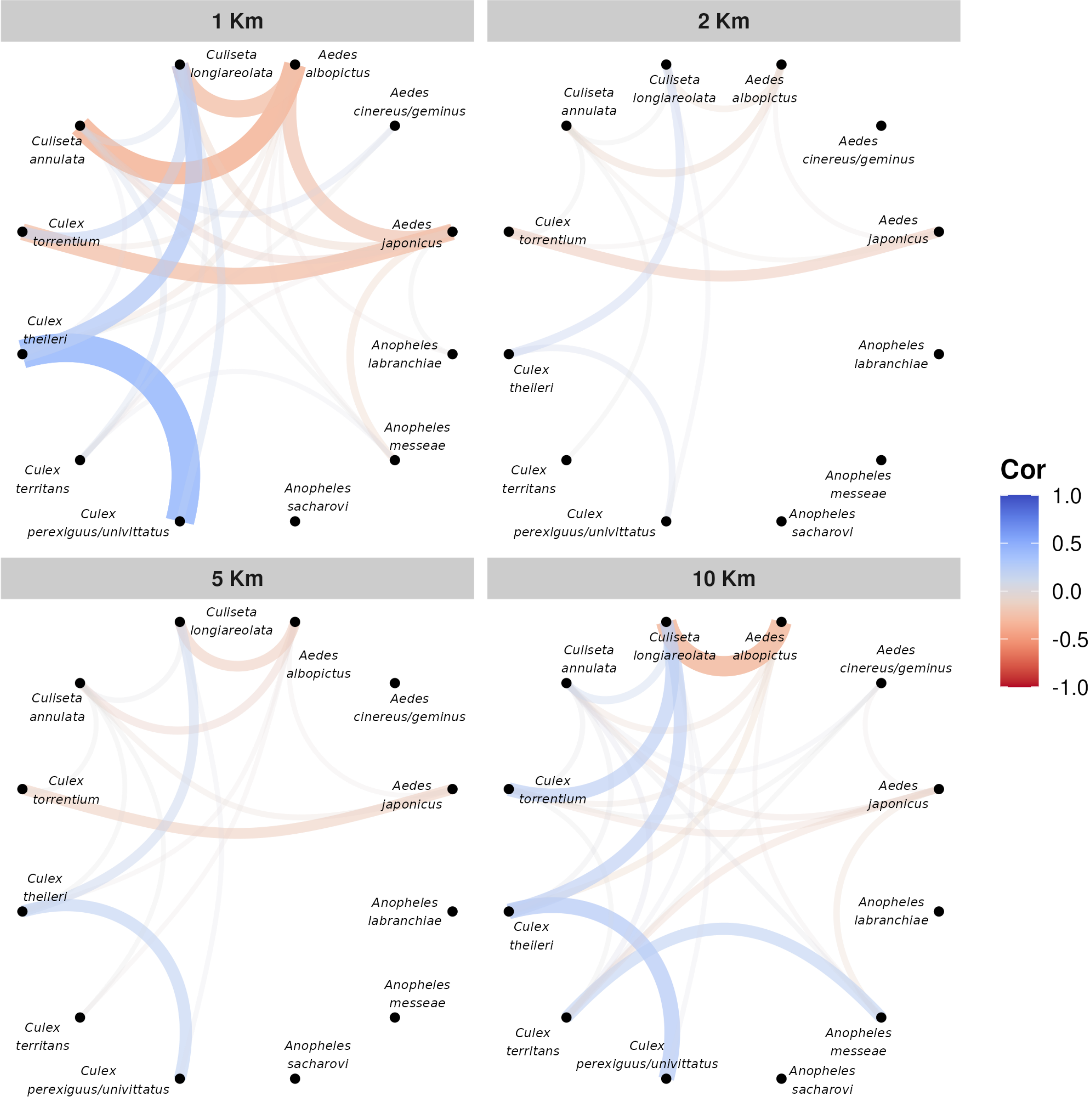

Fig. 3.6 Species residual correlation networks for the Joint Species Distribution Model (JSDM) at 1, 2, 5, and 10 km resolutions. Nodes represent individual species, and edges indicate undirected correlations between species. The width and transparency of each edge are proportional to the squared absolute value of the correlation coefficient, highlighting the strongest correlations.

had the least influence on distribution, affecting only five species. Invasive mosquitoes (*Ae. albopictus* and *Ae. japonicus*) and two prevalent native species (*Cs. annulata* and *An. labranchiae*) showed responsiveness to the widest range of environmental predictors. However, it's worth noting that these *Aedes* species had low overall variance explained by the models and a high proportion of variance attributed to spatial predictors. In contrast, the least prevalent species were significantly influenced by only one predictor each: *Cx. perexiguus/univittatus* showed a positive association with mean annual temperature, while *Cx. territans* was positively associated with population density.

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Invasive mosquitoes (*Ae. albopictus* and *Ae. japonicus*) and two prevalent native species (*Cs. annulata* and *An. labranchiae*) showed responsiveness to the widest range of environmental predictors. In contrast, the least prevalent species (*Cx. perexiguus/univittatus* and *Cx. territans*) exhibited more limited predictor associations. Specifically, *Cx. perexiguus/univittatus* showed a positive association only with mean annual temperature, while *Cx. territans* was solely positively associated with population density. These less prevalent species demonstrated markedly fewer significant predictors compared to the more widespread mosquito species, suggesting potential limitations in their ecological adaptability or detection.

3.5.7 Community predictions at a continental scale

Modelled habitat suitability maps for four mosquito species across Europe, in general, align well with previously observed ranges. *Culex torrentium* appears to favour more northern latitudes, while *Culex theileri* is concentrated in southern regions. Among the invasive species, *Aedes japonicus* shows a broad suitability range spanning central to northern Europe, whereas *Aedes albopictus* remains largely confined to its typical southern distribution, aside from a small, potentially anomalous, suitable area along Norway's northern coast. Full predictions for all mosquito species can be found in Appendix B.

3.6 Discussion

This study represents the first application of JSDMs to predict mosquito communities at a continental scale, assessing the scale-dependent impacts of environmental, biotic, and spatial factors, as well as species prevalence on mosquito distributions. Our results demonstrate that JSDMs can predict distributions with good accuracy for nearly half of the analysed species, despite the relatively low average richness of mosquito communities. This highlights the potential of JSDMs in vector ecology, although the inability to model over 50% of species underscores the need for more comprehensive sampling. Our analysis revealed comparable accuracy across both prevalence-sensitive AUC and prevalence-insensitive TSS metrics, with no significant impact of spatial scale or mosquito species prevalence on model performance for either JSDMs or MSDMs. This finding contrasts with previous studies on other taxa, where species prevalence often influences model accuracy (Santika, 2011; Wisz et al., 2013). Notably, we achieved good models for approximately half of the species studied, suggesting

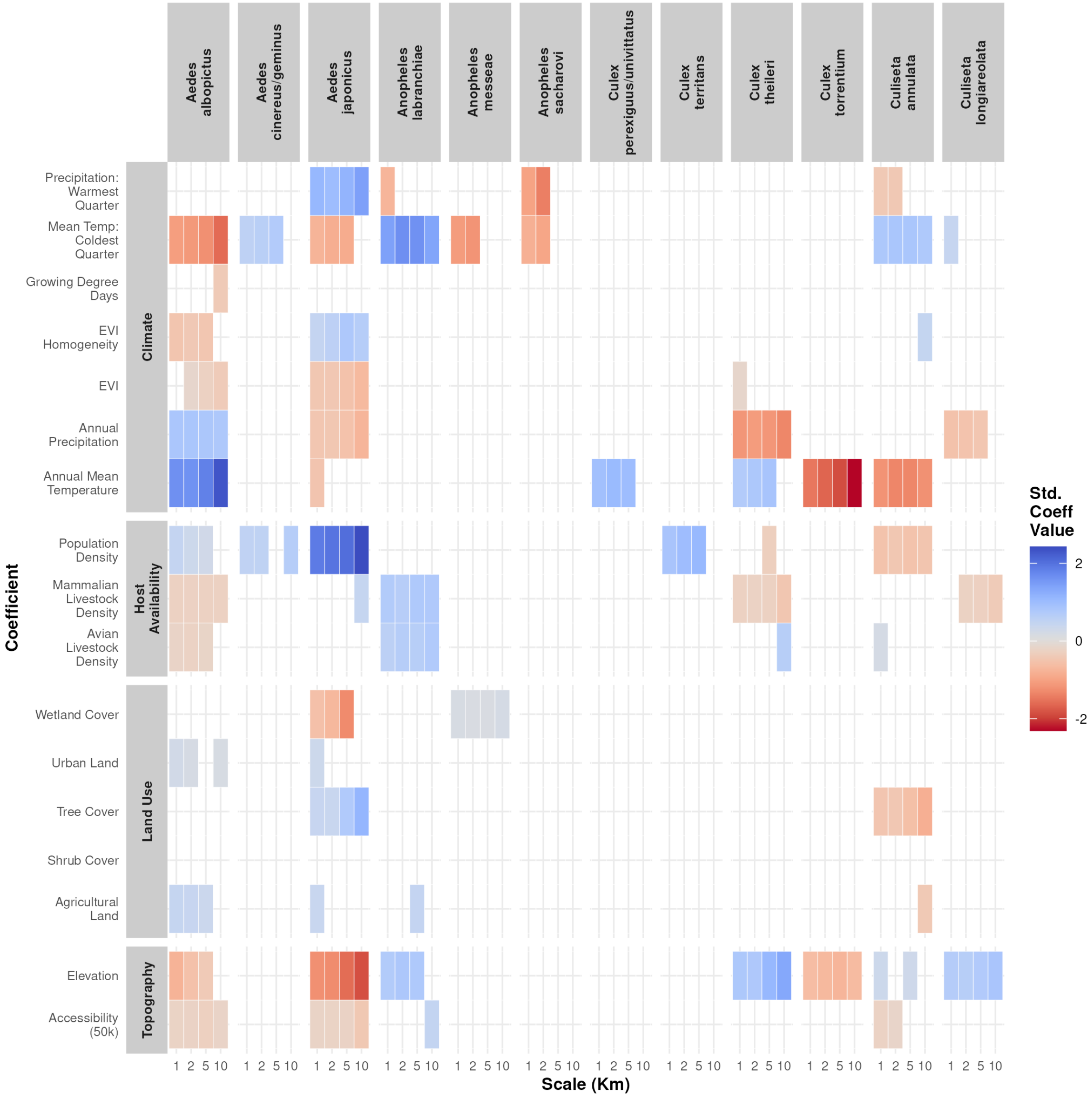

Fig. 3.7 Influence of environmental predictors on the distribution of 12 mosquito species across multiple spatial scales. Standardised coefficients are shown for climatic factors (temperature, precipitation, vegetation), host availability (human, livestock), land use, and topography (elevation, accessibility). The heat-map illustrates the strength and direction (positive or negative) of associations, with colour intensity reflecting the magnitude of the effect. Coefficients were calculated across increasing spatial scales (1-10 Km), revealing variations in species responses to environmental drivers.

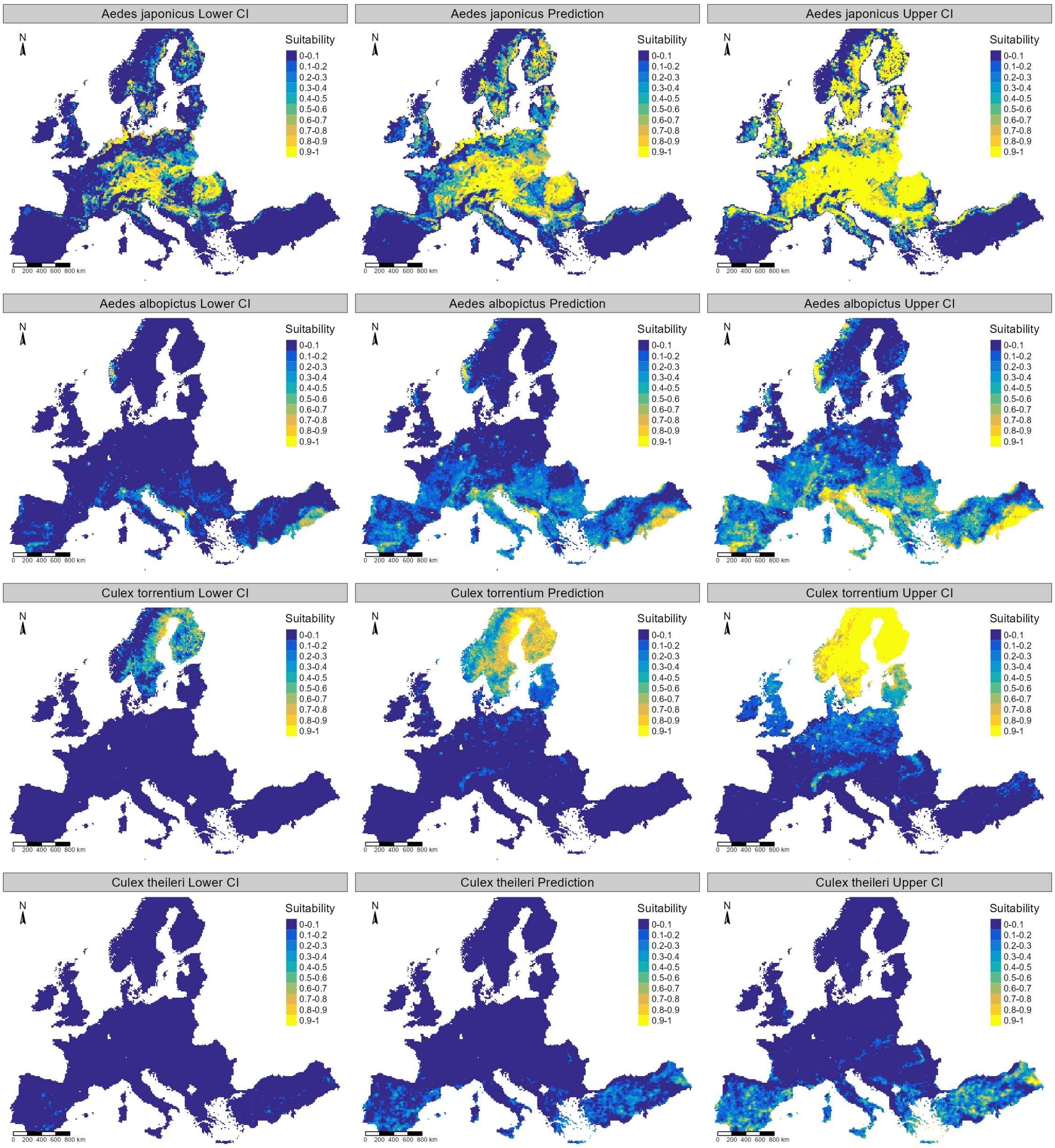

Fig. 3.8 Predicted habitat suitability for four mosquito species in Europe and Upper/Lower Confidence Intervals [CI], generated using our Joint Species Distribution Model (JSDM) at a 10km resolution.

that dense communities are not necessary for effective modelling of mosquito distributions at continental scales. However, this also highlights an important operational implication: less than 50% of species could be modelled successfully at these broad scales, indicating potential limitations in applying these methods to all mosquito species. While traditional SDMs often use balanced pseudo-absence ratios to address prevalence effects and achieve higher accuracy predictions (Barbet-Massin et al., 2012), the community-based nature of JSDM data makes this approach impractical. Nonetheless, our results suggest this limitation may be less critical for mosquito distribution modelling at continental scales.

The prevalence-independence observed was consistent across AUC and TSS metrics and spatial scales. This may indicate that factors not explicitly modelled, such as accounting for dispersal ability or micro-scale habitat data, may be more influential than prevalence in generating highly accurate occurrence predictions. Our results align with recent JSDM studies that found sample size had minor influence on model predictability and species with medium prevalence levels (30-50%) had consistently lower AUC values than rare or common species (Zhang et al., 2018). These findings have intriguing implications for modelling rare species, which are under-represented in current sampling data as they aren't currently associated with MBD risk. However, as demonstrated by the spread of Zika in the Americas, where native vectors are thought to be potential disease spreaders if introduced (Evans et al., 2017), the ability to model rare species effectively could be crucial for anticipating future disease risks.

Ecological theory typically assumes that species interactions are more influential at local scales (Soberón, 2007), with biotic interactions expected to have stronger explanatory power at finer spatial scales (Araújo and Rozenfeld, 2014; Thuiller et al., 2015; Wisz et al., 2013). In insect communities, predator-prey interactions and competition for oviposition sites are thought to have stronger effects at smaller spatial extents (Juliano, 2009; Vonesh and

Blaustein, 2010), with mosquito competition often occurring at the larval stage in localized breeding sites (Costanzo et al., 2011; Reiskind and Lounibos, 2009).

Our analysis using JSDMs challenges these established notions. We found no significant decrease in the biotic contribution to total variance explained at coarser resolutions, aligning with recent studies on woodland bird communities that show improved JSDM performance at coarser resolutions (König et al., 2021). The persistence of biotic effects at broader scales in our mosquito models may reflect the high mobility of adult mosquitoes and potential indirect interactions through shared resources or predators. However, caution is warranted in interpreting these associations as direct biotic interactions; positive correlations between species associations and functional similarity may instead represent shared responses to unobserved environmental predictors (Poggiato et al., 2021; Zurell et al., 2018).

Simulation studies have shown that as spatial scale increases, JSDMs may misinterpret shared environmental responses as positive species associations, even when no true interactions exist (Vallé et al., 2024; Zurell et al., 2018). Notably, our findings suggest that the relationship between invasive and native mosquito species remains consistent across spatial scales, contrasting with trends observed in other taxa where associations were more positive at larger spatial scales (König et al., 2021; Zurell et al., 2020). The consistent negative association of invasive species with natives suggests factors beyond shared environmental responses could be influencing these relationships, potentially reflecting genuine competitive interactions or niche differentiation. Despite potential artifacts in JSDM interpretations, leveraging this information could improve predictions of invasive mosquito species spread in the future (Poggiato et al., 2021).

Environmental factors, particularly temperature, emerged as crucial predictors of mosquito distributions across scales. The significance of fine-scale (1 km) temperature data highlights the importance of capturing thermal conditions critical for mosquito development (Mordecai et al., 2019). Species-specific responses to environmental variables allowed us to infer ecological requirements without directly incorporating life history traits (Lippi et al., 2023a). For example, *Aedes albopictus* and *Aedes japonicus* showed strong associations with urban environments, reflecting their preference for artificial container habitats, while *Aedes japonicus* was uniquely associated with tree cover, aligning with its tree-hole breeding behaviour. However, many species exhibited limited relationships with broad land cover factors, suggesting our models may not fully capture the diverse microhabitats mosquitoes utilize (Rochlin et al., 2016; Sallam et al., 2017). This variability in model performance, especially for invasive and generalist species, indicates the need for more refined environmental variables and consideration of species-specific dispersal mechanisms and non-equilibrium dynamics in future modelling efforts.

The mixed response to land-use drivers across mosquito species underscores the importance of incorporating species-specific life history traits when selecting predictor variables (Lippi et al., 2023a). For example, *Aedes albopictus* and *Aedes japonicus* showed strong associations with urban environments, reflecting their preference for artificial container habitats, while *Aedes japonicus* was uniquely associated with tree cover, aligning with its tree-hole breeding behaviour (Medlock et al., 2012; Mogi et al., 2020). Other species exhibited few significant relationships with broad land cover factors, suggesting these categories may not account for the small, varied, and often ephemeral microclimates that mosquitoes exploit (Rochlin et al., 2016; Sallam et al., 2017; Townroe and Callaghan, 2014). Incorporating host factors yielded mixed but significant results, with population density confirming the affinity of *Aedes* species for human-associated habitats (Benelli et al., 2020; Mogi et al., 2020; Severini et al., 2008). Notably, *Aedes albopictus* showed a negative relationship with farmland but a positive one with livestock density, demonstrating the model's ability to differentiate between habitat and host-based metrics. This nuanced approach offers insights beyond simple environmental proxies, providing a more comprehensive understanding of distributional drivers (Cardador et al., 2014; Hartemink et al., 2015).

Our findings show the utility of host density predictors in modelling mosquito distributions, particularly in the context of vector-borne diseases like West Nile virus, where pathogen transmission often depends on specific mosquito-host assemblages (Kilpatrick et al., 2007; Osório et al., 2012; Savage et al., 2007). However, the generalist feeding behaviour of many mosquito species, which adapt their feeding patterns based on host availability, complicates this relationship (Thiemann et al., 2011). A significant limitation of our study was the exclusion of wild avian and mammalian population data, which are important blood meal sources for various mosquito species and serve as primary reservoirs of mosquito-borne diseases in Europe (Osório et al., 2012; Puente et al., 2012; Tuten et al., 2012). Expanding these models to incorporate a wider array of host data could improve predictions, identify high-risk areas, and inform targeted surveillance efforts. However, empirical validation is necessary to confirm the utility of these models in enhancing disease risk assessments.

Additionally, investigating species interactions at finer spatial resolutions, particularly below 1 km, could yield better insights into mosquito co-occurrence, as interactions among mosquito species likely occur at breeding sites (Bevins, 2008; Braks et al., 2004; Ezeakacha and Yee, 2019). Furthermore, exploring whether the drivers identified in JSDMs influence both juvenile and adult stages of the mosquito life cycle could reveal variations in these relationships across life stages. Addressing these factors may significantly improve the prediction of invasive species distributions by effectively utilizing existing data, particularly in identifying potential areas for invasive species that have not yet reached equilibrium, which are challenging to predict using traditional SDM methods (Poggiato et al., 2021).

Furthermore, leveraging JSDM frameworks that incorporate traits and phylogenetic variables may help refine the interpretation of residual species correlations, offering a way to partially compensate for this uncertainty (Ovaskainen et al., 2016a, 2017b; Tikhonov et al., 2017; Wong et al., 2019). However, trait data for mosquitoes is often scarce and can be significantly influenced by environmental variables due to their developmental stages, which heavily impact phenology (Cator et al., 2020; Chandrasegaran et al., 2020; Mordecai et al., 2019). As a result, species average traits tend to be broad and variable. Traits driven by life history, such as breeding sites and feeding preferences, have demonstrated considerable plasticity, reflecting mosquitoes' adaptability to resource availability and environmental pressures (Chaves et al., 2010; Kilpatrick et al., 2006). This plasticity further complicates the accurate integration of trait data into JSDMs, yet it underscores the importance of considering these factors as additional predictors of transmission and distribution, as in other vector species (Yang and Han, 2018). The species-specific responses to environment seen here, which seem to align with mosquito life history, breeding habits, and traits, strengthen the argument for expanding these models to incorporate trait data.

Ensuring that community data accurately reflects the scale at which a species interacts with others and responds to environmental drivers is challenging but crucial for JSDMs (Araújo and Rozenfeld, 2014; Dormann et al., 2018). This challenge is exacerbated in mosquito surveillance, where limited resources often lead to concentrated sampling efforts along invasion fronts or targeted known vector species. Such biases restrict the range of species captured, which further affects the accuracy of community data and, consequently, the interpretation of JSDMs. Although next-generation sampling and identification methods for arthropods hold promise for addressing some of these issues by generating denser and more representative community data, these methods are not yet sufficiently robust and may only complement existing data (Krol et al., 2019; Schneider et al., 2016).

Moreover, the computational demands of JSDM methods are significant, and incorporating spatial methods at continental scales necessitates innovative use of computational resources and novel hardware solutions (Pichler and Hartig, 2021; Tikhonov et al., 2020a). As such, incorporating additional trait and phylogeny data will likely require compromises in model complexity (Vallé et al., 2024). While JSDMs have limitations in definitively separating true species interactions from shared environmental responses, JSDMs extend our analysis beyond purely spatial and environmental dimensions, providing a foundation to explore potential biotic interactions or unaccounted-for environmental predictors. Despite some trade-offs in individual species accuracy, our study demonstrates that JSDMs can uncover broader community patterns that are otherwise difficult to detect. We have shown that climatic, topographic, and host factors play a crucial role in influencing mosquito distributions, while also emphasizing the importance of considering scale-dependent relationships. The consistently strong biotic influence observed across our models underscores the need to better integrate species interactions and missing environmental variables into our understanding of mosquito distributions. These insights, coupled with continued refinement of JSDM approaches, hold promising potential for enhancing vector surveillance and predicting future disease risks within the context of community ecology.

Chapter 4

Integrating Traits and Community Data in Joint Species Distribution Models: Insights into Mosquito Ecology

4.1 Abstract

Mosquito-borne diseases increasingly threaten public health in Europe, yet our understanding of the ecological drivers shaping vector distributions and community dynamics remains limited. This study presents a novel approach to modelling mosquito communities across Europe by integrating species traits, phylogeny, and environmental data within a joint species distribution modelling (JSDM) framework. Using data from the VectorNet consortium, comprising 4,157 records of 26 mosquito species, we investigated how traits and community interactions influence species distributions across 1 km communities in Europe.

Our model incorporated 16 ecological and behavioural traits, environmental predictors, and phylogenetic information. Results demonstrated that incorporating basic mosquito traits significantly improves model fit and enables a more mechanistic understanding of species-environment interactions. Traits explained 42% of overall variation in species occurrence,

with stronger associations for climate and topographic factors compared to land use metrics. Examination of trait relationships to unknown environmental drivers revealed potential candidates for important unmeasured factors, such as hydrological regimes and habitat fragmentation. Conditional predictions leveraging community information enhanced model accuracy by 10% on average and revealed potential negative impacts on native mosquito species occurrence in communities with invasive species.

This study highlights the value of trait-based approaches in mosquito ecology and the importance of considering community composition in vector surveillance. We emphasize the need for more comprehensive trait databases and investigation of scale-dependent trait relationships to environmental drivers. These insights can improve our understanding of mosquito community interactions and help assess how environmental changes may reshape mosquito communities and associated disease risks in Europe.

4.2 Introduction

In recent years, Europe has witnessed a significant increase in the spread of invasive mosquito species such as *Aedes albopictus* and *Aedes japonicus*, largely driven by the combined forces of climate change and globalization (Gallien and Carboni, 2017; Medlock et al., 2012). These invasive species have attracted substantial attention due to their well-documented role in transmitting a range of arboviruses, including dengue, chikungunya, and Zika (Bhatt et al., 2013; Schaffner and Mathis, 2014; Vorou, 2016). However, the impact of native mosquito species in maintaining and amplifying vector-borne disease cycles remains just as important, especially when native mosquito species may play equally critical roles in disease transmission and viral persistence (Buckley et al., 2003; Kilpatrick et al., 2007; M'ghirbi et al., 2023).

Understandably, surveillance programmes in Europe have focused heavily on monitoring invasive mosquitoes (Schaffner et al., 2013a; Vaux and Medlock, 2015). While this focus has been essential for the early detection and control of invasive species (Cevidanes et al., 2023; Severini et al., 2008), it is important to recognize that the overall impact is determined by native and invasive competent vectors, whose distributions can be shaped by their interactions with other mosquito species and wider biodiversity (Bevins, 2008; Golding et al., 2015; Smith et al., 2024) It is equally important to consider the overall mosquito community composition when investigating the transmission dynamics of both endemic and exotic pathogens, especially considering the broad overlap of many species' ability to vector diseases like West Nile Virus (Osório et al., 2012).

Native mosquito species play significant roles in maintaining and amplifying disease cycles through overwintering and residual circulation of flaviviruses (Folly et al., 2022; M'ghirbi et al., 2023; Sauer et al., 2023). Differences in habitat preferences, feeding preferences and vector competence mean that some species may function as maintenance vectors, facilitating pathogen circulation among reservoir hosts with reduced chance of spillover events, while others serve as bridge vectors, enabling virus transmission from highly competent, infected hosts to susceptible populations (Muñoz et al., 2012; Rizzoli et al., 2015). This means that even at low densities, these species could potentially sustain viral persistence in isolated interactions between mosquito species and reservoir hosts, contributing to broader disease outbreaks if conditions become favourable for more competent disease vectors (Ferraguti et al., 2021). Understanding the biology of native mosquito species, particularly their feeding behaviours, habitat preferences, and vector competence, is crucial for predicting their role in disease transmission. This knowledge may also help forecast the potential impacts of environmental and biotic drivers on their distribution and interactions with other species, as suggested by recent ecological studies (Golding et al., 2015; McDonough and Holloway, 2020; Vallé et al., 2024).

These relationships can often be complex and difficult to disentangle. For example, in Europe, *Culex pipiens* s.l. and *Culex torrentium* are competent vectors in the transmission of flaviviruses like WNV, Sindbis, and Usutu (Bakonyi and Haussig, 2020; Suvanto et al., 2022). The *molestus* form of *Culex pipiens*, thought to be highly anthrophilic, is a significant bridge vector, feeding on both humans and birds. In contrast, reports indicate that *Cx. pipiens* s.s. tends to prefer feeding primarily on birds, which lowers the risk of spillover to humans but contributes to the persistence of flaviviruses in wild bird populations (Bødker et al., 2014; Golding et al., 2012). Furthermore, well adapted species may exhibit life history traits that allow them to overwinter in sheltered environments such as basements and underground systems, entering diapause to survive colder months (Folly et al., 2022; Sauer et al., 2023). Such differences in behaviour between species enables arboviruses to persist through the winter and resume transmission in the spring, potentially triggering early outbreaks when more competent vectors emerge. Invasive species compound this complexity further; the introduced Aedes albopictus has been shown to be competitively superior to native species in their invaded regions in both Europe and the Americas (Aliabadi and Juliano, 2002; Carrieri et al., 2003). Importantly, not only do these invaders then change the composition of mosquito populations and communities through the invasive process and therefore potential disease pressure, but competition itself can change the larval characteristics of mosquitoes which then propagate through to changes in adult abundance and life history traits, ultimately leading to changes in vectorial competence of mosquito species in a community (Bara et al., 2015; Bevins, 2008).

For example, competition between native and invasive mosquito species plays a critical role in shaping vector communities and influencing disease transmission dynamics. For instance, invasive species like *Aedes albopictus* have been shown to outcompete native *Culex pipiens* for breeding sites in urban areas due to their aggressive colonization strategies and higher reproductive rates, potentially altering the local transmission of arboviruses such as West Nile virus (Juliano and Lounibos, 2005; Smith et al., 2004). Similarly, *Aedes japonicus* competes with native mosquitoes in more natural habitats, leveraging its ability to thrive in cooler temperatures and temporary water sources (Alto, 2011). These competitive interactions, both between native and invasive mosquitoes and among native species, are vital for understanding shifts in vectorial capacity and the broader implications for vector-borne disease transmission (Bara et al., 2015; Bursali et al., 2024).

Consequently, it is likely that the mosquito species composition directly influences disease risk, as the mosquito community shapes both virus prevalence in reservoir hosts and the potential for spillover events to humans. Changes to this mosquito community composition either through climate change or in response to invasive species presence is likely to change potential disease dynamics and pressure, but we know comparatively little about the impacts that changes in mosquito community composition have on disease prevalence or indeed how community composition itself related to disease pressure and prevalence (Giunti et al., 2023).

Understanding Mosquito Drivers Through Traits

If mosquito community composition is important for disease risk, it is likely that the specific traits of these mosquitoes explain much of the variance in disease potential. By understanding which species traits are common among mosquito communities, we can gain a more nuanced understanding of native mosquito species' roles in vector-borne disease transmission. This can be achieved by incorporating species-specific trait data into ecological models of both distribution and transmission, leading to more biologically accurate predictions (Cator et al., 2020; Chandrasegaran et al., 2020).

Trait-based approaches, which have been successfully applied to other taxa such as birds, plants, and arthropods, leverage biological and ecological characteristics to predict species distributions and interactions (Vesk et al., 2021; Wong et al., 2019; Zakharova et al., 2019). Traits like habitat preferences, thermal tolerance, and feeding behaviour characteristics are likely to play a significant role in shaping the capacity of mosquito species to transmit pathogens (Cator et al., 2020; Mordecai et al., 2019; Oyewole et al., 2009; Schneider et al., 2011), but these relationships are yet to be quantified across mosquito species and geographical contexts (Chandrasegaran et al., 2020).

Currently, data on the ecological and biological traits of mosquito species, particularly in Europe, remain limited, despite their known importance in determining vector competence. Part of this gap arises from the remarkable plasticity of mosquitoes to their environment. Climate-induced effects on larval mosquitoes can influence adult traits such as body size, wing size, and overall longevity. Furthermore, life history traits can vary within populations due to environmental conditions. For instance, species that can tolerate colder temperatures or exhibit strong overwintering capacity may sustain populations of infected mosquitoes across seasons, in regions where climatic conditions limit the activity of more temperature-sensitive species (Folly et al., 2022; Kreß et al., 2017). In regions with harsh winter climates, some species may enter diapause as larvae or eggs, while in warmer areas, diapause may be delayed or avoided altogether. Additionally, mosquito species that can reproduce without consuming a blood meal could be important in the vertical transmission of arboviruses, a life history characteristic that is restricted to some species of *Culex* (Becker et al., 2010; Lequime et al., 2016).

This variability complicates efforts to integrate detailed trait data into modelling frameworks, as generalizable functional traits are often lacking and increasing evidence points towards trait variability being key in driving both community interactions and vector competence (Cator et al., 2020). However, incorporating aspects of these traits is crucial, as it could significantly enhance our understanding about the underlying processes in generating mosquito communities that are more likely to spread disease. These nuances in mosquito biology are comparatively understudied and hold potential for uncovering more nuanced interactions between mosquito species and disease pressure. Given the hypothesized importance of these traits in shaping vector competence and arbovirus transmission cycles, addressing these data gaps is essential (Giraldo-Calderón et al., 2015).

Phylogenetic relationships among mosquito species also play a crucial role in understanding trait distributions and their ecological implications (Bova et al., 2019; Soghigian et al., 2017, 2023). Closely related species often share similar traits due to their common evolutionary history, a phenomenon that can be detected as phylogenetic signal (Münkemüller et al., 2012; Revell et al., 2008). Incorporating phylogenetic information into trait-based models can help account for this non-independence of species traits, potentially improving model accuracy and interpretability (Ovaskainen et al., 2017b). Moreover, phylogenetic data can provide insights into the evolution of key traits related to habitat preferences, allowing us to predict how these traits might change in response to environmental pressures or how they might manifest in newly invasive species (Renault et al., 2024). By combining trait data with phylogenetic information, we can develop a more comprehensive understanding of the ecological and evolutionary processes shaping mosquito communities.

The Challenges of Predicting Mosquito Distributions

The complexity of mosquito community composition and the importance of species-specific traits highlight the challenges in predicting mosquito distributions and their potential contributions to disease transmission. Species distribution models (SDMs) have become a valuable tool for inferring statistical correlations between species presences and environmental drivers such as climate, topography, and land use characteristics (Barker and MacIsaac, 2022; Lippi et al., 2023a). However, SDMs were not designed to capture the full complexity of species interactions and the diverse data that community ecologists can gather on mosquitoes (Ovaskainen et al., 2017b).

This is particularly pertinent in cases where species occur infrequently or are harder to detect. Native mosquitoes that are not seen as competent vectors and those that occupy niche habitats in hard to access or under-sampled areas can lead to poor predictions of distribution and, consequently, uncertain estimates of their contribution to disease spread (Santika, 2011).

Meanwhile, invasive species like *Aedes albopictus* and *Aedes japonicus* tend to violate some of the assumptions necessary for traditional SDMs, as their rapid range expansion and ecological plasticity make their distributions difficult to predict (Barbet-Massin et al., 2018). However, the distributions of native species, despite being undersampled, could potentially inform predictions about the occurrence of more medically relevant or invasive mosquito species, and shared information on trait based responses to environmental drivers could enhance our inference of these relationships further.

Joint Species Distribution Models (JSDMs) as a Tool for Mosquito Ecology

Joint Species Distribution Models (JSDMs) offer an advanced approach to addressing the limitations of traditional SDMs by incorporating not only environmental variables but also data on species co-occurrences, phylogeny, and ecological traits (Golding and Harris, 2015; Pichler and Hartig, 2021; Tikhonov et al., 2022). While JSDMs may not always provide better predictive performance compared to SDMs, they allow for the sharing of statistical strength across species, potential improving our understanding of drivers for species that are undersampled or sparsely observed (Vallé et al., 2024). Moreover, JSDMs can go beyond traditional SDMs by leveraging information about the presence or absence of one species to make conditional predictions about others, thus providing a more comprehensive picture of mosquito assemblages and potential disease hotspots.

Although JSDMs do not explicitly model species interactions, they offer a way to gain more inferential power about the processes shaping mosquito communities. For example, JSDMs can be used to predict the occurrence of native mosquitoes in areas where invasive species are known to thrive, using shared environmental preferences or co-occurrence patterns. By integrating trait information, such as temperature tolerance, feeding preferences, or habitat specificity into JSDMs, we may gain a deeper understanding of how different mosquito species interact with their environment and with each other (Golding et al., 2015; Smith et al., 2024).

Objectives of the Study

In this study, we leverage continental scale data on mosquito communities, broad species level traits of mosquitoes, and JSDM modelling approaches, to evaluate the role of traits, phylogeny, environmental factors and biotic interactions with other mosquitoes in driving mosquito communities across Europe. Specifically, we are answering the following scientific questions:

1. To what extent do mosquito species' phylogeny, traits, and community interactions contribute to explaining mosquito distributions?
2. Are these integrative models sufficiently accurate for robust predictions of species distributions and vector assemblages for key pathogens affecting Europe?
3. Do statistically significant trait-environment relationships, if any, align with our current understanding of mosquito ecology?
4. Can we leverage additional information on community composition, through conditional predictions from a JSDM model, to improve our predictions of native and invasive mosquito species distributions?

4.3 Methods

We utilized the assembled mosquito community data from Chapter 3, which represents 26 different mosquito species across 1 km communities. This data was derived from mosquito sampling data provided by the VectorNet consortium, comprising 4,157 records of 26 species from 402 studies (see Chapter 3, Braks et al. (2022)).

4.3.1 Mosquito Traits

Mosquito traits were assembled to capture key aspects of species ecology and behaviour that we deemed to be relatively stable across environmental gradients and considered *a priori* to potentially affect species responses to biotic and abiotic factors. Given the ecological plasticity of mosquitoes, we focused on traits that are less likely to be influenced by environmental factors and those that represent broad scale differences in resource use and specialism between species (Hartemink et al., 2015).

These traits encompass various aspects of mosquito life history, including broad habitat preferences for larval and adult mosquitoes, feeding preferences, and breeding and oviposition characteristics. By selecting these relatively stable traits, we aimed to capture the fundamental niche of each species while acknowledging their potential for ecological adaptation (Kellermann and van Heerwaarden, 2019; Wong et al., 2019). The chosen traits are expected to correlate with various environmental drivers and habitat characteristics, such as seasonal temperature patterns, host availability, urbanization, and water body distribution.

Table 4.1 provides a detailed overview of these trait groups and their anticipated associations with specific habitats or environmental factors. Trait information was compiled from literature sources, primarily Becker et al. (2010) and Hawkes et al. (2020), supplemented with data from the Walter Reed Biosystematics Unit (https://wrbu.si.edu/). The specific trait values used in this study are provided in the supplementary information (Table C.1) and Table 4.3.

4.3.2 Phylogenetic Information

We incorporated a phylogenetic component into our model to account for evolutionary relationships among mosquito species. Initially, we attempted to construct a phylogenetic tree using COI and ITS2 sequences but found that species-level genetic data were insufficient for 17 out of the 26 species in our dataset. As an alternative, we generated a taxonomic-level

Table 4.1 Overview of mosquito traits and their *a priori* expected environmental associations.

Trait Group	**Binary Values**	**Description**	**Expected Associations**
Overwintering	Adults, Larvae, Eggs	The life stage in which the species survives unfavourable winter conditions	Associated with seasonal temperature patterns and habitat stability (Crans, 2004; Diniz et al., 2017)
Feeding Preferences	Anthropophilic, Mammalophilic, Ornithophilic	Preferred blood meal sources for adult female mosquitoes	Related to host availability, human population density, and landscape characteristics (Chaves et al., 2010)
Activity Patterns	Day, Crepuscular, Night	Primary periods of adult mosquito flight and host-seeking behaviour	Linked to temperature fluctuations, predation pressure, and host activity patterns (Montarsi et al., 2015)
Breeding Site Preferences	Artificial Container, Temporary Water, Permanent Water	Types of water bodies where females lay eggs and larvae develop	Associated with precipitation patterns, urbanization, and landscape features (Hawkes et al., 2020)
Salinity Tolerance	Salinity tolerant, Salinity intolerant	Ability of larvae to develop in water with elevated salt concentrations	Related to proximity to coastal areas, salt marshes, or inland saline water bodies (Ramasamy et al., 2014)
Habitat Preference	Rural, Urban	General landscape type where the species is most commonly found	Linked to land use patterns, human population density, and availability of specific breeding sites (Sauer et al., 2021)
Life Cycle	Univoltine, Multivoltine	Capacity to produce multiple generations per year under favourable environmental conditions	Associated with length of favourable season, temperature, and resource availability (Becker et al., 2010; Hawkes et al., 2020)

phylogenetic tree using the R packages `taxize` to resolve species names to taxonomic databases (Chamberlain et al., 2024) and `ape` to assemble this information (Paradis and Schliep, 2019). The resulting tree (Figure C.1) was incorporated into our joint species distribution model as the phylogenetic component, enabling us to account for phylogenetic non-independence in species' responses to environmental predictors and in their co-occurrence patterns (Ovaskainen et al., 2017b).

Table 4.2 Summary statistics of environmental predictors across all sampling sites used in the study. The table presents the description, model covariate name, unit of measurement, ecological relevance, mean, and standard deviation for each predictor. Predictors include climate variables, land cover types, topography, human population density, vegetation indices, and livestock density, all of which are potentially important for mosquito ecology and distribution.

Description	**Model Covariate**	**Unit**	**Ecological Relevance**	**Mean**	**Std. Dev**
Accessibility to cities (>50,000 population)	acc_50k	Travel time (minutes)	Human-mosquito interaction potential	3.62	1.17
Agricultural land cover	agriculture	Percentage (%)	Potential larval habitats	50.26	27.84
Annual mean temperature	BIO_01	Degrees Celsius (°C)	Mosquito development and survival	11.42	3.33
Precipitation of warmest quarter	BIO_18	Millimetres (mm)	Breeding site availability	217.69	139.6
Elevation above sea level	elevation	Meters (m)	Species distribution and abundance	316.36	364.8
Enhanced Vegetation Index spatial homogeneity	EVI_Hom	Index value (unitless)	Habitat consistency	4891.39	1194.82
Enhanced Vegetation Index	EVI	Index value (unitless)	Vegetation density and resting sites	2528.49	809.49
Growing Degree Days over 10 °C	GDD	Degree days	Mosquito development rate	10.39	13.42
Avian livestock density	lstock_ave	Log Livestock units per km²	Host availability (ornithophilic species)	8.79	2.3
Mammalian livestock density	lstock_mam	Log Livestock units per km²	Host availability (mammalophilic species)	8.03	1.32
Human population density	pop_den	Log People per km²	Human host availability	4.91	1.63
Shrubland cover	shrubs	Percentage (%)	Potential resting sites	3.41	9.47
Tree cover	trees	Percentage (%)	Microclimate and resting sites	19.61	24.38
Urban/built-up area	urban	Percentage (%)	Artificial breeding sites	10.9	19.31
Wetland cover	wetland	Percentage (%)	Natural breeding sites	0.15	1.09

4.3.3 Environmental Data

Environmental predictors were selected based on their known relevance to mosquito ecology and distribution, following a similar resource-based approach established in Chapter 3. This approach incorporated variables corresponding to mosquito life stage requirements and factors affecting their demographic rates, such as climatic factors and land use characteristics, as well as variables related to anthropogenic pressure and host availability. To address multicollinearity, we removed one of each pair of variables for which Pearson correlation values exceeded 0.7, retaining the variable that we expected *a priori* to have a stronger biological relationship to mosquito occurrence.

In practice, this led to the dropping of mean temperature of the coldest quarter (BIO11) in favour of annual mean temperature (BIO1). We made this choice because we hypothesized that the inclusion of growing degree days above 10 °C could effectively represent the lower thermal limits for mosquito species, capturing the essential information about cold tolerance without the need for BIO11. Additionally, we selected precipitation of the warmest quarter (BIO18) over mean total annual precipitation (BIO12), as it better represents water availability during peak mosquito activity periods and captures the rainfall patterns most relevant to species reliant on temporal or ephemeral floodwaters for breeding. Variables with near-zero variance, such as snow and wetland land cover, were also excluded from the analysis to prevent model instability.

Table 4.3 Trait occurrence across mosquito species in Europe. The table presents binary (0/1) data for 16 ecological and behavioural traits across 26 mosquito species from genera *Aedes*, *Anopheles*, *Coquillettidia*, *Culex*, and *Culiseta*. Traits are categorized into Overwintering Strategies (Adult, Egg, Larvae), Host Preferences (Anthropophilic, Mammalophilic, Ornithophilic), Biting Behaviours (Day, Crepuscular, Night), Oviposition Preferences (Container-breeding, Temporary, Permanent, Salinity), Habitat Preferences (Rural, Urban), and Voltinism (0 = univoltine, 1 = multivoltine). The bottom row shows the prevalence (%) of study species with each trait. Traits were derived from literature, with substantial information from Becker et al. (2020), the Walter Reed Biosystematics Unit Mosquito Catalogue, and Hawkes et al. (2021). Literature used to infer broad trait variables is available in the supplementary information (Table C.1).

Species	**Overwintering Strategy**			**Host Preference**			**Biting Behaviour**			**Oviposition Preferences**				**Habitat**		**Voltinism**
	Adult	**Egg**	**Larvae**	**Anthro.**	**Mammal.**	**Ornith.**	**Day**	**Crep.**	**Night**	**Cont.**	**Temp.**	**Perm.**	**Salinity**	**Rural**	**Urban**	
Aedes albopictus	0	1	0	1	1	1	1	0	0	0	1	0	0	1	1	1
Aedes annulipes/cantans	0	1	0	1	1	1	1	1	0	0	0	1	0	1	0	0
Aedes caspius	0	1	0	1	1	0	1	1	1	0	1	0	1	1	0	0
Aedes cinereus/geminus	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	0
Aedes detritus/coluzzi	0	1	0	1	1	1	0	1	0	0	0	1	1	0	0	1
Aedes geniculatus	0	1	0	1	1	0	1	1	0	0	1	0	0	1	0	1
Aedes japonicus	0	1	0	0	1	1	1	1	0	1	1	0	0	1	1	1
Aedes sticticus	0	1	0	1	1	0	1	1	0	0	1	0	0	1	0	1
Aedes vexans	0	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1
Anopheles atroparvus	1	0	0	0	1	0	0	1	1	1	0	1	1	1	0	1
Anopheles claviger	0	0	1	0	1	0	1	0	0	1	0	1	0	1	0	1
Anopheles labranchiae	1	0	0	1	1	0	0	1	1	1	0	1	1	1	0	1
Anopheles maculipennis	1	0	0	0	1	0	0	1	1	1	0	1	0	1	0	1
Anopheles messeae	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1
Anopheles plumbeus	0	0	1	1	1	0	1	1	1	1	1	0	0	1	1	1
Anopheles sacharovi	1	0	0	1	1	0	1	1	1	1	0	1	1	1	0	1
Coquillettidia richiardii	0	0	1	1	1	0	0	1	0	0	0	1	1	1	0	0
Culex hortensis	1	0	0	0	1	1	0	1	0	1	1	1	0	1	1	1
Culex modestus	0	0	0	1	1	1	1	1	0	1	0	1	1	1	0	1
Culex perexiguus/univitattus	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	1
Culex pipiens	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1
Culex territans	1	0	0	0	0	1	1	1	0	1	0	1	0	1	0	1
Culex torrentium	1	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1
Culiseta annulata	1	0	0	1	1	0	1	1	1	1	0	1	1	1	1	1
Culiseta longiareolata	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1
Trait Prevalence (%)	*42*	*35*	*15*	*58*	*88*	*46*	*54*	*81*	*54*	*62*	*42*	*73*	*46*	*96*	*38*	*85*

4.3.4 Statistical Methods

To fit our models we used an implementation of the Hierarchical Modelling of Species Communities (HMSC) framework based on TensorFlow to improve computational efficiency (Rahman et al., 2024). This HMSC approach allows for the incorporation of species traits and biotic relationships in the modelling process, accounting for residual co-occurrences between species after considering shared responses to environmental drivers. In particular, the HMSC method uses a latent variable approach to account for unmeasured biotic and environmental drivers of species distributions (Ovaskainen et al., 2016a).

All analyses were conducted using the R package `HMSC-HPC` (Tikhonov et al., 2022). We used a probit regression with default priors for all of our HMSC models. All environmental predictors were included in the model as linear fixed effects, and we also included community sample (representing the grid square of our community) as an unstructured random spatial effect. We fitted our HMSC models with three Markov Chain Monte Carlo (MCMC) chains, each consisting of 1,100,000 iterations, with the first 100,000 iterations discarded as burn-in. The posterior estimates of parameter distributions were obtained from 1500 samples thinned from the 1,000,000 iterations. MCMC chain convergence was assessed using the potential scale reduction factors of model parameters and determinants of effective sample size for each parameter from the posterior distribution (Gelman and Rubin, 1992).

To systematically evaluate how incorporating phylogenetic information, species traits, and community associations drives mosquito community composition and distribution, we employed a multi-stage approach.

Model Comparison

First, we generated models to evaluate the importance of three key components in driving mosquito species community distributions: community co-occurrence ($\mathrm{M}_{\mathrm{Community}}$), phylogeny ($\mathrm{M}_{\mathrm{Phylo}}$), and traits ($\mathrm{M}_{\mathrm{Trait}}$). For each of these models, we generated a null model counterpart where the component in question for each model was randomised to statistically infer the impact of the model component in our JSDM (Table 4.4). For the null counterparts of the community and trait components, we implemented a ‘fastball’ version of the curveball algorithm, which preserves species site prevalence and frequencies while generating a new randomly sampled distribution (Godard and Neal, 2022; Harvey et al., 1983). To create the null version of the phylogenetic component, we randomized the species tips of the phylogenetic tree, maintaining tree length and the associated matrix structure while randomizing inter-species relationships (Pigot and Etienne, 2015).

In the case of $\mathrm{M_{Trait}}$ and $\mathrm{M_{Phylo}}$, we fitted these models with the observed matrix of species site co-occurrences to isolate the impact of trait and phylogenetic components on model inference. To evaluate the importance of each component, we compared in-sample model performance metrics (Tjur’s R^2) for each nested model component using paired t-tests. Additionally, to account for the complexity of community structures, we compared the residual co-occurrence patterns generated from our model fitting process with their null counterparts using a Mantel test, quantifying the degree to which our models captured non-random co-occurrence patterns beyond what would be expected by chance (Legendre and Legendre, 2012). This approach enabled us to systematically assess the relative contributions of community structure, phylogenetic relationships, and species traits to mosquito distribution patterns, while controlling for potential confounding factors through the use of null models following best practice (Scherrer et al., 2020).

Full Model and Model Comparison

We fitted a ‘full’ model ($\mathrm{M_{Full}}$) incorporating community, trait, and phylogenetic data to assess the improvement in model inference compared to the individual component models and assess overall relationships between traits, environmental and biotic drivers for mosquito species. Paired t-tests with Tjur’s R^2 were used to evaluate relative performance, as improvements in

Table 4.4 Comparison of ecological models incorporating various combinations of community (C), trait (T), and phylogenetic (P) data. Models assess the relative contributions of these components to explaining the European distributions of mosquito species and communities. Null models use randomised versions of matrices, maintaining species richness and occurrence frequencies while disrupting specific patterns using a modified curveball algorithm. For phylogenetic randomisation, phylogenetic distances between species are kept constant while randomising species placement on the tree.

Model Name	Components	Description	Purpose
Community	C	Community data with environmental covariates and random effects.	Assess effect of community data alone on response variable.
Phylo	C, P	Community data and phylogenetic information.	Evaluate impact of phylogenetic information on community-response relationship.
Trait	C, T	Community data and trait data.	Assess impact of trait data on community-response relationship.
NullCommunity	C (randomised)	Randomised occurrence data, other components as in Community model.	Baseline comparison with randomised occurrence data.
NullTraits	C, T (randomised)	Randomised occurrence and trait data.	Compare influence of randomised trait data on community data.
NullPhylo	C, P (randomised)	Randomised occurrence data and phylogenetic tree.	Compare influence of randomised phylogenetic data on community data.
Full	C, T, P	Comprehensive view with all data types.	Explore combined effects of community, trait, and phylogenetic data.

accuracy (e.g., RMSE, AUC) are only expected when utilising additional information for conditional predictions (Poggiato et al., 2021). We also computed the attributed variance for each environmental component and the variance explicable by traits, following Ovaskainen et al. (2017b). Additionally, we measured the correlation between the full model ($\mathrm{M}_{\mathrm{Full}}$) and model without any trait or phylogenetic information ($\mathrm{M}_{\mathrm{Community}}$). We plotted the species-environment and trait-environment associations that met our threshold of statistical significance (90% Credible Interval). These associations were then evaluated and compared to biological expectations to assess their alignment with known mosquito life history strategies.

To further elucidate the trait-environment relationships present in our full model, we computed factor loadings of traits across the latent variables of the JSDM for each site by comparing average trait values of present species with environmental variation across the latent variable space. This approach, analogous to a Redundancy Analysis (RDA) of the unexplained variation in our HMSC model (defined by latent variable parameters, *Eta*), provides insights into the complex relationships between mosquito traits and any unmeasured environmental components addressed by the latent variable space. It achieved this by mapping trait factor loadings onto the JSDM latent variables, which may uncover subtle ecological patterns not apparent from direct correlations with measured environmental variables.

Improving Predictive Accuracy and Estimations of Community Composition with Conditional Predictions

Lastly, we assessed how we can leverage the relationships uncovered by our JSDM through comprehensive community information by generating conditional predictions from our full model ($\mathrm{M}_{\mathrm{Full}}$) and simulating the impact of invasive species' presences on other mosquito species' predicted occurrence probabilities. These conditional species predictions estimate the probability of occurrence for a target species based on the presence or absence of other species in the community, effectively leveraging the residual species correlation matrix to generate predictions based on these correlations between species, which are determined by shared environmental, trait, and phylogenetic relationships (Poggiato et al., 2021; Wilkinson et al., 2021).

To determine the baseline out-of-sample prediction accuracy of our full model, we computed the Area Under the Receiver Operating Characteristic curve (AUC) through 4-fold cross-validation for both unconditional and conditional predictions from our dataset to illustrate how community information can enhance species prediction accuracy if the state of a community is known. We then utilised these conditional predictions from our full model to simulate hypothetical species distributions of communities in which the invasive species *Aedes albopictus* and *Aedes japonicus* were absent.

We accomplished this by setting *Ae. albopictus* and *Ae. japonicus* as absent across their known occurrence sites and using this known state of occurence to predict other species presence probabilities and how they differ from our normal non-conditional predictions. To determine statistical significance we compared the native community composition for our standard non-conditional predictions to the conditionally predicted communities' occurrence probabilities using a Distance-based Multivariate Analysis of Variance (DMANOVA) with the `dmanova` function from the GUniFrac R package (Chen and Zhang, 2021). The DMANOVA was performed using the scenario as the predictor variable, allowing us to test for significant differences in native community composition and quantify the proportion of variation in native species composition explained by the presence of the invasive species.

4.4 Results

4.4.1 Model Convergence and Diagnostics

The models demonstrated good convergence and overall fit and model runtime was on average 7.4 hours using the tensorflow implementation of HMSC, and measures of effective sample size (ESS) and potential scale reduction factor (PSRF) indicated adequate model convergence. For fixed effects (Beta), the ESS ranged from 399.80 to 2057.66 ($M = 1430.19$, $SD = 243.27$), with no parameters having $ESS < 100$, and a mean PSRF of 1.02 ($SD = 0.0749$). For species traits (Gamma), the ESS ranged from 1311.01 to 1601.74 ($M = 1465.23$, $SD = 87.62$), with no parameters below $ESS < 100$, and a mean PSRF of 1.01 ($SD = 0.0072$). Random effects (Omega 1) had an ESS range of 404.27 to 2581.57 ($M = 1098.13$, $SD = 402.45$), with a PSRF range from 0.99 to 2.76 ($M = 1.083$, $SD = 0.3187$), indicating stable convergence.

4.4.2 Model Comparison and Null Model Validation

The residual species correlations of the community model ($M_{\text{Community}}$) showed a significant positive correlation with its null counterpart with 52% of the residual correlations being similar ($r = 0.522$, $p = 0.014$, Figure 4.1). In contrast, the phylogenetic model (M_{Phylo}) showed a high correlation with its null model ($r = 0.9918$, $p = 0.001$), indicating that phylogenetic information contributed minimally to explaining species residual correlations (Figure 4.1). Similarly, the trait-based model (M_{Trait}) was highly correlated with its null counterpart ($r = 0.9828$, $p = 0.001$), suggesting limited additional explanatory power from traits when considering species residual correlations (Figure 4.1).

Independent t-tests revealed that the Full model (M_{Full}) significantly outperformed both the community ($t(25) = 4.14$, $p = 0.001$, 95% CI [0.0249, 0.0740]) and phylogenetic models ($t(25) = 4.18$, $p = 0.001$, 95% CI [0.0282, 0.0830]) in terms of Tjur R^2. However, there was no significant difference between the Full and Trait models ($t(25) = 1.28$, $p = 0.214$, 95% CI [-0.0109, 0.0462]), indicating that the addition of traits did not significantly enhance model performance when compared to the Full model (Figure 4.3).

The comparative Mantel tests indicated that residual correlations between species are indeed influenced by community composition, evidenced by significant differences between the community model ($M_{\text{Community}}$) and its null counterpart. However, high correlations between $M_{\text{Community}}$ and $M_{\text{NullCommunity}}$ models may indicate incomplete capture of these associations. Phylogenetic (M_{Phylo}) and trait-based (M_{Trait}) models showed minimal additional explanatory power, suggesting either insufficient phylogenetic resolution or limited relevance to mosquito community dynamics in our dataset. While trait-based changes in correlation structure were significant, their magnitude was minor (Figure 4.1). Nevertheless, t-tests confirm that the Full (M_{Full}) and Trait (M_{Trait}) models significantly outperform community ($M_{\text{Community}}$) or phylogeny (M_{Phylo}) models alone.

4.4.3 Trait-based Model Diagnostics

Parameter estimates from the M_{Full} model residual species correlation matrix revealed strong positive co-occurrence among native species, particularly within *Culex*, *Culiseta*, and *Aedes* groups (Figure 4.2). Most residual species associations were strongly positive across clades, with exceptions like *Aedes detritus/coluzzi* and *A. geniculatus* showing fewer strong associations with culicine species. Invasive species exhibited strong negative associations with most others, barring the *Anopheles labranchiae-Aedes japonicus* association. Notably, *Aedes* species showed the weakest correlations with other groups, potentially indicating negative interactions or differing ecological drivers, consistent with their distinct reproductive strategies and life histories.

The full model revealed varying levels of model fit among the studied mosquito species (Figure 4.4A). *Aedes japonicus* ($R^2 = 0.701$), *Aedes albopictus* ($R^2 = 0.657$), and *Anopheles labranchiae* ($R^2 = 0.605$) showed high levels of explained variance, suggesting our environmental drivers reflect the distribution of these species well. Moderate variance was explained for *Aedes sticticus* ($R^2 = 0.497$), *Anopheles maculipennis* ($R^2 = 0.486$), and *Aedes detritus/coluzzi* ($R^2 = 0.370$), suggesting the importance of additional factors. In contrast, *Aedes geniculatus* ($R^2 = 0.0758$), *Culex territans* ($R^2 = 0.152$), and *Anopheles cinereus/geminus*

Fig. 4.1 Heatmaps depicting species residual correlation structures derived from six Hierarchical Modelling of Species Communities (HMSC) models. These models contrast the impact of community composition, phylogenetic relationships, and species traits on residual correlation structure parameters (Omega). Each panel represents a different model configuration with its null counterpart: Top) Community model ($M_{Community}$) vs. Null Community model ($M_{NullCommunity}$); Middle) Phylogeny model (M_{Phylo}) vs. Null Phylogeny model ($M_{NullPhylo}$); Bottom) Trait model (M_{Trait}) vs. Null Trait model ($M_{NullTrait}$). Warm colours (red) indicate positive correlations, while cool colours (blue) represent negative correlations. The intensity of the colour corresponds to the strength of the correlation. Diagonal elements represent self-correlations and are set to 1. Model components and their descriptions can be found in Table 4.4. Plot titles indicate the specific components included in each model (C: Community, P: Phylogeny, T: Traits).

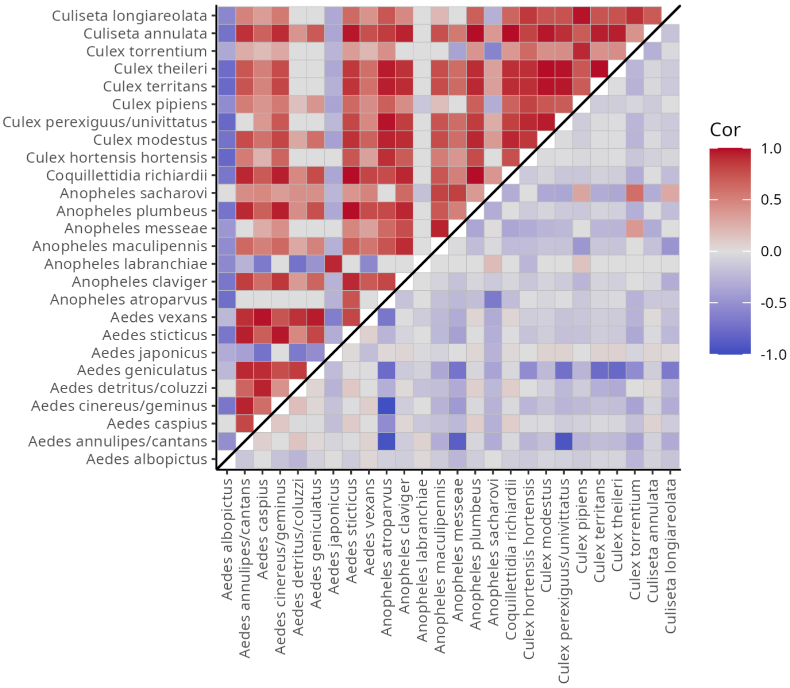

Fig. 4.2 Comparison of Omega residual correlation structures between the M_{Full} (including traits and phylogeny) and the community-only model ($M_{\mathrm{Community}}$). The heatmap is divided into upper and lower triangles. The upper triangle represents the Omega (residual correlation) parameters for the full model, where red indicates positive correlation values between species and blue indicates negative correlation values. The lower triangle represents the absolute difference in correlation values between the full model and the community-only model, with blue indicating correlations that are weaker after adding traits and phylogeny, and red indicating increased strength. In both triangles, colour intensity corresponds to the strength of the correlation or magnitude of the difference.

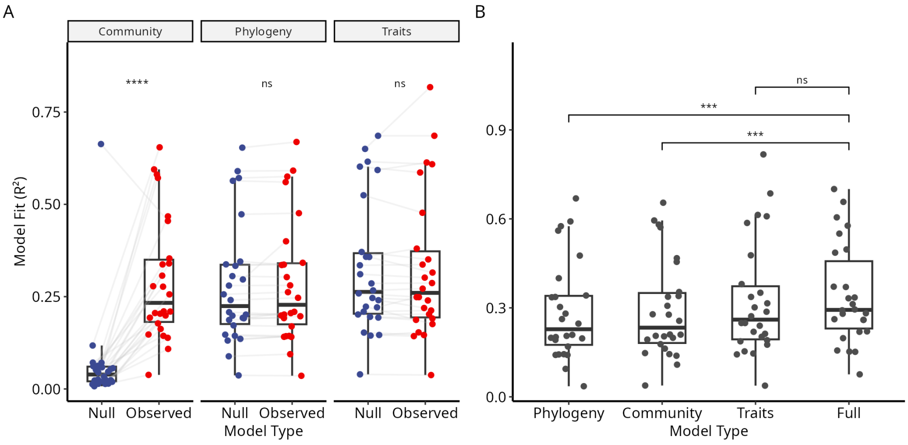

Fig. 4.3 Statistical comparisons of model fit using in-sample Tjur's R^2. (A) Differences between Tjur's R^2 for each species in the model and their null counterparts, with associated statistical tests. (B) Differences in Tjur's R^2 between the non-null community models, including the full model M_{Full} and subsequent component models. Significance levels for paired t-tests are indicated as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$; ns indicates non-significance. These comparisons illustrate the relative performance of different model configurations and the impact of including various ecological factors on model fit.

($R^2 = 0.152$) exhibited low variance explained, implying that unmeasured factors likely play a significant role in their distributions.

Variance partitioning analysis (Figure 4.4B) revealed that the Random Site effect, capturing site-specific factors and unmeasured spatial heterogeneity, accounted for the largest proportion of species response variation ($Mean = 45.2\%$, $SD = 19.1\%$). Topographic Variables ($Mean = 21.0\%$, $SD = 15.3\%$) and Land Use and Vegetation ($Mean = 15.1\%$, $SD = 11.7\%$) played moderate roles in shaping species distributions, reflecting the importance of physical landscape features and habitat characteristics. Anthropogenic Pressure which included human population density and accessibility predictors ($Mean = 11.7\%$, $SD = 9.22\%$) had a lesser influence, indicating that human activities may impact species distributions, though not as strongly as topography or vegetation. Climate ($Mean = 7.02\%$, $SD = 8.71\%$) contributed the least to the observed variation, suggesting a minor role in structuring species assemblages within the study area.

Overall, we found that traits explained 42% of the overall variation in species' occurrence across all sites, a relatively large amount. Variance partitioning also assessed the influence of species' traits on mosquito responses to environmental drivers, quantifying how much traits explained species' responses to different environmental variables (Figure 4.4C). We found that traits explained more variation in species' responses to climate and topographic factors than to land use and habitat metrics, suggesting stronger trait-environment associations for climate and topography. Traits explained considerable variation in species' responses to agricultural habitats, suggesting our trait selection aligns well with agricultural microhabitats suited for specific mosquito species, such as those inhabiting semi-permanent water bodies in agricultural landscapes.

K-fold ($K = 4$) cross-validation of our full HMSC model yielded an average Area Under the Curve (AUC) for all species of $M = 0.76$ ($SD = 0.10$), indicating good overall predictive accuracy scores for the majority of mosquito species. The species with the highest prediction accuracy were *Anopheles labranchiae* (AUC = 0.95) and *Culex perexiguus/univittatus* (AUC = 0.92), while only five of our 26 mosquito species failed to meet an acceptable AUC threshold of 0.70 (Figure 4.4D).

4.4.4 Trait and Environmental Drivers of Mosquito Distribution

Parameter estimates from the full model reveal significant associations between environmental factors and species distributions, with broad-scale climate variables emerging as strong predictors for most species and habitat use eliciting species-dependent responses (Figure 4.5A). The model detects several species-environment relationships that are consistent with our biological expectations. For example, woodland species like *Aedes geniculatus*, *A. japonicus*, and *A. cinereus* show positive associations with warm-quarter precipitation and forested areas, reflecting their tree-hole breeding habits. Conversely, *Culex pipiens/torrentium*, *Aedes*

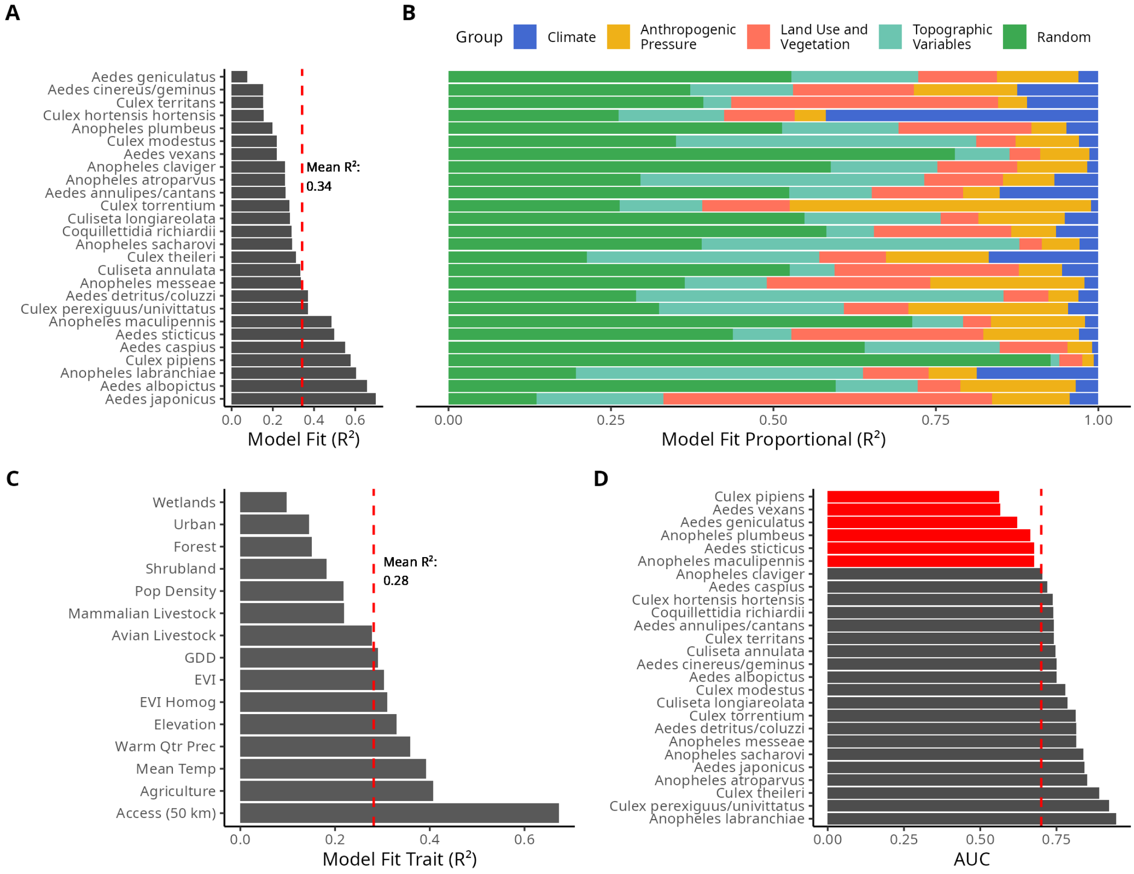

Fig. 4.4 Model fit analysis and environmental factor influence on mosquito species distribution. (A) Total variance explained (Tjur's R^2) by the full model for different mosquito species, with the red dashed line indicating the mean variance explained across species. (B) Variance partitioning analysis showing the relative contribution of different factors to species response variation. Factors include Random Site effect (M = 45.2%, SD = 19.1%), Topographic Variables (M = 21.0%, SD = 15.3%), Land Use and Vegetation (M = 15.1%, SD = 11.7%), Anthropogenic Pressure (M = 11.7%, SD = 9.22%), and Climate (M = 7.02%, SD = 8.71%). (C) Explanatory power of species traits for responses to different environmental variables, highlighting stronger trait-environment associations for climate and topographic factors compared to land use and habitat metrics. The red dashed line indicates the average explanatory power of species traits of 0.28. (D) Predictive accuracy of the full HMSC model based on 4-fold cross-validation, showing Area Under the Curve (AUC) values for each species. The average AUC across all species was 0.76 (SD = 0.10), with *Anopheles labranchiae* (AUC = 0.95) and *Culex perexiguus/univittatus* (AUC = 0.92) showing the highest prediction accuracy. Only five out of 26 species had AUC values below the 0.70 threshold (indicated in red).

japonicus/albopictus, and *Anopheles labranchiae/plumbeus* associate positively with urban habitats, consistent with adaptation to man-made environments.

Agricultural land use emerged as a prominent positive driver for species presence, particularly for anopheline and *Aedes* species, while culicine species showed muted associations. *Anopheles labranchiae* demonstrated strong associations with agricultural water sources, consistent with its anthropophilic tendencies. Unexpectedly, *Anopheles* species showed associations with avian livestock densities. Interestingly, through interpretation of the trait-environment relationships we found that artificial container breeders are associated with areas of high vegetation homogeneity (Figure 4.5B). Similarly, we find that both rural and urban-adapted species are positively correlated with higher precipitation in the summer months.

Analysis of the average trait correlations across model predictions of community composition with the latent variables revealed two primary axes of variation in mosquito ecological strategies (Figure 4.6). To further explore environmental patterns across the latent variable space of our model, we applied k-means clustering to the environmental parameters at each site. The optimal number of clusters was determined using the gap statistic method (Tibshirani et al., 2001), which suggested two clusters as optimal (gap statistic = 1.78, standard error = 0.01). The clustering algorithm revealed a relatively homogeneous distribution of environmental conditions across the latent space, with no distinct areas of environmental similarity, suggesting that the JSDM model effectively accounts for the unknown variation in our environmental drivers. The lack of clear clustering indicates that the model has successfully captured the complex interplay of environmental factors, resulting in a well-mixed representation of ecological conditions in the latent space.

The first latent variable represents a gradient from species adapted to ephemeral, potentially more natural, habitats to those suited for permanent, stable water sources (Figure 4.6). This axis is strongly characterized by overwintering strategies, with egg overwintering negatively correlated ($r = -0.53$) and adult overwintering positively correlated ($r = 0.42$). It also reflects a shift from day-active species to those with nocturnal or crepuscular habits ($r = 0.50$ and 0.42, respectively). The second latent variable axis is associated with a transition from ornithophillic to more generalist feeding behaviours on mammals and humans (Figure 4.6). We see unclear variation in the direction of traits that distinguishes between species adapted to anthropogenic versus natural habitats. This is evidenced by a strong negative correlation with artificial container breeding ($r = -0.66$) and a positive association with anthropophilic behaviour, two traits we would expect to be aligned ($r = 0.55$). Interestingly, both rural and urban traits show negative correlations with this axis ($r = -0.35$ and -0.26, respectively), suggesting a complex relationship with human-modified landscapes.

4.4.5 Impacts of Invasive Species on Native Mosquito Communities from Conditional Predictions

Using our full model, we generated community predictions based on the known occurrence of other species present at the sites to validate the accuracy of conditional predictions on community composition. Predictive improvement was consistently large, with conditional predictions showing, on average, 0.1 higher AUC values (Mean = 0.86, SD = 0.06) compared to non-conditional predictions. This difference was statistically significant (paired t-test: t = 5.84, df = 25, $p < 0.001$). ROC curves for four representative species (Figure 4.7) further illustrate the improvement in model performance with conditional predictions, while highlighting the variability of this improvement across species.

Our analysis comparing species distribution predictions under scenarios with and without conditional species interactions revealed significant variability in the effects of invasive species on native mosquito distributions. While some species showed consistent increases in predicted occurrence, others exhibited considerable variability across different sites, indicating highly site-specific interactions (Figure 4.8).

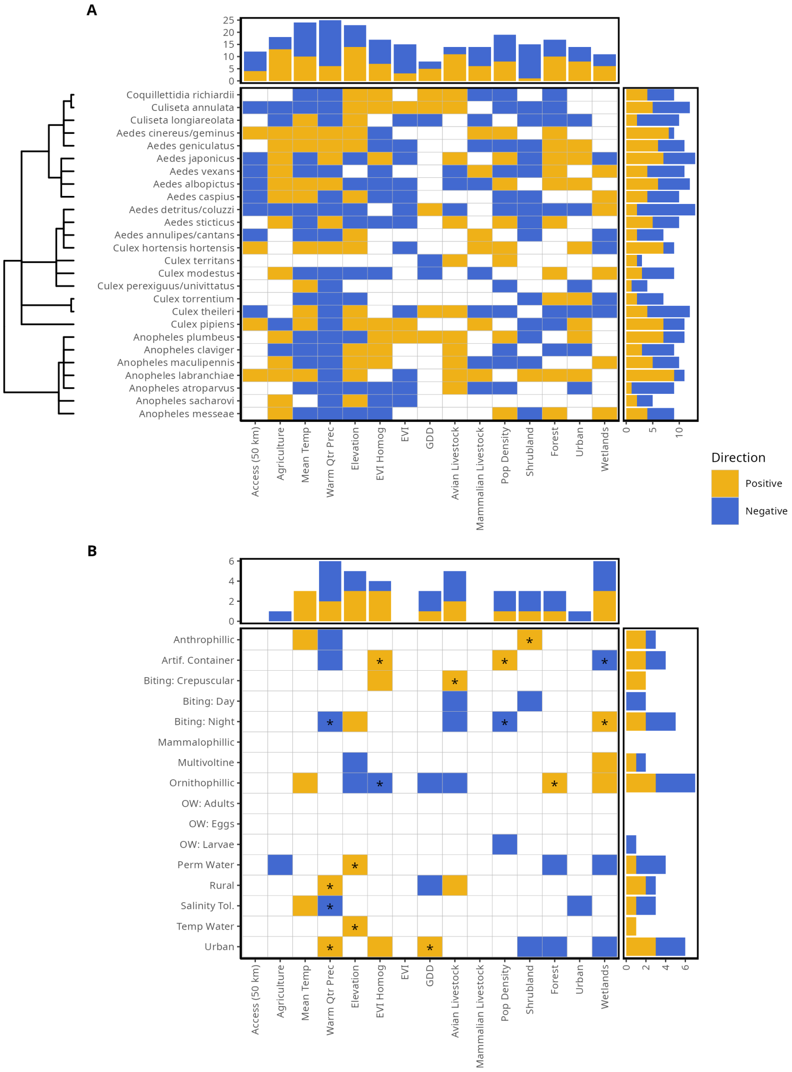

Fig. 4.5 Species-environment (Beta) associations and trait-environment relationships (Gamma). (A) Heatmap showing significant parameter values for species-environment associations from our full model. Only parameters within the 90% credible interval are shown. Sidebars display summed totals of significant responses for both species and environmental drivers. The phylogenetic tree represents the phylogenetic information encoded in the full model. (B) Heatmap illustrating significant trait-environment relationships for gamma parameters of our full model. Significance threshold was relaxed to 85% credible interval to reveal more associations for interpretation. Values marked with an asterisk (*) are above the 90% credible interval.

Fig. 4.6 Scatter plot of the first two latent variable parameters (Eta) from our full model, with each point representing a single site in our dataset. Points are clustered into two environmental groupings based on k-means clustering of environmental parameters at each site. Factor loadings or correlations of average trait values at each site are mapped onto the latent variable space, denoted by their trait name. The size and direction of the arrows indicate the correlation values with the latent variables across two dimensions.

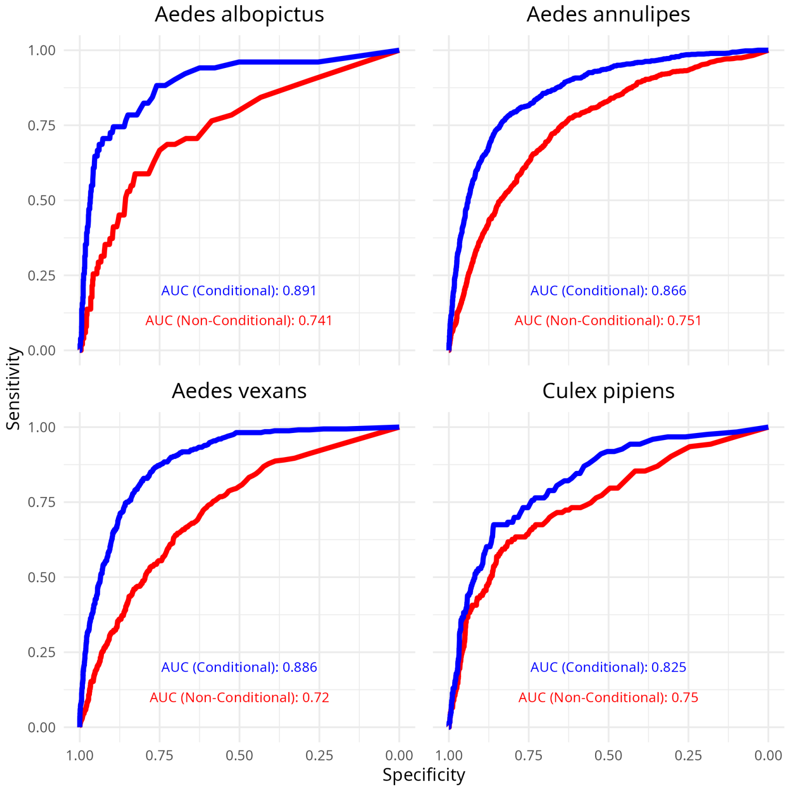

Fig. 4.7 ROC curves comparing conditional (blue) and non-conditional (red) predictions for four mosquito species: *Aedes albopictus*, *Aedes annulipes*, *Aedes vexans*, and *Culex pipiens*. AUC values are shown for each prediction type. Conditional predictions consistently outperform non-conditional predictions across all species, demonstrating improved model performance when accounting for species interactions.

The most substantial median difference was observed for *Culex pipiens* (median = 0.147, SD = 0.210), suggesting that invasive species have a significant and highly variable impact on this species' distribution across locations. *Anopheles maculipennis* also demonstrated a notable median increase (median = 0.0433, SD = 0.125), with considerable variability, highlighting site-dependent responses to invasive species presence. *Aedes vexans* exhibited a moderate increase (median = 0.0227, SD = 0.0563), further supporting the role of local factors in influencing distribution shifts. Other species, such as *Anopheles claviger* (median = 0.0173, SD = 0.0552) and *Culiseta annulata* (median = 0.0173, SD = 0.0527), showed moderate increases; however, they too displayed notable variability across sites. Conversely, species like *Anopheles atroparvus* (median = 0.000667, SD = 0.0148) and *Culex perexiguus/univittatus* (median = 0, SD = 0.0216) showed minimal changes in predicted occurrence, suggesting that invasive species presence had little to no meaningful effect on their distributions.

The DMANOVA confirmed these differences in native community composition between community predictions scenarios with and without invasive species as statistically significant (F = 499.02, df = 1, 8312, $p < 0.001$). The model explained approximately 5.66% of the total variation in native community composition ($R^2 = 0.056$). Despite the high statistical significance, the relatively low R^2 value suggests that while the presence of invasive species does influence native community structure, it accounts for a modest proportion of the overall variation in native community composition. These results provide strong statistical evidence for the indirect impact of invasive species on native community composition.

4.5 Discussion

This study offers a novel and comprehensive approach to understanding mosquito communities by integrating species traits, phylogeny, and environmental data within a JSDM framework. Our findings underscore the value of incorporating mosquito traits into ecological

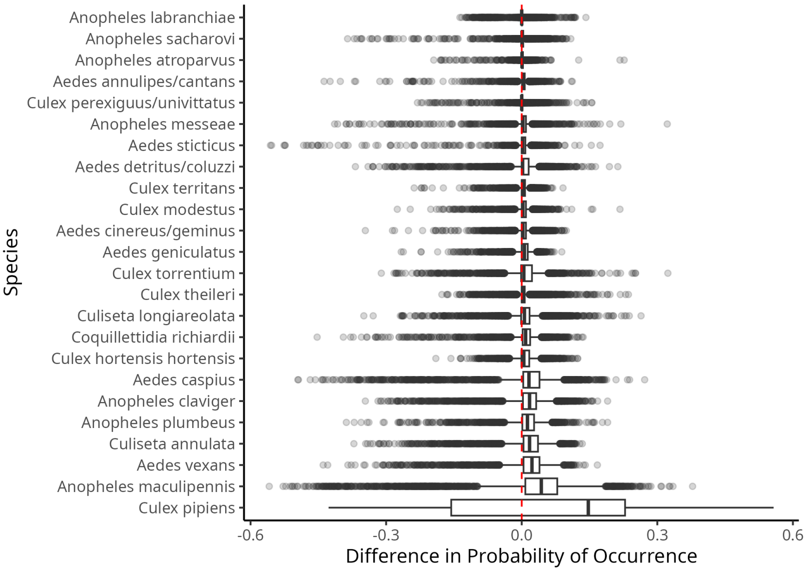

Fig. 4.8 Differences in predicted probability of occurrence for native mosquito species under scenarios with and without invasive species presence across all sites that invasive mosquitoes were originally predicted. The plot shows the distribution of differences across sampling sites for each species. Positive values indicate higher probability of occurrence when invasive species are absent, while negative values indicate higher probability when invasive species are present. Boxplots represent the median (vertical line), interquartile range (box), and 1.5 times the interquartile range (whiskers). Individual points represent outliers. Species are ordered by median difference. The red dashed line at zero represents no change in probability.

models, which allows for a more mechanistic understanding of how mosquito species interact with their environment enabling better understanding of environmental drivers of mosquito species competition (Cator et al., 2020; Chandrasegaran et al., 2020). Furthermore, we demonstrate how leveraging community data enhances the accuracy of distribution models and enables the examination of changing pressures on native mosquito species in the face of ongoing invasive species spread.

4.5.1 The importance of traits in driving species-environment relationships

Our model that fully incorporated traits resolved known trait-environment relationships seen in wild mosquito populations. We found that the traits included in our model were much more likely to explain variation in climate effects than those driven by land use. Broad-scale species traits such as thermal tolerances, overwintering strategies, and voltinism are directly influenced by changes in temperature, humidity, and precipitation - key components of climate variability (Diniz et al., 2017; Kreß et al., 2017; Mordecai et al., 2019). These traits govern fundamental aspects of mosquito fitness, including larval development rate, adult breeding frequency, and overall longevity (Oyewole et al., 2009; Schneider et al., 2011). Overwintering ability allows certain species to survive through colder seasons, while voltinism, highly dependent on temperature, can determine population growth rates (Crans, 2004; Diniz et al., 2017). Oviposition-related behaviours, such as preferences for specific water sources, are closely tied to precipitation patterns and habitat moisture. Host selection may also be influenced by climate-driven changes in the availability or distribution of preferred hosts (Thiemann et al., 2011).

The physiological limitations in mosquitoes' ability to adapt to water body salinity is well understood, applying direct pressure on species fitness based on their tolerance (Ramasamy et al., 2014). We found that salinity tolerance itself was negatively associated with precipitation. Salinity has been shown to drive changes in mosquito community composition both directly as a result of this tolerance, and more broadly in the sense that salinity also correlates with other water body characteristics relevant for mosquito fitness (Emidi et al., 2017; Ramasamy et al., 2014). For instance, freshwater habitats might support a different set of predators or vegetation that is less favourable to salinity-tolerant mosquitoes, further contributing to changes in community composition.

In contrast to climate and vegetation variables, we found that traits associated with broad habitat classifications, such as the gradient between urban and rural environments, may be less directly influenced by physiological factors. Mosquito species exhibit significant behavioural plasticity in habitat use and selection, allowing them to adapt to a wide range of habitat types (Meyer Steiger et al., 2016; Townroe and Callaghan, 2014). Consequently, the lower variance explained in mosquito species responses to these land use types in our model mean that the traits included in our study might not best reflect the drivers of this adaptability to different land use. Considering this, land-use driven variation in mosquito populations may be more gradual or context-specific, whereas climate-driven effects are better captured by these broad-scale traits due to their impact on basic mosquito physiological processes (Diniz et al., 2017; Mordecai et al., 2019). This distinction suggests that while physiological traits can effectively predict responses to climatic factors, behavioural traits related to habitat selection may require more nuanced characterisation to fully capture mosquito responses to land-use changes.

However, we did find that other measures of human-mediated pressure on land use interact in known ways with mosquito ecology. Human population density was significantly associated with artificial container breeding mosquitoes. Such mosquitoes utilise ephemeral water and containers to develop rapidly in an urban environment, often in pots, water butts, and gutters (Townroe and Callaghan, 2014). Use of such water types is highly advantageous for these mosquitoes, evading predation in the larval stage by other insects such as dragonflies and damselflies, whose long life spans can't be supported in urban temporary environments (Collins et al., 2019).

The fact that we find human population density is significantly associated with this type of breeding habitat and not urban habitat further suggests that the relative cover classifications used here might not be the most useful in terms of determining mosquito abundance and occurrence. One would expect urban areas to correlate heavily with population density, and thus we would expect a positive association between both. We should consider alternatives to these classifications in the future as they might not capture the fine-scale variation in microhabitats and microclimates available for mosquito exploitation that shape communities (Rochlin et al., 2016; Meyer Steiger et al., 2016).

Agricultural land use appeared to drive predominantly *Aedes* and *Anopheles* species positively, compared to other mosquito genera. The relationships in agricultural environments are complex; the use of artificial ditches often present in agricultural settings typically favours species able to rapidly colonise areas, sometimes within days (Imbahale et al., 2011; Medlock and Vaux, 2015b). This colonisation ability may be related to drought resistance, a trait in which *Aedes* and *Anopheles* species are known to be significantly more proficient than other genera, a characteristic also observed in similar ephemeral wetland environments (Hawkes et al., 2020; Medlock and Vaux, 2015b). This suggests that traits related to drought tolerance, such as oocyte thickness or other direct measures of desiccation resistance, could significantly influence mosquito community composition in agricultural areas.

Additionally, land use types such as agriculture are often fragmented and highly disturbed. Several studies have shown that both abundance and occurrence of mosquito communities are higher in transitional areas, which agriculture often creates while also providing ample breeding habitat for mosquitoes (Meyer Steiger et al., 2016; Rochlin et al., 2016). Incorporating these trait-environment relationships into mosquito distributional ecology is crucial for understanding the underlying ecological drivers that determine species distributions and, consequently, population dynamics in the face of ongoing global change.

4.5.2 Uncovering hidden mosquito-environment relationships through traits

Hierarchical Modelling of Species Communities (HMSC) leverages latent variables to account for unknown correlations between parameters. In our analysis, we found that these parameters, when mapped onto the trait space, offered different interpretations of unmeasured environmental variables. These latent variables provide insight into the multidimensional nature of mosquito ecological niches and which traits may be associated with similar variation in mosquito occurrence.

We observed diverging patterns between mosquitoes that are predominantly temporary water users (overwintering as eggs) and those that use permanent water bodies (overwintering as adults or larvae) across the latent variable space of the JSDM. This distinct axis of variation in trait use across the latent variables suggests that drivers of mosquito water usage and capitalization may be key in explaining unknown variation. Incorporating environmental drivers that represent the unique nature of mosquito capitalization of water sources may be worthwhile. For instance, measures of soil type and water availability at finer scales have shown to be significant in driving differences in mosquito community composition (Beketov et al., 2010), while other physical characteristics of the water body itself can influence the utility of that water body for different mosquito genera (Becker et al., 2010; Norris, 2004; Smith et al., 2024).

The relative closeness of our traits describing overall mosquito habitat preferences in terms of urban and rural preference in the latent variable space suggest that these broad traits don’t represent that much difference in unexplained environmental variables. This is in line with our other results, which showed how little the traits explained variation in all land use strategies apart from agriculture. The adaptability of mosquitoes across urban to peri-urban and rural habitats may not be accurately represented by such broad traits, and improving upon this likely requires a greater understanding of how microclimates and the traits associated with these different microclimate specializations varies across genera of mosquitoes. For instance, urban areas can support many types of mosquito communities, often those that are used to temporary water sources, but *Culex modestus* is known to be prevalent in underground subways and tunnels in cities (Soto and Delang, 2023), while other species such as *Aedes albopictus* can adapt to relatively hostile urban microclimates (Townroe and Callaghan, 2014). Other species are known to differentially use indoor and outdoor space in order to regulate physiological processes, which can dramatically alter community composition if said microhabitats are available (Benelli et al., 2020). Understanding the distinct tolerances of mosquito species to microclimate needs (thermal limits, humidity needs, etc.) may give us a better understanding of how traits help differentiate between land use types at finer scales.

Interestingly, we found diverging patterns in biting activity across the latent space, with night and day biting activity patterns positioned in opposition to each other. While our current results don't clearly delineate how these traits reflect different associations between environmental drivers of mosquito distribution, we can draw some inferences based on existing knowledge. Mosquito activity patterns are known to shift to target specific host species and vary seasonally (Thiemann et al., 2011). The association between wetland land use types and night biters may reflect the roosting patterns of avian hosts that heavily utilize these areas, with some evidence suggesting avian hosts are bitten more frequently at night (Griffing et al., 2007; Janousek et al., 2014).

However, these traits may be quite plastic, potentially changing in response to fluctuations in resource availability and predation pressure, which mosquitoes modulate through behavioural responses (Collins et al., 2019). As such, traits like biting activity or biting rate might not serve as stable indicators of how mosquito distributions are influenced by long-term environmental drivers, even if they are implicated in influencing overall vectorial potential of mosquitoes (Kilpatrick et al., 2006). Such biotic factors, including the presence and activity patterns of predators and prey, may be important drivers of mosquito behaviour and distribution that were not fully captured by our included variables (Golding et al., 2015; Russell et al., 2022). These behavioural traits, while variable, may still indirectly reflect important environmental and ecological factors shaping mosquito communities (Balenghien et al., 2006).

Additionally, the scale relationships between environment and traits may not be fully captured in our current analysis. Mosquitoes interact with their environment at multiple spatial and temporal scales, from microhabitat selection for oviposition to broader landscape-level movements (Reiskind et al., 2017). Differences in spatial resolution can reveal changes in traits that are evident at different spatial scales; for example, in butterflies, morphological trait variation can be seen at finer spatial scales but becomes less evident at broader resolutions (Kaiser et al., 2016; Laughlin and Messier, 2015; Violle et al., 2012). Our model, while incorporating various environmental variables and traits, may not adequately represent these cross-scale interactions, and variability in these scales can affect phenotypic expression. For instance, the traits we measured might respond differently to environmental factors at local versus regional scales, or there may be emergent properties at larger scales that are not evident when examining individual traits (Suárez-Castro et al., 2018). Furthermore, the resolution of our environmental data may not match the scale at which mosquitoes perceive and respond to their environment (Kitron, 1998). A better understanding of the scales at which traits interact with their environmental drivers would go some way to explaining the complex relationships observed in our study.

4.5.3 Leveraging community information for better mosquito predictions

Incorporating traits, species co-occurrence, and phylogenetic relationships enabled us to produce conditional predictions that significantly improved model accuracy. These predictions offer a way to simulate mosquito community processes under different scenarios, such as the introduction or removal of invasive species (Poggiato et al., 2021; Wilkinson et al., 2021). This feature is particularly important for understanding how invasive mosquitoes, such as *Aedes albopictus* and *Aedes japonicus*, can reshape native mosquito communities through competitive exclusion and other mechanisms which are currently less understood (Aliabadi and Juliano, 2002; Bevins, 2008; Juliano and Lounibos, 2005). By predicting communities with and without invasive species, we demonstrated that invasive mosquitoes can alter predicted community compositions at scale, potentially showcasing the mechanism through which overall community composition could be influenced by the invasion process, and ultimately may influence the likelihood of disease outbreaks due to changes in vector prevalence in these areas (Giunti et al., 2023; Petruff et al., 2020).

In scenarios where invasive mosquitoes were simulated as absent, our predictions based on this community state suggest that native species such as *Culex pipiens*, *Anopheles maculipennis*, *Aedes vexans*, and *Culiseta annulata* would be more prevalent than in cases where the invasive species were present. Such changes in the overall composition of mosquito communities might suggest a reduction in potential vectors of endemic European arboviruses such as West Nile virus and Usutu virus, while an increase in exotic diseases such as Zika or Chikungunya may become more prevalent (Lühken et al., 2023; Medlock and Leach, 2015; Semenza and Suk, 2018). Competitive interactions between these species are well documented, particularly between *Aedes albopictus* and *Culex pipiens*. In many cases, *Ae. albopictus* has been shown to be the superior competitor, especially in constrained container-like habitats, due to its ability to convert food to body mass more efficiently, potentially reducing the abundance of *Cx. pipiens* by up to 70% in some cases (Carrieri et al., 2003; Costanzo et al., 2005; Marini et al., 2017). Less is known about the competitive interactions between *Ae. albopictus* and the other species mentioned here, but it is likely that these characteristics also lend themselves to high competitive proficiency, particularly against species that occupy very similar larval container habitats, such as *Ae. vexans* and *Cs. annulata*. However, the ability to propagate community interactions or residual correlations from JSDMs to regional scales is an exciting use case for understanding shifts in mosquito community composition, especially in the case of community change through invasive species and range shifts of mosquitoes (Carlson et al., 2023; Medley, 2010).

Our analysis has emphasised the underutilisation of mosquito community data from existing sampling efforts, which typically focus on medically relevant species such as *Aedes albopictus* or *Culex pipiens*, often neglecting the broader mosquito community (ECDC, 2021; Medlock et al., 2018; Schaffner et al., 2013a). As we demonstrate, data on native or non-target species is valuable for understanding community dynamics and improving models of mosquito distributions at large scales, either through leveraging conditional predictions or gaining better inference. Including non-medically relevant species in sampling efforts requires more effort but could provide substantial benefits for understanding wider community dynamics of mosquito communities.

A more inclusive approach to mosquito surveillance could significantly enhance our ability to predict changes in mosquito populations in response to environmental changes such as climate change, land use modifications, or the spread of invasive species (Barker and MacIsaac, 2022; Lippi et al., 2023a). Routine inclusion or, at minimum, recording of co-occurrence of non-target species in sampling programmes, which are usually noted as by-catch and in some cases never reported, could also improve our understanding of how mosquito community composition might affect overall disease pressure and disease risk based on the relative composition of potential vectors within these communities. This would allow for more accurate predictions of where and when outbreaks might occur (Santika, 2011). This has clear implications for public health, as understanding mosquito community dynamics at scale can inform more targeted vector control strategies and improve surveillance efforts to mitigate the risks of emerging vector-borne diseases (Ovaskainen et al., 2017a).

4.5.4 Conclusion

This study underscores the significance of integrating trait-environment relationships into mosquito distributional ecology and demonstrates the potential of Hierarchical Modelling of Species Communities (HMSC) to uncover hidden mosquito-environment interactions. By incorporating traits and community information into mosquito distributional models, we not only enhance predictive accuracy but also enable the simulation of community processes under various scenarios.

Our findings also advocate for a more comprehensive understanding and compilation of mosquito traits, including species that may not be the primary focus of sampling programmes. We highlight the current lack of detailed trait databases for mosquitoes, in contrast to other arthropod groups (Homburg et al., 2014; Parr et al., 2017; Shirey et al., 2022), and this gap significantly hinders the further development of trait-based methods in mosquito ecology, though efforts to address this are underway (Lippi et al., 2023b).

This trait-based approach offers a mechanistic understanding of mosquito responses to environmental drivers, potentially bridging the gap between local and laboratory-scale studies and the complex interactions at macro scales. Ultimately, these insights will deepen our understanding of how mosquito populations respond to environmental changes, improving our ability to predict and manage vector populations in the face of ongoing global change.

Chapter 5

Discussion and Synthesis

Community ecology has a long history in ecological research, yet its application to vector-borne disease systems remains limited. Whilst community ecology and distribution modelling are well-developed for many taxa of conservation interest, they are less established for vectors of disease, where public and animal health research typically emphasizes identifying one or two key vector species and understanding their distributions, largely in relation to abiotic environmental drivers. Mosquitoes, despite being one of the deadliest and most medically important taxa in the world, are not currently at the forefront of community-level ecological research. In this thesis, I focus research efforts on taking a broader, more holistic view of mosquito communities, the interactions within these communities, and the environmental drivers that shape them.

By combining joint species distribution modelling and mosquito occurrence data arising from both local-scale stratified ecological study and continental-scale vector surveillance, I show how abiotic and biotic environmental factors can shape overall community composition and distributions at different scales, identifying interactions of relevance to disease transmission and public health. By focusing on communities of mosquitoes, rather than individual species, this work highlights the need to look beyond correlative abiotic drivers of mosquito distributions. The research expands our understanding of how biotic interactions, traits, and phylogeny collectively influence mosquito community structure, offering new perspectives on the ecological dynamics underlying vector-borne disease systems.

5.1 Thesis Overview

In this thesis, I present novel approaches to understanding the impacts of both biotic and abiotic factors on mosquito communities through the use of state-of-the-art Hierarchical Modelling of Species Communities (HMSC) and other Hierarchical Generalized Mixed Bayesian Joint Species Distribution Modelling (JSDM) frameworks. In doing so, I demonstrate the complex interplay between scale, biotic influences, environmental drivers, and traits in shaping communities of mosquitoes. These integrative approaches provide a more nuanced understanding of how mosquito communities are shaped by these different components, impacting overall community composition, which has interesting implications for understanding changes in, and drivers of, mosquito-borne disease risk.

This work represents an important first step towards addressing the challenges of defining communities from sparse datasets, particularly at large spatial scales. By attempting to use these data for inference of biotic interactions, I highlight both the potential and the limitations of employing community data at scale. The methods developed here grapple with the sparsity of data and the spatial and habitat biases inherent in vector surveillance, offering insights into the advantages and challenges of applying community-level analyses to mosquito ecology. Moreover, this research showcases the substantial computational requirements and novel methodological approaches necessary to handle and analyse such data at these scales. This approach not only enhances our understanding of mosquito communities but also contributes to a wider discussion on the applicability and constraints of community data in ecological research.

Ultimately, this work contributes to a more comprehensive view of mosquito ecology, and I hope that some of my findings can be used in the future to investigate the potential of understanding community-level drivers of mosquitoes for public health. The methodologies developed in this thesis offer a framework that could be adapted to explore community dynamics in other vector systems, potentially informing more holistic approaches to vector management and disease control strategies.

5.1.1 Chapter 2: Wetland Management and Mosquito Community Composition

In Chapter 2, I began by exploring how aspects of mosquito community structure can change in response to management and conservation decisions, which might create unintended consequences for overall community composition. My aim was to understand how land and biodiversity management decisions, typically made by policymakers to benefit one species group (in this case, bird taxa), can have ripple effects on other organisms through indirect drivers such as changes in habitat structure and complexity. Importantly, I demonstrated that wetland management changes, combined with interacting biotic factors of predation pressure, are likely crucial in determining local mosquito population structure. Wetland management strategies altered abiotic environmental factors, in this case vegetation composition and structural characteristics of wetland environments, increasing suitable habitat for some mosquito species but leading to reduce habitat suitability for others. These vegetation changes, coupled with inferred biotic interactions between predator species and mosquitoes, ultimately shapes overall community composition through multiple mechanisms.

5.1.2 Chapter 3: Environmental and Biotic Drivers of Mosquito Communities Across Europe: A Multi-Scale Joint Species Distribution Modelling Approach

Chapter 3 addressed this challenge by leveraging novel computational methods and tools to conduct joint distribution modelling across multiple scales (1 km-10 km), quantifying the impact of mosquito species interactions on mosquito communities, alongside environmental factors (hosts, climate, land use, human populations) and space. I found consistent impacts of biotic interactions between mosquito species across these scales, contrasting with ecological theory that these impacts should be strongest and most detectable at finer scales. Importantly, our models revealed that a substantial portion of the variation in species distributions, which in traditional single-species models is typically attributed to spatial and environmental factors, was instead explained by the biotic component in our joint species distribution models. This suggests that species interactions may play a more significant role in shaping mosquito communities at broader scales than previously recognized, and that conventional approaches might be misattributing biotic effects to abiotic factors.

5.1.3 Chapter 4: Leveraging Trait Data and Community Composition for Enhanced Predictions

In Chapter 4, I leveraged the full potential of JSDMs, by including biological traits, phylogenetic relatedness and potential drivers of mosquito species interactions with their environments. JSDMs were used to examine how trait variation between mosquito species influenced responses to environmental drivers and predicted overall distribution. My results demonstrated that trait values related to breeding behaviour, habitat selection, and preference explained several species relationships with environmental drivers that were largely consistent with our current understanding of mosquito ecology. Traits accounted for a substantial portion of the variation in mosquito species' responses to climatic factors but less variation in responses to land use and habitat classification drivers. This was a surprising result, as I had anticipated that the broad resource use traits included in the analysis would correlate more strongly with species responses to land use, habitat, hosts and topography rather than with species' climate responses.

Importantly, using information about how species influence each other through these potential biotic factors can lead to improved predictions of individual species distributions. I discussed how this approach could potentially be used to estimate changes in community composition resulting from the introduction of new species for example, and consequently, how these changes might alter the structure of a mosquito community and competent vector assemblages for different pathogens. Inferring potential species interactions from JSDMs is complementary to mechanistic and empirical approaches for understanding outcomes of interactions between mosquito species, which require intensive data collection (e.g. across *Aedes* invaded ranges).

5.2 Main Findings

5.2.1 Wetland Management and Mosquito Ecology

Habitat structure, modified by wetland management, was found to be a key driver of mosquito community composition at local scales, whilst at continental scales, habitat use traits such as breeding site preferences explained significant variation in mosquito species occurrence. This supports our current understanding about how habitat structure in wetlands can significantly influence mosquito community compositions, with differential impacts on species according to their resource use preferences (Hartemink et al., 2015). It also mirrors findings from other habitat types such as the interface between urban, grassland, and woodland habitats, where in my case aquatic and riparian vegetation can drive changes in overall community compositions (Claflin and Webb, 2017b; Ferraguti et al., 2022, 2021).

Additionally, several potential predator species were implicated in influencing mosquito distributions, highlighting the importance of collecting co-located predator and mosquito data for fully understanding how wetland management and habitat structure may mediate key biotic interactions that constrain mosquito distributions. Such understanding may advance potential for natural vector control options through habitat management that increases predator populations (Beketov and Liess, 2007), as seen in other contexts (Saha et al., 2009). This extends hypotheses of how habitat structure drives composition to a broader context, revealing how multiple species, which we suspect interact with mosquitoes in complex ways, shape these dynamics (Golding et al., 2015).

At local scales, my work untangling the effect of habitat structure effectively advances our understanding of how changes to mosquito communities, especially deliberate management decisions, can impact multiple drivers of mosquito species. By influencing habitat structure and abiotic factors, we also influence the distribution of species that biotically interact with mosquitoes, meaning that these effects can also shape overall community structure (Fouet and Kamdem, 2019; Martinou et al., 2020; Rey et al., 2012). Importantly, I found that indirect changes made to promote broader biodiversity gains and protect key species could inadvertently alter the composition of potential vectors. This serves as a pertinent reminder that while, in this case, mosquito abundance was relatively low and far from heavily populated areas, such changes may have minimal immediate impact. Yet, work in other regions with different wetland compositions (particularly those closer to urban areas through urban greening and wetland expansion plans) has shown that habitat alterations can drive changes in mosquito species composition (Hanford et al., 2020; Roiz et al., 2015).

Therefore, when developing management plans for wetlands, it is crucial to balance the needs of conservation, biodiversity, and ecosystem services with the potential risks of mosquito-borne diseases (MBDs) (Acreman et al., 2011; Martinou et al., 2020). This balance will inevitably vary spatially, depending on local climate and ecosystem conditions and linked ecological community dynamics underpinning hazard, human factors that underpin risks of MBD introduction and exposure, and local MBD risk context. In areas with active MBD outbreaks or higher risk of establishment, management strategies may need to prioritize vector control, while in lower-risk areas, conservation goals might take precedence. However, even in marginal areas for transmission, the potential for future changes in disease dynamics must be considered, particularly in light of climate change or the shifting ranges of host reservoir species (Medlock and Leach, 2015; Medlock and Vaux, 2015b).

As wetland regeneration continues in the study area, or in areas with relatively low MBD risk, it's important not to overlook these risks. We must consider how future climate change, the shifting ranges of host reservoir species, and the presence of invasive species could affect these ecosystems. The disease burden caused by mosquitoes is expected to increase across much of Europe, including the study site, due to various factors (Medlock and Leach, 2015; Medlock and Vaux, 2015b). The United Kingdom, for example, has faced multiple challenges from invasive mosquito species. The invasive *Aedes albopictus* has been detected on at least six occasions, with its establishment thus far prevented through routine control efforts (Vaux et al., 2019). Additionally, other potentially problematic species have emerged, such as the recently detected presence of *Culex modestus*, a competent vector for various pathogens (Golding et al., 2012).

Community-level approaches, particularly through JSDMs, could significantly enhance risk management planning for wetlands by providing more comprehensive predictions of how mosquito assemblages might shift in response to changes in managed habitats. This improved understanding could enable authorities to anticipate potential increases in vector populations or changes in species composition that affect disease transmission risk, allowing for more proactive and targeted interventions (Rey et al., 2012; Willott, 2004). Ultimately, this approach could inform wetland management strategies that minimize the enhancement of mosquito populations or communities of vectors while still achieving other conservation goals.

This work serves as a reminder that while the burden of mosquitoes may currently be low in many areas, the potential for future increases driven by habitat change should not be ignored. Adaptive management approaches that can respond to shifts in climate, vector populations, and disease prevalence will be essential for maintaining this delicate balance between ecosystem services and public health concerns (Fouet and Kamdem, 2019; Martinou et al., 2020). The findings here underline the need for a One Health approach to habitat management, conservation, and public health.

5.2.2 The importance of traits and biotic interactions shaping mosquito communities

Incorporating trait and phylogenetic data into JSDMs offers a promising avenue for improving predictions, particularly in the context of mosquito distributions and their responses to environmental changes. Traits such as salinity tolerance, thermal limits, and breeding habitat preferences were important in explaining species variation in response to environmental drivers like climate, topography, and vegetation (Carver et al., 2009; Mordecai et al., 2019). The detected relationships were in line with biological expectations: species' relationships with salinity depended on their different levels of salinity tolerance, whilst artificial container breeders were positively associated with human population density (Ramasamy et al., 2014; Rochlin et al., 2016). Container-breeding mosquitoes trade off the risk of temporary water drying up with the benefits of reduced predation pressure, as many insect larvae that prey on mosquitoes cannot reproduce in these artificial containers (Carlson et al., 2004).

The predictive power of traits in JSDMs may depend on the specific trait group or mosquito type being studied. For instance, traits related to breeding habitat preferences, such as the utilization of artificial containers, were found to be strongly associated with the distribution of invasive *Aedes* species like *Ae. albopictus* and *Ae. japonicus*. In contrast, traits such as salinity tolerance might be more relevant for predicting the distribution of mosquito species that inhabit coastal or brackish water environments. Furthermore, the predictive power of traits may vary depending on the ecological characteristics of the mosquito species in question. Generalist species with a wide range of habitat preferences and adaptability may be less strongly influenced by specific traits compared to specialist species with narrower ecological niches (Juliano, 2009; Medlock et al., 2012). This could explain why the JSDMs had lower predictive power for some invasive species like *Ae. albopictus*, and the ubiquitous *Culex pipiens*, which are known for their adaptability and wide range of breeding habitats (Medley et al., 2019; Medlock et al., 2012).

Surprisingly, I found that the biotic components of these models consistently detected significant species interactions, even at larger spatial scales. This is particularly interesting because ecological theory suggests that species interactions should weaken as spatial scale increases, with environmental factors like climate becoming more dominant at these scales (Krasnov et al., 2011; Soghigian et al., 2023). While it is possible that the scale at which mosquitoes interact might be larger than expected, a more likely explanation is that missing environmental drivers account for the biotic variation detected by the models (Zurell et al., 2018).

JSDMs allow unmeasured variables to be absorbed into the biotic component, and it is probable that certain key environmental drivers, which were not included in the models, contributed to the observed biotic variation. This hypothesis is supported by several factors in mosquito ecology: the complexity of mosquito habitats (Becker et al., 2010; Wilkerson et al., 2021), which are influenced by numerous, often subtle, environmental variables; rapid temporal dynamics in response to short-term environmental changes; significant human influence through land use changes and control efforts (Gottdenker et al., 2014; Hunt et al., 2017; Meyer Steiger et al., 2016); the role of host availability; and the presence of cryptic species complexes and genetic variation (Cator et al., 2020; Chandrasegaran et al., 2020; Messier et al., 2010; Suárez-Castro et al., 2018). Mosquito ecology can also be driven by fine-scale environmental conditions and resource availability, rather than large-scale species interactions. Thus, the observed biotic variation in the JSDMs is more likely due to unmeasured environmental factors that were absorbed into the biotic component of the model.

However, these findings do not rule out the potential significance of biotic interactions at larger scales. Detecting such interactions, even if partially driven by missing environmental variables, provides valuable insights into how species respond differently to similar environmental drivers. For instance, the negative associations found between invasive *Aedes* species (*Ae. albopictus* and *Ae. japonicus*) and nearly all other mosquito species may not indicate direct competition but rather reflect how these species are driven by unmeasured environmental factors, such as the spread of invasive species through trade (Medlock and Leach, 2015).

5.3 Optimizing JSDMs for Vector-Borne Disease Research

To address the challenges associated with Joint Species Distribution Models (JSDMs), vector-borne disease (VBD) researchers must carefully navigate several trade-offs, which largely depend on the quality, quantity, and type of community data available. The first key decision is defining what constitutes a “community” from often sparse vector data, as this underpins all subsequent stages of analysis. Aggregating such data requires careful consideration, particularly regarding the scale of aggregation, as demonstrated in this thesis. For example, in this work, mosquito data had to be aggregated across both temporal and spatial scales due to limited data availability. Invasive species, highly prevalent species, and rare species each pose unique challenges, and the way these are managed within a dataset can introduce biases.

Researchers must make trade-offs to account for these complexities, balancing precision with feasibility in data collection and analysis.

5.3.1 Understanding the Limitations of Community Data

Traditional SDMs provide various tools for handling imbalances in presence-absence datasets, tools that JSDMs cannot easily utilize without affecting the prevalence and other factors of species in the community dataset. For example, in traditional SDMs, pseudo-absences are commonly used to balance data and improve model performance (Barbet-Massin et al., 2012; Chapman et al., 2019; Phillips et al., 2009). However, in JSDMs, adjusting presence-absence data for one species by selecting pseudo-absences (either randomly or in a stratified manner) can distort the overall community structure and complicate accurate analysis of species interactions. In contrast, JSDMs excel at trying to capture interspecific interactions, such as competition, predation, and facilitation, which are overlooked by SDMs focused on single species (Wilkinson et al., 2019). Therefore, researchers should carefully consider their primary objectives before deciding on the use of modelling methods, especially given the contrasting research showing how Stacked-SDMs can perform across similar data types with the same performance (Zurell et al., 2020).

5.3.2 *A Priori* Assumptions on Abiotic Effects and Scale

In mosquito vector ecology, *a priori* assumptions about abiotic drivers like temperature, precipitation, and habitat characteristics are crucial, especially when considering their scale-dependent effects. Abiotic factors often determine key aspects of vector ecology, but their influence can vary dramatically across spatial scales (Lord et al., 2014). For example, temperature may be a strong predictor at regional scales, while localized factors like water quality or microhabitat structure become more important at smaller scales (Flores Ruiz et al., 2022b; Kraemer et al., 2019a; Murdock et al., 2017a).

Matching abiotic drivers to appropriate scales is essential for accurately modelling mosquito populations and their vectorial capacity. In this thesis, temperature and precipitation were identified *a priori* as critical abiotic factors influencing mosquito resource use, such as breeding habitats and developmental limits using a resource-based framework and utilizing the recent deluge of reviews that cover the various trends in mosquito SDM modelling and drivers therein (Barker and MacIsaac, 2022; Hartemink et al., 2015; Lippi et al., 2023a). However, the strength and consistency of these relationships varied across scales, with broader patterns emerging at regional levels, and more context-specific drivers, like urbanization or water availability, dominating at finer scales which is consistent with other studies (Claflin and Webb, 2017a; Murdock et al., 2017b).

Careful consideration of the scale at which abiotic and biotic drivers operate is required for JSDMs to capture the full complexity of both biotic and abiotic drivers of mosquito communities. Misalignment between the scale of drivers and the ecological processes that influence community composition could lead to inaccurate predictions, particularly when assessing mosquito-borne disease risks (König et al., 2021; Suárez-Castro et al., 2018).

5.3.3 Computational Complexity and Scaling Issues

Another major consideration when using JSDMs is computational complexity, which increases non-linearly as the number of community sites, species, and spatial effects in the model grows (Tikhonov et al., 2020a). Novel approaches are needed to handle large-scale analyses, but even at smaller scales, incorporating additional complexity—such as using abundance data instead of species occurrence—can dramatically increase model run times, making analysis computationally infeasible. For instance, without access to high-performance computing resources, such as graphics processing units (GPUs) needed for machine learning frameworks, the analyses in this thesis would not have been possible (Rahman et al., 2024).

This presents two key challenges for VBD researchers. First, they must prioritize components or drivers based on the ecological question at hand. For example, at larger scales, researchers may want to focus on how species' occurrence probabilities shift within a community to understand how archetypes of mosquito assemblages relate to disease occurrence. At smaller scales, however, understanding how species' abundances change due to co-occurrence effects may be more meaningful, particularly when considering the impact of species interactions on potential disease vectors (Bara et al., 2015). This distinction is important for assessing VBD risk at different scales (Lord et al., 2014). As demonstrated in this thesis, using abundance data for over 400 community sites was computationally infeasible at smaller scales, even though this could have provided valuable insights into how mosquito communities change. However, at larger scales, occurrence data may be more useful for assessing how assemblages of invasive species interact, as discussed in Chapters 3 and 4 (Araújo and Rozenfeld, 2014).

5.3.4 Choosing the Right JSDM Framework

The second challenge is that not all JSDM frameworks are equal. Once researchers define the scale of their ecological question, they must choose tools that best address their research goals. Different frameworks offer different capabilities and trade-offs, which are not always immediately apparent to traditional SDM users. For instance, the *sjSDM* framework, used in Chapter 3 of this thesis to assess biotic interactions at varying scales, is particularly well-suited for incorporating large spatial effects into modelling. However, it lacks the ability to integrate traits or phylogenetic relationships, making it less flexible for studies that require these factors. In contrast, the *HMSC* framework, used in Chapter 2 to assess the local-scale impact of habitat, is highly capable of incorporating multiple levels of mixed effects into the analysis. While this framework was later used to explore trait variation across a continental scale in Chapter 4, its full potential has only recently been realized due to advancements in

Markov Chain Monte Carlo (MCMC) sampling algorithms, yet even these advancements couldn't fully account for scale in this instance.

Therefore, researchers must acknowledge that conducting JSDM analyses often involves compromises, and a perfect solution that is free from assumptions about scale may not be feasible without significant investments in novel sampling methods or computational resources (Ovaskainen and Abrego, 2020; Wilkinson et al., 2021).

5.3.5 Accessibility and Technical Challenges

Another notable challenge is the accessibility of JSDMs for ecologists. Implementing these frameworks has required significant time, effort, and resources, even for an ecologist with experience in computational methods. The complexity of handling large datasets frequently necessitates understanding both ecological and computational limitations, which creates a barrier for many researchers. This contrasts with the more user-friendly frameworks popularized in the 2010s, which required much less computational power and setup (Thuiller et al., 2009). However, the trade-off for simultaneously modelling species interactions is the increased complexity inherent in JSDMs.

Recent software developments have made it easier to implement large-scale JSDMs (Golding, 2019; Pichler and Hartig, 2021; Rahman et al., 2024; Tikhonov et al., 2020a), and this trend is likely to continue as computational power increases and novel approaches, whether through hardware improvements or algorithmic innovations, make analyses more efficient. For example, many MCMC sampling methods, a common backbone of many JSDM statistical frameworks (e.g., *brms*, *HMSC*, *sjSDM*, *greta*), could be accelerated with minimal user input in the future, thanks to updates that handle conversions to hardware-accelerated methods that utilize high-performance probabilistic programming languages, such as *pyMC3*, *JAX*, and *TensorFlow* (Bradbury et al., 2018; Martín Abadi et al., 2015; Salvatier et al., 2016). As these methods become more widespread, implementing and running JSDMs will become increasingly accessible. Nonetheless, researchers must remain mindful of the trade-offs and technical considerations involved before embarking on their use.

5.4 Future Research Areas

While this thesis has made strides in addressing how factors beyond abiotic drivers can shape the distribution of mosquitoes, it has also opened up more questions than it has answered. The integration of biotic interactions into predictive models of mosquito communities has revealed promising insights, yet many challenges remain in fully leveraging this information. Understanding how these biotic factors, such as species interactions, evolutionary relationships, and trait dynamics, intersect with environmental variables is needed to improve predictions of mosquito communities and the estimation of MBD pressure. Future research must work towards a deeper understanding of these complex ecological relationships to refine our approaches.

5.4.1 Understanding Abundance and Temporal Variation

In this thesis, I focused primarily on occurrence data, largely due to limitations in data quality and quantity (Rund et al., 2019), as well as challenges in model convergence and flexibility when working with more complex statistical distributions for abundance data (Ovaskainen and Abrego, 2020). Abundance is likely a key driver in how mosquito communities interact and shape one another. Interactions between mosquito species are density dependent, and rarely lead to the complete exclusion of a species; instead, they often result in reduced abundance and differential niche partitioning (Amarasekare, 2003). These abundance dynamics are also critical for understanding vectorial capacity in a broader context, as density-dependent interactions between hosts, vectors, and humans typically determine the likelihood and extent of mosquito-borne disease (MBD) spillover (Dobson, 2004; Smith et al., 2007). Failing to account for these interactions limits our ability to fully comprehend the dynamics of disease transmission.

Additionally, we should not neglect the importance of the temporal component on mosquito occurrence or abundance probabilities for similar reasons. Although mosquito species are generally active during similar periods of the year, especially in terms of peak abundance, subtle variations in these patterns exist both across seasons and within daily activity patterns (Hawkes et al., 2020; Rund et al., 2016). These shifts in activity at all scales, likely influence how communities of mosquitoes may interact and affect one another, reducing overall competitive interactions through niche partitioning and variable resource use (Laporta and Sallum, 2014). For example, *Culex pipiens* larvae have been shown to be more resistant to encroachment and co-colonization of breeding habitats by *Aedes albopictus* in cooler temperatures early in the year, but are soon outcompeted as conditions warm later in the season (Carrieri et al., 2003).

Neglecting these factors may have significant implications for assessing the usefulness of JSDMs in broader disease ecology and warrants further investigation (Box 1). The abundance and seasonality of competent vectors have far-reaching consequences for overall disease risk and the likelihood of spillover events, which should not be overlooked (William et al., 2018). However, gathering such data requires intensive, routine sampling, meaning that the development of dynamic JSDMs that account for abundance and temporal variation in mosquito populations may only be feasible at small, local scales where consistent monitoring for public health or invasive species control is already in place (Badger et al., 2023; Thorson et al., 2016).

Box 1: The role of abundance and temporal scale

1. **Incorporating species abundance:** How does incorporating species abundance, rather than simple occurrence, into JSDMs of mosquito communities enhance the detection of biotic interactions? Additionally, does accounting for this complexity improve our understanding of community-shaping mechanisms, or is its impact negligible?
2. **Role of seasonality:** What is the role of seasonality in shaping mosquito species' interactions with their ecological niches, and how do seasonal shifts in temperature, rainfall, and habitat availability affect niche partitioning, species interactions, and shape mosquito communities over time?

5.4.2 Moving Towards a Better Understanding of Traits

Research on other arthropod groups has highlighted the importance of scale in trait-environment interactions (Messier et al., 2010; Suárez-Castro et al., 2018). For example, thermal tolerance traits tend to be more predictive at broader, regional, or global scales, where temperature gradients are more pronounced (Flores Ruiz et al., 2022a; Gleiser and Zalazar, 2010; Kaiser et al., 2016). In contrast, traits associated with predator avoidance may be more relevant at finer, habitat-specific scales (Russell et al., 2022; Vonesh and Blaustein, 2010). In mosquitoes, traits related to host-seeking behaviour and larval development are likely to be more detectable at smaller spatial scales, where resource availability becomes a key limiting factor for populations. At larger scales, however, broader phylogenetic patterns may emerge, reflecting evolutionary constraints on species' distributions (Krasnov et al., 2011).

In addition to spatial scale, traits such as body size and feeding behaviour can vary significantly within a single mosquito species depending on local environmental conditions (Ciota et al., 2014; Lahondère and Bonizzoni, 2022; Vinauger and Chandrasegaran, 2024). Understanding this intraspecific variation is critical for capturing the adaptability of mosquito populations and for determining their role in the transmission of mosquito-borne diseases (MBD) (Brass et al., 2024; Cator et al., 2020; Chandrasegaran et al., 2020). Quantifying this variability through metrics such as standard deviations can provide deeper insights into how mosquitoes adapt to different environments, which in turn influences their distribution patterns and vector competence (Brass et al., 2024).

To implement a trait-based approach in mosquito ecology, addressing the scarcity of relevant trait data is essential. This is a crucial step toward developing methods that offer ecologically meaningful explanations of how mosquito species respond to environmental drivers (Lippi et al., 2023b; Wong et al., 2019). Furthermore, testing how traits vary geographically and seasonally, both within and between species, can significantly enhance our understanding of mosquito ecology and improve species distribution models. Aligning trait data with appropriate ecological scales is critical to developing biologically relevant models (Suárez-Castro et al., 2018).

Traits also play a pivotal role in determining mosquito species' invasive potential. Species with broader host ranges are more likely to establish themselves in diverse habitats (Paupy et al., 2009). Phenotypic plasticity, or the ability to rapidly adapt to environmental changes, can enable mosquitoes to expand into areas where they were previously not expected to survive (Sherpa et al., 2019). Comparing the traits of mosquitoes with different vector and invasive statuses can reveal which combinations of traits are most influential in these processes. To effectively capture this variation, trait data should be collected across various spatial scales and populations. Streamlining this process may involve linking traits to genetic markers across species (Beerntsen et al., 2000; Civelek and Lusis, 2014; Mackay et al., 2009) or focusing on species with high genetic variability, which could drive rapid adaptation to new habitats (Brown et al., 2011). However, the high cost of genetic sequencing limits the feasibility of such studies, making them practical only for the most important vector species (Dritsou et al., 2015).

Traits that influence vector competence often overlap with those that promote invasiveness. Mosquitoes with broad host ranges are not only more adaptable but also serve as efficient bridge vectors for zoonotic diseases (Kilpatrick et al., 2006; Takken and Verhulst, 2013). Traits like overwintering and diapause can greatly increase the potential for virus transmission across seasons and facilitate mosquito dispersal through trade routes (Folly et al., 2022). Mosquito species that exhibit both invasive potential and predisposition to transmit arboviruses pose a significant threat to public health, particularly in naïve populations, where these traits converge to create highly efficient vectors of disease (Medlock and Leach, 2015; Schaffner et al., 2013c).

In summary, while incorporating traits into mosquito ecological research holds great promise for understanding disease risk, several key challenges remain (Box 2). These include selecting biologically relevant traits, capturing trait variation across scales and within species, and integrating insights from other taxa where trait-based approaches are more established. By addressing these considerations and streamlining trait data collection, researchers can develop a more comprehensive understanding of mosquito ecology and improve our ability to predict and mitigate disease risk in a changing world. Drawing on the experiences and methodologies used in other taxonomic groups can provide valuable guidance for refining trait-based approaches in mosquito ecology.

Box 2: Key gaps in understanding the role of traits

- **Scale-dependent trait interactions:** How do key mosquito traits (e.g., thermal tolerance, host-seeking behaviour, larval development characteristics) interact with environmental drivers across different spatial scales to influence mosquito distribution and community composition?
- **Improving trait data availability:** What strategies and sources of information can be employed to improve the estimation of mosquito trait values at sufficient scale and throughput, addressing the current scarcity of trait data?
- **Intraspecific trait variation:** How does accounting for intraspecific variation in traits such as body size and feeding behaviour improve our understanding of mosquito species' ecological flexibility, distribution patterns, and potential as disease vectors?

5.4.3 Application of Community Models to Mosquito Surveillance and Disease Risk

Despite the trade-offs in overall accuracy and complexity inherent to Joint Species Distribution Models (JSDMs), my research demonstrated that leveraging fully realized conditional predictions within this framework could achieve significant improvements in model accuracy. This approach is particularly promising for mosquito surveillance, as routine sampling practices already provide comprehensive data on community composition in many areas (ECDC, 2014; Schaffner et al., 2013b).

The power of conditional predictions lies in their ability to estimate the probability of occurrence for species not directly observed at a given site. For instance, in a network of established monitoring locations, JSDMs can generate predictions for potential invasive species based on the presence of known native species and environmental factors. If surveillance at Site A consistently detects native species X, Y, and Z, the model can estimate the likelihood of an invasive species I occurring there, even if it hasn't been directly observed.

This method offers several advantages for vector management:

1. Identification of potential invasion hotspots without additional sampling efforts
2. Prioritization of sites for enhanced monitoring or preemptive control measures
3. Cost-efficient direction of limited resources towards high-risk areas
4. Creation of a dynamic tool for adaptive management through continual model updates

For example, if the model predicts a high probability of an invasive species across multiple sites in a region, despite its absence in current samples, that area could be flagged for increased surveillance or expanded sampling protocols. This approach not only maximizes the utility of existing data but also provides a framework for proactive vector management.

While the potential of this method is significant, it's important to note that detailed research in this area is currently limited beyond the results presented in Chapter 4 (Poggiato et al., 2021). However, given the established infrastructure for routine mosquito surveillance, particularly for medically significant and invasive species, mosquitoes present ideal candidates for further exploration and refinement of these techniques.

JSDMs offer valuable insights into community-level dynamics and species interactions, particularly at finer spatial resolutions. However, they face limitations when applied to broader scales, where traditional SDMs often excel in capturing larger environmental and climatic drivers efficiently. Considering both the limitations and benefits of JSDMs, I believe there is a place for multiscale approaches to distribution modelling that could combine both traditional SDM methods and JSDM approaches. For instance, JSDMs could be applied at finer spatial resolutions to explore species interactions, while predictions from traditional SDMs could be used at broader scales to capture larger environmental and climatic drivers when investigating distributions of important assemblages (Jones et al., 2010). This hybrid approach could offer a more comprehensive understanding of species distributions by leveraging the strengths of both SDMs and JSDMs in tandem.

Another intriguing research direction is to investigate whether certain mosquito community archetypes are more prone to amplifying disease potential. Given that vector species like *Aedes albopictus* and *Culex pipiens* are ubiquitous across Europe, yet disease spillover events are geographically concentrated, it would be valuable to explore whether specific community compositions correlate with higher mosquito-borne disease risk (Ferraguti, 2024; Ferraguti et al., 2021). Characterizing community structures in areas where diseases like West Nile Virus or dengue are more likely to emerge could reveal how the interactions between species influence vector competence. Such studies would enhance our current understanding of the relationship between mosquito presence and disease risk, and may also help explain why certain regions experience more frequent outbreaks (Lippi et al., 2023a).

Archetypal categorization of communities and habitat types are frequently used in conservation to attribute resources most effectively, and there is no reason such methods couldn't be explored for mosquito-borne diseases (Moilanen, 2007). In fact, this approach is already being implemented in recent studies of potential Rift Valley fever introduction, where stacked SDMs have been employed to identify potential incursion hotspots (Wint et al., 2020). By applying similar community-based approaches to mosquito populations, we could potentially identify high-risk assemblages that are more likely to facilitate disease transmission. This could lead to more targeted surveillance and control efforts, focusing resources on areas where specific community compositions indicate a higher likelihood of disease emergence or persistence. Moreover, understanding these community archetypes could provide valuable insights into the ecological factors that contribute to disease risk, potentially informing broader strategies for mosquito-borne disease management and prevention across diverse landscapes.

Understanding how community composition across larger spatial scales influences MBD transmission potential offers valuable insights for vector-borne disease forecasting. JSDMs, when combined with other modelling techniques, present an opportunity to maximize their strengths at local scales where intervention and management can take palce (ECDC, 2021; Schaffner et al., 2013a). By integrating JSDMs with routinely sampled data from well-monitored areas, researchers can capitalize on the practical application of these techniques. Such techniques have been used in mapping the distribution of invasive plant species, which showed that combinations of fine-scale models and larger models could overcome some of the inherent challenges of non-equilibrium assumptions for invasive species modelling (Jones et al., 2010). Access to biotic interactions to aid these approaches would prove to be a novel step towards understanding the true usefulness in vector ecology (Poggiato et al., 2021). Establishing a robust research program focused on utilizing JSDMs for these purposes is crucial for ensuring their effective and practical implementation. Such a program could start by addressing several key research questions (Box 3).

Box 3: Applying JSDMs to surveillance and risk mapping

- **Combining JSDM and SDM strengths:** What are the advantages and limitations of integrating JSDMs into multiscale modelling frameworks, and can they provide ecological insights that enhance the broad-scale accuracy of SDMs when combined?
- **Disease and communities:** How does mosquito community composition correlate with the likelihood of mosquito-borne disease outbreaks, and can specific assemblages of mosquito species be used as indicators of increased disease transmission risk?
- **Conditional predictions:** How can routine sampling and monitoring improve predictions of mosquito invasion risk in vulnerable areas by leveraging species relationships in conditional predictions, and what role can long-term sampling data play in enhancing early detection and risk assessments for future invasions?

5.5 Conclusion

Community-based approaches offer a more holistic understanding of mosquito ecology, taking into account how species interact within their environments and with each other. These approaches can provide a more accurate representation of mosquito populations and their potential to transmit diseases, as they incorporate both biotic interactions and environmental drivers. By moving beyond single-species models, community-level studies can identify ecological interactions that may either facilitate or suppress vector populations, providing valuable insights for vector control strategies.

The long-term potential of integrating community-level approaches into mosquito research lies in the ability to enhance disease management. By improving our understanding of how mosquito species interact within ecosystems, we may develop more targeted interventions to reduce the risk of transmission. These models will be essential for predicting how shifts in mosquito populations in response to climate change and habitat modification ultimately contribute to changes in overall community composition, giving us a better understanding of the many driving factors behind the diseases spread by mosquitoes.

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Appendix A

Appendix: Chapter 2

A.1 Background to the ESA

1. The ESA extends over 29,260 hectares of the central Somerset lowlands, bounded by the Mendips to the north, low limestone escarpments to the east, the Blackdown Hills to the south and the Quantock Hills to the west. The moors comprise an extensive area of very low-lying basin peat, with a few remnants of raised bog, surrounded by alluvial clay and silt. The peat is overlain by riverine clay. Westwards from the moors lies an extensive area of slightly higher estuarine alluvium known as the Levels, most of which is excluded from the ESA. Grassland predominates and, traditionally, has been used for summer cattle grazing and hay cutting.

2. The whole area forms the largest remaining lowland wet grassland system in Britain and is consequently of outstanding environmental interest. The ecological interest is associated with the wet, often species-rich pastures and meadows and the surrounding network of ditches with their aquatic flora and invertebrate interest. This wet grassland area supports overwintering wildfowl and breeding waders for which part of the area is designated as a Ramsar/SPA site. The landscape value lies in the rectilinear pattern

of traditionally managed fields and drainage channels within a low-lying wet and expansive grassland area. In addition, there is a wealth of archaeological interest, ranging from prehistoric wooden trackways to more recent buildings and structures.

3. In the 1970s and early 1980s the drainage of large areas of the Moors was improved. This, along with the increased use of chemicals and fertilisers resulted in the grassland being improved or converted to arable. This threat has been countered by the designation of 13 moors as Sites of Special Scientific Interest (SSSIs) and the establishment of the area as an ESA.

4. This is a 'part-farm' scheme which started in 1987. In 1992 it was extended by 530 ha and by a further 1,580 ha when the revised scheme was introduced in 1997. Overall uptake at the end of 1998 was c. 16,748 hectares.

5. A priority objective is to sensitively manage the grassland and water levels in the surrounding ditches (most tiers). Tier 1a helps to achieve enhancement by protecting the semi-improved, improved and unimproved species rich grassland through reduced inputs. To help achieve enhancement a new tier (Tier 1A) has been introduced to protect the semi-improved and unimproved species-rich grassland, through reduced inputs. The management requirements are similar to Tier 2, but without the water level restrictions. A water level supplement is also available on a site-specific basis, and is designed to benefit birds or rare plant species. These tiers and supplements are the main mechanism for achieving the Biodiversity Action Plan (BAP) targets in the area.

6. A further objective is to maintain the traditional landscape character, including the field boundary and historic features, by encouraging appropriate grassland management (all tiers). Enhancement of features such as ditches, pollarded willows, gates/wing fences and historic artefacts is encouraged through the Conservation Plans.

7. A new all-year penning supplement (for Tiers 1, 1A & 2) has been introduced to maintain summer penning levels throughout the winter to protect the peat resource and its associated archaeological remains.

8. A new buffer strip supplement has been introduced for arable land to create fertiliser-free grass buffer strips adjacent to water courses. These are designed to reduce the run-off of agricultural inputs into the ditches, thus protecting the diverse, aquatic plant and insect communities.

A.1.1 Tier 1 Permanent grassland

Scheme Prescriptions

1. Maintain grassland, do not plough, level or reseed land. You may use a chain harrow or roller but no other form of cultivation is allowed.

2. Graze with cattle or sheep but avoid poaching, under-grazing or over-grazing.

3. If you cut the grass for hay or silage, graze the aftermath.

4. Do not exceed your existing level of inorganic fertiliser and in any case do not exceed 75kg of nitrogen, 37.5kg of phosphate and 37.5kg of potash per hectare (60 units of nitrogen, 30 units of phosphate and 30 units of potash per acre). Do not exceed your existing level of home produced organic fertiliser and do not apply any other organic fertiliser.

5. Do not use fungicides or insecticides.

6. Do not apply herbicides except to control creeping buttercup, soft rush, nettles, spear thistle, creeping or field thistle, curled dock, broad-leaved dock or ragwort. Apply herbicides by weed wiper or spot treatment

7. Do not apply lime, slag or any other acidity reducing substance.
8. Do not install under-drainage, do not mole drain, and do not subsoil or tunnel plough. Do not substantially modify your existing drainage system.
9. Maintain existing field gutters, surface piping, rig and furrow, ditches or rhynes by mechanical means, not sprays. Do not install additional surface piping.
10. Do not spray irrigate your land.
11. Maintain hedges, trees and pollarded willows in accordance with local custom.
12. Do not plant any additional trees or allow natural establishment of additional trees/ bush without prior agreement.
13. Do not damage or destroy any features of historic interest.
14. Obtain written advice on siting and materials before constructing buildings, roads or any other engineering operations which do not require planning permission or prior notification determination by the Local Planning Authority.
15. Maintain existing gates with wing fencing but do not erect any additional permanent fencing without prior consent.
16. Water levels in ditches and rhynes must either be:
    - From 1 April to 31 October maintained at or above the penning level, provided since 1987, by the relevant Internal Drainage Board (IDB) or the Environment agency (EA) (as appropriate) and from 1 November to 31 March maintained at or above the winter level provided since 1987 by relevant IDB or the EA (as appropriate) with at least 15 cm 15 cm (6") of water in the bottom of the ditches/rhynes at all times.

Or, to obtain a supplementary payment:

- From 1 May to 30 November water levels in ditches and rhynes must be maintained at not more than 30 cm (12") below mean field level and from 1 December to 30 April maintained at not less than mean field levels so as to cause conditions of surface splashing.

17. Agreement holders must not pump below these levels which will be fixed for reference to gauge boards set to Ordnance Datum Newlyn.

18. You must abide by the Codes of Good Agricultural Practice (Annex IVII) for the Protection of Water, Soil and Air, published by the Ministry (references PB 0587, PB 0617 and PB 0618) as amended from time to time.

Agronomic Impact

1. No significant consequences for Income Forgone.

2. No significant consequences for Income Forgone.

3. No significant consequences for Income Forgone.

4. As a consequence of not being able to reseed and a required reduction in fertiliser application from the pre-ESA rate of (200 kg N, 40 kg P2O5, 30 kg K2O)/ha to (75 kg N, 37½ kg P2O5, 37½ kg K2O)/ha, the stocking rate will be reduced from 1.65 GLU/ha to 1.2 GLU/ha. This results in a decrease in livestock gross margin. Costs will be saved from reduced forage inputs, labour and interest on working capital.

5. No significant consequences for Income Forgone.

6. Typically this will involve a switch from using cheaper hormone based herbicides on an overall basis to spot treatment or wick application of more expensive chemicals.

Both spot and wick application methods are more labour intensive techniques. Topping is also used to control weeds in both the non-ESA and ESA situation.

7. No significant consequences for Income Forgone.
8. No significant consequences for Income Forgone.
9. ESA agreement holders will have to clean out their ditches and rhynes at a greater frequency than non-agreement holders.
10. No significant consequences for Income Forgone.
11. Extra costs of hedge management involving hedge laying on a 15 year cycle and regular hedge trimming traditional to the area. Additional costs will be incurred for maintenance of pollarded willows in accordance with the local custom. Little pollarding is undertaken by non-ESA farmers.
12. No significant consequences for Income Forgone.
13. No significant consequences for Income Forgone.
14. No significant consequences for Income Forgone.
15. Extra costs associated with the maintenance of wooden gates and winged fencing compared to replacement steel gates.
16. No significant consequences for Income Forgone.
17. No significant consequences for Income Forgone.
18. No significant consequences for Income Forgone

A.1.2 Tier 1A - Extensive permanent grassland

Scheme Prescriptions

Observe prescriptions 1-18 plus additional prescriptions set out below:

19. Do not use a chain harrow or roller between 31 March and 1 July.
20. Do not exceed your existing level of inorganic fertiliser and in any case do not exceed 25kg of nitrogen, 12.5kg of phosphate and 12.5kg of potash per hectare (20 units of nitrogen, 10 units of phosphate and 10 units of potash per acre) each year.
21. Unless traditionally the land has been used for grazing each year mow at least one third (or one year in three) of the land but not before 1 July and do not graze the land prior to laying it up.
22. Do not cut or top the grass after 31 August.
23. Do not graze with sheep from 1 September to 1 March.
24. Do not use herbicides to control creeping buttercup.
25. Water levels in ditches and rhynes must be:
    - From 1 April to 31 October at or above the penning level, provided since 1987, by the relevant IDB or the EA (as appropriate) and from 1 November to 31 March maintained at or above the winter level provided since 1987 by relevant IDB or the EA (as appropriate) with at least 15 cm (6") of water in the bottom of the ditches/rhynes at all times.
26. Agreement holders must not pump below these levels which will be fixed by reference to gauge boards set to Ordnance Datum Newlyn.

Agronomic Impact

19-20. A small amount of sward deterioration will result in a slight reduction in stocking rate. This coupled with a reduction in the quantity of fertiliser applied from (200 kg N: 40 kg P2O5 :30 K2O)/ha to (25 kg N: 12 ½ kg P2O5 , 12 ½ kg K2O)/ha will decrease the stock carrying capacity. This in conjunction with the maintenance of higher water levels will reduce stocking rate from 1.65 GLU/ha to 1.0 GLU/ha. Reduced forage inputs, requirement for labour and interest on working capital will produce cost savings.

19. As for prescription 19.
20. This will result in potential loss of land for silage production. The hay produced will be of lower energy value than silage and therefore extra concentrate feed will be required.
21. No significant consequences for Income Forgone.
22. This will result in loss of winter grazing for sheep and therefore incur extra costs associated with winter keep.
23. No significant consequences for Income Forgone.
24. No significant consequences for Income Forgone.
25. No significant consequences for Income Forgone

A.1.3 Tier 2 - Wet permanent grassland

Scheme Prescriptions

Observe prescriptions 1-18 plus additional prescriptions set out below:

27. Do not use a chain harrow or roller between 31 March and 1 July.

28. Do not exceed your existing level of inorganic fertiliser and in any case do not exceed 25kg of nitrogen, 12.5kg of phosphate and 12.5kg of potash per hectare (20 units of nitrogen, 10 units of phosphate and 10 units of potash per acre) each year.

29. Unless traditionally the land has been used just for grazing each year mow at least one third (or one year in three) of the land but not before 1 July and do not graze the land prior to laying it up.

30. Do not cut or top the grass after 31 August.

31. Do not graze with sheep from 1 September to 1 March.

32. Do not use herbicides to control creeping buttercup.

33. Water levels in ditches and rhynes must be either:

    - From 1 April to 31 October maintained at or above the penning level, provided since 1987 by the relevant IDB or the EA (as appropriate) and in any case not more than 45 cm (18") below mean field level and from 1 November to 31 March, maintained at or above the winter level provided since 1987 by the relevant IDB or the EA (as appropriate) with at least 30 cm (12") of water in the bottom of the ditches/rhynes at all times.

    Or, to obtain a supplementary payment:

    - From 1 May to 30 November water levels in ditches and rhynes must be maintained at not more than 30 cm (12") below mean field level and from 1 December to 30 April, maintained at not less than mean field level so as to cause conditions of surface splashing.

34. Agreement holders must not pump below these levels which will be fixed by reference to gauge boards set to Ordnance Datum Newlyn.

Agronomic Impact

27. A small amount of sward deterioration will result in a slight reduction in stocking rate. This coupled with a reduction in the quantity of fertiliser applied from (200 kg N :40 kg P2O5 :30 K2O)/ha to (25 kg N: 12 ½ kg P2O5 , 12 ½ kg K2O)/ha will decrease the stock carrying capacity from 1.65 GLU/ha to 0.9 GLU/ha and therefore produce a substantial decrease in the livestock gross margin. Reduced forage inputs, the requirement for labour and interest on working capital will produce cost savings.

28. As for prescription 27.

29. Mow one third of land each year. This will result in potential loss of land for silage production. The hay produced will be of lower energy value than silage and therefore extra concentrate feed will be required.

30. No significant consequences for Income Forgone.

31. Do not graze with sheep from 1 September to 1 March. This will result in loss of winter grazing for sheep and therefore incur extra costs associated with winter keep.

32. No significant consequences for Income Forgone.

33. No significant consequences for Income Forgone.

34. No significant consequences for Income Forgone

A.1.4 Tier 3 - Permanent grassland raised water level areas

Scheme Prescriptions

Observe prescriptions 1-18 plus additional prescriptions set out below:

35. Do not carry out mechanical operations between 31 March and 1 July.

36. Apply no inorganic fertiliser and do not exceed your existing level of organic manure provided it is only home produced cattle farmyard manure and does not exceed 25 tonnes per hectare (10 tones per acre) per annum. No slurry should be applied.
37. Graze only with cattle but do not graze before 20 May in any year.
38. Do not exceed a grazing density of one animal per 0.75 hectare (one animal per 1.8 acres) from 20 May to 8 July. Do not cause poaching, over-grazing or under-grazing.
39. Do not make silage. Unless traditionally the land has been used just for grazing each year mow at least one third of the land (or mow one year in three) but not before 8 July. Do not graze the land prior to laying it up.
40. Do not cut or top grass after 31 August.
41. Do not use herbicides to control creeping buttercup.
42. Water levels in ditches and rhynes must:
    - From 1 May to 30 November be maintained at not more than 30 cm (12") below mean field level and from 1 December to 30 April, maintained at not less than mean field level so as to cause conditions of surface splashing.
43. To further the objective of conserving, enhancing or protecting landscape, wildlife and historical features the Minister may specify different water level requirements.
44. Agreement holders must not pump below these levels which will be fixed by reference to gauge boards set to Ordnance Datum Newlyn.

Agronomic Impact

35. A small amount of sward deterioration will result in a slight reduction in stocking rate and the prohibition of inorganic and organic fertiliser will only permit a very low

stocking rate of 0.25 GLU/ha. This will result in an 80% reduction of livestock gross margin. Reduced forage inputs, labour and interest on working capital will produce cost savings.

36. As for prescription 35.

37. No significant consequences for Income Forgone.

38. No significant consequences for Income Forgone.

39. Hay can only be made after 8 July. This will result in a reduction in forage digestibility. As a result extra feed will have to be purchased as feed barley.

40. No significant consequences for Income Forgone.

41. No significant consequences for Income Forgone.

42. Surface splash conditions have to be maintained between 1 December to 30 April. This will result in a loss of winter grazing, and therefore incur extra costs associated with winter keep. Even after drainage surface conditions remain too wet to permit grazing before 20 May. In some years grazing cannot be carried out until early June. This will result in the loss of early spring grazing and restrict the growing season. This prescription will result in the replacement of agricultural grasses with less productive native species.

43. No significant consequences for Income Forgone.

44. No significant consequences for Income Forgone

Table A.1 Combined Results of Bayesian Hierarchical Models for Environmental Variables in ESA Tiers 1 and 3. Models were fitted using the brms package in R with default weakly informative priors. Gaussian models were used for Dissolved Oxygen, pH, Vertical Vegetation, Salinity, Water Temperature, Ditch Width, Emergent Vegetation Height, and Turbidity. Beta models were used for Floating Cover and Shaded Area. All models included random effects for site, year, and year:season interaction. Fixed effects show the contrast between Tier 1 (reference level) and Tier 3. Estimates are presented with standard errors and 95% credible intervals. SD parameters represent the standard deviation of random effects and residuals. Phi, ZOI (Zero One Inflated), COI (Continuous One Inflated), and HU (Hurdle) parameters are specific to beta and hurdle models.

Variable	Parameter	Estimate	Std. Error	Conf. Low	Conf. High
Dissolved Oxygen	Intercept	145.66	12.10	121.66	170.00
	Tier T3	-6.56	5.52	-17.32	4.49
	SD Site	10.49	2.34	6.96	15.97
	SD Year	12.44	12.00	0.32	43.23
	SD Year:Season	23.16	8.55	12.11	45.15
	SD Residual	12.47	0.88	10.82	14.23
pH	Intercept	6.37	1.24	3.99	8.94
	Tier T3	-0.30	0.17	-0.63	0.04
	SD Site	0.29	0.08	0.17	0.49
	SD Year	2.30	1.28	0.71	5.55
	SD Year:Season	0.41	0.41	0.07	1.59
	SD Residual	0.60	0.05	0.50	0.69
Floating Cover	Intercept	-0.02	0.80	-1.62	1.66

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Variable	Parameter	Estimate	Std. Error	Conf. Low	Conf. High
	Phi Intercept	0.68	0.16	0.37	1.00
	ZOI Intercept	0.19	0.17	-0.14	0.52
	COI Intercept	-2.73	0.47	-3.73	-1.89
	Tier T3	-0.97	0.33	-1.67	-0.35
	Phi Tier T3	0.85	0.22	0.42	1.28
	ZOI Tier T3	-0.19	0.23	-0.64	0.25
	COI Tier T3	-0.58	0.75	-2.08	0.86
	SD Site	0.49	0.19	0.15	0.91
	SD Year	1.04	0.89	0.05	3.43
	SD Year:Season	0.69	0.53	0.07	2.09
Vertical Vegetation	Intercept	4.44	0.44	3.58	5.29
	HU Intercept	-0.58	0.17	-0.92	-0.25
	Tier T3	0.03	0.09	-0.15	0.20
	HU Tier T3	-1.10	0.27	-1.64	-0.57
	SD Site	0.14	0.04	0.07	0.24
	SD Year	0.53	0.60	0.03	2.15
	SD Year:Season	0.20	0.15	0.05	0.61
	SD Residual	0.34	0.02	0.31	0.38
Salinity	Intercept	0.44	0.11	0.25	0.66
	Tier T3	-0.01	0.07	-0.15	0.12
	SD Site	0.13	0.03	0.09	0.20
	SD Year	0.11	0.19	0.00	0.61

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Variable	Parameter	Estimate	Std. Error	Conf. Low	Conf. High
	SD Year:Season	0.02	0.02	0.00	0.06
	SD Residual	0.08	0.01	0.07	0.09
Water Temperature	Intercept	16.66	1.56	13.45	19.70
	Tier T3	0.86	0.72	-0.61	2.24
	SD Site	1.38	0.31	0.91	2.09
	SD Year	1.61	1.59	0.05	5.67
	SD Year:Season	2.90	1.06	1.54	5.62
	SD Residual	1.56	0.11	1.34	1.78
Shaded Area	Intercept	-0.36	0.59	-1.44	0.79
	Phi Intercept	0.85	0.11	0.63	1.05
	ZOI Intercept	-2.63	0.33	-3.34	-2.03
	COI Intercept	0.14	0.66	-1.17	1.45
	Tier T3	-0.30	0.35	-0.98	0.39
	Phi Tier T3	0.47	0.16	0.16	0.77
	ZOI Tier T3	1.04	0.38	0.31	1.83
	COI Tier T3	-3.53	1.23	-6.26	-1.38
	SD Site	0.63	0.15	0.41	0.98
	SD Year	0.62	0.72	0.03	2.59
	SD Year:Season	0.24	0.21	0.01	0.76
Ditch Width	Intercept	43.22	7.89	27.36	58.69
	Tier T3	8.42	7.62	-6.85	23.49
	SD Site	14.64	3.28	9.62	22.44

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Variable	Parameter	Estimate	Std. Error	Conf. Low	Conf. High
	SD Year	7.85	8.17	0.29	29.52
	SD Year:Season	3.39	3.09	0.12	11.30
	SD Residual	20.58	1.21	18.19	22.96
Emergent Vegetation Height	Intercept	3.37	0.63	1.75	4.19
	HU Intercept	0.96	0.18	0.61	1.33
	Tier T3	-0.28	0.13	-0.56	-0.02
	HU Tier T3	-1.22	0.24	-1.70	-0.75
	SD Site	0.18	0.08	0.03	0.36
	SD Year	0.49	0.74	0.01	2.61
	SD Year:Season	0.37	0.23	0.14	0.98
	SD Residual	0.43	0.03	0.37	0.49
Turbidity	Intercept	0.57	0.16	0.28	0.86
	Tier T3	-0.02	0.08	-0.19	0.15
	SD Site	0.16	0.04	0.11	0.25
	SD Year	0.16	0.26	0.01	0.88
	SD Year:Season	0.02	0.02	0.00	0.07
	SD Residual	0.10	0.01	0.08	0.11

Table A.2 Detailed Variance Partitioning results for taxa across different environmental components, including Chemical, Vegetation, Structural, and Random Effects (spatial, season, year). Values represent the proportion of variance explained by each component for the respective taxa.

Taxa	Chemical	Vegetation	Structural	Random: plot_id	Random: season	Random: year
An. maculipennis	0.59	0.26	0.09	0.02	0.02	0.02
An. claviger	0.49	0.06	0.25	0.17	0.01	0.02
Cx. pipiens	0.11	0.05	0.02	0.80	0.01	0.00
Cs. annulata	0.09	0.03	0.01	0.85	0.01	0.01
Corixidae	0.18	0.11	0.03	0.12	0.05	0.51
Coleoptera larvae	0.17	0.28	0.06	0.28	0.03	0.18
Coleoptera	0.15	0.14	0.06	0.30	0.11	0.24
Zygoptera larvae	0.18	0.12	0.11	0.31	0.09	0.19
Anisoptera larvae	0.36	0.25	0.19	0.10	0.04	0.05
Ilyocoris	0.39	0.27	0.20	0.06	0.04	0.04
Nepa cinerea	0.41	0.31	0.16	0.04	0.04	0.05
Gammaridae	0.32	0.26	0.22	0.13	0.05	0.03

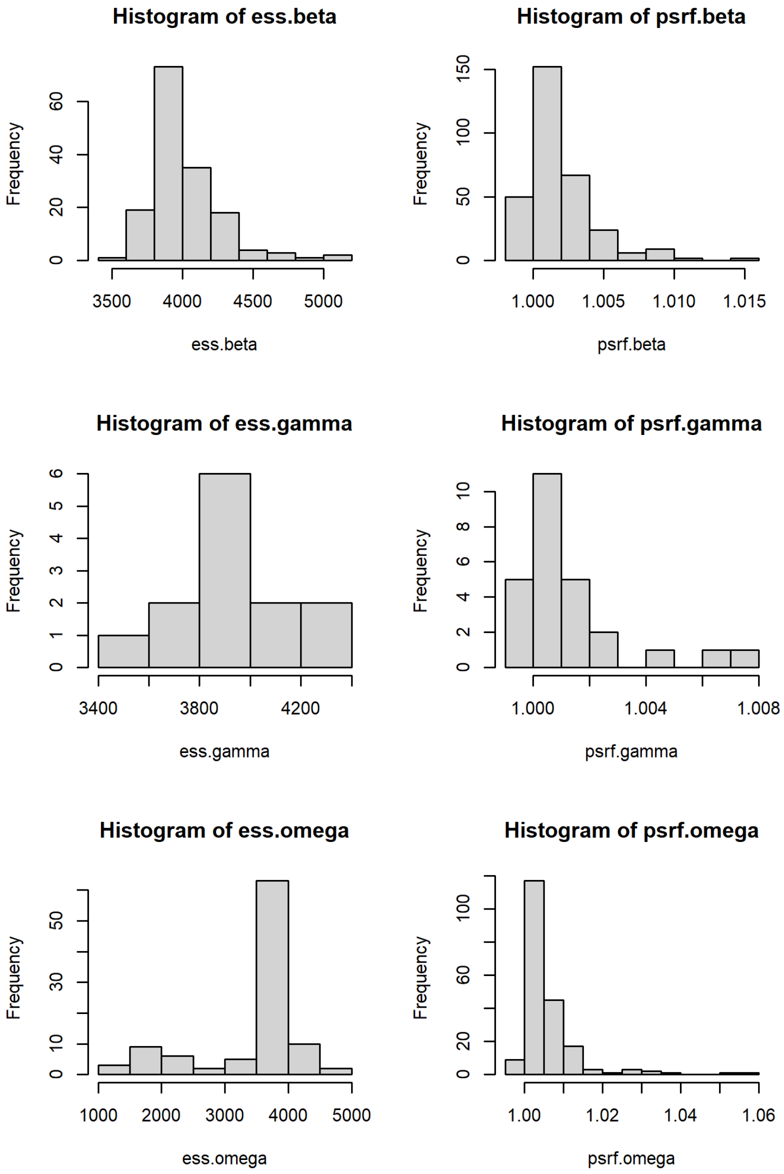


Fig. A.1 Fitted model convergence metrics for the Beta, Omega and Gamma parameters of the HMSC model. Effective Sample Size (ESS) over 1000 indicate good fit, while Potential Scale Reduction Factors (PSRF) values of under 1.1 (though ideally 1.01) are considered converged for MCMC sampling.

Appendix B

Appendix: Chapter 3

Table B.1 Species that were grouped together to form morphologically similar distributions or species groups.

Species	New Group
Aedes annulipes	*Aedes annulipes/cantans*
Aedes cantans	*Aedes annulipes/cantans*
Aedes cinerus	*Aedes cinerus/geminus*
Aedes geminus	*Aedes cinerus/geminus*
Aedes detritus	*Aedes detritus/coluzzi*
Aedes coluzzi	*Aedes detritus/coluzzi*
Culex perexiguuus	*Culex perexiguss/univittatus*
Culex univittatus	*Culex perexiguss/univittatus*

Table B.2 This table provides a comprehensive overview of the predictor variables employed in the joint species distribution models (JSDMs) and multi-species distribution models (MSDMs) for European mosquito species. It includes climatic, topographic, land cover, and anthropogenic variables, detailing their descriptions, data sources, original temporal and spatial resolutions, and the transformations applied to standardize the data for analysis. All variables were resampled to match the study's focal resolutions (1 km, 2 km, 5 km, and 10 km) using the EPSG:3035 coordinate reference system, which is optimised for spatial accuracy in Europe. The diverse set of predictors was selected to capture the range of environmental and human-influenced factors that potentially impact mosquito habitat suitability and distribution across the continent.

Predictor Variable	Description	Source	Original Temporal Resolution	Original Spatial Resolution	Transformation
Mean Temperature	Annual mean temperature (BIO_01)	CHELSA Climate Data [1]	1979-2013	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Coldest Quarter Temperature	Mean temperature of coldest quarter (BIO_11)	CHELSA Climate Data [1]	1979-2013	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Annual Precipitation	Annual precipitation sum (BIO_12)	CHELSA Climate Data [1]	1979-2013	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Precipitation Warmest Quarter	Precipitation of warmest quarter (BIO_18)	CHELSA Climate Data [1]	1979-2013	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Growing Degree Days 10 °C	Growing degree days above 10°C (GDD10)	CHELSA Climate Data [1]	1979-2013 climatology	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Evergreen or Deciduous Trees	Percent cover of evergreen and deciduous trees (CLASS_1)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035

Predictor Variable	Description	Source	Original Temporal Resolution	Original Spatial Resolution	Transformation
Evergreen Trees	Percent cover of evergreen trees (CLASS_2)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Deciduous Trees	Percent cover of deciduous trees (CLASS_3)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Mixed Trees	Percent cover of mixed trees (CLASS_4)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Shrubs	Percent cover of shrubs (CLASS_5)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Agriculture	Percent cover of agriculture (CLASS_7)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Wetlands	Percent cover of wetlands (CLASS_8)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Urban	Percent cover of urban areas (CLASS_9)	EarthEnv Land Cover [2]	2001-2005	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035
Elevation	Elevation above sea level	EarthEnv Topography [3]	Static	30 arc-seconds (∼1 km at equator)	Bilinear interpolation to EPSG:3035

Predictor Variable	Description	Source	Original Temporal Resolution	Original Spatial Resolution	Transformation
Habitat Heterogeneity (Homogeneity)	Measure of habitat heterogeneity	EarthEnv Habitat Heterogeneity [4]	Static	30 arc-seconds ($\sim$1 km at equator)	Bilinear interpolation to EPSG:3035
Habitat Heterogeneity (Mean)	Mean habitat heterogeneity	EarthEnv Habitat Heterogeneity [4]	Static	30 arc-seconds ($\sim$1 km at equator)	Bilinear interpolation to EPSG:3035
Livestock Density	Density of livestock, aggregated from mammalian species (cattle, pigs, sheep, goats)	Global Livestock Data [5]	2010	3 arc-minutes ($\sim$5 km at equator)	Bilinear interpolation to EPSG:3035
Population Density	Human population density	Gridded Population of the World v4 [6]	2010	30 arc-seconds ($\sim$1 km at equator)	Bilinear interpolation to EPSG:3035

Data Sources:

1. Karger, D.N., et al. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122.

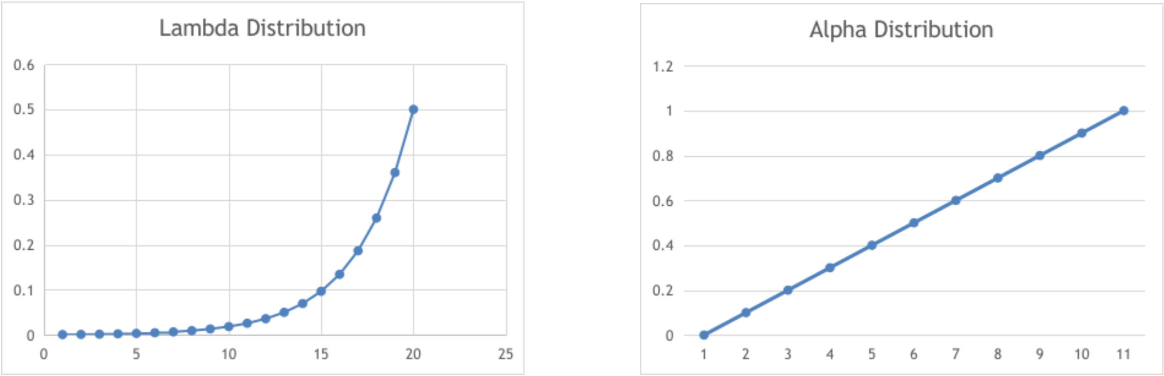
2. Tuanmu, M.N. & Jetz, W. (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 23(9), 1031-1045.

3. Amatulli, G., et al. (2018). A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, 5, 180040.

4. Tuanmu, M.N. & Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 24(11), 1329-1339.

5. Gilbert, M., et al. (2018). Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. *Scientific Data*, 5, 180227.

6. Center for International Earth Science Information Network - CIESIN - Columbia University. (2018). Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC).



(a) Lambda Distribution

(b) Alpha Distribution

Fig. B.1 Distributions that hyperparameters were randomly drawn from for Lambda and Alpha hyperparameters during elastic net regularisation

Table B.3 AUC (Area Under the Curve) values for different mosquito species across various spatial resolutions. AUC measures the overall predictive accuracy of the JSDM and MSDM models, with higher values indicating better performance.

	JSDM				**MSDM**			
Species	1 Km	2 Km	5 Km	10 Km	1 Km	2 Km	5 Km	10 Km
Aedes albopictus	0.71	0.72	0.72	0.69	0.73	0.71	0.73	0.70
Aedes annulipes/cantans	0.70	0.75	0.81	0.68	0.75	0.65	0.66	0.75
Aedes caspius	0.59	0.65	0.63	0.61	0.68	0.64	0.63	0.65
Aedes cinereus/geminus	0.72	0.78	0.82	0.68	0.67	0.61	0.77	0.70
Aedes detritus/coluzzi	0.64	0.65	0.64	0.70	0.62	0.63	0.65	0.64
Aedes geniculatus	0.62	0.58	0.62	0.62	0.60	0.59	0.64	0.60
Aedes japonicus	0.75	0.80	0.76	0.77	0.73	0.77	0.76	0.76
Aedes sticticus	0.67	0.69	0.65	0.60	0.66	0.61	0.71	0.76
Aedes vexans	0.61	0.59	0.54	0.61	0.60	0.55	0.57	0.60
Anopheles atroparvus	0.65	0.79	0.71	0.63	0.66	0.73	0.77	0.64
Anopheles claviger	0.68	0.71	0.70	0.65	0.70	0.74	0.67	0.65
Anopheles labranchiae	0.96	0.96	0.96	0.92	0.95	0.96	0.96	0.90
Anopheles maculipennis	0.59	0.63	0.57	0.63	0.61	0.63	0.62	0.64
Anopheles messeae	0.70	0.75	0.67	0.62	0.75	0.75	0.66	0.81
Anopheles plumbeus	0.60	0.58	0.61	0.64	0.57	0.62	0.59	0.67
Anopheles sacharovi	0.65	0.75	0.85	0.75	0.70	0.67	0.72	0.74
Coquillettidia richiardii	0.63	0.59	0.66	0.69	0.70	0.68	0.66	0.78
Culex hortensis hortensis	0.70	0.65	0.68	0.68	0.67	0.62	0.71	0.62
Culex modestus	0.60	0.63	0.62	0.65	0.63	0.60	0.62	0.62
Culex perexiguus/univittatus	0.89	0.90	0.91	0.89	0.92	0.89	0.91	0.86
Culex pipiens	0.53	0.57	0.55	0.58	0.54	0.56	0.54	0.56
Culex territans	0.65	0.68	0.78	0.77	0.75	0.67	0.85	0.72
Culex theileri	0.78	0.89	0.75	0.77	0.83	0.81	0.79	0.79
Culex torrentium	0.75	0.75	0.77	0.80	0.78	0.80	0.78	0.82
Culiseta annulata	0.67	0.70	0.77	0.68	0.68	0.69	0.73	0.62
Culiseta longiareolata	0.70	0.76	0.63	0.68	0.75	0.69	0.75	0.66

Table B.4 TSS (True Skill Statistic) values for different mosquito species across various spatial resolutions. TSS evaluates model performance based on sensitivity and specificity, with higher values indicating better predictive power.

	JSDM				**MSDM**			
Species	1 Km	2 Km	5 Km	10 Km	1 Km	2 Km	5 Km	10 Km
Aedes albopictus	0.35	0.37	0.39	0.36	0.39	0.35	0.40	0.35
Aedes annulipes/cantans	0.30	0.49	0.49	0.29	0.37	0.24	0.26	0.16
Aedes caspius	0.21	0.26	0.25	0.25	0.29	0.25	0.26	0.30
Aedes cinereus/geminus	0.37	0.49	0.60	0.39	0.32	0.29	0.45	0.38
Aedes detritus/coluzzi	0.25	0.29	0.26	0.36	0.25	0.25	0.29	0.18
Aedes geniculatus	0.28	0.16	0.27	0.27	0.19	0.20	0.26	0.26
Aedes japonicus	0.45	0.50	0.47	0.49	0.38	0.47	0.45	0.47
Aedes sticticus	0.21	0.32	0.29	0.15	0.21	0.17	0.37	0.49
Aedes vexans	0.21	0.17	0.14	0.28	0.20	0.13	0.16	0.24
Anopheles atroparvus	0.29	0.41	0.38	0.18	0.23	0.45	0.44	0.10
Anopheles claviger	0.36	0.40	0.38	0.32	0.36	0.43	0.35	0.29
Anopheles labranchiae	0.89	0.87	0.88	0.84	0.87	0.88	0.88	0.77
Anopheles maculipennis	0.17	0.23	0.18	0.26	0.22	0.25	0.24	0.30
Anopheles messeae	0.34	0.38	0.37	0.31	0.51	0.44	0.33	0.54
Anopheles plumbeus	0.25	0.18	0.21	0.36	0.16	0.21	0.22	0.36
Anopheles sacharovi	0.25	0.41	0.67	0.45	0.39	0.36	0.38	0.35
Coquillettidia richiardii	0.24	0.23	0.31	0.34	0.37	0.31	0.33	0.61
Culex hortensis hortensis	0.33	0.25	0.33	0.36	0.30	0.26	0.42	0.25
Culex modestus	0.19	0.30	0.25	0.28	0.27	0.25	0.26	0.20
Culex perexiguus/univittatus	0.73	0.74	0.76	0.70	0.72	0.68	0.73	0.76
Culex pipiens	0.09	0.13	0.12	0.20	0.10	0.13	0.09	0.15
Culex territans	0.27	0.27	0.57	0.58	0.58	0.35	0.65	0.44
Culex theileri	0.57	0.73	0.52	0.54	0.65	0.59	0.61	0.56
Culex torrentium	0.41	0.45	0.43	0.52	0.48	0.50	0.49	0.55
Culiseta annulata	0.36	0.38	0.53	0.35	0.36	0.36	0.46	0.26
Culiseta longiareolata	0.37	0.47	0.27	0.38	0.49	0.33	0.47	0.32

Table B.5 This table presents a detailed breakdown of variance explained for each mosquito species across different model types (Joint Species Distribution Models [JSDMs] and Multi-Species Distribution Models [MSDMs]) and spatial resolutions (1 km, 2 km, 5 km, and 10 km). The variance is decomposed into three primary components: environmental, spatial, and biotic. For each species, the table reports the total variance explained and the proportion attributed to each component. Species are listed alphabetically, and values are presented as percentages with associated variance in estimate.

	Environmental		**Biotic**		**Spatial**	
Species	**JSDM**	**MSDM**	**JSDM**	**MSDM**	**JSDM**	**MSDM**
Aedes albopictus	0.273 (±0.041)	0.182 (±0.043)	0.088 (±0.022)	0.017 (±0.009)	0.089 (±0.042)	0.225 (±0.046)
Aedes annulipes/cantans	0.302 (±0.078)	0.593 (±0.071)	0.182 (±0.066)	0.015 (±0.012)	0.231 (±0.027)	0.111 (±0.062)
Aedes caspius	0.081 (±0.076)	0.193 (±0.009)	0.287 (±0.053)	0.012 (±0.008)	0.253 (±0.095)	0.400 (±0.009)
Aedes cinereus/geminus	0.439 (±0.03)	0.501 (±0.109)	0.048 (±0.034)	0.019 (±0.006)	0.19 (±0.031)	0.159 (±0.094)
Aedes detritus/coluzzi	0.53 (±0.025)	0.482 (±0.04)	0.1 (±0.036)	0.004 (±0.007)	0.043 (±0.04)	0.183 (±0.03)
Aedes geniculatus	0.268 (±0.125)	0.457 (±0.057)	0.132 (±0.074)	0.038 (±0.024)	0.264 (±0.064)	0.171 (±0.071)
Aedes japonicus	0.495 (±0.032)	0.484 (±0.04)	0.037 (±0.018)	0.001 (±0.001)	0.038 (±0.017)	0.075 (±0.03)
Aedes sticticus	0.099 (±0.068)	0.058 (±0.035)	0.128 (±0.038)	0.029 (±0.01)	0.491 (±0.074)	0.631 (±0.041)
Aedes vexans	0.116 (±0.058)	0.170 (±0.025)	0.260 (±0.077)	0.009 (±0.005)	0.217 (±0.086)	0.400 (±0.009)
Anopheles atroparvus	0.369 (±0.091)	0.536 (±0.042)	0.273 (±0.075)	0.017 (±0.012)	0.079 (±0.049)	0.172 (±0.044)
Anopheles claviger	0.114 (±0.062)	0.193 (±0.009)	0.334 (±0.025)	0.006 (±0.004)	0.141 (±0.066)	0.362 (±0.022)
Anopheles labranchiae	0.628 (±0.038)	0.632 (±0.043)	0.039 (±0.013)	0.005 (±0.003)	0.032 (±0.028)	0.067 (±0.043)
Anopheles maculipennis	0.07 (±0.023)	0.202 (±0.013)	0.259 (±0.038)	0.004 (±0.003)	0.187 (±0.048)	0.279 (±0.023)
Anopheles messeae	0.496 (±0.024)	0.581 (±0.017)	0.145 (±0.02)	0.006 (±0.005)	0.070 (±0.036)	0.127 (±0.013)
Anopheles plumbeus	0.127 (±0.092)	0.161 (±0.045)	0.275 (±0.021)	0.016 (±0.006)	0.239 (±0.075)	0.454 (±0.057)
Anopheles sacharovi	0.449 (±0.065)	0.476 (±0.055)	0.143 (±0.054)	0.012 (±0.005)	0.129 (±0.043)	0.239 (±0.057)
Coquillettidia richiardii	0.133 (±0.105)	0.162 (±0.068)	0.297 (±0.017)	0.014 (±0.016)	0.24 (±0.112)	0.484 (±0.07)
Culex hortensis hortensis	0.465 (±0.053)	0.425 (±0.142)	0.085 (±0.076)	0.005 (±0.004)	0.095 (±0.043)	0.211 (±0.125)
Culex modestus	0.284 (±0.016)	0.489 (±0.138)	0.138 (±0.037)	0.012 (±0.008)	0.266 (±0.027)	0.19 (±0.129)
Culex perexiguus/univittatus	0.51 (±0.095)	0.642 (±0.044)	0.129 (±0.032)	0.036 (±0.039)	0.075 (±0.076)	0.038 (±0.017)
Culex pipiens	0.014 (±0.003)	0.065 (±0.004)	0.172 (±0.015)	0.002 (±0.002)	0.021 (±0.013)	0.039 (±0.009)
Culex territans	0.396 (±0.096)	0.577 (±0.077)	0.128 (±0.07)	0.015 (±0.008)	0.176 (±0.134)	0.11 (±0.067)
Culex theileri	0.504 (±0.071)	0.496 (±0.08)	0.016 (±0.014)	0.011 (±0.006)	0.129 (±0.055)	0.141 (±0.065)
Culex torrentium	0.628 (±0.022)	0.626 (±0.015)	0.015 (±0.019)	0.008 (±0.002)	0.017 (±0.009)	0.027 (±0.011)
Culiseta annulata	0.223 (±0.051)	0.11 (±0.04)	0.276 (±0.015)	0.016 (±0.011)	0.093 (±0.055)	0.44 (±0.03)
Culiseta longiareolata	0.299 (±0.074)	0.184 (±0.135)	0.137 (±0.091)	0.025 (±0.015)	0.222 (±0.073)	0.444 (±0.116)

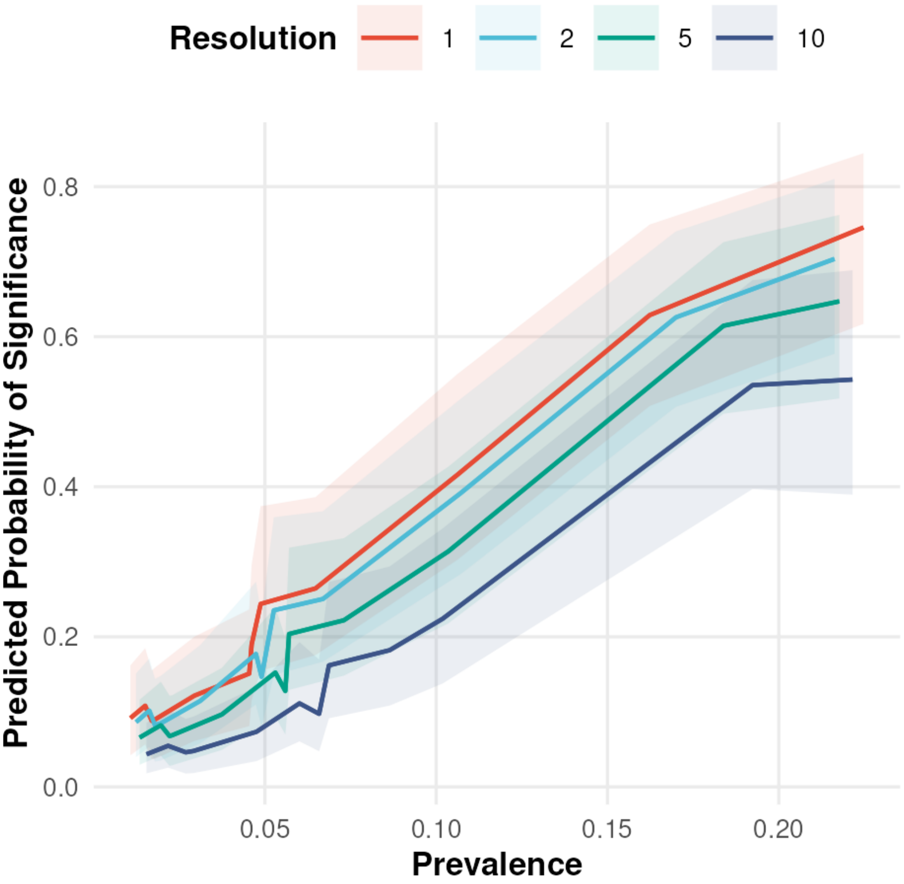


Fig. B.2 Predicted probability of significant predictors for mosquito species distribution as a function of species prevalence. Median predictions (lines) and 95% credible intervals (shaded regions) illustrate how environmental variable significance varies across species prevalence and different ecological resolutions.

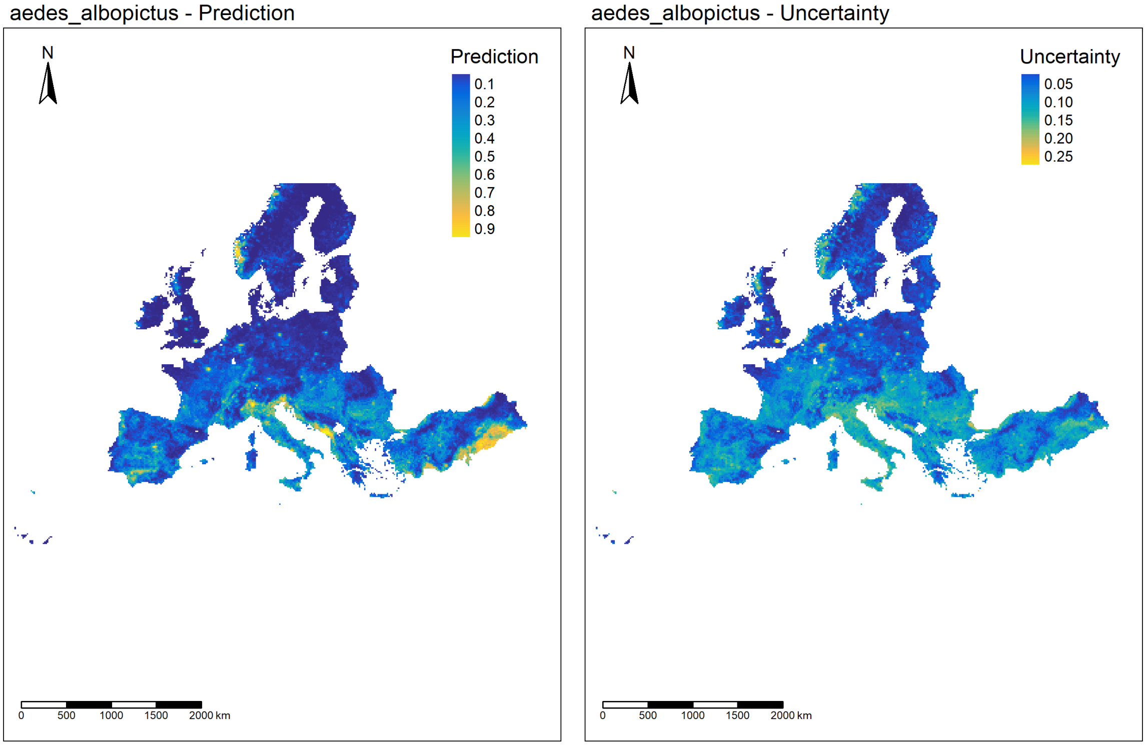


Fig. B.3 Predictions for *Aedes albopictus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

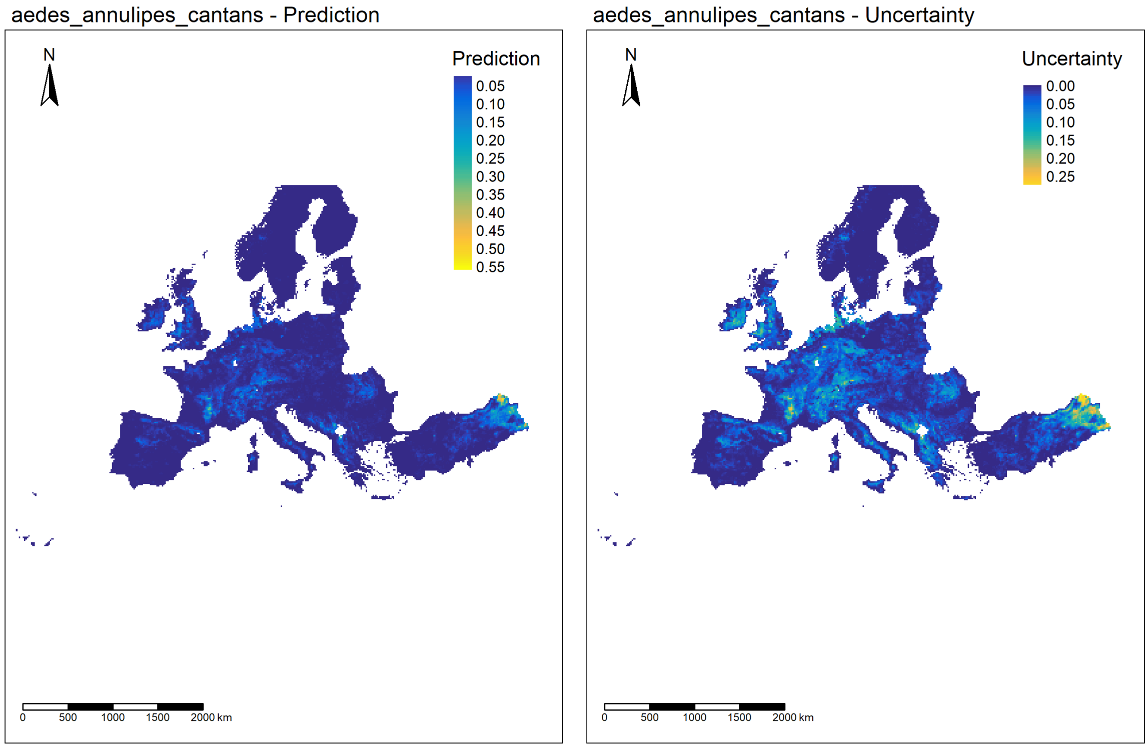


Fig. B.4 Predictions for *Aedes annulipes/cantans* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

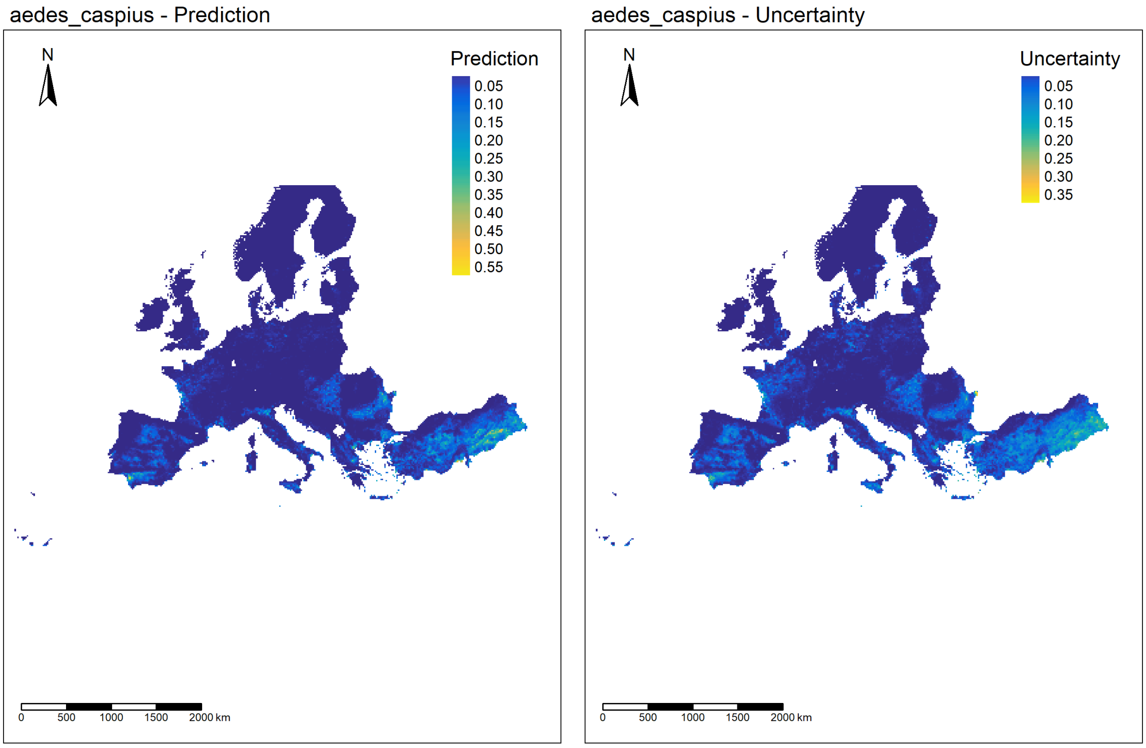


Fig. B.5 Predictions for *Aedes caspius* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

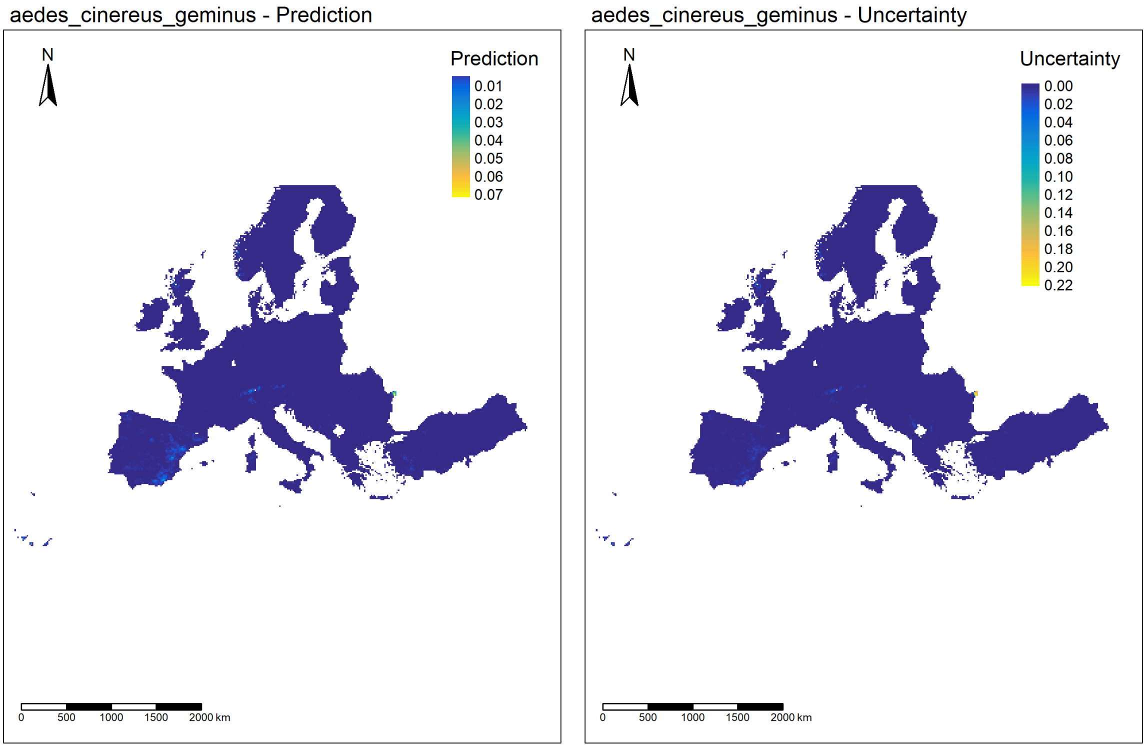


Fig. B.6 Predictions for *Aedes cinereus/geminus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

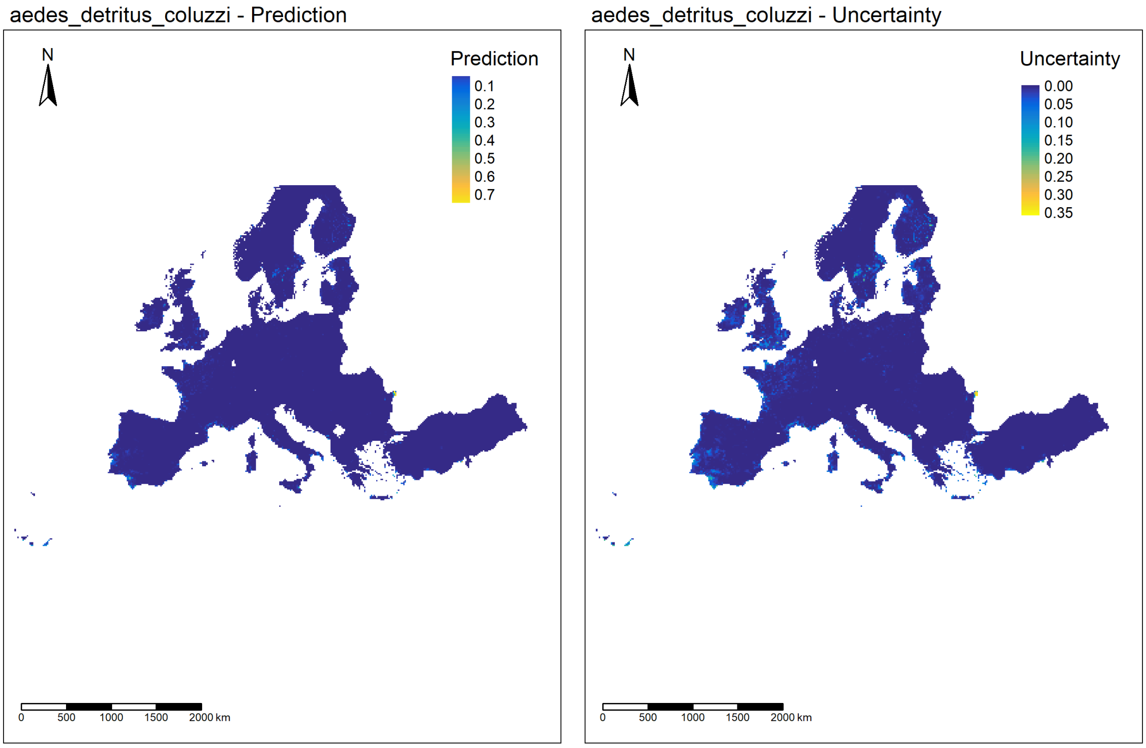


Fig. B.7 Predictions for *Aedes detritus/coluzzi* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

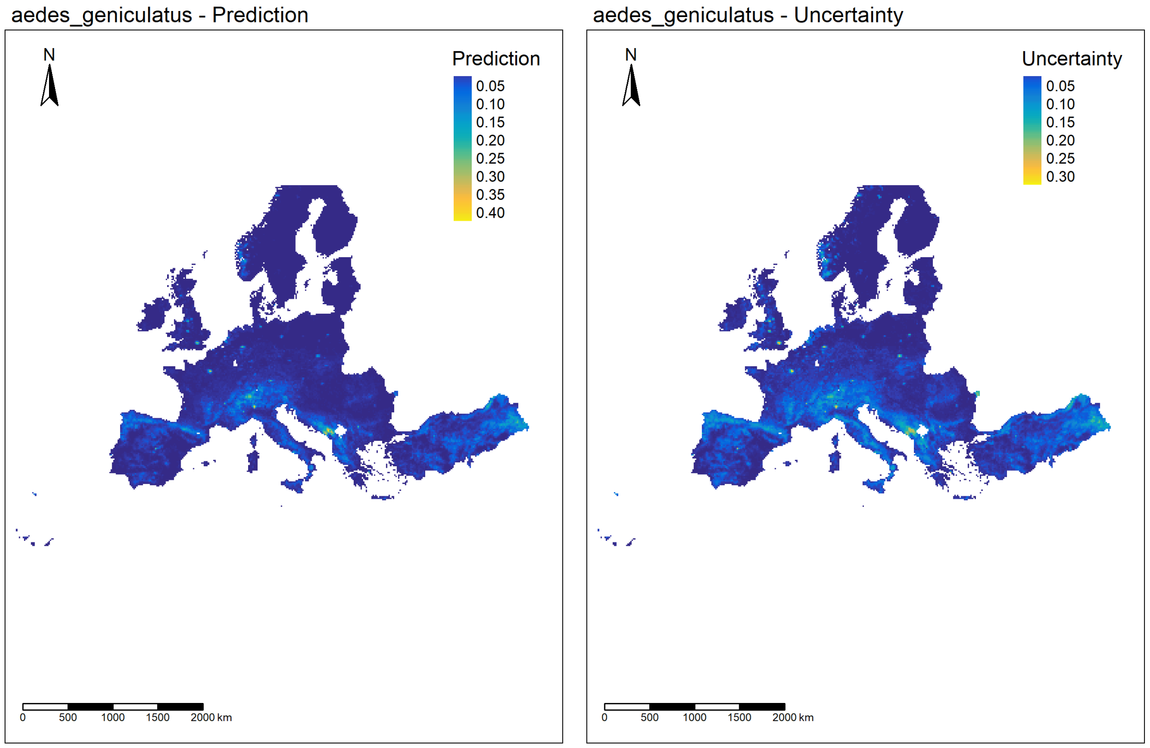


Fig. B.8 Predictions for *Aedes geniculatus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

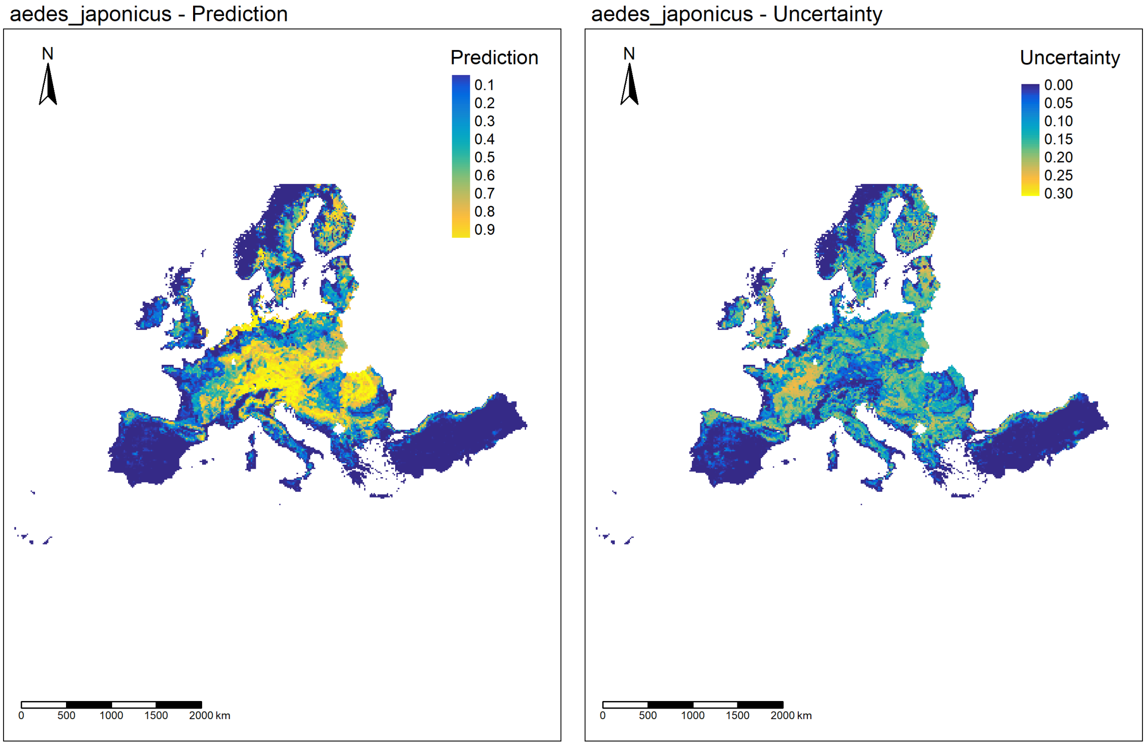


Fig. B.9 Predictions for *Aedes japonicus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

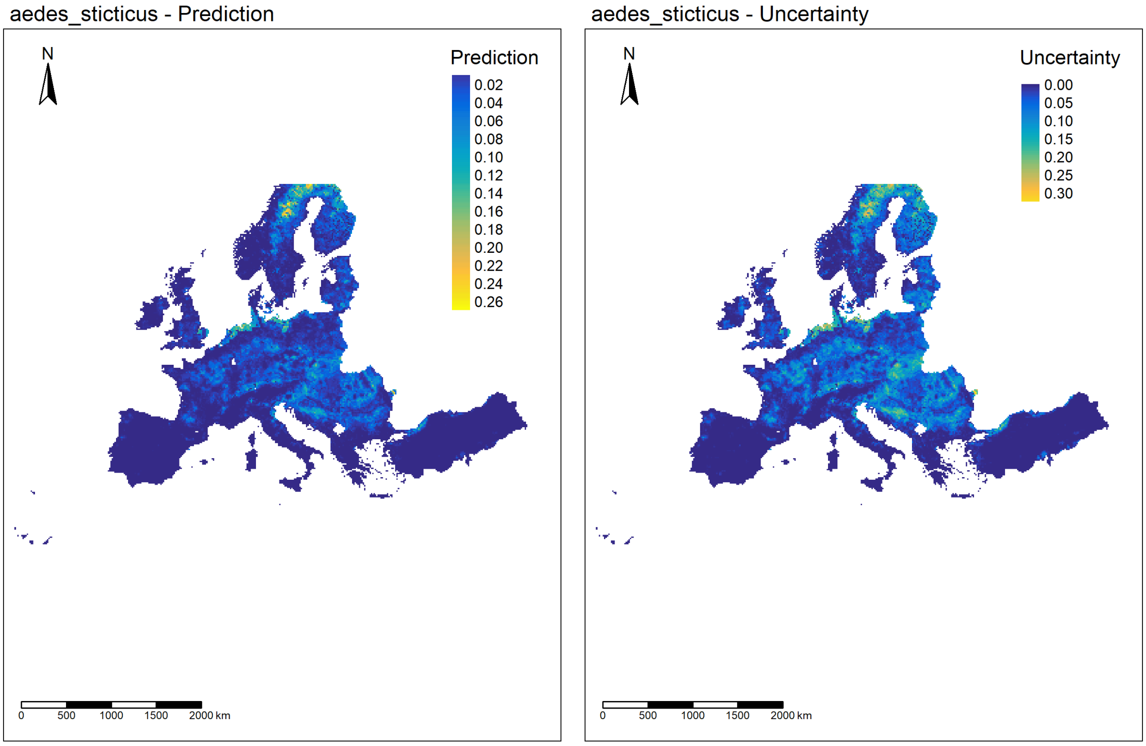


Fig. B.10 Predictions for *Aedes sticticus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

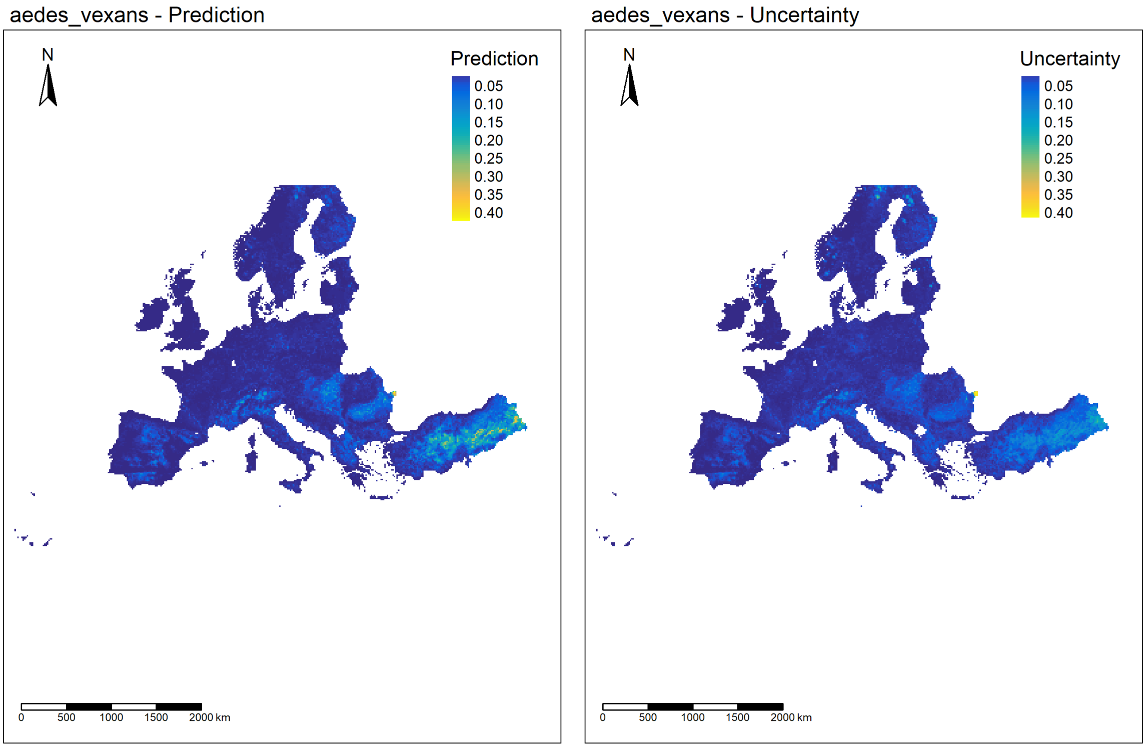


Fig. B.11 Predictions for *Aedes vexans* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

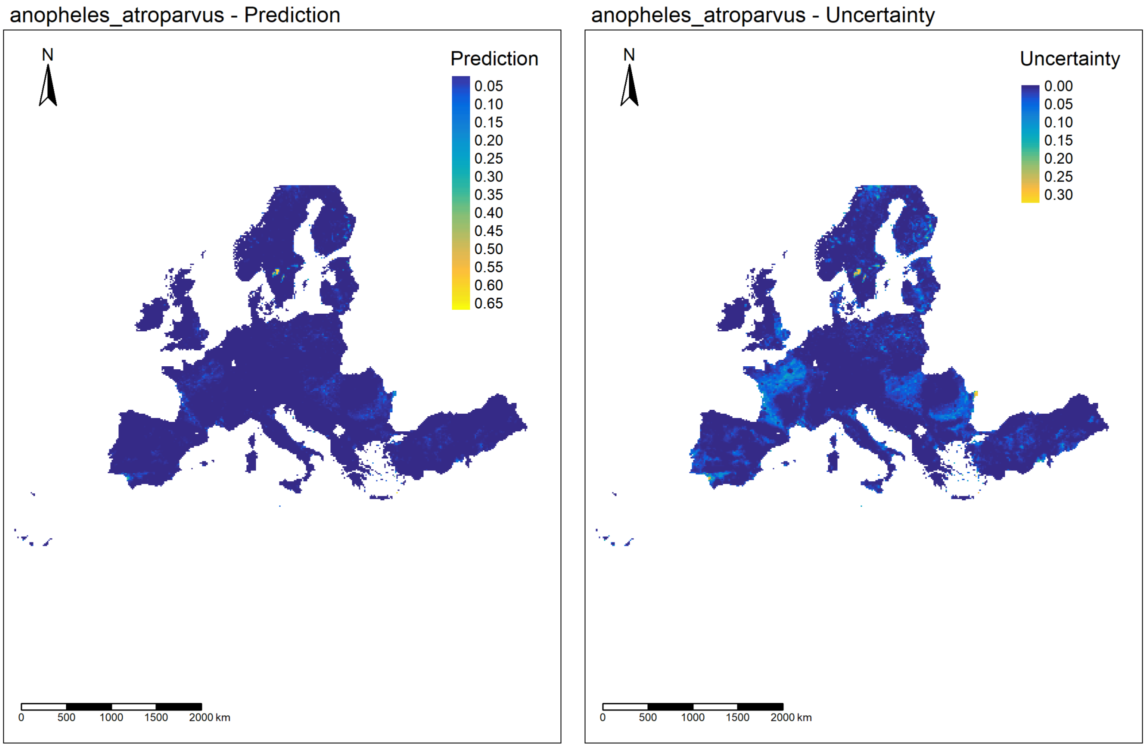


Fig. B.12 Predictions for *Anopheles atroparvus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

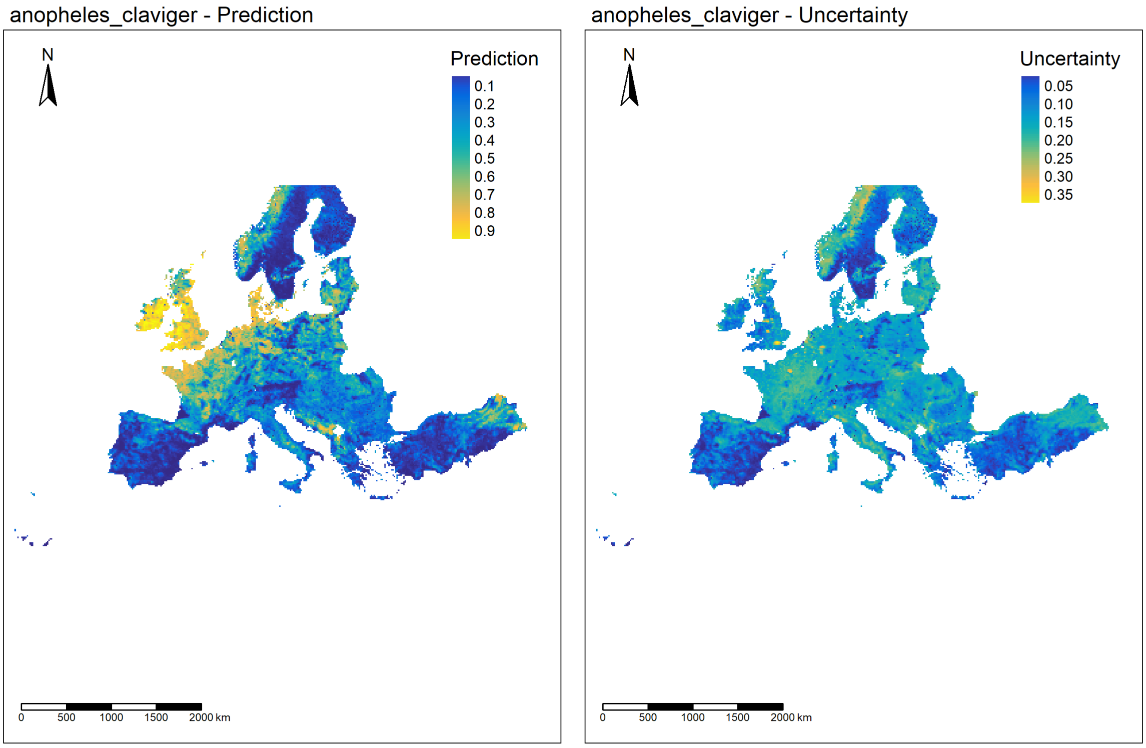


Fig. B.13 Predictions for *Anopheles claviger* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

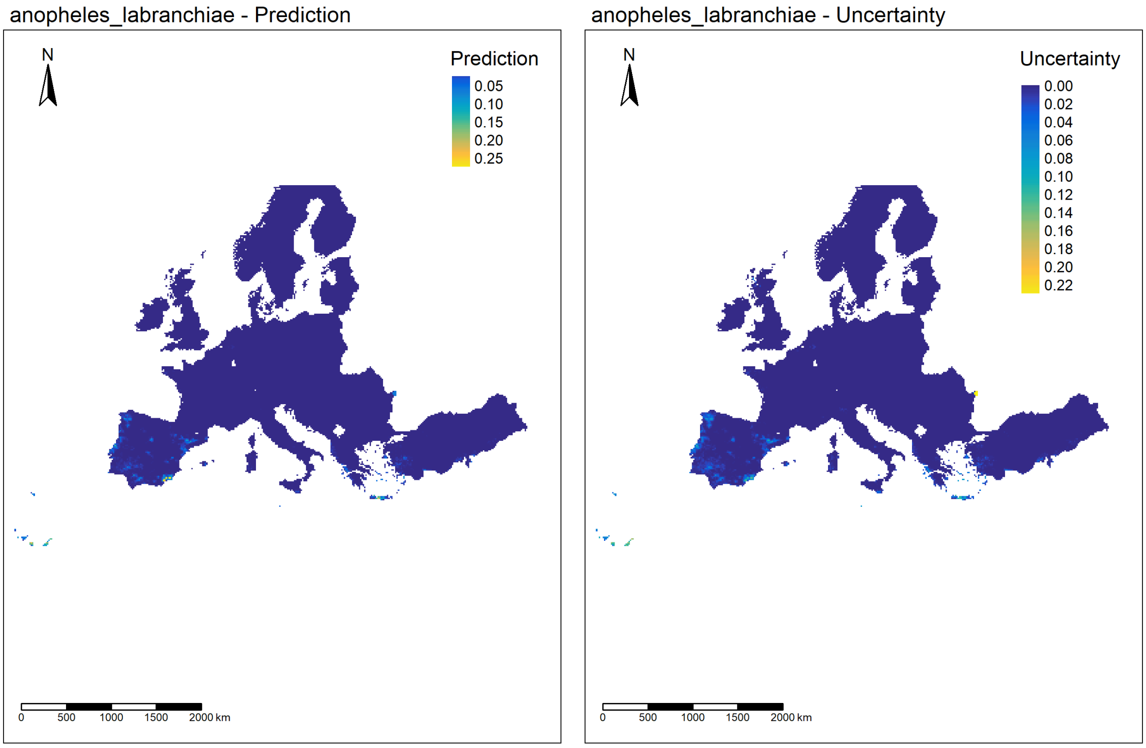
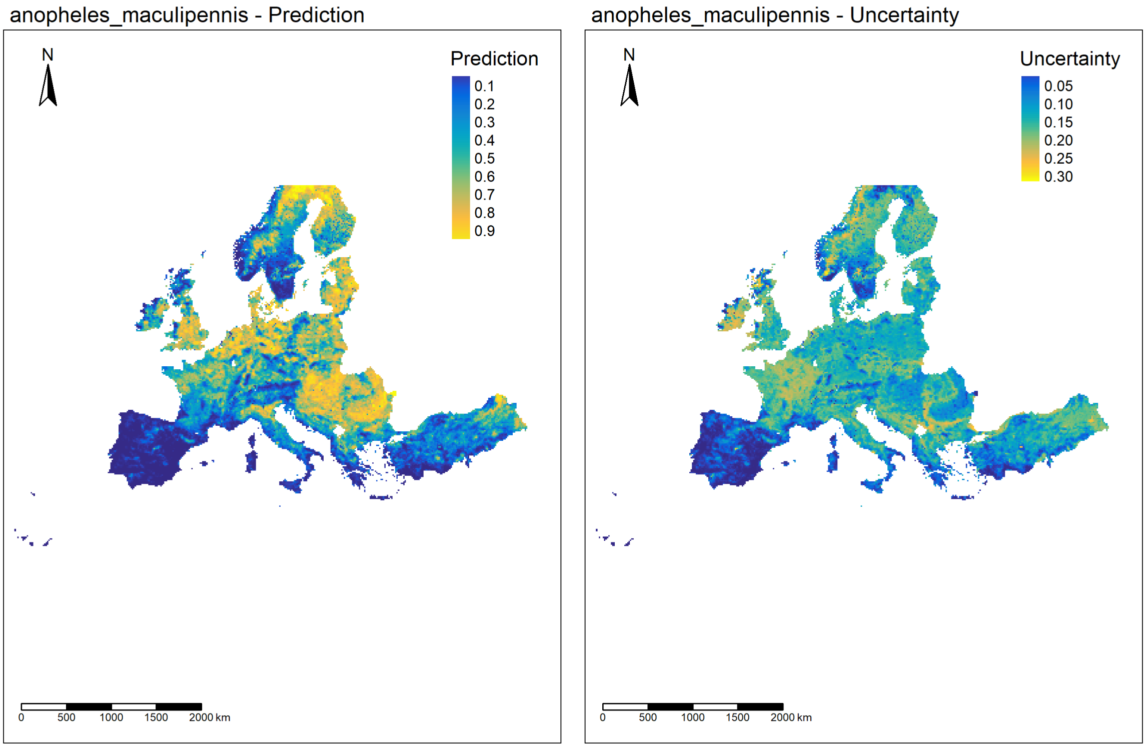


Fig. B.14 Predictions for *Anopheles labranchiae* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.


anopheles_maculipennis - Prediction

anopheles_maculipennis - Uncertainty

Fig. B.15 Predictions for *Anopheles maculipennis* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

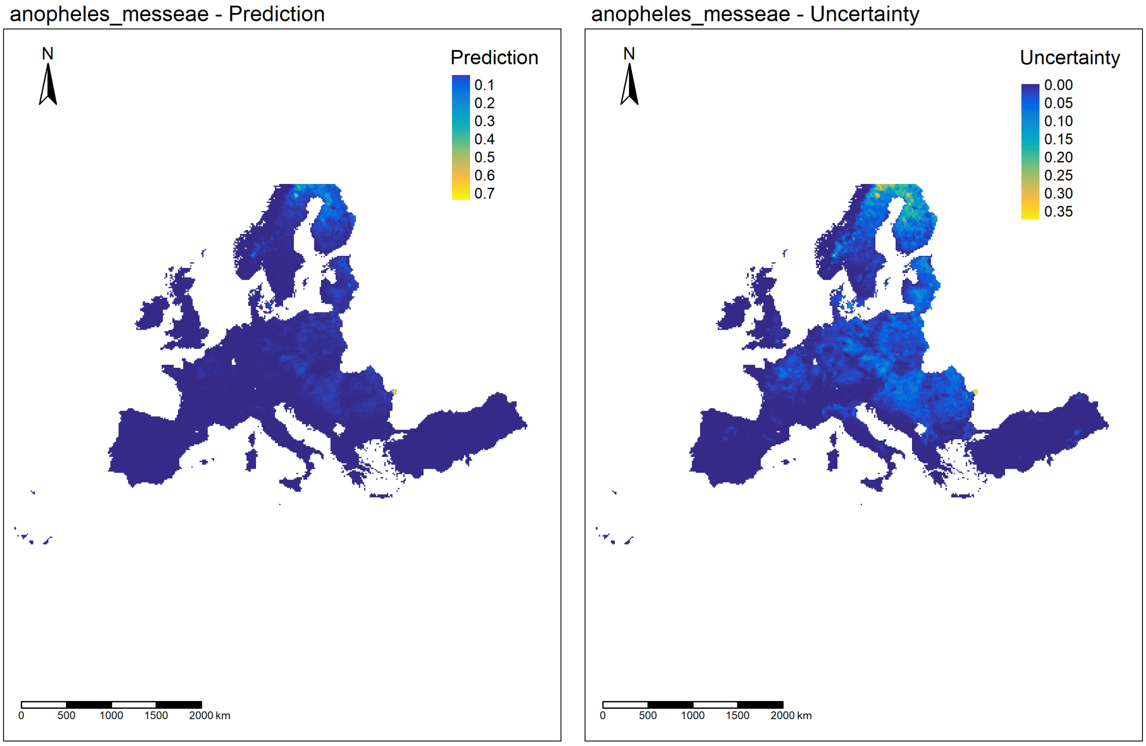


Fig. B.16 Predictions for *Anopheles messeae* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

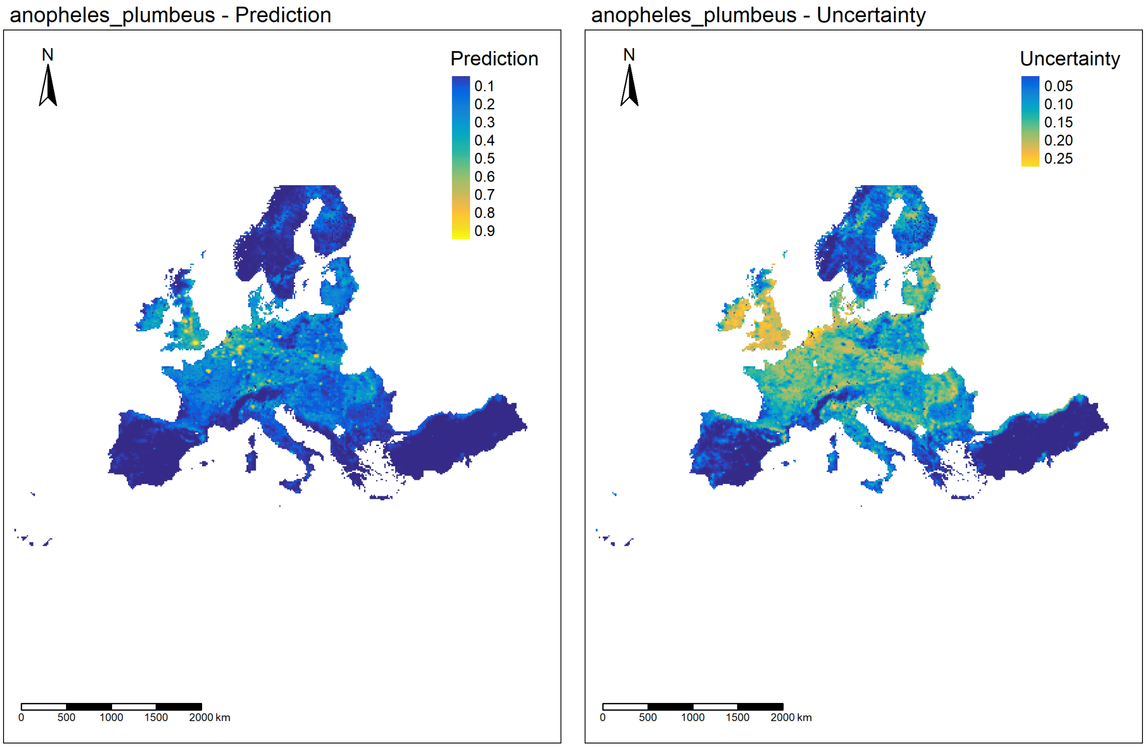


Fig. B.17 Predictions for *Anopheles plumbeus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

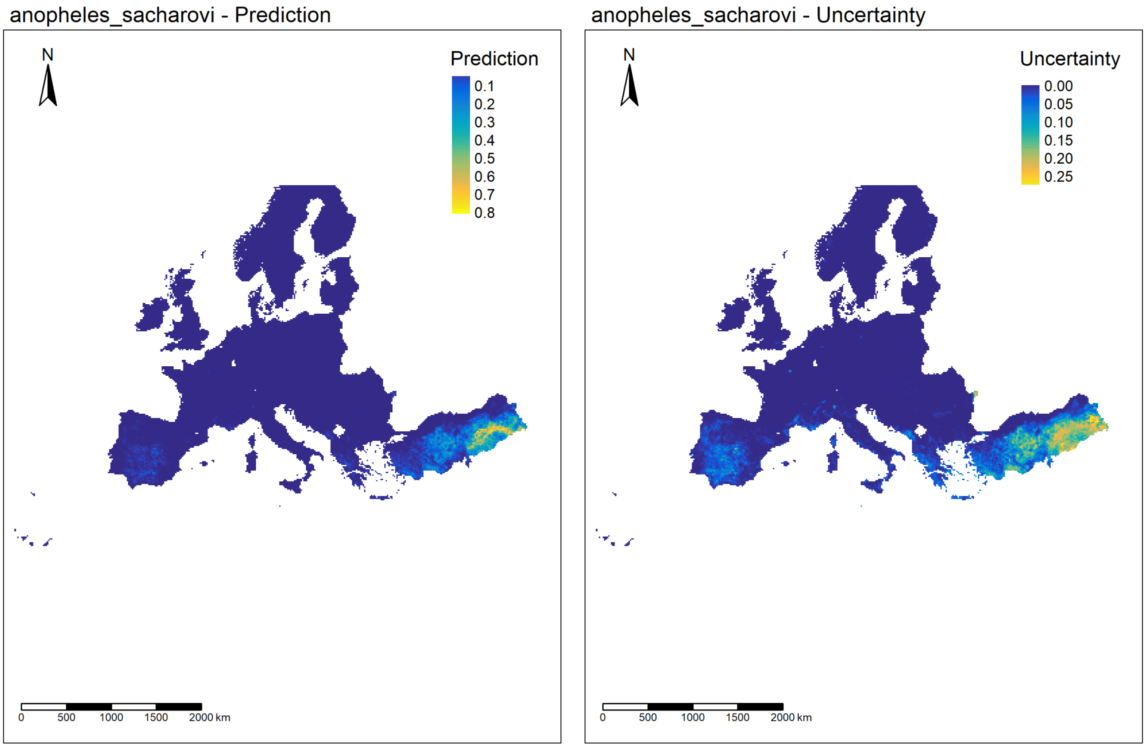


Fig. B.18 Predictions for *Anopheles sacharovi* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

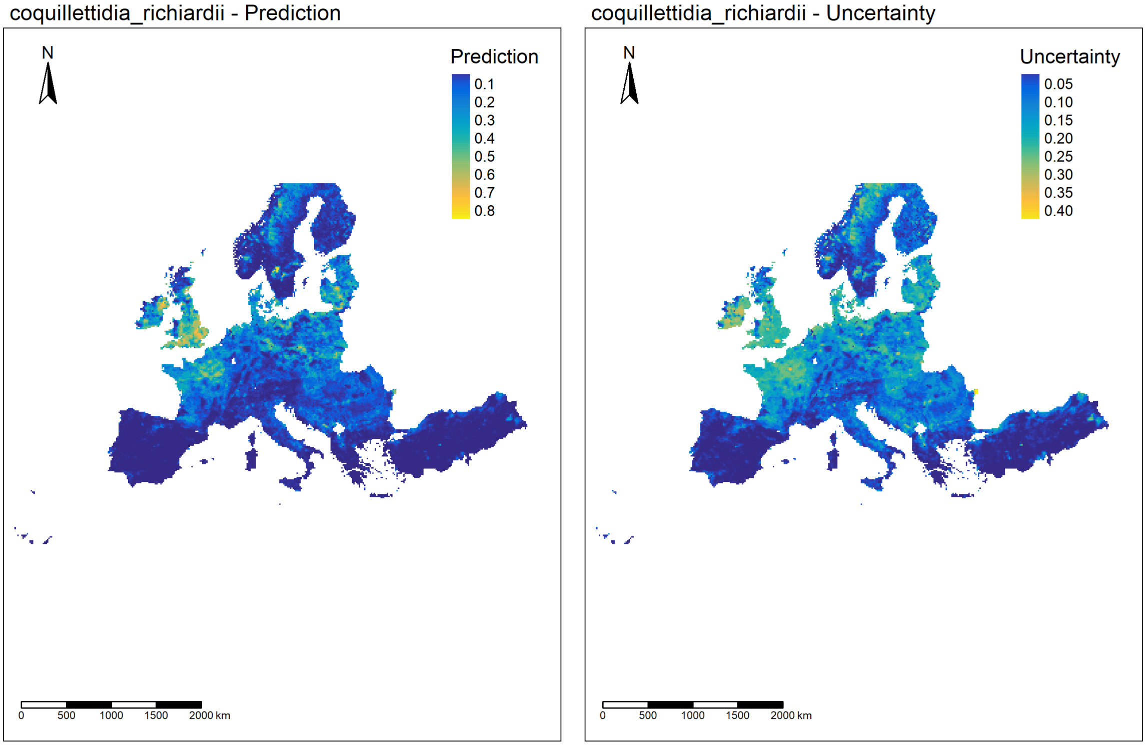


Fig. B.19 Predictions for *Coquillettidia richiardii* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

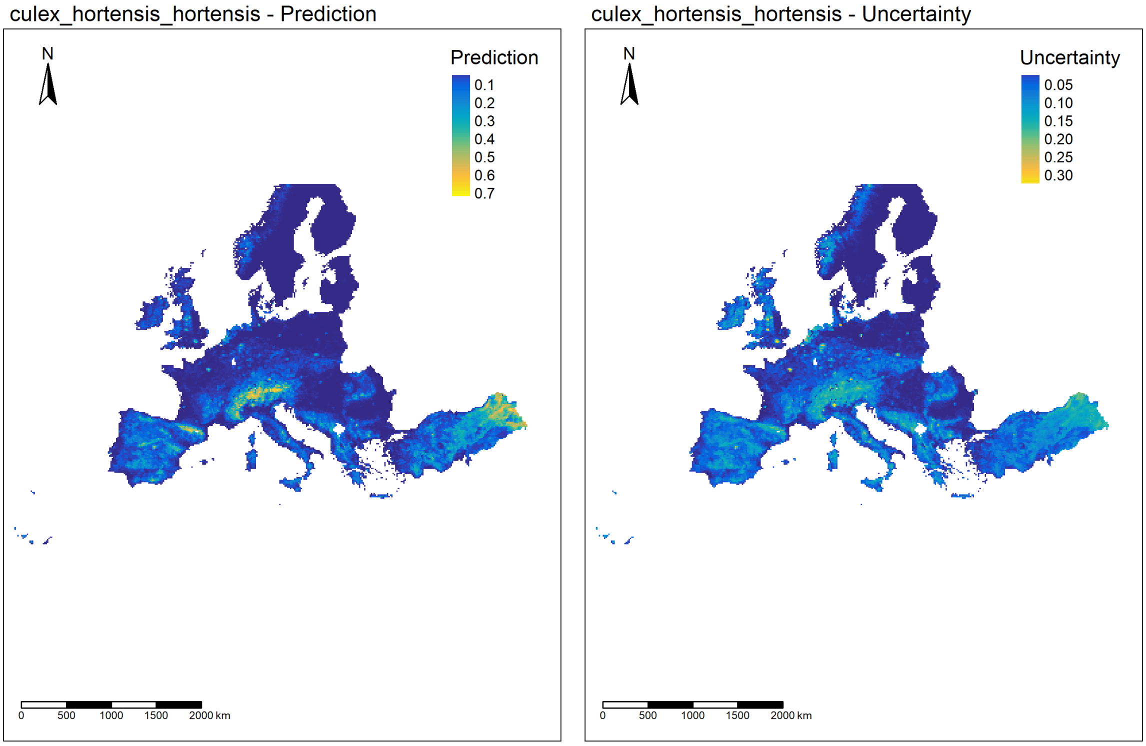


Fig. B.20 Predictions for *Culex hortensis hortensis* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

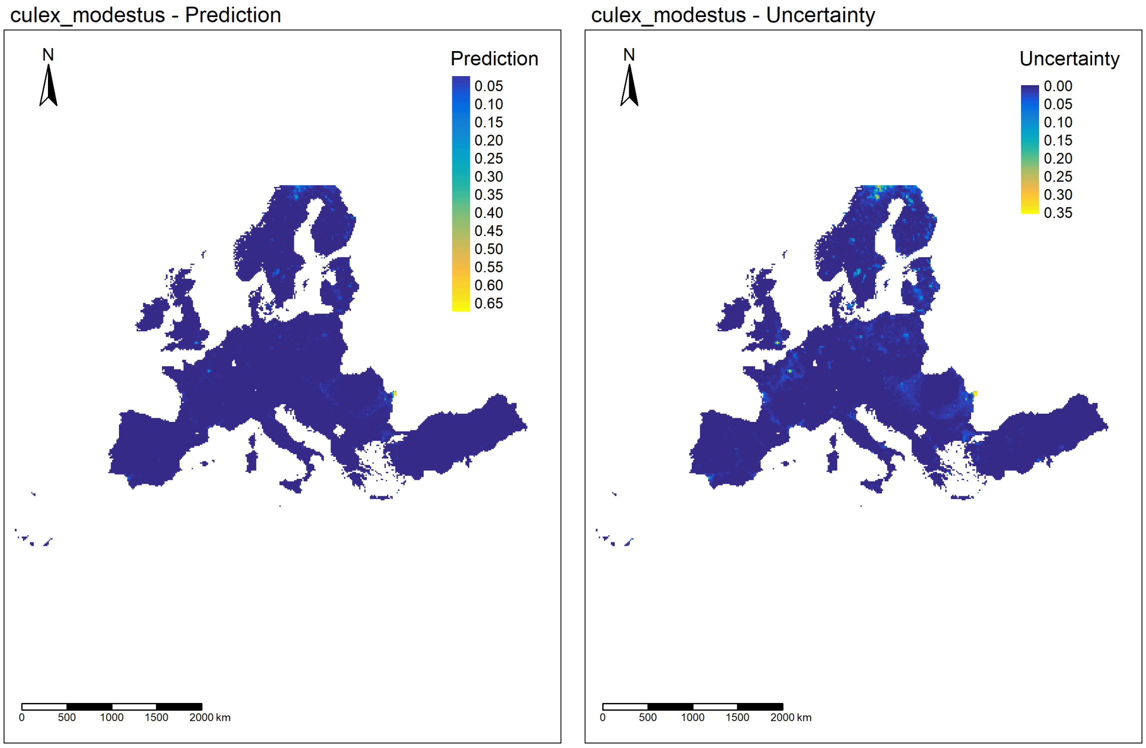


Fig. B.21 Predictions for *Culex modestus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

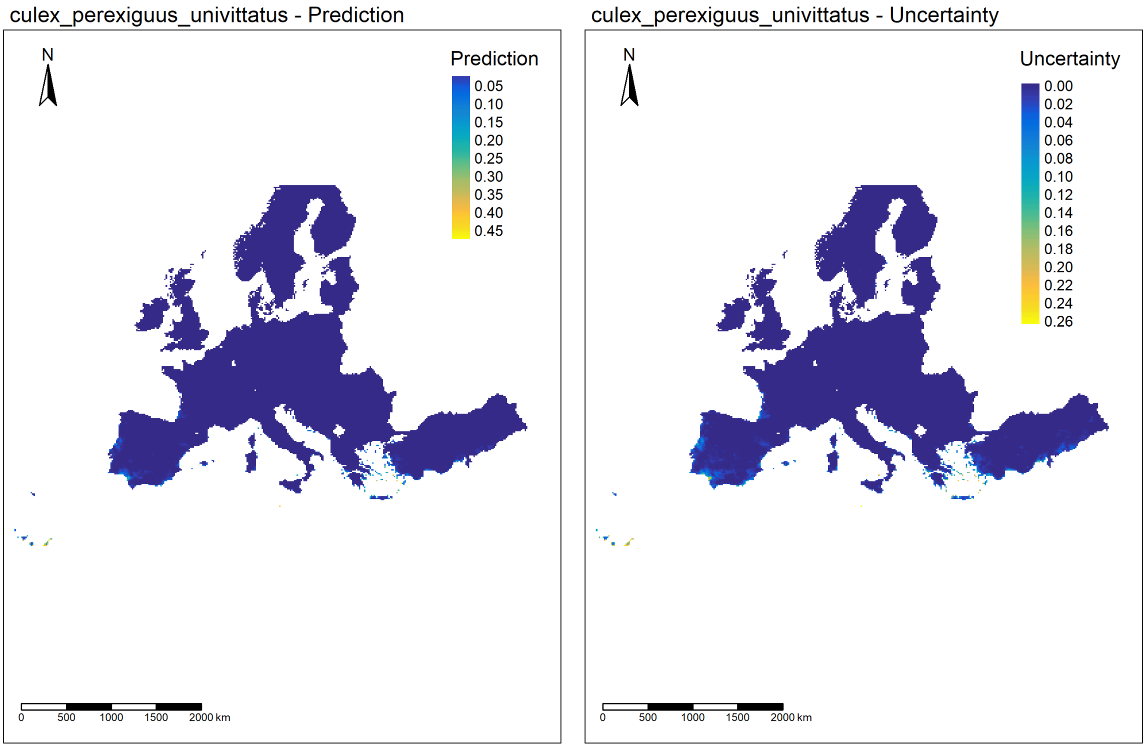


Fig. B.22 Predictions for *Culex perexiguus/univittatus* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

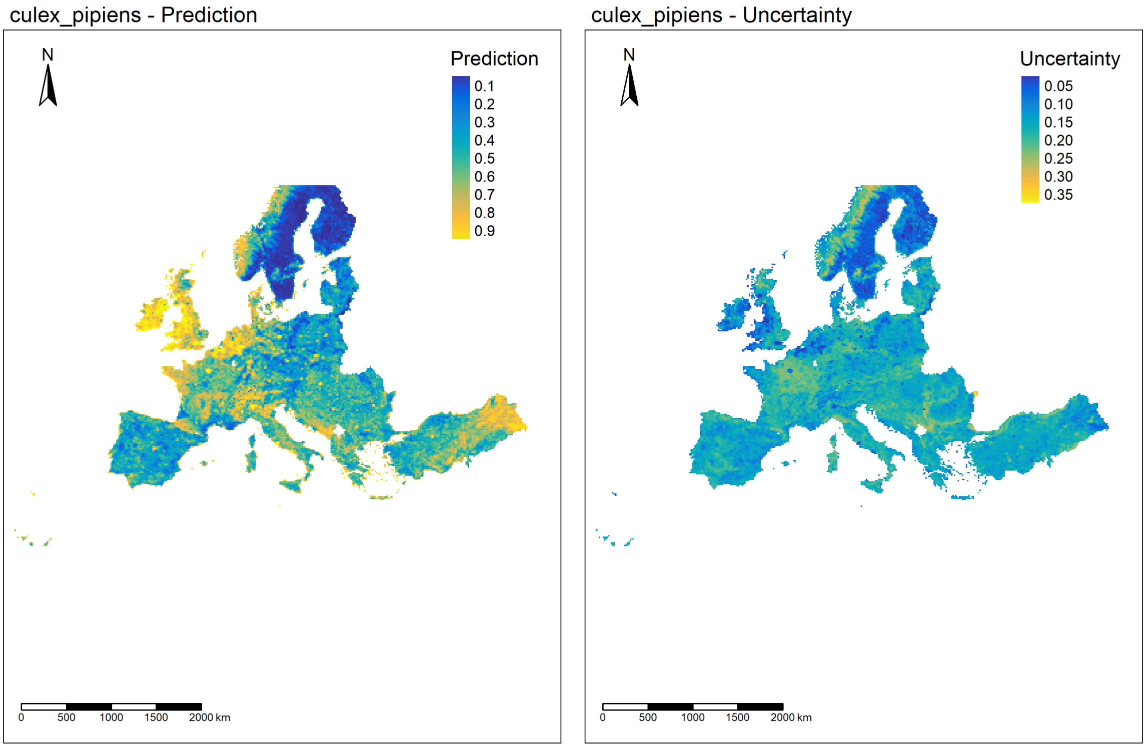
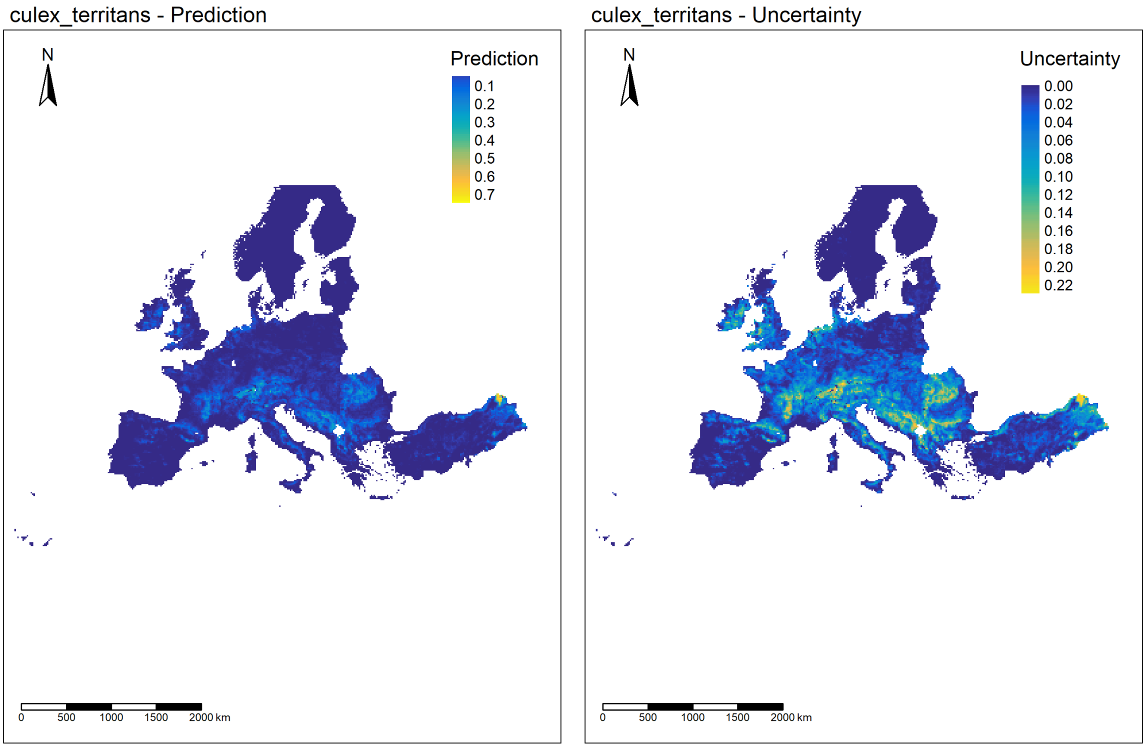


Fig. B.23 Predictions for *Culex pipiens* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.



culex_territans - Prediction

culex_territans - Uncertainty

Fig. B.24 Predictions for *Culex territans* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

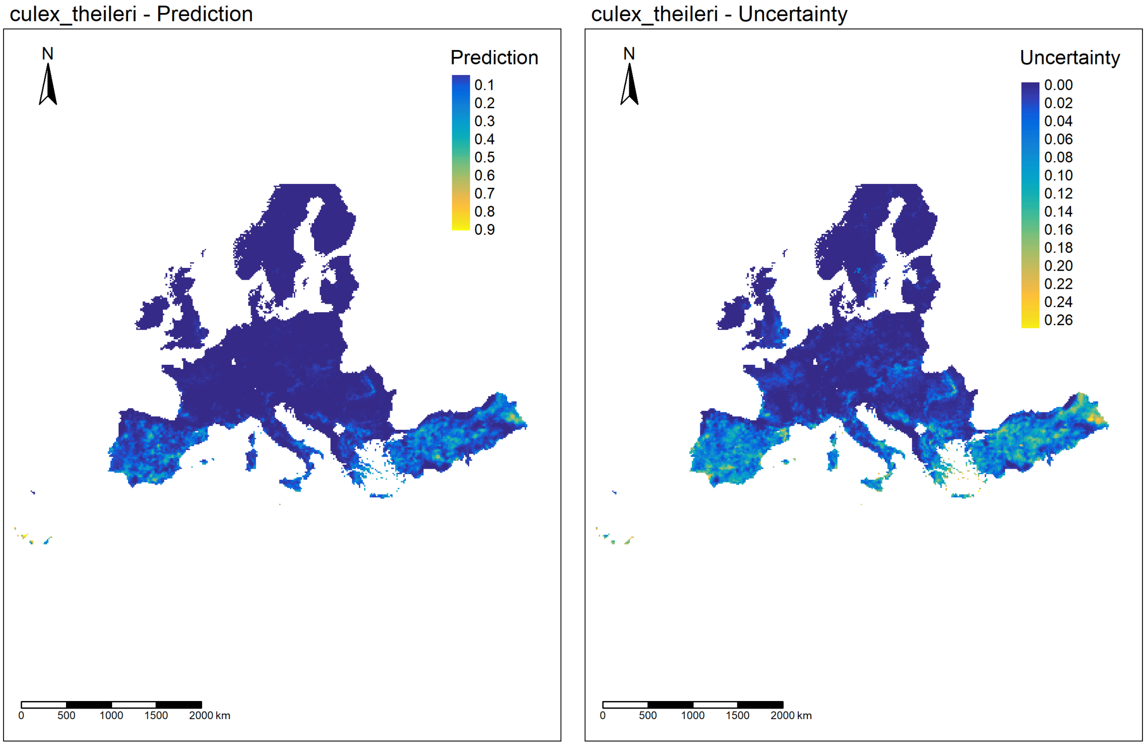


Fig. B.25 Predictions for *Culex theileri* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

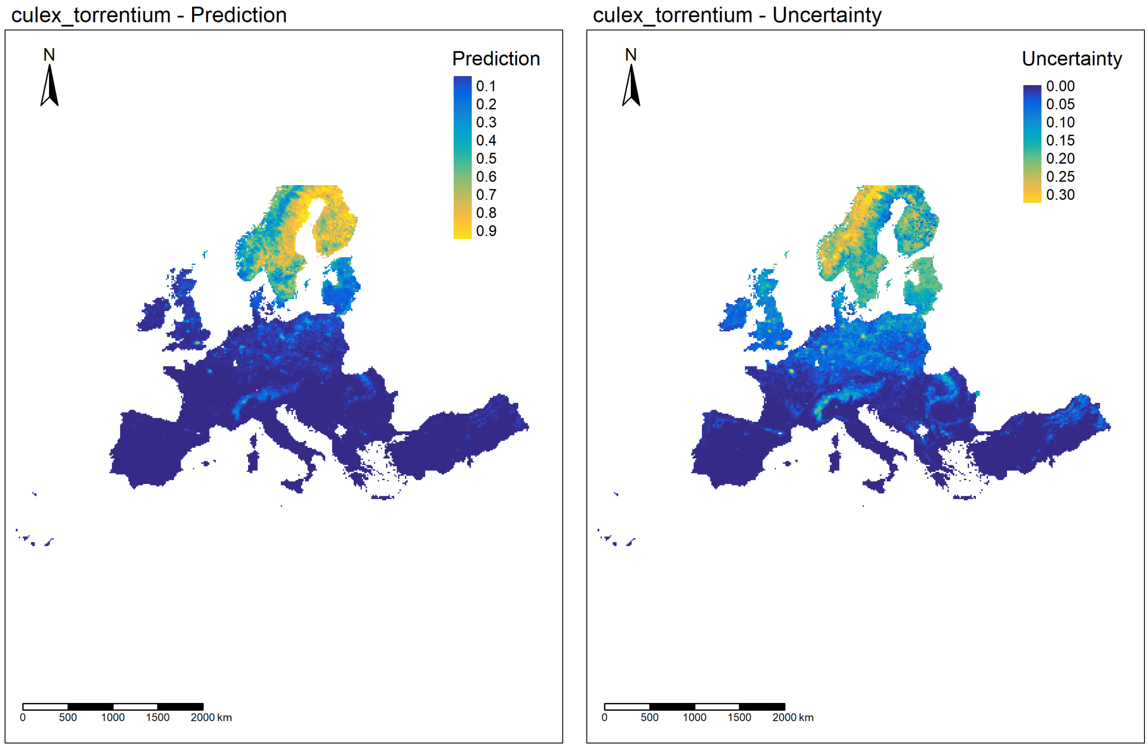


Fig. B.26 Predictions for *Culex torrentium* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

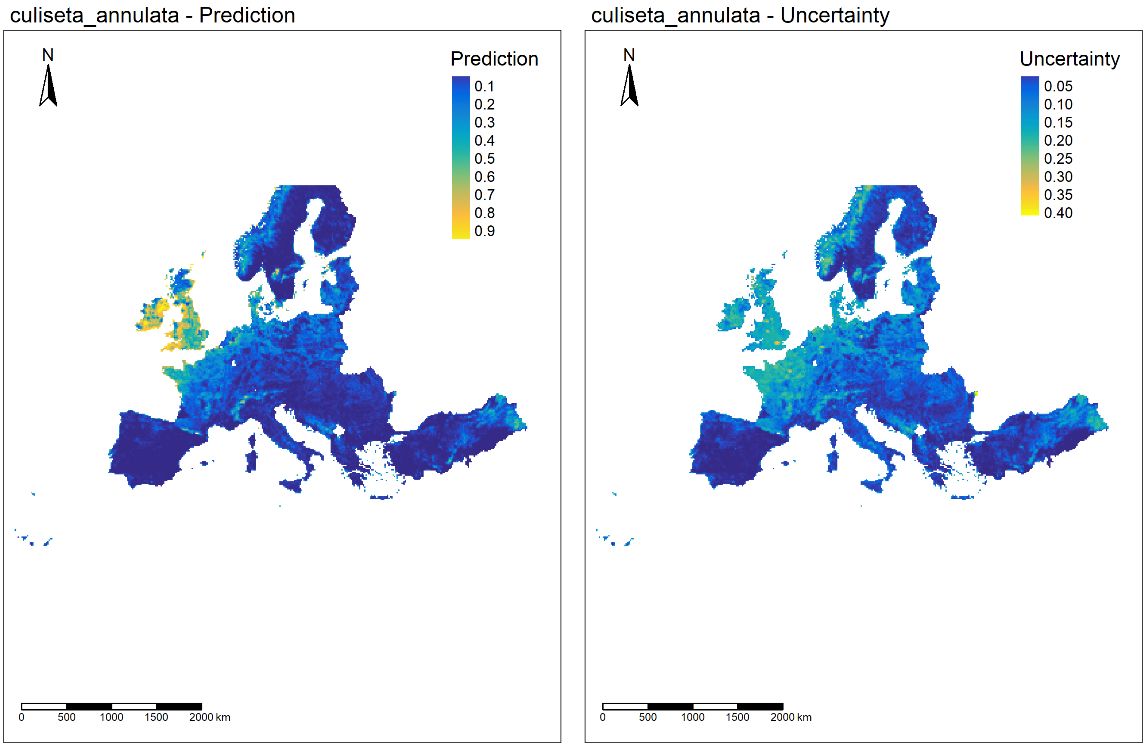


Fig. B.27 Predictions for *Culiseta annulata* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

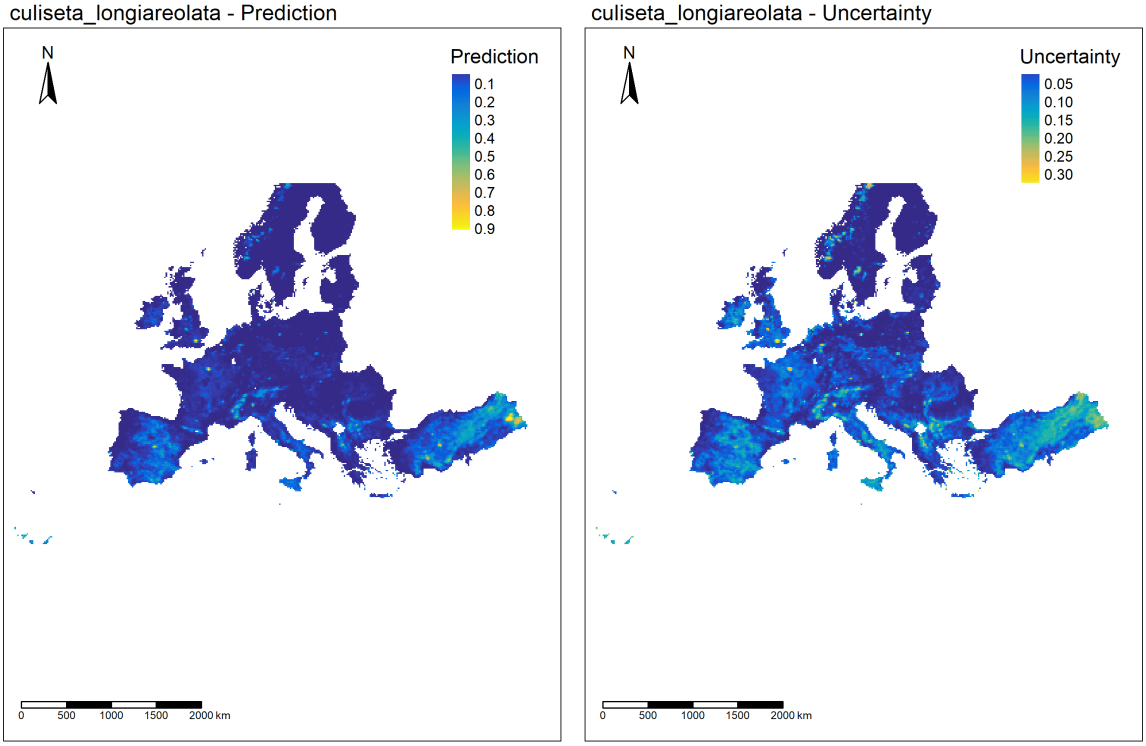


Fig. B.28 Predictions for *Culiseta longiareolata* distribution across the European region. These maps show 5km resolution predictions from the Joint Species Distribution Model (JSDM), including uncertainty estimates generated from bootstrap predictions.

Appendix C

Appendix: Chapter 4

Table C.1 Summary of mosquito species traits used for binary trait inference. The table includes various traits such as habitat, water source, feeding preferences, and behaviour, which were inferred from published data sources. The references are listed at the bottom of the table, corresponding to the numerical reference identifiers in the last column.

Species	Trait	Value(s)	Reference
Aedes albopictus	Water Source	Artifical, Natural	1
Aedes albopictus	Water Permanence	Temporary	1
Aedes albopictus	Water Type	Freshwater	1
Aedes albopictus	Habitat	Forest	1
Aedes albopictus	Vegetation Density	High	1
Aedes albopictus	Main Overwintering Stage	Larvae, Eggs	1
Aedes albopictus	Primarily Anthrophillic	Yes	2
Aedes albopictus	Primarily Mammalophillic	Yes	1
Aedes albopictus	Primarily Ornithophillic	Yes	1
Aedes albopictus	Day	Yes	1
Aedes albopictus	Crepuscular	No	1
Aedes albopictus	Night	No	1
Aedes albopictus	Voltinism	Multivoltine	1
Aedes albopictus	Vector	Yes	1
Aedes annulipes/cantans	Water Source	Natural	1

Species	Trait	Value(s)	Reference
Aedes annulipes/cantans	Water Permanence	Semi-permanent	1
Aedes annulipes/cantans	Water Type	Freshwater	1
Aedes annulipes/cantans	Habitat	Forest, Rural	1
Aedes annulipes/cantans	Vegetation Density	High	1
Aedes annulipes/cantans	Main Overwintering Stage	Eggs	1
Aedes annulipes/cantans	Primarily Anthrophillic	Yes	3
Aedes annulipes/cantans	Primarily Mammalophillic	Yes	4
Aedes annulipes/cantans	Primarily Ornithophillic	Yes	4
Aedes annulipes/cantans	Day	Yes	1
Aedes annulipes/cantans	Crepuscular	Yes	3
Aedes annulipes/cantans	Night	No	1
Aedes annulipes/cantans	Voltinism	Univoltine	1
Aedes annulipes/cantans	Vector	No	4
Aedes caspius	Water Source	Natural	1
Aedes caspius	Water Permanence	Temporary, Permanent	1
Aedes caspius	Water Type	Freshwater, Brackish, Saline	1
Aedes caspius	Habitat	Coastal, Rural	1
Aedes caspius	Vegetation Density	Medium	3
Aedes caspius	Main Overwintering Stage	Eggs	1
Aedes caspius	Primarily Anthrophillic	Yes	1
Aedes caspius	Primarily Mammalophillic	Yes	1
Aedes caspius	Primarily Ornithophillic	No	5
Aedes caspius	Day	Yes	6

Species	Trait	Value(s)	Reference
Aedes caspius	Crepuscular	Yes	6
Aedes caspius	Night	Yes	6
Aedes caspius	Voltinism	Univoltine	1
Aedes caspius	Vector	Yes	1
Aedes cinereus/geminus	Water Source	Natural	1
Aedes cinereus/geminus	Water Permanence	Semi-permanent	1
Aedes cinereus/geminus	Water Type	Freshwater	1
Aedes cinereus/geminus	Habitat	Forest, Floodplains, Sedge marshes, Sphagnum bogs	1
Aedes cinereus/geminus	Vegetation Density	High	1
Aedes cinereus/geminus	Main Overwintering Stage	Eggs	1
Aedes cinereus/geminus	Primarily Anthrophillic	Yes	1
Aedes cinereus/geminus	Primarily Mammalophillic	Yes	1
Aedes cinereus/geminus	Primarily Ornithophillic	Yes	7
Aedes cinereus/geminus	Day	No	1
Aedes cinereus/geminus	Crepuscular	Yes	1
Aedes cinereus/geminus	Night	Yes	3
Aedes cinereus/geminus	Voltinism	Bivoltine (at least two generations per year)	1
Aedes cinereus/geminus	Vector	Yes	1
Aedes detritus/coluzzi	Water Source	Natural	1
Aedes detritus/coluzzi	Water Permanence	Semi-permanent	1
Aedes detritus/coluzzi	Water Type	Brackish, Saline	1
Aedes detritus/coluzzi	Habitat	Coastal	1
Aedes detritus/coluzzi	Vegetation Density	Low	1
Aedes detritus/coluzzi	Main Overwintering Stage	Eggs, Larvae	1
Aedes detritus/coluzzi	Primarily Anthrophillic	Yes	1
Aedes detritus/coluzzi	Primarily Mammalophillic	Yes	3
Aedes detritus/coluzzi	Primarily Ornithophillic	Yes	3
Aedes detritus/coluzzi	Day	No	3
Aedes detritus/coluzzi	Crepuscular	Yes	1

Species	Trait	Value(s)	Reference
Aedes detritus/coluzzi	Night	No	3
Aedes detritus/coluzzi	Voltinism	Multivoltine	1
Aedes detritus/coluzzi	Vector	Yes	3
Aedes geniculatus	Water Source	Natural	1
Aedes geniculatus	Water Permanence	Temporary	1
Aedes geniculatus	Water Type	Freshwater	1
Aedes geniculatus	Habitat	Forest	1
Aedes geniculatus	Vegetation Density	High	1
Aedes geniculatus	Main Overwintering Stage	Eggs, Larvae	1
Aedes geniculatus	Primarily Anthrophillic	Yes	1
Aedes geniculatus	Primarily Mammalophillic	Yes	3
Aedes geniculatus	Primarily Ornithophillic	No	3
Aedes geniculatus	Day	Yes	1
Aedes geniculatus	Crepuscular	Yes	1
Aedes geniculatus	Night	No	1
Aedes geniculatus	Voltinism	Multivoltine	3
Aedes geniculatus	Vector	No	8
Aedes japonicus	Water Source	Natural, Artificial	1
Aedes japonicus	Water Permanence	Temporary	1
Aedes japonicus	Water Type	Freshwater	1
Aedes japonicus	Habitat	Forest, Urban	1
Aedes japonicus	Vegetation Density	High	1
Aedes japonicus	Main Overwintering Stage	Eggs, Larvae	1
Aedes japonicus	Primarily Anthrophillic	No	1
Aedes japonicus	Primarily Mammalophillic	Yes	1
Aedes japonicus	Primarily Ornithophillic	Yes	1
Aedes japonicus	Day	Yes	1
Aedes japonicus	Crepuscular	Yes	1
Aedes japonicus	Night	No	1
Aedes japonicus	Voltinism	Multivoltine	1
Aedes japonicus	Vector	Yes	1
Aedes sticticus	Water Source	Natural	1
Aedes sticticus	Water Permanence	Temporary	1

Species	Trait	Value(s)	Reference
Aedes sticticus	Water Type	Freshwater	1
Aedes sticticus	Habitat	Forest, Rural	1
Aedes sticticus	Vegetation Density	High	1
Aedes sticticus	Main Overwintering Stage	Eggs	1
Aedes sticticus	Primarily Anthrophillic	Yes	1
Aedes sticticus	Primarily Mammalophillic	Yes	9
Aedes sticticus	Primarily Ornithophillic	No	9
Aedes sticticus	Day	Yes	1
Aedes sticticus	Crepuscular	Yes	1
Aedes sticticus	Night	No	1
Aedes sticticus	Voltinism	Multivoltine	10
Aedes sticticus	Vector	Yes	11
Aedes vexans	Water Source	Natural	12
Aedes vexans	Water Permanence	Temporary	12
Aedes vexans	Water Type	Freshwater	12
Aedes vexans	Habitat	Rural	12
Aedes vexans	Vegetation Density	High	12
Aedes vexans	Main Overwintering Stage	Eggs	12
Aedes vexans	Primarily Anthrophillic	Yes	12
Aedes vexans	Primarily Mammalophillic	Yes	12
Aedes vexans	Primarily Ornithophillic	No	12
Aedes vexans	Day	No	13
Aedes vexans	Crepuscular	No	13
Aedes vexans	Night	Yes	13
Aedes vexans	Voltinism	Multivoltine	12
Aedes vexans	Vector	Yes	12
Anopheles atroparvus	Water Source	Natural, Artificial	12
Anopheles atroparvus	Water Permanence	Semi-permanent, Permanent	12
Anopheles atroparvus	Water Type	Freshwater, Brackish	12
Anopheles atroparvus	Habitat	Coastal, Rural	12
Anopheles atroparvus	Vegetation Density	High	12
Anopheles atroparvus	Main Overwintering Stage	Adults	12

Species	Trait	Value(s)	Reference
Anopheles atroparvus	Primarily Anthrophillic	No	12
Anopheles atroparvus	Primarily Mammalophillic	Yes	12
Anopheles atroparvus	Primarily Ornithophillic	No	12
Anopheles atroparvus	Day	No	12
Anopheles atroparvus	Crepuscular	Yes	12
Anopheles atroparvus	Night	Yes	12
Anopheles atroparvus	Voltinism	Multivoltine	3
Anopheles atroparvus	Vector	Yes	12
Anopheles claviger	Water Source	Natural, Artificial	12
Anopheles claviger	Water Permanence	Permanent, Semi-permanent	12
Anopheles claviger	Water Type	Freshwater	12
Anopheles claviger	Habitat	Forest, Rural	12
Anopheles claviger	Vegetation Density	High	12
Anopheles claviger	Main Overwintering Stage	Larvae	3
Anopheles claviger	Primarily Anthrophillic	No	12
Anopheles claviger	Primarily Mammalophillic	Yes	14
Anopheles claviger	Primarily Ornithophillic	No	12
Anopheles claviger	Day	Yes	3
Anopheles claviger	Crepuscular	No	3
Anopheles claviger	Night	No	3
Anopheles claviger	Voltinism	Multivoltine	12
Anopheles claviger	Vector	Yes	12
Anopheles labranchiae	Water Source	Natural, Artificial	12
Anopheles labranchiae	Water Permanence	Permanent, Semi-permanent	12
Anopheles labranchiae	Water Type	Freshwater, Brackish	12
Anopheles labranchiae	Habitat	Coastal, Rural	12
Anopheles labranchiae	Vegetation Density	High	12
Anopheles labranchiae	Main Overwintering Stage	Adults	12
Anopheles labranchiae	Primarily Anthrophillic	Yes	12
Anopheles labranchiae	Primarily Mammalophillic	Yes	12

Species	Trait	Value(s)	Reference
Anopheles labranchiae	Primarily Ornithophillic	No	12
Anopheles labranchiae	Day	No	12
Anopheles labranchiae	Crepuscular	Yes	8
Anopheles labranchiae	Night	Yes	12
Anopheles labranchiae	Voltinism	Multivoltine	8
Anopheles labranchiae	Vector	Yes	12
Anopheles maculipennis	Water Source	Natural, Artificial	12
Anopheles maculipennis	Water Permanence	Permanent, Semi-permanent	12
Anopheles maculipennis	Water Type	Freshwater	15
Anopheles maculipennis	Habitat	Rural, Mountain	15
Anopheles maculipennis	Vegetation Density	Variable	15
Anopheles maculipennis	Main Overwintering Stage	Adults	3
Anopheles maculipennis	Primarily Anthrophillic	No	15
Anopheles maculipennis	Primarily Mammalophillic	Yes	15
Anopheles maculipennis	Primarily Ornithophillic	No	15
Anopheles maculipennis	Day	No	14
Anopheles maculipennis	Crepuscular	Yes	14
Anopheles maculipennis	Night	Yes	14
Anopheles maculipennis	Voltinism	Multivoltine	3
Anopheles maculipennis	Vector	Yes	15
Anopheles messeae	Water Source	Natural	15
Anopheles messeae	Water Permanence	Permanent, Semi-permanent	15
Anopheles messeae	Water Type	Freshwater	15
Anopheles messeae	Habitat	Rural	15
Anopheles messeae	Vegetation Density	High	15

Species	Trait	Value(s)	Reference
Anopheles messeae	Main Overwintering Stage	Adults	15
Anopheles messeae	Primarily Anthrophillic	No	15
Anopheles messeae	Primarily Mammalophillic	Yes	15
Anopheles messeae	Primarily Ornithophillic	No	15
Anopheles messeae	Day	Yes	3
Anopheles messeae	Crepuscular	No	3
Anopheles messeae	Night	No	3
Anopheles messeae	Voltinism	Multivoltine	3
Anopheles messeae	Vector	Yes	15
Anopheles plumbeus	Water Source	Natural, Artificial	15
Anopheles plumbeus	Water Permanence	Temporary	15
Anopheles plumbeus	Water Type	Freshwater	15
Anopheles plumbeus	Habitat	Forest, Rural, Urban	15
Anopheles plumbeus	Vegetation Density	High	15
Anopheles plumbeus	Main Overwintering Stage	Eggs, Larvae	15
Anopheles plumbeus	Primarily Anthrophillic	Yes	12
Anopheles plumbeus	Primarily Mammalophillic	Yes	3
Anopheles plumbeus	Primarily Ornithophillic	No	12
Anopheles plumbeus	Day	Yes	15
Anopheles plumbeus	Crepuscular	Yes	15
Anopheles plumbeus	Night	Yes	8
Anopheles plumbeus	Voltinism	Multivoltine	3
Anopheles plumbeus	Vector	Yes	15
Anopheles sacharovi	Water Source	Natural, Artificial	15
Anopheles sacharovi	Water Permanence	Permanent, Semi-permanent	15
Anopheles sacharovi	Water Type	Freshwater, Brackish	15
Anopheles sacharovi	Habitat	Coastal, Rural	15
Anopheles sacharovi	Vegetation Density	High	15
Anopheles sacharovi	Main Overwintering Stage	Adults	15
Anopheles sacharovi	Primarily Anthrophillic	Yes	15

Species	Trait	Value(s)	Reference
Anopheles sacharovi	Primarily Mammalophillic	Yes	15
Anopheles sacharovi	Primarily Ornithophillic	No	15
Anopheles sacharovi	Day	Yes	15
Anopheles sacharovi	Crepuscular	Yes	8
Anopheles sacharovi	Night	Yes	15
Anopheles sacharovi	Voltinism	Multivoltine	15
Anopheles sacharovi	Vector	Yes	15
Coquillettidia richiardii	Water Source	Natural	15
Coquillettidia richiardii	Water Permanence	Permanent	15
Coquillettidia richiardii	Water Type	Freshwater, Brackish	15
Coquillettidia richiardii	Habitat	Rural	15
Coquillettidia richiardii	Vegetation Density	High	15
Coquillettidia richiardii	Main Overwintering Stage	Larvae	3
Coquillettidia richiardii	Primarily Anthrophillic	Yes	3
Coquillettidia richiardii	Primarily Mammalophillic	Yes	3
Coquillettidia richiardii	Primarily Ornithophillic	No	14
Coquillettidia richiardii	Day	No	3
Coquillettidia richiardii	Crepuscular	Yes	3
Coquillettidia richiardii	Night	No	3
Coquillettidia richiardii	Voltinism	Univoltine	3
Coquillettidia richiardii	Vector	Yes	15
Culex hortensis hortensis	Water Source	Natural, Artificial	15
Culex hortensis hortensis	Water Permanence	Permanent, Temporary	15
Culex hortensis hortensis	Water Type	Freshwater	15
Culex hortensis hortensis	Habitat	Rural, Urban	15
Culex hortensis hortensis	Vegetation Density	Variable	15
Culex hortensis hortensis	Main Overwintering Stage	Adults	15
Culex hortensis hortensis	Primarily Anthrophillic	No	15

Species	Trait	Value(s)	Reference
Culex hortensis hortensis	Primarily Mammalophillic	Yes	14
Culex hortensis hortensis	Primarily Ornithophillic	Yes	14
Culex hortensis hortensis	Day	No	15
Culex hortensis hortensis	Crepuscular	Yes	8
Culex hortensis hortensis	Night	No	8
Culex hortensis hortensis	Voltinism	Adult	8
Culex hortensis hortensis	Vector	No	8
Culex modestus	Water Source	Natural, Artificial	15
Culex modestus	Water Permanence	Permanent, Semi-permanent	15
Culex modestus	Water Type	Freshwater, Brackish	12
Culex modestus	Habitat	Rural	15
Culex modestus	Vegetation Density	High	3
Culex modestus	Main Overwintering Stage	Adult	3
Culex modestus	Primarily Anthrophillic	Yes	15
Culex modestus	Primarily Mammalophillic	Yes	15
Culex modestus	Primarily Ornithophillic	Yes	15
Culex modestus	Day	Yes	16
Culex modestus	Crepuscular	Yes	3
Culex modestus	Night	No	15
Culex modestus	Voltinism	Multivoltine	15
Culex modestus	Vector	Yes	15
Culex perexiguus/univittatus	Water Source	Natural, Artificial	15
Culex perexiguus/univittatus	Water Permanence	Permanent, Semi-permanent	15
Culex perexiguus/univittatus	Water Type	Freshwater, Brackish	15
Culex perexiguus/univittatus	Habitat	Rural, Urban	15

Species	Trait	Value(s)	Reference
Culex perexiguus/univittatus	Vegetation Density	Medium	15
Culex perexiguus/univittatus	Main Overwintering Stage	Adult	8
Culex perexiguus/univittatus	Primarily Anthrophillic	No	15
Culex perexiguus/univittatus	Primarily Mammalophillic	Yes	15
Culex perexiguus/univittatus	Primarily Ornithophillic	Yes	15
Culex perexiguus/univittatus	Day	No	17
Culex perexiguus/univittatus	Crepuscular	Yes	17
Culex perexiguus/univittatus	Night	Yes	12
Culex perexiguus/univittatus	Voltinism	Multivoltine	8
Culex perexiguus/univittatus	Vector	Yes	15
Culex pipiens	Water Source	Natural, Artificial	15
Culex pipiens	Water Permanence	Permanent, Semi-permanent, Temporary	15
Culex pipiens	Water Type	Freshwater, Brackish	15
Culex pipiens	Habitat	Rural, Urban	15
Culex pipiens	Vegetation Density	Variable	15
Culex pipiens	Main Overwintering Stage	Adults	3
Culex pipiens	Primarily Anthrophillic	No	3
Culex pipiens	Primarily Mammalophillic	Yes	3
Culex pipiens	Primarily Ornithophillic	Yes	14
Culex pipiens	Day	No	15
Culex pipiens	Crepuscular	Yes	14
Culex pipiens	Night	Yes	14
Culex pipiens	Voltinism	Multivoltine	3
Culex pipiens	Vector	Yes	15
Culex territans	Water Source	Natural, Artificial	15

Species	Trait	Value(s)	Reference
Culex territans	Water Permanence	Permanent, Semi-permanent	15
Culex territans	Water Type	Freshwater	15
Culex territans	Habitat	Rural	15
Culex territans	Vegetation Density	High	15
Culex territans	Main Overwintering Stage	Adults	15
Culex territans	Primarily Anthrophillic	No	15
Culex territans	Primarily Mammalophillic	No	15
Culex territans	Primarily Ornithophillic	Yes	15
Culex territans	Day	Yes	8
Culex territans	Crepuscular	Yes	8
Culex territans	Night	No	8
Culex territans	Voltinism	Univoltine, Multivoltine	15
Culex territans	Vector	No	18
Culex theileri	Water Source	Natural, Artificial	15
Culex theileri	Water Permanence	Permanent, Semi-permanent, Temporary	15
Culex theileri	Water Type	Freshwater, Brackish	15
Culex theileri	Habitat	Rural, Urban	15
Culex theileri	Vegetation Density	Variable	15
Culex theileri	Main Overwintering Stage	Adults	19
Culex theileri	Primarily Anthrophillic	Yes	20
Culex theileri	Primarily Mammalophillic	Yes	20
Culex theileri	Primarily Ornithophillic	No	20
Culex theileri	Day	No	21
Culex theileri	Crepuscular	Yes	21
Culex theileri	Night	Yes	21
Culex theileri	Voltinism	Multivoltine	15
Culex theileri	Vector	Yes	15
Culex torrentium	Water Source	Natural, Artificial	15
Culex torrentium	Water Permanence	Permanent, Semi-permanent	15

Species	Trait	Value(s)	Reference
Culex torrentium	Water Type	Freshwater	15
Culex torrentium	Habitat	Rural, Urban	15
Culex torrentium	Vegetation Density	Variable	15
Culex torrentium	Main Overwintering Stage	Adults	3
Culex torrentium	Primarily Anthrophillic	No	3
Culex torrentium	Primarily Mammalophillic	No	3
Culex torrentium	Primarily Ornithophillic	Yes	3
Culex torrentium	Day	No	15
Culex torrentium	Crepuscular	No	15
Culex torrentium	Night	Yes	15
Culex torrentium	Voltinism	Multivoltine	3
Culex torrentium	Vector	Yes	15
Culiseta annulata	Water Source	Natural, Artificial	15
Culiseta annulata	Water Permanence	Permanent, Semi-permanent	15
Culiseta annulata	Water Type	Freshwater, Brackish	15
Culiseta annulata	Habitat	Rural, Urban	15
Culiseta annulata	Vegetation Density	Variable	15
Culiseta annulata	Main Overwintering Stage	Adults	3
Culiseta annulata	Primarily Anthrophillic	Yes	3
Culiseta annulata	Primarily Mammalophillic	Yes	3
Culiseta annulata	Primarily Ornithophillic	No	3
Culiseta annulata	Day	Yes	14
Culiseta annulata	Crepuscular	Yes	14
Culiseta annulata	Night	Yes	14
Culiseta annulata	Voltinism	Multivoltine	3
Culiseta annulata	Vector	Yes	15
Culiseta longiareolata	Water Source	Natural, Artificial	15
Culiseta longiareolata	Water Permanence	Permanent, Temporary	15
Culiseta longiareolata	Water Type	Freshwater, Brackish	15
Culiseta longiareolata	Habitat	Rural, Urban	15
Culiseta longiareolata	Vegetation Density	Low	15

Species	Trait	Value(s)	Reference
Culiseta longiareolata	Main Overwintering Stage	Larvae	15
Culiseta longiareolata	Primarily Anthrophillic	No	22
Culiseta longiareolata	Primarily Mammalophillic	No	22
Culiseta longiareolata	Primarily Ornithophillic	Yes	15
Culiseta longiareolata	Day	Yes	8
Culiseta longiareolata	Crepuscular	Yes	8
Culiseta longiareolata	Night	Yes	8
Culiseta longiareolata	Voltinism	Multivoltine	15
Culiseta longiareolata	Vector	Yes	15

1 Becker, N., Petric, D., Zgomba, M., Boase, C., Madon, M. B., Dahl, C., and Kaiser, A. *Mosquitoes: Identification, Ecology and Control*. Springer Nature, 2020.

2 Sawabe, K. et al. (2010). "Host-Feeding Habits of *Culex pipiens* and *Aedes albopictus* (Diptera: Culicidae) Collected at the Urban and Suburban Residential Areas of Japan," *Journal of Medical Entomology*, 47(3), pp. 442–450.

3 Hawkes, F.M. et al. (2020). *Wetland Mosquito Survey Handbook: Assessing Suitability of British Wetlands for Mosquitoes*. Chatham, UK: Natural Resources Institute.

4 Kay, B.H., Boreham, P.F.L., and Williams, G.M. (1979). "Host preferences and feeding patterns of mosquitoes (Diptera: Culicidae) at Kowanyama, Cape York Peninsula, northern Queensland," *Bulletin of Entomological Research*, 69(3), pp. 441–457.

5 Gutierrez-Lopez, R. et al. (2019). "Effects of host sex, body mass, and infection by avian *Plasmodium* on the biting rate of two mosquito species with different feeding preferences," *Parasites & Vectors*, 12(1), p. 87.

6 Nunez, A.I. et al. (2019). "European *Aedes caspius* mosquitoes are experimentally unable to transmit Zika virus," *Parasites & Vectors*, 12(1), p. 363.

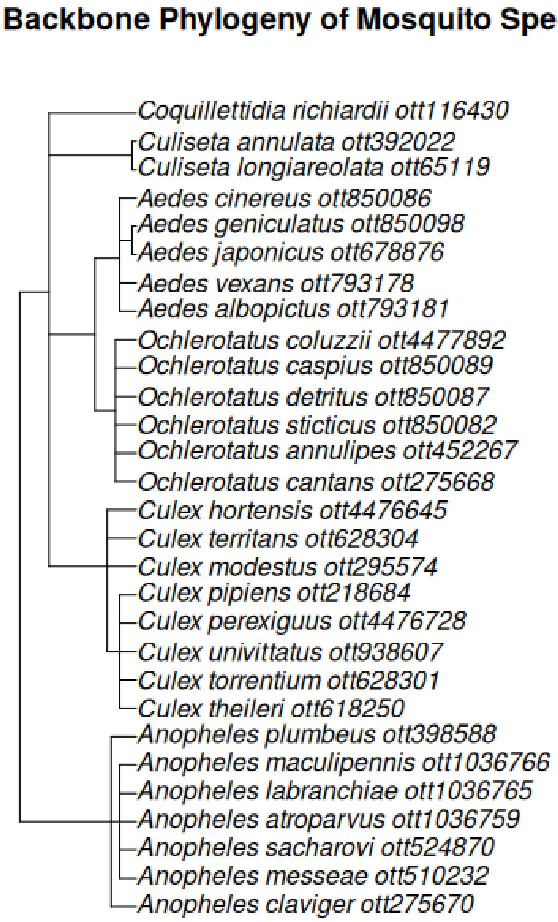


Fig. C.1 Phylogenetic tree of mosquito species used in this study, constructed based on taxonomic relationships. The tree was generated using the taxize and ape R packages.

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