

META-ANALYSIS OPEN ACCESS

Diversity and Plasticity in Mosquito Feeding Patterns: A Meta-Analysis of ‘Universal’ DNA Diet Studies

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ABSTRACT

Aim: Although mosquitoes can have innate preferences for particular blood-meal hosts, their realised feeding patterns on different host species can be modified under climate and land use change with implications for disease spread. Therefore, it is important to understand the niche breadth of vectors and the extent to which shifts in feeding patterns can be predicted.

Location: Global.

Time Period: 2000–2019.

Major Taxa Studied: Six prominent disease-vectoring mosquitoes: *Aedes aegypti*, *Ae. albopictus*, *Anopheles funestus*, *An. gambiae*, *Culex pipiens*, *Cx. quinquefasciatus*.

Methods: Focusing on blood-meal studies that used ‘universal’ molecular methods with broad taxonomic coverage, we compiled evidence from > 15,600 blood-meals. We estimated mosquito’s host niche breadth and we used hierarchical Dirichlet regression models to investigate shifts in feeding patterns among different functional and taxonomic groups of host species in relation to host and environmental factors.

Results: We estimated host ranges of 179–321 species for each of the two *Culex* mosquitoes and 26–65 species for *Aedes* mosquitoes, comprising considerably broader host niche breadths than previously anticipated. For the two *Anopheles* species, we estimated host ranges of 7–29 species. We found some evidence that shifts in feeding patterns among different host functional and taxonomic groups were associated with environmental conditions such as temperature and livestock density, while our results also demonstrate that with the currently available evidence, global predictions of shifts in mosquito feeding patterns are impeded by significant uncertainty.

Main Conclusions: Our global meta-analysis afforded first insights into the shifts of feeding patterns in variable environments, suggesting that host choice is not a simple function of host availability, but contingent on other environmental drivers. Improving resolution and consistency of data gathering and reporting will improve the precision of how blood-meal studies can inform us of present and potential risks of pathogen transmission events.

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1 | Introduction

The contingency of female mosquito blood-feeding patterns on the environment is likely to have consequences for the transmission of vector-borne pathogens. For example, increased feeding on human hosts for blood-meals can increase the transmission of pathogens between humans, while mixed host utilisation increases the risk for zoonotic pathogen transmission (Fikrig and Harrington 2021). With a global rise in arboviral spread (Messina et al. 2015; Weaver et al. 2018) understanding how changing environmental conditions affect blood-feeding patterns would improve prediction of pathogen spillover.

Certain mosquito species have innate preferences for certain hosts. For example, some mosquitos of the genera *Anopheles* and *Aedes* are considered to exhibit strong and consistent preferences for feeding on humans in both laboratory and field contexts (McBride 2016; Richards et al. 2006). However, other mosquito blood-feeding patterns are modified by additional intrinsic and extrinsic factors such as host-seeking cues and host detection, behavioural plasticity, host availability, and pathogen infection (Harrington et al. 2014; Lyimo and Ferguson 2009; Yan et al. 2021). For example, *An. arabiensis* feeds relatively more often on livestock than on humans with increasing livestock density (Mayagaya et al. 2015). Host availability is generally considered a strong environmental factor impacting host selection of some mosquito species, with studies of forage ratios (i.e., the ratio of actual blood-meals over available host species) prevailing in research since the late 1960s (Edman and Taylor 1968; Tempelis et al. 1965). However, these forage ratio studies consistently show that host selection is determined not only by host availability but also by environmental factors that, for example, can affect mosquito behaviour and host detection (Riccetti et al. 2022; Yan et al. 2021). Such variability in host selection appears to be species- or even biotype-specific; for example, some forms of the *Culex pipiens* species complex are considered bird specialists, whereas other forms appear to predominantly feed on mammals and hybrids readily generalise to feed on both birds and mammals (Fonseca et al. 2004).

Changing climate is modifying the distribution of vectors and hosts (Altizer et al. 2013) and anthropogenic land use entails mosquito habitat changes at multiple scales from regional habitat suitability to microhabitats, such that artificial water bodies in more urbanised environments may offer novel and resilient breeding environments (Rose et al. 2020). Environmental changes also modify vector phenotypes and the complex interactions that determine host choice. Nutrient or temperature-induced stress can change the frequency and selectivity of mosquito host seeking behaviour, as has been evidenced in laboratory studies (reviewed in Carvajal-Lago et al. 2021). To better understand these interaction dynamics, we can make use of existing studies of mosquitoes feeding in the wild.

There is a considerable body of work that looks at the dietary choices of mosquitoes in situ that stretches to over a hundred years, launched when (King and Bull 1923) published a study that used a molecular antigen-binding technique (precipitin) to determine the origins of blood-meals recovered from guts of engorged female mosquitos captured from the wild. Numerous

studies have since used various molecular techniques to identify what species mosquitoes are feeding on. Some of these are very targeted in host detection (identifying one species such as human or cattle), whereas other molecular methods can identify a broad range of hosts (Apperson et al. 2002; Kent 2009; Mukabana et al. 2002; Takken and Verhulst 2013). The advantages of using such broad approaches, typically referred to as ‘universal’, is that they do not presuppose the identity of the blood-meal host of the mosquitoes, and allow more accurate identification of host range and forage ratios (Alcaide et al. 2009; Ferraguti et al. 2021; Hernández-Andrade et al. 2019; Melgarejo-Colmenares et al. 2022). Universal approaches have also uncovered exciting new information into the unexpected diversity of mosquito host ranges including the importance of amphibians, reptiles, fish and even some invertebrates as hosts (Börstler et al. 2016; Harrington et al. 2014; Molaei et al. 2006; Reeves and Burkett-Cadena 2022). Universal studies constitute a rather small percentage of the host diet studies conducted thus far (especially for taxa such as *An. funestus*, *An. gambiae* and *An. arabiensis*) but are expanding our insights into the plasticity of host selection and have the potential to inform us of the local transmission risk of vector-transmitted pathogens (Hernández-Andrade et al. 2019).

Most meta-analyses on mosquito feeding patterns conducted so far have combined universal and species-specific methods that target expected/known hosts (especially humans and livestock) and risk missing out on wider host shifts that might be expected under global change scenarios (Cebrián-Camisón et al. 2020; Chaves et al. 2010; Stephenson et al. 2019). Here, we compile studies based on universal PCR methods to explore how gradients in host densities, climate, and land use influences mosquito blood-feeding patterns. This quantitative meta-analysis focuses on compositional data compiled on the realised host utilisation of six common mosquito species that pose zoonotic disease risks and exhibit various degrees of host feeding fidelity. Our approach, although correlative (rather than mechanistic), provides new insights into vector feeding behaviour and, consequently, the factors driving vector-mediated disease transmission in a changing global environment.

2 | Material and Methods

2.1 | Focal Species and Blood-Meal Data Extraction

We focused on six mosquito species: *Aedes aegypti*, *Aedes albopictus*, *Anopheles gambiae*, *Anopheles funestus*, *Culex pipiens* s.l., and *Culex quinquefasciatus*. These are of considerable interest as vectors of infectious diseases and feed to various extents on humans (Chaves et al. 2010; Takken and Verhulst 2013). We conducted a systematic literature search to collect empirical evidence of mosquitos feeding on different blood-meal hosts under different environmental conditions throughout their geographic ranges. Our literature search was conducted between July and September 2023 on the Web-of-Science database (Clarivate Analytics Ltd) and involved two steps. The first used the phrase ‘bloodmeal*’ OR ‘blood meal’ OR ‘blood-meal’ and the names (including synonyms) of the focal mosquito species. If the search returned > 200 hits for any of the species, then additional ‘methods’ search terms

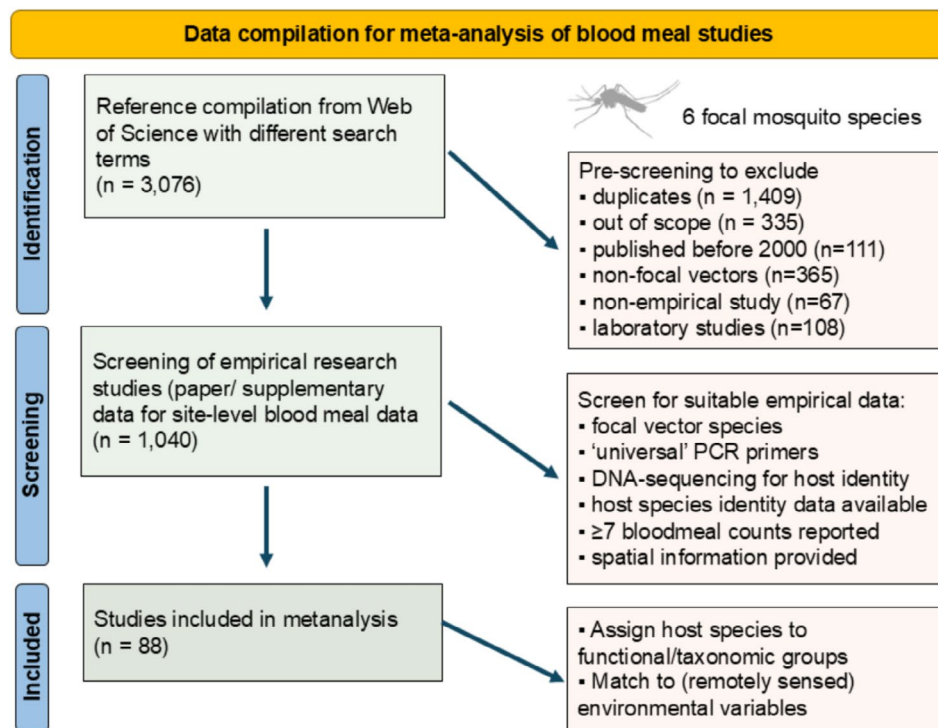


FIGURE 1 | Flow chart for identification and selection of studies included in the meta-analysis on blood-meal counts from the six focal mosquito species.

(Table S1) were added to narrow down the number of papers. The second search used publications of popular PCR primer sets as a search term (Table S1). If the search returned >200 hits, then the number of linked articles was refined using the search term 'mosquito*' (Table S1). These searches yielded an initial list of 3076 references. After pre-screening, we identified 1040 published research articles (Figure 1), which were then further filtered based on the following criteria:

1. The arthropod vector was one of six focal species.
2. PCR primers used to identify blood-meal hosts were 'universal' (for vertebrates/mammals/birds) and not targeted to particular species (Table S1).
3. Either Sanger (dideoxy) sequencing or high-throughput DNA sequencing is used at some point to confirm host identity.
4. Host species identity data was available.
5. For any given mosquito species and sampling site, there must be ≥7 bloodmeals (corresponding to an ~80% chance of detecting an uncommon host present in ~20% of samples).
6. Spatial information was provided as either geographical coordinates or salient location names and sampling sites were not pooled over spatial extents > 50 km in diameter.

This resulted in a total of 88 studies that covered 120 different sites ('s', some studies provided data for multiple sites, see Figure S1 for location map, Table S4 for references) with data collected between 2000 and 2019 (74 of these studies were conducted outdoors and covered 100 sites). From these we generated a database of geographical coordinates, counts of

blood-meals and the host species (resolved to smallest taxonomic unit) for each mosquito species. Counts of blood-meal origins were assigned to both hosts in the 16 studies that recorded mosquitos feeding on multiple hosts (e.g., 'human + cow'). All extracted scientific species names were checked and aligned to the Integrated Taxonomic Information System (ITIS) database, using the *taxize* 0.9.1 R package (Chamberlain and Szöcs 2013).

For sites with missing geographical coordinates, we identified coordinates for location names at the smallest available administrative units using various online maps and search engines. If multiple nearby trap locations were recorded from the same region within a study (e.g., multiple trap locations with coordinates within a single city or forest aggregation), we computed the average of coordinates as the corresponding site for our analyses.

2.2 | Host Functional and Taxonomic Groups

Host functional groups were derived and consisted of: (f1) 'Human', (f2) 'Mammal—pets' (cat, dog, rabbits if specified as domestic), (f3) 'Mammal—farmed' (cattle, buffalo, donkey, goat, horse, sheep, pigs unless explicitly recorded as wild), (f4) 'Mammal—wild' (all other mammalian species), (f5) 'Bird—farmed' (commensal chickens, goose, ducks if recorded as farmed animals), and (f6) 'Bird—wild' (all free-roaming wild birds). All other origins were grouped as 'other' (including zoo animals, caged ornamental birds, reptiles, and amphibians; none of these groups included sufficient data to warrant considering them as independent groups in statistical analyses). We also grouped host species in taxonomic groups using different taxonomic levels according to 4% overall sample origins thresholds. These were 'Homo', (t2) 'Gallus', (t3) 'Canidae', (t5) 'Felidae', (t6) 'Bovidae', (t7) 'Mammalia' (others, not included

in groups at finer taxonomic resolution), (t8) 'Cardinalidae', (t9) 'Columbidae', (t10) 'Corvidae', (t11) 'Turdidae', (t12) 'Aves' (others, not included in any group at finer taxonomic resolution), (t13) 'others' (amphibian and reptiles).

The total number of recorded blood-meals per vector and the number of sites (s) were: *Ae. aegypti*: 1803 ($s=18$), *Ae. albopictus*: 1769 ($s=22$); *An. funestus*: 308 ($s=5$); *An. gambiae*: 631 ($s=15$); *Cx. pipiens* complex: 11,172 ($s=87$) with *Cx. pipiens* s.l.: 4886 ($s=48$); *Cx. quinquefasciatus*: 5449 ($s=36$). Out of the *Cx. pipiens* s.l. samples, 1061 ($s=8$) were more specifically assigned to the *Cx. pipiens* f. *pipiens* biotype and 45 ($s=4$) to the *Cx. pipiens* f. *molestus* biotype.

2.3 | Environmental Variables

We systematically quantified landscape features of the environment surrounding mosquito survey sites by selecting nine environmental predictor variables from a larger set of environmental variables (by ordination of land cover variables and by removing correlated variables with $r \geq 0.7$, Table S2, Figures S2 and S3). We used 3-km buffers for characterising environmental features around the centre of mosquito survey sites; while this spatial extent likely covers a larger area than mosquito local foraging ranges, the remotely generated environmental features are assumed to be representative following comparison with available information on local conditions described in some studies.

Specifically, the selected environmental predictor variables were: (x.1) 'annual mean temperature' (bio1), (x.2) 'annual rainfall' (bio12), and (x.3) 'rainfall of driest month' (bio14). These three climate variables were selected to cover three key aspects of large scale climate gradients and were obtained from the WorldClim database of gridded climate data at a 0.01° resolution (Fick and Hijmans 2017, <http://worldclim.org/version2>). Land use type classification were based on the yearly layers of the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type (MCD12Q1 version 6.1, <https://lpdaac.usgs.gov/products/mcd12q1v006/>); land cover categories were 'urban', 'water bodies', 'cropland', 'grassland', 'shrubland', and 'tree cover'. We quantified overall vegetation density based on the normalised difference vegetation index (NDVI, computed as mean and one SD of all repeated measures within the corresponding year) from the MODIS MOD13Q1 layer (version 6.1, <https://lpdaac.usgs.gov/products/mod13q1v006/>). Since MODIS data were only available from 2001 onwards, we characterised sites surveyed for mosquitoes in 2000 with the MODIS data from 2001. As land cover variables are typically highly correlated, we used principal component analysis (PCA) to generate two principal components. The first was (x.4) 'urbanisation' (PC1), where increasing values represent mainly increasing urban land cover and decreasing NDVI. PC1 explained 30% of the variation in land cover variables across sites. The second was (x.5) 'natural vegetation' (PC2) where increasing values mainly represent increasing tree and grassland cover and decreasing cropland and explained 21% of land cover variation across sites (Figure S5, Table S3). Next, (x.6) 'human population density' was based on the Gridded Population of the World version 4.0 dataset (GPW4) (Center for International Earth Science Information Network 2018). The (x.7) 'ruminant livestock' density pooled local numbers of sheep, goats, cattle, and buffalo and (x.8)

'poultry density' pooled local numbers of chickens and ducks using the Gridded Livestock of the World (GLW3) in 2010 at approximately 10 km² resolution (Gilbert et al. 2018). Finally, we included (x.9) latitude as an environmental predictor variable to account for the large-scale variation in biological diversity and other factors along this prominent gradient. We considered studies that were conducted indoors (or indoors and outdoors) for reporting host ranges only (Section 3.1), while we excluded indoor studies from the statistical analysis of feeding patterns (Sections 3.2. and 3.3; see Supporting Information for equivalent that included indoor studies).

2.4 | Statistical Analysis

Our key aims were to explore variation in mosquito host utilisation across sites and to identify shifts in host selection associated with environmental predictor variables for each of six focal mosquito species. We implemented the model described below through a Bayesian workflow with different model versions fitted to simulated and empirical data for optimisation. The final model was fitted separately for each mosquito species (and biotype), but for *Culex* mosquitoes, we additionally ran the model for the '*Cx. pipiens* complex' as a whole (to account for studies that did not differentiate between members of the complex).

Dirichlet regression was used because it allows us to model the relationship between the parameters representing the proportions of distinct host categories/taxa and environmental predictor variables, resembling data structures commonly analysed in diet and microbiome compositional studies (Douma and Weedon 2019). We combined the Dirichlet model in a hierarchical multivariate modelling framework with a Binomial model of the counts of blood-meals originating from different host groups to account for uncertainty in proportions arising from small and unequal sample sizes. We modelled the proportions of blood-meals $\theta_{g,s}$ that originated from any host group g out of $G=7$ at site s based on the number of mosquitoes $n_{g,s}$ with blood-meals reported from that group and the total number of mosquitoes N_s for which blood-meals were identified at that site as:

$$n_{g,s} \sim \text{Binomial}(N_s, \theta_{g,s}).$$

Here, $\theta_{g,s}$ is assumed to be a G -simplex Q_s of the interlaced feeding proportions of the four different host groups Q_s subject to the constraint that proportions sum to one.

We therefore modelled

$$Q_s \sim \text{Dirichlet}(M_s)$$

whereby the vector M_s comprises a normalised exponential function of the four joint linear predictors terms $\mu_{g,s}$:

$$\mu_{g,s} = a_g + B_g X,$$

where a_g is the group-specific intercept, X is a matrix of the environmental predictor variables described above and B is a vector of coefficient estimates for the predictors denoted in the matrix X .

We fitted models for parameter estimation in Stan (Carpenter et al. 2017; Stan Development Team 2023) via the *CmdStanr* interface (<https://mc-stan.org/cmdstanr/>). Stan's probabilistic modelling framework based on Hamiltonian Monte Carlo enables efficient Bayesian workflows for model specification and diagnostics and exploring the uncertainty in estimates for challenging problems (Betancourt 2017). Using this sampling approach, we randomly imputed missing covariate data (in GLW3 and GPW4) by averaging over the uncertainty in their values (randomly drawn from $Normal(\mu=0, \sigma=1)$ distributions for variables scaled to have variance equal to 1).

Since feature selection and parameter estimation in multiple regression models can be challenged by high-dimensional feature space for sparse data (Piironen et al. 2020) we tested $Normal(\mu=0, \sigma=1)$, $Student.t(v=3, \mu=0, \sigma=1)$, and regularised horseshoe (RHS) priors with various global and local shrinkage priors (Piironen and Vehtari 2017) for the coefficient estimates of B . We then iteratively fitted the model to simulated and real data with each of four chains sampling 1000 posterior draws after warmups of 10,000 iterations for optimising prior specifications. We used trace plots and rank normalised split- \hat{R} for convergence diagnostics and computed the sum of squared residuals for comparing model fits with different priors. We scaled all covariates (centred around zero and variance equal to one) for parameter estimation. Model fit was similar for all three prior specifications, while the RHS priors shrunk more posterior distributions towards zero; we therefore reported results from models with RHS only as the most conservative approach. We assumed those coefficients for which estimates did not overlap zero based on 90% highest posterior density credible intervals (CI) represent meaningful trends and report these as the odds ratios (OR) from the scaled covariates. We used posterior estimates of the model intercepts a_g to draw Dirichlet posterior estimates of the 'global' average feeding proportions Ψ_g and interpreted upper/lower CIs as maximum/minimum feeding proportions on different host groups. We calculated species richness estimates based on Chao's species richness estimator and rarefaction curves based on Hill numbers in the packages iNEXT (Hsieh et al. 2016), using the cumulative number of blood-meal counts from different host species for *Aedes* and *Culex* species (the available data were insufficient to draw robust rarefaction curves for *Anopheles* species). For species richness estimates, we also considered studies with < 7 total blood-meals reported (totalling $n = 101$ studies) in order to maximise the evidence of known host ranges. We used R v4.3.0 (R Core Team 2023) for all analyses and graphics.

3 | Results

3.1 | Host Ranges of *Culex* Are Considerably Larger Than for *Aedes* Species

Culex quinquefasciatus had the largest host range of 170 reported host species from 70 families (including 130 bird and 33 mammalian species), followed by *Cx. pipiens* s.l. which had 138 host species from 62 different families (including 115 bird and 20 mammalian species) (Table 1). A total of 25 host species from 21 families (including 9 bird and 15 mammalian species)

were reported for *Aedes aegypti* and 29 host species from 25 families (including 7 bird and 19 mammalian species) for *Ae. albopictus*. *Anopheles funestus* had 7 host species (including the wild bird *Crinifer piscator*) and *An. gambiae* had 8 host species reported (including domestic chicken and the rodent *Thryonomys swinderianus*). Host species richness estimates were 242 (95% CI: 207–309) for *Cx. quinquefasciatus*, 225 (95% CI: 179–321) *Cx. pipiens* s.l., and only 28 (95% CI: 24–45) for *Ae. aegypti* and 37 (95% CI: 30–65) for *Ae. albopictus*, respectively (Table 1). Rarefaction curves indicate distinct host-species discovery rates for the genera *Aedes* and *Culex* (Figure 2). The limited sample sizes of *Anopheles* blood-meals precluded the robust application of species richness estimators.

3.2 | Global Scale Feeding Patterns

Across all sites included in the meta-analysis the feeding patterns of all focal mosquito species varied in their utilisation of human, other mammalian, and avian hosts (and occasionally amphibians or reptiles—Figure 3). The 'global' average proportions of blood-meals from humans, according to global Ψ_{human} estimates, were highest for *Anopheles gambiae* (Ψ_{human} CI of 64%–93%) and *Aedes aegypti* (Ψ_{human} CI of 40%–84%). The large credible intervals in these estimates were partly explained by the strong variation in feeding patterns across outdoor sites. For *Ae. aegypti*, for example, > 70% of blood-meals originated from humans at 4 out of 14 sites (according to θ_{human} lower CIs) but < 40% of blood-meals originated from humans at another 3 sites (according to θ_{human} upper CIs, Figure 4). The *Culex* species in this study were clearly identified as ornithophilic and fed frequently on birds but less often on humans (all Ψ_{human} CIs 1%–60%) than the *Aedes* and *Anopheles* species (Figure 3).

Functional group utilisation clearly differed among mosquito genera (Figure 4). In most cases, *Aedes* fed predominantly on humans but also fed frequently on mammalian pets, including

TABLE 1 | The number of recorded host species (host range), host families and Chao species richness estimations for the six focal mosquito species based on blood-meal records extracted from the 86 studies included in this meta-analysis (based on 'universal' PCR primers for vertebrates/mammals/birds and were not targeted to particular species).

Species	Host range	Host families	Chao estimate
<i>Culex quinquefasciatus</i>	170	70	242 (207–309)
<i>Culex pipiens</i> s.l.	138	62	225 (179–321)
<i>Aedes aegypti</i>	25	21	25 (26–45)
<i>Aedes albopictus</i>	29	25	29 (31–65)
<i>Anopheles funestus</i>	7	5	7 (7–29)
<i>Anopheles gambiae</i>	8	6	8 (8–9)

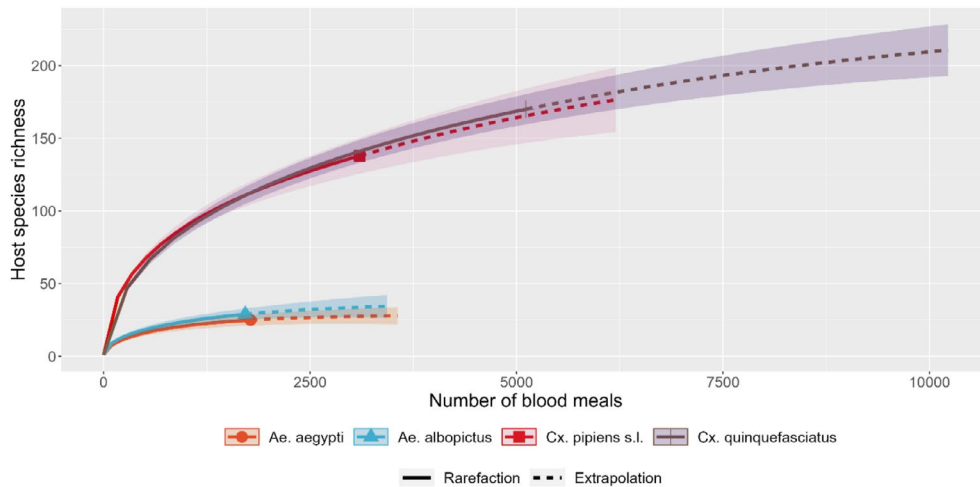


FIGURE 2 | Rarefied host species richness estimates and predictions based on the cumulative number of host species recorded in blood-meal studies for common mosquito species. Estimates (lines) and 95% confidence intervals (shaded areas) are based on Hill numbers. Solid lines refer to the rarefied samples, dashed lines to extrapolated predictions of the same number of samples. Abbreviated genera names correspond to *Aedes* and *Culex*.

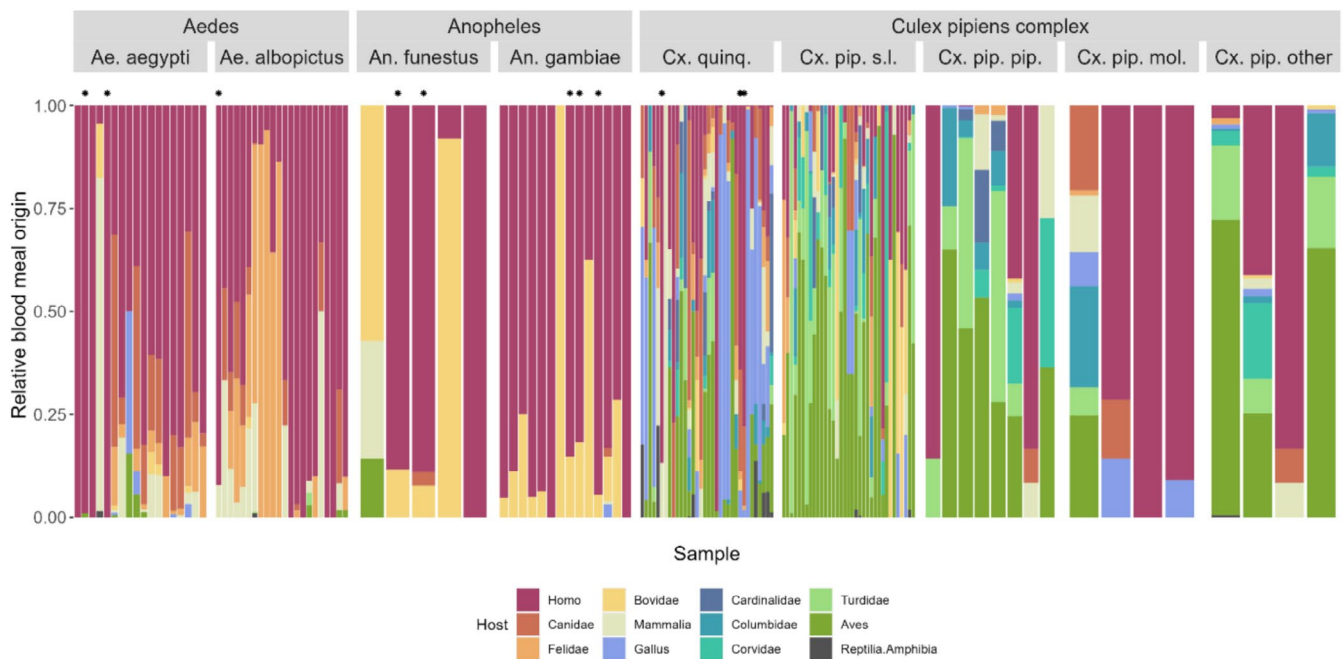


FIGURE 3 | Taxonomic composition of mosquito blood-meal origins from vertebrate hosts plotted as the relative proportion of blood-meals recorded from each host groups at different sampling sites for the focal mosquito species. The plot is faceted by mosquito species with *Aedes* and *Anopheles* species on the left and members of the *Culex pipiens* complex on the right. The latter is comprised of *Cx. quinquefasciatus* and *Cx. pipiens* sensu lato, which is divided into the biotypes *Cx. pipiens f. molestus* and *Cx. pipiens f. pipiens* where known. The 'Cx. pip. other' category refers to other specimens that are part of the complex or, more often, studies where members of the complex could not be determined. Asterisks mark those samples from studies conducted indoors (excluded from analysis of feeding patterns).

Canidae and Felidae ($\geq 30\%$ of blood-meals originated from mammalian pets at 3 out of 14 and 6 out of 21 outdoor study sites for *Ae. aegypti* and *Ae. albopictus*, respectively) and to a lesser extent wild mammals. *Aedes* fed occasionally on wild birds or poultry. *Anopheles* species, in turn, also deviated occasionally from feeding on humans and shifted towards feeding on farmed mammals, including Bovidae (Figure 4).

Culex species fed on a broad range of bird and mammal hosts, including wild, farmed, and pet species, with the relative use of these host groups varying considerably across sites (Figure 4). *Culex quinquefasciatus* fed frequently on farmed birds including domestic chicken *Gallus* ($\geq 60\%$ meals from farmed birds at 5 out of 28 outdoor sites), whereas *Cx. pipiens* s.l. predominantly fed less on farmed birds ($\leq 44\%$ at all

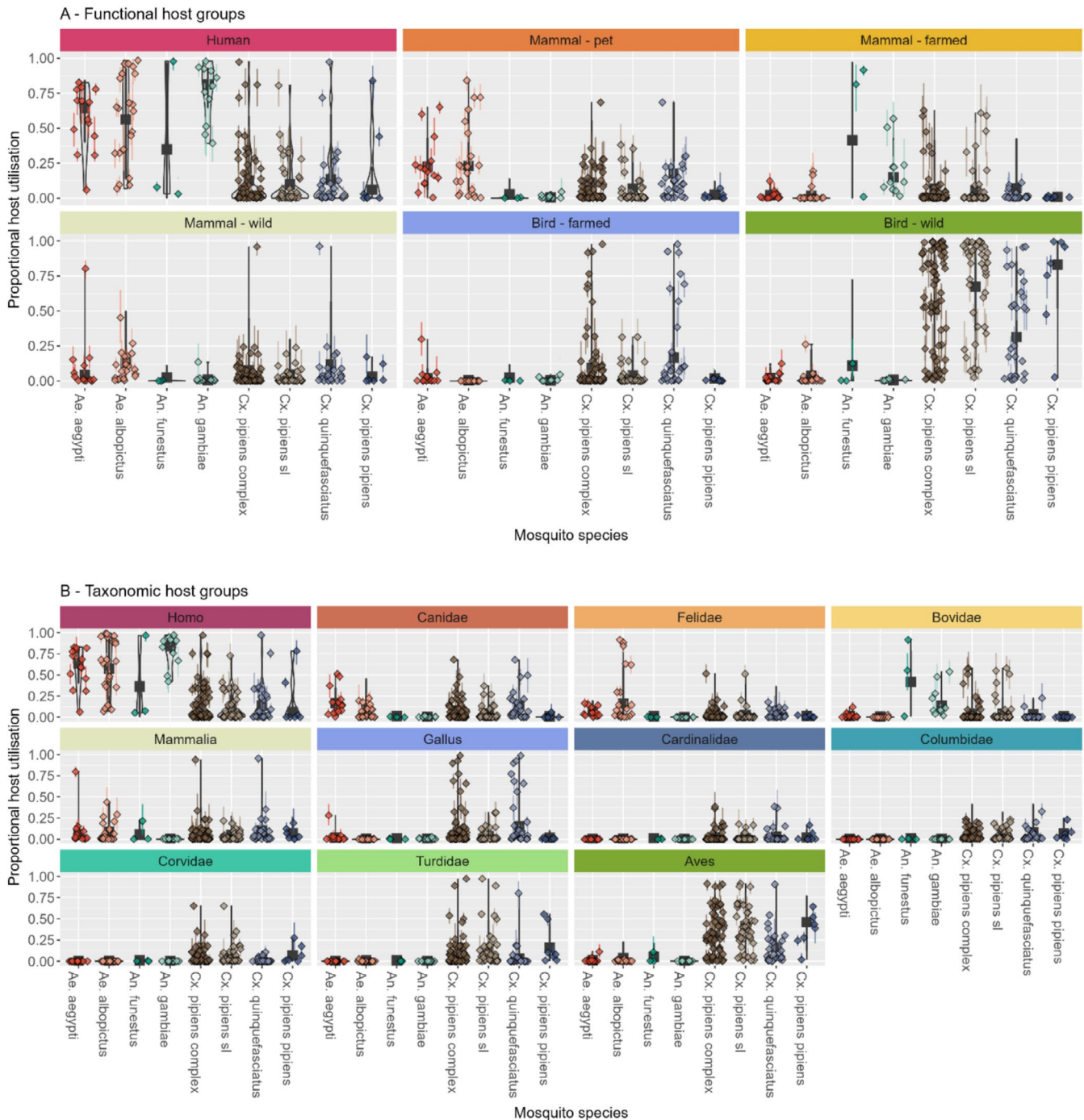


FIGURE 4 | Variation in host feeding patterns of six common mosquito species reported from blood-meal studies at different sites (outdoor sites, only). Coloured point clusters within violins show the relative host utilisation frequencies of (A) different functional host groups (humans, domestic and wildlife species) and (B) different taxonomic host groups (genera/families/classes of mammals and birds according to relative abundance in the overall data set) at different study sites, with vertical error bars around points representing 95% highest posterior credible intervals of the probabilistic frequencies linked to data observations. Black squares and error bars represent the 'average' posterior estimates based on a hierarchical hyperprior modelling approach. Abbreviated genera names correspond to *Aedes*, *Anopheles* and *Culex*. *Culex. pipiens* s.l. and *Cx. quinquefasciatus* samples were also combined into *Cx. pipiens complex* and we also conducted analysis for *Cx. pipiens* f. *pipiens* and *Cx. pipiens* f. *molestus* biotypes.

41 study outdoors sites with records for this species Figure 4). *Culex pipiens* f. *pipiens* fed $\geq 60\%$ on wild birds at 4 out of 5 outdoor sites and $\geq 60\%$ on humans at another outdoor site. Since the data for *Cx. pipiens* f. *molestus* were all conducted indoors, no valid comparison among the two biotypes was possible.

3.3 | Shifts in Feeding Patterns Across Environmental Gradients

We found some signals of environmental conditions predicting changes in feeding patterns across sites (Figure 5, Table S5), despite the overall sparse data for some species. For



FIGURE 5 | Relative effects of different environmental predictors on the shifts in mosquito blood-meal origin from different functional (panel A) and taxonomic (panel B) host groups. Points and error bars represent the scaled coefficient estimates (mean and 90% CI credible intervals) from models of variation in relative host utilisation frequencies for humans (red), mammalian pets (blue), mammalian wildlife (green) and wild birds (dark blue), whereby only estimates not overlapping one are displayed in thick-lined colour and those overlapping one in thin-lined grey (including all host groups for which no relationship were evidenced). Abbreviated genera names correspond to *Aedes*, *Anopheles* and *Culex*. *Culex pipiens* s.l. and *Cx. quinquefasciatus* samples were also combined into *Cx. pipiens complex* and we also conducted analysis for *Cx. pipiens f. pipiens* and *Cx. pipiens f. molestus* biotypes.

Ae. aegypti, higher proportions of blood-meals originated from wild mammals with higher ruminant density (OR: 1.27–6.82), and higher proportions of blood-meals originated from mammalian pets with higher mean temperatures (OR: 1.02–3.82). For *An. gambiae*, higher proportions of blood-meals originated from humans at higher latitude (OR: 1.22–4.51). For

mosquitoes from the *Cx. pipiens* complex, smaller proportions of blood-meals originated from wild birds with higher mean temperatures (OR: 0.49–0.87). For *Cx. pipiens pipiens*, higher proportions of blood-meals originated from wild birds with increasing natural vegetation (PC2, OR: 1.01–12.1). The analysis with taxonomically refined grouping of hosts confirmed

that with higher ruminant density, more blood-meals of *Ae. aegypti* originated from wild mammals (OR: 1.38–6.27). The taxonomic grouping of hosts revealed also some different relationships, in that with higher ruminant density, more blood-meals of mosquitoes from the *Cx. pipiens* complex originated from Bovidae (OR: 1.14–2.32). With increasing precipitation in the driest months, mosquitoes from the *Cx. pipiens* complex fed more often on Cardinalidae (OR: 1.09–2.75). With higher temperatures, more blood-meals of mosquitoes from the *Cx. pipiens* complex originated from domestic chicken (OR: 1.1–2.27) but less originated from Turdidae (OR: 0.31–0.73).

Some of these correlations were similar when adding the indoor studies to the analysis, but the latitude effect on feeding patterns of *Ae. aegypti*, and the urban-suburban space effect of feeding patterns on *Cx. pipiens pipiens* disappeared when including indoor studies in the analysis (Figure S4). Also, including indoor studies in the analysis suggested additional effects, with more feeding of *Ae. aegypti* on humans with higher poultry density, less feeding on wild birds, and more feeding on humans of *Cx. pipiens* s.l. with higher ruminant density, and less feeding of *Cx. quinquefasciatus* on Turdidae with increasing temperature (Figure S4). These findings highlight the uncertainty introduced by potential sampling biases in the currently available data.

4 | Discussion

By compiling globally available evidence of host feeding patterns for six prominent disease-vectoring mosquitoes, with a focus on blood-meal studies that used universal molecular methods, we present new host range estimates that show higher host discovery rates than previously anticipated. In addition, we provide first insights into the plasticity in host feeding patterns in response to changes in host density and environmental conditions across regions.

4.1 | Host Ranges Revealed in Global Data

Our meta-analysis revealed a total of 341 host species across all six focal mosquito species (avian: 267, mammal: 60, reptile: 13, amphibian: 1). The discovery of novel hosts per sampling effort (Figure 2) was more than double the rate found in other meta-analyses (Bellekom et al. 2021). Focusing on papers that used ‘universal’ detection methods, we reduced the bias that is inherent to species richness estimates and species accumulation curves from molecular methods that are not capable to detect full host ranges (i.e., methods that limit the number of hosts discoverable will always tend to plateau before methods that don’t have such limits). This focus not only provides a more comprehensive picture of host ranges but also enhances our understanding of mosquito host selection. This is because universal methods are less likely to underestimate the actual range of hosts utilised in the wild, making shifts in host selection from one host species or group to another more detectable. The greatest host richness was witnessed in *Cx. quinquefasciatus* and *Cx. pipiens* s.l. and, which had host range estimates of 207–309 and 179–321 host species respectively. *Ae. aegypti* and *Ae. albopictus* were also found to feed on more host species than typically anticipated from regional studies (host range estimates of 26–45

and 31–65 species respectively), though their host niche breaths were considerably lower than for the two *Culex* species. This accords with previous studies (Martinet et al. 2019) and most probably reflects the higher diversity of bird than mammalian species across global habitats (Barrowclough et al. 2016), which may enable mostly ornithophilic *Culex* species to exploit a broader host spectrum than the mostly mammalophilic *Aedes* species. For *Anopheles* species, the host range estimates were relatively small (7–29 for *An. funestus* and 8–9 for *An. gambiae*), while we anticipate that the limited number of total blood-meals counts and sites surveyed with universal primers for *Anopheles* species could mean that these estimates were well below their true but unknown fundamental host ranges. Overall, these host range estimates, based on a compiled ‘global’ dataset, demonstrate that the fundamental host range of the focal mosquito species may be considerably larger than anticipated based on regionally realised host ranges. This highlights the need for future sampling across diverse habitats and zoogeographical regions to obtain a more comprehensive understanding of host ranges and host specificity under variable natural conditions.

4.2 | The Innate vs. Realised Host Niche

Many studies have established that mosquito species have innate host preferences (Lyimo and Ferguson 2009; Main et al. 2016) that vary from strong to weak (e.g., Mayagaya et al. 2015). Although variations can be resolved with laboratory-based behavioural studies, the real-world variation in regional host species assemblages and environmental contingencies is immense (Fikrig and Harrington 2021), which is why we also need to look at field studies on realised feeding patterns in natural environments. The observed feeding patterns of the examined mosquito species were mostly as expected, e.g., *Anopheles* fed predominantly on mammals. However, there are a few reports of *Anopheles* feeding also on birds (Diallo et al. 2013; Ogola et al. 2017; Omondi et al. 2015). Notably, these studies looked at more diverse landscapes and host species assemblages than had previously been considered for this genus, showing that with only a few universal primers studies available for *Anopheles* blood-meals, there is more to discover about their diet composition. For *Aedes*, host composition varies considerably across sites with blood-meals sourced from both humans and non-human mammals (Figure 2), which is broadly consistent with previous observations (e.g., Little et al. 2022). This reinforces the caution recommended in assuming *Aedes* species are highly anthropophilic (Bellekom et al. 2021; Ponlawat and Harrington 2005). Notably, we found that a few host taxa dominate, with humans and cats constituting large proportions of hosts of *Ae. albopictus* (as reported at the regional level by Little et al. 2021; Ogola et al. 2017), whereas *Ae. aegypti* studies predominantly reported meals on humans and, to a lesser extent, dogs (e.g., Estrada-Franco et al. 2021; Hopken et al. 2021). We found no statistical evidence for the recently debated assumption that *Cx. pipiens* f. *molestus* is mammalophilic and exhibits a distinct host preference from the ornithophilic feeding of *Cx. pipiens* f. *pipiens* (Börstler et al. 2016; Farajollahi et al. 2011; Fonseca et al. 2004). Besides the small numbers of only eight and four sites for which these two biotypes were identified, all data from the *molestus* biotype were from indoor studies and did not allow a systematic comparison of outdoor studies that allow us to better

distinguish host availability from other drivers of feeding patterns (Martínez-de la Puente et al. 2016).

4.3 | Plasticity in Host Feeding Patterns Associations With Environmental Conditions

Compiling blood-meal evidence from a range of studies, we explored the variation in host-feeding patterns of six mosquito species in response to changes in standardised global environmental data as landscape-scale predictor variables in a hierarchical Dirichlet regression model. There were several cases where the feeding selection of mosquitoes on a given host group was correlated with temperature, precipitation, or the density of another vertebrate group, latitude, or vegetation cover (Figure 5). With increasing ruminant density, host selection of *Culex* species (*Cx. pipiens* complex) shifted towards Bovidae, whereas, with increasing ruminant density, host selection of *Ae. aegypti* shifted towards wild mammals. This could be due to landscapes with higher ruminant densities indirectly creating landscape-scale conditions that are favourable for a selected subset of wild or commensal mammals to proliferate, such that correlations of feeding patterns with livestock density do not reflect the true underlying mechanism even if livestock density serves as a predictor variable in correlative models (in our dataset, relatively high feeding rates of *Ae. aegypti* on wild mammals involved unspecified bats and the hyrax *Procavia capensis* in mixed landscapes of high anthropogenic impact in Kenya; Chepkorir et al. 2018; Fitzpatrick et al. 2019).

Mean annual temperature, which spatially covaries with distance to the equator across regions, was positively correlated with *Ae. aegypti* feeding on mammalian pets. For *Culex* mosquitoes, we found temperature to inversely correlate with *Cx. pipiens* s.l. feeding on species from the thrush genera *Turdus*, whereas with increasing temperature, *Culex* feeding (*Culex pipiens* complex) increased on the domestic chicken genus *Gallus*. Further climate-related shifts in feeding patterns were indicated by an increase in *Culex* feeding (*Culex pipiens* complex) on Cardinalidae with increasing precipitation in the driest month. Closer inspection of the underlying studies revealed that for *Culex* species, a plausible argument for this relationship is that feeding on thrushes occurred in geographic regions with more pronounced climate seasonality (with a lower mean annual temperature) and sampling in these studies were predominantly conducted during the summer when migratory thrush species were present (Hamer et al. 2009; Komar et al. 2018; Kothera et al. 2020). Unfortunately, the studies we analysed often pooled data across dates, and due to the sparse data situation, we were not able to more precisely model mosquito feeding behaviour as a function of season and related shifts in the relative availability of migratory bird species. The climate-related shift of *Ae. aegypti* feeding on mammalian pets lacks a plausible explanation without further detailed research. However, in line with our overall findings, we propose that this shift towards increased feeding on pets could be linked to a reduced availability of alternative wildlife hosts. Alternatively, it might be driven by variations in the availability of mammalian pets, or by differences in how pets are kept (e.g., indoors versus outdoors) and their changing exposure to mosquitoes across regions; these hypotheses, however, await empirical testing. Likewise the climate-induced

shift in *Culex* feeding on chicken, lacks a plausible explanation without further research, especially as this effect was not found for any particular species such as *Cx. quinquefasciatus* despite its frequent feeding on chickens (Hopken et al. 2021; Kading et al. 2013).

In terms of land-use, induced shifts in feeding patterns, we found the feeding of *Cx. pipiens pipiens* to shift towards more feeding on wild birds with increasing natural vegetation (opposed to higher land cover with agricultural areas, as represented by PC2). *Cx. pipiens* is considered to be highly abundant in urban areas (Figueroa et al. 2022; Gutiérrez-López et al. 2025), and at a closer inspection of the underlying studies, we found the high feeding of *Cx. pipiens pipiens* on wild birds to take place in temperate, mixed landscapes (Brugman et al. 2017; Kothera et al. 2020), where parks or remnant forest patches could be possible 'natural' vegetation to support the feeding on wild birds. Thrushes, for example, such as the American robin, are common in suburban parks and gardens where they have high reproductive success and survival (Evans et al. 2015; Morneau et al. 1995). *Anopheles gambiae* feeding rates were higher on humans with higher latitude—this is more difficult to explain and could be a sampling artefact or a proxy for some unknown regional condition, given that available data from outdoor sampling were restricted to a few locations from Guinea, Kenya, and Mali only (Figure S1).

In line with previous forage ratio studies, these patterns suggest that host choice is not necessarily a simple function of host availability per se, but contingent on other drivers (Ricetti et al. 2022; Yan et al. 2021). Overall, the found relationships between feeding patterns and environmental predictors demonstrate that even if shifts in feeding patterns may be to some extent predictable by environmental conditions, considerably more future research is necessary to more thoroughly understand how such shifts are either linked to differences in host availability and exposure, or other factors such as the availability of mosquito breeding grounds or factors shaping mosquito behaviour.

Potential biases in observed feeding preferences may also stem from study design and the selection of study sites. For instance, studies are more likely to be conducted in accessible agricultural or urban areas for convenience, while natural environments may be underrepresented due to logistical constraints. If sampling is biased towards more accessible anthropogenic landscapes, conclusions regarding mosquito feeding behaviour could be skewed towards host species from these areas, with wildlife species from remote, forested regions being underrepresented.

While any of these correlations may help to predict shifts in feeding patterns, they do not allow rigorous insights into the underlying mechanisms, and we anticipate that beside more data for increasing predictive power, different kinds of experimental studies would be necessary to understand the true drivers of shifting feeding patterns in variable environments.

4.4 | Areas for Future Method/Data Developments

This pioneering study was an opportunity to explore the current state of evidence of host diversity and feeding patterns of six

prominent disease-vectoring mosquito species. Although there are clear limitations regarding sample size and data quality, it identifies areas that need to be addressed going forward. A key feature of this study is the use of global environmental indicators to replace the site-specific environmental characterisation derived from locally conducted mosquito diet studies, which were inconsistently reported and insufficient for generating meaningful local predictor variables. The climate and land use data used were collected at a 0.01-degree resolution (~1.1 km) and averaged within a 3 km radius of each sample site. While this is highly resolved at the global scale, it is relatively coarse if we consider the scale at which mosquitoes generally live (Martínez-de la Puente et al. 2020; Moore and Brown 2022) even though some mosquitoes may disperse 10–100 km (Huestis et al. 2019). For domestic livestock density, we were able to use data and projections from Gilbert et al. (2018) and the GPW4 for human density (Center for International Earth Science Information Network 2018); however, similar data for wild animal and pet densities as predictor variables was not available.

It is unfortunate that seasonality or more highly resolved land use change information could not be included in our models. These impact host availability because of migration, natural succession, or habitat suitability, while mosquitoes may seasonally switch from feeding on birds to mammals in cooler months (first observed in Tempelis et al. 1965). Season and local landscape features also impact mosquito physiology and behaviour, with host seeking behaviour being impacted by plant availability (nutritious sugar sources important for mosquito development and behaviour), rainfall, temperature, and daylight hours (Carvajal-Lago et al. 2021; Farajollahi et al. 2011). With the increasing availability of more studies and systematically reported meta-data, it will also be important to consider study details that may introduce biases in the mosquito sampling process, including, for example, indoor/outdoor sampling (see Figure S3), trapping methods, the proximity of livestock farms and zoos, and local-scale habitat features.

4.5 | Limitations in Study Methods

We omitted many studies because of our strict inclusion criteria. Notably, our literature search returned 1040 publications since 2000, which were manually checked and only 88 met our criteria. Most exclusions were because of our criteria that studies use ‘universal’ molecular methods to detect hosts. The biggest impact of this was on *Anopheles funestus* and *Anopheles gambiae* for which we recovered only 14 studies that used universal methods, but a considerable number of studies used ELISA ($n=44$), highly targeted PCR methods ($n=9$), or a precipitin test ($n=1$). The ‘loss’ of many studies in our data compilation was offset by the advantage that methods which do not make a priori assumptions about host range provided us with a deeper, less biased understanding of vector ecology and a more accurate account of the frequency with which *Anopheles* fed on unexpected host species (Diallo et al. 2013; Ogola et al. 2017; Omondi et al. 2015). Some studies were also excluded because they did not systematically report the sampling locations. In many studies molecular feeding data is frequently pooled across locations or timepoints, which means local environmental or seasonal features are lost. We included these studies, to ensure that we had sufficient data

to run our model, while exploring finer spatial and temporal resolution requires more refined data and awaits further research.

4.6 | Wider Implications of Research and Conclusion

From an epidemiological perspective, vector-borne pathogen transmission between different host species is the outcome of several features, including: host and vector range, host and vector competence, and host selection plasticity (Campos et al. 2023; Mordecai et al. 2019; Takken and Verhulst 2013). Mosquitoes that feed on diverse hosts present the greatest risk for transmitting pathogens between host species. However, this can limit the spread of highly specialised pathogens. For example, *Culex* mosquitoes may successfully transmit West Nile virus between competent bird species, but blood feeding on mammals as additional hosts may dilute the transmission of this virus as viral loads in mammals are typically too low for transmission (Hamer et al. 2009). If vectors and pathogens specialise in the same host species, then this can also increase transmission (Fikrig and Harrington 2021). Intermediate feeding patterns should favour transmission of multihost pathogens. Moreover, some pathogens are spread by various mosquito species, which may differ in their vector competence and capacity. Some *Culex* species, for instance, play a major role in transmitting pathogens (e.g., WNV, Sindbis virus), while others contribute less to the transmission cycles due to lower vector competence or more opportunistic feeding behaviour (Figueroa et al. 2022; Gutiérrez-López et al. 2025; McMillan et al. 2019). Thus, a better understanding of the drivers that cause plasticity in feeding patterns of mosquitoes is crucial for better predicting pathogen transmission risks in natural environments and improving the targeting of control efforts.

5 | Conclusion

We found that a focus on molecular studies that use ‘universal’ methods considerably increased the discovery rate of novel hosts per sample measured and thus highlight that the host niche breadth of common *Culex* and *Aedes* mosquito species might be much broader than previously anticipated. This is mostly because although mosquitoes generally feed on the hosts that they are expected to—there are also many unexpected host species associations (e.g., mammalophilic mosquitoes feeding on birds or reptiles). Our meta-analysis set out to understand what we can learn by putting local blood-meal studies in a global context. We confirm that the host selection is not solely determined by innate preference and host availability but also by other environmental features. While our strict criteria for inclusion meant that only 88 out of 1040 studies were included in the analysis, these results suggest that universal molecular methods are a means towards understanding how the environment shapes mosquito blood feeding and the corresponding risks of disease transmission and spillover.

Author Contributions

Meshach Lee: data curation (contribution; explored preliminary data as part of his BSc dissertation at Swansea University supervised by K.W.); review and editing (equal). Nicholas Clark: formal analysis

(contribution); review and editing (equal). Richard O'Rorke: conceptualisation (equal); data curation (lead); writing – review and editing (equal). Tamsyn Uren Webster: conceptualisation (equal); data curation (contribution); review and editing (equal). Konstans Wells: conceptualisation (lead); data curation (equal); writing – original draft (lead); formal analysis (lead); writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and computer code used for data compilation/manipulation and analysis are freely available on Dryad, [10.5061/dryad.18931zd70](https://doi.org/10.5061/dryad.18931zd70).

Unique, permanent digital object identifier (DOI): <https://doi.org/10.5061/dryad.18931zd70>. The temporary reviewer URL. <http://datadryad.org/stash/share/t-CCotZ0RRd5ltDFm-GHVpIDMZiX7XQNg1t7l2SVQnA>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.