Landscape Ecology

Original Research Article

Local tree cover predicts mosquito species richness and disease vector presence in a tropical countryside landscape

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Abstract

Context

Land use change and deforestation drive both biodiversity loss and zoonotic disease transmission in tropical countrysides. For mosquito communities that can include disease vectors, forest loss has been linked to reduced biodiversity and increased vector presence. The spatial scales at which land use and tree cover shape mosquito communities present a knowledge gap relevant to both biodiversity and public health.

Objectives

We investigated the responses of mosquito species richness and *Aedes albopictus* disease vector presence to land use and to tree cover surrounding survey sites at different spatial scales. We also investigated species compositional turnover across land uses and along environmental gradients.

Methods

We paired a field survey of mosquito communities in agricultural, residential, and forested lands in rural southern Costa Rica with remotely sensed tree cover data. We compared mosquito richness and vector presence responses to tree cover measured across scales from 30m to 1000m, and across land uses. We analyzed compositional turnover between land uses and along environmental gradients of tree cover, temperature, elevation, and geographic distance.

Results

Tree cover was both positively correlated with mosquito species richness and negatively correlated with the presence of the common invasive dengue vector *Ae. albopictus* at small spatial scales of 90 – 250m. Land use predicted community composition and *Ae. albopictus* presence.

Conclusions

The results suggest that local tree cover preservation and expansion can support mosquito species richness and reduce disease vector presence. The identified spatial range at which tree cover shapes mosquito communities can inform the development of land management practices to protect both ecosystem and public health.

Introduction

Humans have modified more than half of Earth's land surface through activities such as deforestation, agricultural intensification and expansion, and urbanization (Hooke *et al.*, 2012). Land use and land cover change fundamentally alter ecosystems, with strong impacts on biodiversity including species endangerment, loss, and invasion (e.g., Sala, 2000; Pereira *et al.*, 2010; Maxwell *et al.*, 2016; Giam, 2017). For communities containing species that transmit human diseases, the impacts of land use change on biodiversity can also impact human health. For example, the growing land area used for pineapple production in Costa Rica corresponds to an increase in highly suitable habitat for the malaria vector *Anopheles albimanus* (Rhodes *et al.*, 2022). Developing land management solutions that benefit both biodiversity and public health is particularly important for countryside landscapes characterized by natural habitat remnants patchworked with human residential and agricultural infrastructure. These landscapes are globally dominant, are disproportionately impacted by land use change and zoonoses, and are critical to biodiversity conservation (Norris, 2008; Chazdon *et al.*, 2009; Maxwell, 2016; Sokolow *et al.*, 2022). Percent tree cover at small spatial scales of <100m has emerged as a reliable predictor of biodiversity for taxa in Latin American tropical countrysides including birds, non-flying mammals, and bats (Mendenhall *et al.*, 2016), suggesting that local tree cover management holds promise as a practicable conservation tool. However, major knowledge gaps remain surrounding how local tree cover relates to invertebrate biodiversity, including for arthropod vectors of human diseases.

Mosquito communities (family Culicidae) are relevant to biodiversity and public health in countryside landscapes because they are sensitive to tree cover and habitat type, act as prey, predators, and detritivores in aquatic and terrestrial food webs (Addicott, 1974; Heard, 1994;

99 Daugherty, Alto and Juliano, 2000; Poulin, Lefebvre and Paz, 2010), and can include species that
100 are important vectors of diseases including malaria, dengue, chikungunya, Zika, yellow fever,
101 West Nile fever, and arboviral encephalitis (Garmendia, Van Kruiningen and French, 2001;
102 Lemon, 2008; LaPointe, Atkinson and Samuel, 2012; World Health Organization, 2021).
103 Previous studies show associations between forest conversion and low mosquito biodiversity,
104 and suggest that high rates of land use change and active invasions by major vector species are
105 together reshaping mosquito communities in ways that increase disease risk (Ferraguti *et al.*,
106 2016; Meyer Steiger, Ritchie and Laurance, 2016; Burkett-Cadena and Vittor, 2018; Chaves *et*
107 *al.*, 2021). These patterns are likely shaped by abiotic and biotic conditions associated with tree
108 cover and land use context that affect the presence and abundance of mosquito species that vary
109 in their thermal niches, aquatic breeding habitat requirements, and preferred groups of
110 vertebrates for blood meals (Laird, 1988; Gutman *et al.*, 2004; Mordecai *et al.*, 2019; Prevedello
111 *et al.*, 2019). Clarifying the spatial scales at which these landscape features shape mosquito
112 communities is critical to understanding how tree cover management might balance biodiversity
113 conservation, public health, and economic needs.
114 The countryside of Costa Rica is an ideal system in which to study relationships between
115 land cover, mosquito community characteristics, and disease vector occurrence. This region, like
116 neighboring Latin American countries, has a large burden of mosquito-borne diseases, including
117 dengue virus, with two invasive *Aedes* spp. vectors potentially contributing to transmission
118 (Rezza, 2012; Kraemer *et al.*, 2015; WHO, 2021). *Aedes aegypti* is considered the primary
119 dengue vector in Costa Rica, but the ongoing, patchily described invasion by the globally
120 important vector species *Aedes albopictus* is potentially reshaping disease risk (Troyo *et al.*,
121 2006; Calderón-Arguedas *et al.*, 2010; Calderón-Arguedas *et al.*, 2015; Rojas-Araya *et al.*,

122 2017). Globally, *Ae. albopictus* and *Ae. aegypti* are predominantly associated with rural and
123 urban human settlements, respectively, suggesting that *Ae. albopictus* and its responses to tree
124 cover may play particularly important roles in countryside dengue transmission (Braks *et al.*,
125 2003; Tsuda *et al.*, 2006). Additionally, intensive long-term research in this system has
126 characterized many links between landscape context, biodiversity, and ecosystem services (e.g.,
127 Daily *et al.*, 2001; Ricketts *et al.*, 2004; Karp *et al.*, 2013; Frank *et al.*, 2017; Hendershot *et al.*,
128 2020; Langhans *et al.*, 2022), but the corresponding links to mosquito biodiversity and disease
129 vector presence remain undescribed.

130 Here, we combine field observations of mosquito communities in forested, agricultural, and
131 residential settings in a rural area of southern Costa Rica with remotely-sensed land cover data in
132 order to investigate mosquito community responses to forest cover and land use. We ask: How
133 do mosquito community characteristics vary with tree cover measured at different spatial scales,
134 among land use types, and along environmental gradients? We hypothesize that lower local tree
135 cover and non-forest land uses are associated with lower mosquito species richness but higher
136 presence of human-associated *Aedes* spp. vectors. By improving scientific understanding of how
137 landscape context influences mosquito community assembly in Costa Rica, this study contributes
138 to a more general understanding of links between land cover, biodiversity, and ecosystem
139 services through the lens of entomological factors that influence disease risk.

140

141 **Methods**

142 *Study area*

143 This study was conducted in the cantons of Coto Brus, Corredores, and Golfito (8°43′14″N,
144 82°57′20″W), located in the southern Puntarenas region of Costa Rica along the border with

Panama (Figure 1). The region ranges from coastal lowland tropical rainforest (0 m above sea level) to high elevation cloud forest (1500 m above sea level) and has distinct wet and dry seasons. The study area is predominately composed of rural communities surrounded by agriculture interspersed with forest patches, and also includes the protected Las Cruces forest reserve. In this area, dengue is endemic, *Ae. aegypti* is common, and *Ae. albopictus* has a growing presence (World Health Organization, 1994; Troyo *et al.*, 2008, 2009; Rojas-Araya *et al.*, 2017).

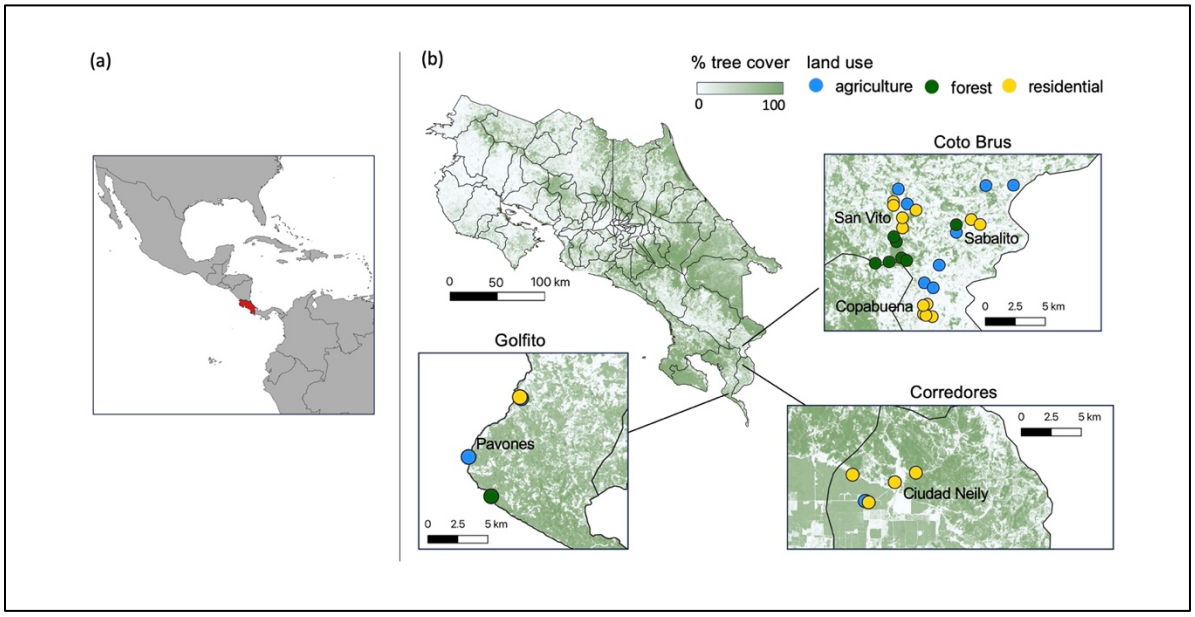

Figure 1. Tree cover and land use varied across study sites in Costa Rica. (A) Location of Costa Rica in Central America is highlighted in red. (B) Map of Costa Rica with canton boundaries delineated by lines, tree cover (remotely sensed at 30 m resolution) indicated in shades of green, and sampling sites indicated by colored points within the three insets. Insets shows study sites within Golfito, Corredores, and Coto Brus cantons. Blue, green, and yellow points denote agricultural, forest, and residential land uses, respectively. Text labels within insets denote districts.

Study sites

With landowner permission, we accessed 37 sites representing three broad land use classes that were determined on-site by the survey team: residential (N = 17), agricultural (N = 12), and

forest (N = 8) (Figure 1). In the Coto Brus canton (N = 12 residential sites, 8 agricultural, 7 forest), sites were in the districts San Vito, Sabalito, and Copabuena; in Corredores canton (N = 4 residential, 2 agricultural), sites were in Ciudad Neily district; in Golfito canton, (N = 1 residential, 2 agricultural, 1 forest), sites were in Pavones district. Residential site collections took place in the yards of residences in urban and peri-urban areas; agricultural site collections took place in the agricultural fields of coffee plantations, an oil palm plantation, a pine plantation, one mixed crop field, and one pasture; forest site trapping took place in primary and secondary forest edges, interiors, and fragments, on both protected and unprotected lands.

Environmental variables

To quantify percent tree cover, we used a 30 m resolution map of tree cover in Costa Rica created by Echeverri et. al (2022) from multi-sensor satellite observations (2005 – 2017) and fine-scale tree cover maps (Figure 1). From this map, we calculated percent tree cover at different spatial scales surrounding each site using the R package "raster" (Hijmans *et al.*, 2015). Specifically, we began by calculating percent tree cover within a radius of 30 m; we then increased this radius by increments of 10 m up to 200 m, and by increments of 50 m for radii between 200 m and 1000 m (following Mendenhall *et. al*, 2014). To account for mosquito interspecific variation in sensitivity to thermal conditions (Mordecai *et al.,* 2019), which could affect observed relationships between land cover and mosquito community characteristics along the 1500 m elevational gradient surveyed, we additionally extracted mean annual temperature data from 1970 – 2000 for each study site from the WorldClim 1 km^2 resolution mean annual temperature dataset (Fick and Hijmans, 2017).

Sample collection

186 We trapped mosquitoes during the rainy season, visiting all sites twice between June 19
187 and August 9, 2017, excepting the four sites in Pavones, which were trapped once (N = 70 trap
188 nights). The interval between collections at a given site ranged from 8 to 36 days (mean = 22
189 days, SD = 8 days) (Table S1). In order to detect mosquito species with a variety of habitat and
190 blood meal host preferences, we used a mix of trapping and manual collection methods
191 (Thongsripong *et al.*, 2013; Hoshi *et al.*, 2014; Giordano *et al.*, 2020; Romero-Vega *et al.*, 2023).
192 Specifically, at each site, we placed a total of four traps overnight for a 12-16 hour period within
193 an area of 30 m in radius: one unlighted CDC trap baited with carbon dioxide produced by a
194 mixture of Fleischmann's Dry Active Yeast, household refined sugar, and water to mimic
195 vertebrate respiration; one BG Sentinel baited with a BG-Lure and octanol to attract human-
196 specialist mosquitoes; and two BG-GAT traps furnished with yellow sticky cards, corn oil, and a
197 mixture of water and local leaf litter to attract gravid female mosquitoes. Trap locations within
198 sites were chosen per BioGents recommendations, and square metal frames covered in large
199 black plastic bags were placed over BG Sentinel and BG-GAT traps for protection from rainfall.
200 To supplement the overnight trapping, during each trapping session, mosquito larvae were
201 collected from breeding habitats and one of three trained members of the field team carried out
202 20 minutes of direct aspiration, over a standardized time and area.
203
204 *Mosquito identification*
205 Four field team members trained to morphologically identify *Ae. albopictus* and *Ae.*
206 *aegypti* picked out, sexed, and counted individuals of these species collected at each site. All
207 morphological identifications were confirmed by the field team lead to ensure consistency. All
208 other mosquitoes were counted, stored, and transported to Stanford University for molecular

209 identification. We extracted and amplified DNA from the mitochondrial CO1 gene from pooled
210 samples of mosquitoes from each trap night at each site (N = 70 pools) using MyTaq RedMix
211 (Meridian Bioscience, Cincinnati, OH), following the protocol provided by the manufacturer.
212 Amplified DNA libraries were prepared for next-generation sequencing with Nextera (Illumina,
213 Inc., San Diego, CA) and sequenced via Illumina MISEQ, with samples containing *Aedes*
214 *albopictus* and *Culex tarsalis* DNA as positive controls. We removed primer sequences and
215 paired forward and reverse reads from the sequencing data with the R package "dplyr", and then
216 used the R package "dada2" to filter and trim the DNA sequences to 473 bp, with a minimum
217 overlap of 20 bases and a maximum of 5 expected errors (Callahan *et al.*, 2016; Wickham *et al.*,
218 2023). We estimated taxonomic placement for the sequenced mosquitoes by using the R
219 packages "Biostrings" and "DECIPHER" to group DNA sequences into operational taxonomic
220 units (OTUs, henceforth referred to as species) of 97% sequence similarity, and comparing
221 representative sequences for each species to the BOLD and GenBank database records (Altschul
222 *et al.*, 1990; Ratnasingham and Hebert, 2007; Wright, 2016; Pagès *et al.*, 2022). Species were
223 identified based on top matches with sequence similarity ≥ 97% (Hardulak *et al.*, 2020). When
224 sequence similarity to the top match was < 97%, a higher level of taxonomic identification (e.g.,
225 genus) was assigned based on placement within a phylogenetic tree of the BOLD database
226 sequences.
227
228 *Statistical analyses*
229 We described mosquito communities in terms of species richness and species
230 composition by combining presence data from the morphologically identified *Aedes* data and the
231 sequencing data. To assess the completeness of species pool sampling for each land use type, we

232 plotted species accumulation curves with the function "accumcomp" in the package
233 BiodiversityR (Kindt and Coe, 2005). To quantify relationships between species richness and
234 percent tree cover, we used generalized linear models (GLMs) with negative binomial error
235 corrections for overdispersion and mean-centered independent variables. To assess the spatial
236 scales at which tree cover best predicted species richness, we compared AIC values for GLMs
237 that included percent tree cover surrounding each site calculated at radii ranging from 30 m to
238 1000 m. We used binomial logistic regression to analyze relationships between *Ae. albopictus*
239 disease vector presence/absence and percent tree cover across spatial scales. For the 1000 m
240 spatial scale where climate data were available, we additionally assessed the relative influence of
241 mean annual temperature on species richness and *Aedes* vector presence with GLMs including
242 mean annual temperature and its interaction with tree cover.

243 To compare species richness and *Aedes* vector presence between forest, agricultural, and
244 residential land uses, we used Kruskal-Wallis tests with Bonferroni p-value adjustments to
245 account for multiple comparisons.

246 To compare species composition among land use types and along environmental
247 gradients, we first calculated the Jaccard coefficient of community similarity for each pair of
248 sites for use in statistical tests and ordination. We then tested for differences in community
249 similarity among land uses with permutational analysis of variation (PERMANOVA), first for all
250 land use types, and then with pairwise adonis functions. Because PERMANOVA is sensitive to
251 heterogeneity in dispersion among groups (Anderson and Walsh, 2013), we additionally tested
252 whether dispersion differed among land use types using Tukey's Honest Significant Differences
253 method with betadisper() calculations of group average distances to the median. To visualize
254 community similarity across land uses, we used non-metric multidimensional scaling (NMDS).

All the above analyses of compositional similarity among land uses were run using the R package "vegan" (Oksanen *et al.*, 2013); for the pairwise PERMANOVA analyses, we used the R package "ecole" which provides wrapper functions for "vegan" (Smith, 2022). Finally, to quantify compositional turnover along environmental gradients of tree cover, mean temperature, elevation, and geographic distance, we used the R package "gdm" for generalized dissimilarity modeling (GDM), a form of nonlinear matrix regression that is robust to collinearity (Fitzpatrick *et al.*, 2022). As above, we compared GDM models that incorporated tree cover at radii ranging from 30 – 1000 m to identify the spatial scale at which tree cover best explained compositional turnover.

All analyses were performed in R version 4.2.1. In addition to the R packages cited above, we used the packages "tidyverse" (Wickham *et al.*, 2019), "cowplot" (Wilke *et al.*, 2019), "MASS" (Ripley *et al.*, 2013), "interactions" (Long, 2019), "gridExtra" (Auguie *et al.*, 2017), and "reshape2" (Wickham, 2007) for data analysis and figure generation.

Results

Environmental variables

Across sites, tree cover ranged from 0% to 100% (mean = 27.9%, SD = 34.8%) at the smallest spatial scale we considered, a 30 m radius. Surrounding tree cover within a 1000 m radius, the largest spatial scale considered, ranged from 8.2% to 74.8% (mean = 33.4%, SD = 20.3%). The lowest and highest site elevations were 12 m and 1451 m above sea level, respectively (mean = 776 m, SD = 473.2 m). Mean annual temperature ranged from 18.8 to 26.4 ºC (mean = 22.6 ºC, SD = 2.3 ºC).

Mosquito collections

278 A total of 1,283 mosquitoes representing 48 species in 13 genera were collected from 37
279 sites (Figure 2, Table S2). The number of mosquitoes collected at a site ranged from one to 244
280 (mean = 35, SD = 64) (Table S1). Of these, 99 individuals from 14 residential and five
281 agricultural sites were morphologically identified as *Ae. albopictus*, and five total *Ae. aegypti*
282 individuals were identified from one forest, one agricultural, and one residential site. *Ae.*
283 *albopictus* DNA was detected in the pooled samples of molecularly identified mosquitoes from
284 seven of the 19 sites where *Ae. albopictus* individuals were also morphologically identified, and
285 no sites without morphologically identified specimens. The five most common species were *Ae.*
286 *albopictus*, *Culex quinquefasciatus*, *Cx. nigripalpus*, *Wyeomyia adelpha/Guatemala,* and
287 *Limatus durhamii* (Figure 2, Table S3).
288

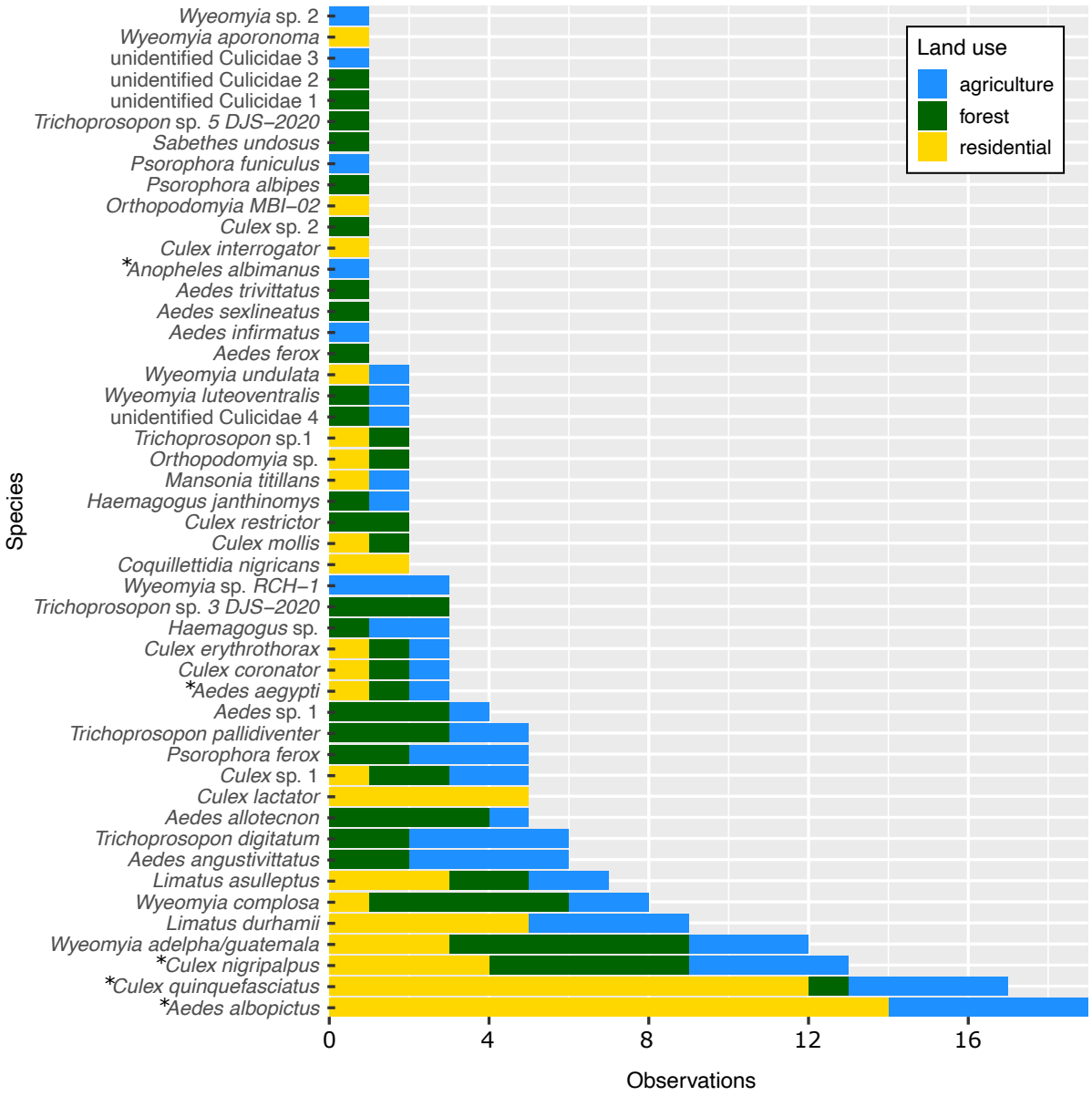

Figure 2. The commonness of 48 observed mosquito species varied both overall and among land use types. Blue bars show the number of agricultural sites in which each species was present, green bars show forest sites, and yellow bars show residential sites. Asterisks indicate species known to vector human diseases.

Species richness

Site-level species richness ranged from one to 19 (mean = 4.89, SD = 4.1) (Table S2). Overall species counts for forest, agricultural, and residential land uses were 33, 29, and 21, respectively. Ten species (21%) were observed in all three land uses. Nineteen species (40%)

were shared among forest and agricultural land uses, 13 species (27%) were shared among agricultural and residential land uses, and twelve species (25%) were shared among forest and residential land uses (Figure 2, Table S3). Eleven species (23%) were found only in forested settings, six species (13%) were found only in agricultural settings, and six species (13%) were found only in residential settings (Figure 2, Table S3). Two species, *Ae. albopictus* and *Culex quinquefasciatus*, were common (observed at >50% of sites) in residential settings, no species were common in agricultural settings, and three species—*Culex nigripalpus*, *Wyeomyia complosa*, and *Wyeomyia adelpha/guatemala*—were common in forested settings (Table S1). Species accumulation curves indicate that more species would have been observed in each land use class with additional sampling, but at a lower rate in residential compared to forest and agricultural land uses (Figure S1).

Disease vectors

At least five of the mosquito species observed are known vectors of human diseases. Three of these—the dengue and chikungunya virus vector *Ae. albopictus* (present at 19 sites) and the St. Louis Encephalitis virus vectors *Cx. quinquefasciatus* (present at 17 sites) and *Cx. nigripalpus* (present at 13 sites)—were the three most frequently observed species (Reisen, 2003; Simmons *et al.*, 2012). Rarely observed vector species included the dengue, chikungunya, yellow fever, and Zika virus vector *Ae. aegypti* (present at three sites spanning all three land use types) and the malaria vector *Anopheles albimanus* (present at one agricultural site) (Zimmerman, 1992; Simmons *et al.*, 2012). In contrast to *Ae. aegypti, Cx. nigripalpus,* and *Cx. quinquefasciatus*, which were observed in all land use types, *Ae. albopictus* was observed only in residential and agricultural settings associated with intensive human modification.

Model results

Mosquito species richness was explained by tree cover, but not by land use type. Comparisons of GLMs using tree cover calculated for radii ranging between 30 m and 1000 m surrounding each site indicated that species richness was positively correlated with tree cover at radii between 90 m and 650 m, and tree cover at a 250 m radius had the largest effect size (estimated effect = 1.40×10^{-2}, SE = 5.00×10^{-3}, z-value = 2.8, p-value = 5.08×10^{-3}) (Figure 3a, Table S4). At the 1000 m spatial scale where both tree cover and climate data were available, the interaction between tree cover and mean annual temperature had a significant effect on species richness (estimated effect = -9.48×10^{-3}, SE = 3.48×10^{-3}, z-value = -2.72, p-value = 6.48×10^{-3} (Table S5). Specifically, at high temperatures, species richness was low even when tree cover was high (Figure S2). By contrast, Kruskal-Wallis test results indicated that species richness did not differ significantly among forested, agricultural, and residential sites (chi-squared = 2.84, df = 2, p-value = 0.24) (Figure 3b). Notably, the highest species richness was observed at a site in the Coto Brus forest reserve (Figure 3b).

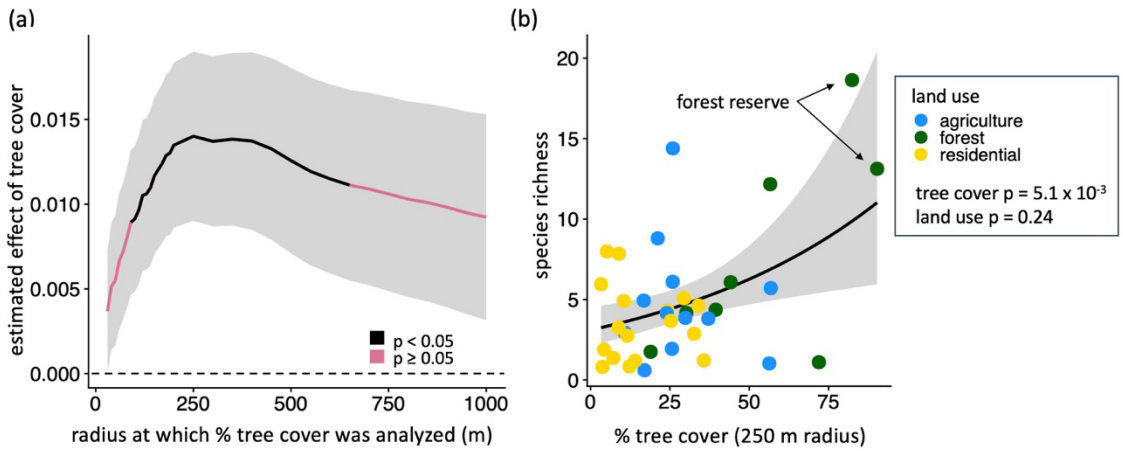

Figure 3. Species richness is correlated with tree cover surrounding survey sites for radii between 90 m and 650 m. *(a) The estimated effect of surrounding tree cover calculated across spatial scales on species richness. Radii where the relationship between tree cover and species richness is significant ($p < 0.05$) are shown in black; others are shown in pink. Values above the dashed line are positive. (b) Species richness increases with percent tree cover at a 250 m radius: the scale identified as having the strongest effect. Land use (colored points) and species richness are not significantly correlated. The site with the highest species richness and the site with the highest surrounding tree cover were both located in the Las Cruces forest reserve (arrows). In both panels, gray shading shows +/- 1 SE.*

Relationships of Ae. albopictus *presence to tree cover and land use*

From the *Aedes* disease vector survey, we present results only for *Ae. albopictus* because observations of *Ae. aegypti* were insufficient for statistical analysis. Both tree cover and land use type predicted *Ae. albopictus* presence. Comparisons of GLMs using tree cover calculated for radii ranging between 30 m and 1000 m surrounding each site indicated that *Ae. albopictus* presence was negatively correlated with tree cover at radii between 30 m and 250 m, and was best explained by tree cover at a 110 m radius (estimated effect = -4.46×10^{-2}, SE = 1.83×10^{-2}, z-value = -2.44, p-value = 1.47×10^{-2}) (Figure 4a, Table S6). At the 1000 m spatial scale where we additionally assessed the influence of climate, *Ae. albopictus* presence was negatively correlated with tree cover and positively correlated with temperature (tree cover estimated effect = -8.34×10^{-2}, SE = 3.61×10^{-2}, z-value = -2.31, p-value = 2.08×10^{-2}; mean annual temperature

estimated effect = 9.36 x 10^{-1}, SE = 4.2 x 10^{-1}, z-value = 2.23, p-value = 2.5 x 10^{-2}) (Figure S3, Table S7). Land use type also predicted *Ae. albopictus* presence (Kruskal-Wallis chi-squared = 15.02, p-value = 5.48 x 10^{-4}). Specifically, *Ae. albopictus* was significantly more likely to be observed in residential settings (present at 14/17 sites) than in forested settings (present at 0/8 sites) (Kruskal-Wallace chi-squared = 14.37, Bonferroni-adjusted p-value = 4.49 x 10^{-4}), and its presence in agricultural settings (present at 5/12 sites) did not differ significantly compared to either residential (Kruskal-Wallace chi-squared = 4.98, adjusted p-value = 7.8x 10^{-2}) or forested (Kruskal-Wallace chi-squared = 4.22, adjusted p-value = 1.20 x 10^{-1}) settings. Eighteen of the 19 sites where *Ae. albopictus* was present were surrounded by less than 35% tree cover within a 110 m radius. The only site within a pine plantation was a clear outlier, where *Ae. albopictus* was present under 75% tree cover (Figure 4B).

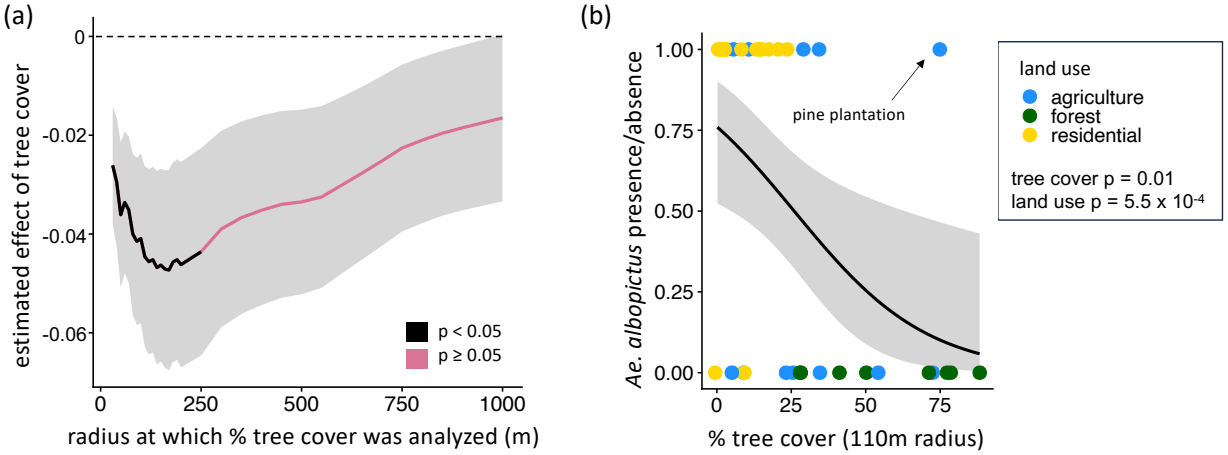

Figure 4. *Aedes albopictus* is most likely to be found at low tree cover levels and in residential settings. *(a) The estimated effects of tree cover across spatial scales on* Ae. albopictus *presence, where black lines indicate statistically significant (p < 0.05) effects and pink lines indicate non-significant (p > 0.05) relationships. Values below the dashed line are negative. (b) Land use type (colored points), percent tree cover, and* Ae. albopictus *presence/absence at the highest-significance 110 m radius. In both panels, gray shading shows +/- 1 SE.*

Species composition across land uses

In contrast to species richness, community composition and dispersion were predicted by land use type. PERMANOVA results comparing all three land uses showed that land use significantly affected community composition (sum of squares = 2.24, R^2 = 0.16, F-value = 3.24, p-value = 0.001), and pairwise PERMANOVAs showed that agricultural and forest mosquito communities differed significantly from residential communities (Table 1). Wider dispersion among agricultural compared to residential mosquito communities (average distance to the median: agriculture = 0.618, forest = 0.572, residential = 0.496; Tukey test adjusted p-values: residential – agricultural = 0.0104, residential – forested = 0.218, forested – agricultural = 0.604) likely contributed to the community dissimilarity detected between these land uses (Anderson and Walsh, 2013). Supporting these statistical results, NMDS visualization of communities grouped by land use type highlights that agricultural communities bridge distinct forest and residential communities (NMDS stress = 0.12) (Figure 5). The wider variation among agricultural sites is also evident from the species observation table: no single species was observed at more than 1/3 of all agricultural sites, whereas *Ae. albopictus* and Unidentified Culicidae 1 were both observed at >70% of residential sites, and *Culex nigripalpus*, *Wyeomyia adelpha/guatemala*, and *Wyeomyia complosa* were each observed at >60% of forested sites (Tables S2, S3). On the NMDS plot, forest land use sites falling far outside of the 95% CI included the single forest fragment and two of four forest edges surveyed (Figure S4). Agricultural land use outliers clustering near the residential group included both oil palm plantations surveyed and one coffee plantation, and those clustering nearer the forest group included three coffee plantations (Figure S4). Each site in the geographically distinct Pavones district that was sampled only once fell outside of the 95% CIs for its land use type (Figure S4).

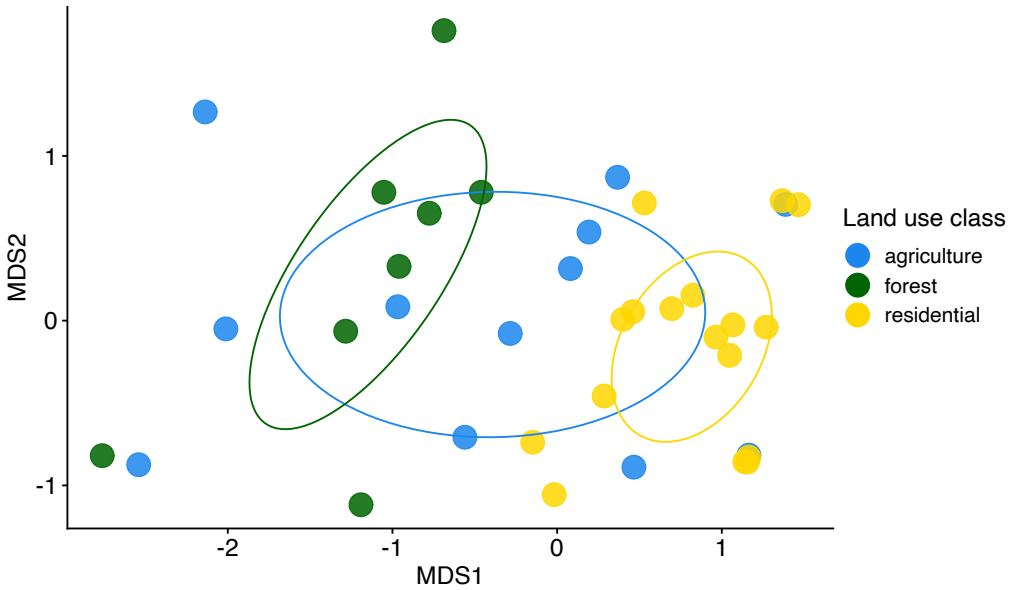

Figure 5. Distinct mosquito communities were observed in forest and residential land uses, while communities in agricultural settings overlapped with both other land use types. *NMDS ordination visualization groups sites by community similarity, with colors indicating land use types (blue: agriculture, green: forest, yellow: residential). Each point represents the community at one study site, and the distance between points is smaller for more similar communities. Ellipses show 95% confidence intervals for ordination of agriculture, forest, and residential mosquito communities.*

Table 1. PERMANOVA results for community composition compared among land use types. Asterisks indicate p < 0.05.

Land use pair	Sum of squares	F-Value	R^2	Bonferroni-adjusted p-value
agriculture vs. forest	0.645	1.59	0.0813	0.117
agriculture vs. residential	0.846	2.52	0.0853	0.018 *
forest vs. residential	1.82	5.87	0.203	0.003 *

Species turnover along environmental gradients

Finally, generalized dissimilarity modeling (GDM) indicated that environmental gradients explained little of the species turnover among sites. Among the spatial scales for which tree cover was calculated, the model using the 130m radius explained the highest amount of species turnover among sites (Table S8). The model that included mean annual temperature,

geographic distance, and tree cover at the 130m radius explained 7% of species turnover among sites. Elevation showed no relationship with species turnover. Whereas increasing tree cover was associated with a consistent increase in community turnover, increasing temperature was associated with a steep increase in community turnover up to a plateau around 22 ºC, and increasing geographic distance was associated with comparatively limited turnover (Figure 6).

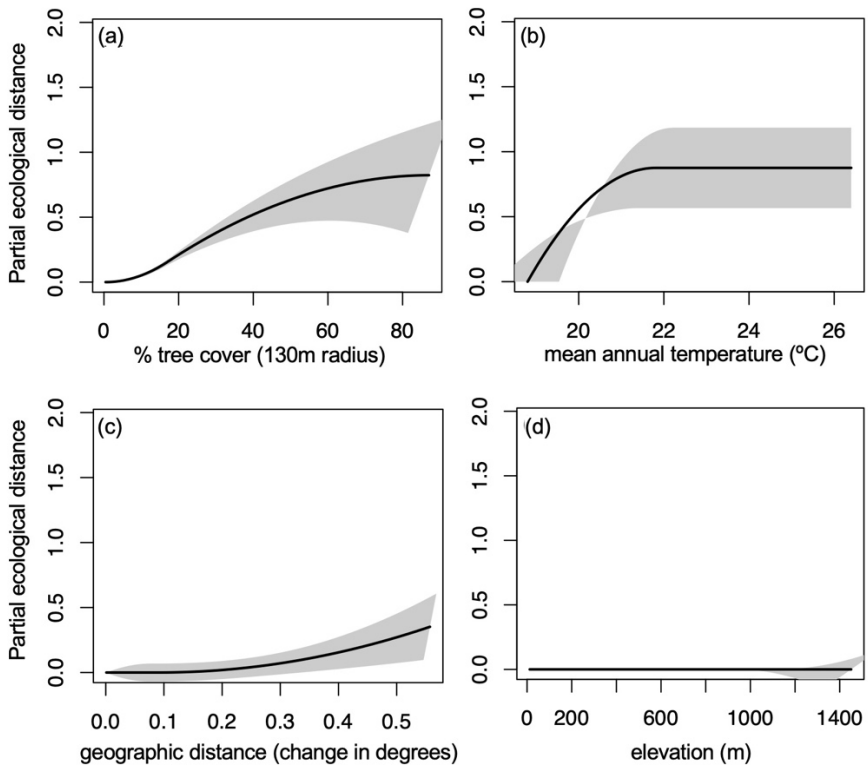

Figure 6. Generalized dissimilarity modelling (GDM) of community dissimilarity indicated that (a) percent tree cover and (b) mean annual temperature explained 7% of deviation from the null. *(c) geographic distance contributed minimally and (d) elevation did not significantly contribute to community turnover. In each panel, the x-axis shows the environmental gradient and the y-axis shows the amount of compositional turnover, measured as partial ecological distance. The maximum height the spline reaches on the y-axis indicates the total amount of compositional turnover the gradient is associated with, and the slope shows how the rate of compositional turnover varies along the environmental gradient. The difference in height between any two points along the I-spline corresponds to the modeled contribution of that predictor variable to the difference between those points. Grey shading shows +/- 1 standard deviation when 70% of sites are sampled 10 times.*

Discussion

We found that local tree cover, but not land use (residential, agricultural, or forest), predicted mosquito species richness, suggesting that more diverse communities occur at higher tree cover. By contrast, community composition was more predictable for forested and residential land uses, and more variable among agricultural sites, but environmental gradients of tree cover, climate, and geographic distance explained only 7% of species turnover among sites. *Ae. albopictus* presence varied significantly with both tree cover and land use, but in the opposite direction from mosquito richness: increasing with lower tree cover and in residential compared to forested sites (with intermediate probability in agricultural sites). Overall, our results add to support from both mosquitoes and other taxa that natural and semi-natural habitat, including tree cover, sustains substantial biodiversity and ecosystem services—here, in the form of protection against mosquitoes that vector human disease (Millennium Ecosystem Assessment, 2005; Jose, 2009; Mendenhall *et al*., 2014, 2016; Frank *et al*., 2017; Barrios *et al.*, 2018; Burkett-Cadena and Vittor, 2018; Frishkoff *et al.,* 2019; Langhans *et al.*, 2022; Perrin *et al.*, 2023).

Mosquito richness and species composition

The spatial scales at which tree cover predicted mosquito species richness were small (90-650 m), and comparable to previous findings for other taxa in the same study area, highlighting the disproportionately positive impact of small patches of trees on biodiversity (Mendenhall *et al.* 2014, 2016; Frank *et al.*, 2017). The radius at which tree cover best predicted species richness was 250 m; by comparison, biodiversity was correlated with tree cover at small spatial scales for non-flying mammals (70 m), bats (50 - 60 m), birds (30 m), reptiles (50 m), and amphibians (80 m) in the same region of Costa Rica (Mendenhall *et al.,* 2014, 2016; Frank *et al.,*

456 2017). Although the radius at which mosquito species richness responded most strongly to tree
457 cover was larger compared to previously studied taxa, the spatial scale remained local, and
458 significant effects of tree cover were found at radii as small as 90 m. Our observation of a
459 positive relationship between species richness and tree cover aligns with those of many other
460 studies of mosquito diversity along land cover gradients in locations including Latin America,
461 Asia, and Europe (e.g., Johnson, Gómez and Pinedo-Vasquez, 2008; Thongsripong *et al.*, 2013;
462 Ferraguti *et al.*, 2016; Chaverri *et al.*, 2018), and our analysis of the distance around sampling
463 sites at which tree cover shapes mosquito communities contributes to clarifying the spatial scales
464 at which mosquitoes respond to landscape features.

465 Our observation that mosquito community composition was distinct among different land
466 uses is consistent with patterns observed both for other taxa in this system, and for mosquitoes in
467 other regions (Mendenhall *et al.*, 2014, 2016; Meyer Steiger, Ritchie and Laurance, 2016; da
468 Silva Pessoa Vieira *et al.*, 2022). In agricultural settings, relatively high species richness and
469 community similarity with forested settings support the argument that farmlands can contribute
470 substantially to biodiversity (e.g., Norris, 2008). However, the high proportion of species unique
471 to forest habitats and the high species richness observed inside the large Las Cruces forest
472 reserve also reaffirm the importance of forests and protected areas as refugia for biodiversity
473 (Coetzee, Gaston and Chown, 2014; Mendenhall *et al.*, 2016). Additionally, the compositional
474 variability among agricultural settings and the close community resemblance between some
475 agricultural and residential sites indicate a need for additional research on how mosquito
476 communities respond to specific land uses, crop assemblages, or management practices that can
477 result in similar levels of tree cover. For example, organic farming methods are associated with
478 higher arthropod diversity globally compared to conventional methods, and Kenyan ricelands

479 that rely on natural rather than artificial irrigation have higher mosquito species richness (Muturi
480 *et al.*, 2006; Lichtenberg *et al.*, 2017). Costa Rican croplands that are less intensively farmed
481 support greater bird species richness, a pattern that may also hold for mosquitoes (Hendershot *et*
482 *al.*, 2020).

483 Environmental gradients of tree cover and temperature shaped species turnover, but
484 explained only 7% of variance in community composition, suggesting that additional habitat
485 characteristics may play important roles in determining species composition. Such factors might
486 include local microclimates, differences among types of tree cover (e.g., agricultural types,
487 primary versus secondary forest), and/or the presence of vertebrate hosts preferred by different
488 mosquito species. Differences in species abundances and community evenness, which were not
489 quantified here, might also respond more strongly to gradual environmental change than the
490 identities of the species present. Additionally, undersampling of communities may have
491 contributed to this result by limiting the repeatability of community composition observed at
492 environmentally similar sites. However, our result that land use predicts species composition,
493 while land cover predicts species richness, aligns with patterns of abundance-based Dipteran and
494 Culicid diversity observed in the tropical Australian countryside (Smith and Mayfield, 2015;
495 Meyer Steiger, Ritchie and Laurance, 2016).

496

497 *Disease vectors*

498 The most frequently observed disease vector, *Ae. albopictus*, was more likely to be
499 observed in sites with lower surrounding tree cover and agricultural or residential land uses,
500 suggesting that rural landscapes with more forest and tree cover may be more resistant to
501 invasion by this species. These observations align with this species' well-established preferences

502 for taking blood meals from humans and livestock (Niebylski *et al.*, 1994; Richards *et al.*, 2006),
503 and its association with rural, agricultural, suburban, and/or deforested settings in the Americas,
504 Asia, and Africa (Gilotra, Rozeboom and Bhattacharya, 1967; Braks *et al.*, 2003; Young *et al.*,
505 2017; Câmara *et al.*, 2020; Canelas *et al.*, 2023). The 30 – 250 m radii at which tree cover
506 negatively affected *Ae. albopictus* presence fell within the 90 – 650 m range at which tree cover
507 positively affected species richness, suggesting promise for local tree cover management as a
508 means of supporting both public health and biodiversity conservation. Protection against
509 mosquito disease vectors conferred by tree cover may extend beyond *Ae. albopictus* to include at
510 least 16 other significant vectors of human diseases that are favored by deforestation, including
511 *Ae. aegypti,* multiple Anopheline malaria vectors, and the Amazonian malaria vector
512 *Nyssorhynchus darlingi* (Burkett-Cadena and Vittor, 2018; Chaves *et al.*, 2021).
513 Our finding that *Ae. albopictus* was associated with, but inconsistently observed in,
514 agricultural settings (present in 33% of agriculture sites) reinforces that agricultural lands have
515 the potential to either harbor or resist invasive species, and suggests vector associations with
516 agricultural subtypes as a key future research direction. In our survey, factors that differentiated
517 the high tree-cover pine plantation and two of the six surveyed coffee plantations as suitable
518 habitat for *Ae. albopictus* are of particular interest. For example, *Ae. albopictus* larvae were
519 found in banana leaves and stumps in a shade-grown coffee plantation. Understanding vector
520 responses to agriculture is particularly important because this land use is the most likely
521 candidate for local tree cover management in Costa Rica due to its spatial extent, the established
522 Payment for Ecosystem Services program for incentivizing landowner forest retention and tree
523 planting, and a previous finding that urban tree cover is correlated with dengue incidence in this

region, while forest cover at the district level is negatively associated with dengue hospitalizations and outbreaks (Sánchez-Azofeifa *et al.*, 2007; Troyo *et al.*, 2009; Piaggio, 2024).

The findings of this study are subject to several limitations resulting from incomplete sampling of the mosquito community. Extensive sampling is required to fully capture the high arthropod biodiversity present in tropical areas (Coddington *et al.* 2009), such that unsaturated species accumulation curves are common in these systems (e.g., Novotný and Basset, 2003; Responte and Nuneza, 2016; Thormann *et al.*, 2016; Romero-Vega *et al.*, 2023; Kirmse, 2024). Many more mosquito species may have been observed with increased collection time at each site, particularly with additional coverage to include the dry season, as highlighted by seasonal mosquito species richness and abundances observed in Costa Rica by Romero-Vega *et al.* (2023). The sequencing approach we took to identify species other than *Ae. albopictus* and *Ae. aegypti* allowed us to efficiently identify specimens compared to a traditional morphological approach, but was limited by sequencing success and the availability of database entries for comparison. Additionally, the pooling of sequenced mosquitoes by site and trap night prevented measurements of species abundances and evenness, which are likely sensitive to tree cover and are key indicators of community structure and functioning, including the potential for vector species to transmit diseases (Franklinos *et al*., 2019). Despite these limitations, the number of mosquitoes collected and species richness we observed are on par with other mosquito studies in Costa Rica (Calderón-Arguedas *et al.*, 2008; Burkett-Cadena *et al.,* 2013; Chaverri *et al.*, 2018; Romero-Vega *et al.*, 2023), and the statistically significant environmental responses of mosquito community characteristics were consistent with hypotheses grounded in the findings of other studies with much larger sample sizes (e.g., Braks *et al.*, 2003; Johnson, Gómez and Pinedo-Vasquez, 2008; Chaves *et al.*, 2021; da Silva Pessoa Vieira *et al.*, 2022). We hypothesize that

547 additional sampling in this system might uncover more species in all sites and land use types but
548 also (1) significantly lower species richness in residential compared to forest and agricultural
549 land uses, based on the comparatively shallow slope of the residential species accumulation
550 curve; (2) a stronger signal of species turnover along environmental gradients, based on the large
551 uncertainty in the GDM results; and (3) rare occurrences of *Ae. albopictus* in forest edge
552 habitats, based on the association of this species with the urban-forest interface in Brazil (Pereira
553 dos Santos *et al.*, 2018; Hendy *et al.*, 2023).

554 To improve understanding of how local tree cover shapes mosquito biodiversity and
555 public health risk, future studies should aim to capture species richness and abundance along tree
556 cover gradients and across seasons (Calderón-Arguedas *et al.*, 2008; Troyo *et al.*, 2008; Romero-
557 Vega *et al.*, 2023); assess effects of other factors in habitats that have similar tree cover but differ
558 in aspects such as crop type or tree cover geometry; and use reforestation efforts or experimental
559 tree cover additions at relevant spatial scales to test mosquito community responses. In the study
560 region, tree cover responses of *Ae. aegypti* and *An. albimanus* require clarification, as we
561 observed these regionally important vectors too rarely for statistical analysis; in particular, the
562 canonically widespread and urban vector *Ae. aegypti* was unexpectedly rare and generalist,
563 occurring in one site of each of the three land use types (Troyo *et al.*, 2006; Cáceres *et al.*, 2012).
564 Additionally, the extent to which local tree cover effects on vector presence shape the potential
565 for disease transmission should be tested with human pathogen surveillance in field-captured
566 mosquitoes from different environments, and by comparison of disease case data to mosquito
567 community data. In addition to dengue, Zika, and malaria, St. Louis Encephalitis Virus should be
568 considered for surveillance in rural areas where humans and animals live in close proximity,
569 because two potential vectors—*Cx. quinquefasciatus* and *Cx. nigripalpus*—were common, and

570 this unmonitored disease is already widespread among both domesticated and wild animal hosts
571 in Costa Rica (Medlin *et al.*, 2016; Chaves *et al.*, 2021; Piche-Ovares *et al.*, 2023).
572
573 *Conclusions*
574 Overall, our findings follow patterns observed repeatedly across the globe associating
575 tree cover with higher mosquito species richness and lower disease vector presence. We showed
576 that tree cover both increases mosquito species richness and decreases *Ae. albopictus* presence at
577 small spatial scales of 90 – 250m. We also found that at larger spatial scales of 1000m, warm
578 mean annual temperatures increase habitat suitability for *Ae. albopictus* and limit tree cover
579 contributions to species richness, but note that other factors that covary with climate across the
580 study region may contribute to this result. Although the specific mechanisms and characteristics
581 by which tree cover inhibits disease vectors remain unclear, the alignment of local tree cover
582 effects on mosquito communities with other benefits for biodiversity and ecosystem services
583 adds support to the idea that countryside landscapes can be managed to foster both human and
584 ecosystem health.
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964 Field collections and sample exports were carried out under general insect collecting permit R-
965 036-2017-OT-CONAGEBIO, Costa Rica export permit 434-DGVS-2016, USDA veterinary
966 import permit 134109, and Health and Human Services permit 2017-08-079.

967

968 **Author contributions**

969 All authors contributed to the study conception and design. MH, JS, and CA collected the data.
970 MH and JF prepared the data, and JF analyzed the data. The first draft of the manuscript was
971 written by JF, and all authors contributed to subsequent versions of the manuscript. All authors
972 read and approved the final manuscript.

973

974 The authors have no competing interests to declare.

975

976 **Data availability**

977 The data presented in this manuscript are available in the DRYAD repository at
978 https://doi.org/10.5061/dryad.p8cz8w9xg.