Climate, human population density, and land cover link the distributions of two globally important dengue vectors from local to continental scales

Christopher B. Anderson, Erin A. Mordecai, Lisa Mandle, Jeffrey R. Smith, Gretchen C. Daily

Department of Biology, Natural Capital Project, Stanford University

Introduction

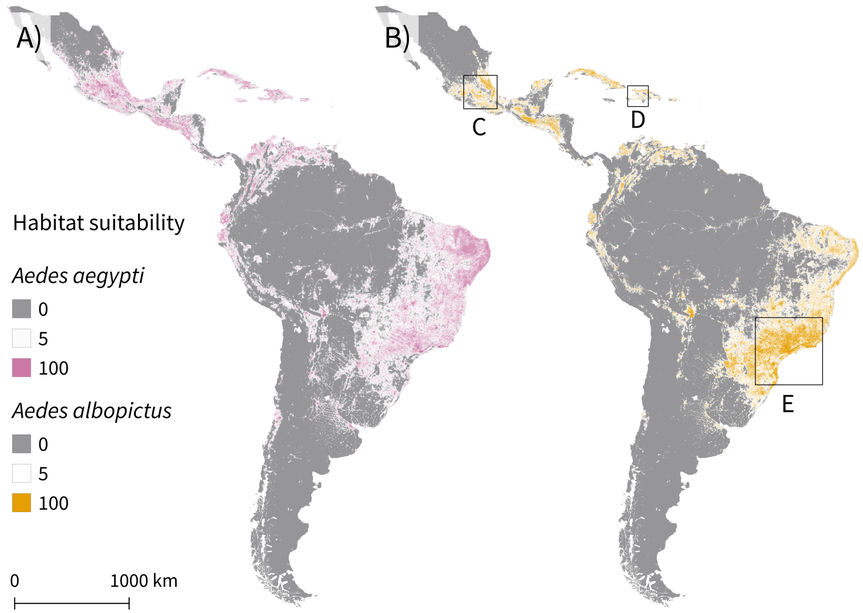
The distributions of mosquito vectors are expected to shift with rising temperatures due to climate change. But other global change patterns, like land cover change and human population growth, are simultaneously occurring. How will these changes interact to shift the future distributions of these vectors? Here, we analyzed how climate, land cover, and human population density regulate and predict habitat for two mosquito species, *Aedes aegypti* and *Ae. albopictus*, the primary vectors of dengue, Zika and chikungunya.

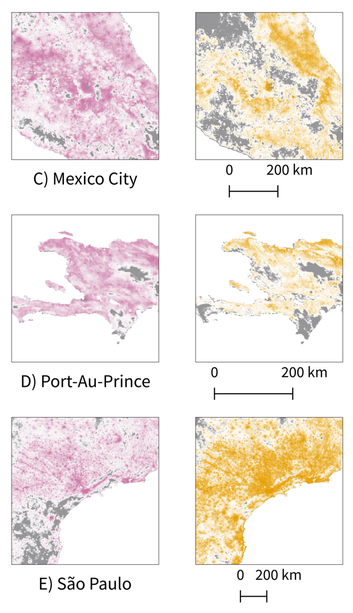
Research questions

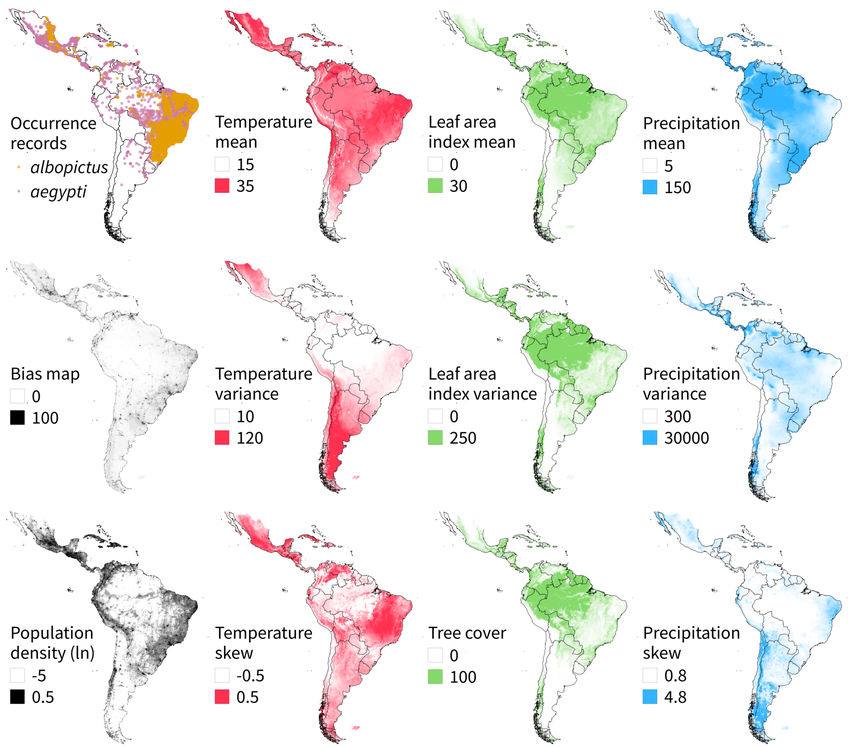
1. How do environmental response curves derived from vector occurrence data compare to lab-derived responses?
2. Based on these environmental response curves, which drivers best predict the spatial distribution of each vector?
3. Are environmental responses derived from large-scale (continental) occurrence data consistent at fine spatial scales?

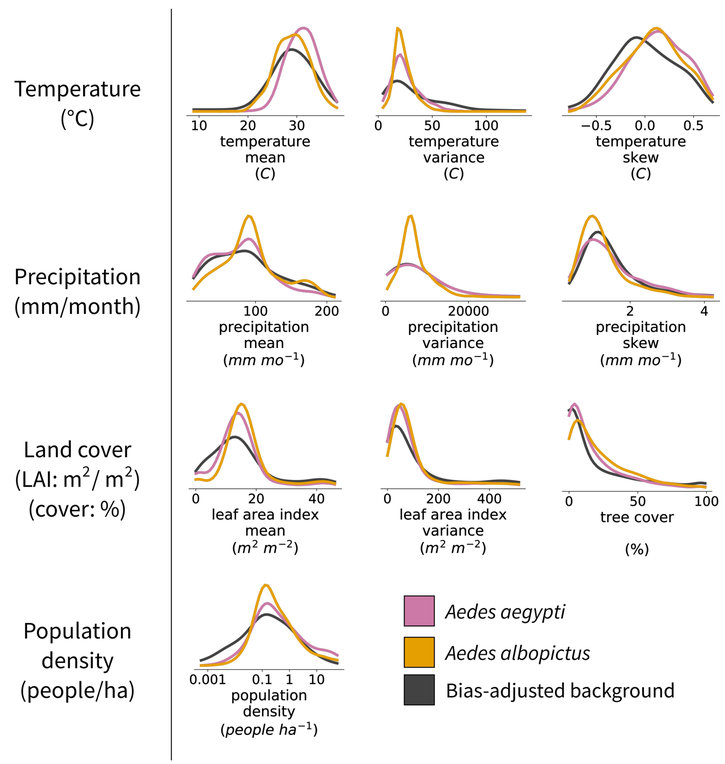
Methods

Using species distribution models, we analyzed 6,317 *Ae. aegypti* occurrence records, 3,629 *Ae. albopictus* records, 10 satellite-derived environmental covariates, and two independent field surveys over 134 sites. Occurrence records were aggregated from two global datasets. All covariates were measured at or resampled to 1 km^2 grid cells. We derived pixel-wise mean, variance, and skewness statistics from all MODIS temperature (°C) and TRMM precipitation measurements (mm mo^{-1}) over 2002-2017, capturing 16 years of spatial and temporal climatic variation. Land cover covariates included tree cover (%) and the mean and variance of leaf area index (LAI; m^2 m^{-2}) from 2002-2017. We included just one human population covariate, population density (people ha^{-1}), which was natural log-transformed. We used the target group selection method to generate a sampling bias map. We assumed that neither the vectors nor the vector sampling efforts were uniformly distributed. Suitability was therefore calculated relative to a statistically derived null distribution of locations where people live to account for these biases







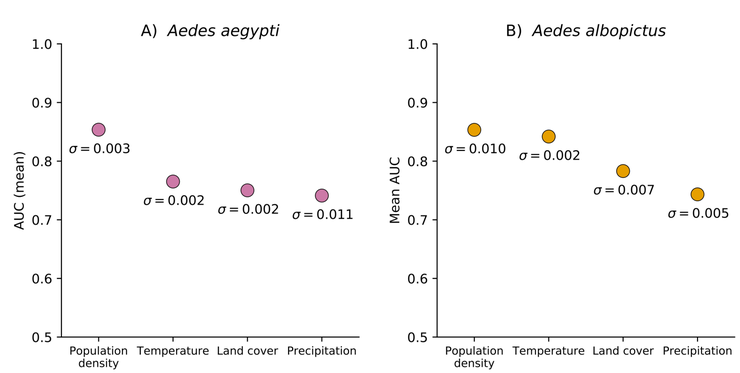


Results

Ae. albopictus tended to occur in areas with slightly lower mean temperatures (mean = 29.1 °C) than *Ae. aegypti* (mean = 31.0 °C), and these mean observed values are slightly higher than lab-derived predictions of dengue transmission optima (26.4 °C for *Ae. albopictus*, 29.1 °C for *Ae. aegypti*). *Ae. albopictus* records were not significantly different from the background mean temperature ($p = 0.738$), but were significantly different from *Ae. aegypti* distributions ($p < 0.001$). Both vectors were observed in areas of higher population density than would be predicted by randomly sampling human populations, and in areas with low temperature variance, in areas skewed towards higher extreme temperatures, and with high variance in leaf area index (all distributions tested for stochastic equality using the two-sided, nonparametric Brunner-Munzel test, all with $p < 0.001$).

For Ae. aegypti, we found that human population density alone best predicted habitat suitability (AUC $\mu = 0.853$, $\sigma = 0.003$), followed by temperature (AUC $\mu = 0.765$, $\sigma = 0.002$), land cover (AUC $\mu = 0.750$, $\sigma = 0.002$), and precipitation (AUC $\mu = 0.741$, $\sigma = 0.010$). We found similar trends for *Ae. albopictus*, where population density best predicted habitat suitability (AUC $\mu = 0.853$, $\sigma = 0.010$), followed closely by temperature (AUC $\mu = 0.842$, $\sigma = 0.002$), land cover (AUC $\mu = 0.783$, $\sigma = 0.007$), and precipitation (AUC $\mu = 0.743$, $\sigma = 0.005$).

Population density was the most important covariate for each vector based on both percent contribution (68.4% for *Ae. aegypti*, 48.7% for *Ae. albopictus*) and permutation importance (72.5% for *Ae. aegypti*, 53.1% for *Ae. albopictus*). The next three most important covariates (based on percent contribution) were tree cover (15.5%), mean temperature (5.5%) and precipitation variance (4.0%) for *Ae. aegypti*, and temperature variance (20.3%), tree cover (17.0%) and precipitation variance (7.0%) for *Ae. albopictus*. These final models performed better than any of the independent model runs reported above (cross-validation AUC $\mu = 0.897$, $\sigma = 0.002$ for *Ae. aegypti*, $\mu = 0.917$, $\sigma = 0.002$ for *Ae. albopictus*). The joint spatial predictions cluster around population centers, with differences between vector distributions driven by vector-specific responses to the underlying covariate data.



Ranked importance of environmental covariates

Aedes aegypti			*Aedes albopictus*		
Variable	**Percent contribution**	**Permutation importance**	**Variable**	**Percent contribution**	**Permutation importance**
Population density	68.4	72.5	Population density	48.7	53.1
Land cover - tree cover	15.5	0.6	Temperature - variance	20.3	20.2
Temperature - mean	5.5	6.1	Land cover - tree cover	17	1.8
Precipitation - variance	4	9.3	Precipitation - variance	7	11.6
Temperature - variance	2.9	2.1	Land cover - LAI mean	2.1	1.7
Land cover - LAI variance	2	3.6	Precipitation - mean	1.4	6
Land cover - LAI mean	0.7	2.3	Land cover - LAI variance	1.3	2.4
Precipitation - mean	0.7	2.9	Temperature - mean	1.2	1.1
Temperature - skew	0.2	0.6	Temperature - skew	0.7	0.9
Precipitation - skew	0.1	0	Precipitation - skew	0.3	1.1