Rapid range shifts in African *Anopheles* mosquitoes over the last century

Colin J. Carlson[1,†,*], Ellen Bannon[2,*], Emily Mendenhall[2,3], Timothy Newfield[1,4], Shweta Bansal[1]

Affiliations:

[1] Department of Biology, Georgetown University, Washington, DC 20057, U.S.A.

[2] Science, Technology, and International Affairs Program, Edmund A. Walsh School of Foreign Service, Georgetown University, Washington, DC 20057, U.S.A

[3] Developmental Pathways for Health Research Unit, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

[4] Department of History, Georgetown University, Washington, DC 20057, U.S.A.

[†] Corresponding author: cjc322@georgetown.edu

* These authors contributed equally.

Abstract

Anopheles mosquitoes are the vector of malaria and several neglected tropical diseases, such as lymphatic filariasis and O'nyong'nyong fever. Like many species, mosquitoes are expected to track warming temperatures in a changing climate, possibly introducing disease into previously protected higher-latitude and higher-elevation communities. Tracking range shifts is fundamental for forecasting disease risk, but has proven challenging to do in real-time. Here, we use historical data to trace those shifts in *Anopheles* for the first time. We test for range shifts using a new comprehensive dataset of *Anopheles* occurrences in sub-Saharan Africa, with over 500,000 species-locality pair records spanning 1898 to 2016. We propose a simple regression-based method of measuring range shifts in larger datasets, which identifies a more coherent signal in anopheline range shifts than the Mann-Whitney method popular in ecology. We estimate range-shifting species gained 1.56 meters of elevation annually, and moved southward 6.28 km per year in their outer range limits, a full order of magnitude faster than some "rapid" shifts observed in the literature. We expect these results to have major implications for malaria control work in sub-Saharan Africa, and for our broader picture of vector responses to climate change.

Introduction

In the coming century, scientific consensus predicts a massive redistribution of global biodiversity, including the reservoirs, vectors, and pathogens that are most consequential to human health. [1–3] A seminal 2011 study estimated that species are moving higher in elevation and latitude at a median rate of roughly 11 meters per decade and 17 kilometers per decade, respectively [4]; crop pests and pathogens have been estimated to be moving at a slightly faster pace of roughly 3 kilometers a year. [5] But despite the widespread model prediction and oft-repeated assumption that mosquitoes and other human disease vectors will track climate change, very little work explicitly documents these shifts, with no mosquitoes included in the 2011 estimate. Perhaps the most is known about the global expansion of *Aedes aegypti* and *Ae. albopictus*, which a recent study suggests have expanded up to 250 and 150 kilometers per year respectively. [6] But these are some of the best-documented vector ranges [7], and their rapid velocity is indicative of several global wavefronts of invasion in new landscapes, not climate change acting on equilibrium ranges. Almost no data exists on range shifts of non-invasive mosquitoes, and we know of no studies documenting a long-term signal in *Anopheles* mosquitoes, the vectors of malaria worldwide.

The genus *Anopheles* (Diptera: Culicidae) contains roughly 460 species of mosquito found on every inhabited continent. Roughly one quarter of species have the ability to transmit infectious diseases, including O'nyong'nyong virus, lymphatic filiariasis, and most significantly malaria (*Plasmodium* spp.). Malaria vectors exist all over the world, but the majority of the disease burden, especially from the most clinically severe species (*P. falciparum*), lies in sub-Saharan Africa. In 2017, of the 219 million cases of malaria worldwide, 92% of cases and 93% of deaths occurred in sub-Saharan Africa. [8] As for most vector-borne diseases, the severity and stability of malaria is determined by a handful of interacting and often covarying sociecological factors, including poverty, primary healthcare, migration, land use change, and climate. [9] As a result of heterogeneity in these factors, the burden of malaria is heavily clustered in national and regional hotspots; in 2017, Nigeria, the Democratic Republic of the Congo, Mozambique, India, and Uganda alone accounted for almost half of all cases. [8] As a consequence of vector and pathogen limits, areas of lower temperatures and higher elevation have historically been protected from malaria [9], especially in East Africa (Burundi, Eritrea, Ethiopia, Kenya, Rwanda,

and Tanzania) and isolated mountain ranges in countries like Cameroon, the DRC, and Zimbabwe. [10] However, in a changing climate, many fear warming temperatures may allow malaria to infiltrate these high altitude regions.

The problem of documenting range shifts in malaria is complicated by the semi-independence of the pathogen, the vector, human populations, and underlying changes in climate, land use, healthcare, and drug resistance. Since the 20th century, several explosive epidemics of malaria have been observed at high elevations in east Africa. [11,12] In the early 2000s, researchers proposed increases in these outbreaks might be driven by a changing climate [13], but some originally argued these trends were weak [14], or were driven by emerging drug resistance and failures of vector control, and not climate change. [15,16] Over time, these data been carefully re-evaluated alongside new evidence, with current consensus largely indicating temperature-linked elevational shifts in malaria in countries such as Burundi, Ethiopia, Kenya, Rwanda, and Uganda. [9,17,18] The thermal bounds of malaria transmission are now fairly well resolved [19,20], and most studies project that areas suitable for malarial transmission will experience net increases across sub-Saharan Africa, and low-temperature areas protected from malaria will contract significantly. [21–24] But most climate models of *Plasmodium* simply assume mosquito range shifts will not be a limiting factor [22], and most work has focused on malaria incidence separate from vector range boundaries.

Despite a handful of anecdotal records noting mosquito arrival at higher elevations [25], no broad evidence as yet exists documenting anopheline mosquito range shifts. In this study, we follow an approach common in global change biology [26] to test for evidence of range shifts in historical records of mosquito occurrences. We focus on *Anopheles* mosquitoes in sub-Saharan Africa, specifically on the dominant vectors of malaria. We test the idea that mosquitoes are moving southwards (away from the equator) and upwards (gaining elevation), by looking for a historical signal of mosquito range changes in the 20th century. (We focus on range shifts at the southern margin, measured in absolute latitude, given that the Sahel poses a hard dispersal barrier in most cases.) In answering these, we aim to provide what we believe is the first data-driven estimate of the velocity of mosquito range shifts at a continental scale, outside of those occurring during a global biological invasion. [6]

Methods

Data

To investigate evidence of range shifts in *Anopheles* mosquitoes, we used a recently published compendium of occurrence data, focused on sub-Saharan Africa over the interval 1898 to 2016. [27] These data are a compendium of several sources, including both deliberate methodic records (entomological surveys from malaria research and control programs) and opportunistic data collected incidentally to other research projects. Data sources include such a mix of carefully maintained datasets, technical reports, theses and individual studies, and archival records that it is difficult to generalize any uniform sampling biases in the data over space and time. There are noticeable variations in completeness of the data due to the Global Malaria Eradication Programme (1955-1969) and subsequent neglect of malaria projects in Africa for several decades. **(Figure S1)** However, even when attention shifted elsewhere in the post-GMEP era, over 5,000 species-locality pairs were generated every year—an essentially unparalleled depth of data for such a narrowly defined taxonomic group.

To format these data for our study, we expanded every survey with a start and end year one or more years apart into a separate record for every year. We eliminated all secondary vectors and concatenated records of dominant vector presence as separate occurrences in year/location pairs. This produced a total of 504,314 unique records from 48 countries, spanning 1898 to 2016. For elevational data, we used the GTOPO30 global digital elevation model (DEM) downloaded as a 30 arc-second resolution grid for Africa from Data Basin (www.databasin.org). We extracted elevation for each distinct occurrence record, using the 'raster' package in R version 3.3.2.

Region delineation

For elevation analyses, we aggregated countries into four regions of Sub-Saharan Africa, defined based on the Global Burden of Disease study and previously used to describe population at risk from mosquito-borne disease. [28] Those regions are:

- **Central Africa:** Angola, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Gabon, Republic of Congo

- **East Africa:** Burundi, Comoros, Djibouti, Eritrea, Ethiopia, Kenya, Madagascar, Malawi, Mozambique, Reunion, Rwanda, Somalia, South Sudan, Sudan, Tanzania, Uganda, Zambia, Mayotte, Zanzibar
- **Southern Africa:** Botswana, Lesotho, Namibia, South Africa, Swaziland, Zimbabwe
- **West Africa:** Benin, Burkina Faso, Cameroon, Cape Verde, Chad, Cote d'Ivoire, Gambia, Ghana, Guinea Bissau, Liberia, Mali, Mauritania, Nigeria, Niger, Guinea, Sao Tome and Principe, Senegal, Sierra Leone, Togo

Models

Our study design reflects the need for comparable estimates of elevational and latitudinal shifts to most animal and plant species, allowing us to avoid a handful of methodological problems. First, by focusing only on southward latitudinal shifts, we avoid the question of what the maximum traveling speed of *Anopheles* ranges is in any direction, which would require more complicated approaches, like spatial generalized additive models or kernel methods. Second, we assume that *Anopheles* ranges started as close to equilibrium as any other species did in the 20th century, and that their spread did not follow a traveling wave-front. [6,29] By making this assumption, we focus on simple linear and directional trends in range shifts, and largely avoid any questions about underlying patterns of resistance on the landscape, or "points of introduction" (which would be a poor model for the underlying process). Finally, we assume that the question of interest is range *margin* shifts and not range *core* shifts, which would reflect more of the complex geography of malaria across African nations and over a century of social shifts. [30] Future work could potentially follow on this by using methods which test for, and then fit, unimodal curves in response to environmental gradients like elevation. [31]

Within these constraints, we chose to try two basic methods of testing for range shifts. The first is adapted from the classic ecological literature on climate-driven range shifts, and involves using a Mann-Whitney U test to compare the top or bottom *n* values (usually n = 10; see studies cited in [4]) of elevation or latitude between two non-overlapping intervals. The range shift velocity assigned is the difference in means divided by the time between the midpoints of the two intervals. While this method became extremely popular in the first decade of the 2000s [31–34], it comes with clear disadvantages, namely that it is designed for the kind

of resurveys that are common in community ecology. For continuously-recorded data, it has two forms of information loss: first in the aggregation of discrete years into intervals, and second in the discarding of data in-between the intervals.

As a simple alternative to the Mann-Whitney approach, we propose a comparatively simple, regression-based approach loosely adapted from Bebber *et al.* [5], in which the maximum n points (for elevation or latitude) are taken every year and analyzed using regression, with species as a fixed effect, and with year nested within species. The number of points used represents a tradeoff between using a few points capturing the most extreme values, which give the best approximation of where range edges lie, and using more data, which increases statistical power but also risks muddling the distinction between the range core and the range edge. In the main text we use $n = 3$ points, which already increases the number of records used over an order of magnitude from the Mann-Whitney method. However, in the supplement we show the same analyses using $n = 10$, and using an optimal linear estimator as a "distance-to-edge" model. [35]

We used the new 'rangeshifts' R package to implement both of these analyses. In both approaches, we applied a significance cutoff of $p = 0.05$ to determine whether range shifts were significant. For elevation and latitude, we used Mann-Whitney tests to compare species ranges based on a baseline before the start of the Global Malaria Eradication Programme, and ten years after it ended to the present (1898—1955 vs. 1979—2019). We only used the Mann-Whitney approach to test for significance, and not to quantify range shift speed, given the large period of aggregation we used. For elevation, we repeated the Mann-Whitney method separating countries into five regions (North, West, East, Central, and Southern Africa), delineated based on the Global Burden of Disease study regions.

We then analyzed both elevation and latitude using regression approach, with the maximum $n = 3$ points from every year. For elevation, we treated geographic divisions as a random effect to account for spatial heterogeneity in the landscape (and the fact that several elevational fronts can be expanding within a single range). Here, we decided our data was complete enough—and Africa is a large enough continent—that we used country as that random effect. (This also allowed us to decompose range shifts in a way we could not with the Mann-Whitney tests—with 49 countries and 26 species represented in the dataset, there would be a total of 1,274 possible pairwise comparisons.)

Results

Our models suggested that the majority of species have experienced at least some range shift over the past few years. Using the Mann-Whitney approach for maximum latitude, we found that 16 species exhibited a significant global shift including two significant contractions (northwards towards the equator). For maximum elevation, 17 of 26 exhibited a significant global shift, including six contractions (downwards). It is possible that the sign-reversed shifts represent actual range shifts driven by vector control either during the Global Malaria Eradication Programme (GMEP) or occurring since, corresponding to an overall century-long reduction in *Plasmodium falciparum* prevalence due in at least some part to vector control. [30] It is equally plausible, though, that they are an artefact of the crude Mann-Whitney approach and the information loss that is required to run it.

By region, results of the Mann-Whitney tests on elevation were even more mixed. In West Africa, 6 species (out of 21 with enough data to run comparisons) had a significant shift, all being range expansions. In East Africa, 13 of 22 total were significant, including 8 expansions and 5 contractions. In Central Africa, 10 of 13 were significant, but only 2 were expansions. Data was most limited in Southern Africa, where five of seven possible tests were significant, and all were contractions. Overall, these results offer little cohesive explanation of long-term trends, and highlight the downside of the interval comparison method—especially in the number of species which had to be omitted due to sample size issues.

The linear regression approach, on the other hand, painted a more cohesive picture. For latitude, we found that 24 out of 26 species had a significant trend (adjusted $R^2 = 0.947$); all but two were negative. (**Figure 2**) Species with a significant trend displayed an average (±s.e.) range velocity of 6.28 ± 1.4 km per year (5.92 ± 1.21 for all species regardless of species:year intercept significance). For elevation, in the mixed-effects model (conditional $R^2 = 0.674$), we found that 22 species had a significant trend, of which 19 were positive. (**Figure 3**) Species had an average significant range shift of 1.56 ± 0.3 meters per year (for all species: 1.27 ± 0.27). We found no significant correlation between latitudinal and elevational shift (**Figure 4**), possibly suggesting different traits predispose those shifts (per a similar finding by [34]), or that species do not differ in dispersal capacity, and are probably tracking local climate and anthropogenic landscapes.

Discussion

Our study presents compelling—and concerning—evidence of rapid range shifts in anopheline mosquitoes. At a surprising maximum pace of 3.8 meters per year in elevation and 20 kilometers per year in latitude, these shifts are more than an order of magnitude greater than others considered "rapid" for climate-driven shifts. [4] While still an order of magnitude less than the maximum speeds observed during the invasion of *Aedes aegypti* and *Aedes albopictus* in Europe and the United States [6], ours are the first estimates that set the pace of native range shifts, a process that is almost universally slower. In comparison to prior estimates of the velocity of climate change in Africa (with a maximum around 10 km per year; [36]), our results suggest that mosquitoes—especially the vectors most responsible for the burden of malarial disease—will have little trouble keeping pace with shifting thermal optima. While this largely agrees with modeling projections, it challenges the long-standing idea in historical epidemiology that mosquito ranges are mostly stationary over decades, centuries, or millennia. [37,38]

Previous studies have either focused on modeling vector shifts or pathogen shifts [39], and many models of vector-borne illness have been qualified by a disclaimer that worst-case scenarios assume the presence of mosquitoes, without much certainty or data about their range expansions. Without apparent dispersal constraints on mosquitoes, evidence seems unanimous that most tropical and sub-tropical areas previously protected from vector-borne disease are likely to experience the onset of new health regimes in the immediate future. These projections agree with those made in parallel work on arboviruses, which has predicted future expansions in high-altitude and high-latitude areas for chikungunya, dengue, Zika, and other illnesses. Within countries, prioritization schemes for vector control and surveillance will have to change rapidly to include new at-risk areas. In Ecuador, for example, models have projected that under the most extreme climate change scenarios, the range of the *Aedes aegypti* mosquito should expand 4,215 km^2 into mountainous terrain, impacting over 12,000 people. [40] But at the global scale, the number of countries facing these problems will also increase, with *Aedes aegypti* and *Ae. albopictus* expected in 159 and 197 countries by 2080. [6] As *Anopheles* shift to the south and to higher elevations, they will similarly produce new regional populations at risk from malaria, lymphatic filariasis, and other pathogens.

Mosquito range shifts during the 20th century were influenced by several other factors in addition to climate change, and the same is true for malaria. The impact that vector shifts have on the global incidence of malaria will depend on several interacting (and often correlated) factors, including deforestation and land degradation [41,42], insecticide resistance in mosquitoes [43], emerging drug resistance [44,45], migration and human rights crises [46,47], poverty [38], and conflict between malaria control and other aspects of sustainable development. [49] In combination with these problems, the ability of malaria vectors to track shifting climate optima at the pace of climate change is immensely problematic for control programs, and the already stretched-thin healthcare infrastructure that many countries will struggle to maintain in the face of climate change. New rapid diagnostics for malaria, and global efforts to integrate and bolster mosquito surveillance, will help researchers tackle these threats, as will future efforts to maintain and expand long-term datasets like the one we use here. [50–52] We recommend that focusing some of these efforts in the highlands of eastern Africa and Madagascar, and on the southern range limits of *Anopheles gambiae* complex, will likely be the strongest line of defense against the expansion of malaria epidemics into new populations in a changing climate.

Author Contributions: EB initiated the idea for the study. CJC and EB collected data. CJC performed all analyses. All authors contributed to the writing and editing of the manuscript.

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Figures

Figure 1. Number of locality-species pairs by year increases rapidly, peaks during the GEMP, declines after and returns in recent years.

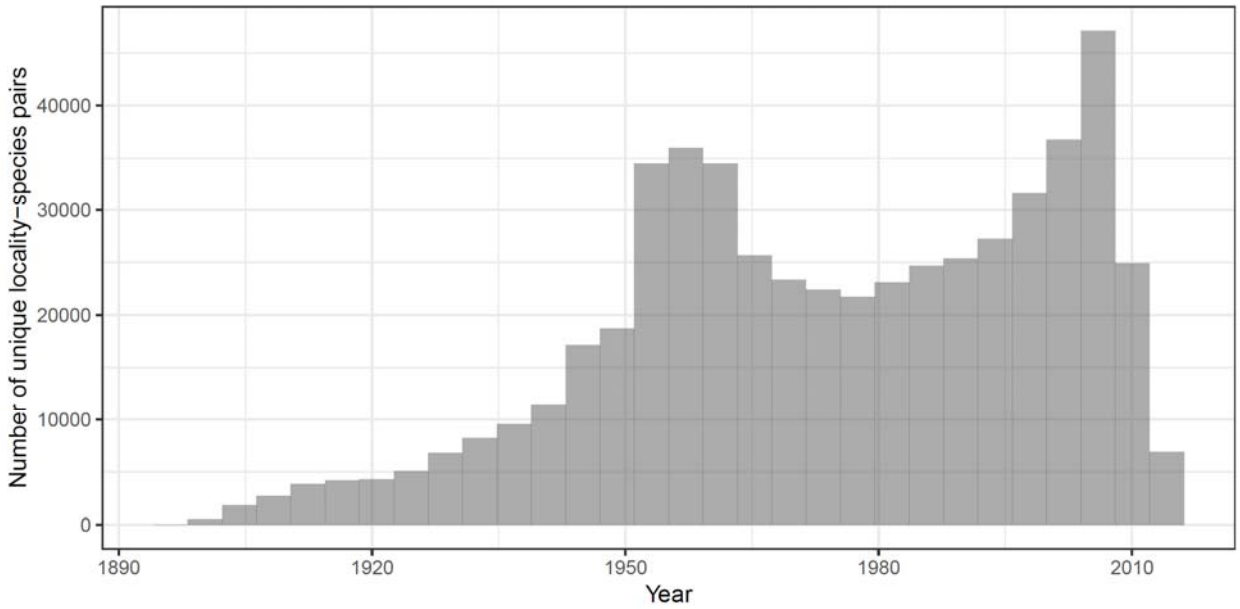

Figure 2. A century of range margin shifts in elevation and absolute latitude. Lines represent species' individual trends estimated from a linear model. Bounds are the standard error from linear models.

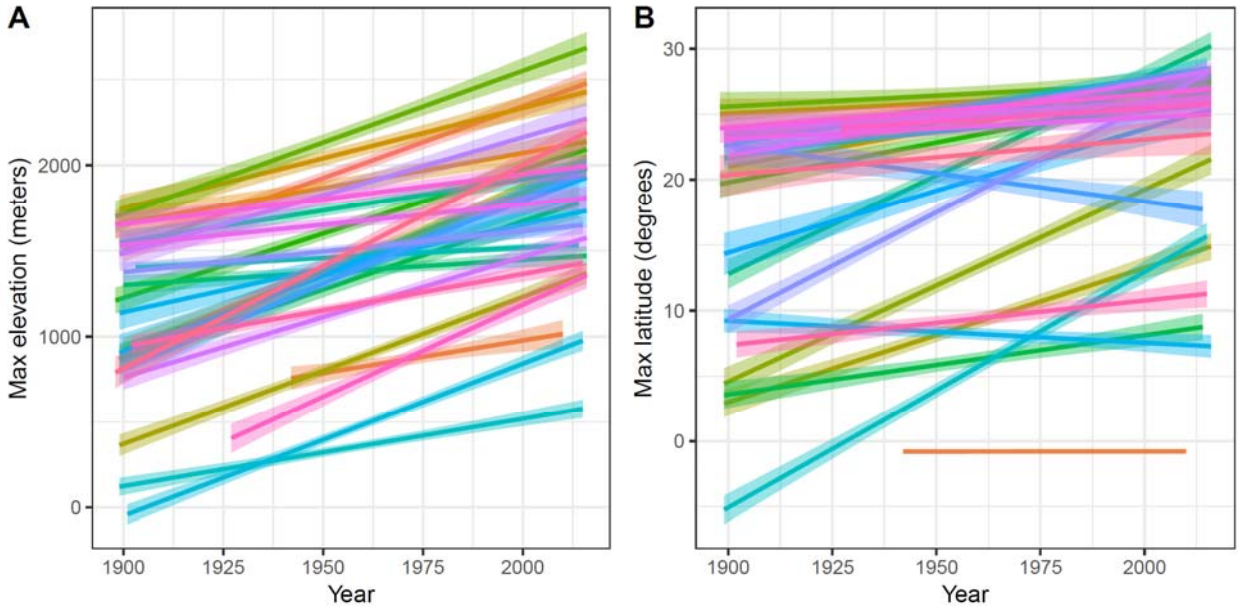

Figure 3. Latitudinal shifts estimated using the regression approach. (Units in left panel are degrees of absolute latitude).

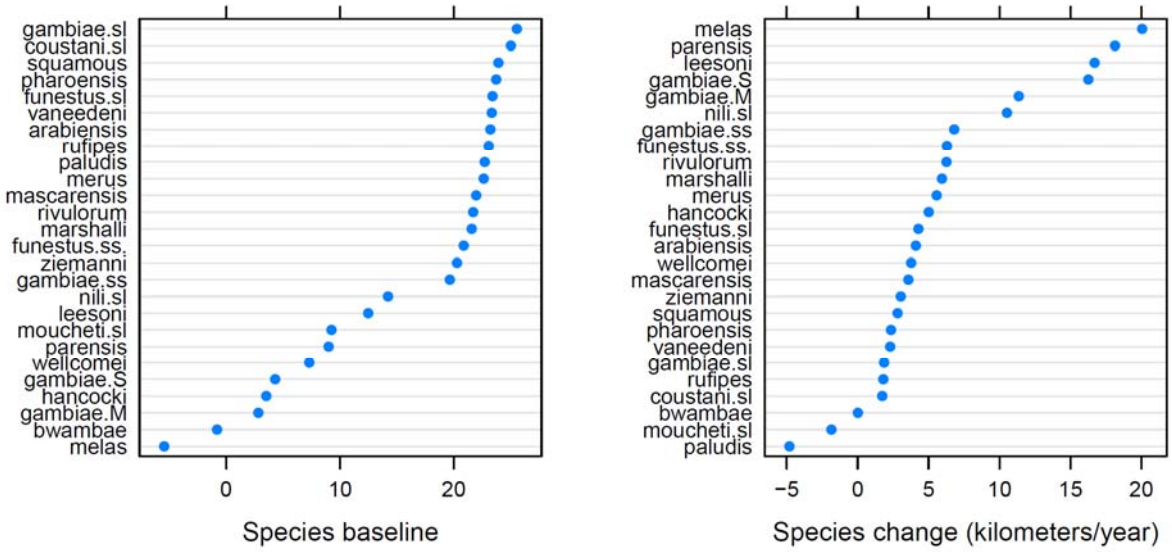

Figure 4. Elevational shifts estimated using the regression approach.

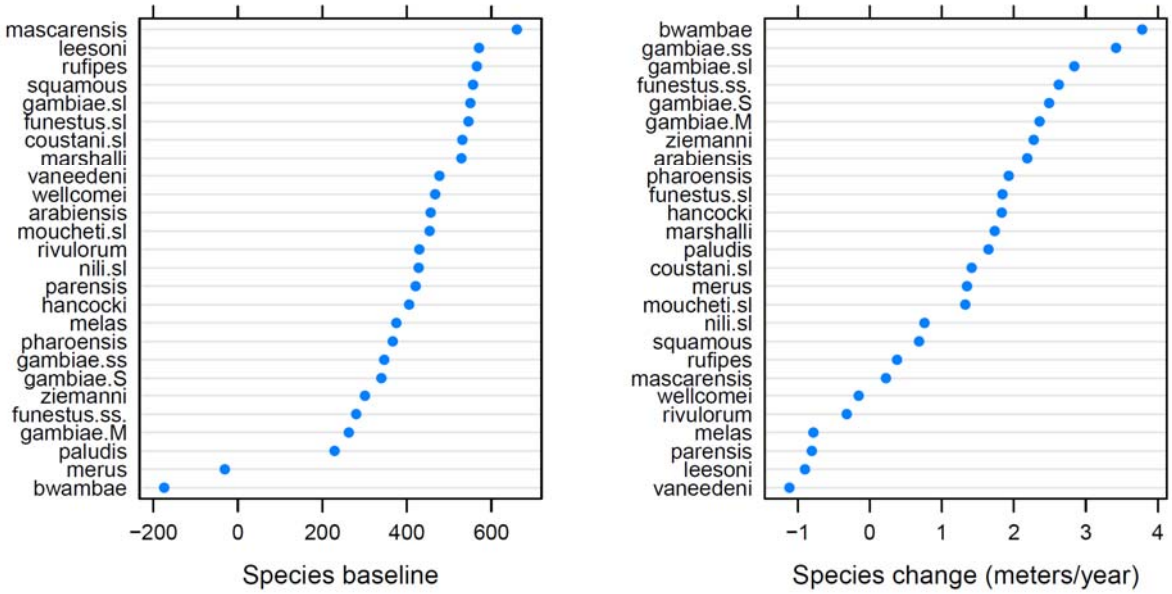
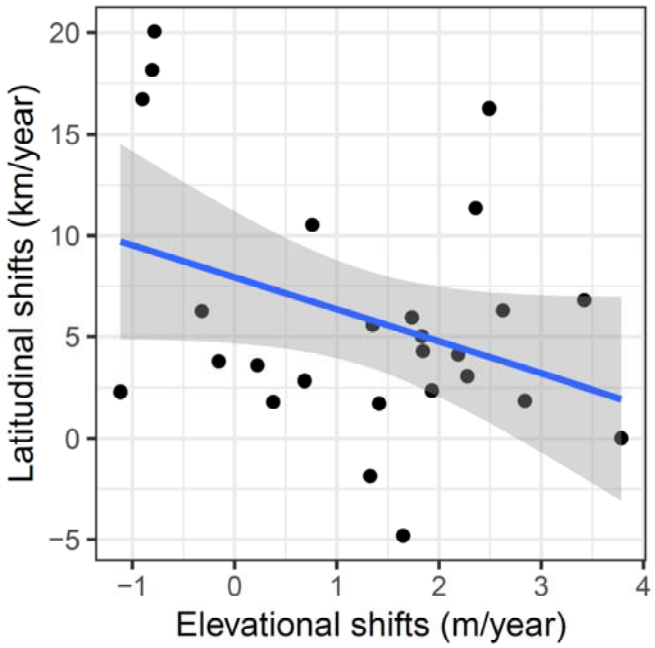
Figure 5. Maximum-based elevational and latitudinal shifts had no significant relationship (p = 0.076), implying the landscapes species are moving on may determine more about these shifts than intrinsic, species-level dispersal capacity.