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

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14

15   **Abstract**

16

17   *Anopheles* mosquitoes are the vector of malaria and several neglected tropical diseases, such as

18   lymphatic filariasis and O'nyong'nyong fever. Like many species, mosquitoes are expected to

19   track warming temperatures in a changing climate, possibly introducing disease into previously

20   protected higher-latitude and higher-elevation communities. Tracking range shifts is fundamental

21   for forecasting disease risk, but has proven challenging to do in real-time. Here, we use historical

22   data to trace those shifts in *Anopheles* for the first time. We test for range shifts using a new

23   comprehensive dataset of *Anopheles* occurrences in sub-Saharan Africa, with over 500,000

24   species-locality pair records spanning 1898 to 2016. We propose a simple regression-based

25   method of measuring range shifts in larger datasets, which identifies a more coherent signal in

26   anopheline range shifts than the Mann-Whitney method popular in ecology. We estimate range-

27   shifting species gained 1.56 meters of elevation annually, and moved southward 6.28 km per

28   year in their outer range limits, a full order of magnitude faster than some "rapid" shifts observed

29   in the literature. We expect these results to have major implications for malaria control work in

30   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,

62   and Tanzania) and isolated mountain ranges in countries like Cameroon, the DRC, and

63   Zimbabwe. [10] However, in a changing climate, many fear warming temperatures may allow

64   malaria to infiltrate these high altitude regions.

65   The problem of documenting range shifts in malaria is complicated by the semi-

66   independence of the pathogen, the vector, human populations, and underlying changes in

67   climate, land use, healthcare, and drug resistance. Since the 20th century, several explosive

68   epidemics of malaria have been observed at high elevations in east Africa. [11,12] In the early

69   2000s, researchers proposed increases in these outbreaks might be driven by a changing climate

70   [13], but some originally argued these trends were weak [14], or were driven by emerging drug

71   resistance and failures of vector control, and not climate change. [15,16] Over time, these data

72   been carefully re-evaluated alongside new evidence, with current consensus largely indicating

73   temperature-linked elevational shifts in malaria in countries such as Burundi, Ethiopia, Kenya,

74   Rwanda, and Uganda. [9,17,18] The thermal bounds of malaria transmission are now fairly well

75   resolved [19,20], and most studies project that areas suitable for malarial transmission will

76   experience net increases across sub-Saharan Africa, and low-temperature areas protected from

77   malaria will contract significantly. [21–24] But most climate models of *Plasmodium* simply

78   assume mosquito range shifts will not be a limiting factor [22], and most work has focused on

79   malaria incidence separate from vector range boundaries.

80   Despite a handful of anecdotal records noting mosquito arrival at higher elevations [25],

81   no broad evidence as yet exists documenting anopheline mosquito range shifts. In this study, we

82   follow an approach common in global change biology [26] to test for evidence of range shifts in

83   historical records of mosquito occurrences. We focus on *Anopheles* mosquitoes in sub-Saharan

84   Africa, specifically on the dominant vectors of malaria. We test the idea that mosquitoes are

85   moving southwards (away from the equator) and upwards (gaining elevation), by looking for a

86   historical signal of mosquito range changes in the 20th century. (We focus on range shifts at the

87   southern margin, measured in absolute latitude, given that the Sahel poses a hard dispersal

88   barrier in most cases.) In answering these, we aim to provide what we believe is the first data-

89   driven estimate of the velocity of mosquito range shifts at a continental scale, outside of those

90   occurring during a global biological invasion. [6]

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92

93   **Methods**

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95   *Data*

96   To investigate evidence of range shifts in *Anopheles* mosquitoes, we used a recently published

97   compendium of occurrence data, focused on sub-Saharan Africa over the interval 1898 to 2016.

98   [27] These data are a compendium of several sources, including both deliberate methodic records

99   (entomological surveys from malaria research and control programs) and opportunistic data

100   collected incidentally to other research projects. Data sources include such a mix of carefully

101   maintained datasets, technical reports, theses and individual studies, and archival records that it

102   is difficult to generalize any uniform sampling biases in the data over space and time. There are

103   noticeable variations in completeness of the data due to the Global Malaria Eradication

104   Programme (1955-1969) and subsequent neglect of malaria projects in Africa for several

105   decades. **(Figure S1)** However, even when attention shifted elsewhere in the post-GMEP era,

106   over 5,000 species-locality pairs were generated every year—an essentially unparalleled depth of

107   data for such a narrowly defined taxonomic group.

108   To format these data for our study, we expanded every survey with a start and end year

109   one or more years apart into a separate record for every year. We eliminated all secondary

110   vectors and concatenated records of dominant vector presence as separate occurrences in

111   year/location pairs. This produced a total of 504,314 unique records from 48 countries, spanning

112   1898 to 2016. For elevational data, we used the GTOPO30 global digital elevation model (DEM)

113   downloaded as a 30 arc-second resolution grid for Africa from Data Basin (www.databasin.org).

114   We extracted elevation for each distinct occurrence record, using the 'raster' package in R

115   version 3.3.2.

116

117   ***Region delineation***

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119   For elevation analyses, we aggregated countries into four regions of Sub-Saharan Africa, defined

120   based on the Global Burden of Disease study and previously used to describe population at risk

121   from mosquito-borne disease. [28] Those regions are:

122   • **Central Africa:** Angola, Central African Republic, Democratic Republic of the Congo,

123   Equatorial Guinea, Gabon, Republic of Congo

124   •   **East Africa:** Burundi, Comoros, Djibouti, Eritrea, Ethiopia, Kenya, Madagascar,

125   Malawi, Mozambique, Reunion, Rwanda, Somalia, South Sudan, Sudan, Tanzania,

126   Uganda, Zambia, Mayotte, Zanzibar

127   •   **Southern Africa:** Botswana, Lesotho, Namibia, South Africa, Swaziland, Zimbabwe

128   •   **West Africa:** Benin, Burkina Faso, Cameroon, Cape Verde, Chad, Cote d'Ivoire,

129   Gambia, Ghana, Guinea Bissau, Liberia, Mali, Mauritania, Nigeria, Niger, Guinea, Sao

130   Tome and Principe, Senegal, Sierra Leone, Togo

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132   *Models*

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134   Our study design reflects the need for comparable estimates of elevational and latitudinal shifts

135   to most animal and plant species, allowing us to avoid a handful of methodological problems.

136   First, by focusing only on southward latitudinal shifts, we avoid the question of what the

137   maximum traveling speed of *Anopheles* ranges is in any direction, which would require more

138   complicated approaches, like spatial generalized additive models or kernel methods. Second, we

139   assume that *Anopheles* ranges started as close to equilibrium as any other species did in the 20th

140   century, and that their spread did not follow a traveling wave-front. [6,29] By making this

141   assumption, we focus on simple linear and directional trends in range shifts, and largely avoid

142   any questions about underlying patterns of resistance on the landscape, or "points of

143   introduction" (which would be a poor model for the underlying process). Finally, we assume that

144   the question of interest is range *margin* shifts and not range *core* shifts, which would reflect

145   more of the complex geography of malaria across African nations and over a century of social

146   shifts. [30] Future work could potentially follow on this by using methods which test for, and

147   then fit, unimodal curves in response to environmental gradients like elevation. [31]

148   Within these constraints, we chose to try two basic methods of testing for range shifts.

149   The first is adapted from the classic ecological literature on climate-driven range shifts, and

150   involves using a Mann-Whitney U test to compare the top or bottom *n* values (usually n = 10;

151   see studies cited in [4]) of elevation or latitude between two non-overlapping intervals. The

152   range shift velocity assigned is the difference in means divided by the time between the

153   midpoints of the two intervals. While this method became extremely popular in the first decade

154   of the 2000s [31–34], it comes with clear disadvantages, namely that it is designed for the kind

155   of resurveys that are common in community ecology. For continuously-recorded data, it has two

156   forms of information loss: first in the aggregation of discrete years into intervals, and second in

157   the discarding of data in-between the intervals.

158   As a simple alternative to the Mann-Whitney approach, we propose a comparatively

159   simple, regression-based approach loosely adapted from Bebber *et al.* [5], in which the

160   maximum *n* points (for elevation or latitude) are taken every year and analyzed using regression,

161   with species as a fixed effect, and with year nested within species. The number of points used

162   represents a tradeoff between using a few points capturing the most extreme values, which give

163   the best approximation of where range edges lie, and using more data, which increases statistical

164   power but also risks muddling the distinction between the range core and the range edge. In the

165   main text we use *n = 3* points, which already increases the number of records used over an order

166   of magnitude from the Mann-Whitney method. However, in the supplement we show the same

167   analyses using *n = 10*, and using an optimal linear estimator as a "distance-to-edge" model. [35]

168   We used the new 'rangeshifts' R package to implement both of these analyses. In both

169   approaches, we applied a significance cutoff of $p = 0.05$ to determine whether range shifts were

170   significant. For elevation and latitude, we used Mann-Whitney tests to compare species ranges

171   based on a baseline before the start of the Global Malaria Eradication Programme, and ten years

172   after it ended to the present (1898—1955 vs. 1979—2019). We only used the Mann-Whitney

173   approach to test for significance, and not to quantify range shift speed, given the large period of

174   aggregation we used. For elevation, we repeated the Mann-Whitney method separating countries

175   into five regions (North, West, East, Central, and Southern Africa), delineated based on the

176   Global Burden of Disease study regions.

177   We then analyzed both elevation and latitude using regression approach, with the

178   maximum *n = 3* points from every year. For elevation, we treated geographic divisions as a

179   random effect to account for spatial heterogeneity in the landscape (and the fact that several

180   elevational fronts can be expanding within a single range). Here, we decided our data was

181   complete enough—and Africa is a large enough continent—that we used country as that random

182   effect. (This also allowed us to decompose range shifts in a way we could not with the Mann-

183   Whitney tests—with 49 countries and 26 species represented in the dataset, there would be a

184   total of 1,274 possible pairwise comparisons.)

185

186 **Results**

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188 Our models suggested that the majority of species have experienced at least some range shift

189 over the past few years. Using the Mann-Whitney approach for maximum latitude, we found that

190 16 species exhibited a significant global shift including two significant contractions (northwards

191 towards the equator). For maximum elevation, 17 of 26 exhibited a significant global shift,

192 including six contractions (downwards). It is possible that the sign-reversed shifts represent

193 actual range shifts driven by vector control either during the Global Malaria Eradication

194 Programme (GMEP) or occurring since, corresponding to an overall century-long reduction in

195 *Plasmodium falciparum* prevalence due in at least some part to vector control. [30] It is equally

196 plausible, though, that they are an artefact of the crude Mann-Whitney approach and the

197 information loss that is required to run it.

198   By region, results of the Mann-Whitney tests on elevation were even more mixed. In

199 West Africa, 6 species (out of 21 with enough data to run comparisons) had a significant shift, all

200 being range expansions. In East Africa, 13 of 22 total were significant, including 8 expansions

201 and 5 contractions. In Central Africa, 10 of 13 were significant, but only 2 were expansions. Data

202 was most limited in Southern Africa, where five of seven possible tests were significant, and all

203 were contractions. Overall, these results offer little cohesive explanation of long-term trends, and

204 highlight the downside of the interval comparison method—especially in the number of species

205 which had to be omitted due to sample size issues.

206   The linear regression approach, on the other hand, painted a more cohesive picture. For

207 latitude, we found that 24 out of 26 species had a significant trend (adjusted $R^2 = 0.947$); all but

208 two were negative. (**Figure 2**) Species with a significant trend displayed an average (±s.e.) range

209 velocity of 6.28 ± 1.4 km per year (5.92 ± 1.21 for all species regardless of species:year intercept

210 significance). For elevation, in the mixed-effects model (conditional $R^2 = 0.674$), we found that

211 22 species had a significant trend, of which 19 were positive. (**Figure 3**) Species had an average

212 significant range shift of 1.56 ± 0.3 meters per year (for all species: 1.27 ± 0.27). We found no

213 significant correlation between latitudinal and elevational shift (**Figure 4**), possibly suggesting

214 different traits predispose those shifts (per a similar finding by [34]), or that species do not differ

215 in dispersal capacity, and are probably tracking local climate and anthropogenic landscapes.

216

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.

247   Mosquito range shifts during the 20th century were influenced by several other factors in

248 addition to climate change, and the same is true for malaria. The impact that vector shifts have

249 on the global incidence of malaria will depend on several interacting (and often correlated)

250 factors, including deforestation and land degradation [41,42], insecticide resistance in

251 mosquitoes [43], emerging drug resistance [44,45], migration and human rights crises [46,47],

252 poverty [38], and conflict between malaria control and other aspects of sustainable development.

253 [49] In combination with these problems, the ability of malaria vectors to track shifting climate

254 optima at the pace of climate change is immensely problematic for control programs, and the

255 already stretched-thin healthcare infrastructure that many countries will struggle to maintain in

256 the face of climate change. New rapid diagnostics for malaria, and global efforts to integrate and

257 bolster mosquito surveillance, will help researchers tackle these threats, as will future efforts to

258 maintain and expand long-term datasets like the one we use here. [50–52] We recommend that

259 focusing some of these efforts in the highlands of eastern Africa and Madagascar, and on the

260 southern range limits of *Anopheles gambiae* complex, will likely be the strongest line of defense

261 against the expansion of malaria epidemics into new populations in a changing climate.

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393 **Figures**

394 **Figure 1.** Number of locality-species pairs by year increases rapidly, peaks during the GEMP, declines

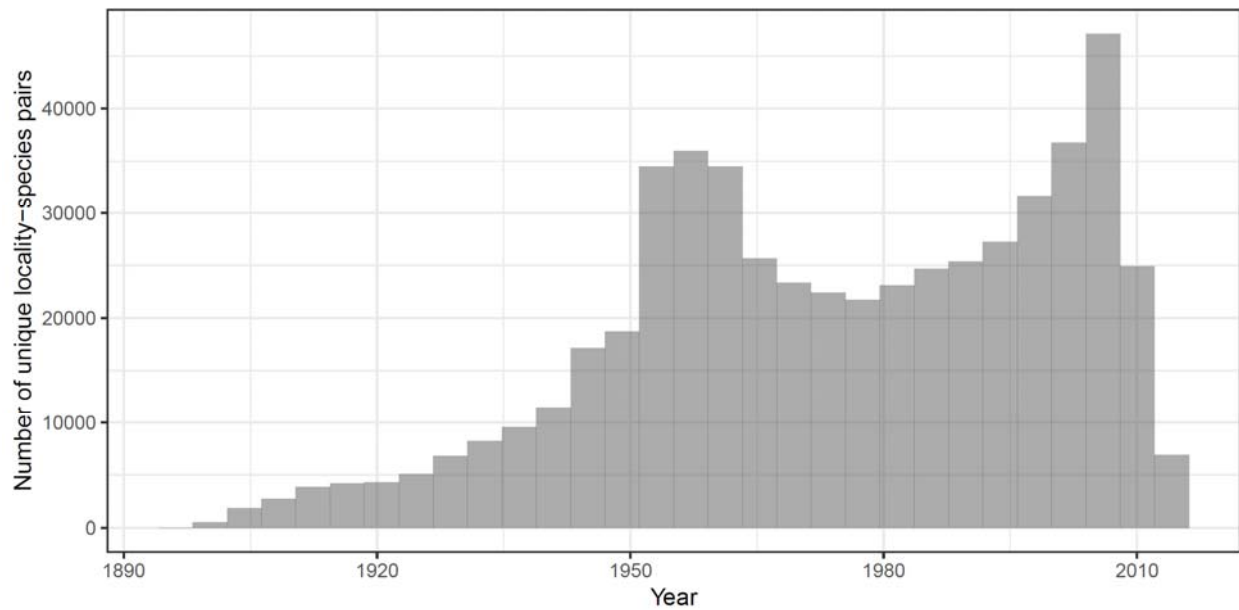395 after and returns in recent years.

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398 **Figure 2.** A century of range margin shifts in elevation and absolute latitude. Lines represent species'

399 individual trends estimated from a linear model. Bounds are the standard error from linear models.
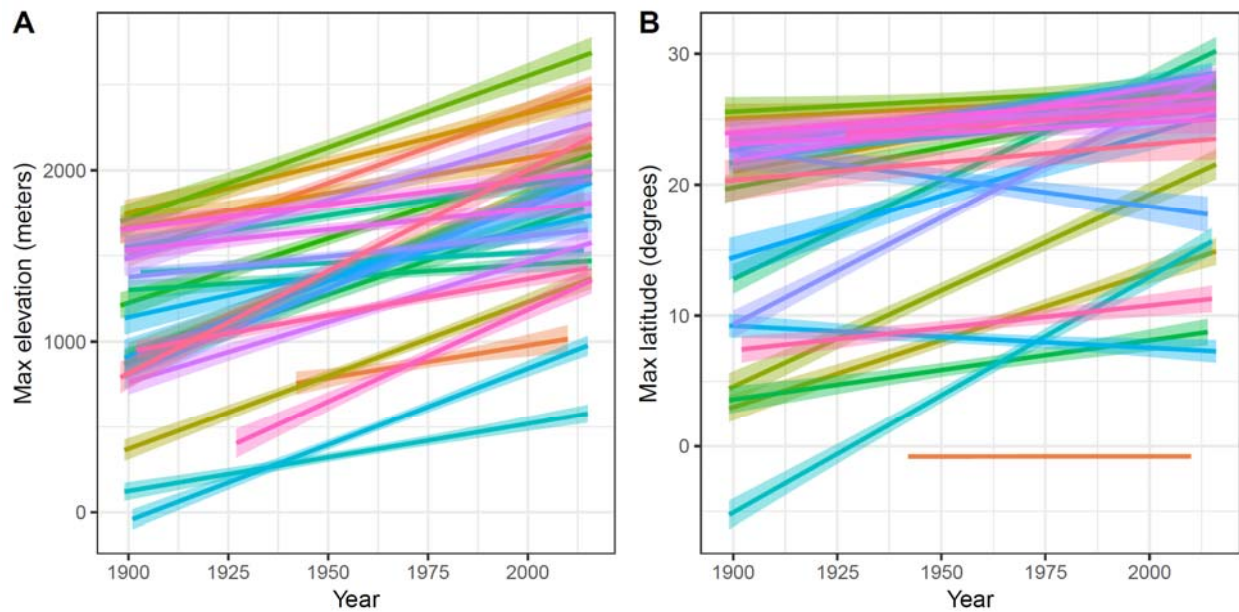
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404   **Figure 3.** Latitudinal shifts estimated using the regression approach. (Units in left panel are degrees of
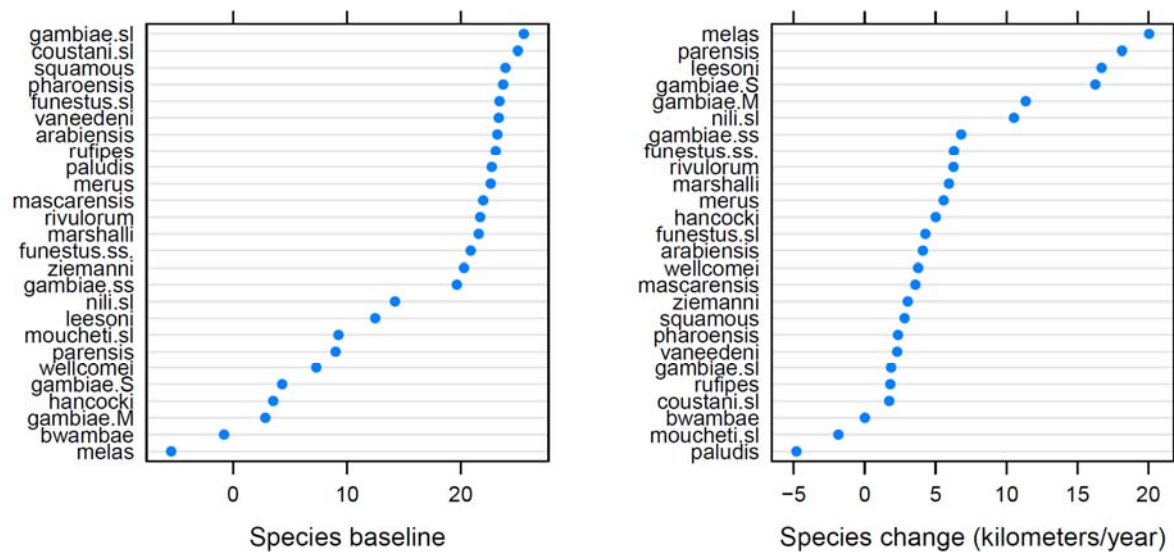
405   absolute latitude).

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407   **Figure 4.** Elevational shifts estimated using the regression approach.
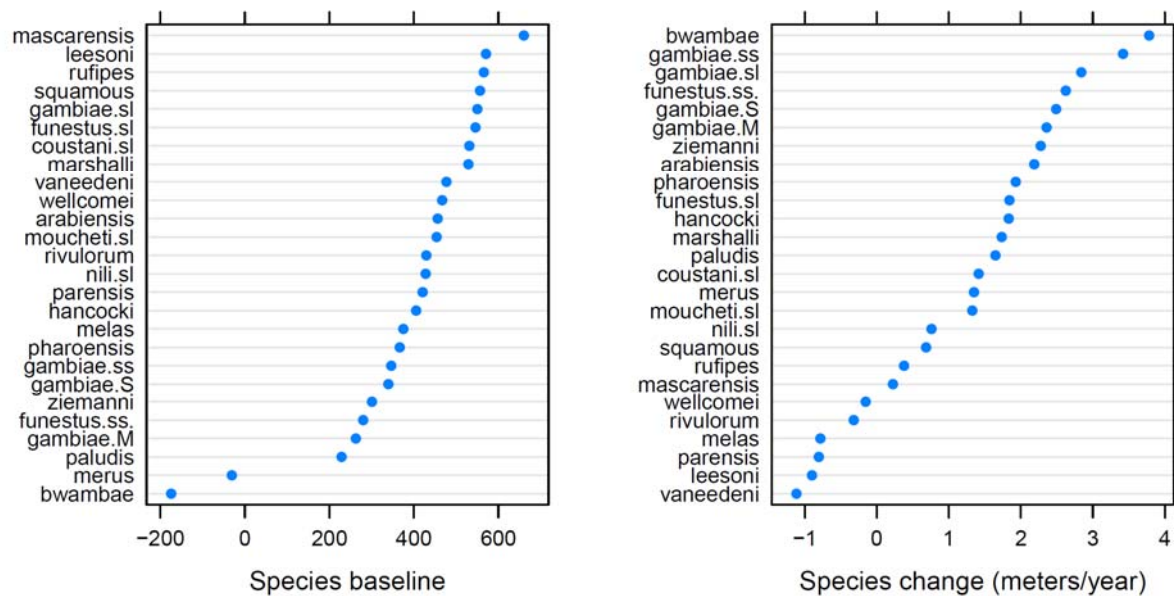

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411   **Figure 5.** Maximum-based elevational and latitudinal shifts had no significant relationship (p = 0.076),

412   implying the landscapes species are moving on may determine more about these shifts than intrinsic,

413   species-level dispersal capacity.

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