



21 **ABSTRACT**

22

23 Sandflies of the family Psychodidae show notable diversity in both disease vector status  
24 and climatic niche. Some species (in the subfamily Phlebotominae) transmit *Leishmania*  
25 parasites, responsible for the disease leishmaniasis. Other Psychodidae species do not.  
26 Psychodid species' ranges can be solely tropical, confined to the temperate zones, or  
27 span both. Studying the relationship between the evolution of disease vector status and  
28 that of climatic niche affords an understanding not only of the climate conditions  
29 associated with the presence and species richness of *Leishmania* vectors, but also  
30 allows the study of the extent to which psychodid flies' climatic niches are conserved, in  
31 a context with implications for global human health. We obtained observation site data,  
32 and associated climate data, for 223 psychodid species to understand which aspects of  
33 climate most closely predict distribution. Temperature and seasonality are strong  
34 determinants of species occurrence within the clade. We built a mitochondrial DNA  
35 phylogeny of Psychodidae, and found a positive relationship between pairwise genetic  
36 distance and climate niche differentiation, which indicates strong niche conservatism.  
37 This result is also supported by strong phylogenetic signals of metrics of climate  
38 differentiation. Finally, we used ancestral trait reconstruction to infer the tropicality (i.e.,  
39 proportion of latitudinal range in the tropics minus the proportion of the latitudinal range  
40 in temperate areas) of ancestral species, and counted transitions to and from tropicality  
41 states, finding that tropical and temperate species respectively produced almost entirely  
42 tropical and temperate descendant species, a result consistent for vector and non-  
43 vector species. Taken together, these results imply that while vectors of *Leishmania* can  
44 survive in a variety of climates, their climate niches are strongly predicted by phylogeny.  
45

## 46 INTRODUCTION

47 Climatic variables affect how individual species are distributed across the globe  
48 as well as patterns of diversification for clades of species (Haffer 1997; Barnagaud et  
49 al. 2012; Ali and Aitchison 2014). A notable pattern that has emerged from studying the  
50 climatic niche distribution across related species is that related species tend to have  
51 similar climatic niches. This pattern, known as niche conservatism, has been reported  
52 for multiple taxa across the tree of life including frogs (Wiens et al. 2006), mammals  
53 (Cooper et al. 2011), and angiosperms (Kerkhoff et al. 2014). Niche conservatism in  
54 climatic tolerances specifically may have implications for speciation, and how clades  
55 have expanded geographically over time. In particular, this pattern has been invoked as  
56 a potential explanation for the higher species diversity in the tropics because tropical  
57 species might not be able to evolve the ability to colonize temperate areas of the planet  
58 (Wiens and Donoghue 2004). Niche conservatism also has important implications for  
59 how species are expected to respond to global climate change because increases in  
60 global temperature will likely affect tropical and temperate clades differently (Wiens and  
61 Graham 2005).

62 Sandflies of the genera *Lutzomyia* and *Phlebotomus* are the only known vectors  
63 of *Leishmania*, a trypanosome parasite responsible for the disease leishmaniasis.  
64 *Lutzomyia* (Diptera: Psychodidae) is endemic to the New World and encompasses over  
65 400 species (Young and Duran 1994). *Phlebotomus* (Diptera: Psychodidae) is endemic  
66 to the Old World and encompasses 50 species (Lewis and Lane 1976). At least 120  
67 species from these two genera transmit leishmaniasis. Some of the *Leishmania*-vector  
68 species and others not known to transmit *Leishmania* also transmit Bartonellosis and  
69 arboviral infections (Caceres et al. 1997; Villaseca et al. 1999; Ulloa et al. 2018). For  
70 leishmaniasis alone, more than 12 million people are infected and over 2 million new  
71 cases are reported annually (Desjeux 2004; Karimkhani et al. 2016; Bailey et al. 2017).  
72 Even though species within two other genera in the family (*Sergentomyia* and *Warileya*,  
73 (Lawyer et al. 1990; Mukherjee et al. 1997; Campino et al. 2013; Kanjanopas et al.  
74 2013; Moreno et al. 2015)) can be infected with *Leishmania*, they do not transmit the  
75 parasite. All other species in the family are known as moth-flies, some of which can

76 cause human myiasis (i.e., infection of skin tissue with larvae (Sarkar et al. 2018;  
77 Pijáček and Kudělková 2020)) and are commonly human commensals (Sparkes and  
78 Anderson 2010).

79 Despite the negative impacts that *Leishmania*-vectoring species (subfamily  
80 Phlebotominae) can have on human well-being, the potential drivers of geographic  
81 distribution remain highly unexplored for this group. While there are significant gaps in  
82 our knowledge of the genetics and evolutionary history of the Psychodidae, the  
83 geographic ranges of the genera in the family, in particular *Lutzomyia* and *Phlebotomus*,  
84 have been extensively characterized. In non-psychodid taxa, previous ecological niche  
85 modelling efforts have predicted the inferred range of individual vector species (Oliveira  
86 et al. 2017), and whether certain vectors are likely to expand their geographical range  
87 (Cromley 2003; Bouzid et al. 2014; Kamal et al. 2018). However, to our knowledge, the  
88 efforts to reconstruct the relationships between psychodid species have focused on  
89 taxonomic classifications and have not addressed how climate tolerance traits have  
90 evolved in the clade. For example, no study has addressed whether the distributions of  
91 these vectors are influenced by their phylogenetic relationships; namely, whether  
92 closely related species of vectors show similar geographic distributions and climatic  
93 niches or, on the contrary, have experienced climatic niche shifts over time. This is an  
94 important question because understanding the environmental variables associated with  
95 species occurrence sheds light on the potential drivers of niche evolution but also allows  
96 prediction concerning whether their ranges will expand over time (Pearman et al. 2008,  
97 2010).

98 Macroecological analyses that combine environmental data with species  
99 occurrence records can reveal the extent of climatic variation across the geographic  
100 range of a species group (Diniz-Filho and Bini 2008; Keith et al. 2012). Coupled with  
101 phylogenetic analyses, macroecological data can reveal the extent of climate niche  
102 evolution in a group. In the case of vectors, these analyses can reveal whether the  
103 clinical importance of these species is likely to increase as they expand their range.  
104 Despite significant gaps in our knowledge of the genetics and evolutionary history of the  
105 Psychodidae, the geographic ranges of the genera in the family, in particular *Lutzomyia*

106 and *Phlebotomus*, have been studied for decades. Extensive collections exist of these  
107 vectors and previous ecological niche modelling efforts have predicted the inferred  
108 range of individual vector species (Oliveira et al. 2017), and whether certain vectors are  
109 likely to expand their geographical range (Cromley 2003; Bouzid et al. 2014; Kamal et  
110 al. 2018).

111 In this study, we used geolocated occurrence data to determine the primary axes  
112 of climatic variation that distinguish geographic ranges of *Lutzomyia*, *Phlebotomus* and  
113 related genera. We find extensive variation in the climatic niche among genera within  
114 the Psychodidae and among species within the two vector genera. We find evidence  
115 that the climate niche has a strong phylogenetic signal in the family. Thermal niche  
116 differentiation between species pairs increases as divergence increases, following the  
117 expectations of niche conservatism. Temperate species are more likely to give rise to  
118 temperate species, tropical species are more likely to give rise to other tropical species,  
119 and transitions between these latitudinal zones are rare. Our work constitutes a  
120 systematic treatment of niche evolution in a family of vectors.

## 121 **METHODS**

122

### 123 Occurrence data

124 We obtained coordinates for the collections of 223 species in the Psychodidae  
125 family from Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>). The  
126 dataset included species from the genera *Lutzomyia* (45), *Pericoma* (24), *Phlebotomus*  
127 (26), *Psychoda* (26), *Sergentomyia* (15), *Telmatoscopus* (15), *Brumptomyia* (14),  
128 *Satchelliella* (12), *Psychodopygus* (9), *Trichomyia* (8), *Evandromyia* (6), *Clytocerus* (5),  
129 *Philosepedon* (4), *Psathyromyia* (4), *Pintomyia* (4), *Micropygomyia* (3), *Migonemyia* (2),  
130 and *Warileya* (1). The DOIs for each of the datasets are listed in Table S1. We only  
131 included the 126 extant species for which at least five georecorded locations were  
132 available.

133

### 134 Estimating species' climatic niche

135

136 Our first goal was to describe how the abiotic environment varies across sites  
137 where psychodid species have been observed. We used the collection location data  
138 described above and bioclimatic variables extracted from publicly available databases  
139 to estimate variation in the abiotic environments of Psychodidae species. For each  
140 psychodid occurrence record, we extracted four climatic variables from BIOCLIM  
141 (Booth et al. 2014) warmest-month maximum temperature, coldest-month minimum  
142 temperature, annual precipitation, seasonality of precipitation; Booth et al. 2014) plus  
143 elevation (Fick and Hijmans 2017). We chose to only consider five environmental  
144 variables to avoid overfitting, given that 70% of species had fewer than 20 occurrence  
145 records. For each of these five climate variables, we calculated 25th, 50th, and 75th  
146 percentiles of the distribution for each species. We conducted a principal component  
147 analysis (function *prcomp*; library *stats*, (R Core Team 2016)) using the 25th and 75th  
148 percentile of each trait for each species (10 total variables) in order to capture the  
149 climatic breadth of each species. However, because the eigenvectors associated with  
150 25th versus 75th percentile were highly correlated within each climatic variable (see  
151 Results), we opted to instead use a PCA of the medians of each variable (5 total

152 variables). To measure the extent of the differentiation along each principal component  
153 (PC) axis, we use One-Way ANOVAs where each PC was the response and the genus  
154 was the only fixed effect (function *lm*, library ‘*stats*’, (R Core Team 2016)). We followed  
155 the ANOVA with Tukey’s honest difference post-hoc comparisons (function *glht*, library  
156 ‘*multcomp*’, (Hothorn et al. 2020)).

157

### 158 Mean latitude and tropicality index

159 We calculated the mean latitude of occurrence for each species as one way of  
160 characterizing geographical distribution. However, mean latitude is unable to distinguish  
161 between a range-restricted tropical species and a cosmopolitan species with an  
162 identical range centroid. As such, we additionally calculated Kerkhoff et al.’s ([Kerkhoff et  
163 al. 2014](#)) tropicality index (TI) for each species as the proportion of its latitudinal range  
164 that falls within the tropics minus the proportion of the latitudinal range that falls within  
165 the temperate zone. The index ranges between  $-1$  (strictly temperate species) to  $1$   
166 (strictly tropical species). Values of  $0$  correspond to species whose distribution is half-  
167 temperate and half-tropical. Following Kerkoff et al. (2014), we further assigned species  
168 to one of four distributional categories based on the tropicality index: “tropical” species  
169 with  $TI > 0.5$  (75% or more of the range within the tropics), “semitropical” species with  $0$   
170  $< TI \leq 0.5$ , “semitemperate” species with  $-0.5 < TI \leq 0$ , and “temperate” species with  $TI$   
171  $\leq -0.5$  (75% or more of the range within the temperate zone).

172

### 173 mtDNA genealogy

174 In spite of the rich geographical range dataset for Psychodidae, few efforts have  
175 addressed the phylogenetic relationships between species of the family. We obtained  
176 sequences of the mitochondrial locus Cytochrome Oxidase I data (*COI*) for 125 species  
177 from GenBank. All the accession numbers are listed in Table S2. Of these 125 species,  
178 74 also had geographic information (described above, Table S1). We aligned the  
179 sequences using Clustal Omega (Sievers et al. 2011; Sievers and Higgins 2018) with  
180 the following specifications: `-dealign -t --seqtype={DNA} --outfmt=phylip -v`. We included  
181 the *COI* sequence for *Aedes albopictus* to serve as an outgroup and root the tree (Table  
182 S1).

183 We generated a phylogenetic tree for the 74 species for which we have both  
184 mtDNA and geographic information using IQTREE, and these species formed the core  
185 of our analyses for this study. We used the -m TEST option (jModelTest, (Posada 2008;  
186 Darriba et al. 2012)) for model selection. To estimate support of the branches we used  
187 SH-aLRT support (%) and ultrafast bootstrap support (%) using 1,000 replicates. We  
188 only kept nodes with 60% bootstrap support. Here, we do not aim to infer all the  
189 genealogical relationships between species in the Psychodidae, as more data than just  
190 the *COI* locus would be required for this task. The DRYAD data package (DOI:TBD)  
191 contains the log files for the run.

192

### 193 Phylogenetic signal

194 We estimated the phylogenetic signal of the climatic niche (characterized by the  
195 PC1 score from the ordination above), the mean latitude of each species, and the  
196 tropicity index across the Psychodidae tree using two different metrics: Blomberg's *K*  
197 (Blomberg et al. 2003), and Pagel's  $\lambda$ . Both metrics were calculated using the function  
198 '*phylosig*' (library *phytools*, (Revell 2012)) with 1,000 simulations to determine if the  
199 calculated value differed from zero. Blomberg's *K* (Blomberg et al. 2003) indicates  
200 whether the association between the tree and the trait follows the expectations under a  
201 Brownian model of evolution (i.e., the trait value changes randomly, in both direction  
202 and magnitude, over the course of evolution). If *K* equals 1, the evolution of species'  
203 traits (climatic niche, mean latitude, tropicity index) conforms to a model of Brownian  
204 motion evolution in which trait values of descendant species diverge slowly from the  
205 ancestral value. A *K* lower than one suggests that relatives resemble each other less  
206 than expected under Brownian motion evolution and is evidence against phylogenetic  
207 niche conservatism (Cooper et al. 2010). A *K* higher than 1 suggests that close relatives  
208 are more similar than expected under Brownian motion evolution. This can be caused  
209 by phylogenetic constraints or niche conservatism (Cooper et al. 2010).

210 The second metric, Pagel's  $\lambda$ , is a measure of phylogenetic signal which  
211 estimates the extent to which the phylogenetic history of a clade is predictive of the trait  
212 distribution at the tree tips. Values of  $\lambda$  lower than 1.0 represent traits being less similar  
213 amongst species than expected from their phylogenetic relationships. A  $\lambda$  equal to 1.0



214 suggests that traits covary with phylogeny (Pagel 1997, 1999) and is consistent with,  
215 but not diagnostic of, niche conservatism (Cooper et al. 2010).

216

### 217 Climatic niche divergence

218

219 To additionally assess whether genetic divergence and climate niche differentiation  
220 were associated, we used regression analyses. Our goal was to determine whether the  
221 relationship between genetic divergence and climatic niche differentiation had a positive  
222 slope (i.e., species became more differentiated in climate niche as genetic distance  
223 increased). To score the divergence between two species in their climatic niche, we  
224 calculated the difference between their mean PC1 values ( $\Delta PC1$ ). We then fit a linear  
225 regression and calculated the slope of the relationship between  $\Delta PC1$  and genetic  
226 distance (function *lm*, library *stats*; (R Core Team 2016)). We bootstrapped the  
227 regression coefficients using the function *Boot* (library *simpleboot*, (Peng 2008)). These  
228 analyses are conceptually related to the calculation of phylogenetic signal because  
229 cases where the difference in the climatic niche of a pair of species increases as  
230 divergence accrues should also have a strong phylogenetic signal.

231 Closely related species do not behave independently and their similarity is likely  
232 to be the result of shared history (Huey et al. 2019). We therefore used two  
233 phylogenetic non-independence corrections. First, we use a variant of phylogenetic  
234 regressions in which the genetic relationships of the species are considered a random  
235 effect in a linear mixed model. We used the function *force.ultrametric* (library '*phytools*',  
236 (Revell 2012)) to make an ultrametric tree and the function *cophenetic* (library '*stats*', (R  
237 Core Team 2016)) to generate a genetic distance matrix. We used a linear mixed model  
238 in which the difference in PC1 was the response, genetic distance was a continuous  
239 variable, and the two species in the comparison were considered random effects using  
240 the function *lmer* (library '*lme4*', (De Boeck et al. 2011; Bates et al. 2013)). We used the  
241 function *bootMer* (library '*lme4*', (Bates et al. 2013)) to bootstrap the regression (1,000  
242 replicates). To compare the slope of the phylogenetically-corrected and the non-  
243 corrected regressions, we used a Wilcoxon rank sum test with continuity correction  
244 (function *wilcox.test*, library *stats*; (R Core Team 2016)).

245           Second, we fitted a generalized linear mixed model using Markov chain Monte  
246 Carlo. We used the function *ginvn* (library *MASS*, (Venables 2002; Venables et al.  
247 2003)) to find the generalized inverse of the (1-genetic distance) matrix as proposed by  
248 Castillo (Castillo 2017). We fitted a linear model using the package *MCMCglmm*  
249 (Hadfield 2010) in which the difference between climatic PC1 was the response, genetic  
250 distance was a predictor variable and the phylogenetic covariance matrix was a random  
251 effect. We ran five independent MCMC chains. To determine if the model converged in  
252 each of the chains, we used the function *gelman.diag* (library *coda*, (Plummer et al.  
253 2006)). A chain was considered converged if all scale reduction factors for all variables  
254 (both fixed and random effects) were  $\leq 1.1$  for each of the two chains. We calculated the  
255 95% confidence interval for the intercept and the slope using the function *HPDinterval*  
256 (library *coda*, (Plummer et al. 2006)).

257           Next, to understand the dynamics of diversification of climatic niche in Psychodid  
258 species, we fitted seven different models of trait evolution using the function  
259 *fitContinuous* (library '*geiger*', (Harmon et al. 2008; Pennell et al. 2014). Models varied  
260 in the tempo and mode of trait evolution and ranged from no phylogenetic signal (i.e.,  
261 white noise) to different modes of evolution. The details of the seven models are  
262 described in Table 1. First, and following (Cooper et al. 2010; Wiens et al. 2010), we  
263 compared three models of trait evolution: white noise, Ornstein–Uhlenbeck (OU), and  
264 Brownian. Support for the latter two suggests evidence of niche conservatism (Cooper  
265 et al. 2010). Next, we compared all seven models using their Akaike Information  
266 Criterion (AIC) values and calculating their Akaike weights (*wAIC*) using the equation:

267

$$268 \qquad wAIC_i = \exp(-0.5 * \Delta AIC_i)$$

269

270           Where  $\Delta AIC_i$  is the difference between the AIC of model *i* and the model with the lowest  
271 AIC. We used the function *aic.w* (library *phytools*, (Revell 2012)) for these calculations.

272

273 Ancestral trait reconstruction and rates of transition

274

275 We inferred the climatic niche of each node in the Psychodidae tree using the *COI* gene  
276 genealogy for three proxies of climate niche: *i*) tropicality index (TI), *ii*) mean latitude,  
277 and *iii*) PC1 (described in 'Estimating species' climatic niche').

278 We used the function '*collapse.singles*' (library *ape*, (Paradis and Schliep 2019))  
279 to resolve polytomies. Trees were then checked with the function '*is.binary.tree*' (library  
280 *ape*, (Paradis and Schliep 2019)). We used the function '*anc.ML*' (library *phylo*, (Revell  
281 2012)) for the ancestral trait reconstruction of each of the three traits mentioned above  
282 with a maximum of 5,000 iterations using a Brownian movement model. (Similar runs  
283 using other models gave identical results.) Trees were drawn using the function  
284 '*contMap*' (library *phylo*, (Revell 2012)). Finally, we used ancestral niche reconstruction  
285 to examine the rate at which species in the Psychodidae transitioned among and  
286 between the four latitudinal range categories (tropical, semitropical, semitemperate, and  
287 temperate) based on TI as described above (Kerkhoff et al. 2014). First, we inferred the  
288 latitudinal category for each node in the tree using *anc.ML* (Revell 2012). Ancestral trait  
289 reconstructions using other approaches (*anc.Bayes* and *fastAnc* (Revell 2012)) gave  
290 similar results. Then, for each latitudinal category, we selected all of the ancestral nodes  
291 inferred to be in that category, and calculated the proportion of immediately descendant  
292 nodes or tips that fell into each of the four latitudinal categories. Doing this for each  
293 category yielded 16 transition rates describing the frequency of transitions between any  
294 pair of latitudinal states.

295

296

## 297 RESULTS

### 298 Geographic distribution of Psychodidae genera

299

300 First, we calculated the mean latitude of 223 species in the Psychodidae family  
301 as a proxy of their distribution. We find that there are two peaks of diversity in the family,  
302 one in the tropics around the Equator and a smaller one slightly below the Arctic circle  
303 (Figure S1). Figure S2 shows the mean latitude for species within 12 genera in the  
304 Psychodidae family. The moth-fly genera *Clytocerus*, *Philosepedon*, *Satcheliella*, and  
305 *Telmatoscopus* are all of temperate distribution. The genera *Pericoma* and *Psychoda*  
306 are largely temperate but some species have a tropical distribution. Among *Leishmania*-  
307 harboring genera, some patterns are also salient. The genera *Lutzomyia* and  
308 *Brumptomyia* are mostly restricted to the tropics. *Phlebotomus* on the other hand shows  
309 high diversity in the northern subtropical region. These results indicate that different  
310 genera in the family show strong differences in their distribution and suggest the  
311 possibility of climate niche evolution among and within genera.

312 Given the strong differences in mean latitude between genera, we first tested for  
313 a relationship between environmental variables and occurrence records of each species  
314 within the different genera of psychodids included in our dataset. We found that the  
315 eigenvectors for the 25th and 75th percentiles' contributions to the largest principal  
316 components were highly correlated (Pearson's product-moment correlation, PC1:  $r =$   
317  $0.993$ ,  $p < 0.001$ ; PC2:  $r = 0.980$ ,  $p = 0.003$ ; PC3:  $r = 0.999$ ,  $p < 0.001$ ). In light of this  
318 correlation, we opted to use the 50th percentile of each climate variable for each  
319 species distribution for all further analyses. A PCA revealed the relative importance of  
320 elevation, temperature, and temperature seasonality for occurrence. Table S3 shows  
321 the loadings for the PCA. The first three PCs explain the vast majority of the variance  
322 (93.96%) so we restricted our analyses to these PCs. All environmental variables had  
323 relatively high loadings on PC1 (56.72% of variation). Positive values on PC1 indicate  
324 locations that are relatively seasonal and cool, while more negative values are indicative  
325 of locations that are less seasonal and warmer (Figure 1). Genera differed along PC1  
326 (LMM:  $X^2_1=469.69$ ,  $P < 1 \times 10^{-10}$ , Figure 1B), but not PC2 (LMM:  $X^2_1= 8.48$ ,  $P = 0.58$ ),  
327 which is largely dominated by elevation (Table 2) and explained 18.37% of the variance.

328 Finally, PC3 (17.36%), which is mostly influenced by amount and seasonality of  
329 precipitation, also differed among genera ( $X^2_{7} = 72.98$ ,  $P < 1 \times 10^{-10}$ ). Pairwise  
330 comparisons for these PCs all suggested strong differences across genera (Tables S4-  
331 S6).

332

### 333 **Comparative phylogenetic analyses**

334

335 COI gene genealogy. We generated a gene genealogy based on mtDNA to get an  
336 approximation of the phylogenetic relationships within the family Psychodidae. Over  
337 90% of branches had bootstrap support of >60% (Figure S3). Our sample contains  
338 genera from two different taxonomic subfamilies: Phlebotominae and Psychodinae. We  
339 recovered these two subfamilies as monophyletic groups (Figure 4A, Figure S3) but not  
340 all genera appear monophyletic (e.g., *Phlebotomus*). The hematophagous clade was  
341 monophyletic (*Lutzomyia*, *Phlebotomus*, *Brumptomyia* and *Sergentomyia*) but the  
342 *Leishmania* vectors were not.

343

344 Phylogenetic signal. We used the COI genealogy to study macroevolutionary trends of  
345 the evolutionary history of climate niche in the family. We used two complementary  
346 indices that summarise patterns of trait evolution on a phylogeny for each of our three  
347 proxies of climatic niche: TI, mean latitude, and PC1. First, we found that Blomberg's *K*  
348 was significantly higher than 1 for each of the three metrics of geographic range (Figure  
349 2, Table 2), indicating that the climatic niches of close relatives are more similar to each  
350 other than expected under a pure model of Brownian motion evolution (1,000  
351 randomizations,  $P < 0.001$ ; Figure 2). Second, we found that Pagel's  $\lambda$  was significantly  
352 higher than 0 and lower than 1 for the three proxies (Figure 2). Broadly, these two  
353 metrics suggest that climatic descriptors of niche have a strong phylogenetic signal in  
354 the Psychodidae tree.

355 Consistent with niche conservatism, we found that the genetic divergence  
356 between species pairs is positively associated with the extent of their climate niche  
357 differentiation (Figure 3; One-way ANOVA:  $F_{1,2484} = 1,754.6$ ,  $P < 1 \times 10^{-10}$ ). This result  
358 suggests that closely related species are the most similar in their climatic niche, and

359 that the climate niche of Psychodidae species becomes more dissimilar as divergence  
360 increases. This result is qualitatively identical for a phylogenetically corrected dataset  
361 where the species identity are considered random effects (LMM:  $F_1=1,824.06$ ,  $P < 1 \times$   
362  $10^{-10}$ ; Figure 3, blue lines). The magnitude of the regression slope is significantly lower  
363 in the phylogenetically-corrected regression than for the non-corrected dataset  
364 ( $\text{Slope}_{\text{Corrected}}=0.365$ ,  $\text{Slope}_{\text{Non-corrected}}=1.457$ ; Wilcoxon rank sum test with continuity  
365 correction:  $W = 1 \times 10^6$ ,  $P < 1 \times 10^{-10}$ ). Finally, a MCMC-based phylogenetic correction  
366 revealed the same pattern, as the slope of the regression is also positive (95% CI =  
367 0.0676-0.273). The results from all these analyses (i.e., a positive correlation between  
368 divergence in climatic traits and age of divergence) are consistent with our phylogenetic  
369 signal analyses, which suggest that climatic niche evolution in the species from the  
370 Psychodidae family follows the expectation of niche conservatism.

371

372 Models of trait evolution. We fit seven different models of trait evolution to determine  
373 which fit best the evolution of climatic niche in the Psychodidae family. These models  
374 range from no phylogenetic signal (i.e., white-noise) to punctuated changes of trait  
375 evolution associated with speciation events (i.e., *kappa*). Table 3 shows the fit and the  
376 parameters inferred for each of the seven models for TI; Tables S4 and S5 show the  
377 parameters for PC1 and mean latitude, respectively. Consistent with the results from the  
378 summary indices, we find that models with a phylogenetic signal fit better than the only  
379 model with no phylogenetic signal for all three proxies of geographic range. When we  
380 restricted the comparisons to the white-noise, OU, and Brownian models, the latter  
381 model had the lowest AIC for the three proxies of climate niche (Tables 3, S7 and S8).  
382 These results suggest evidence for niche conservatism (Wiens et al. 2010).  
383 Nonetheless, when we included four additional models, the three proxies differed in the  
384 model that best fit their mode of evolution. For PC1, the best fitting model was still a  
385 Brownian motion model of trait evolution (*BM* model  $\text{AIC}_{\text{BM-PC1}} = 153.618$ ). The best  
386 fitting model for mean latitude and TI was the early burst model (*EB* model  $\text{AIC}_{\text{EB-Latitude}}$   
387  $= 606.419$ ; *EB* model  $\text{AIC}_{\text{EB-TI}} = 99.379$ ) where climatic habitat changes are consistent  
388 with the occupation of a variety of climatic niches early in the divergence of the family  
389 and a decline of trait evolution as diversification of the family proceeded. These results

390 indicate that even though the evolution of climate niche in Psychodidae has evidence of  
391 niche conservatism, macroevolutionary models of trait evolution also suggest the  
392 existence of transitions in the phylogenetic history of the group.

393

394 Ancestral trait reconstruction and transition rates. Figure 4 shows the extant tropicality  
395 indexes in the Psychodidae family (marked by color) and the inferred states along the  
396 phylogenetic tree. Figure S4 shows similar trees for PC1 and mean latitude. Our best  
397 estimate is that the ancestor of the Psychodidae family had a semitropical to tropical  
398 distribution (inferred state at the root for tropicality index under a BM model of trait  
399 evolution,  $Z_0 = 0.54$ ;  $Z_0$  values with other models are listed in Table 3). Extant subtropical  
400 and temperate species, such as most moth-flies, have a climatic niche that appears to  
401 be derived in the family. The clade encompassing vector genera also has an inferred  
402 semitropical origin (inferred TI value = 0.39). Within *Phlebotomus*, ancestral character  
403 reconstruction suggests that the ancestor of the genus had a semitemperate distribution  
404 (inferred TI value = -0.26), suggesting that the colonization of temperate habitats is  
405 derived from a semitemperate or semitropical ancestor.

406 In general, we found that evolutionary transitions to new latitudinal ranges were  
407 rare (Figure 5). 92% of transitions from tropical ancestors and 91% of transitions from  
408 temperate ancestors resulted in descendant nodes or tips remaining in the same  
409 latitudinal zone. Further, all of the remaining 8% of transitions from tropical nodes and  
410 9% of transitions from temperate nodes were to semitropical and semitemperate zones,  
411 respectively. By contrast, transitions from the more intermediately defined semitropical  
412 and semitemperate zones to adjacent zones were more common and only 33% and  
413 38%, respectively, of descendants from these nodes shared their ancestors' states.

414

## 415 **DISCUSSION**

416 In this report, we used georeferenced collections and studied the evolution of  
417 climate niche in the Psychodidae family which includes *Leishmania*-vector species.  
418 Even though the family distribution spans the tropics to the Arctic circle, our results  
419 suggest that different genera within the Psychodidae differ in their climatic niche. Within  
420 the family, most species have either a tropical or temperate distribution but rarely span



421 the full hemisphere. Moreover, the phylogenetic distribution of climatic niche  
422 components suggests that climate niche has undergone few transitions in Psychodidae.  
423 As they have diversified, tropical species have mostly produced tropical species, and  
424 temperate species have given rise to more temperate species.

425         Studies on the evolution of niche divergence as genetic divergence proceeds are  
426 rare. In California Jewelflowers, habitat isolation accumulates quickly and remains high  
427 (Christie and Strauss 2018) and acts as a barrier against hybridization. This result is  
428 qualitatively similar to our findings in *Lutzomyia*, as climatic niche becomes more  
429 differentiated as divergence increases. Nonetheless, the scale of the ranges of  
430 divergence time differs between the two studies. The study of climatic differentiation in  
431 Jewelflowers aimed to understand how barriers to hybridization accumulate between  
432 potential interbreeding species, and our goal was to assess the extent of climate  
433 differentiation across the whole family, regardless of whether they hybridize or not.  
434 Systematic assessments of the magnitude of climatic differentiation across taxa,  
435 including those considering the potential effects of climate niche differentiation as a  
436 barrier to gene flow via hybridization, are sorely needed to measure the rate of evolution  
437 of niche differentiation across the tree of life.

438         The work presented here has several limitations. Our inference on phylogenetic  
439 relationships is largely consistent with previous efforts but should be taken as  
440 preliminary. Only a more comprehensive sampling of the variation of the genomes in  
441 these dipterans will reveal the true phylogenetic relationships between species. This  
442 lack of a fully resolved phylogeny also might affect our results. mtDNA provides low  
443 resolution in instances where there has been introgression (e.g., (McVay et al. 2017)). A  
444 genome-wide phylogenetic tree that reconstructs the species tree without the limitations  
445 of a single gene genealogy is sorely needed. A logical next step in the research of  
446 thermal niche differentiation will be to assess whether different species have differences  
447 in their realized thermal physiology (reviewed in (Angilletta Jr et al. 2002; Bennett et al.  
448 2019)), in their thermal preference (e.g., (Matute et al. 2009; Cooper et al. 2018)), or in  
449 both. Also, the number of transitions from a tropical or temperate node is higher (78 and  
450 46 respectively) than from a semitemperate or semitropical ancestor (6 and 16  
451 respectively) and we thus have more power to detect differences in transition rates



452 between the former categories. Integrating physiological and performance-based traits  
453 with analyses of climatic niche evolution can provide a window to understanding  
454 differences between physiological and realized niches, ultimately revealing the  
455 ecological implications of climatic divergence (Gunderson et al. 2018).

456 Despite these caveats, our finding of climate niche evolution in the Psychodidae  
457 family opens the possibility of new research avenues. First, incorporating a climatic  
458 dimension to the study of the evolution of vectors can inform to what extent climate  
459 plays a role in the coevolution of parasites and vectors. In the specific case of  
460 *Lutzomyia* and *Phlebotomus*, these studies will reveal whether there is an association  
461 between carrying *Leishmania* and a tropical climate niche. Second, studies that address  
462 the limits of climate niche will also inform which vectors are most likely to move across  
463 climatic zones as climate change changes the thermal characteristics of the planet.  
464 Finally, comparing the rates of transition between different latitudinal categories can  
465 inform whether different taxa show different rates of conservatism. Only one other study  
466 has calculated the rates of transition between latitudinal zones (angiosperms; (Kerckhoff  
467 et al. 2014)) but the comparison is still informative. The rates of transitions we observed  
468 among tropicality values obtained for Psychodidae and those observed for angiosperms  
469 are similar and both reveal strong niche conservatism.

470 As climatic shifts occur globally, changes in environmental conditions will lead to  
471 new species distributions (Hitch and Leberg 2007; Rosenberg et al. 2019) or, in the  
472 extreme, extinction (Møller et al. 2008). Of particular importance for human health are  
473 potential changes in disease vector ranges and abundances, which depend on the  
474 extent to which disease vectors exhibit niche conservatism, a phenomenon still poorly  
475 examined. Cunze and colleagues (Cunze et al. 2018) suggested niche conservatism in  
476 two species of *Aedes* mosquitoes, the vectors of dengue, because none of the two  
477 species has filled the entirety of the ecological niche in areas where they have recently  
478 invaded. While this evidence shows that *Aedes* have the potential to expand their range  
479 in the near future, it does not inform about the extent of conservatism in the genus.  
480 Pairwise comparisons of the ecological niche of six pairs of triatomid bugs, vectors of  
481 Chagas disease (Ibarra-Cerdeña et al. 2014) suggest that pairs of related species are  
482 more similar in their niche than pairs of distantly-related species. While these tests have

483 revealed that niche conservatism might exist for the few species pairs that have been  
484 surveyed, the evidence for niche conservatism at the phylogenetic level is still scant.  
485 Studies on the climate evolution of species, and in particular of vectors, are important,  
486 because species in clades with phylogenetically conserved climatic niches are more  
487 likely to shift their geographic distributions in response to changing climate (Tingley et  
488 al. 2009, La Sorte and Jetz 2012, Martinez-Meyer and Peterson 2006, Oliveira et al.  
489 2017), raising the possibility of poleward shifts of many vector species that are currently  
490 confined to the tropics. Some species of *Lutzomyia*, for example, have expanded their  
491 range northward (Comer et al. 1994; Reeves et al. 2008; Minter et al. 2009; Florin et al.  
492 2011; Florin and Rebollar-Téllez 2013) which could potentially expand the endemicity of  
493 leishmaniasis (Grosjean et al. 2003; Rosypal et al. 2003, 2005; Schaut et al. 2015).

494 Understanding the underlying causes of species distribution can inform how  
495 species respond to climate change. This is of particular importance to understand how  
496 vectors of disease will be distributed around the globe as global warming progresses.  
497 Modelling of potential occurrence has revealed that increasing temperatures might  
498 increase the potential range of a handful of species (Andrade-Filho et al. 2017; da  
499 Costa et al. 2018). Our results suggest that most Psychodidae vector species show a  
500 tropical distribution and that an assessment of the potential range expansions given  
501 multiple temperature change scenarios might be useful to monitor how vectors expand  
502 their niche along latitude and altitude.

503

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510

## 511 **TABLES**

512 **TABLE 1. Models of trait evolution fitted to climatic niche data in the Psychodidae**  
513 **family.**

514

<b>Model</b>	<b>Assumptions</b>	<b><i>fitContinuous</i> option</b>
<b>White-noise</b>	The trait values come from a single normal distribution with no covariance structure among species.	model="white"
<b>Lambda</b>	A model in which phylogeny predicts covariance among trait values (Pagel 1999). The model transforms the tree using a scalar, $\lambda$ , that ranges between 0 (a star-like phylogeny) and 1 (the BM model, see below). Equivalent to calculating a form of phylogenetic signal ( $\lambda$ , see Methods).	model="lambda"
<b>Early Burst</b>	The rate of evolution increases or decreases exponentially through time, under the model $r_t = r_0 \times e^{(a \cdot t)}$ , where $r_0$ is the initial rate, $a$ is the rate change parameter, and $t$ is time.	model="EB"
<b>Ornstein Uhlenbeck (OU)</b>	Trait evolution is best-explained by a random walk with a central tendency and an attraction strength determined by the parameter alpha, which ranges between $\sim 0$ and 2.72 (Butler and King 2004).	model="OU"
<b>Brownian motion model</b>	The correlation structure among trait values is proportional to the extent of shared ancestry for pairs of species (Felsenstein 1973).	model="BM"
<b>Kappa</b>	Character divergence is associated with speciation events in the tree (Pagel	model="kappa"

	1999). kappa ranges between ~0 and 1.	
<b>Delta</b>	A model that fits relative contributions of early versus late evolution in the tree to the covariance of species trait values (Pagel 1999). Delta values larger than 1 suggest recent evolution has been relatively fast; delta lower than 1, suggest recent evolution has been comparatively slow.	model="delta"

515

516 **TABLE 2. Different proxies of climatic niche have a strong phylogenetic signal.**

517 Blomberg's K and  $\lambda$  estimates for three different proxies of geographic range in the  
518 Psychodidae family.

	<b>Blomberg's K</b>	<b><math>\lambda</math></b>
<b>Mean latitude</b>	2.557, P=0.001	0.999
<b>PC1</b>	2.678, P=0.001	0.999
<b>TI</b>	2.175, P=0.001	0.999

519

520 **TABLE 3. Trait-evolution models suggest that TI in Psychodidae evolves**

521 **according to an Early-Burst model.**  $\sigma^2$  is the average amount of change expected in  
522 each time step.  $z_0$  is the trait value at the root of the tree. Similar analyses and results  
523 for PC1 and mean latitude are shown in Table S4 and S5.

524

<b>model</b>	<b><math>\sigma^2</math></b>	<b><math>z_0</math></b>	<b>Additional parameters</b>	<b>AIC</b>	<b>wAIC</b>
White-noise	0.807	0.231	NA	198.316	0.000

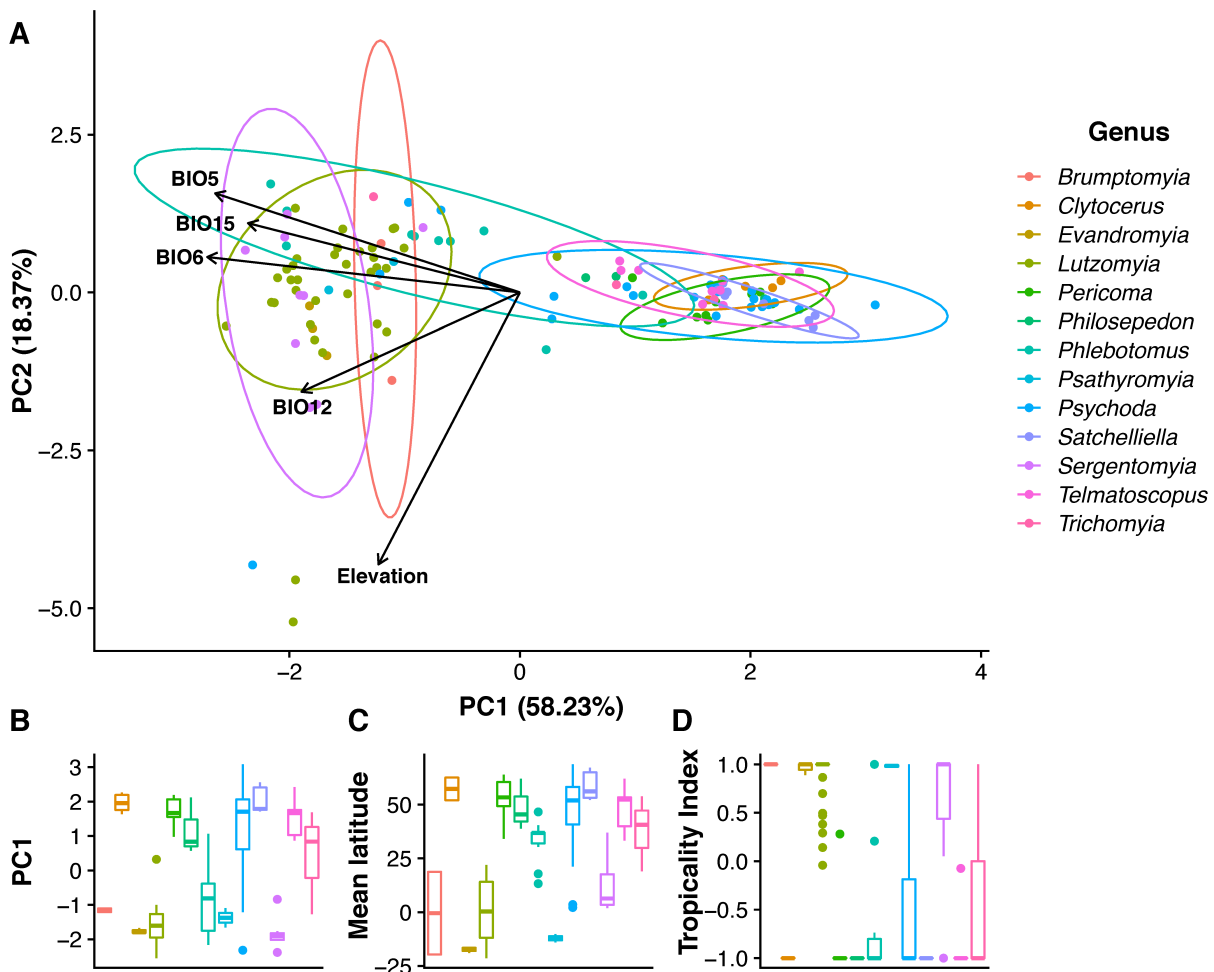
Lambda	1.303	0.554	$\lambda = 1.000$	103.090	0.058
Early burst	4.232	0.540	$a = -3.871$	99.379	0.371
OU	1.303	0.554	alpha = 0.000	101.874	0.058
Brownian motion	1.303	0.554	NA	100.916	0.172
Kappa	0.678	0.508	kappa = 0.751	100.285	0.106
Delta	2.420	0.556	delta = 0.362	103.090	0.235

525

526

527 **FIGURES**

528 **FIGURE 1. Different genera within the Psychodidae family differ from each other**  
529 **in their climatic niche. A.** PCA based on the Worldclim variables suggests that the  
530 occurrence of different genera within the family are associated with climatic variables.  
531 **B.** Boxplot showing the mean species values for PC1. This PC is mostly explained by  
532 temperature and precipitation. **C.** Boxplot showing the mean species values for  
533 latitudinal distribution. **D.** Boxplot showing the mean species values for TI.



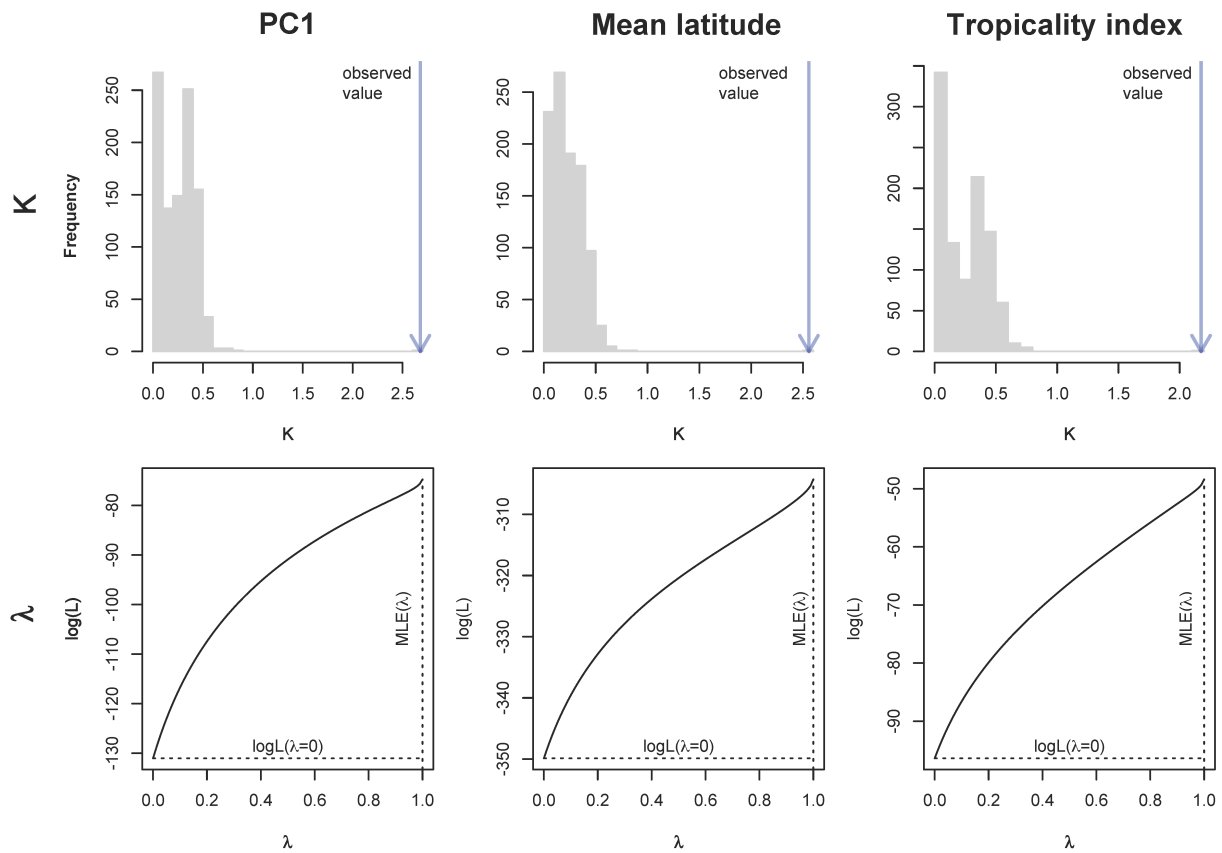
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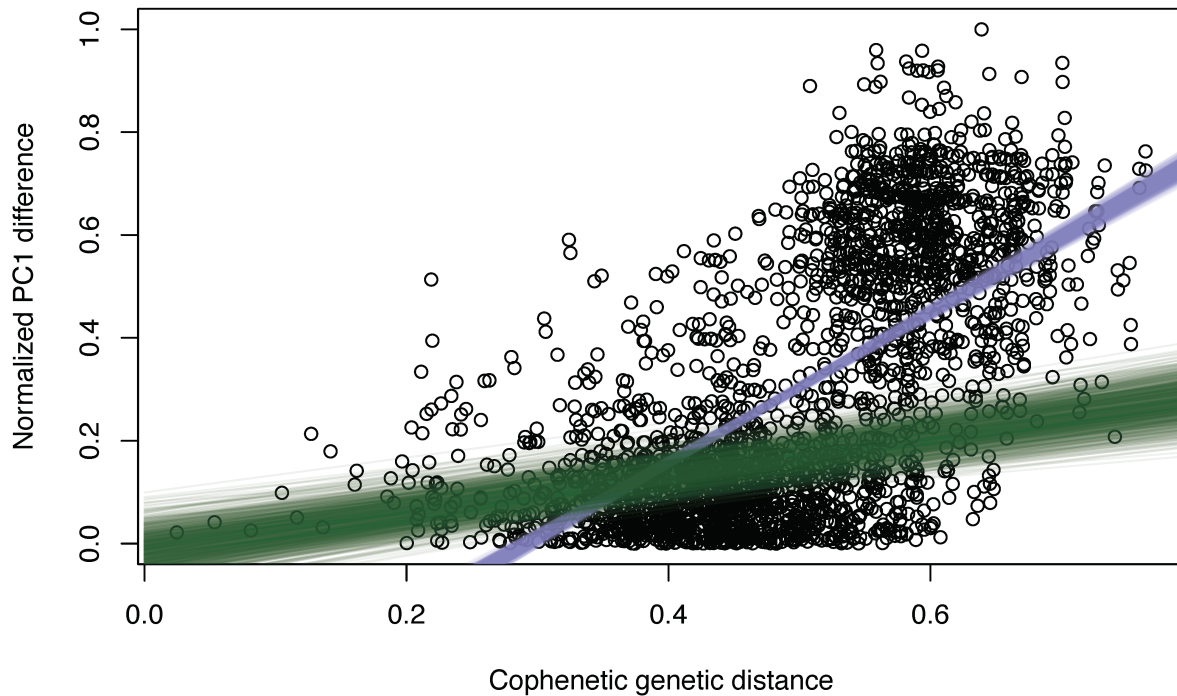
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538 **FIGURE 2. Climatic niche shows strong phylogenetic signal in the Psychodidae**  
539 **family.** Top panels show the distribution of simulated and observed Blomberg's K.  
540 Bottom panels show values of the maximum likelihood estimate (MLE) of  $\lambda$  and the  
541 maximum likelihood of the model when  $\lambda$  is zero. Left-side panels show metrics for PC1.  
542 Center panels show metrics for median latitude. Right-side panels show metrics for  
543 tropicality index.



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550

551 **FIGURE 3. Habitat differentiation increases with genetic distance in the**  
552 **Psychodidae family.** Blue lines show 1,000 bootstrapped linear regressions with this  
553 non-phylogenetically-corrected dataset. Green lines show 1,000 bootstrapped linear  
554 regressions with a species-identity random effect to account for phylogenetic non-  
555 independence. Both models show a monotonic increase with genetic distance.

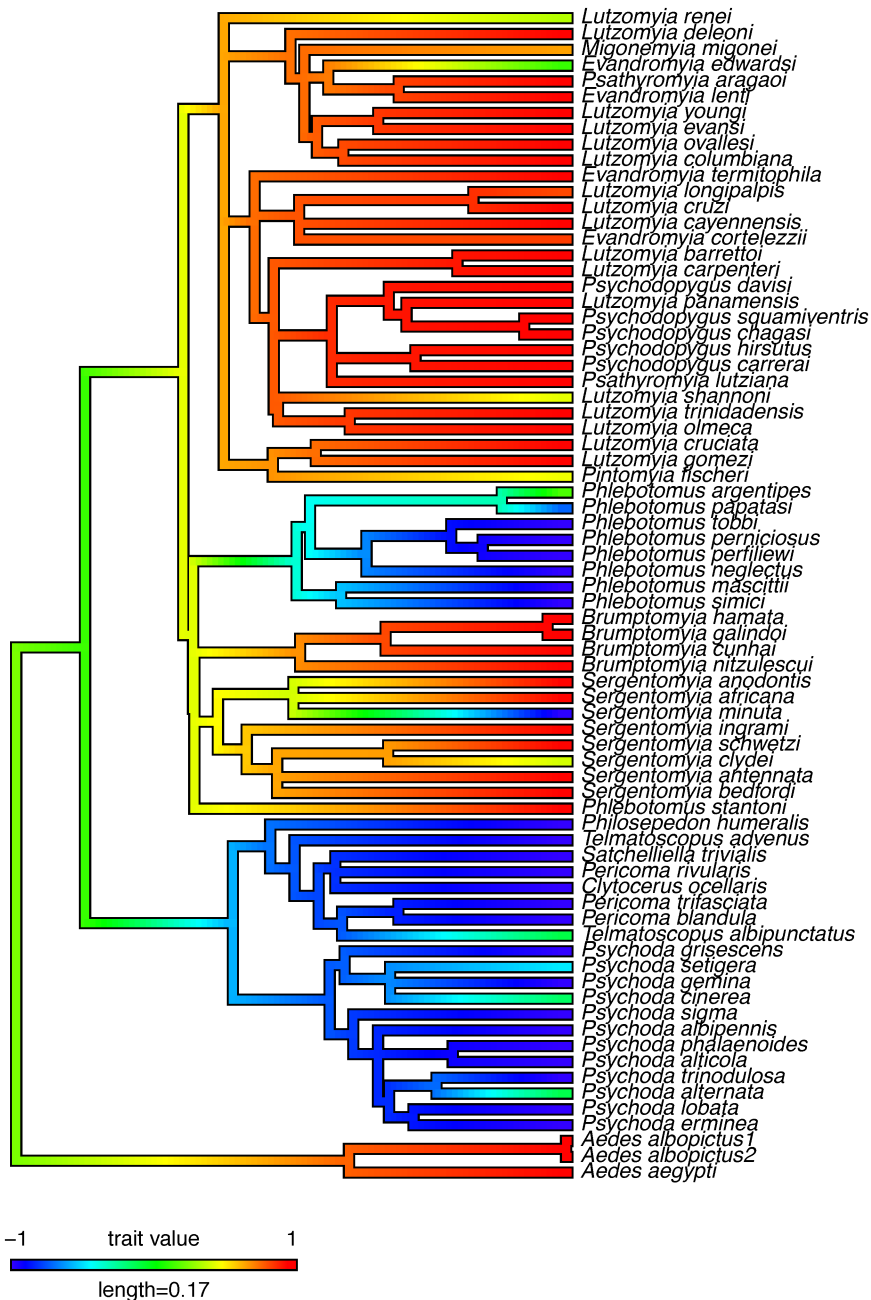


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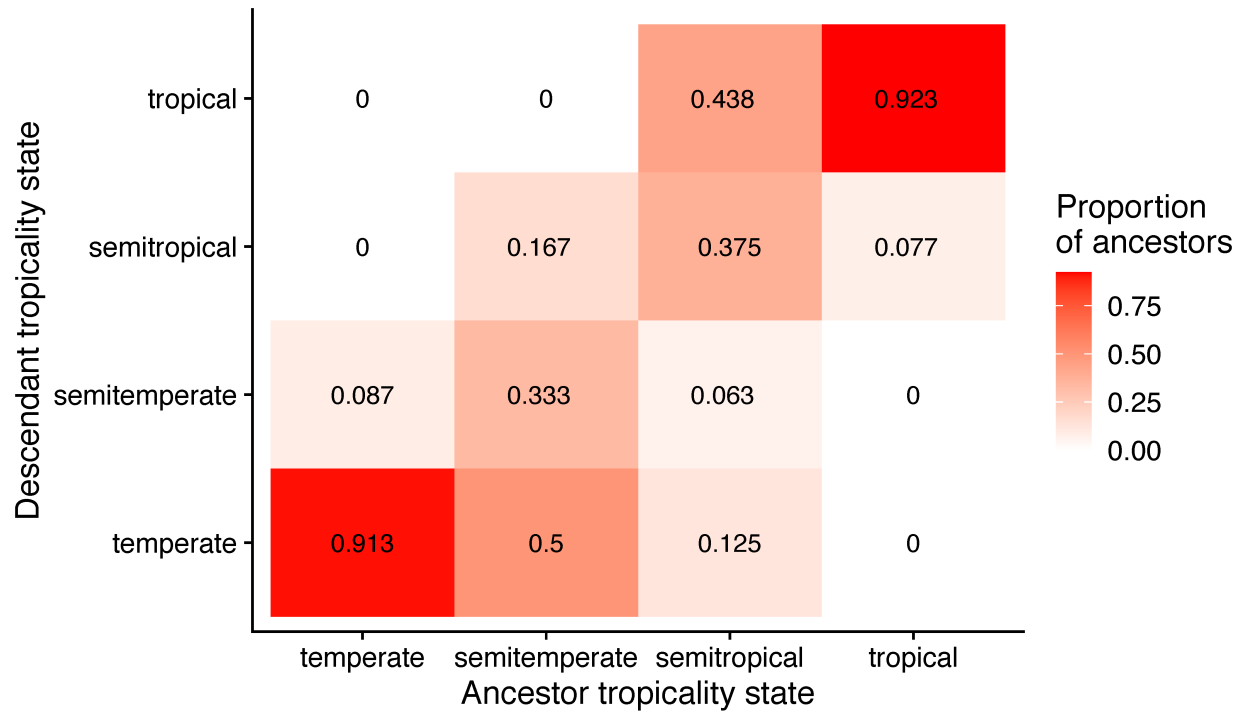


558 **FIGURE 4. Ancestral reconstruction of TI across the Psychodidae tree shows few**  
559 **transitions in tropicity index.** The color of each branch shows the inferred TI values  
560 for each node and branch. All ancestral reconstructions used *anc.ML* (*phytools*, (Revell  
561 2012)). Similar trees for PC1 and mean latitude are shown in Figure S4.



562

563 **FIGURE 5. Transitions between latitudinal states, as defined by the tropicity**  
564 **index (TI), are rare in the Psychodidae family.** The color of a cell reflects the  
565 likelihood of a transition rate. Values in the diagonal represent the likelihood of staying  
566 in the same latitudinal band.



567

568

569 **REFERENCES**

- 570 Ali, J. R., and J. C. Aitchison. 2014. Exploring the combined role of eustasy and oceanic  
571 island thermal subsidence in shaping biodiversity on the Galápagos. *Journal of*  
572 *Biogeography* 41:1227–1241.
- 573 Andrade-Filho, J. D., R. G. C. Scholte, A. L. G. Amaral, P. H. F. Shimabukuro, O. S.  
574 Carvalho, and R. L. Caldeira. 2017. Occurrence and Probability Maps of  
575 *Lutzomyia longipalpis* and *Lutzomyia cruzi* (Diptera: Psychodidae:  
576 Phlebotominae) in Brazil. *Journal of Medical Entomology* 54:1430–1434.
- 577 Angilletta Jr, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal  
578 physiology in ectotherms. *Journal of thermal Biology* 27:249–268. Elsevier.
- 579 Bailey, F., K. Mondragon-Shem, P. Hotez, J. A. Ruiz-Postigo, W. Al-Salem, Á. Acosta-  
580 Serrano, and D. H. Molyneux. 2017. A new perspective on cutaneous  
581 leishmaniasis—Implications for global prevalence and burden of disease  
582 estimates. *PLOS Neglected Tropical Diseases* 11:e0005739. Public Library of  
583 Science.
- 584 Barnagaud, J.-Y., V. Devictor, F. Jiguet, M. Barbet-Massin, I. L. Viol, and F. Archaux.  
585 2012. Relating Habitat and Climatic Niches in Birds. *PLOS ONE* 7:e32819. Public  
586 Library of Science.
- 587 Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. lme4: Linear mixed-effects  
588 models using Eigen and S4. R package version.
- 589 Bennett, S., C. M. Duarte, N. Marbà, and T. Wernberg. 2019. Integrating within-species  
590 variation in thermal physiology into climate change ecology. *Philosophical*  
591 *Transactions of the Royal Society B* 374:20180550. The Royal Society.

- 592 Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for Phylogenetic Signal in  
593 Comparative Data: Behavioral Traits Are More Labile. *Evolution* 57:717–745.
- 594 Booth, T. H., H. A. Nix, J. R. Busby, and M. F. Hutchinson. 2014. bioclim: the first  
595 species distribution modelling package, its early applications and relevance to  
596 most current MaxEnt studies. *Diversity and Distributions* 20:1–9.
- 597 Bouzid, M., F. J. Colón-González, T. Lung, I. R. Lake, and P. R. Hunter. 2014. Climate  
598 change and the emergence of vector-borne diseases in Europe: case study of  
599 dengue fever. *BMC Public Health* 14:781.
- 600 Butler, M. A., and A. A. King. 2004. Phylogenetic comparative analysis: a modeling  
601 approach for adaptive evolution. *The American Naturalist* 164:683–695. The  
602 University of Chicago Press.
- 603 Caceres, A. G., E. A. Galati, F. Le Pont, and C. Velasquez. 1997. Possible role of  
604 *Lutzomyia maranonensis* and *Lutzomyia robusta* (Diptera: Psychodidae) as  
605 vectors of human bartonellosis in three provinces of region nor Oriental del  
606 Marañon, Peru. *Rev Inst Med Trop Sao Paulo* 39:51–52.
- 607 Campino, L., S. Cortes, L. Dionisio, L. Neto, M. O. Afonso, C. Maia, L. Campino, S.  
608 Cortes, L. Dionisio, L. Neto, M. O. Afonso, and C. Maia. 2013. The first detection  
609 of *Leishmania major* in naturally infected *Sergentomyia minuta* in Portugal.  
610 *Memórias do Instituto Oswaldo Cruz* 108:516–518. Fundação Oswaldo Cruz.
- 611 Castillo, D. M. 2017. Factors contributing to the accumulation of reproductive isolation: A  
612 mixed model approach. *Ecology and Evolution* 7:5808–5820.
- 613 Christie, K., and S. Y. Strauss. 2018. Along the speciation continuum: Quantifying  
614 intrinsic and extrinsic isolating barriers across five million years of evolutionary

615 divergence in California jewelflowers. *Evolution* 72:1063–1079. Wiley Online  
616 Library.

617 Comer, J. A., W. S. Irby, and D. M. Kavanaugh. 1994. Hosts of *Lutzomyia shannoni*  
618 (Diptera: Psychodidae) in relation to vesicular stomatitis virus on Ossabaw Island,  
619 Georgia, USA. *Medical and veterinary entomology* 8:325–330. Wiley Online  
620 Library.

621 Cooper, B. S., A. Sedghifar, W. T. Nash, A. A. Comeault, and D. R. Matute. 2018. A  
622 Maladaptive Combination of Traits Contributes to the Maintenance of a *Drosophila*  
623 Hybrid Zone. *Current Biology*, doi: 10.1016/j.cub.2018.07.005.

624 Cooper, N., R. P. Freckleton, and W. Jetz. 2011. Phylogenetic conservatism of  
625 environmental niches in mammals. *Proceedings of the Royal Society B: Biological*  
626 *Sciences* 278:2384–2391. Royal Society.

627 Cooper, N., W. Jetz, and R. P. Freckleton. 2010. Phylogenetic comparative approaches  
628 for studying niche conservatism. *Journal of Evolutionary Biology* 23:2529–2539.

629 Cromley, E. K. 2003. GIS and Disease. *Annual Review of Public Health* 24:7–24.

630 Cunze, S., J. Kochmann, L. K. Koch, and S. Klimpel. 2018. Niche conservatism of *Aedes*  
631 *albopictus* and *Aedes aegypti* - two mosquito species with different invasion  
632 histories. *Scientific Reports* 8:7733. Nature Publishing Group.

633 da Costa, S. M., J. L. P. Cordeiro, and E. F. Rangel. 2018. Environmental suitability for  
634 *Lutzomyia (Nyssomyia) whitmani* (Diptera: Psychodidae: Phlebotominae) and the  
635 occurrence of American cutaneous leishmaniasis in Brazil. *Parasites Vectors*  
636 11:155.

- 637 Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models,  
638 new heuristics and parallel computing. *Nature methods* 9:772–772. Nature  
639 Publishing Group.
- 640 De Boeck, P., M. Bakker, R. Zwitser, M. Nivard, A. Hofman, F. Tuerlinckx, and I.  
641 Partchev. 2011. The estimation of item response models with the lmer function  
642 from the lme4 package in R. *Journal of Statistical Software* 39:1–28.
- 643 Desjeux, P. 2004. Leishmaniasis: current situation and new perspectives. *Comparative*  
644 *Immunology, Microbiology and Infectious Diseases* 27:305–318.
- 645 Diniz-Filho, J. A. F., and L. M. Bini. 2008. Macroecology, global change and the shadow  
646 of forgotten ancestors. *Global Ecology and Biogeography* 17:11–17.
- 647 Felsenstein, J. 1973. Maximum likelihood and minimum-steps methods for estimating  
648 evolutionary trees from data on discrete characters. *Systematic Biology* 22:240–  
649 249. Society of Systematic Zoology.
- 650 Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate  
651 surfaces for global land areas. *International Journal of Climatology* 37:4302–4315.
- 652 Florin, D. A., S. J. Davies, C. Olsen, P. Lawyer, R. Lipnick, G. Schultz, E. Rowton, R.  
653 Wilkerson, and L. Keep. 2011. Morphometric and molecular analyses of the sand  
654 fly species *Lutzomyia shannoni* (Diptera: Psychodidae: Phlebotominae) collected  
655 from seven different geographical areas in the southeastern United States.  
656 *Journal of medical entomology* 48:154–166. Oxford University Press Oxford, UK.
- 657 Florin, D. A., and E. A. Rebollar-Téllez. 2013. Divergence of *Lutzomyia* (*Psathyromyia*)  
658 *shannoni* (Diptera: Psychodidae: Phlebotominae) is indicated by morphometric  
659 and molecular analyses when examined between taxa from the southeastern

660 United States and southern Mexico. *Journal of medical entomology* 50:1324–  
661 1329. Oxford University Press Oxford, UK.

662 Grosjean, N. L., R. A. Vrable, A. J. Murphy, and L. S. Mansfield. 2003. Seroprevalence  
663 of antibodies against *Leishmania* spp among dogs in the United States. *Journal of*  
664 *the American Veterinary Medical Association* 222:603–606. Am Vet Med Assoc.

665 Gunderson, A. R., D. L. Mahler, and M. Leal. 2018. Thermal niche evolution across  
666 replicated *Anolis* lizard adaptive radiations. *Proceedings of the Royal Society B:*  
667 *Biological Sciences* 285:20172241. Royal Society.

668 Hadfield, J. D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed  
669 Models: The MCMCglmm R Package. *J. Stat. Soft.* 33.

670 Haffer, J. 1997. Alternative models of vertebrate speciation in Amazonia: an overview.  
671 *Biodiversity and Conservation* 6:451–476.

672 Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER:  
673 investigating evolutionary radiations. *Bioinformatics* 24:129–131. Oxford  
674 University Press.

675 Hitch, A. T., and P. L. Leberg. 2007. Breeding distributions of North American bird  
676 species moving north as a result of climate change. *Conservation Biology* 21:534–  
677 539. Wiley Online Library.

678 Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S.  
679 Scheibe. 2020. multcomp: Simultaneous Inference in General Parametric Models.

680 Huey, R. B., T. Garland, and M. Turelli. 2019. Revisiting a Key Innovation in Evolutionary  
681 Biology: Felsenstein’s “Phylogenies and the Comparative Method.” *The American*  
682 *Naturalist* 193:755–772. The University of Chicago Press.

- 683 Ibarra-Cerdeña, C. N., A. Zaldívar-Riverón, A. T. Peterson, V. Sánchez-Cordero, and J.  
684 M. Ramsey. 2014. Phylogeny and Niche Conservatism in North and Central  
685 American Triatomine Bugs (Hemiptera: Reduviidae: Triatominae), Vectors of  
686 Chagas' Disease. PLOS Neglected Tropical Diseases 8:e3266. Public Library of  
687 Science.
- 688 Kamal, M., M. A. Kenawy, M. H. Rady, A. S. Khaled, and A. M. Samy. 2018. Mapping  
689 the global potential distributions of two arboviral vectors *Aedes aegypti* and *Ae.*  
690 *albopictus* under changing climate. PLOS ONE 13:e0210122.
- 691 Kanjanopas, K., S. Siripattanapipong, U. Ninsaeng, A. Hitakarun, S. Jitkaew, P.  
692 Kaewtaphaya, P. Tan-ariya, M. Mungthin, C. Charoenwong, and S. Leelayoova.  
693 2013. *Sergentomyia (Neophlebotomus) gemmea*, a potential vector of *Leishmania*  
694 *siamensis* in southern Thailand. BMC Infect Dis 13:333.
- 695 Karimkhani, C., V. Wanga, L. E. Coffeng, P. Naghavi, R. P. Dellavalle, and M. Naghavi.  
696 2016. Global burden of cutaneous leishmaniasis: a cross-sectional analysis from  
697 the Global Burden of Disease Study 2013. The Lancet Infectious Diseases  
698 16:584–591.
- 699 Keith, S. A., T. J. Webb, K. Böhning-Gaese, S. R. Connolly, N. K. Dulvy, F. Eigenbrod,  
700 K. E. Jones, T. Price, D. W. Redding, I. P. F. Owens, and N. J. B. Isaac. 2012.  
701 What is macroecology? Biology Letters 8:904–906. Royal Society.
- 702 Kerkhoff, A. J., P. E. Moriarty, and M. D. Weiser. 2014. The latitudinal species richness  
703 gradient in New World woody angiosperms is consistent with the tropical  
704 conservatism hypothesis. PNAS 111:8125–8130. National Academy of Sciences.



- 705 Lawyer, P. G., P. M. Ngumbi, C. O. Anjili, S. O. Odongo, Y. B. Mebrahtu, J. I. Githure, D.  
706 K. Koech, and C. R. Roberts. 1990. Development of *Leishmania major* in  
707 *Phlebotomus duboscqi* and *Sergentomyia schwetzi* (Diptera: Psychodidae). The  
708 American Journal of Tropical Medicine and Hygiene 43:31–43. The American  
709 Society of Tropical Medicine and Hygiene.
- 710 Lewis, D. J., and R. P. Lane. 1976. A taxonomic review of *Phlebotomus*  
711 (*Idiophlebotomus*) (Psychodidae). Systematic Entomology 1:53–60.
- 712 Matute, D. R., C. J. Novak, and J. A. Coyne. 2009. Temperature-based extrinsic  
713 reproductive isolation in two species of *Drosophila*. Evolution 63:595–612.
- 714 McVay, J. D., A. L. Hipp, and P. S. Manos. 2017. A genetic legacy of introgression  
715 confounds phylogeny and biogeography in oaks. Proceedings of the Royal  
716 Society B: Biological Sciences 284:20170300. Royal Society.
- 717 Minter, L., B. Kovacic, D. M. Claborn, P. Lawyer, D. Florin, and G. C. Brown. 2009. New  
718 state records for *Lutzomyia shannoni* and *Lutzomyia vexator*. Journal of medical  
719 entomology 46:965–968. Oxford University Press Oxford, UK.
- 720 Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species  
721 that did not show a phenological response to climate change are declining.  
722 Proceedings of the National Academy of Sciences 105:16195–16200. National  
723 Acad Sciences.
- 724 Moreno, M., C. Ferro, M. Rosales-Chilama, L. Rubiano, M. Delgado, A. Cossio, M. A.  
725 Gómez, C. Ocampo, and N. G. Saravia. 2015. First report of *Warileya*  
726 *rotundipennis* (Psychodidae: Phlebotominae) naturally infected with *Leishmania*

- 727 (Viannia) in a focus of cutaneous leishmaniasis in Colombia. *Acta Tropica*  
728 148:191–196.
- 729 Mukherjee, S., M. Q. Hassan, A. Ghosh, K. N. Ghosh, A. Bhattacharya, and S. Adhya.  
730 1997. Short Report: Leishmania DNA in *Phlebotomus* and *Sergentomyia* Species  
731 during a Kala-Azar Epidemic. *The American Journal of Tropical Medicine and*  
732 *Hygiene* 57:423–425. The American Society of Tropical Medicine and Hygiene.
- 733 Oliveira, S. V. de, D. Romero-Alvarez, T. F. Martins, J. P. dos Santos, M. B. Labruna, G.  
734 S. Gazeta, L. E. Escobar, and R. Gurgel-Gonçalves. 2017. *Amblyomma* ticks and  
735 future climate: Range contraction due to climate warming. *Acta Tropica* 176:340–  
736 348.
- 737 Pagel, M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta*  
738 26:331–348. Wiley Online Library.
- 739 Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–  
740 884. Nature Publishing Group.
- 741 Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics  
742 and evolutionary analyses in R. *Bioinformatics* 35:526–528. Oxford University  
743 Press.
- 744 Pearman, P. B., M. D’Amen, C. H. Graham, W. Thuiller, and N. E. Zimmermann. 2010.  
745 Within-taxon niche structure: niche conservatism, divergence and predicted  
746 effects of climate change. *Ecography* 33:990–1003.
- 747 Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. Niche dynamics in  
748 space and time. *Trends in Ecology & Evolution* 23:149–158.
- 749 Peng, R. D. 2008. simpleboot: Simple bootstrap routines. R package version 1.1-3.

- 750 Pennell, M. W., J. M. Eastman, G. J. Slater, J. W. Brown, J. C. Uyeda, R. G. FitzJohn, M.  
751 E. Alfaro, and L. J. Harmon. 2014. geiger v2. 0: an expanded suite of methods for  
752 fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30:2216–  
753 2218. Oxford University Press.
- 754 Pijáček, M., and L. Kudělková. 2020. Drain fly-*Clogmia albipunctata* (Diptera:  
755 Psychodidae)-a fly with epidemiological potential and posing risk of myiasis.  
756 *Epidemiologie, Mikrobiologie, Immunologie: Casopis Spolecnosti pro Epidemiologii*  
757 *a Mikrobiologii Ceske Lekarske Spolecnosti JE Purkyne* 69:142–147.
- 758 Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: convergence diagnosis  
759 and output analysis for MCMC. *R News* 6:7–11.
- 760 Posada, D. 2008. jModelTest: phylogenetic model averaging. *Molecular biology and*  
761 *evolution* 25:1253–1256. Oxford University Press.
- 762 R Core Team. 2016. R Development Core Team.
- 763 Reeves, W. K., C. Y. Kato, and T. Gilchrist. 2008. Pathogen screening and bionomics  
764 of *Lutzomyia apache* (Diptera: Psychodidae) in Wyoming, USA. *Journal of the*  
765 *American Mosquito Control Association* 24:444–447. BioOne.
- 766 Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and  
767 other things). *Methods in ecology and evolution* 3:217–223. John Wiley & Sons,  
768 Ltd (10.1111).
- 769 Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J.  
770 C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the  
771 North American avifauna. *Science* 366:120–124. American Association for the  
772 Advancement of Science.

- 773 Rosypal, A. C., G. C. Troy, A. M. Zajac, R. B. Duncan Jr, K. Waki, K.-P. CHANG, and D.  
774 S. Lindsay. 2003. Emergence of zoonotic canine leishmaniasis in the United  
775 States: Isolation and immunohistochemical detection of *Leishmania infantum* from  
776 foxhounds from Virginia. *Journal of Eukaryotic Microbiology* 50:691–693. Wiley  
777 Online Library.
- 778 Rosypal, A. C., G. C. Troy, A. M. Zajac, G. Frank, and D. S. Lindsay. 2005.  
779 Transplacental transmission of a North American isolate of *Leishmania infantum*  
780 in an experimentally infected beagle. *Journal of Parasitology* 91:970–972.
- 781 Sarkar, S. D., D. S. Mandal, and D. Banerjee. 2018. First report of drain fly,  
782 *Telmatoscopus albipunctata* (Vaillant, 1972)(Diptera: Psychodidae): causative  
783 agent of a rare urinary myiasis from India. *JMSCR* 6:70–74.
- 784 Schaut, R. G., M. Robles-Murguia, R. Juelsgaard, K. J. Esch, L. C. Bartholomay, M.  
785 Ramalho-Ortigao, and C. A. Petersen. 2015. Vectorborne transmission of  
786 *Leishmania infantum* from hounds, United States. *Emerging infectious diseases*  
787 21:2209. Centers for Disease Control and Prevention.
- 788 Sievers, F., and D. G. Higgins. 2018. Clustal Omega for making accurate alignments of  
789 many protein sequences. *Protein Science* 27:135–145.
- 790 Sievers, F., A. Wilm, D. Dineen, T. J. Gibson, K. Karplus, W. Li, R. Lopez, H. McWilliam,  
791 M. Remmert, J. Söding, J. D. Thompson, and D. G. Higgins. 2011. Fast, scalable  
792 generation of high-quality protein multiple sequence alignments using Clustal  
793 Omega. *Mol. Syst. Biol.* 7:539.
- 794 Sparkes, J., and M. Anderson. 2010. The possibility of drain flies being a public health  
795 pest. *International Pest Control* 52:206–210. Research Information Ltd.

- 796 Ulloa, G. M., F. Vásquez-Achaya, C. Gomes, L. J. del Valle, J. Ruiz, M. J. Pons, and J.  
797 del V. Mendoza. 2018. Molecular Detection of *Bartonella bacilliformis* in  
798 *Lutzomyia maranonensis* in Cajamarca, Peru: A New Potential Vector of Carrion's  
799 Disease in Peru? The American Journal of Tropical Medicine and Hygiene  
800 99:1229–1233. The American Society of Tropical Medicine and Hygiene.
- 801 Venables, W. N. 2002. Modern applied statistics with S / W.N. Venables, B.D. Ripley.  
802 Venables, W. N. (William N. ), B. D. Ripley, and W. N. (William N. ). Venables. 2003.  
803 Modern Applied Statistics With S. Technometrics 45:111–111.
- 804 Villaseca, P., C. Padilla, G. Ventura, F. Samalvides, H. Yañez, L. Chevarría, B. Ellis, L.  
805 Rotz, J. Leake, and L. Beati. 1999. Importancia de la *Lutzomyia peruensis* en la  
806 transmisión de la Enfermedad de Carrion en el Valle Sagrado de los Incas,  
807 Urubamba-Cusco, Perú. Revista Peruana de Medicina Experimental y Salud  
808 Publica 16:28–30. Instituto Nacional de Salud.
- 809 Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I.  
810 Damschen, T. Jonathan Davies, J.-A. Grytnes, and S. P. Harrison. 2010. Niche  
811 conservatism as an emerging principle in ecology and conservation biology.  
812 Ecology letters 13:1310–1324. Wiley Online Library.
- 813 Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species  
814 richness. Trends in ecology & evolution 19:639–644. Elsevier.
- 815 Wiens, J. J., T. N. Engstrom, and P. T. Chippindale. 2006. Rapid Diversification,  
816 Incomplete Isolation, and the “Speciation Clock” in North American Salamanders  
817 (genus *Plethodon*): Testing the Hybrid Swarm Hypothesis of Rapid Radiation.  
818 Evolution 60:2585–2603.

819 Young, D. G., and M. A. Duran. 1994. Guide to the identification and geographic  
820 distribution of *Lutzomyia* sand flies in Mexico, the West Indies, Central and South  
821 America (Diptera: Psychodidae). WALTER REED ARMY INST OF RESEARCH  
822 WASHINGTON DC.  
823  
824