

Phylogenetic climatic niche conservatism in sandflies (Diptera: Phlebotominae) and their relatives

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Received September 28, 2021

Accepted May 4, 2022

Phylogenetic niche conservatism is a pattern in which closely related species are more similar than distant relatives in their niche-related traits. Species in the family Psychodidae show notable diversity in climatic niche, and present an opportunity to test for phylogenetic niche conservatism, which is as yet rarely studied in insects. Some species (in the subfamily Phlebotominae) transmit *Leishmania* parasites, responsible for the disease leishmaniasis, and their geographic range has been systematically characterized. Psychodid genus ranges can be solely tropical, confined to the temperate zones, or span both. We obtained observation site data, and associated climate data, for 234 psychodid species to understand which aspects of climate most closely predict distribution. Temperature and seasonality are strong determinants of species occurrence within the clade. Next, we built a phylogeny of Psychodidae, and found a positive relationship between pairwise genetic distance and climate niche differentiation, which indicates strong niche conservatism. This result is also supported by strong phylogenetic signals of metrics of climate differentiation. Finally, we used ancestral trait reconstruction to infer the tropicality (i.e., proportion of latitudinal range in the tropics minus the proportion of the latitudinal range in temperate areas) of ancestral species, and counted transitions to and from tropicality states. We find that tropical and temperate species produced almost entirely tropical and temperate descendant species, respectively. Taken together, our results imply that climate niches in psychodids are strongly predicted by phylogeny, and represent a formal test of a key prediction of phylogenetic niche conservatism in a clade with implications for human health.

Aspects of climate affect how individual species are distributed across the globe as well as patterns of diversification for clades of species (Haffer 1997; Barnagaud et al. 2012; Ali and Aitchison 2014). A notable pattern that has emerged from studying the climatic niche distribution across related species is that related species tend to have similar climatic niches because species retain

ecological characteristics from their ancestors (Peterson et al. 1999; Wiens and Graham 2005; Losos 2008; Wiens et al. 2010). This pattern, known as niche conservatism, has been reported for multiple taxa across the tree of life including frogs (Wiens et al. 2006), mammals (Cooper et al. 2011), and angiosperms (Kerkhoff et al. 2014). Niche conservatism in climatic tolerances

specifically has been invoked as a potential explanation for the higher species diversity in the tropics, because tropical species might not be able to evolve the ability to colonize temperate areas of the planet (Wiens and Donoghue 2004). Despite the evidence for niche conservatism in some clades, whether ecological niches are expected to be conserved or labile remains debated (Wiens and Graham 2005; Losos 2008). Tests are universally needed to assess whether niche conservatism is a common effect of ecological diversification.

The family Psychodidae includes 4000 species distributed globally (Rutledge and Gupta 2002; Munstermann 2019). Species from the family occupy a variety of climatic niches ranging from almost exclusively polar to exclusively tropical species. Among the family, two genera have been the main foci of research. Sandflies of the genera *Lutzomyia* and *Phlebotomus* are the only known vectors of *Leishmania*, a trypanosome parasite responsible for the disease leishmaniasis. *Lutzomyia* (Diptera: Psychodidae) is endemic to the New World and encompasses over 400 species (Young and Duran 1994). *Phlebotomus* (Diptera: Psychodidae) is endemic to the Old World and encompasses 50 species (Lewis and Lane 1976). At least 120 species from these two genera transmit leishmaniasis. Even though species within two other genera in the family (*Sergentomyia* and *Wari-leya*; Lawyer et al. 1990; Mukherjee et al. 1997; Campino et al. 2013; Kanjanopas et al. 2013; Moreno et al. 2015) can be infected with *Leishmania*, they do not transmit the parasite. All other species in the family are known as moth-flies, some of which can cause human myiasis (i.e., infection of skin tissue with larvae; Sarkar et al. 2018; Pijáček and Kudělková 2020) and are commonly human commensals (Sparkes and Anderson 2010).

Despite the negative impacts that psychodids can have on human well-being, the potential drivers of geographic distribution remain highly unexplored for this group. Although there are significant gaps in our knowledge of the genetics and evolutionary history of the Psychodidae, the geographic ranges of the genera in the family, in particular *Lutzomyia* and *Phlebotomus*, have been extensively characterized. However, to our knowledge, the efforts to reconstruct the relationships between psychodid species have focused on taxonomic classifications and have not addressed how climate tolerance traits have evolved in the clade. For example, no study has addressed whether the distributions of these vectors, and their related species, are influenced by their phylogenetic relationships; namely, whether closely related species show similar geographic distributions and climatic niches or, on the contrary, have experienced climatic niche shifts over time. Macroecological analyses that combine environmental data with species occurrence records can reveal the extent of climatic variation across the geographic range of a species group (Diniz-Filho and Bini 2008; Keith et al. 2012). When coupled with phylogenetic

analyses, macroecological data can also reveal the extent of climate niche evolution in a group.

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

Methods

OCCURRENCE DATA

We obtained coordinates for the collections of 234 species in the Psychodidae family from Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>). The dataset included species from the genera *Lutzomyia* (55), *Pericoma* (23), *Phlebotomus* (28), *Psychoda* (25), *Sergentomyia* (15), *Telmatoscopus* (14), *Brumptomyia* (14), *Satchelliella* (12), *Psychodopygus* (9), *Trichomyia* (8), *Evandromyia* (4), *Clytrocercus* (5), *Philosepedon* (4), *Psathyromyia* (4), *Pintomyia* (4), *Micropygomyia* (3), *Migone-myia* (2), and *Warileya* (2). The DOIs for each of the datasets are listed in Table S1. We then filtered our dataset to only include the 133 extant species for which at least five georecorded locations were available.

ESTIMATING SPECIES' CLIMATIC NICHE

Our first goal was to describe how the abiotic environment varies across sites where psychodid species have been observed. We used the collection location data described above and bioclimatic variables extracted from publicly available databases to estimate variation in the abiotic environments of Psychodidae species. For each psychodid occurrence record, we extracted four climatic variables from BIOCLIM (warmest-month maximum temperature, coldest-month minimum temperature, annual precipitation, and seasonality of precipitation; Booth et al. 2014) and one from WorldClim (elevation; Fick and Hijmans 2017). The resolution for both the WorldClim and BIOCLIM datasets was 2.5 min of a degree (in other words, $2.5 \times 1/60$ of a degree). We only considered five environmental variables to avoid overfitting, given that 70% of species had fewer than 20 occurrence records. For each of these five climate variables, we calculated 25th, 50th, and 75th percentiles of the distribution for each species. We conducted a

principal component analysis (PCA) (function *prcomp*; library *stats* [R Core Team 2016]) using the 25th and 75th percentiles of each trait for each species (10 total variables) to capture the climatic breadth of each species. However, because the eigenvectors associated with 25th versus 75th percentile were highly correlated within each climatic variable (see *Results*), we opted to instead use a PCA of the medians of each variable (five total variables). To measure the extent of the differentiation along each principal component (PC) axis, we use linear mixed models (LMM) where each PC was the response, the genus was the only fixed effect, and the species was a random effect (function *lme*, library *nlme*; Pinheiro et al. 2017). We used a type III ANOVA to assess the significance of the genus effect (function *Anova*, library *car*; Fox et al. 2007; Fox and Weisberg 2019). We followed the LMM with a Tukey's honest difference post hoc comparisons (function *lsmeans*, library *lsmeans*; Lenth et al. 2015; Lenth 2016).

MEAN LATITUDE AND TROPICALITY INDEX

We calculated the mean latitude of occurrence for each species as one way of characterizing geographical distribution. However, mean latitude is unable to distinguish between a range-restricted tropical species and a cosmopolitan species with an identical range centroid. As such, we additionally calculated Kerkhoff et al.'s (2014) tropicality index (TI) for each species as the proportion of its latitudinal range that falls within the tropics, defined as the region between the Tropic of Cancer (23.43641° N) and the Tropic of Capricorn (23.43641° S), minus the proportion of the latitudinal range that falls within the temperate zone. The index ranges between -1 (strictly temperate species) to 1 (strictly tropical species). Values of 0 correspond to species whose distribution is half-temperate and half-tropical. Following Kerkhoff et al. (2014), we further assigned species to one of four distributional categories based on the tropicality index: "tropical" species with $TI > 0.5$ (75% or more of the range within the tropics), "semitropical" species with $0 < TI \leq 0.5$ (50%–75% of the range in the tropics), "semitemperate" species with $-0.5 < TI \leq 0$ (25%–50% of the range in the tropics), and "temperate" species with $TI \leq -0.5$ (less than 25% of the range within the tropics).

PHYLOGENETIC TREE

In spite of the rich geographical range dataset for Psychodidae, few efforts have addressed the phylogenetic relationships between species of the family (but see Grace-Lema et al. 2015). To address this gap, we inferred the phylogenetic relationships between species of the family Psychodidae. We used a set of 79 species of the Psychodidae family that had been genotyped with nuclear (18S rDNA and ITS) and mtDNA (COI and cytochrome B) markers. We list their all the accession numbers in Table S2. We aligned the sequences using Clustal Omega

(Sievers et al. 2011; Sievers and Higgins 2018) with the following specifications: `-dealign -t -seqtype = {DNA} -outfmt = phylip -v`. We included sequences for *Aedes albopictus* and *Aedes aegypti* to serve as an outgroup and root the tree (Table S2). We concatenated the four loci into a supermatrix using the function *concatenateAlignments* (library *"chopper"*; Michonneau 2022). The total alignment used 81 species and 6095 markers. Next, we used this matrix to generate an ultrametric phylogenetic tree using BEAST (Drummond and Rambaut 2007; Drummond and Bouckaert. 2015). We used an HKY substitutions model with estimated base frequencies, Coalescent: Constant size, an uncorrelated relaxed clock, and a UPGMA starting tree. The input tree for BEAST was prepared using BEAUti (Drummond and Rambaut 2007; Drummond and Bouckaert. 2015). We ran 10,000,000 steps on the chain and use TreeAnnotator (Drummond and Rambaut 2007; Drummond and Bouckaert. 2015) to select the most credible tree discarding the 100,000 states as burnin. This approach generated a rooted ultrametric tree for the Psychodidae family. We used the resulting tree for all following analyses. We also inferred the topology using other 11 BEAST specifications and they all showed a lower posterior (Table S3). Nonetheless, we compared the phylogenies resulting with different specifications using the Robinson-Foulds symmetric difference (Robinson and Foulds 1981; Bryant and Steel 2001; function *treedist*, library *"phangorn"*, Schliep 2011). All run files are available in the DRYAD package (<https://doi.org/10.5061/dryad.m63xsj44g>).

PHYLOGENETIC SIGNAL

We used the ultrametric tree to estimate the phylogenetic signal of the climatic niche (characterized by the PC1 score from the ordination above), the mean latitude of each species, and the tropicality index across the Psychodidae tree using two different metrics, Pagel's λ (Pagel 1999) and Blomberg's K (Blomberg et al. 2003). Both metrics were calculated using the function *"phylosig"* (library *phytools*, Revell 2012) with 1000 simulations to determine if the calculated value differed from zero. The first metric, Pagel's λ , is a measure of phylogenetic signal that estimates the extent to which the phylogenetic history of a clade is predictive of the trait distribution at the tree tips. Values of λ lower than 1.0 represent traits being less similar among species than expected from their phylogenetic relationships. A λ equal to 1.0 suggests that traits covary with phylogeny (Pagel 1997, 1999) and is consistent with, but not diagnostic of, niche conservatism (Cooper et al. 2010). The second metric, Blomberg's K (Blomberg et al. 2003), indicates whether the association between the tree and the trait follows the expectations under a Brownian model of evolution (i.e., the trait value changes randomly, in both direction and magnitude, over the course of evolution). If K equals 1 , the evolution of species' traits (climatic niche, mean latitude, TI) conforms to

Table 1. Models of trait evolution fitted to climatic niche data in the Psychodidae family.

Model	Assumptions	<i>fitContinuous</i> Option
White noise	The trait values come from a single normal distribution with no covariance structure among species.	model = “white”
Lambda	A model in which phylogeny predicts covariance among trait values (Pagel 1999). The model transforms the tree using a scalar, λ , that ranges between 0 (a star-like phylogeny) and 1 (the BM model, see below). Equivalent to calculating a form of phylogenetic signal (λ , see <i>Methods</i>).	model = “lambda”
Early burst	The rate of evolution increases or decreases exponentially through time, under the model $r_t = r_0 \times e^{(a \times t)}$, where r_0 is the initial rate, a is the rate change parameter, and t is time.	model = “EB”
Ornstein-Uhlenbeck (OU)	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 ~ 0 and 2.72 (Butler and King 2004).	model = “OU”
Brownian motion model	The correlation structure among trait values is proportional to the extent of shared ancestry for pairs of species (Felsenstein 1973).	model = “BM”
Kappa	Character divergence is associated with speciation events in the tree (Pagel 1999). kappa ranges between ~ 0 and 1.	model = “kappa”
Delta	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; deltas lower than 1 suggest recent evolution has been comparatively slow.	model = “delta”

a model of Brownian motion evolution in which trait values of descendant species diverge slowly from the ancestral value. A K lower than 1 suggests that relatives resemble each other less than expected under Brownian motion evolution and is evidence against phylogenetic niche conservatism (Cooper et al. 2010). A K higher than 1 suggests that close relatives are more similar than expected under Brownian motion evolution. This observation that species are more similar in the niche than expected by Brownian motion models is consistent with a pattern of niche conservatism (Losos 2008; Revell et al. 2008; Cooper et al. 2010). We repeated these analyses for 11 other BEAST specifications to confirm the inference of phylogenetic signal was robust to differences in the topology caused by choices of phylogenetic models.

Additionally, we studied whether λ was sufficient to explain the mode of evolution of climatic niche in the family, or whether a more complex model would provide a better fit. We fitted seven different models of trait evolution using the function *fitContinuous* (library “*geiger*”; Harmon et al. 2008; Pennell et al. 2014). Models varied in the tempo and mode of trait evolution and ranged from no phylogenetic signal (i.e., white noise) to different modes of evolution. The details of the seven models are described in Table 1. We compared all seven models using their

Akaike information criterion (AIC) values and calculating their Akaike weights (*wAIC*) using the equation:

$$wAIC_i = \exp(-0.5 \times \Delta AIC_i),$$

where ΔAIC_i is the difference between the AIC of model i and the model with the lowest AIC. We used the function *aic.w* (library *phytools*; Revell 2012) for these calculations.

CLIMATIC NICHE DIVERGENCE

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

niche of a pair of species increases as divergence accrues should also have a strong phylogenetic signal.

Closely related species do not behave independently, and their similarity is likely to be the result of shared history (Huey et al. 2019). We therefore used two corrections for phylogenetic nonindependence. First, we use a variant of phylogenetic regression in which the genetic relationships of the species are considered a random effect in a linear mixed model. We used the function *cophenetic* (library “stats”; R Core Team 2016) to convert the ultrametric tree into a genetic distance matrix. We used a linear mixed model in which the difference in PC1 was the response, genetic distance was a continuous variable, and the two species in the comparison were considered random effects using the function *lmer* (library “lme4”; De Boeck et al. 2011; Bates et al. 2013). We used the function *bootMer* (library “lme4”; Bates et al. 2013) to bootstrap the regression (1000 replicates). To compare the slope of the phylogenetically corrected and the noncorrected regressions, we used a Wilcoxon rank sum test with continuity correction (function *wilcox.test*, library *stats*; R Core Team 2016).

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

ANCESTRAL TRAIT RECONSTRUCTION AND RATES OF TRANSITION

We inferred the climatic niche of each ancestral node in the Psychodidae phylogenetic tree for three proxies of climate niche: (i) tropicality index (TI), (ii) mean latitude, and (iii) PC1 (described in ESTIMATING SPECIES' CLIMATIC NICHE). We used the function “*anc.ML*” (library *phylo*; Revell 2012) for the ancestral trait reconstruction of each of the three traits mentioned above with a maximum of 5000 iterations using a Brownian movement model. (Similar runs using other models gave identical results.) Trees were drawn using the function “*contMap*” (library *phylo* [Revell 2012]). Finally, we used ancestral niche reconstruction to examine the rate at which species in the Psychodi-

dae transitioned among and between the four latitudinal range categories (tropical, semitropical, semitemperate, and temperate) based on TI as described above (Kerkhoff et al. 2014). First, we inferred the latitudinal category for each node in the tree using *fastAnc* (Revell 2012). Ancestral trait reconstructions using other approaches (*anc.Bayes* and *anc.ML*; Revell 2012) gave similar results. Then, for each latitudinal category, we selected all of the ancestral nodes inferred to be in that category, and calculated the proportion of immediately descendant nodes or tips in each of the four latitudinal categories. Doing this for each category yielded 16 transition rates describing the frequency of transitions between any pair of latitudinal states.

Results

GEOGRAPHIC DISTRIBUTION OF PSYCHODIDAE GENERA

First, we calculated the mean latitude of 234 species in the Psychodidae family as a proxy of their distribution. We find that there are two peaks of diversity in the family, one in the tropics around the Equator and a smaller one slightly below the Arctic circle (Fig. S1). Figure S2 shows the mean latitude for species within 12 genera in the Psychodidae family. The moth-fly genera *Clytocerus*, *Philosepedon*, *Satcheliella*, and *Telmatoscopus* are all of temperate distribution. The genera *Pericoma* and *Psychoda* are largely temperate but some species have a tropical distribution. Among *Leishmania*-harboring genera, some patterns are also salient. The genera *Lutzomyia* and *Brumptomyia* are mostly restricted to the tropics. *Phlebotomus* on the other hand shows high diversity in the northern subtropical region.

Given the strong differences in mean latitude between genera, we first tested for a relationship between environmental variables and occurrence records of each species within the different genera of psychodids included in our dataset. We found that the eigenvectors for the 25th and 75th percentiles' contributions to the largest principal components were highly correlated (Pearson's product-moment correlation, PC1: $r = 0.997$, $P < 0.001$; PC2: $r = 0.986$, $P = 0.002$; PC3: $r = 0.999$, $P < 0.001$). In light of this correlation, we opted to use the 50th percentile of each climate variable for each species distribution for all further analyses. A PCA revealed the relative importance of elevation, temperature, and temperature seasonality for occurrence. Table S4 shows the loadings for the PCA. The first three PCs explain the vast majority of the variance (93.89%), so we restricted our analyses to these PCs. All environmental variables had relatively high loadings on PC1 (57.04% of variation). Positive values on PC1 indicate locations that are relatively seasonal and cool, whereas more negative values are indicative of locations that are less seasonal and warmer (Fig. 1). Genera differed along PC1 (LMM: $\chi^2_{12} = 522.16$, $P < 1 \times 10^{-10}$;

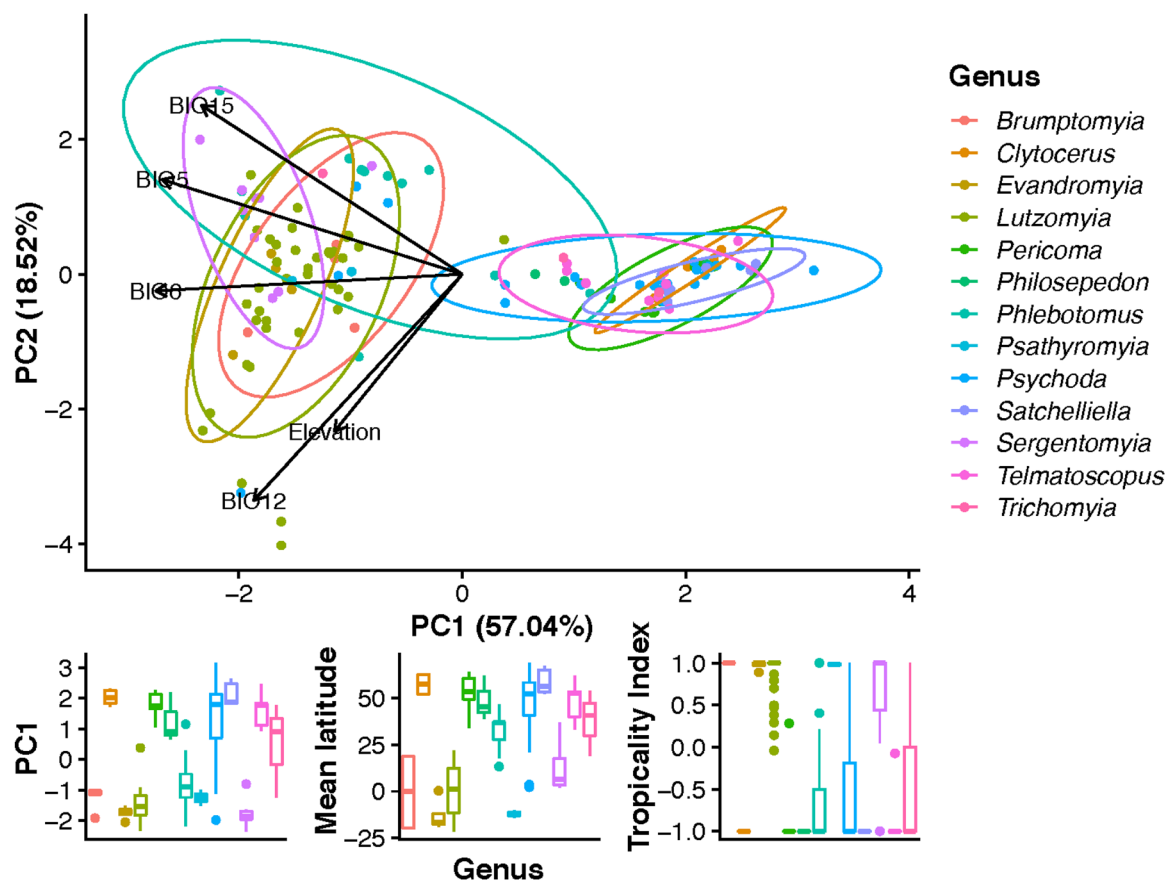


Figure 1. Different genera within the Psychodidae family differ from each other in their climatic niche. (a) PCA based on the WorldClim and BIOCLIM variables suggests that the occurrence of different genera within the family is associated with climatic variables. (b) Boxplot showing the mean species values for PC1. This PC is mostly explained by temperature and precipitation. (c) Boxplot showing the mean species values for latitudinal distribution. (d) Boxplot showing the mean species values for TI.

Fig. 1b) and PC2 (LMM: $\chi^2_{12} = 34.71$, $P = 5.2 \times 10^{-4}$), which is largely dominated by elevation and explained 18.52% of the variance. Finally, PC3 (18.33%), which is mostly influenced by amount and seasonality of precipitation, also differed among genera ($\chi^2_{12} = 36.15$, $P = 3.07 \times 10^{-4}$). Pairwise comparisons for these PCs all suggested strong differences across genera (Tables S5–S7).

COMPARATIVE PHYLOGENETIC ANALYSES

Phylogenetic relationships

We generated a Bayesian phylogeny based on concatenated nuclear and mtDNA markers to get an approximation of the phylogenetic relationships within the family Psychodidae (Open Tree of Life: TBD; Fig. S3). Our sample contains genera from two different taxonomic subfamilies: Phlebotominae and Psychodinae. We recovered these two subfamilies as monophyletic groups (Fig. S3), but not all genera appear monophyletic (e.g., *Phlebotomus*). The hematophagous clade was monophyletic (*Lutzomyia*, *Phlebotomus*, *Brumptomyia*, and *Sergentomyia*) but the *Leishmania* vectors were not.

Phylogenetic signal

We used the phylogenetic tree to study macroevolutionary trends of the evolutionary history of climate niche in the family. We used two complementary indices that summarized patterns of trait evolution on a phylogeny for each of our three proxies of climatic niche: TI, mean latitude, and PC1. First, we found that Pagel's λ was significantly higher than 0 and lower than 1 for the three proxies (Fig. 2). Second, we found that Blomberg's K was significantly higher than 1 for each of the three metrics of geographic range (Fig. 2; Table 2), indicating that the climatic niches of close relatives are more similar to each other than expected under a pure model of Brownian motion evolution (1000 randomizations, $P < 0.001$; Fig. 2). The prior specifications of BEAST had little impact on these conclusions as all three proxies showed high levels of phylogenetic signal in the majority of phylogenetic reconstructions (Table S3).

Broadly, these two metrics suggest that climatic descriptors of niche have a strong phylogenetic signal in the Psychodidae tree.

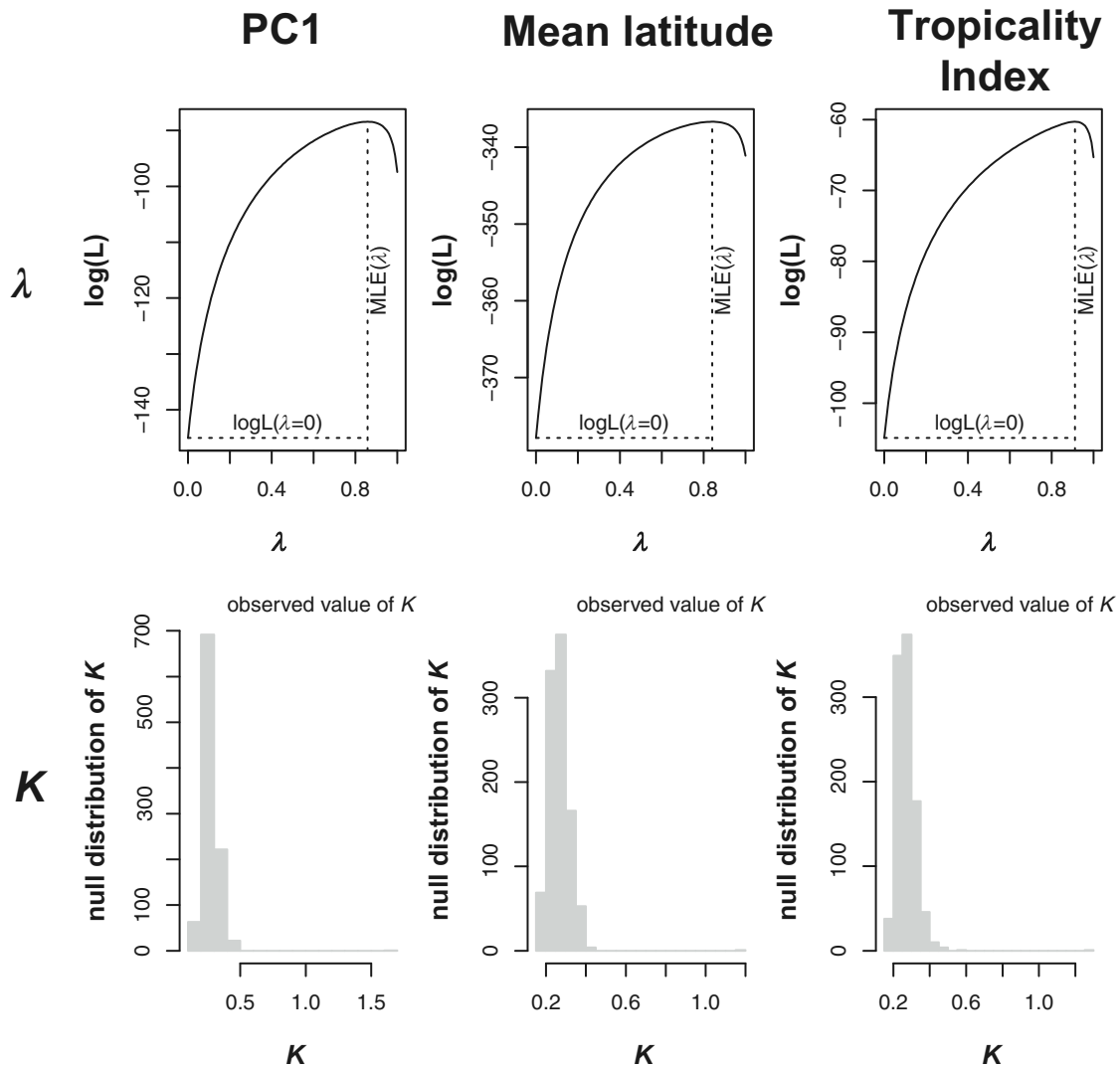


Figure 2. Climatic niche shows strong phylogenetic signal in the Psychodidae family. Top panels show the distribution of simulated and observed Blomberg's K . Bottom panels show values of the maximum likelihood estimate (MLE) of λ and the maximum likelihood of the model when λ is zero. Left-side panels show metrics for PC1. Center panels show metrics for median latitude. Right-side panels show metrics for tropicality index.

Table 2. Different proxies of climatic niche have a strong phylogenetic signal.

	Blomberg's K	λ
Mean latitude	1.170, $P = 0.001$	0.841, $P < 0.001$
PC1	1.645, $P = 0.001$	0.858, $P < 0.001$
TI	1.276, $P = 0.001$	0.912, $P < 0.001$

Note: Blomberg's K and λ estimates for three different proxies of geographic range in the Psychodidae family.

Additionally, we studied whether the model with *lambda* as the only parameter was sufficient to describe the history of climate niche evolution in the phylogenetic tree of the Psychodi-

dae. We fit seven different models of trait evolution to determine which one fitted best the evolution of climatic niche in the Psychodidae family. These models range from no phylogenetic signal (i.e., white noise) to punctuated changes of trait evolution associated with speciation events (i.e., *kappa*). Table 3 shows the fit and the parameters inferred for each of the seven models for TI; Tables S8 and S9 show the parameters for PC1 and mean latitude, respectively. Consistent with the results from the summary indices, we find that models with a phylogenetic signal fit better than the only model with no phylogenetic signal for all three proxies of geographic range. For the three proxies of climate niche, the model that best fit their mode of evolution was the *lambda* model that assumes phylogenetic history predicts covariance among trait values. These results indicate that the

Table 3. Trait-evolution models suggest that a *lambda* model best explains the evolution of TI in Psychodidae.

Model	σ^2	z_0	Additional Parameters	AIC	wAIC
White noise	0.781	0.200	NA	213.951	0.000
Lambda	2.474	−0.126	$\lambda = 1.000$	126.594	0.917
Early burst	3.624	−0.120	$a = 0.00$	136.646	0.006
OU	4.395	−0.114	$\alpha = 2.718$	134.651	0.016
Brownian motion	3.624	−0.120	NA	134.646	0.016
Kappa	1.150	−0.114	$\kappa = 0.672$	133.370	0.031
Delta	2.326	−0.111	$\delta = 1.798$	135.076	0.013

Note: σ^2 is the average amount of change expected in each time step. z_0 is the trait value at the root of the tree. Similar analyses and results for PC1 and mean latitude are shown in Tables S4 and S5.

evolution of climate niche in Psychodidae shows signs of niche conservatism.

Consistent with niche conservatism, we found that the genetic divergence between species pairs is positively associated with the extent of their climate niche differentiation (one-way ANOVA: $F_{1,3079} = 4165.49$, $P < 1 \times 10^{-10}$). These results suggest that closely related species are the most similar in their climatic niche, and that the climate niche of Psychodidae species becomes more dissimilar as divergence increases. This result is qualitatively identical for a phylogenetically corrected dataset where the species identity is considered a random effect (LMM: $\chi^2 = 3348.04$, $P < 1 \times 10^{-10}$). The magnitude of the regression slope is lower in the phylogenetically corrected regression than for the noncorrected dataset ($\text{Slope}_{\text{Corrected}} = 10.09 \pm 0.16$, $\text{Slope}_{\text{Noncorrected}} = 9.82 \pm 0.17$; Wilcoxon rank sum test with continuity correction: $W = 883,679.0$, $P < 1 \times 10^{-10}$; Fig. 3). Finally, an MCMC-based phylogenetic correction revealed the same pattern, as the slope of the normalized difference regression is also positive (95% CI = 0.081–0.287). The results from all these analyses (i.e., a positive correlation between divergence in climatic traits and age of divergence) are consistent with our phylogenetic signal analyses, which suggest that climatic niche evolution in the species from the Psychodidae family is consistent with niche conservatism.

Ancestral trait reconstruction and transition rates

Figure 4 shows the extant tropicality indexes in the Psychodidae family (marked by color) and the inferred states along the phylogenetic tree. Figure S4 shows similar trees for PC1 and mean latitude. Our best estimate is that the ancestor of the Psychodidae family had a semitropical to tropical distribution (inferred state at the root for tropicality index under a *lambda* model of trait evolution, $Z_0 = -0.13$; Z_0 values with other models are listed in Table 3). Extant subtropical and temperate species, such as most moth-flies, have a climatic niche that appears to be derived in the family. The clade encompassing vector genera also

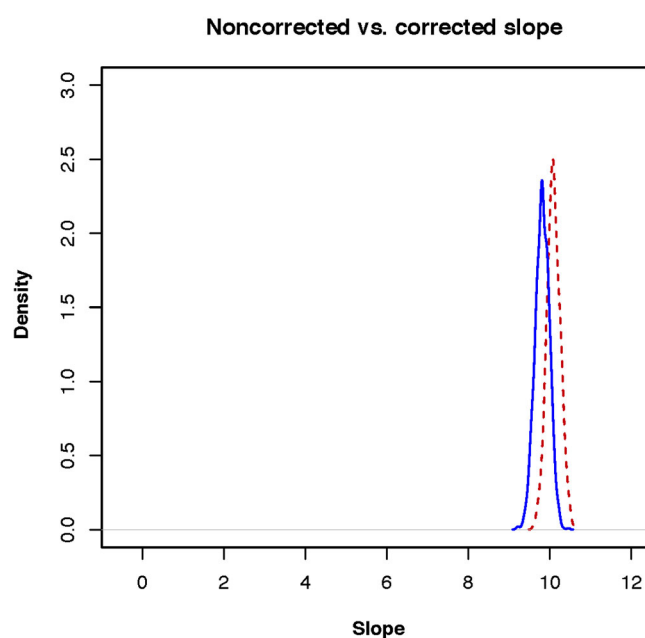
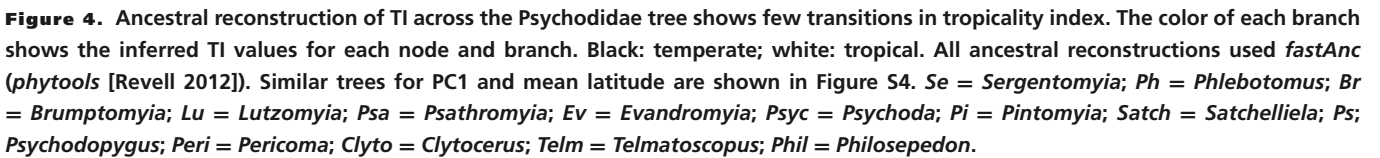


Figure 3. Habitat differentiation increases with genetic distance in the Psychodidae family. Both models show a monotonic increase with genetic distance. The blue distribution shows a noncorrected linear regression; the red-dashed distribution shows a linear mixed model that accounts for the species effect.

has an inferred semitropical origin (inferred TI value = 0.21). Within *Phlebotomus*, ancestral character reconstruction suggests that the ancestor of the genus had a tropical distribution (inferred TI value = 0.03), suggesting that the colonization of temperate habitats is derived from a tropical ancestor.

In general, we found that evolutionary transitions to new latitudinal ranges were rare (Fig. 5). A total of 91.9% transitions from tropical ancestors and 91.7% transitions from temperate ancestors resulted in descendant nodes or tips remaining in the same latitudinal zone. Further, all of the remaining 8.1% transitions from tropical nodes and 8.3% transitions from temperate nodes were to semitropical and semitemperate zones,



Discussion

ther a tropical or temperate distribution but rarely span the full latitudinal gradient. Moreover, the phylogenetic distribution of climatic niche components suggests that climate niche has undergone few transitions in Psychodidae. As they have diversified, tropical species have mostly produced tropical species, and temperate species have given rise to more temperate species. Our results constitute a systematic test of phylogenetic niche conservatism in tropical and temperate species.

Phylogenetic niche conservatism, as a pattern, has been proposed to be ubiquitous across clades (Wiens and Graham 2005) but the evidence for the prevalence of this pattern is varied and in some instances, noncomparable (reviewed in Wiens et al. 2010, Peterson 2011, and Crisp and Cook 2012). In angiosperms, climatic niche shows evidence of conservatism in tropical and

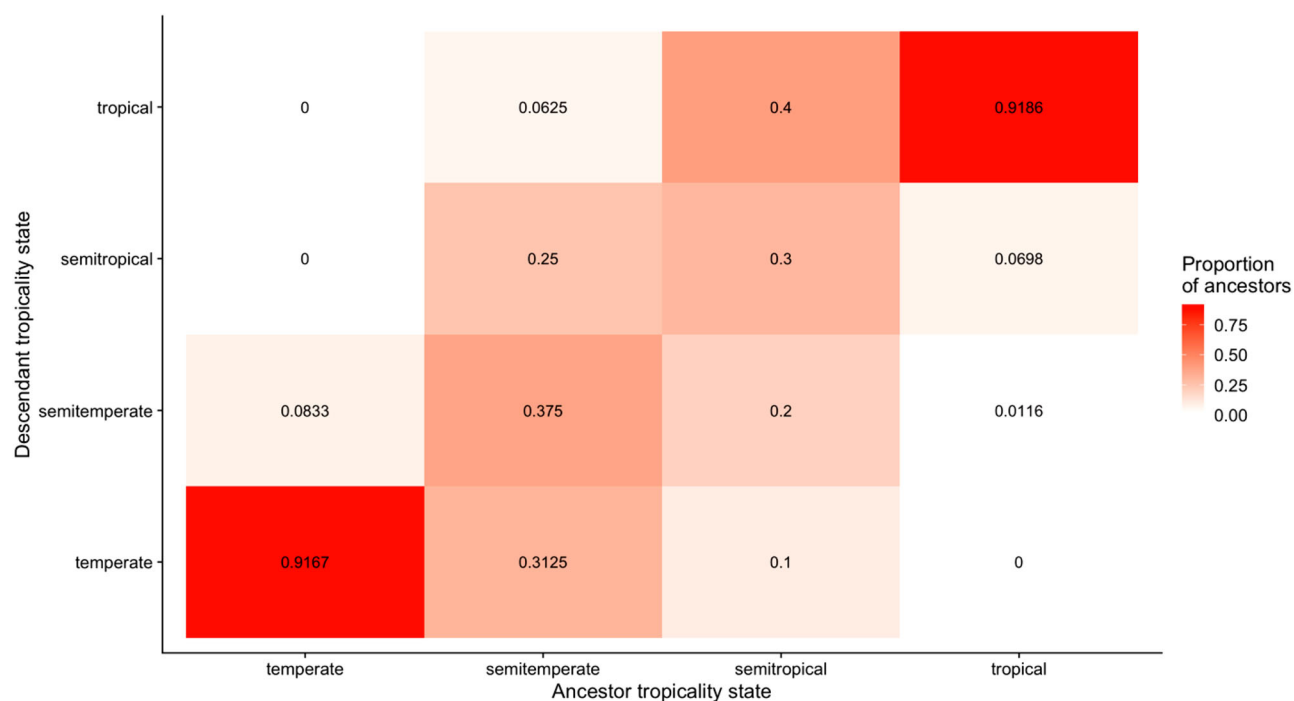


Figure 5. Transitions between latitudinal states, as defined by the tropicality index (TI), are rare in the Psychodidae family. The color of a cell reflects the likelihood of a transition rate. Values in the bottom-left to top-right diagonal represent the likelihood of staying in the same tropicality state.

temperate clades (Kerkhoff et al. 2014). In animals, the majority of the research has been done in vertebrate clades. In *Desmognathus* and eastern *Plethodon* salamanders, climatic variables show evidence of niche conservatism (table 2 in Kozak and Wiens 2010), which in turn explains the time to speciation and the altitudinal diversity patterns in these groups. Thermal physiology traits in birds and mammals show evidence of niche conservatism in tropical but not temperate assemblages (Khaliq et al. 2015). Initial surveys suggest that diet traits might show evidence of niche conservatism in birds (Kissling et al. 2009) but not in mammals (fig. 2 in Olalla-Tárraga et al. 2017). This rich field of research in vertebrates will benefit from a unified methodological approach to study whether ecological niches tend to be conserved or labile during divergence.

In insects, data on phylogenetic niche conservatism are more scant. Metrics of ecological niche such as mean annual air temperature, mean annual rainfall, and vegetation type show evidence of phylogenetic niche conservatism in Hawaiian *Drosophila*, *Laupala*, and *Tetragnatha* (table S6 in Hiller et al. 2019). Elevational niche shows moderate signatures of phylogenetic niche conservatism in Fijian *Homalictus* bees (Dorey et al. 2020). A third study conducted pairwise comparisons of the ecological niche of six pairs of triatomid bugs, vectors of Chagas disease (Ibarra-Cerdeña et al. 2014), and suggested that pairs of related species are more similar in their niche than pairs of distantly related species. Our results add to the body of work that

suggests that climate niche is phylogenetically conserved in at least some insect clades.

The work presented here has two limitations. Our inference of the phylogenetic relationships in the group is largely consistent with previous results (e.g., Grace-Lema et al. 2015), but only a comprehensive sampling of the variation of the genomes in these dipterans will reveal the true phylogenetic relationships between species. A logical next step in the research of climate niche differentiation will be to assess whether different species have differences in their realized thermal physiology (reviewed in Angilletta Jr. et al. 2002; Bennett et al. 2019), in their thermal preference (e.g., Matute et al. 2009; Cooper et al. 2018), or in both. More generally, the current granularity of our data only allows us to conclude the existence of a pattern of phylogenetic niche conservatism but does not allow us to speculate on the mechanisms behind the pattern (Wiens and Graham 2005; Pyron et al. 2015).

Despite these caveats, our finding of climate niche evolution in the Psychodidae family opens the possibility of new research avenues. First, incorporating a climatic dimension to the study of the evolution of vectors can inform to what extent climate plays a role in the coevolution of parasites and vectors. In the specific case of *Lutzomyia* and *Phlebotomus*, these studies will reveal whether there is an association between carrying *Leishmania* and a tropical climate niche. Second, studies that address the limits of climate niche will also inform which vectors are most likely to move across climatic zones as climate change changes

the thermal characteristics of the planet. Finally, comparing the rates of transition between different latitudinal categories can inform whether different taxa show different rates of conservatism. Only one other study has calculated the rates of transition between latitudinal zones (angiosperms; Kerkhoff et al. 2014) but the comparison is still informative. The rates of transitions we observed among tropicality values obtained for Psychodidae and those observed for angiosperms are similar and both reveal strong niche conservatism. The number of transitions from a tropical or temperate node is higher (78 and 46, respectively) than from a semitemperate or semitropical ancestor (6 and 16, respectively) and we thus have more power to detect differences in transition rates between the former categories. Integrating physiological and performance-based traits with analyses of climatic niche evolution can provide a window to understanding differences between physiological and realized niches, ultimately revealing the ecological implications of climatic divergence (Gunderson et al. 2018).

As climatic shifts occur globally, changes in environmental conditions will lead to new species distributions (Hitch and Leberg 2007; Rosenberg et al. 2019) or, in the extreme, extinction (Møller et al. 2008). Of particular importance for human health are potential changes in disease vector ranges and abundances, which depend on the extent to which disease vectors exhibit niche conservatism, a phenomenon still poorly examined. Studies on the climate evolution of species, and in particular of vectors, are important, because species in clades with phylogenetically conserved climatic niches are more likely to shift their geographic distributions in response to changing climate (Martinez-Meyer et al. 2004; Tingley et al. 2009; La Sorte and Jetz 2010; Oliveira et al. 2017), raising the possibility of poleward shifts of many vector species that are currently confined to the tropics. Some species of *Lutzomyia*, for example, have expanded their range northward (Comer et al. 1994; Reeves et al. 2008; Minter et al. 2009; Florin et al. 2011; Florin and Rebollar-Téllez 2013) that could potentially expand the endemicity of leishmaniasis (Grosjean et al. 2003; Rosypal et al. 2003, 2005; Schaut et al. 2015). Modeling of potential occurrence has revealed that increasing temperatures might further increase the potential range of a handful of species (Andrade-Filho et al. 2017; da Costa et al. 2018). Our results suggest that most Psychodidae vector species show a tropical distribution and that an assessment of the potential range expansions given multiple temperature change scenarios might be useful to monitor how vectors expand their niche along latitude and altitude.

ACKNOWLEDGMENTS

We thank J. Coughlan, A. Dagilis, the Matute Lab, and two anonymous reviewers for constructive feedback on the manuscript. This work was supported by the National Science Foundation (Dimensions of Biodiver-

sity award 1737752 to DRM). The funders had no role in any aspect of study design, data collection and analysis, or decisions with respect to publication.

AUTHOR CONTRIBUTIONS

ERRDA, AHH, AAC, and DRM conceptualized the idea of the study. RV, LR, EB, AHH, AAC, and ADRM designed the methodology. ERRDA and DRM collected and curated data. ERRDA, AHH, AAC, and DRM performed formal analysis. ERRDA, AHH, AAC, and DRM wrote the original draft. ERRDA, AHH, AAC, and DRM reviewed and edited the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

All code and raw data can be found at: <https://doi.org/10.5061/dryad.m63xsj44g>; the Phylogenetic tree used in this study was deposited in the Open Tree of Life.

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Associate Editor: R. Unckless
Handling Editor: T. Chapman

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

TABLE S1. Data accessibility. DOIs for the geographical occurrences of each species included in this study.

TABLE S2. Genbank accession numbers used to generate a phylogenetic tree for the Psychodidae family.

TABLE S3. Phylogenetic signal calculations using different BEAST specifications to generated the tree. K: Blomberg's K; λ : Pagel's lambda. The posterior of the tree shown in the main text was -55,973.52.

TABLE S4. PC loadings for the Psychodidae family-level PCA.

TABLE S5. Tukey pairwise comparisons for PC1.

TABLE S6. Tukey tests for PC2.

TABLE S7. Tukey tests for PC3.

TABLE S8. Trait-evolution models suggest that PC1—a proxy of climatic niche evolution—in Psychodidae evolves according to a lambda model of trait evolution.

TABLE S9. Trait-evolution models suggest that mean latitude proxy of climatic niche evolution—in Psychodidae evolves according to a lambda model of trait of trait evolution.

FIGURE S1. Geographic distribution of the samples included in this study. A. Location of the included samples. B. Mean latitude distribution for all species in the Psychodidae family. The solid black line marks the equator; dashed black lines mark the boundaries of the tropics

FIGURE S2. Mean latitude distribution for 72 species from 12 genera in the Psychodidae family. All species had at least five georeferenced records. Solid black line marks the equator; dashed black lines mark the boundaries of the tropics. Purple bars represent non-hematophagous species, orange bars represent hematophagous species who do not carry Leishmania. Purple bars represent hematophagous vector species.

FIGURE S3. Phylogenetic tree for the Psychodidae family based on four markers. Values on each node show the posterior probability. Blue bars show the 95% confidence interval of the node height.

FIGURE S4. Ancestral trait reconstruction using three different proxies of geographical distribution values suggest the ancestor of the Psychodidae family had a climatic niche akin to a tropical species. A. PC1 of climatic variation. B. Mean latitude. Figure 4 shows the ancestral niche reconstructions for TI.