

1 Associations between Afrotropical bats, parasites, and microbial symbionts

2

3 Lutz HL^{1,2}, Jackson EW³, Webala PW⁴, Babyesiza WS⁵, Kerbis Peterhans JC^{2,6}, Demos

4 TC², Patterson BD², Gilbert JA^{1,7}

5

6 ¹ Department of Surgery, University of Chicago, Chicago, Illinois, USA.

7 ² Integrative Research Center, Field Museum of Natural History, Chicago, Illinois, USA

8 ³ Department of Microbiology, Cornell University, Ithaca, New York, USA

9 ⁴ Department of Forestry and Wildlife Management, Maasai Mara University, Narok,

10 Kenya

11 ⁵ Department of Wildlife Management, Sokoine University of Agriculture, Morogoro,

12 Tanzania

13 ⁶ Department of Biological Sciences, Roosevelt University, Chicago, Illinois, USA

14 ⁷ Biosciences Division, Argonne National Laboratory, Argonne, Illinois, USA

15

16 Corresponding author:

17 Holly L. Lutz & Jack A. Gilbert

18 Department of Surgery

19 University of Chicago

20 5851 S. Maryland Avenue

21 Chicago, IL 60637 - 1508

22 hlutz@surgery.bsd.uchicago.edu

23 gilbertjack@uchicago.edu

24 ABSTRACT

25

26 Bats are among the most diverse animals on the planet and harbor numerous bacterial,
27 viral, and eukaryotic symbionts. The interplay between bacterial community composition
28 and parasitism in bats is not well understood and may have important implications for
29 studies of similar systems. Here we present a comprehensive survey of dipteran and
30 haemosporidian parasites, and characterize the gut, oral, and skin microbiota of
31 Afrotropical bats. We identify significant correlations between bacterial community
32 composition of the skin and dipteran ectoparasite prevalence across four major bat
33 lineages, as well as links between the oral microbiome and malarial parasitism, suggesting
34 a potential mechanism for host selection and vector-borne disease transmission in bats.
35 Mirroring recent studies of host-microbiome co-speciation in mammals, we find a weak
36 correlation between chiropteran phylogenetic distances and bacterial community
37 dissimilarity across the three anatomical sites, suggesting that host environment is more
38 important than shared ancestry in shaping the composition of associated bacterial
39 communities.

40

41

42 Keywords: microbiome, malaria, vector-borne disease, Afrotropics, Chiroptera

43

44

45

46

47 SIGNIFICANCE

48

49 Animals rely on bacterial symbionts for numerous biological functions, such as digestion

50 and immune system development. Increasing evidence suggests that host-associated

51 microbes may play a role in mediating parasite burden. This study is the first to provide a

52 comprehensive survey of bacterial symbionts from multiple anatomical sites across a

53 broad taxonomic range of Afrotropical bats, demonstrating significant associations

54 between the bat microbiome and parasite prevalence. This study provides a framework for

55 future approaches to systems biology of host-symbiont interactions across broad

56 taxonomic scales, which will allow for the recognition of the interdependence between

57 microbial symbionts and vertebrate health in the study of wild organisms and their

58 natural history.

59

60

61

62

63

64

65

66

67

68

69

70 \body

71

72 INTRODUCTION

73

74 Humans and other animals rely on bacterial symbionts for numerous biological
75 functions, such as digestion and immune system development (1, 2). Many studies have
76 found significant associations between host phylogeny (shared common ancestry) and
77 bacterial community composition (3, 4), while others have identified spatiotemporal
78 variables as significant drivers of host-microbe associations over the course of individual
79 lifespans (5-7). The influence of microbes on their hosts may be context dependent, such
80 that the presence of a particular microbe may be beneficial under one set of ecological
81 conditions and harmful under another. Thus, patterns of association between vertebrates
82 and bacterial symbionts provide a unique lens through which to explore evolutionary and
83 ecological phenomena.

84 Recognition of the interdependence between microbial symbionts and vertebrate
85 health has led to a growing paradigm shift in the study of wild organisms and their
86 natural history. Vertebrate species not only exhibit inherent life history characteristics,
87 but serve as hosts to myriad bacteria, archaea, viruses, fungi, and eukaryotic organisms
88 that abound in their environments. Many relationships between eukaryotic parasites and
89 hosts have ancient origins, and the same may be true for host-microbial associations.
90 Indeed, it is possible that bacterial symbionts of vertebrate hosts interact with eukaryotic
91 parasites, viruses, or fungal symbionts in ways that could ultimately shape host evolution
92 (8). For example, evidence from human and anthropophilic mosquito interactions

93 suggests that the skin microbiome can influence vector feeding preference, thereby
94 affecting transmission patterns of mosquito-borne pathogens (such as WNV, yellow
95 fever, dengue, malaria, etc.), and ultimately imposing selective pressures on human
96 populations - indeed, positive selection of malaria-protective genes can be seen in the
97 human genome (9). Despite the potential significance of such interactions between hosts,
98 microbes, and pathogen-transmitting vectors, they have not been well studied in most
99 wild vertebrate systems.

100 Bats (Mammalia: Chiroptera) are an important system for comparison of the
101 relative contributions of evolutionary and ecological factors driving host-symbiont
102 associations. In addition to being one of the most speciose orders of mammals (second
103 only to the order Rodentia), bats frequently live in large colonies, are long-lived, and
104 volant, granting them access to a wide geographic range relative to their non-volant
105 mammalian counterparts. The associations of diverse eukaryotic parasites (e.g. dipteran
106 insects, haemosporidia, helminths) within numerous bat lineages have been well-
107 characterized (10-13). Furthermore, bats have received increasing attention due to their
108 role as putative vectors of human pathogens (*e.g.* Ebola, Marburg, SARS (14, 15)).
109 Indeed, numerous serological surveys have supported the role of Afrotropical bats as
110 reservoirs for a number of viruses (16-18). Taken together, these features make bats an
111 appealing and tractable model for studying the interaction of bacterial symbionts and
112 non-bacterial parasites and pathogens.

113 In this study, we conduct the first broad-scale study of Afrotropical bat-associated
114 microbes. We test associations between bacterial community composition in the
115 gastrointestinal tract, skin, and oral cavities from nine families and nineteen genera of

116 bats. We pair this information with host-parasite associations between bats and
117 ectoparasites in the superfamily Hippoboscoidea (obligate hematophagous dipteran
118 insects), and haemosporidian (malarial) parasites putatively vectored by these
119 hippoboscoid insects. Using a combination of machine learning, network theory, and
120 negative binomial distribution models, we test the hypothesis that host-associated
121 bacterial communities predict prevalence of parasitism by obligate dipteran and malarial
122 parasites.

123

124 RESULTS

125

126 1) Ectoparasite and malarial parasite prevalence among Afrotropical bats

127

128 Sampling was conducted across 20 sites in Kenya and Uganda from July–August
129 of 2016. Sites ranged from sea level to ~2500m in elevation (Fig. 1; Table S1). We
130 collected gut, oral, and skin samples for bacterial community characterization from a total
131 of 495 individual bats, comprising 9 families, 19 genera, and 28 recognized species. Bat
132 families with the greatest representation included Hipposideridae ($n = 80$), Miniopteridae
133 ($n = 116$), Rhinolophidae ($n = 88$), and Pteropodidae ($n = 106$). All host and parasite
134 vouchers are accessioned at the Field Museum of Natural History (Chicago, IL, USA)
135 (Table S2). Miniopterid bats experienced the highest prevalence of both ectoparasitism
136 (*M. minor*, 89%) and malarial parasitism (*M. minor*, 67%) (Table 1). Bats with similarly
137 high ectoparasite prevalence at the host species level included *Rhinolophus eloquens* (79%

138 prevalence), *Stenonycteris lanosus* (62%), and *Triaenops afer* (60%). Unlike miniopterid
139 bats, these bat species did not harbor any detectable malarial parasites (Table 1).

140

141 2) Bacterial richness of bat skin drastically exceeds that of gut or oral communities

142

143 Across all samples, 51,136 Exact Sequence Variants (ESVs) were identified using
144 Deblur (19). Gut microbial communities exhibited the lowest overall diversity (9,804
145 ESVs), followed by oral (13,629 ESVs), and skin (46,904 ESVs), the latter being
146 significantly greater than gut or oral ($p < 2.2e-16$, Kruskal-Wallis; Bonferroni corrected
147 p -value $p < 1e-113$, Dunn's test) (Fig. 2A). Aggregate mean observed ESVs by host
148 genus were 70, 93, and 531 for gut, oral, and skin samples, respectively (Table 2). As with
149 observed ESV richness counts, the Shannon index of bat skin microbial communities was
150 significantly greater than that of either gut or oral microbiota ($p < 2.2e-16$, Kruskal-
151 Wallis; Bonferroni corrected p -value $p < 1e-119$, Dunn's Test) (Fig. 2B). Based on
152 weighted UniFrac distances, measures of intraspecific beta dispersion revealed a
153 continuum of dissimilarities across all host species (Fig. 3). Mean beta dispersion among
154 anatomical sites differed significantly ($p < 1.2e-7$, Kruskal-Wallis; Bonferroni corrected
155 p -value $p < 0.01$, Dunn's Test). Measures of intraspecific beta dispersion among
156 unweighted UniFrac and Bray-Curtis distances also showed a continuum of
157 dissimilarities across host species, and exhibited significant differences in mean beta
158 dispersion across anatomical sites (Fig. S1).

159

160 3) Microbial communities significantly correlate with geographic locality, anatomical site,
161 and host taxonomy, but not host phylogeny

162

163 Permutational analysis of variance (PERMANOVA) identified geographic
164 locality, host taxonomy, and anatomical sampling site (gut, oral, skin) as significant
165 factors explaining variation in three independent measures of microbial beta diversity
166 (Bray-Curtis, unweighted UniFrac, and weighted UniFrac) ($p < 0.001$, ADONIS) (Table
167 4). Secondary analysis of sites by elevation revealed that bats at higher elevations tended
168 to host increased alpha diversity across gut, oral, and skin microbiomes ($p < 2e-16$, linear
169 regression) (Fig. S2). In general, gut microbiota were dominated by Proteobacteria
170 (Enterobacteraceae) and Firmicutes (Bacillaceae). Oral microbiota were dominated by
171 Proteobacteria (Neisseriaceae, Pasteurellaceae). The oral microbiota of several insect bat
172 families (Miniopteridae, Nycteridae, Rhinolophidae) were enriched for Firmicutes in the
173 Mycoplasmataceae family, while the oral microbiota of fruit bats (Pteropodidae) were
174 enriched for Firmicutes in the Streptococacceae family. Similar to gut and oral microbiota,
175 skin also showed a high relative abundance of Proteobacteria (Moraxellaceae,
176 Enterobacteraceae) and Firmicutes (Bacillaceae), with a pronounced increase in relative
177 abundance of Actinobacteria and Bacteroidetes (Fig. 4).

178 Linear regression analyses of host phylogenetic distances and microbial
179 community dissimilarity (unweighted UniFrac (uf) and weighted UniFrac (wuf)
180 distances) revealed weak correlations for gut (uf: $R^2 = 0.013$, $p < 0.05$; wuf: $R^2 = 0.002$, p
181 $= 0.752$; $R^2 = 0.0007$, $p = 0.2643$; $R^2 = 0.0015$, $p = 0.522$), oral ($R^2 = 0.009$; $p < 0.05$), and
182 skin ($R^2 = 0.024$; $p < 0.005$) microbiota and host evolutionary relatedness (Fig. S3).

183

184 4) The microbiome is associated with parasitism in African bats

185

186 To test for significant associations between bacterial communities and eukaryotic
187 parasites (obligate ectoparasitic dipteran insects, and obligate endoparasitic malarial
188 parasites), we employed a combination of machine learning techniques, network analyses,
189 and negative binomial distribution models (see methods). PERMANOVA analysis
190 identified ectoparasite status and malarial infection status as significant predictors of
191 bacterial beta diversity dissimilarity among skin and oral microbiota, respectively ($p <$
192 0.001 , ADONIS). Tests of three independent measures of beta diversity (weighted
193 UniFrac, unweighted UniFrac, and Bray-Curtis) produced congruent results, with the
194 exception of oral microbiome, which was not significantly predictive of malarial infection
195 based on unweighted UniFrac analysis (Table 3).

196 Supervised machine learning analyses (random forests; see methods) produced
197 models that could classify the anatomical source of microbial communities and the host
198 genus of gut, oral, and skin microbial samples with reasonable accuracy (ratio of baseline
199 to observed classification error ≥ 2 ; *i.e.* random forest models performed at least twice as
200 well as random). Random forest models also performed well when classifying ectoparasite
201 status based on skin bacterial community composition, but less well for classification of
202 malarial status based on oral bacterial community composition (Table 5).

203 Following the application of statistical and machine learning approaches, we
204 employed network analyses to characterize the co-occurrence topology of microbial
205 communities (in terms of the relative abundance of co-occurring ESVs) across the skin

206 microbiota of our four most well-sampled bat families (Hipposideridae ($n = 80$),
207 Miniopteridae ($n = 116$), Rhinolophida ($n = 88$), and Pteropodidae ($n = 106$)). Network
208 analyses produced strikingly consistent results, revealing a significant decrease in cluster
209 size ($p < 0.05$, Mann-Whitney-Wilcoxon rank sum test) and median node degree ($p <$
210 0.05 , t test), as well as reduced network connectivity for parasitized bats from three of the
211 four bat families examined (Fig. 5; Fig. S4).

212

213 5) Bacterial taxa on skin correlated with presence or absence of obligate dipteran

214 ectoparasites

215

216 Negative binomial distribution (*e.g.* DESeq) models applied to skin microbiota in
217 four well-sampled bat families (Hipposideridae, Miniopteridae, Rhinolophidae,
218 Pteropodidae) identified a number of ESVs that were significantly associated with either
219 ectoparasitized or non-ectoparasitized bats (Fig. 6). Overall, we identified 89 and 24
220 ESVs significantly associated with parasitized and non-parasitized bats, respectively
221 (Table S3). Bacterial classes with the greatest representation among significant results
222 were Actinobacteria (16 families), Gammaproteobacteria (11 families), Bacilli (5
223 families), and Alphaproteobacteria (3 families). ESVs significantly enriched in parasitized
224 bats from at least three out of four bat families included Mycobacteraceae
225 (Actinobacteria), and Xanthomonadaceae (Gammaproteobacteria). ESVs significantly
226 enriched in parasitized bats from at least two out of four bat families included
227 Hyphomicrobiaceae (Alphaproteobacteria), Alcaligenaceae (Betaproteobacteria),
228 Moraxellaceae (Gammaproteobacteria), Planococcaceae (Bacilli), Flavobacteraceae

229 (Flavobacteria), Halobacteraceae (Halobacteria), and Chitinophagaceae (Saprospirae)
230 (Fig. 6).

231

232 DISCUSSION

233

234 The bacterial diversity we observed among gut, oral, and skin microbiota of bats
235 fall within ranges similarly observed in other vertebrate groups (3, 20-23). Although few
236 studies have simultaneously compared gut, oral, and skin microbiota from the same
237 individuals, our data reflect an apparent trend in the literature of skin bacterial diversity
238 among vertebrates significantly outnumbering gut or oral bacterial diversity (24-27). Our
239 data corroborate the findings of Nishida and Ochman (3), revealing no relationship
240 between chiropteran phylogeny and gut bacterial community dissimilarity. We found the
241 same absence of phylogenetic signal among oral and skin microbial communities. As
242 suggested in other studies of volant vertebrates (bats and birds), convergent adaptations
243 driven by the evolution of flight may be influencing the nature and composition of
244 microbial communities in both bats and birds (28-30).

245 Microbial community specificity can be assessed as a function of intraspecific
246 variation in dissimilarity (beta dispersion), where low dispersion suggests a tight and
247 perhaps co-evolutionary link between hosts and symbionts, whereas high dispersion
248 suggests more random associations between hosts and symbionts (31). Measures of beta
249 dispersion among bats revealed a continuum for all three anatomical sites, with oral
250 bacterial communities showing lower levels of beta dispersion (for weighted UniFrac
251 distances) than gut or skin communities (Fig. 3). This continuum suggests a possible

252 gradient of host-symbiont specificity across different bat species that may be influenced
253 by evolutionary history or host ecology. Given that we found no association between
254 bacterial community dissimilarity and host phylogenetic distance, variation in beta
255 dispersion is more likely a reflection of host ecology than evolutionary history.

256 Similar to recent studies in North American bats (32), we found sampling locality
257 to be a significant factor influencing skin, gut and oral microbial composition (Table 4).
258 Furthermore, we observed an apparent trend in increasing Shannon diversity and
259 observed ESV richness along an elevational gradient that was most pronounced for skin
260 microbiota (Fig. S2). A positive correlation between bacterial richness and elevation has
261 been observed in studies of amphibian skin (33) and montane soil, and this pattern may
262 be the result of climatological and other abiotic factors (*e.g.* pH) found along elevational
263 gradients (34, 35).

264 We found the general composition of gut microbiota in East African bats to be
265 similar to that of Neotropical bats, with Proteobacteria being the dominant bacterial
266 phylum present (36). Regardless of diet (insectivorous or frugivorous), the distal bat gut is
267 dominated by bacteria in the family Enterobacteriaceae (Phylum: Proteobacteria), though
268 fruit bats do have an increased relative abundance of bacteria in the family Clostridiaceae
269 (Phylum: Firmicutes) relative to insectivorous bats. In their study of neotropical bats,
270 Phillips et al. (37) noted an increased relative abundance of Lactobacillales in frugivorous
271 bats, and we note a similar pattern among pteropodid fruit bats in this study, which
272 exhibited a slightly higher proportion of Streptococcaceae (Order: Lactobacillales)
273 relative to insectivorous bats. Overall, the domination of the chiropteran gut by

274 Proteobacteria differs markedly from other mammalian gut microbiomes, which are
275 generally dominated by Firmicutes (21, 38, 39).

276 Among most bat families, the oral microbiome was dominated by Pasteurellaceae
277 (Phylum: Proteobacteria), and in some cases a high relative abundance of bacteria in the
278 families Mycoplasmataceae (in nycterids), Neisseriaceae (in vespertilionids and
279 rhinonycterids), and Streptococcaceae (in pteropodids) was also observed. Although the
280 oral microbiome has received less attention than that of the gut, several studies have
281 found diverse Pasteurellaceae and Neisseria lineages present in the oral microbiota of
282 animals, including domestic cats (20) and marine mammals (40). Pasteurellaceae lineages
283 have also recently been documented in the oral microbiota of Tasmanian devils (23, 41).
284 In humans, Pasteurallaceae (genera *Haemophilus* and *Aggregatibacter*) and Neisseriaceae
285 (genera *Neisseria*, *Kingella*, and *Eikenella*) play an important role in the formation
286 supragingival plaque (22). Though these bacterial groups are present in lower proportions
287 in other animals relative to bats, their presence in a broad range of host taxa suggest a
288 conserved evolutionary niche.

289 Our analysis identified links between ectoparasitism, malarial parasitism, and
290 bacterial communities on the skin and in oral cavities, respectively. Network analyses
291 identified consistent, stable, and species-rich clusters of bacteria on the skin of non-
292 ectoparasitized bats, compared to relatively disconnected and apparently transient bacteria
293 on the skin of bats harboring ectoparasites. This result mirrors that found in human-
294 mosquito interactions, in which individuals with lower bacterial diversity on the skin are
295 significantly more attractive to blood-seeking mosquitoes than individuals with higher
296 diversity (42). In humans, skin bacteria play a known role in attracting mosquitoes via

297 their production of volatile organic compounds (VOCs), and studies have shown that
298 variation in skin microbial community composition can increase or decrease human
299 attractiveness to blood-seeking mosquitoes (42-44). Similar mechanisms may be at play
300 in the bat-ectoparasite system, particularly given the phylogenetic proximity of
301 hippoboscoid bat parasites to mosquitoes.

302 Several bacterial families exhibited significant associations with presence of
303 ectoparasitism in bats based on DESeq analyses. Bacteria found across multiple host
304 families included (but were not limited to) Alcaligenaceae, Chitinophagaceae,
305 Flavobacteriaceae, Moraxellaceae, Mycobacteriaceae (*Mycobacterium* spp.), and
306 Xanthomonadaceae. In many cases, these bacterial families were associated with
307 parasitism in some bat families, and absence of parasitism in others, suggesting a
308 potential mechanism by which ectoparasites might be distinguishing between “correct”
309 and “incorrect” hosts. As suggested by human-mosquito interaction studies (42, 43, 45),
310 bacteria positively associated with increased rates of blood-feeding dipteran host selection
311 may be producing VOCs on which the insects rely to identify their hosts. Bacteria that
312 are negatively associated with such insects may be consuming the products of the former,
313 or may be producing VOCs of their own that mask those of the former (suggested by
314 Verhulst et al. (42)). To better understand the mechanisms underlying these correlations
315 in wild populations, future experiments should consider including sampling of VOCs *in*
316 *vivo*.

317 PERMANOVA analyses identified associations between the oral microbiome
318 and malarial parasite prevalence among bats in the family Miniopteridae, although these
319 associations were less robust than those of the skin bacteria and ectoparasitism. Upon

320 further exploration of this potential association, we identified a single bacterial ESV in
321 the genus *Actinobacillus* (99% similar to *A. porcinus* based on NCBI blastn search) as
322 significantly reduced in malaria-free bats (baseMean 7.61, $-24.2 \log_2 \text{FoldChange}$, $p =$
323 $1.7\text{E}-20$). Network analyses indicated no significant differences in connectivity or node
324 degree distribution (results not shown). Because no other bat groups experienced rates of
325 malarial parasitism adequate for statistical analyses, we were unable to explore this
326 relationship further. Future studies that incorporate greater sampling of malaria-positive
327 species may reveal more robust microbial associations, as have been documented in
328 numerous experiments with controlled rodent and human malaria infections (45-47).

329 Although we cannot ascertain causality of differences in the microbial
330 composition of skin in this study, our results support the hypothesis that these differences
331 may provide a mechanism by which ectoparasites can locate or distinguish hosts.
332 Alternatively, observed differences in microbial composition could result from microbial
333 transfer from parasites to hosts. Given the known effect of locality and apparent absence
334 of host phylogenetic signal in microbial community composition of skin, one possible
335 explanation is that local environmental variables play a greater role in determining host-
336 bacteria associations in bats. Indeed, in North America, multiple bat species have been
337 found to share many bacterial genera with soil and plant material (32). Thus, local
338 conditions and bacterial composition of bat roosts are likely playing an important role in
339 driving the composition of skin bacteria, and via mechanisms similar to the camouflage
340 hypothesis, could subsequently influence which individuals become parasitized.

341

342 METHODS

343

344 1) Sampling

345

346 Sampling for this study was conducted from the eastern coast of Kenya to the northern
347 border of Uganda during August–October 2016 (Fig. 1; Table S1, S2). Eight families
348 and nineteen genera of bats (order: Chiroptera) were collected as part of bird and small
349 mammal biodiversity inventories. All sampling was conducted in accordance with the
350 Field Museum of Natural History IACUC and voucher specimens are accessioned at the
351 Field Museum of Natural History (Table S2). Blood samples were collected and screened
352 for haemosporidia and haemosporidian taxonomy was assigned using previously described
353 molecular methods (13). Following blood sampling, ectoparasites were removed with
354 forceps and placed directly into 95% EtOH; ectoparasites taxonomy was assigned based
355 on morphological features. For the purposes of analysis with microbiome data,
356 ectoparasite and malarial status were each scored separately as 1 (present) or 0 (absent).
357 Gut, skin, and oral samples were taken for each bat for microbial analyses. Gut samples
358 consisted of fecal material collected directly from the distal end of the colon using
359 sterilized tools, and preserved on Whatman® FTA® cards for microbiome analyses. For
360 oral microbiome analyses, we preserved both buccal swabs in LN_2 and tongue biopsies in
361 95% ethanol (EtOH). Comparison of ESV diversity obtained from paired subsets of each
362 sample type revealed greater diversity recovered from tongue biopsies (data not shown);
363 tongues were therefore used for characterization of oral microbiomes in this study. Lastly,
364 skin samples from five regions of the body (ear, wing membrane, tail membrane, chest,
365 back) were collected and pooled in 95% EtOH using sterile Integra® Miltex® 5mm

366 biopsy punches. The goal of sampling from five body regions was to maximize bacterial
367 diversity recovered from the external skin surface of each individual. We based our
368 storage media selections on the recent study by Song et al. (48). Host sequencing and
369 phylogenetic methods are described in Fig. S2.

370

371 2) Microbiome sequencing, characterization, and parasite association

372

373 DNA extractions were performed on gut, tongue, and skin samples using the MoBio
374 PowerSoil 96 Well Soil DNA Isolation Kit (Catalog No. 12955-4, MoBio, Carlsbad,
375 CA, USA). We used the standard 515f and 806r primers (49-51) to amplify the V4
376 region of the 16S rRNA gene, using mitochondrial blockers to reduce amplification of
377 host mitochondrial DNA. Sequencing was performed using paired-end 150 base reads
378 on an Illumina HiSeq sequencing platform. Following standard demultiplexing and
379 quality filtering using the Quantative Insights Into Microbial Ecology pipeline
380 (QIIME2) (52) and vsearch8.1 (53), ESVs were identified using the Deblur method (19)
381 and taxonomy was assigned using the Greengenes Database (May 2013 release;
382 <http://greengenes.lbl.gov>). Libraries containing fewer than 1000 reads were removed
383 from further analyses. Negative controls all contained fewer than 1000 reads and were
384 filtered at this step. We did not rarefy the data, based on the recommendations of
385 McMurdie and Holmes (54). Data were then subset for analyses according to sample
386 type, host genus, and locality (or some combination thereof). Site-specific analyses were
387 only performed for sites from which five or more individual bats were sampled. We
388 calculated alpha diversity for each sample type (gut, oral, skin) using the Shannon index,

389 and measured species richness based on actual observed diversity. Significance of differing
390 mean values for each diversity calculation was determined using the Kruskal-Wallis rank
391 sum test, followed by a post-hoc Dunn test with bonferroni corrected p -values. Three
392 measures of beta diversity (unweighted UniFrac, weighted UniFrac, and Bray-Curtis)
393 were calculated using relative abundances of each ESV (calculated as ESV read depth
394 over total read depth per library). Significant drivers of community similarity were
395 identified using the ADONIS test with Bonferroni correction for multiple comparisons
396 using the R package Phyloseq (55). Complete code for microbiome analyses can be found
397 at <http://github.com/hollylutz/BatMP>.

398

399 3) Machine learning and network analyses

400

401 A supervised machine learning approach was used to produce random forests (RF) for the
402 classification of different variables. RFs were constructed using 500 decision trees and
403 subsets of ESV data via the supervised_learning.py script implemented in QIIME (52).
404 We tested the ability of RFs to accurately classify 1) anatomical site (using all data), 2)
405 host genus (using gut, oral, or skin microbial data separately), 3) ecotparasite status (using
406 skin microbial data), and 4) malarial status (using oral microbial data). RF performance
407 was assessed by comparing the out-of-bag estimated error (OOB) with baseline (random)
408 error. If the ratio of OOB to baseline error was less than or equal to two, the model was
409 considered to perform reasonably well, as it performed at least twice as well as random
410 (56). To reconstruct microbial networks for skin and oral bacterial communities within
411 bat family groupings (which were further sub-divided into parasitized or non-

412 parasitized), we utilized the R package Sparse Inverse Covariance Estimation for
413 Ecological Association Inference (SPIEC-EASI) (57). All network datasets were filtered
414 to contain only ESVs that appeared in at least three individuals within each respective
415 dataset. Network results produced with SPIEC-EASI were summarized using the R
416 packages CAVnet (58) and igraph (59). Network stability was assessed by sequentially
417 removing network nodes (ordered by betweenness centrality and degree) and observing
418 natural connectivity (*i.e.* eigenvalue of the graph adjacency matrix) as nodes are removed.
419 To determine which, if any, bacterial ESVs were significantly associated with ectoparasite
420 or malarial prevalence, we performed analyses based on the negative binomial distribution
421 of ESVs relative abundance, utilizing the R package DESeq2 (60). False discovery rate
422 (FDR) was calculated using the Benjamini-Hochberg method (default method in
423 DESeq), and p -values were adjusted accordingly.

424

425 ACKNOWLEDGMENTS

426

427 We thank the Kenya Wildlife Service and the Uganda Wildlife Authority for permission
428 to conduct research in national parks. For logistical support and assistance in the field, we
429 thank Mike Bartonjo of the National Museums of Kenya, Phausia Kweyu of Karatina
430 University, Dr. Robert Kityo, Solomon Sebuliba, and Cissy Akoth of the Makerere
431 University Zoological Museum, Drs. Brian Amman, Jonathan Towner, and Rebecca
432 Tiller of the Centers for Disease Control and Prevention, and Lauren Lutz. We thank
433 Neil Gottel for his knowledge and assistance with laboratory processing of microbial
434 samples, and other members of the Gilbert Lab, including Alyson Yee, Cesar Cardona,

435 Thomas Kuntz, Drs. Bea Penalver, Melissa Dsouza, and Naseer Sangwan for the
436 assistance with bacterial 16s analyses.

437

438 AUTHOR CONTRIBUTIONS

439 H.L.L. designed the research and wrote the first draft; H.L.L., E.W.J., T.C.D. analyzed
440 data; H.L.L., P.W.W., W.B.S., J.C.K. conducted field research; J.A.G., B.D.P. provided
441 funding and research support; all authors interpreted results and contributed to writing.

442

443 REFERENCES

444

445

- 446 1. Human Microbiome Project C (2012) Structure, function and diversity of the
447 healthy human microbiome. *Nature* 486(7402):207-214.
- 448 2. Thaïss CA, Zmora N, Levy M, & Elinav E (2016) The microbiome and innate
449 immunity. *Nature* 535(7610):65-74.
- 450 3. Nishida AH & Ochman H (2018) Rates of gut microbiome divergence in
451 mammals. *Mol Ecol* 27(8):1884-1897.
- 452 4. Moeller AH, *et al.* (2014) Rapid changes in the gut microbiome during human
453 evolution. *Proc Natl Acad Sci U S A* 111(46):16431-16435.
- 454 5. Kundu P, Blacher E, Elinav E, & Pettersson S (2017) Our Gut Microbiome: The
455 Evolving Inner Self. *Cell* 171(7):1481-1493.
- 456 6. Li X, *et al.* (2017) Composition of Gut Microbiota in the Gibel Carp (*Carassius*
457 *auratus gibelio*) Varies with Host Development. *Microb Ecol* 74(1):239-249.
- 458 7. Kolodny o, *et al.* (2017).

- 459 8. McFall-Ngai M, *et al.* (2013) Animals in a bacterial world, a new imperative for
460 the life sciences. *Proc Natl Acad Sci U S A* 110(9):3229-3236.
- 461 9. Kwiatkowski DP (2005) How malaria has affected the human genome and what
462 human genetics can teach us about malaria. *Am. J. Hum. Genet.* 77:171-190.
- 463 10. Dittmar K, Morse, Solo F., Dick, Carl W., Patterson, Bruce D. (2015) Bat fly
464 evolution from the Eocene to the present (Hippoboscoidea, Streblidae and
465 Nycteribiidae). *Parasite Diversity and Diversification: Evolutionary Ecology Meets*
466 *Phylogenetics*, ed S. Morand BRK, D. T. J. Littlewood (Cambridge University
467 Press, Cambridge, U. K.).
- 468 11. Dick CW, Patterson, B. D. (2006) *Micromammals and Macroparasites: From*
469 *Evolutionary Ecology to Management* (Springer, Kato Bunmeisha, Japan).
- 470 12. Schaer J, *et al.* (2013) High diversity of West African bat malaria parasites and a
471 tight link with rodent Plasmodium taxa. *Proceedings of the National Academy of*
472 *Sciences* 100:17415-17419.
- 473 13. Lutz HL, *et al.* (2016) Diverse sampling of East African haemosporidians reveals
474 chiropteran origin of malaria parasites in primates and rodents. *Mol Phylogenet*
475 *Evol* 99:7-15.
- 476 14. Bausch DG, Schwarz, L. (2014) Outbreak of Ebola virus disease in Guinea:
477 where ecology meets economy. *PLoS Negl Trop Dis* 8(7):e3056.
- 478 15. Hayman DT, Bowen, R.A., Cryan, P.M., McCracken, G.F., O'Shea, T.J., Peel,
479 A.J., Gilbert, A., Webb, C.T., Wood, J.L. (2013) Ecoogy of zoonotic infectious
480 diseases in bats: current knowledge and future directions. *Zoonoses and Public*
481 *Health* 60:2-21.

- 482 16. Towner JS, *et al.* (2009) Isolation of genetically diverse Marburg viruses from
483 Egyptian fruit bats. *PLoS Pathog* 5(7):e1000536.
- 484 17. Olival KJ & Hayman DT (2014) Filoviruses in bats: current knowledge and
485 future directions. *Viruses* 6(4):1759-1788.
- 486 18. Amman BR, *et al.* (2015) A Recently Discovered Pathogenic Paramyxovirus,
487 Sosuga Virus, is Present in Rousettus aegyptiacus Fruit Bats at Multiple
488 Locations in Uganda. *J Wildl Dis* 51(3):774-779.
- 489 19. Amir A, *et al.* (2017) Deblur Rapidly Resolves Single-Nucleotide Community
490 Sequence Patterns. *mSystems* 2(2).
- 491 20. Sturgeon A, Pinder SL, Costa MC, & Weese JS (2014) Characterization of the
492 oral microbiota of healthy cats using next-generation sequencing. *Vet J*
493 201(2):223-229.
- 494 21. Ley RE, *et al.* (2008) Evolution of mammals and their gut microbes. *Science*
495 320(5883):1647-1651.
- 496 22. Mark Welch JL, Rossetti BJ, Rieken CW, Dewhirst FE, & Borisy GG (2016)
497 Biogeography of a human oral microbiome at the micron scale. *Proc Natl Acad Sci*
498 *USA* 113(6):E791-800.
- 499 23. Brix L, Hansen MJ, Kelly A, Bertelsen MF, & Bojesen AM (2015) Occurrence
500 of Pasteurellaceae Bacteria in the Oral Cavity of the Tasmanian Devil
501 (*Sarcophilus Harrisii*). *J Zoo Wildl Med* 46(2):241-245.
- 502 24. Grice EA & Segre JA (2011) The skin microbiome. *Nat Rev Microbiol* 9(4):244-
503 253.

- 504 25. Ursell LK, *et al.* (2012) The interpersonal and intrapersonal diversity of human-
505 associated microbiota in key body sites. *J Allergy Clin Immunol* 129(5):1204-1208.
- 506 26. Costello EK, *et al.* (2009) Bacterial community variation in human body habitats
507 across space and time. *Science* 326(5960):1694-1697.
- 508 27. Chiarello M, Villéger, S., Bouvier, C., Bettarel, Y., Bouvier, T. (2015) High
509 diversity of skin-associated bacterial communities in marine fishes is promoted by
510 their high variability among body parts, individuals and species. *FEMS Microbiol*
511 *Ecol* 91(7):1-12.
- 512 28. Caviedes-Vidal E, McWhorter, T. J., Lavin, S. R., Chediak, J. G., Tracy, C. R.,
513 Karasov, W. H. (2007) The digestive adaptation of flying vertebrates: High
514 intestinal paracellular absorption compensates for smaller guts. *PNAS*
515 104(48):19132-19137.
- 516 29. Price ER, Brun A, Caviedes-Vidal E, & Karasov WH (2015) Digestive
517 adaptations of aerial lifestyles. *Physiology (Bethesda)* 30(1):69-78.
- 518 30. Caviedes-Vidal E, *et al.* (2008) Paracellular absorption: a bat breaks the mammal
519 paradigm. *PLoS One* 3(1):e1425.
- 520 31. Thomas T, *et al.* (2016) Diversity, structure and convergent evolution of the
521 global sponge microbiome. *Nat Commun* 7:11870.
- 522 32. Avena CV, *et al.* (2016) Deconstructing the Bat Skin Microbiome: Influences of
523 the Host and the Environment. *Front Microbiol* 7:1753.
- 524 33. Muletz Wolz CR, Yarwood SA, Campbell Grant EH, Fleischer RC, & Lips KR
525 (2018) Effects of host species and environment on the skin microbiome of
526 Plethodontid salamanders. *J Anim Ecol* 87(2):341-353.

- 527 34. Bryant JA, Lamanna, C., Morlon, H., Kerkhoff, A. J., Enquist, B. J., Green, J. L.
528 (2008) Microbes and mountainsides: contrasting elevational patterns of bacterial
529 and plan diversity. *PNAS* 105:11505-11511.
- 530 35. Singh D, *et al.* (2014) Strong elevational trends in soil bacterial community
531 composition on Mt. Halla, South Korea. *Soil Biology and Biochemistry* 68:140-149.
- 532 36. Carrillo-Araujo M, *et al.* (2015) Phyllostomid bat microbiome composition is
533 associated to host phylogeny and feeding strategies. *Front Microbiol* 6:447.
- 534 37. Phillips CD, *et al.* (2012) Microbiome analysis among bats describes influences of
535 host phylogeny, life history, physiology and geography. *Mol Ecol* 21(11):2617-
536 2627.
- 537 38. Eckburg PB, Bik, E. M., Bernstein, C. N., Purdom, E., Dethlefsen, L., Sargent,
538 M., Gill, S. R., Nelson, K. E., Relman, D. A. (2005) Diversity of human
539 intestinal microbial flora. *Science* 308(5728):1635-1638.
- 540 39. Yildirim S, *et al.* (2010) Characterization of the fecal microbiome from non-
541 human wild primates reveals species specific microbial communities. *PLoS One*
542 5(11):e13963.
- 543 40. Bik EM, *et al.* (2016) Marine mammals harbor unique microbiotas shaped by and
544 yet distinct from the sea. *Nat Commun* 7:10516.
- 545 41. Gutman N, Hansen MJ, Bertelsen MF, & Bojesen AM (2016) Pasteurellaceae
546 bacteria from the oral cavity of Tasmanian devils (*Sarcophilus Harrisii*) show high
547 minimum inhibitory concentration values towards aminoglycosides and
548 clindamycin. *Lett Appl Microbiol* 62(3):237-242.

- 549 42. Verhulst NO, *et al.* (2011) Composition of human skin microbiota affects
550 attractiveness to malaria mosquitoes. *PLoS One* 6(12):e28991.
- 551 43. Busula AO, Takken W, JG DEB, Mukabana WR, & Verhulst NO (2017)
552 Variation in host preferences of malaria mosquitoes is mediated by skin bacterial
553 volatiles. *Med Vet Entomol* 31(3):320-326.
- 554 44. Verhulst NO, *et al.* (2009) Cultured skin microbiota attracts malaria mosquitoes.
555 *Malar J* 8:302.
- 556 45. Robinson A, *et al.* (2018) Plasmodium-associated changes in human odor attract
557 mosquitoes. *Proc Natl Acad Sci U S A* 115(18):E4209-E4218.
- 558 46. De Moraes CM, *et al.* (2014) Malaria-induced changes in host odors enhance
559 mosquito attraction. *Proc Natl Acad Sci U S A* 111(30):11079-11084.
- 560 47. de Boer JG, *et al.* (2017) Odours of Plasmodium falciparum-infected participants
561 influence mosquito-host interactions. *Sci Rep* 7(1):9283.
- 562 48. Song SJ, Amir, A., Metcalf, J. L., Amato, K. R., Xu, Z. Z., Humphrey, G.,
563 Knight, R. (2016) Preservation methods differ in fecal microbiome stability,
564 affecting suitability for field studies. *mSystems* 1(3):1 - 12.
- 565 49. Caporaso JG, Lauber, C. L., Walters, W. A., Berg-Lyons, D., Lozupone, C. A.,
566 Turnbaugh, P. J., Fierer, N., Knight, R. (2011) Global patterns of 16S rRNA
567 diversity at a depth of millions of sequences per sample. *PNAS* 108:4516-4522.
- 568 50. Caporaso JG, *et al.* (2012) Ultra-high-throughput microbial community analysis
569 on the Illumina HiSeq and MiSeq platforms. *ISME J* 6(8):1621-1624.
- 570 51. Kozich JJ, Westcott, S. L., Baxter, N. T., Highlander, S. K., Schloss, P. D.
571 (2013) Development of a dual-index sequencing strategy and curation pipeline for

- 572 analyzing amplicon sequence data on the MiSeq Illumina sequencing platform.
573 *Applied and Environmental Microbiology* 79(17):5122-5120.
- 574 52. Caporaso JG, Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D.,
575 Costello, E. K., Fierer, N., Gonzalez Peña, A., Goodrich, E. K., Gordon, J. I.,
576 Huttley, G. A., Kelley, S. T., Knights, D., Koenig, J. E., Ley, R. E., Lozupone,
577 C. A., McDonald, D., Muegge, B. D., Pirrung, M., Reeder, J., Sevinsky, J. R.,
578 Turnbaugh, P. J., Walters, W. A., Widmann, J., Yatsunenko, T., Zaneveld, J.,
579 Knight, R. (2010) QIIME allows analysis of high-throughput community
580 sequencing data. *Nature Methods* 7(5):335 - 336.
- 581 53. Rognes T, Flouri T, Nichols B, Quince C, & Mahe F (2016) VSEARCH: a
582 versatile open source tool for metagenomics. *PeerJ* 4:e2584.
- 583 54. McMurdie PJ, Holmes, S. (2014) Waste not, want not: Why rarefying
584 microbiome data is inadmissible. *PLoS Comput Biol* 10(4):1-12.
- 585 55. McMurdie PJ & Holmes S (2013) phyloseq: an R package for reproducible
586 interactive analysis and graphics of microbiome census data. *PLoS One*
587 8(4):e61217.
- 588 56. Breiman L (2001) Random Forests. *Machine Learning* 45:5-32.
- 589 57. Kurtz ZD, *et al.* (2015) Sparse and compositionally robust inference of microbial
590 ecological networks. *PLoS Comput Biol* 11(5):e1004226.
- 591 58. Cardona C (2017) CAVNet: Creation Analysis and Visualization of Networks).
- 592 59. Csardi G, Nepusz, T. (2006) The Igraph Software Package for Complex Network
593 Research. *InterJournal, Complex Systems* 1695.

- 594 60. Love MI, Huber W, & Anders S (2014) Moderated estimation of fold change
595 and dispersion for RNA-seq data with DESeq2. *Genome Biol* 15(12):550.
- 596 61. Teeling EC, Springer, M. S., Madsen, O., Bates, P., O'Brien, S. J., Murphy, W.
597 J. (2005) A molecular phylogeny for bats illuminates biogeography and fossil
598 record. *Science* 307:580-584.
- 599
- 600
- 601
- 602
- 603
- 604
- 605
- 606
- 607
- 608
- 609
- 610
- 611
- 612
- 613
- 614
- 615
- 616

617 FIGURE LEGENDS

618

619 Figure 1. Sampling localities and elevation, grouped by district. Colors correspond to
620 elevation, and white numbers and size of points correspond to number of bats collected.

621

622 Figure 2. Alpha diversity of Exact Sequence Variants (ESVs) by anatomical sites,
623 including (A) Observed richness, (B) Shannon index of diversity, (C) ESVs shared
624 between anatomical sites. Asterisks indicate significant differences between groups
625 (Dunn's Test, Bonferroni corrected p -value $p < 0.0001$).

626

627 Figure 3. Intraspecific variation across anatomical sites measured as beta dispersion of
628 weighted UniFrac distances. Dotted lines indicate mean dispersion for anatomical
629 groupings; numbers in parentheses indicate sample size per bat species. White and gray
630 boxes correspond to the chiropteran suborders Yangochiroptera (microbats) and
631 Yinpterochiroptera (fruit bats and kin), respectively.

632

633 Figure 4. (A) Relative abundance of top 6 bacterial phyla grouped by anatomical site,
634 with each bar corresponding to individual libraries. (B) Relative abundance of the most
635 prevalent eight bacterial families across all anatomical sites, grouped by bat family.

636 Phylogeny based on Teeling et al. (61).

637

638 Figure 5. (A) Distribution of skin microbial network clusters for parasitized and non-
639 parasitized bats, grouped by bat family (* indicates significance at $p < 0.005$, Kruskal-

640 Wallis) (B) Visualization of skin bacterial networks (based on Fruchterman-Reingold
641 algorithm); colored nodes correspond to unique clusters of co-occurring ESVs within
642 each network.

643

644 Figure 6. Log₂fold change in relative abundance of skin-associated ESVs from the four
645 most-sampled bat families. ESVs shown were found to be significantly associated with
646 ectoparasite status in bats based on analysis of negative binomial distributions of relative
647 abundance (Benjamini-Hochberg FDR corrected p -value $p < 0.05$). Positive values
648 correspond to ESVs found to be enriched on parasitized bats, and negative values
649 correspond to ESVs found to be enriched on non-parasitized bats. Gray bars highlight
650 ESVs in bacterial families that were enriched in parasitized bats for three out of four bat
651 families.

652

Table 1. Bat sampling, ectoparasite prevalence (n_{ecto}), and malarial parasite prevalence (n_{haem}) and identification.

Bat family	Bat species	n_{bats}	n_{ecto} (%)	n_{haem} (%)
Emballonuridae	<i>Coleura afra</i>	11	2 (18)	0
Hipposideridae	<i>Hipposideros caffer</i>	47	18 (38)	0
	<i>Hipposideros camerunensis</i>	2	0	0
	<i>Hipposideros ruber</i>	21	16 (76)	0
	<i>Macronycteris vittatus</i>	10	0	0
Miniopteridae	<i>Miniopterus africanus</i>	22	13 (59)	11 (50)
	<i>Miniopterus natalensis</i>	54	16 (30)	13 (24)
	<i>Miniopterus rufus</i>	22	20 (61)	20 (91)
	<i>Miniopterus minor</i>	18	16 (89)	12 (67)
Molossidae	<i>Chaerephon bivittatus</i>	14	0	0
	<i>Otomops harrisoni</i>	33	1 (3)	0
Nycteridae	<i>Nycteris arge</i>	3	0	0
	<i>Nycteris thebaica</i>	7	1 (14)	0
	<i>Nycteris</i> sp.	6	0	0
Pteropodidae	<i>Epomophorus labiatus</i>	2	0	0
	<i>Epomophorus wahlbergi</i>	11	0	3 (27)
	<i>Micropteropus pusillus</i>	4	0	0
	<i>Myonycteris angolensis</i>	4	0	0
	<i>Rousettus aegyptiacus</i>	48	24 (50)	0
	<i>Stenonycteris lanosus</i>	37	23 (62)	0
Rhinolophidae	<i>Rhinolophus clivosus</i>	43	8 (19)	0
	<i>Rhinolophus eloquens</i>	24	19 (79)	0
	<i>Rhinolophus hildebrandti</i>	4	1 (25)	0
	<i>Rhinolophus landeri</i>	14	0	3 (21)
	<i>Rhinolophus</i> sp.	3	0	0
Rhinonycteridae	<i>Triaenops afer</i>	10	6 (60)	0
Vespertilionidae	<i>Myotis tricolor</i>	9	8 (89)	3 (33)
	<i>Neoromicia nana</i>	1	0	0
	<i>Neoromicia</i> sp.	3	0	0
	<i>Pipistrellus</i> sp.	1	0	0
	<i>Scotoecus hindei</i>	4	1 (25)	0
	<i>Scotophilus dingani</i>	3	0	0
Total		495	193	65

Table 2. Alpha diversity of microbial communities across anatomical sites within each host genus, measured by Shannon Index of diversity (S-I) and observed sOTU richness (obs); n corresponds to number of libraries included in each calculation (following quality filtering).

Host Family	Host Genus	Fecal			Oral			Skin		
		S-I	obs	n_{fecal}	S-I	obs	n_{oral}	S-I	obs	n_{skin}
Emballonuridae	<i>Chaerephon</i>	1.16	52	12	1.39	57	14	3.57	547	14
Hipposideridae	<i>Hipposideros</i>	1.70	79	65	2.01	155	52	4.95	439	74
	<i>Macronycteris</i>	1.82	74	9	2.12	110	9	4.94	883	7
Miniopteridae	<i>Miniopterus</i>	1.41	70	92	1.55	87	74	4.12	403	114
Molossidae	<i>Coleura</i>	1.59	52	11	0.38	41	11	4.01	566	11
	<i>Otomops</i>	0.88	53	26	0.35	22	26	3.88	288	33
Nycteridae	<i>Nycteris</i>	1.60	80	10	1.62	78	14	4.48	807	14
Pteropodidae	<i>Epomophorus</i>	1.44	49	11	1.42	46	11	3.78	566	13
	<i>Micropteropus</i>	1.90	39	3	2.21	39	4	2.30	84	3
	<i>Myonycteris</i>	1.14	117	4	1.29	195	5	5.21	1246	4
	<i>Rousettus</i>	1.62	93	32	1.95	84	34	4.90	1207	34
	<i>Stenonycteris</i>	1.55	61	41	1.72	97	38	4.59	855	33
Rhinolophidae	<i>Rhinolophus</i>	1.34	62	58	1.95	81	59	4.71	543	79
Rhinonycteridae	<i>Triaenops</i>	1.69	82	9	1.28	414	9	4.03	508	10
Vespertilionidae	<i>Myotis</i>	1.62	54	1	1.33	72	6	5.41	771	3
	<i>Neoromicia</i>	2.13	65	4	1.47	37	4	3.76	267	4
	<i>Pipistrellus</i>	1.05	NA	1	NA	NA	0	4.80	360	2
	<i>Scotoecus</i>	1.86	92	4	1.97	17	3	4.20	360	4
	<i>Scotophilus</i>	1.23	64	3	0.38	96	1	4.08	459	2
Mean		1.51	69	n_{fecal} 396	1.47	96	n_{oral} 375	4.30	587	n_{skin} 458

Table 3. Nonparametric permutational multivariate analysis of variance using distance matrices (via ADONIS), with distance matrices among sources of variation partitioned by host taxonomy (species nested within genus), ectoparasite status, malarial infection status, and locality included as strata to constrain permutation across this variable; * indicates p-value < 0.05.

Site	Partition Variable	Weighted UniFrac			Unweighted UniFrac			Bray-Curtis		
		F	R2	Pr(>F)	F	R2	Pr(>F)	F	R2	Pr(>F)
Fecal	(Host genus (species))	4.27	0.162	0.001*	3.15	0.120	0.001*	2.89	0.110	0.001*
	Ectoparasite status	0.47	0.001	0.912	1.42	0.004	0.048*	1.40	0.004	0.097
	Malarial status	1.34	0.004	0.21	1.33	0.004	0.077	1.98	0.005	0.011*
Oral	(Host genus (species))	6.82	0.279	0.001*	3.50	0.143	0.001*	6.69	0.274	0.001*
	Ectoparasite status	0.51	0.001	0.836	1.41	0.004	0.057	1.00	0.003	0.447
	Malarial status	2.78	0.008	0.015*	1.17	0.003	0.2	1.98	0.006	0.019*
Skin	(Host genus (species))	7.68	0.329	0.001*	3.98	0.170	0.001*	5.60	0.240	0.001*
	Ectoparasite status	2.42	0.006	0.01*	1.54	0.004	0.02*	2.07	0.005	0.001*
	Malarial status	0.92	0.002	0.513	1.02	0.002	0.363	1.06	0.003	0.32

Table 4. Permutational multivariate analysis of variance using distance matrices, with distance matrices among sources of variation partitioned by host taxonomy (species nested within genus), locality, and anatomical site.

Partition Variable	Weighted UniFrac			Unweighted UniFrac			Bray-Curtis		
	SumSq	F	Pr(>F)	SumSq	F	Pr(>F)	SumSq	F	Pr(>F)
Anatomical site	10.67	198.01	0.001*	56.52	82.90	0.001*	38.2	36.97	0.001*
Host Genus	3.77	13.09	0.001*	25.54	7.02	0.001*	85.30	15.06	0.001*
Locality	1.56	11.00	0.001*	20.62	11.34	0.001*	23.85	8.42	0.001*
Host Genus:species	1.39	4.08	0.001*	11.20	2.59	0.001*	25.25	1.33	0.001*

Table 5. Supervised machine learning results, showing random forest model performance with respect to different classification variables and input data sets (fecal, oral, skin microbiome). Model performance is assessed by measuring the ratio of Out-of-bag estimated error (OOB) to baseline error.

Classification variable	Input Data	Baseline error	OOB error	Baseline:OOB
Anatomical site	All data	0.68	0.14	4.8
Host Genus	Skin	0.75	0.17	4.3
Host Genus	Oral	0.78	0.24	3.2
Host Genus	Gut	0.77	0.35	2.2
Ectoparasite Status	Skin	0.53	0.27	2.0
Malarial Status (Miniopteridae only)	Oral	0.46	0.38	1.2

FIGURE 1

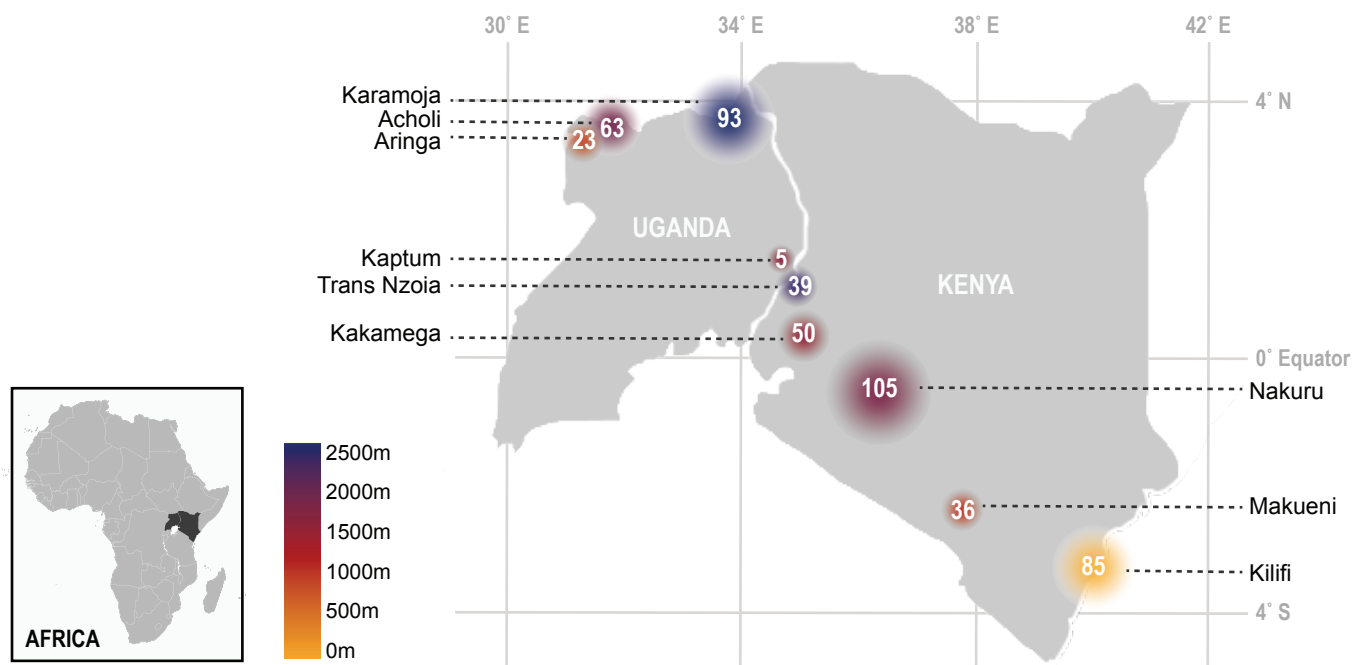


FIGURE 2

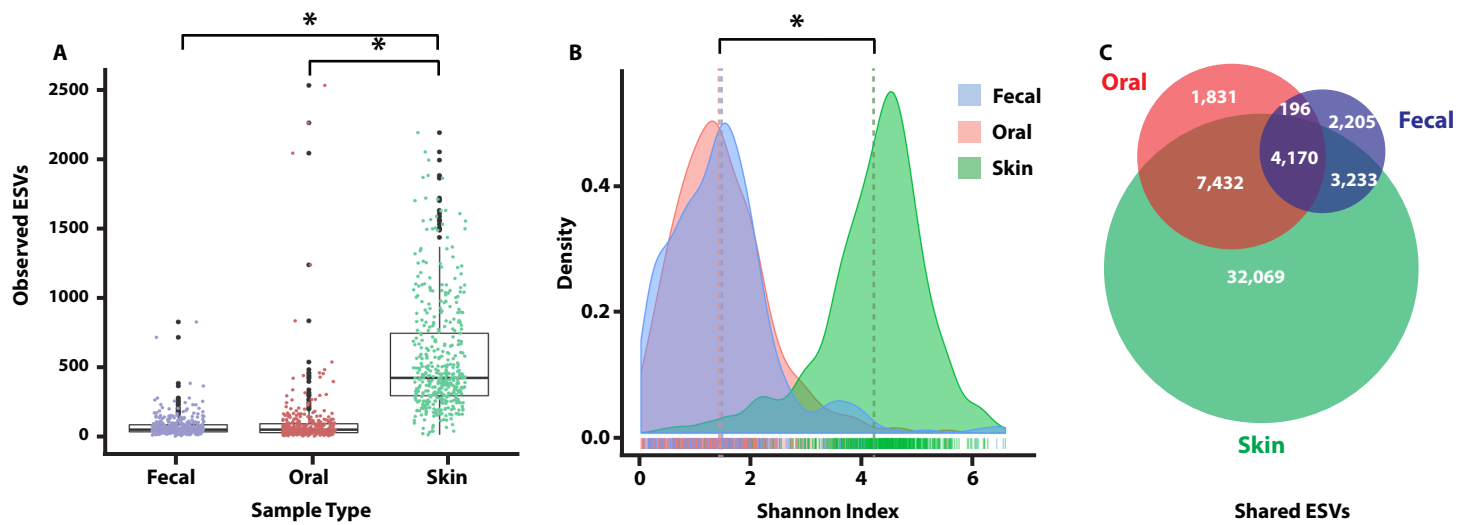


FIGURE 3

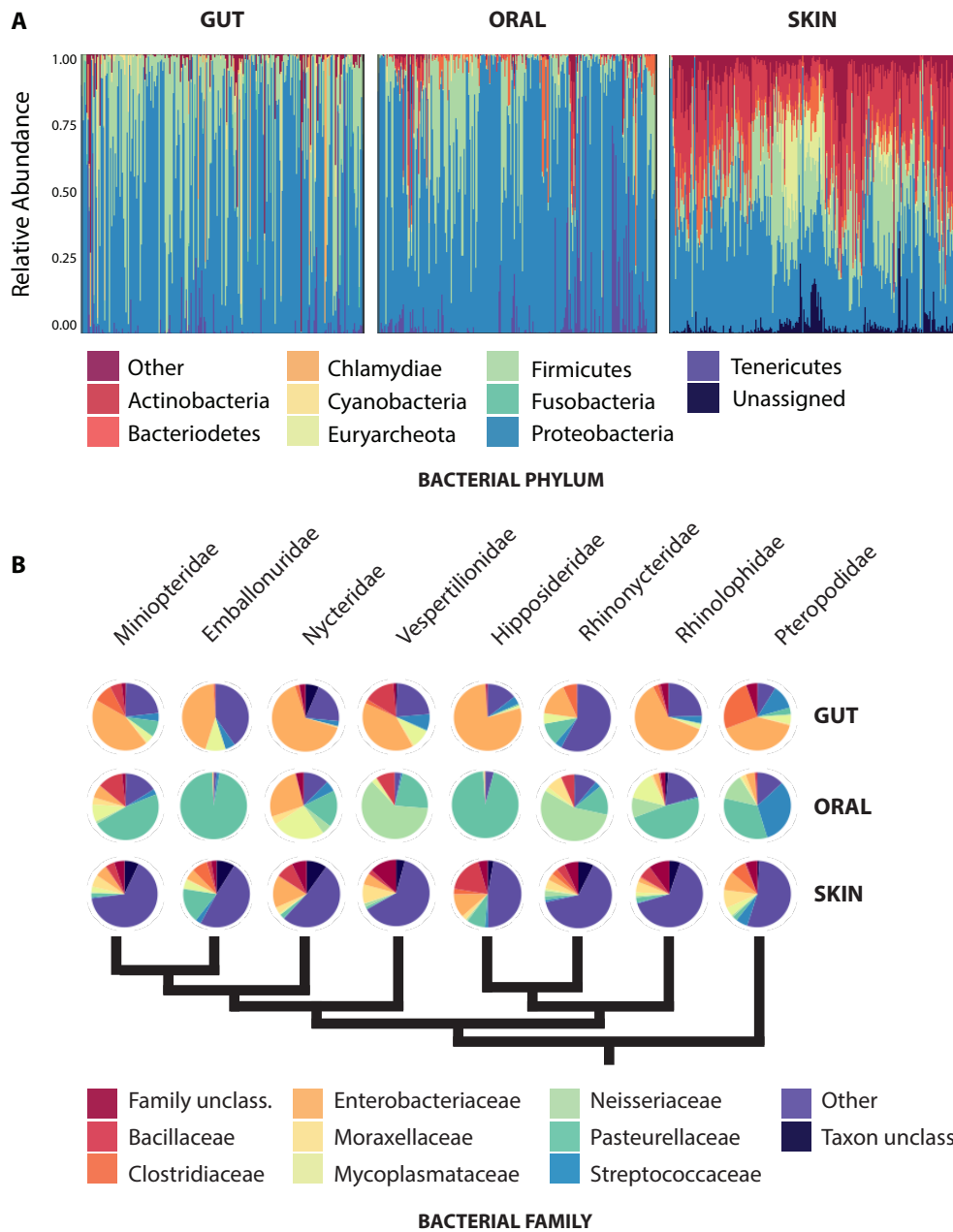


FIGURE 4

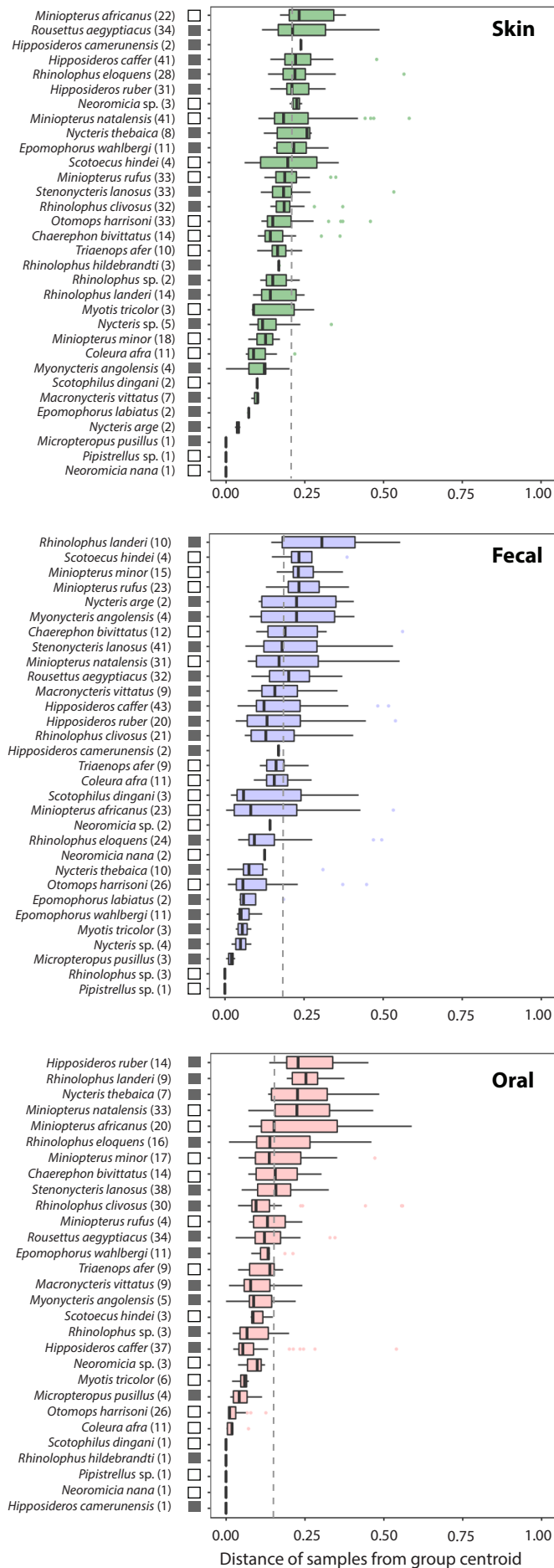


FIGURE 5

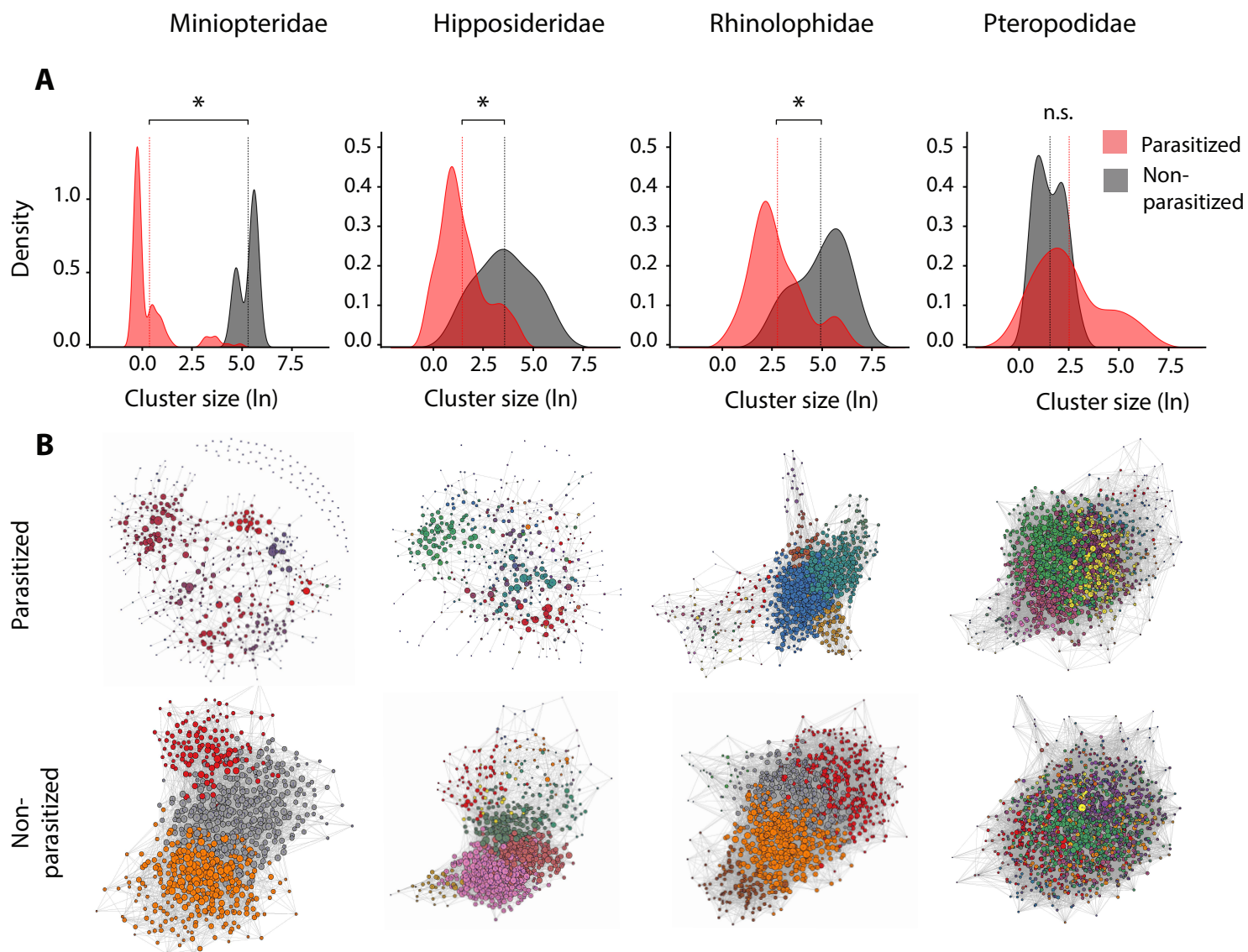


FIGURE 6

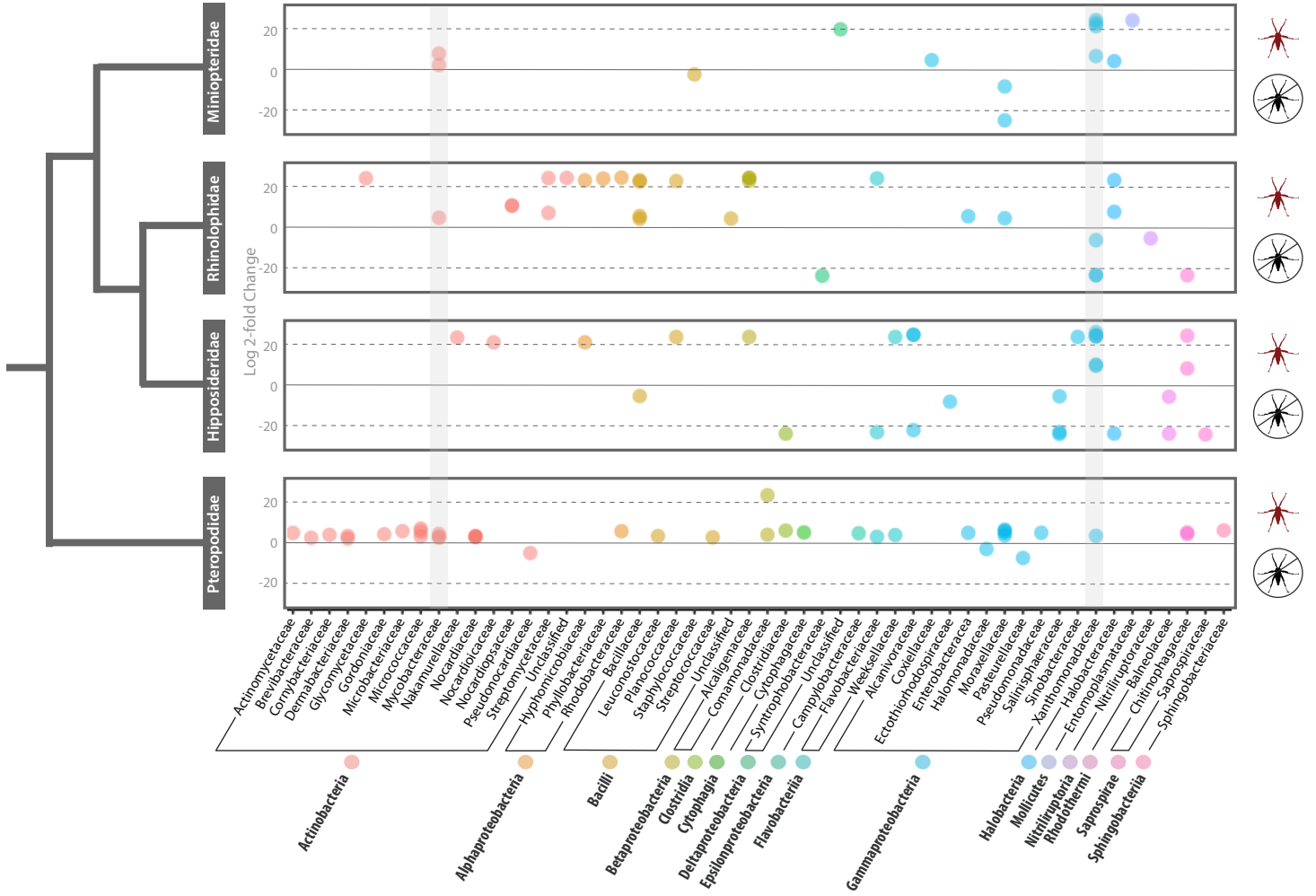


Figure S1. Measures of intraspecific beta dispersion among (A) unweighted UniFrac and (B) Bray-Curtis distances. Dotted gray line indicates mean beta dispersion for each anatomical group and dissimilarity measure.

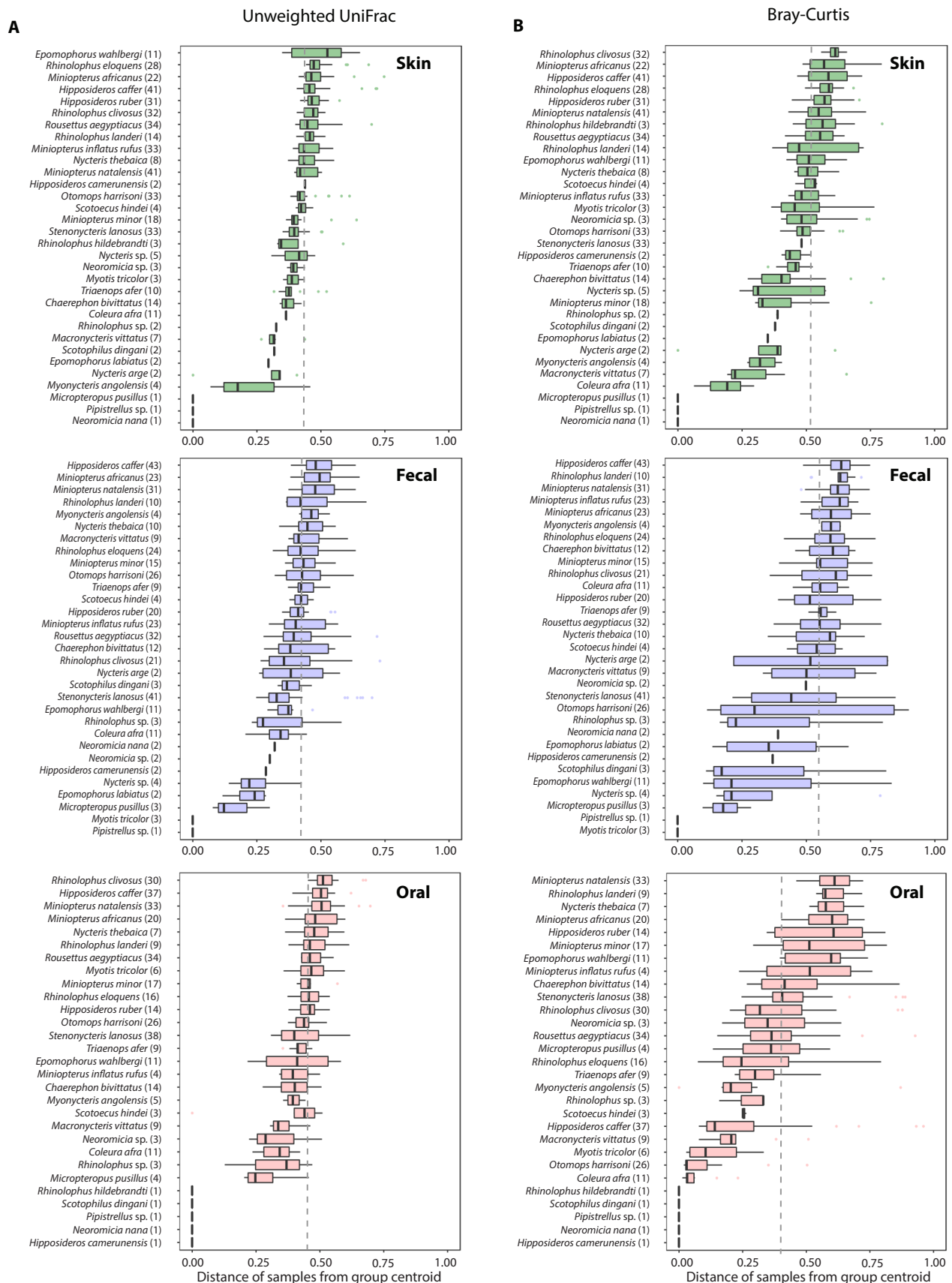


Figure S2. Linear regression of (A) Shannon diversity and (B) observed ESV richness of gut, oral, and skin microbiomes against elevation from which host was sampled (~0 - 2500 meters above sea level). R^2 and significance values are provided within each plot.

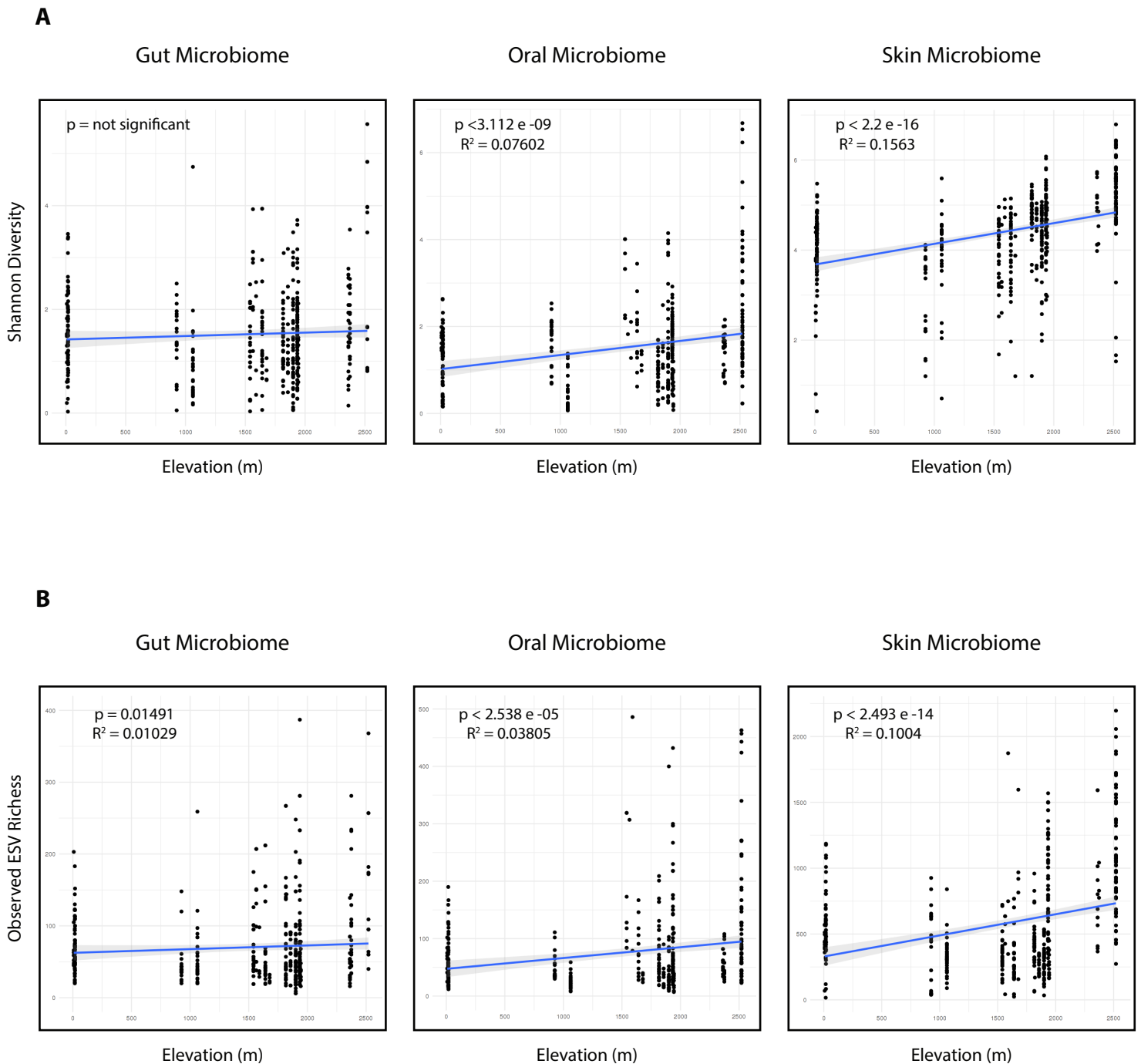


Figure S3.A Linear regression of patristic distances between microbial community dissimilarity (unweighted and weighted UniFrac) and phylogenetic distances between individual bat species sampled in this study.

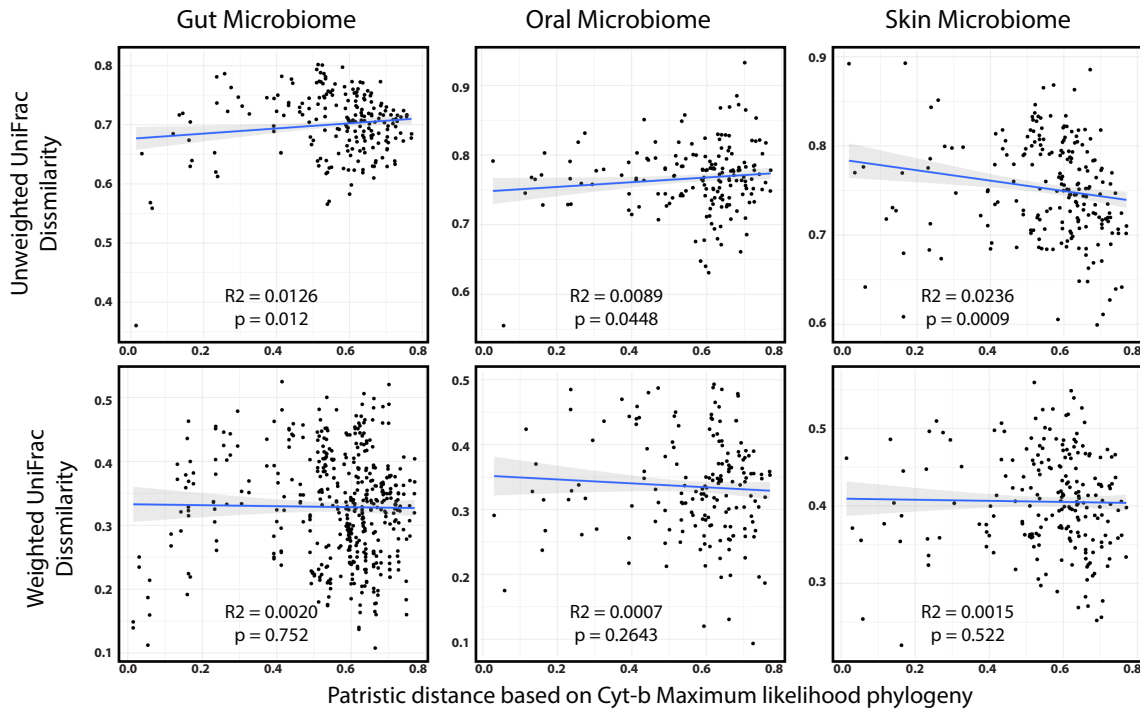


Figure S3.B Maximum likelihood phylogeny of bat species. Phylogenetic distances were calculated as patristic distances based on maximum likelihood reconstruction of bat species-level phylogeny with 1000 bootstrap (bs) replicates. Closed circles > 95% bs support, open black circles > 90% bs support, open gray circles >75% bs support.

Methods: DNA was extracted from pectoral muscle tissue of bat specimens, and sequenced for mitochondrial Cytochrome-b (cyt-b) using the primer pair LGL 765F and LGL 766R to amplify the entire cyt-b gene (1, 2). PCR amplification and sequencing were carried out as in Demos et al. (3). The best-supported model of nucleotide substitution for cyt-b was determined using the BIC on the maximum-likelihood topology estimated independently for each model in jMODELTEST2 (4) on CIPRES Science Gateway v.3.1 (5). Maximum-likelihood estimates of cyt-b gene trees and concatenated gene trees were made using the program RAxML-HPC v.8 (6) on the CIPRES portal. We conducted analyses using the rapid bootstrapping algorithm and searched for best-scoring ML tree algorithm under the GTRGAMMA model with 1000 bootstrap replicates (references listed on next page).

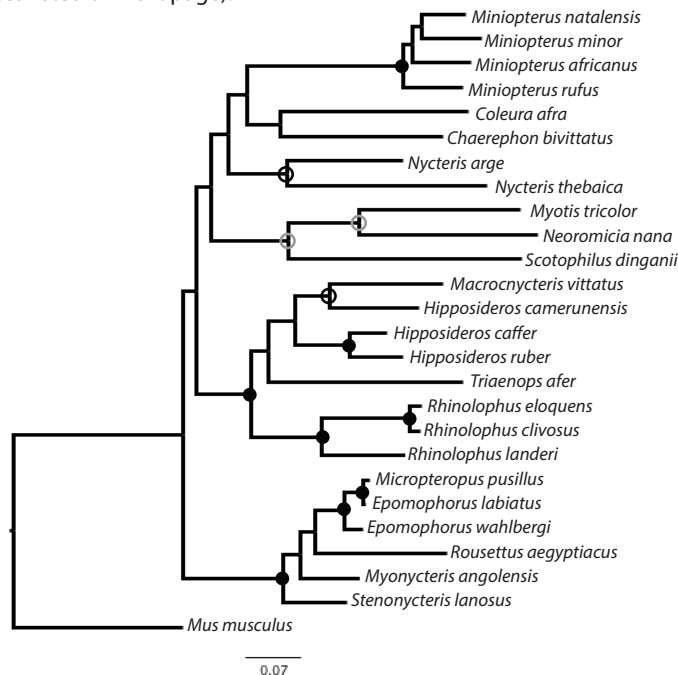


Figure S4. Network Analyses - (A) Node degree distribution of parasitized and non-parasitized bats, grouped by family. (B) Network fragility plots, showing natural network connectivity with sequential removal of nodes ordered by betweenness and degree.

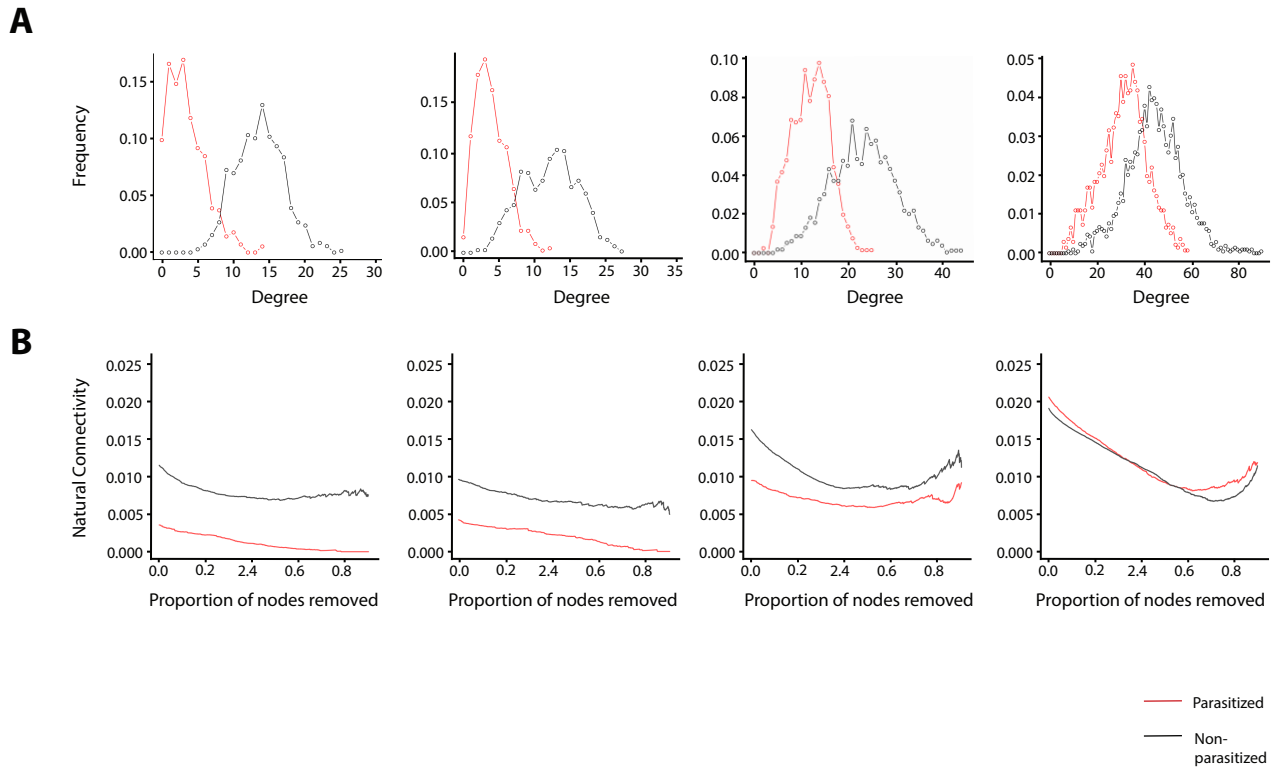


Table S1. Full sampling locality data. Loc_name corresponds to map labels in main text, Figure 1.

Loc_name	Country	County	Specific locality	GPS Coordinates	Elevation (m)
Acholi	Uganda	Acholi	Agoro-Agu Forest Reserve	N 3.81039 E32.92264	1935
Aringa	Uganda	Aringa	Aringa Bridge	N 3.71665 E 32.89481	926
Chyulu	Kenya	Makueni	Guano cave 3, Chyulu Hills National Park	S 02.33952 E 037.70911	1062
Lirhanda	Kenya	Kakamega	Lirhanda cave, Kakamega Forest	N 00.21176 E 034.89856	1540
Buzambuli	Kenya	Kakamega	Buzambuli Trail 3, Kakamega Forest National Reserve	N 00.34375 E 034.85660	1564
Ikhondo	Kenya	Kakamega	Ikhondo Junction, Kakamega Forest National Reserve	N 00.35293 E 034.86720	1590
Buyangu	Kenya	Kakamega	Buyangu KWS HQ, Kakamega Forest National Reserve	N 00.35500 E 034.86567	1618
Mahiakalo	Kenya	Kakamega	Mahiakalo cave, Kakamega Forest	N 00.24454 E 034.90688	1641
Kaptum	Uganda	Kaptum	Kaptum Cave	N 1.4474 E 34.5769	1678
Karamoja	Uganda	Karamoja	Mount Morungole	N 03.81083 E 34.02931	2520
Watamu	Kenya	Kilifi	Watamu cave, Gede	S 03.35109 E 040.01544	8
Makuruhi	Kenya	Kilifi	Makuruhi cave, Gede	S 03.32319 E 040.04153	17
Kaboga	Kenya	Kilifi	Kaboga cave, Gede	S 03.33452 E 040.03074	19
Kitum	Kenya	Trans Nzoia	Kitum cave, Mount Elgon National Park	N 01.02937 E 034.75580	2362
Makingeny	Kenya	Trans Nzoia	Makingeny cave, Mount Elgon National Park	N 01.03553 E 034.75305	2374
Lionhill	Kenya	Nakuru	Lion Hill cave, Lake Nakuru National Park	S 00.34589 E 036.11918	1816
Soysambu	Kenya	Nakuru	Monkey Bridge campsite, Soysambu Conservancy	S 00.39227 E 036.21117	1821
Kariandusi	Kenya	Nakuru	Kariandusi mines, Gilgil	S 00.45143 E 036.28194	1856
Diatomite	Kenya	Nakuru	Diatomite cave, Gilgil	S 00.43010 E 036.17368	1900
Pipeline	Kenya	Nakuru	Pipeline cave, Gilgil	S 00.53911 E036.29431	1943

FMNH233880	PWW.3445	Chiroptera	Rhinolophidae	Rhinolophus	landeri	F	Nakuru	Kenya	Kariandusi mines Gilgil	1856	25	10	2016	0	0	0	0	0
FMNH233881	PWW.3446	Chiroptera	Rhinolophidae	Rhinolophus	landeri	F	Nakuru	Kenya	Kariandusi mines Gilgil	1856	25	10	2016	0	0	0	0	0
FMNH233882	PWW.3447	Chiroptera	Rhinolophidae	Rhinolophus	landeri	F	Nakuru	Kenya	Kariandusi mines Gilgil	1856	25	10	2016	0	0	0	0	0
FMNH233824	PWW.3355	Chiroptera	Rhinolophidae	Rhinolophus	sp.	F	Makueni	Kenya	Guano cave 3 Chyulu Hills National Park	1062	20	10	2016	0	0	1	Hippoboscidae	Phthiridium hoogstraali
FMNH233823	PWW.3354	Chiroptera	Rhinolophidae	Rhinolophus	sp.	M	Makueni	Kenya	Guano cave 3 Chyulu Hills National Park	1062	20	10	2016	0	0	0	0	0
FMNH233825	PWW.3357	Chiroptera	Rhinolophidae	Rhinolophus	sp.	M	Makueni	Kenya	Guano cave 3 Chyulu Hills National Park	1062	20	10	2016	0	0	0	0	0
FMNH234082	PWW.3369	Chiroptera	Rhinonycteridae	Trienops	afes	F	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	0	0	0
FMNH234086	PWW.3373	Chiroptera	Rhinonycteridae	Trienops	afes	F	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	1	Streblidae	Raymondia sp.
FMNH234088	PWW.3375	Chiroptera	Rhinonycteridae	Trienops	afes	F	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	1	Streblidae	Raymondia sp.
FMNH234090	PWW.3377	Chiroptera	Rhinonycteridae	Trienops	afes	F	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	1	Streblidae	Raymondia sp.
FMNH234091	PWW.3378	Chiroptera	Rhinonycteridae	Trienops	afes	F	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	1	0	1	Streblidae	Raymondia sp.
FMNH234083	PWW.3370	Chiroptera	Rhinonycteridae	Trienops	afes	M	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	0	0	0
FMNH234085	PWW.3372	Chiroptera	Rhinonycteridae	Trienops	afes	M	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	1	0	0
FMNH234089	PWW.3376	Chiroptera	Rhinonycteridae	Trienops	afes	M	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	1	Macronyssidae	Macronyssidae
FMNH234084	PWW.3371	Chiroptera	Rhinonycteridae	Trienops	afes	M	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	1	Streblidae	Raymondia sp.
FMNH234087	PWW.3374	Chiroptera	Rhinonycteridae	Trienops	afes	M	Kilifi	Kenya	Makuruhi cave Gede	17	21	10	2016	0	0	1	Streblidae	Raymondia sp.
FMNH232112	JCK.10026	Chiroptera	Vespertilionidae	Myotis	tricolor	F	Karamoja	Uganda	Mount Morungole	2520	25	7	2016	0	0	1	Nycteribiidae	Nycteribia latiterna
FMNH232118	JCK.10139	Chiroptera	Vespertilionidae	Myotis	tricolor	F	Karamoja	Uganda	Mount Morungole	2520	28	7	2016	1	Polychromophilus muri	1	Nycteribiidae	Nycteribia latiterna
FMNH232117	JCK.10072	Chiroptera	Vespertilionidae	Myotis	tricolor	M	Karamoja	Uganda	Mount Morungole	2520	26	7	2016	0	0	1	0	0
FMNH232119	JCK.10259	Chiroptera	Vespertilionidae	Myotis	tricolor	M	Karamoja	Uganda	Mount Morungole	2520	1	8	2016	0	0	1	Ixodidae	Ixodidae
FMNH232111	JCK.10025	Chiroptera	Vespertilionidae	Myotis	tricolor	M	Karamoja	Uganda	Mount Morungole	2520	25	7	2016	1	Polychromophilus muri	1	Nycteribiidae	Nycteribia latiterna
FMNH232113	JCK.10028	Chiroptera	Vespertilionidae	Myotis	tricolor	M	Karamoja	Uganda	Mount Morungole	2520	26	7	2016	1	Polychromophilus muri	1	Nycteribiidae	Nycteribia latiterna
FMNH232114	JCK.10029	Chiroptera	Vespertilionidae	Myotis	tricolor	M	Karamoja	Uganda	Mount Morungole	2520	26	7	2016	0	0	1	Nycteribiidae	Nycteribia latiterna
FMNH232115	JCK.10030	Chiroptera	Vespertilionidae	Myotis	tricolor	M	Karamoja	Uganda	Mount Morungole	2520	26	7	2016	0	0	1	Nycteribiidae	Nycteribia latiterna
FMNH232116	JCK.10031	Chiroptera	Vespertilionidae	Myotis	tricolor	M	Karamoja	Uganda	Mount Morungole	2520	26	7	2016	0	0	1	Nycteribiidae	Nycteribia latiterna
FMNH234713	PWW.3617	Chiroptera	Vespertilionidae	Neoromicia	nana	M	Kakamega	Kenya	Ikhondo Junction Kakamega Forest National Reserve	1590	1	11	2016	0	0	0	0	0
FMNH234596	PWW.3439	Chiroptera	Vespertilionidae	Neoromicia	sp.	F	Kilifi	Kenya	Kaboga cave Gede	19	22	10	2016	0	0	0	0	0
FMNH234597	PWW.3440	Chiroptera	Vespertilionidae	Neoromicia	sp.	F	Kilifi	Kenya	Kaboga cave Gede	19	22	10	2016	0	0	0	0	0
FMNH234598	PWW.3443	Chiroptera	Vespertilionidae	Neoromicia	sp.	M	Kilifi	Kenya	Kaboga cave Gede	19	22	10	2016	0	0	0	0	0
FMNH232432	JCK.10376	Chiroptera	Vespertilionidae	Pipistrellus	sp.	F	Acholi	Uganda	Agoro-Agu Forest Reserve	1935	9	8	2016	0	0	1	0	0
FMNH232514	JCK.10396	Chiroptera	Vespertilionidae	Scotoecus	hindei	F	Acholi	Uganda	Agoro-Agu Forest Reserve	1935	11	8	2016	0	0	0	0	0
FMNH232516	JCK.10398	Chiroptera	Vespertilionidae	Scotoecus	hindei	F	Acholi	Uganda	Agoro-Agu Forest Reserve	1935	11	8	2016	0	0	0	0	0
FMNH232513	JCK.10356	Chiroptera	Vespertilionidae	Scotoecus	hindei	F	Acholi	Uganda	Agoro-Agu Forest Reserve	1935	9	8	2016	0	0	1	Hippoboscidae	Basilia ansifera
FMNH232515	JCK.10397	Chiroptera	Vespertilionidae	Scotoecus	hindei	M	Acholi	Uganda	Agoro-Agu Forest Reserve	1935	11	8	2016	0	0	0	0	0
FMNH234475	PWW.3602	Chiroptera	Vespertilionidae	Scotophilus	dingani	F	Kakamega	Kenya	Buzambuli Trail 3 Kakamega Forest National Reserve	1564	31	10	2016	0	0	0	0	0
FMNH234476	PWW.3616	Chiroptera	Vespertilionidae	Scotophilus	dingani	M	Kakamega	Kenya	Ikhondo Junction Kakamega Forest National Reserve	1590	1	11	2016	0	0	0	0	0
FMNH234474	PWW.3441	Chiroptera	Vespertilionidae	Scotophilus	dingani	F	Kilifi	Kenya	Kaboga cave Gede	19	22	10	2016	0	0	1	Nycteribiidae	Nycteribia schmidlii
FMNH232110	JCK.10180	Chiroptera	Vespertilionidae	Vespertilionid	sp.	M	Karamoja	Uganda	Mount Morungole	2520	30	7	2016	0	0	0	Spinturnicidae	Spinturnicidae

Table S3. DESeq results: ESVs from the skin that were identified as significantly enriched in either non-ectoparasitized (positive log2FoldChange values; black or ectoparasitized (negative log2FoldChange values; red) bats.

Host_family	baseMean	log2FoldChange	lfcSE	stat	pvalue	padj	Rank1	Rank2	Rank3	Rank4	Rank5	Rank6	Rank7
Hipposideridae	33.3360233	-25.65717963	2.84165626	-9.0289526	1.73E-19	4.77E-17	Bacteria	Bacteroidetes	[Saprosirae]	[Saprosirales]	Saprosiraceae	Unclassified	Unclassified
Hipposideridae	24.9053051	-25.44743324	2.961084869	-8.5939561	8.40E-18	1.54E-15	Bacteria	Proteobacteria	Gammaproteobacteria	Salinisphaerales	Salinisphaeraceae	Salinisphaera	Unclassified
Hipposideridae	21.6441823	-25.2429634	2.961117027	-8.5248111	1.53E-17	2.68E-15	Bacteria	Bacteroidetes	[Rhodothermi]	[Rhodothermales]	[Balneolaceae]	KSA1	Unclassified
Hipposideridae	35.4879494	-25.2388568	2.420732479	-10.426124	1.88E-25	3.63E-22	Bacteria	Firmicutes	Clostridia	Clostridiales	Clostridiaceae	Unclassified	Unclassified
Hipposideridae	20.5283726	-25.17048193	2.799904489	-8.9897645	2.48E-19	6.36E-17	Archaea	Euryarchaeota	Halobacteria	Halobacteriales	Halobacteriaceae	Natronomonas	Unclassified
Hipposideridae	33.6261871	-24.50404309	2.849792516	-8.5985358	8.07E-18	1.54E-15	Bacteria	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Unclassified	Unclassified
Hipposideridae	11.6313092	-24.40177521	2.306373551	-10.580149	3.68E-26	1.42E-22	Bacteria	Proteobacteria	Gammaproteobacteria	Salinisphaerales	Salinisphaeraceae	Salinisphaera	Unclassified
Hipposideridae	5.78175293	-23.45826935	2.497594017	-9.3923469	5.87E-21	3.23E-18	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Alcanivoracaceae	Alcanivorax	Unclassified
Hipposideridae	44.391983	-9.110914131	2.339431242	-3.8944996	9.84E-05	0.01148019	Bacteria	Proteobacteria	Gammaproteobacteria	Chromatiales	Ectothiorhodospiraceae	Unclassified	Unclassified
Hipposideridae	277.237854	-6.60493886	1.518580924	-4.3494151	1.37E-05	0.00175176	Bacteria	Bacteroidetes	[Rhodothermi]	[Rhodothermales]	[Balneolaceae]	KSA1	Unclassified
Hipposideridae	70.8563568	-6.389388446	1.413078047	-4.5216104	6.14E-06	0.00081475	Bacteria	Proteobacteria	Gammaproteobacteria	Salinisphaerales	Salinisphaeraceae	Salinisphaera	Unclassified
Hipposideridae	403.611788	-6.270630576	1.107148163	-5.6637682	1.48E-08	2.28E-06	Bacteria	Firmicutes	Bacilli	Bacillales	Bacillaceae	Unclassified	Unclassified
Hipposideridae	44.8861438	7.644821161	1.885374384	4.05480271	5.02E-05	0.00615871	Bacteria	Bacteroidetes	[Saprosirae]	[Saprosirales]	Chitinophagaceae	Unclassified	Unclassified
Hipposideridae	15.8097063	9.002077621	2.222664025	4.05012972	5.12E-05	0.00615871	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Luteibacter	rhizovicinus
Hipposideridae	36.9729559	9.667104592	2.044794813	4.72766486	2.27E-06	0.00032385	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Hipposideridae	0.89485376	20.86870844	2.959888545	7.05050482	1.78E-12	2.86E-10	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiodiaceae	Unclassified	Unclassified
Hipposideridae	0.89485376	20.86870883	2.959888544	7.05050495	1.78E-12	2.86E-10	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Hyphomicrobiaceae	Devosia	Unclassified
Hipposideridae	4.93611809	23.27919885	2.527845745	9.20910578	3.29E-20	1.06E-17	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nakamurellaceae	Unclassified	Unclassified
Hipposideridae	6.0392616	23.56015701	2.546061692	9.25356879	2.17E-20	8.36E-18	Bacteria	Firmicutes	Bacilli	Bacillales	Planococcaceae	Unclassified	Unclassified
Hipposideridae	6.15431009	23.58277186	2.72388647	8.65776607	4.81E-18	9.75E-16	Bacteria	Bacteroidetes	Flavobacteriia	Flavobacteriales	[Weeksellaceae]	Unclassified	Unclassified
Hipposideridae	6.20940611	23.59952012	2.545088156	9.27257473	1.82E-20	7.77E-18	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Sinobacteraceae	Unclassified	Unclassified
Hipposideridae	7.48028504	23.62760844	2.562780411	9.21952124	2.98E-20	1.04E-17	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Alcaligenaceae	Unclassified	Unclassified
Hipposideridae	6.8718056	23.73606007	2.731340242	8.69026118	3.62E-18	7.73E-16	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Hipposideridae	8.66930761	24.05903572	2.574969728	9.3432468	9.33E-21	4.49E-18	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Hipposideridae	10.1050997	24.23263237	2.758293021	8.78537276	1.56E-18	3.53E-16	Bacteria	Bacteroidetes	[Saprosirae]	[Saprosirales]	Chitinophagaceae	Unclassified	Unclassified
Hipposideridae	11.7961065	24.49313991	2.767890018	8.84902931	8.83E-19	2.12E-16	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Hipposideridae	13.3303502	24.62715736	2.597856709	9.4797982	2.55E-21	1.63E-18	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Alcanivoracaceae	Alcanivorax	Unclassified
Hipposideridae	15.0738992	24.73109623	2.44240381	10.1257196	4.25E-24	4.09E-21	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Alcanivoracaceae	Alcanivorax	Unclassified
Hipposideridae	33.8904008	25.96995682	2.521288461	10.300272	7.03E-25	9.02E-22	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Miniopterus	9.91594853	-25.58567541	2.017479186	-12.682002	7.44E-37	1.13E-33	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	Alkanindiges	Unclassified
Miniopterus	9.86344729	-8.50285269	2.025199058	-4.1985269	2.69E-05	0.00870641	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	Acinetobacter	Unclassified
Miniopterus	606.594629	-2.376277139	0.559035525	-4.2506729	2.13E-05	0.00743821	Bacteria	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Staphylococcus	Unclassified
Miniopterus	475.832275	2.315050715	0.485464246	4.76873577	1.85E-06	0.00076463	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Mycobacteriaceae	Mycobacterium	Unclassified
Miniopterus	92.5081738	4.319454662	1.138716109	3.79326737	0.00014868	0.04497011	Archaea	Euryarchaeota	Halobacteria	Halobacteriales	Halobacteriaceae	Halococcus	Unclassified
Miniopterus	96.4689286	4.819654198	1.073981799	4.4876498	7.20E-06	0.00272717	Bacteria	Proteobacteria	Gammaproteobacteria	Legionellales	Coxiellaceae	Rickettsiella	Unclassified
Miniopterus	16.2221811	6.873850559	1.233974991	5.57049422	2.54E-08	1.15E-05	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Miniopterus	59.749205	8.111218933	1.329825481	6.09946121	1.06E-09	5.37E-07	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Mycobacteriaceae	Mycobacterium	Unclassified
Miniopterus	0.98024775	20.38460648	2.931930405	6.9526229	3.59E-12	2.03E-09	Bacteria	Proteobacteria	Deltaproteobacteria	Myxococcales	unclassified	Unclassified	Unclassified
Miniopterus	15.314646	21.98481035	1.96908894	11.16496	6.05E-29	5.49E-26	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Miniopterus	46.8275783	23.45661248	1.763147258	13.3038306	2.20E-40	4.99E-37	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Miniopterus	10.2817702	23.72426544	2.024424912	11.7190148	1.02E-31	1.16E-28	Bacteria	Cyanobacteria	Chloroplast	Stramenopiles	unclassified	Unclassified	Unclassified
Miniopterus	29.1518671	24.8954245	2.440446386	10.2011766	1.96E-24	1.27E-21	Bacteria	Tenericutes	Mollicutes	Entomoplasmatales	Entomoplasmataceae	Entomoplasma	Unclassified
Miniopterus	26.8833469	25.05865373	1.665395292	15.0466702	3.63E-51	1.65E-47	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Pteropodidae	197.918879	-7.705987738	1.445731453	-5.3301654	9.81E-08	4.38E-05	Bacteria	Proteobacteria	Gammaproteobacteria	Pasteurellales	Pasteurellaceae	Avibacterium	Unclassified
Pteropodidae	11.6562082	-5.19327303	1.577955943	-3.2911394	0.00099782	0.0306917	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Pseudonocardiaceae	Actinomycetospora	Unclassified
Pteropodidae	46.3280145	-3.177959536	0.941405521	-3.3757605	0.00073612	0.02626475	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Halomonadaceae	Candidatus Portiera	Unclassified
Pteropodidae	222.317519	2.145584572	0.618996233	3.46623203	0.00052781	0.02264072	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Dermabacteraceae	Brachy bacterium	Unclassified
Pteropodidae	726.212554	2.457775804	0.700785138	3.50717455	0.00045289	0.02244331	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Brevibacteriaceae	Brevibacterium	aureum
Pteropodidae	13.2685055	2.509635649	0.824569764	3.04356982	0.00233789	0.04739544	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Mycobacteriaceae	Mycobacterium	Unclassified

Pteropodidae	372.152047	2.716938071	0.870978721	3.1194081	0.00181215	0.0413651	Bacteria	Firmicutes	Bacilli	Lactobacillales	Streptococcaceae	Lactococcus	garvieae
Pteropodidae	151.569379	2.914848464	0.882657155	3.30235635	0.00095876	0.03054341	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Mycobacteriaceae	Mycobacterium	Unclassified
Pteropodidae	169.414871	2.947354462	0.768660819	3.83440197	0.00012587	0.01122762	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	Rhodococcus	Unclassified
Pteropodidae	26.3950706	2.995492927	0.915443259	3.2721776	0.00106723	0.03107064	Bacteria	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Unclassified	Unclassified
Pteropodidae	41.0912537	3.061484864	0.845280699	3.62185588	0.0002925	0.01922586	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	Rhodococcus	fascians
Pteropodidae	59.1688549	3.074215379	0.962941686	3.19252497	0.00141035	0.03787161	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	Rhodococcus	Unclassified
Pteropodidae	16.0799288	3.184695056	0.974251879	3.26886211	0.00107981	0.03107064	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	Micrococcus	Unclassified
Pteropodidae	9.96279949	3.352163162	1.00234675	3.34431489	0.00082486	0.02829906	Bacteria	Firmicutes	Bacilli	Lactobacillales	Leuconostocaceae	Unclassified	Unclassified
Pteropodidae	32.229834	3.388681904	0.985558957	3.43833505	0.0005853	0.0233889	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	Nocardia	Unclassified
Pteropodidae	98.8625562	3.419943337	1.062502587	3.21876236	0.00128745	0.03588771	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Dermabacteraceae	Unclassified	Unclassified
Pteropodidae	14.4704316	3.468398712	1.001388823	3.4635884	0.00053302	0.02264072	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Xanthomonas	Unclassified
Pteropodidae	30.8523866	3.610840904	1.090269038	3.31188063	0.00092671	0.03054341	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	Alkanindiges	Unclassified
Pteropodidae	219.403137	3.882183276	1.095733525	3.54299945	0.0003956	0.02075755	Bacteria	Bacteroidetes	Flavobacteriia	Flavobacteriales	[Weeksellaceae]	Chryseobacterium	Unclassified
Pteropodidae	837.095064	3.968944289	1.296094202	3.06223443	0.00219691	0.04557318	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Corynebacteriaceae	Corynebacterium	Unclassified
Pteropodidae	14.0749496	4.010380328	1.304276362	3.07479339	0.00210648	0.04473771	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Unclassified	Unclassified
Pteropodidae	56.4996028	4.25907289	1.336892154	3.1858014	0.00144354	0.03787161	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Gordoniaceae	Gordonia	Unclassified
Pteropodidae	15.8728715	4.356749352	1.20558942	3.61379196	0.00030175	0.01922586	Bacteria	Bacteroidetes	[Saprosirae]	[Saprosirales]	Chitinophagaceae	Unclassified	Unclassified
Pteropodidae	178.794782	4.452743212	1.409556552	3.15896741	0.00158329	0.03817017	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Mycobacteriaceae	Mycobacterium	Unclassified
Pteropodidae	6.21886086	4.663028428	1.469938289	3.17226136	0.00151257	0.04473771	Bacteria	Bacteroidetes	[Saprosirae]	Unclassified	Unclassified	Unclassified	Unclassified
Pteropodidae	5.96221438	4.749096228	1.363012276	3.48426519	0.00049349	0.02264072	Bacteria	Proteobacteria	Epsilonproteobacteria	Campylobacterales	Campylobacteraceae	Arcobacter	Unclassified
Pteropodidae	20.9436783	4.932987454	1.557435665	3.167378	0.0015382	0.03811324	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetaceae	Unclassified	Unclassified
Pteropodidae	29.9474311	5.001377895	1.606855019	3.11252592	0.00185494	0.0413651	Bacteria	Proteobacteria	Gammaproteobacteria	Enterobacteriales	Enterobacteriaceae	Unclassified	Unclassified
Pteropodidae	10.2541137	5.014078622	1.385069977	3.62009047	0.0002945	0.01922586	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Pseudomonas	Unclassified
Pteropodidae	3.24100976	5.123619144	1.650426241	3.10442177	0.00190651	0.04147829	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	Perlucidibaca	Unclassified
Pteropodidae	3.37516681	5.18178447	1.510624461	3.43022677	0.00060308	0.0233889	Bacteria	Bacteroidetes	Cytophagia	Cytophagales	Cytophagaceae	Spirosoma	Unclassified
Pteropodidae	4.95612079	5.221601557	1.59942147	4.50160516	6.74E-06	0.00104039	Bacteria	Bacteroidetes	[Saprosirae]	[Saprosirales]	Chitinophagaceae	Chitinophaga	Unclassified
Pteropodidae	36.3126387	5.658834091	1.377583532	4.10779743	3.99E-05	0.0476996	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	Micrococcus	Unclassified
Pteropodidae	4.87593266	5.711005131	1.671272559	3.41715964	0.00063278	0.02351838	Bacteria	SR1	Unclassified	Unclassified	Unclassified	Unclassified	Unclassified
Pteropodidae	36.6191086	5.804559353	1.291697739	4.4937443	7.00E-06	0.00104039	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Paracoccus	aminovorans
Pteropodidae	15.5814282	5.859034147	1.441500053	4.06453967	4.81E-05	0.00476996	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Unclassified	Unclassified
Pteropodidae	46.66724	6.009936763	1.620417793	3.708881	0.00020818	0.01688128	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	Unclassified	Unclassified
Pteropodidae	6.52515097	6.131913909	1.715182193	3.57508021	0.00035012	0.02075755	Bacteria	Firmicutes	Clostridia	Clostridiales	Clostridiaceae	Clostridium	Unclassified
Pteropodidae	6.99054863	6.230715904	1.991565377	3.12855203	0.0017567	0.0412362	Bacteria	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Sphingobacteriaceae	Unclassified	Unclassified
Pteropodidae	12.8455406	6.606968105	1.445297111	4.57135634	4.85E-06	0.00104039	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	Alkanindiges	Unclassified
Pteropodidae	139.44463	7.14102869	1.506630904	4.73973332	2.14E-06	0.00063629	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	Micrococcus	luteus
Pteropodidae	11.7853444	23.96508235	1.691972713	14.1639887	1.53E-45	1.37E-42	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Rhodoferax	Unclassified
Rhinolophidae	6.21690977	-23.8707008	2.717367908	-8.7844935	1.57E-18	1.61E-16	Bacteria	Proteobacteria	Deltaproteobacteria	Syntrophobacteriales	Syntrophobacteraceae	Unclassified	Unclassified
Rhinolophidae	5.44483902	-23.68996395	2.90593782	-8.1522611	3.57E-16	1.83E-14	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Dokdonella	Unclassified
Rhinolophidae	5.33513131	-23.65059387	2.705098902	-8.7429683	2.27E-18	2.09E-16	Bacteria	Bacteroidetes	[Saprosirae]	[Saprosirales]	Chitinophagaceae	Unclassified	Unclassified
Rhinolophidae	4.69629323	-23.4884648	2.695621731	-8.7135612	2.94E-18	2.46E-16	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Lysobacter	Unclassified
Rhinolophidae	6.34244731	-6.063086547	1.884632095	-3.2171194	0.00129485	0.04075613	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Unclassified	Unclassified
Rhinolophidae	10.1070747	-5.160488069	1.60780803	-3.2096419	0.001329	0.04075613	Bacteria	Actinobacteria	Nitriiliruptoria	Nitriiliruptorales	Nitriiliruptoraceae	Unclassified	Unclassified
Rhinolophidae	52.5912353	4.708233337	1.396062002	3.3725102	0.00074486	0.0263567	Bacteria	Firmicutes	Bacilli	Bacillales	Bacillaceae	Lentibacillus	Unclassified
Rhinolophidae	286.783152	4.793488406	1.121747608	4.27323256	1.93E-05	0.00088623	Bacteria	Firmicutes	Bacilli	Bacillales	Unclassified	Unclassified	Unclassified
Rhinolophidae	29.0374515	4.948438459	1.493176523	3.31403446	0.0009196	0.03021549	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	Acinetobacter	Unclassified
Rhinolophidae	74.9680408	5.175528257	1.379008178	3.75308018	0.00017468	0.00669587	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Mycobacteriaceae	Mycobacterium	Unclassified
Rhinolophidae	7.84537579	5.932305883	1.610067389	3.68450782	0.00022915	0.00843254	Bacteria	Proteobacteria	Gammaproteobacteria	Enterobacteriales	Enterobacteriaceae	Unclassified	Unclassified
Rhinolophidae	30.9715879	6.023183129	1.795897484	3.35385688	0.00079694	0.02715485	Bacteria	Firmicutes	Bacilli	Bacillales	Bacillaceae	Unclassified	Unclassified
Rhinolophidae	20.7504911	7.6085716	1.87930866	4.04860136	5.15E-05	0.00215467	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Streptomycetaceae	Streptomycetes	Unclassified
Rhinolophidae	128.396363	8.116688524	1.731467878	4.68774999	2.76E-06	0.00013375	Archaea	Euryarchaeota	Halobacteria	Halobacteriales	Halobacteriaceae	Halobococcus	Unclassified
Rhinolophidae	226.682754	11.28161549	2.703490864	4.17298081	3.01E-05	0.00131709	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiopsaceae	Unclassified	Unclassified
Rhinolophidae	384.620387	11.30748268	2.903543181	3.89437387	9.85E-05	0.00393811	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiopsaceae	Nocardiopsis	exhalans

Rhinolophidae	13.121515	23.36634892	1.952101243	11.9698448	5.11E-33	4.70E-30	Bacteria	Firmicutes	Bacilli	Bacillales	Bacillaceae	Unclassified	Unclassified
Rhinolophidae	7.95472357	23.56150973	2.263836033	10.407781	2.28E-25	5.26E-23	Bacteria	Firmicutes	Bacilli	Bacillales	Planococcaceae	Sporosarcina	Unclassified
Rhinolophidae	25.9764381	23.68310583	2.905014398	8.15249172	3.57E-16	1.83E-14	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Alcaligenaceae	Pigmentiphaga	Unclassified
Rhinolophidae	30.0313576	23.92603537	2.691733283	8.88870956	6.18E-19	7.11E-17	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Hyphomicrobiaceae	Devosia	Unclassified
Rhinolophidae	10.4559986	23.94359103	2.596320604	9.22212418	2.91E-20	3.83E-18	Bacteria	Firmicutes	Bacilli	Bacillales	Bacillaceae	Lentibacillus	Unclassified
Rhinolophidae	11.1543769	24.03396481	2.050336281	11.7219624	9.84E-32	4.52E-29	Archaea	Euryarchaeota	Halobacteria	Halobacteriales	Halobacteriaceae	Halococcus	Unclassified
Rhinolophidae	19.2709528	24.79580547	2.876512782	8.62009223	6.69E-18	3.85E-16	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Phyllobacteriaceae	Mesorhizobium	Unclassified
Rhinolophidae	20.7016756	24.89752797	2.664359714	9.34465712	9.22E-21	1.41E-18	Bacteria	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Unclassified	Unclassified
Rhinolophidae	22.0885461	24.99090392	2.888308394	8.65243614	5.04E-18	3.37E-16	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Glycomycetaceae	Glycomyces	Unclassified
Rhinolophidae	23.5924593	25.07911141	2.905037058	8.6329747	5.98E-18	3.67E-16	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Streptomycetaceae	Streptomyces	Unclassified
Rhinolophidae	24.5114842	25.12952762	2.905027754	8.65035715	5.13E-18	3.37E-16	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Alcaligenaceae	Unclassified	Unclassified
Rhinolophidae	69.9247038	25.15739443	2.904873199	8.66041053	4.70E-18	3.37E-16	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Unclassified	Unclassified	Unclassified
Rhinolophidae	26.6336435	25.18897948	2.687384143	9.3730476	7.05E-21	1.30E-18	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Alcaligenaceae	Unclassified	Unclassified
Rhinolophidae	27.999455	25.32174644	2.382913512	10.6263808	2.25E-26	6.89E-24	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Unclassified	Unclassified