

1 **Title:** Testing for niche partitioning and specialization in plant–frugivore interactions using
2 generalized joint attribute modeling

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26 **Short–running title (45):** Bat–plant trait interactions

27 **Keywords (10):** trophic interactions, functional traits, *Piper*, *Carollia*, Bayesian hierarchical
28 models, generalized joint attribute modeling, bats, mutualism, Phyllostomidae, niche
29 partitioning

30 **Type of Article:** Letter

31 **Word count:** Abstract, Main Text, Text Box

32 **Number of References:** 46

33 **Number of Figures:** 3

34 **Number of Tables:** 1

35 **Number of Text Boxes:** 0

36 **Statement of Authorship:** LBM, ZAK, SRW and SES collected primary data, and LRY and
37 LMD designed and performed the analyses. All authors contributed to the discussion of the
38 results and the writing of the manuscript.

39 **Data Accessibility Statement:** All data, scripts, and results will be deposited onto Dryad.

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51 **ABSTRACT**

52 We use generalized joint attribute modeling (GJAM) to estimate how the proclivity to consume
53 different *Piper* species varies among three syntopic *Carollia* species my depend on bat traits
54 (e.g., body size and age) or *Piper* fruit traits. How these ecologically and morphologically
55 similar bats coexist is unclear. Compared to the *Piper*-specialist *Carollia castanea*,
56 generalist *C. perspicillata* had a higher proclivity for several *Piper* species that were the lowest
57 ranked for the specialist, indicating some degree of niche partitioning. *Piper* proclivity
58 estimates were associated with bat forearm length and age after controlling for bat species,
59 reproductive condition and sex. However, neither fruit nor seed shape influence dietary
60 differences among bats. Understanding the mechanisms of coexistence for closely related
61 species with a high degree of morphological and behavioral similarity is complex, but
62 simultaneously controlling for multiple sources of variation among different data types
63 allowed us to discover key differences in resource consumption and traits contributing to
64 niche partitioning among frugivores.

65

66 INTRODUCTION

67 Fruiting plants and frugivores are central to many ecosystems, and their interactions
68 have important ecological and evolutionary consequences (Cordeiro & Howe 2003;
69 Sekercioglu 2006; Schleuning *et al.* 2011). Effective seed dispersal by animals can be critical
70 to the plant life cycle because failure to disperse results in less reproduction and higher
71 probability of extinction (Pratt & Stiles 1985; Harms *et al.* 2000; Nathan & Muller-Landau
72 2000). In turn, frugivores obtain energy from fruits and benefit from the relative predictability
73 of fruiting plants as a food source (Kalko *et al.* 1996; Wendeln *et al.* 2000; Norconk *et al.*
74 2009). Advantages to both plants and animals are thought to explain the broad spread of
75 animal-mediated seed dispersal: the seeds of up to 90% of tropical angiosperms are
76 dispersed via consumption and subsequent defecation by birds and mammals (Bascompte
77 & Jordano 2007). The importance and prevalence of these associations, as well as the
78 staggering diversity of plants dependent on seed-dispersing frugivores make the study of
79 seed dispersal mutualisms crucial to understanding how ecological interactions persist.

80 Neotropical *Piper* plants (Piperales: Piperaceae) and *Carollia* bats (Fig. 1; Chiroptera:
81 Phyllostomidae) are a mutualistic system whose ecology has been well documented. *Piper*
82 are both diverse and abundant in tropical ecosystems worldwide (Gentry 1988) and provide
83 a constant supply of ripe fruit throughout the year through continuous or staggered fruiting
84 patterns among sympatric species (Thies & Kalko 2004). Many neotropical *Piper* species
85 depend on *Carollia* for seed dispersal (Dyer & Palmer 2004), and *Piper* fruits dominate these
86 bats' diets throughout the year and across their range (Fleming 1991). Because of the
87 apparent high dietary overlap and morphological similarity among syntopic *Carollia* species,
88 they are ideal for testing predictions from evolutionary and ecological hypotheses, including
89 ecological character displacement and ecological fitting. In Costa Rica, three species of
90 syntopic *Carollia* feed on at least a dozen *Piper* species, with *C. perspicillata* being the most
91 generalist frugivore, *C. sowelli* being intermediate, and *C. castanea* being the most
92 specialized on *Piper* (Fleming 1991).

93 From an evolutionary perspective, stable species coexistence instead of competitive
94 exclusion is enabled by (1) enough niche space that can be occupied by a diverse set of
95 species within a guild, (2) differentiation of functional traits, and (3) tradeoffs in species
96 performance across niche axes such that niche differentiation can occur (e.g., Weinstein &
97 Graham (2017) but see Sexton *et al.* (2017)). How do closely related, ecologically,
98 behaviorally, and morphologically similar syntopic species meet these requirements? And
99 how do their realized versus fundamental niches compare to one another as a result? These
100 questions are particularly puzzling in specialists like *Carollia* bats, which live in hyper-diverse
101 ecological communities with seemingly conserved trophic niches.

102 We develop a framework to simultaneously measure the role of traits of both fruits
103 and bats in structuring their ecological interactions. We use Bayesian generalized joint
104 attribute modeling (GJAM) to contrast realized dietary niche breadths and estimate the
105 proclivity of three syntopic species of *Carollia* for *Piper* species, as well as the influence of
106 bat traits on these estimates. In turn, we relate *Piper* fruit traits to these estimates, testing
107 their influence on bat consumption. Analyzing the trophic interactions among bats and
108 plants, and among competing congeners, requires the integration of several types of
109 ecological data (e.g., continuous traits, presence/absence of food resources), and has
110 been historically challenging to model (Clark 2016; Clark *et al.* 2017). Joint attribute

111 modeling is able to account for multiple sources of variation and multiple predictors of
112 different data types to obtain robust estimates of responses (Clark *et al.* 2017). We predicted
113 divergence of bat proclivities to consume different *Piper* species and evolved functional traits
114 that minimize competition among congeners. Additionally, we tested if differential proclivity
115 to consume *Piper* species is related to specific *Piper* traits. We discovered two *Carollia*
116 species show realized dietary niches that are divergent, complementary, and associated with
117 divergent morphological traits of the bats. *Piper* traits examined showed no relationships to
118 bat proclivities, suggesting these may not be involved in fruit selection by bats. Despite only
119 subtle trait differences among the bat species studied, our analyses uncovered key
120 differences in resource consumption contributing to niche partitioning among frugivores.

121

122 MATERIALS AND METHODS

123 To investigate mechanisms of co-existence among *Carollia* bats, we collected data from
124 co-occurring individuals of bats and plants at La Selva Biological Station, Sarapiquí, Costa
125 Rica. We used these data to build three types of Bayesian models. The first models link bats
126 and their traits to *Piper* species represented in bat feces. The second model estimates the
127 relationship between bat morphometric (*e.g.*, body size) and performance (*i.e.*, bite force)
128 traits related to feeding, and the third quantifies the effects of *Piper* traits on modeled bat
129 proclivities to consume *Piper* species.

130

131 *Piper Consumption by Bats*

132 To determine how *Carollia* species and traits relate to particular proclivity to consume *Piper*,
133 we quantified the diets of the three syntopic *Carollia* species at La Selva. All procedures for
134 bat capture and handling were approved by the Institutional Animal Care and Use Committee
135 (IACUC) of the University of Washington, Seattle, USA (protocol #4307-02). We used mist
136 nets to capture bats between 1800–2200 h along trails throughout the forest during the wet
137 season, when there is a greater incidence of fruiting peaks for *Piper* (July and September –
138 December 2015). We collected fecal samples from 318 individuals from the three *Carollia*
139 species (Fig. 1): *C. perspicillata* ($N = 84$), *C. sowelli* ($N = 111$), and *C. castanea* ($N = 123$)
140 by placing individual bats in cloth bags for up to two hours. If the bat defecated, we collected
141 fecal pellets, which we dried in an air-conditioned room for 1–2 days. Samples were then
142 transported to UW for seed identification. We identified seed species in rehydrated fecal
143 pellets using morphological characters and by comparison to a seed reference library that
144 included *Piper* and non-*Piper* species native to La Selva. The reference library was built from
145 seeds removed from ripe fruits collected directly from the parent plant, and plants were
146 identified by LBM, ZAK, Orlando Vargas (OTS), and confirmed via genetic markers (see
147 (Santana *et al.* 2021)). If we could not identify the species of a particular seed, we classified
148 them as a morphotype (*e.g.*, *Piper* Type 1). We coded each plant species as present or
149 absent in the individual fecal sample (Data S1).

150

151 *Bat Traits*

152 We recorded age class (adult, sub-adult, juvenile), sex (male, female), reproductive
153 condition (reproductive, non-reproductive), mass, and forearm length (Data S1) for each
154 bat that produced a fecal sample. Using these bat-specific variables as covariates, we built
155 a model to estimate the relationship between bat traits and species and *Piper* species

156 represented in the feces (i.e., to examine how bat traits and species designation influence
 157 their dietary records). We call these modeled coefficients of bat species and traits “*Piper*
 158 bat proclivities”. Our data set was composed of multiple data types, including a zero-inflated
 159 matrix of *Piper* species in the bat fecal samples (e.g., 0 if *Piper* species is not present; 1 if
 160 *Piper* species is present) and correlates of those data: discrete categories of *Carollia*
 161 species, continuous bat size traits, as well as the categorical traits of sex and reproductive
 162 condition. Simultaneously estimating relationships among bat species, their traits, and the
 163 *Piper* species consumed by bats, is a challenge to general linear models. We implemented
 164 the flexible framework of generalized joint attribute modeling (GJAM) (Clark *et al.* 2017),
 165 which uses a Bayesian multivariate approach to infer the parameters of the linear model
 166 based on a series of joint distributions of both the bat traits and the *Piper* fecal abundances,
 167 while simultaneously accommodating multifarious trait data, in this case from bats.

168

169 *Generalized Joint Attribute Modeling*

170 For each observation i of n bat individuals, there is a set $\{x_i, y_i\}^n$, in which each x_i
 171 observation has Q predictors to result in a vector of predictors $x_{iq}: 1 \dots Q$. In our case $Q = 6$,
 172 with predictors species, age class, sex, reproductive condition, mass, and forearm length.
 173 The set of responses is a vector of $y_{ip}: 1 \dots P$, where P is the total number of *Piper* species
 174 ($P = 18$) observed across all fecal samples. For y_{ip} , each vector of bat individual i is the
 175 presence or absence of *Piper* species p . Seven *Piper* species were removed from the
 176 analysis, as they accounted for less than 1% of the observations. Most of the observations
 177 in y_{ip} are 0, meaning most *Piper* species are not observed in a sample. To accommodate
 178 this zero-inflation, GJAM implements a Tobit regression. The representations of x_i and y_i
 179 are composed of partitions of discrete and continuous space, and GJAM applies a
 180 connection between the two, which we represent as I in our model. Thus, it is possible to
 181 estimate a continuous response w_i from multifarious data such that for each observation,

182

$$183 \quad w_i | x_i, y_i \sim \mathcal{N}(B', E) * I$$

184

185 where B' is the matrix of coefficients and E is a $P \times P$ correlation matrix to represent the
 186 covariances among the response variables. For detailed explanations of the calculations of
 187 I , E , and w , see further discussion in Clark *et al.* (2017). We estimated the coefficients
 188 using the R package `gjam` v. 2.1.6 for 20,000 generations, discarding 4,000 as burn-in. We
 189 applied a series of dimension reduction options ($N = 2, 5$, by $r = 2, 5$) to facilitate
 190 convergence amidst the multiple dimensions of covariance space and adopted the one that
 191 yielded the lowest model deviance. Note that we compared both fractional composition
 192 models (continuous on (0,1)) and presence-absence models (discrete). Medians of the
 193 posterior distributions of the continuous response w_i were used for further modeling.

194

195 *Bat Functional Traits*

196 Bite force is a metric of feeding performance linked to the mechanical demands of the food
 197 a species can process (e.g., Aguirre *et al.* 2002; Santana *et al.* 2010; Santana & Miller
 198 2016). Following methods by Santana *et al.* (2010), we measured deep bilateral, voluntary
 199 bite forces for at least ten wild individuals per *Carollia* species using a piezoelectric force
 200 transducer (Kistler 9203; range ± 500 N, accuracy 0.01–0.1 N) attached to a handheld

201 charge amplifier (Kistler 5995A). The force transducer was mounted between two metal
202 plates covered with medical tape to provide a non-skid biting surface and to protect the
203 bats' teeth. We adjusted the distance between the bite plates for each individual to
204 accommodate a moderate gape angle of approximately 30°, following Santana *et al.*
205 (2010). To avoid variation from age (Santana & Miller 2016) and stress to reproductive
206 females, we only measured adult males and adult non-pregnant, non-lactating females.
207 We recorded five to eight measurements for each bat and chose the highest value to
208 represent maximum bite force. Following bite force measurements, we recorded head
209 length, width, and height measured to the nearest 0.1 mm (Fig. S1B), as well as mass and
210 forearm length for most individuals (Data S1).

211

212 *Piper Fruit and Seed Traits*

213 Physical traits of fruits and seeds can constrain whether and how bats of different sizes can
214 process them. We collected dimensions of whole *Piper* infructescences (the unit consumed
215 by *Carollia*, herein called “fruits” for simplicity) and individual seeds to estimate how these
216 traits relate to bat proclivities to consume *Piper* species. We measured length and width
217 from five ripe fruits from each *Piper* species to the nearest 0.001 mm, and used ImageJ
218 (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Maryland, USA) to measure
219 seed length and seed width from digital photographs of three seeds from each fruit. Seed
220 photos were taken with a Leica MZ 95 microscope camera coupled with Clemex Captiva
221 software. We used these fruit and seed measurements to calculate a ratio (length/width) as
222 an estimate of fruit and seed shape, respectively.

223

224 *Bayesian Hierarchical Modeling*

225 After determining that both sex and head length were linear predictors of bite force in
226 regressions with either a sample-wide intercept (male sex coefficient $t_{(27)} = 2.29$, P -value =
227 0.03, head length coefficient $t_{(27)} = 7.60$, P -value = $3.54e-08$), or species-specific
228 intercepts (male sex coefficient $t_{(27)} = 4.23$, P -value $1.20e-04$, head length coefficient $t_{(27)}$
229 = 2.44, P -value = 0.01), we modeled bite force as a function of bat body size traits while
230 controlling for both sex and head length, which may explain bite force. We used Jags v.3.3.0
231 (Plummer 2003) to code these models, and ran them in the R package R2jags v.0.04-01
232 (Su & Yajima 2012). These models included species-specific intercepts whose prior was
233 drawn from a normal distribution. Priors for both between- and within-population variances
234 were modeled as half-Cauchy distributions with variance of at least 100,000. These priors
235 do not make any assumptions about the relative contribution of variation from different levels
236 in the hierarchy (Gelman & Hill 2006). For each model, four independent chains ran for
237 500,000 iterations with 250,000 iterations as burn-in, and samples were taken every 250
238 generations. Convergence was assessed by both the effective sampling size of model
239 parameters (>1000 in every case), and the potential scale reduction factor (PSRF), which
240 approaches 1 at convergence (Gelman & Rubin 1992). The models coded measures of error
241 to estimate the variance explained, as outlined by Gelman & Pardoe (2006).

242 We used the *Piper* traits as regressors in Bayesian models of *Piper* bat proclivities
243 estimated by GJAM analysis. Thus, these models connect the differential use of *Piper*
244 resources by bats (e.g., across species, age class, or body sizes) to the *Piper* traits that
245 might underlie those differences. We used the R package MCMCglmm (Hadfield 2010) to

246 code the models, and accounted for the correlation structure of the data due to evolutionary
247 relatedness by including a molecular phylogeny of *Piper* (Santana *et al.* 2021) as a species-
248 specific (random) effect. We applied a parameter-expanded prior with the parameters $V =$
249 1 $\nu = 1$ for the residual variance (Rojas *et al.* 2018), and a proper Cauchy prior defined by
250 $V = 0.5$ $\nu = 1$ and $\alpha.\mu = 0$ and $\alpha.V = 10^3$ for the random term (Hadfield 2019).
251 Each model ran for 200,000 iterations, sampling every 100, with 10,000 generations as
252 burn-in. Convergence of the resulting posteriors was assessed by the effective sampling
253 size of model parameters (>1000 in every case). In total, we ran four models corresponding
254 to the modeled proclivities associated with bat forearm, body mass, and *C. castanea* and
255 *C. perspicillata*.

256

257 RESULTS

258 As expected, the percentage of *Piper* presence in the diet was highest in the specialist *C.*
259 *castanea* (67.5%) and lowest in the generalist *C. perspicillata* (45.2%). *C. sowelli* was
260 intermediate (60.5%) (Fig. S2). For the period sampled, *Piper* Type 4 was the most common
261 species in the diets of *C. castanea* and *C. sowelli*, while *P. hispidum* was the most common
262 for *C. perspicillata*. Dietary proportions are displayed in Fig. S2 and raw diet data in Data
263 S1.

264

265 *Bat species proclivities to Piper*

266 Model fit was assessed through DIC (Deviance Information Criterion) and posterior predictive
267 output and the fractional composition model (as opposed to presence-absence)
268 demonstrated a much better fit (Fig. 2A, 2B). In GJAM, the sensitivity of the covariate inputs
269 can be interpreted as the amount of information each input contributes to estimating the
270 model coefficients (Clark *et al.* 2017). Bat species (particularly *C. castanea* and *C.*
271 *perspicillata*), body size (forearm length), age, and reproductive status all showed sensitivity
272 values greater than one, suggesting they were much more informative than sex or body mass
273 in explaining the presence of *Piper* species in the diet of *Carollia* (i.e., *Piper* bat proclivities;
274 Table S1; Fig. 2C). Figure 3 illustrates the posterior probabilities for each *Piper* species
275 estimated by the proclivity of each bat species to consume that particular *Piper* species
276 (details in Table S2). While the 95% highest posterior density (HPD) credible interval crossing
277 zero corresponds to a weak relationship between the covariate and the *Piper* species, an
278 HPD not overlapping zero can be interpreted as a strong response. Consequently, *C.*
279 *perspicillata* showed a strong positive response to six species of *Piper* (in order of highest
280 proclivity: *P. hispidum* (median: 0.45; 95% HPD: [0.22, 0.66]), *P. colonense* (0.45 [0.20,
281 0.66]), *P. silvivagum* (0.45 [0.20, 0.68]), Type 4 (0.36 [0.13, 0.56]), *P. aduncum* (0.35
282 [0.10, 0.59]), and Type 10 (0.31 [0.001, 0.59])). The *Piper* specialist *C. castanea* also
283 has the lowest proclivities for five of these six species (Fig. 3); *P. colonense* (-0.52 [-0.75,
284 -0.24]), *P. hispidum* (-0.34 [-0.56, -0.09]), *P. silvivagum* (-0.34 [-0.58, -0.07]), *P.*
285 *aduncum* (-0.33 [-0.58, -0.07]), and Type 4 (-0.32 [-0.54, -0.08]). *C. castanea* also
286 showed a negative proclivity for *P. sancti-felicis* (-0.33 [-0.63, -0.01]), towards which *C.*
287 *sowelli* (the bat species that exhibits intermediate specialization on *Piper*) also demonstrated
288 a positive proclivity (0.22 [0.02, 0.41]). *C. perspicillata* only showed a negative proclivity
289 towards *Piper* Type 1 (-0.29 [-0.58, -0.01]). Table S2 shows coefficient estimates for all
290 *Piper* species.

291

292 *Influence of bat traits on Piper proclivities*

293 The sensitivity of bat traits and their influence on proclivity to *Piper* species varied (Table S1;
294 Fig. 2C). The magnitude of these coefficients reflects the influence of the trait on the
295 proclivity or response to each *Piper* species. One covariate representing body size (forearm
296 length) had strong sensitivity on responses for *Piper* species (Fig. 2C; Fig. 4). The presence
297 of *P.* Type 1 showed the strongest positive response to forearm length (0.70 [0.34, 1.01]).
298 There was a strong positive influence of forearm length in four other *Piper* species (Fig. 4;
299 *P. peracuminatum*: 0.41 [0.13, 0.73]; *P. paulowniifolium*: 0.34 [0.04, 0.70], *P. sancti-*
300 *felicis*: 0.27 [0.01, 0.59], and *P. multiplivervium*: 0.26 [0.03, 0.52]). A strong negative
301 response to forearm was estimated for *Piper* Type 4 (-0.21 [-0.37, -0.06]), which also had
302 anticorrelated proclivities favoring *perspicillata* (0.36 [0.13, 0.56]) and negative for
303 *castanea* (-0.31 [-0.54, -0.08]). Although age showed the second highest sensitivity
304 among all covariates (Fig. 2C), no *Piper* species had a posterior that entirely excluded zero
305 (Fig. S4), likely because there were few observations of juveniles and subadults. It is worth
306 noting that despite this variation, *P. paulowniifolium* showed the strongest response with
307 adult bats and Type 1 and *P. hispidum* showed the strongest response in juveniles and
308 subadults (Fig. S4). There was no meaningful bat sex or reproductive condition influence on
309 *Piper* species consumed. Table S2 summarizes estimates for each categorical or continuous
310 covariate of this model.

311

312 *Bat functional traits*

313 We modeled the scaling of bite force with head and body dimensions using hierarchical
314 models and in the natural log scale in every case. Although head length did not differ among
315 species ($F_{2,27} = 1.443$, $p = 0.256$), it was a positive covariate of maximum bite force with
316 high variance explained (multiple regression $R^2 = 0.90$, after controlling for sex), and a
317 consistently positive posterior coefficient distribution (Table S3). Similar results were
318 obtained in combination with body mass (multiple regression $R^2 = 0.90$), and forearm length
319 (multiple regression $R^2 = 0.90$ and lowest deviance), with the forearm length coefficient
320 indicating negative trends with bite force after controlling for head length (Table S4). Head
321 and forearm length were positively correlated ($R = 0.76$, $t_{28} = 6.2306$, $p = 9.862e-07$). In
322 short, once the effect of head size is accounted for, and acknowledging that larger bats
323 have larger heads, the marginal relationship between forearm length and bite force tends to
324 be negative. Male bats always had greater bite force compared to females, even after
325 controlling for head length, or body size (Table S3).

326

327 *Piper fruit traits and Bat-Piper responses*

328 Phylogenetic hierarchical Bayesian models sought to relate bat responses to *Piper* species
329 to *Piper* traits (seed shape index, fruit shape index). These models examined whether *Piper*
330 traits could predict the relative strength of GJAM coefficients reflecting the likelihood that a
331 given bat will consume a given *Piper* species (*i.e.*, *Piper* bat proclivities). Neither of the fruit
332 traits was a statistically significant predictor of *C. castanea* proclivities (Table S4), or of
333 proclivities estimated based on forearm length or body mass for *C. perspicillata*.

334

335 DISCUSSION

336 Niche theory predicts that coexisting, closely related species will select different resources
337 to minimize competition, evolving specializations over time to avoid competitive interactions
338 with phenotypically similar species (Schluter 2000). We built a framework to estimate bat
339 species proclivities to consume plant species within an assemblage of *Piper* and *Carollia*
340 species. Using these estimates, we tested both how bat traits contributed to responses or
341 proclivities to an array of *Piper* species, and whether plant traits showed a reciprocal
342 influence on bat consumption. Our study has three key findings: [1] the *Piper* species most
343 consumed by the *Piper* generalist *C. perspicillata* were the same ones least probable in the
344 diet of the specialist *C. castanea*; [2] body size sometimes influences these interactions
345 and is a weakly negative correlate of feeding performance ability (bite force) at the
346 intrageneric level; and [3] the fruit traits analyzed do not influence *Piper*–*Carollia*
347 interactions. In short, we found evidence for niche partitioning among bat frugivores that is
348 sometimes associated with bat traits, but no corresponding matching by the plant traits
349 examined.

350 Despite great morphological similarity, we expected syntopic *Carollia* species to use
351 different co-occurring plants and to exhibit traits that match the consumption of these
352 divergent resources. Indeed, of the six *Piper* species with the highest probability of being
353 consumed by the generalist *C. perspicillata* (Fig. 3), five also had the lowest probability of
354 being consumed by the specialist *C. castanea* (Fig. 3). This finding stands in contrast to
355 past work that found no evidence for differential use of *Piper* across *Carollia*
356 species (Maynard *et al.* 2019), suggesting that the models in GJAM that allow for
357 simultaneous inference of multiple covariates with different variance structures help to
358 elucidate the complex patterns of species interaction within this guild. This inverse proclivity
359 to a suite of *Piper* species is strong evidence that *C. perspicillata* is using *Piper* species that
360 *C. castanea* uses very little, contributing to niche partitioning. We interpret these patterns to
361 mean that, rather than support for traditional concept of niche partitioning in which different
362 coexisting species are adapted to eat different resources, rather *C. perspicillata* is eating
363 several *Piper* species that *C. castanea* does not (or rarely does). Nearly all other *Piper*
364 species had overlapping probabilities of being found in the diet of the three bat species (Fig.
365 3), indicating a relatively high degree of food niche overlap among the *Carollia* species.
366 Niche partitioning between *perspicillata* and *castanea* may also be facilitated by a greater
367 proportion of non-*Piper* species consumed by *perspicillata* (Fig. S2). These two bat species
368 may also use their habitat differently or at different times, or be in active competition on an
369 ecological time scale. We propose that in the presence of a competing species such as *C.*
370 *perspicillata*, the realized niche is smaller for the specialist *C. castanea*, such that
371 specializing on different *Piper* resources.

372 Dietary specialization should be reflected in bat traits, and we found bat body size
373 traits to influence consumption probability for some *Piper* species, including two that are
374 differentially consumed by *C. castanea* and *C. perspicillata* (Type 1, Type 4) and one that
375 is differentially consumed by *C. castanea* and *C. sowelli* (*Piper sancti-felicis*). With head
376 size a reliable positive predictor of bite force, specialization may involve greater bite force
377 by the larger *perspicillata* (which would enable access to harder fruit). This interpretation is
378 indirect, however, as head size could not be directly included in *Piper* consumption models.
379 The traits analyzed here do not exhaust the universe of traits potentially involved in
380 specialization, as there is evidence for plant–bat specialization mediated by bat perception

381 through the sense of smell (Yohe *et al.* 2021) and fruit scent specifically in *Piper* (Santana
382 *et al.* 2021). Alternatively, these bat species may use habitat differentially, but such
383 partitioning was found to be linked to age (Maynard *et al.* 2019) rather than species, and
384 age also had the highest sensitivity of all bat traits in our study. Together, these findings
385 suggest habitat use across the sampled localities does not correspond to bat species and
386 therefore cannot explain the differential use of certain *Piper* we found. Finally, *perspicillata*
387 may be in direct competition with *castanea* for access to some *Piper* species; even though
388 *castanea* does consume all the *Piper* underrepresented in its diet, these could possibly be
389 more highly represented were it not for the presence of its larger congener. As there were
390 no bat traits consistently associated with species specific proclivities (other than for Type
391 4), this is also a viable explanation for the niche partitioning found. Experiments excluding
392 *perspicillata* can help distinguish between ongoing strong competition (Maynard *et al.* 2019)
393 and the longstanding hypothesis that *castanea* is a more specialized frugivore than its
394 congeners (Dyer & Palmer 2004; Salazar *et al.* 2013).

395 While body size may predict consumption of some *Piper* species, we found little
396 evidence that body size independent of head size underlies differences in a functional trait,
397 bite force. Body size —measured by body mass or forearm length— does not explain bite
398 force differences among *Carollia*, but head length and sex do, after controlling for species
399 (Table S3). Bite performance might be important to reduce competition among bats like
400 *Carollia*; higher bite force allows access to tougher foods, thereby expanding the species'
401 fundamental niche (Meyers & Irschick 2015; Villalobos–Chaves *et al.* 2016). The link between
402 bite force and *Piper* proclivities is indirect (as the *Piper* consumption model lacked head
403 length data, and bite force was not measured for individuals therein). But head and forearm
404 length are positively correlated, implying that the influence of forearm length on *Piper*
405 proclivities (Fig. 3) correspond to bite force as well. Structuring of *Piper* proclivities by size
406 —which connects to bite force— aligns our results with comparative analyses for all
407 phyllostomids (Santana *et al.* 2010b). Although nowhere near the relatively high bite forces
408 crucial for phyllostomids that eat hard fruit (Dumont *et al.* 2009), our models indicate that
409 partitioning by body size (forearm length) and positively associated with higher bite force
410 could be important for explaining differential consumption for some *Piper* species.

411 Yet, *Carollia* feed on ripe *Piper* fruits, most of which become very soft when ripe, and
412 all of which are cylindrical. Hence, gape and consumption speed may be more important
413 than force in food processing (Freeman & Lemen 2007). Indeed, field observations show
414 *Carollia* eat *Piper* fruit like corn on the cob (Fig. 1D), and very rapidly when compared to
415 other phyllostomid frugivores (Fleming 1988). Despite differences in body size (Fig. S4),
416 *Carollia* species have similar head dimensions, and this is reflected in similar posterior
417 distributions for bite force across species (Table S3). In addition to different bite forces, the
418 differences in body size that structure proclivities to *Piper* might indicate differences in dietary
419 niche breadth, because niche breadth can increase with body size in bats (Barclay &
420 Brigham 1991). In the latter case, instead of specialization, *Piper* proclivities might be related
421 to *Piper* distribution and bat dispersal ability. In effect, and although we did not focus on
422 non-*Piper* species, the larger generalist *C. perspicillata* eats fruits from several other types
423 of plants too. Relating niche breadth to body size would thus support ongoing competition
424 among bat congeners.

425 In the context of coevolution driven by mutualisms, a reciprocal correlation between
426 frugivore phenotype and traits of the food resources is expected, as in the case of beak size
427 and shape, and seed size and hardness in Galapagos finches (Schluter & Grant 1984;
428 Schluter *et al.* 1985). While we found no relationship between *Piper* traits and any proclivity
429 estimates, many other traits might be involved in this plant–bat interaction. Traits such as
430 fruiting time (Thies & Kalko 2004), plant habit, or secondary metabolite profiles (Whitehead
431 *et al.* 2016) have been proposed as being more important to differential consumption than
432 the physical traits of fruit we measured. There is also strong support for chemical
433 communication between plants and bats, with behavioral evidence for *Carollia* using the
434 sense of smell to locate ripe fruit (Thies *et al.* 1998; Leiser–Miller *et al.* 2020), and bat
435 olfactory receptor diversity scaling to dietary diversity (Yohe *et al.* 2021). Chemical bouquet
436 composition both differs sharply and evolved adaptively among *Piper* species (Santana *et*
437 *al.* 2021), so those traits may affect and better reflect reciprocal adaptation to bat
438 consumption. In short, while we found no evidence of an effect of fruit and seed dimensions
439 on bat consumption, behavioral and chemical evidence suggest scent traits are likely to be
440 more important in structuring niche partitioning across bat species.

441 Though the inverse relationship in proclivities for *Piper* may indicate ongoing
442 specialization in food resources in two *Carollia* species, there is some indication that
443 behavioral aspects, such as learning, may contribute to differential resource use. While no
444 *Piper* species showed a significant association to bat age, age had high sensitivity and some
445 interesting patterns of contrasting consumption tendencies in adult versus juvenile bats
446 warrant further exploration (Fig. S3). A previous study has found that adults used a lower
447 percentage of mid- to late-successional species than juveniles, partitioning *Piper* by habitat
448 (Maynard *et al.* 2019). We hypothesize that older, more experienced bats can locate and
449 exploit resources better than younger, naïve bats –whether through spatial learning, or
450 familiarity with less conspicuous fruit cues.

451 Because our model both accounts for several sources of variation and can
452 incorporate many different types of ecological data, we were able to discover partitioning
453 and estimate the influence of various traits on plant–frugivore interactions. Identifying such
454 patterns both uncovered ecological factors contributing to coexistence and provided
455 quantitative evidence of the relationships between differential resource use and frugivore
456 traits. We discovered that, while the use of different fruit resources is related to putatively
457 adaptive differences in body size traits, age may also play an important role in defining the
458 dietary niche of syntopic species. As body size both may confer niche breadth and underlies
459 functional traits such as bite force, our findings are consistent with both specialization
460 through adaptation and ongoing competition. While there was not an effect of the plant traits
461 examined on bat consumption, mounting evidence for plant chemical adaptation and
462 specialization suggests plant–bat interactions may not be mediated by gross fruit
463 morphology. Thus, this approach enabled us to both uncover the most informative predictors
464 of differential plant use, and hint at new mechanisms underlying the evolutionary ecology of
465 fruit–frugivore interactions.

466 467 **Acknowledgements**

468 This project was made possible by the scientists and administrators at La Selva Biological
469 Research Station in Sarapiquí, Costa Rica. We specifically acknowledge Bernal Rodriguez

470 Hernandez, Bernal Matarrita, Orlando Vargas, David Villalobos Chaves, and Minor Porras for
471 their technical assistance and help with permits. This project was funded via the National
472 Science Foundation DEB-1442142, DEB-1456375, DEB-1856776, and the Postdoctoral
473 Research Fellowship in Biology (NSF DBI-1812035).

474 **References**

- 475 Aguirre, L.F., Herrel, A., van Damme, R. & Matthysen, E. (2002). Ecomorphological
476 analysis of trophic niche partitioning in a tropical savannah bat community. *Proc. R.*
477 *Soc. B Biol. Sci.*, 269, 1271–1278.
- 478 Barclay, R.M.R. & Brigham, R.M. (1991). Prey detection, dietary niche breadth, and body
479 size in bats: why are aerial insectivorous bats so small? *Am. Nat.*, 137, 693–703.
- 480 Bascompte, J. & Jordano, P. (2007). Plant–animal mutualistic networks: The architecture
481 of biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 38, 567–593.
- 482 Clark, J.S. (2016). Why species tell more about traits than traits about species: Predictive
483 analysis. *Ecology*, 97, 1979–1993.
- 484 Clark, J.S., Nemergut, D., Seyednasrollah, B., Turner, P.J. & Zhang, S. (2017).
485 Generalized joint attribute modeling for biodiversity analysis: Median–zero,
486 multivariate, multifarious data. *Ecol. Monogr.*, 87, 34–56.
- 487 Cordeiro, N.J. & Howe, H.F. (2003). Forest fragmentation severs mutualism between seed
488 dispersers and an endemic African tree. *Proc. Natl. Acad. Sci.*, 100, 14052–14056.
- 489 Dumont, E.R., Herrel, A., Medellín, R.A., Vargas–Contreras, J.A. & Santana, S.E. (2009).
490 Built to bite: Cranial design and function in the wrinkle–faced bat. *J. Zool.*, 279, 329–
491 337.
- 492 Dyer, L.A. & Palmer, A.D.N. (2004). *Piper: a model genus for studies of phytochemistry,*
493 *ecology, and evolution.* Springer, New York.
- 494 Fleming, T.H. (1988). *The short–tailed fruit bat: a study in plant–animal interactions.*
495 University of Chicago Press.
- 496 Fleming, T.H. (1991). The relationship between body size, diet, and habitat use in
497 frugivorous bats, Genus *Carollia* (Phyllostomidae). *J. Mammal.*, 72, 493–501.
- 498 Freeman, P.W. & Lemen, C.A. (2007). Using scissors to quantify hardness of insects: do
499 bats select for size or hardness? *J. Zool.*, 271, 469–476.
- 500 Gelman, A. & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical*
501 *models.* Cambridge university press.
- 502 Gelman, A. & Pardoe, I. (2006). Bayesian measures of explained variance and pooling in
503 multilevel (hierarchical) models. *Technometrics*, 48, 241–251.
- 504 Gelman, A. & Rubin, D.B. (1992). Inference from iterative simulation using multiple
505 sequences. *Stat. Sci.*, 7, 457–472.
- 506 Gentry, A.H. (1988). Tree species richness of upper Amazonian forests. *Proc. Natl. Acad.*
507 *Sci.*, 85, 156–159.
- 508 Hadfield, J. (2019). MCMCglmm course notes. *Unpubl. Manuscript, Univ. Edinburgh.*
- 509 Hadfield, J.D. (2010). MCMC methods for multi–response generalized linear mixed
510 models: the MCMCglmm R package. *J. Stat. Softw.*, 33, 1–22.
- 511 Harms, K.E., Wright, S.J., Caldero, O. & Herre, E.A. (2000). Pervasive density–dependent
512 recruitment enhances seedling diversity in a tropical forest. *Nature*, 30, 493–495.
- 513 Kalko, E.K. V., Herre, E.A. & Handley Jr., C. (1996). Relation of fig fruit characteristics to
514 fruit–eating bats in the New and Old World tropics. *J. Biogeogr.*, 23, 565–576.
- 515 Leiser–Miller, L., Kaliszewska, Z., Lauterbur, M., Mann, B., Riffell, J. & Santana, S.E.
516 (2020). A fruitful endeavor: scent cues and echolocation behavior used by *Carollia*
517 *castanea* to find fruit. *Integr. Org. Biol.*, 2.
- 518 Maynard, L.D., Ananda, A., Sides, M.F., Burk, H. & Whitehead, S.R. (2019). Dietary

519 resource overlap among three species of frugivorous bat in Costa Rica. *J. Trop.*
520 *Ecol.*, 35, 165–172.

521 Meyers, J.J. & Irschick, D.J. (2015). Does whole-organism performance constrain
522 resource use? A community test with desert lizards. *Biol. J. Linn. Soc.*, 115, 859–
523 868.

524 Nathan, R. & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal , their
525 determinants and consequences for recruitment. *TRENDS Ecol. Evol.*, 15, 278–285.

526 Norconk, M.A., Wright, B.W., Conklin-Brittain, N.L. & Vinyard, C.J. (2009). Mechanical
527 and nutritional properties of food as factors in Platyrrhine dietary adaptations. In:
528 *South American Primates* (eds. Garber, P., Estrada, A., Bicca-Marques, J.C.,
529 Heymann, E.W. & Strier, K.B.). Springer, New York, NY, pp. 279–319.

530 Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using
531 Gibbs sampling. In: *Proceedings of the 3rd international workshop on distributed*
532 *statistical computing*. Vienna, Austria.

533 Pratt, T.K. & Stiles, E.W. (1985). The influence of fruit size and structure on composition
534 of frugivore assemblages in New Guinea. *Biotropica*, 17, 314–321.

535 Rojas, D., Pereira, M.J., Fonseca, C. & Davalos, L.M. (2018). Eating down the food
536 chain: generalism is not an evolutionary dead end for herbivores. *Ecol. Lett.*, 21, 402–
537 410.

538 Salazar, D., Kelm, D.H. & Marquis, R.J. (2013). Directed seed dispersal of *Piper* by
539 *Carollia perspicillata* and its effect. *Ecology*, 94, 2444–2453.

540 Santana, S.E., Dumont, E.R. & Davis, J.L. (2010a). Mechanics of bite force production
541 and its rel to diet in bats. *Funct. Ecol.*, 24, 776–784.

542 Santana, S.E., Dumont, E.R. & Davis, J.L. (2010b). Mechanics of bite force production
543 and its relationship to diet in bats. *Funct. Ecol.*, 24, 776–784.

544 Santana, S.E., Kaliszewska, Z.A., Leiser-Miller, L.B., Lauterbur, M.E., Arbour, J.H.,
545 Dávalos, L.M., *et al.* (2021). Fruit odorants mediate co-specialization in a
546 multispecies plant-animal mutualism. *Proc. R. Soc. B Biol. Sci.*, 288, 20210312.

547 Santana, S.E. & Miller, K. (2016). Extreme postnatal scaling in bat feeding performance: a
548 view of ecomorphology from ontogenetic and macroevolutionary perspectives. *Integr.*
549 *Comp. Biol.*, 56, 1–10.

550 Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H.M. & Böhning-
551 Gaese, K. (2011). Specialization and interaction strength in a tropical plant – frugivore
552 network differ among forest strata. *Ecology*, 92, 26–36.

553 Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, New
554 York.

555 Schluter, D. & Grant, P.R. (1984). Determinants of morphological patterns in communities
556 of Darwin’s finches. *Am. Nat.*, 123, 175–196.

557 Schluter, D., Price, T.D. & Grant, P.R. (1985). Ecological character displacement in
558 Darwin’s finches. *Science (80-.)*, 227, 1056–9.

559 Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *TRENDS*
560 *Ecol. Evol.*, 21, 464–471.

561 Sexton, J.P., Montiel, J., Shay, J.E., Stephens, M.R. & Slatyer, R.A. (2017). Evolution of
562 ecological niche breadth. *Annu. Rev. Ecol. Evol. Syst.*, 48, annurev-ecolsys-110316-
563 023003.

564 Su, Y.-S. & Yajima, M. (2012). R2jags: A Package for running jags from R. *R Packag.*
565 *version 0.03-08*, URL <http://CRAN.R-project.org/package=R2jags>.
566 Thies, W. & Kalko, E.K. (2004). Phenology of neotropical pepper plants (Piperaceae) and
567 their association with their main dispersers, two short-tailed fruit bats,. *Oikos*, 2, 362–
568 376.
569 Thies, W., Kalko, E.K. V. & Schnitzler, H.-U. (1998). The roles of echolocation and
570 olfaction in two Neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea*,
571 feeding on *Piper*. *Behav. Ecol. Sociobiol.*, 42, 397–409.
572 Villalobos-Chaves, D., Padilla-Alvarez, S. & Rodriguez-Herrera, B. (2016). Seed
573 predation by the wrinkle-faced bat *Centurio senex*. A new case of this unusual feeding
574 strategy in Chiroptera. *J. Mammal.*, 97, 726–733.
575 Weinstein, B.G. & Graham, C.H. (2017). Persistent bill and corolla matching despite
576 shifting temporal resources in tropical hummingbird-plant interactions. *Ecol. Lett.*, 20,
577 326–335.
578 Wendeln, M.C., Runkle, J.R. & Kalko, E.K. V. (2000). Nutritional values of 14 fig species
579 and bat feeding preferences in Panama. *Biotropica*, 32, 489–501.
580 Whitehead, S.R., Obando Quesada, M.F. & Bowers, M.D. (2016). Chemical tradeoffs in
581 seed dispersal: defensive metabolites in fruits deter consumption by mutualist bats.
582 *Oikos*, 125, 927–937.
583 Yohe, L.R., Leiser-Miller, L.B., Kaliszewska, Z.A., Donat, P., Santana, S.E. & Davalos,
584 L.M. (2021). Diversity in olfactory receptor repertoires is associated with dietary
585 specialization in a genus of frugivorous bat. *G3 Genes/Genomes/Genetics*, 11,
586 jkab260.
587

588 **Figure Legends**

589

590 **Figure 1.** Headshots of the three sympatric short-tailed fruit bats (*Carollia*) found in our study
591 locality in Costa Rica: (A) *Carollia perspicillata*, (B) *C. sowelli*, and (C) *C. castanea*. (D) *C.*
592 *perspicillata* feeding on *Piper sancti-felicis*. Photo credit: David Villalobos Chaves (A–C) and
593 Susan Whitehead (D).

594

595 **Figure 2.** Parameters (A) richness and (B) diversity calculated as posterior predictive checks
596 of model fit for the relative abundance fractional composition model. Model fit of the
597 generalized joint attribute modeling in predicting *Piper* bat proclivities. The brown histogram
598 in (A) and (B) is the distribution of the observed data and the dashed lines are the 1:1
599 diagonals of the observed values and predictions. (A) Richness represents a predictive
600 posterior check, such that richness is responses predicted that are greater than 0. (B) More
601 diverse “sites” had a better fit, as less diverse “sites” are more rare. (C) Sensitivity of the
602 covariate inputs can be interpreted as the amount of information each input contributes to
603 estimating the model coefficients. The higher the sensitivity, the more informative the
604 covariate to the model.

605

606 **Figure 3.** Posterior distributions of bat species responses for each *Piper* species (*Piper* bat
607 proclivities), ordered by median. Bat species response to *Piper* can be interpreted as the
608 probability of a particular *Carollia* species to show a proclivity towards a particular *Piper*
609 species. Asterisks and black species names refer to *Piper* in which 95% of the highest
610 posterior density intervals did not cross zero, indicating a strong positive or negative
611 response.

612

613 **Figure 4.** Posterior distributions of bat body size trait responses of forearm length for *Piper*
614 species that indicate strong positive or negative responses (from Fig. 3), determined by the
615 entire 95% highest posterior density being entirely above or below zero.