

Towards a functional classification of poorly known tropical insects: The case of rhinoceros beetles (Coleoptera, Dynastinae) in Panama

by Basset, Y., Blažek, P., Souto-Vilarós, D., Vargas, G., Ramírez Silva, J.A., Barrios, H., Perez, F., Bobadilla, R., Lopez, Y., Ctvrtecka, R., Šípek, P., Solís, A., Segar, S.T. and Lamarre, G.P.A.

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1 **Towards a functional classification of poorly known tropical insects:**

2 **The case of rhinoceros beetles (Coleoptera, Dynastinae) in Panama**

3

4 Yves Basset^{1,2,3,4*}, Petr Blažek^{2,3}, Daniel Souto-Vilarós³, Gersey Vargas¹, José Alejandro Ramírez Silva^{1,4},

5 Héctor Barrios⁴, Filonila Perez¹, Ricardo Bobadilla¹, Yacksecari Lopez¹, Richard Ctvrtecka^{2,3}, Petr Šípek⁵,

6 Angel Solís⁶, Simon T. Segar⁷ & Greg P. A. Lamarre^{1,3}

7

8

9 ¹ForestGEO, Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panamá.

10 ²Faculty of Science, University of South Bohemia, 370 05 Ceske Budejovice, Czech Republic.

11 ³Biology Centre of the Czech Academy of Sciences, Institute of Entomology, 370 05 Ceske Budejovice, Czech
12 Republic.

13 ⁴Maestria de Entomologia, Universidad de Panamá, 080814 Panama City, Republic of Panama.

14 ⁵Department of Zoology, Faculty of Science, Charles University, 128 00 Praha 2, Czech Republic.

15 ⁶BioAlfa Barcoding Project, Santo Domingo de Heredia, Heredia, Costa Rica.

16 ⁷Agriculture & Environment Department, Harper Adams University, Newport, Shropshire, TF10 8NB, UK.

17

18 *Correspondence: Yves Basset, ForestGEO, Smithsonian Tropical Research Institute, Apartado 0843-03092,
19 Balboa, Ancon, Panamá. E-mail: bassety@si.edu.

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22

23 ORCID numbers:

24

25 Yves Basset: 0000-0002-1942-5717

26 Petr Blažek: 0000-0002-0901-4578

27 Gersey Vargas: 0000-0002-5625-8284

28 José Alejandro Ramírez Silva: 0000-0001-6799-5207

29 Daniel Souto-Vilarós: 0000-0002-8803-5173

30 Héctor Barrios: 0000-0002-0542-1731

- 31 Filonila Perez: NA
- 32 Ricardo Bobadilla: NA
- 33 Yacksecari Lopez: NA
- 34 Richard Ctvrtecka: 0000-0002-0599-6850
- 35 Petr Šipek: 0000-0002-2769-2217
- 36 Angel Solís: 0000-0001-8622-4555
- 37 Simon Segar: 0000-0001-6621-9409
- 38 Greg P.A. Lamarre: 0000-0002-7645-985X
- 39
- 40

41 **Abstract**

42

43 1. The population dynamics of most tropical insects are unknown and long-term monitoring programs are
44 urgently needed to evaluate a possible insect decline in the tropics. In this context, functional groups
45 can be used effectively to summarize time-series for species-rich taxa. Neotropical dung beetles have
46 often been catalogued into functional groups, but close relatives also of ecological significance, the
47 Dynastinae, are awaiting such a classification.

48 2. Here we examine the functional groups of Dynastinae at the regional (Panama: 147 species) and local
49 (Barro Colorado Island, BCI: 56 species) scales. Our optimum classification of Panamanian species
50 distinguished five groups, one of which is probably artificial and accounts for species ecologically
51 poorly known.

52 3. Ecological attributes or species traits mainly influencing the delineation of groups were geographical
53 distribution, body length, seasonal aggregation, larval food and whether the adult may be present in
54 decaying wood.

55 4. Our analyses indicated that (1) missing trait values and the high percentage of “cryptic” species (25%)
56 influenced the delineation of groups; (2) the dendrogram similarity of functional groups vs.
57 phylogenetic tree was low, although some traits were phylogenetically conserved; and (4) the overall
58 structure of functional groups was conserved when comparing regional and local data, suggesting no
59 drastic loss of functional groups locally.

60 5. To proceed with the functional classification of poorly known tropical insects, we recommend a
61 cautious selection of traits a priori, inclusion of “cryptic” species recognized by DNA barcoding, and
62 building phylogenies which may allow a careful taxonomic imputation to complete species-traits
63 matrices.

64

65 **Key words:** Barro Colorado Island, cryptic species, DNA barcoding, pollinator, species traits.

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71 **Introduction**

72

73 In recent years there have been alarming reports concerning insect decline, particularly in temperate countries
74 (Hallmann *et al.*, 2017; Sánchez-Bayo & Wyckhuys, 2019; Wagner *et al.*, 2021). This attrition has been
75 attributed mainly to habitat loss, pesticide use and climate change (Sánchez-Bayo & Wyckhuys, 2019). In this
76 context, Basset and Lamarre (2019) stressed that the population dynamics of most tropical insects were
77 unknown and that we urgently need accurate long-term monitoring programs to evaluate a possible insect
78 decline in the tropics. The situation is potentially of great concern because ectothermic organisms such as
79 insects are at great risk of extinction in the tropics due to their limited tolerance to a warmer world (Deutsch *et*
80 *al.*, 2008; Kaspari *et al.*, 2014). To compound the challenge, the taxonomy of most tropical insects is poorly
81 known, and local species richness can easily be an order of magnitude higher than in temperate countries.

82

83 In these conditions, summarizing insect population dynamics for that many species represents a challenge.

84 Moreover, the public and decision makers are often little interested in insects (Basset & Lamarre, 2019).

85 Climate change may generate similar responses among species with similar attributes (species traits), but not
86 necessarily sharing a common phylogeny. Thus, interpreting species response to climate change may be easier
87 when considering functional groups, characterized by species traits, than a more traditional species-specific
88 approach (Violle *et al.*, 2007; Pau *et al.*, 2011). In this study, we seek to delineate functional groups for a local
89 assemblage of tropical insects with the subsequent aim of forecasting their population dynamics.

90

91 Functional traits are defined as measurable characteristics associated with species fitness and ecological function
92 (Wong *et al.*, 2019). This represents a powerful approach for plants (e.g., Körner, 1994) and vertebrates (e.g.,
93 Luck *et al.*, 2012). For invertebrates, the use of functional groups is well established in marine and aquatic
94 communities (Usseglio-Polatera *et al.*, 2000) and in soil assemblages (Pey *et al.*, 2014), but the concept is
95 relatively new for other terrestrial invertebrates (Májeková *et al.*, 2016; Wong *et al.*, 2019). For insects the
96 concept of functional groups is particularly popular for taxa whose ecology is relatively well documented, such
97 as butterflies (Eskildsen *et al.*, 2015), some moths (Slade *et al.*, 2013), ants (Parr *et al.*, 2017), and beetles such
98 as carabids (Pakeman *et al.*, 2014) or dung beetles (Audino *et al.*, 2014). However, since the ecology of tropical
99 insects is not as well-known when compared to temperate taxa, discerning functional groups of tropical insects
100 is often challenging (Basset *et al.*, 2017). Many species traits may be missing for tropical species thus limiting

101 the delineation of functional groups or estimation of functional diversity (Májeková *et al.*, 2016). Another
102 challenge is the high occurrence of cryptic species in tropical assemblages, which may complicate analyses as
103 many traits may not be available for these species (Hebert *et al.*, 2004). In the tropics, dung beetles
104 (Scarabaeinae and related taxa) represent good examples of well-studied insect assemblages using the concept
105 of functional groups (e.g., Slade *et al.*, 2007; Audino *et al.*, 2014; Gagic *et al.*, 2015; Raine *et al.*, 2018). In
106 comparison, their close relatives, the Dynastinae, have been comparatively far less studied. Here, we examine
107 the functional groups of Dynastinae within a tropical country, Panama. To the best of our knowledge, this
108 represents the first attempt towards a functional classification of rhinoceros beetles.

109

110 Rhinoceros beetles (Coleoptera: Scarabaeidae: Dynastinae) include ca. 800 species in the Neotropics (Ratcliffe,
111 2003). The taxonomy of the subfamily is reasonably well-known, and many species are rather popular as adults
112 are sizeable and bear cephalic horns. These characteristics make them ideal subjects for ecological and
113 conservation studies. Adults of nearly all species are nocturnal or crepuscular, and most are readily attracted to
114 lights at night, further making them ideal target taxa for long-term monitoring. Larvae are primarily
115 saprophagous or phytophagous and live in the soil or in decaying logs where they are crucial in nutrient cycling
116 by fragmenting large amounts of wood (Ratcliffe & Cave, 2008). Other species may be plague of crops, at the
117 larval or adult stage (Moore & Jameson, 2013). Adults of the species-rich genus *Cyclocephala* are floral visitors
118 of some plant families in the core eudicots (such as Araceae and Annonaceae) and can have a destructive impact
119 by damaging flowers or a beneficial impact by providing pollination (Moore & Jameson, 2013; Moore *et al.*,
120 2018). Some of these relationships are mutualistic, where the visitor in the floral cavity in exchange of
121 pollination services is rewarded with mating site, food, and floral heat, allowing beetles to remain active during
122 longer periods of time and pre-flight warm-up (Seymour *et al.*, 2009). Since floral heat appears to be an
123 important reward, increasing ambient temperatures due to global warming may disrupt visiting patterns of these
124 beetles, thus preventing the effective pollination of associated plant species (Seymour *et al.*, 2009).

125

126 The Forest Global Earth Observatory (ForestGEO) is a network of 72 permanent vegetation plots (mostly in the
127 tropics) and dedicated mainly to monitor forest dynamics over time (Anderson-Teixeira *et al.*, 2015). In 2009,
128 the ForestGEO Arthropod Initiative started long-term monitoring of selected insect taxa, including Dynastinae,
129 at the ForestGEO site of Barro Colorado Island (BCI) in Panama (Lamarre *et al.*, 2020). This program aims at

130 detecting long-term changes in the abundance and composition of focal assemblages representing a variety of
131 phylogenies and life histories.

132

133 In this contribution we take advantage of (a) an exceptional taxonomic and ecological coverage of all
134 Dynastinae species in Panama (Ratcliffe, 2003), a compilation rarely equaled for any insect group in the tropics;
135 and (b) ten years of monitoring data for BCI Dynastinae to delineate and discuss functional groups of this taxon
136 in Panama and on BCI. This represents the first step of an analytical approach analyzing the long-term
137 population dynamics of Dynastinae on BCI, summarizing the information either by clades and/or functional
138 groups (Eskildsen *et al.*, 2015; Basset *et al.*, 2017). Here, our sets of specific questions are mostly
139 methodological (1-4 below), but also have ecological implications (5):

140

- 141 1. Which of the species traits are most important (and easy to measure or estimate) to explain the
142 delineation of functional groups in Panamanian Dynastinae? Which traits should be captured if limited
143 time and funding are available?
- 144 2. Once traits are selected, what is the influence of missing traits in the species trait matrix for the
145 Dynastinae assemblage in Panama? In particular, is the delineation of functional groups very different
146 when considering many species with many missing traits or a few species with all traits well
147 documented?
- 148 3. Does the occurrence of cryptic or unidentified species have any impact on the delineation of functional
149 groups locally (Barro Colorado Island) or can we safely ignore these species for this purpose?
- 150 4. Are functional groups relatively independent from phylogeny? Could we use phylogeny as a surrogate
151 for functional groups? Are species traits measured phylogenetically conserved? If yes, could these traits
152 help in refining matrices of species traits?
- 153 5. Which functional groups may be missing or underrepresented when we compare Dynastinae
154 assemblages between the whole country of Panama and a local subset of this regional dataset, such as
155 BCI? Can we explain the possible deficit of functionality at the local scale?

156

157 **Material and methods**

158

159 *Study site and acquisition of data*

160
161 Local Dynastinae assemblages were surveyed on Barro Colorado Island (9.15°N, 79.85°W; 120–160 m asl) in
162 Panama, which receives an average annual rainfall of 2,662 mm, with an annual average daily maximum and
163 minimum air temperatures of 31.0 °C and 23.6 °C, respectively (Anderson-Teixeira *et al.*, 2015). The 1,542 ha
164 island is covered with lowland tropical forest and was created around 1910, when the Chagres River was
165 dammed to fill the Panama Canal. Dynastinae were collected within and near the 50 ha ForestGEO plot, which
166 is thoroughly described in Anderson-Teixeira *et al.* (2015). Compilation of species for the whole country of
167 Panama was obtained from Ratcliffe (2003; 37,716 specimens recorded). To compile species occurring on BCI
168 we considered again Ratcliffe (2003), with additions from the database Symbiota (Symbiota, 2021; 444 records
169 for BCI) and the data from the ForestGEO Arthropod Initiative (3,231 records for BCI). Most specimens (89%)
170 collected on BCI by the ForestGEO Arthropod Initiative were obtained at 10W black light traps during 2009-
171 2018 (Appendices S1, S2), as nearly all adult Dynastinae are nocturnal (Ratcliffe, 2003). The rest of specimens
172 were manually collected on BCI in various situations.

173
174 Specimens were identified with keys provided by Ratcliffe (2003). Additionally, DNA Cytochrome c oxidase
175 subunit I (COI, “DNA barcode”) sequences were obtained from ForestGEO specimens collected in Panama and
176 INBio specimens collected in Costa Rica by AS and colleagues. Specimens were sequenced at the Biodiversity
177 Institute of Ontario, University of Guelph, using methods described in Wilson (2012). In total, we obtained 209
178 sequences from 292 Panamanian specimens, and 459 sequences from 526 Costa Rican specimens, which were
179 deposited in project BCIDY and dataset DS-CRPADYNA of the database of the Barcode of Life Data System
180 (<http://www.barcodinglife.org/index.php>). Molecular data were used to confirm identifications based on
181 morphology and to examine the possible occurrence of cryptic species. All species delineated by molecular data
182 were referred to by their Barcode Index Number (BIN), which can be used as a proxy taxonomic unit
183 (Ratnasingham & Hebert, 2013). Morphospecies not yet formally described (notably in Ratcliffe, 2003, 2011)
184 but with distinct BINs are termed “cryptic” species, even if in some cases they can be distinguished
185 morphologically from other species. For sake of brevity, we extend the definition of “cryptic species” in this
186 study to all morphospecies that do not have a proper Latin binomial (i.e., morphospecies that could not be
187 identified using Ratcliffe, 2003, 2011 and lacking sequences). Specimens collected on BCI were vouchered in
188 the collection of the ForestGEO Arthropod Initiative at the Smithsonian Tropical Research Institute in Panama.
189

190 *Species traits*

191

192 Arthropods and plants differ in many life-history traits, which are often far better refined in the latter than in the
193 former (Wong *et al.*, 2019). Hence, while species traits are narrowly defined for plants (e.g., Violle *et al.*, 2007),
194 they often include wider and broader concepts for terrestrial arthropods, including behavioral traits and
195 ecological preferences/ranges, such as micro-habitat specialization, matrix use or biogeographical distribution
196 (Thomas, 1991; Koh *et al.*, 2004; Barbaro & Van Halder, 2009; Slade *et al.*, 2013; Pey *et al.*, 2014; Wong *et al.*,
197 2019). We considered a total of 31 functional and ecological attributes, including ecological preferences
198 (hereafter “species traits” for sake of brevity). We selected variables that may potentially affect the population
199 dynamics of species with respect to global warming. We emphasize that including different traits, if available,
200 may result in a better characterization of, for example, ecological services. The traits were distributed in six
201 categories that summarized for each species spatial and temporal distributions, adult and larval ecology,
202 morphometrical traits and color lightness (Table 1). Our trait variables include most of the traits advocated for
203 beetles by Fountain-Jones *et al.* (2015), except for variables related to voltinism and breeding season, which
204 were unknown for most species. Details about the measurement of traits are described in Appendix S1.

205

206 *Final selection of species traits*

207

208 We followed the rationale of Petchey and Gaston (2006) and Villéger *et al.* (2008) who argue that species traits
209 should be selected *a priori* for the delineation of functional groups. The need to describe each function or
210 ecological preference should lead the selection of the traits, while avoiding redundancy between traits (i.e.,
211 trivial correlations). If traits are carefully selected, then any correlation between traits in the species–trait matrix
212 may be considered a relevant aspect of species distribution in functional trait space (Villéger *et al.*, 2008). Thus,
213 we selected traits so that relevant ecological aspects were represented and trivial correlations were avoided. We
214 retained at least one variable in each of our six trait categories, with different rationale for initial selection
215 (Table 1). Further, trait distributions were visually checked, and highly positively skewed variables were \log_{10} -
216 transformed to reduce the leverage of outliers, following the recommendation of Májeková *et al.* (2016) (Table
217 1). Then, the relationships between all variables were explored using a matrix of Pearson correlations
218 (categorical variables were converted to dummy variables to enable this comparison). We removed variables

219 either if the variable was difficult to measure and/or when it was highly correlated ($r > 0.7$) with other variables.
220 The final selection of traits is further explained in Appendix S3.

221

222 *Delineation of functional groups*

223

224 We considered different matrices of species-traits, as indicated below (methods to answer Questions 1-5). For
225 each matrix, we first calculated a species dissimilarity matrix using the Gower metric, which handles a mixture
226 of numeric and categorical traits (Gower 1971). Missing values did not require any special treatment as
227 distances were calculated based on available trait values in each species pair. Variables were weighted to
228 balance their influence on the dissimilarity matrix, accounting for different distributions, using an iterative
229 approach (Pavoine *et al.*, 2009; de Bello *et al.*, 2021). Resulting weights, calculated with all Panamanian
230 species, are indicated in Table S1, and were used with all matrices.

231

232 Then, hierarchical agglomerative clustering using Ward's method (function *agnes*; Murtagh & Legendre, 2014)
233 was performed on the species dissimilarity matrix. The functional tree obtained was pruned to form distinct
234 clusters according to three methods: (a) the Kelley-Gardner-Sutcliffe penalty (lower penalties are better; Kelley
235 *et al.*, 1996); (b) plots of silhouette width (larger silhouette widths are better; Rousseeuw, 1987); and (c) matrix
236 (Mantel) correlations between the distance matrix and binary matrices representing partitions (higher
237 correlations are better; Borcard *et al.*, 2011). The same number of clusters identified as optimal for the complete
238 dataset was used also in subsequent functional trees. Functional groups were interpreted by (1) graphical
239 summary of trait values in each group; (2) an ordination diagram of a distance-based redundancy analysis
240 (dbRDA) to visualize the main axes of trait variation and the distinction of the functional groups in the
241 multivariate space; and (3) species assignment to the clusters. A multivariate analysis of variance (MANOVA)
242 was also computed to get an overall r^2 characterizing how much trait variation was captured by the functional
243 groups (permutation test with 999 permutations). All analyses were carried out in R 3.6.2 (R Core Team, 2020),
244 using the packages 'cluster' (Maechler *et al.*, 2019), 'maptree' (White and Gramacy, 2012), 'vegan' (Oksanen *et*
245 *al.*, 2020) and 'corrplot' (Wei and Simko, 2017).

246 *Question 1: importance of traits*

247

248 To answer this question, we used the full matrix of species present in Panama (n=147) with the 11 traits
249 ultimately selected (see results). To evaluate the importance of each trait we considered (1) the graphical
250 summary of trait values in each group and Kruskal-Wallis tests and Chi-square test testing for differences in
251 numerical and categorical variables, respectively, among groups; and (2) the squared correlation coefficients
252 between trait values and constrained axes of the redundancy analysis (dbRDA), as obtained with the function
253 *envfit* of ‘vegan’ (Oksanen *et al.*, 2020).

254

255 *Question 2: missing trait values*

256

257 We first plotted a histogram of the number of available trait values per species (Fig. S1). Out of the 11 traits
258 eventually selected (see results), less than half of the Panamanian species (61 species) had between 8 and 11
259 trait values measured (11 species with 11 trait values measured, 7.5% of the total number of species), whereas
260 most species had only 3 to 7 trait values measured. We selected species that had more trait values available than
261 the mode of the distribution in Fig. S1 (7 trait values) as our first matrix. We compared the delineation of
262 functional groups obtained with this matrix (n=61, 85.0% of available values) with a second matrix represented
263 by all species occurring in Panama (n=147, 68.9% of available values). This comparison tested whether results
264 obtained with data including missing values were similar to results obtained with fewer but “cleaner” data.

265

266 The resulting dendrograms obtained with the two matrices were compared using several methods. (1) Visually,
267 we drew tanglegrams with the R package ‘dendextend’ (Galili, 2015). (2) With the same R package, we
268 calculated the cophenetic correlation between the two hierarchical classifications (trees). This index measures
269 how good the pairwise distances are preserved between dendrograms and compares complete trees with their
270 hierarchy and fine structure. The value can range between -1 to 1. Negative values indicate negative association
271 of trees (-1 is absolute mismatch), 0 no association (random match) and positive values indicate positive
272 association (+1 is perfect match; Galili, 2015). (3) We also calculated Cramer’s V (Cramer, 1946) to compare
273 the final classification of species. Unlike cophenetic correlation, Cramer’s V compares only the resulting
274 functional groups with no hierarchy, using contingency table of two factors. It is a measure of association
275 between two nominal variables, ranging between 0 and +1. A Cramer’s V in the range of [0, 0.3] is considered
276 as weak, [0.3,0.7] as medium and > 0.7 as strong (Signorell *et al.*, 2021). For these various comparisons, trees or
277 matrices were pruned to include only species present in both trees, thus testing the congruence between the

278 assignment to functional groups of these species between the two trees. A G test was used to compare the
279 species counts in the functional groups between the two classifications (functional group \times matrix type), testing
280 whether the species loss in the matrix with fewer species was proportional to each functional group of the main
281 classification.

282

283 *Question 3: influence of cryptic species*

284

285 We compared the following species-traits matrices: (1) all species present on BCI (n=56) and (2) all species
286 present on BCI excluding cryptic species (listed in Appendix S2; n=46). To compare the congruence between
287 the resulting classifications, we used the same methods as described in Question 2.

288

289 *Question 4: comparison of functional groups and phylogeny*

290

291 Cytochrome Oxidase subunit I (COI) sequences from the BOLD dataset DS-CRPADYNA were manually
292 inspected to include only specimens with BIN. To increase coverage and resolution of our phylogeny, we
293 included sequences from Costa Rican species, available in the GenBank database. A phylogenetic tree was built
294 with these data as explained in Appendix S1. To evaluate whether some species traits were phylogenetically
295 conserved, the phylogeny was pruned to include only Panamanian species with available traits (104 species),
296 using the *match.phylo.comm* command implemented in the ‘picante’ package in R (Kembel *et al.*, 2010). We
297 then used the ‘phyloSignal’ R package (Keck *et al.*, 2016) to test for phylogenetic signal on continuous traits
298 based on a variety of indices within the *phyloSignal* function of the same package (such as Abouheif’s C_{mean} and
299 Pagel’s λ), as well as calculated on randomly simulated values along the phylogeny and trait simulation under a
300 Brownian motion model of evolution. Although Pagel’s λ is based on autocorrelation, sensitivity analyses have
301 suggested both these indices to be appropriate methods for testing for phylogenetic signal (Münkenmüller *et al.*,
302 2012). We calculated the Local Indicator of Phylogenetic Association (LIPA; based on local Moran’s I) to
303 identify regions of the phylogeny where the signal was located. To test for phylogenetic clustering in categorical
304 traits, we calculated the standardized effect size of mean pairwise phylogenetic distance and the standardized
305 effect size of the mean nearest taxon based on cophenetic distance matrices using the functions *ses.mpd* and
306 *ses.mntd*, respectively, implemented in the R package ‘picante’ (Kembel *et al.* 2010; see Appendix S1).
307 Eventually, we compared the functional dendrogram based on the trait matrix of all Panamanian species to the

308 phylogenetic tree of Panamanian species, using a tanglegram and cophenetic correlation. Since one functional
309 group was recognized as being artificial (see results), we drew the tanglegram with and without the artificial
310 group.

311

312 *Question 5: functional groups in Panama and BCI*

313

314 Using the methods indicated in Question 2, we contrasted the matrix species-traits including all species present
315 in Panama (n=147) with that including all species present on BCI (n=56). Eventually, to appreciate the relative
316 importance of issues encapsulated in Questions 2-5 for delineating functional groups, we rank the four
317 tanglegram pairs according to their similarity.

318

319 **Results**

320

321 Our compilation indicated that at least 147 species are present in Panama and 56 species on BCI (38.1% of the
322 Panamanian fauna). Out of the BCI species, 32 were collected by light traps of the ForestGEO Arthropod
323 Initiative during the period 2009-2018. Appendix S2 details all species, along with their species traits. This
324 includes 133 and 46 species with identification at the species level in Panama and on BCI, respectively. We
325 recorded 14 cryptic species, including 10 with BINs. In total we obtained 105 BINs from Panama, representing
326 71.4% of the Panamanian fauna and 78.5% of the local fauna on BCI. The most common species in Panama as
327 recorded by Ratcliffe (2003) were *Cyclocephala lunata*, *Aspidolea singularis* and *C. melanocephala*, whereas
328 on BCI light trap records indicated that *C. fulgurata*, *C. brevis* and *C. carbonaria* were most common.

329

330 *Selection of species traits*

331

332 Out of the 31 traits that we initially considered, 11 traits were retained for final analyses (Fig. S2). The rationale
333 for excluding or retaining each variable is detailed in Appendix S3. The variables retained were: elevational
334 range, spatial aggregation and number of provinces in the category spatial distribution; seasonal aggregation in
335 the category temporal distribution; host-plant specialization at the family level and whether associated with
336 decaying wood in the category adult ecology; larval food in the category larval ecology; body length (from
337 Ratcliffe, 2003), variation in body surface and wing loading in the category morphometry; and variation in

338 lightness in the category lightness (Table 1). The correlation matrices between all variables and variables
339 retained for the analyses are presented in Fig. S2.

340

341 *Importance of traits and functional groups*

342

343 When considering all Panamanian species, our analyses indicated that the optimal number of clusters was five
344 (Fig. S3). As often happens, analyses may select a low number of clusters as being optimal ($k < 5$), but this
345 trivial solution is not interesting in ecological terms (Borcard *et al.*, 2011). Conversely, a high number of
346 clusters ($k > 13$) is also difficult to interpret. The Kelley–Gardner–Sutcliffe penalty and Mantel correlations
347 designated five as the optimal cluster number. The silhouette plots also suggested that this was a good solution
348 when low numbers of clusters were dismissed (Fig. S3). The assignment of species to functional groups is
349 detailed in Appendix 2 and the overall dendrogram for all Panamanian species is drawn in Fig. 1. To reveal
350 which traits underlie this classification (Question 1), the distributions of traits per functional groups are
351 indicated in Fig. 2 and 3. All selected traits were significantly different among functional groups (Kruskal-
352 Wallis or Chi-square tests, usually $P < 0.001$), apart from wing loading and CV of lightness (Fig. 2). This
353 suggest that all but the last two traits are important for the delineation of functional groups. The MANOVA
354 captured 53.1% of the variation in the original matrix of selected traits (adjusted $r^2 = 0.518$). The traits with the
355 highest squared correlation coefficients with dbRDA axes were, for the whole model: number of provinces,
356 body length, seasonal aggregation and larval food; for Axis 1: body length, larval food, adult presence in
357 decaying wood; for Axis 2: number of provinces; for Axis 3: seasonal aggregation; and for Axis 4: adult
358 presence in decaying wood and larval food (Fig. 3, Table S2).

359

360 These results suggest the following interpretation of Functional Groups 1-5 (Figs 2, 3). Functional Group 1
361 includes mostly small species with a wide distribution (number of provinces), often aggregated seasonally and
362 spatially with a mixed diet as larval food. They recruit mostly from Cyclocephalini (genus *Cyclocephala*) and
363 Pentodontini. Group 2 also often includes small species of *Cyclocephala*, often widely distributed (number of
364 provinces, elevational range) with a high wing loading and mixed diet, but with low seasonal aggregation. The
365 larval habitat for most species in Groups 1 and 2 is soil. Group 3 include large species with adults present in
366 decaying wood, often with larvae feeding on rotting wood, not so widely distributed (number of provinces) and
367 often recruiting from Phileurini. Group 4 includes large species recruiting from tribes Dynastini, Oryctini and

368 Phileurini, with many species feeding of rotting wood or dead organic debris. Group 5 include medium-sized
 369 species from a variety of tribes but often from Cyclocephalini, often with high seasonal aggregation and high
 370 endemism (number of provinces = 1). The proportion of species with low number of traits measured is very
 371 high in this group (83.3%, compared to 43-53% in the other groups) and 11 out of 14 cryptic species belong to
 372 this group. Hence Group 5 may combine mainly species that are ecologically poorly known. The percentages of
 373 species included in each group to the total number of species in Panama were 29.9%, 14.3%, 11.6%, 11.6% and
 374 32.7% for Groups 1-5, respectively. Adult pollinators (only genera *Cyclocephala* and *Aspidolea*; 68 confirmed
 375 species) recruited from functional groups 1 (44.1% of species within that group), 2 (20.6%) and 5 (35.3%;
 376 Appendix S2).

377

378 *Questions 2-5: missing traits, cryptic species, relation with phylogeny and comparison Panama-BCI*

379

380 The four tanglegram pairs relevant to Questions 2-5 are drawn in Fig. 4. Although perfect match did not occur,
 381 correlations between tanglegram pairs were reasonably strong, except for the comparison involving functional
 382 groups and phylogenetic tree (Fig. 4c; in this case only the cophenetic correlation could be calculated). The
 383 strongest correlations between dendrogram pairs in terms of correlation structure and congruence of the
 384 classification of species could be ranked as follows: comparison Panamanian species vs. BCI species (r
 385 cophenetic / Cramer = $0.80 / 0.70$) > comparison Panamanian species vs. species with most traits ($0.62 / 0.75$) \approx
 386 comparison BCI species vs. BCI species without cryptic species ($0.57 / 0.80$) > comparison functional groups all
 387 Panamanian species vs. their phylogenetic tree ($0.40 / NA$). Regarding the later comparison, removing the
 388 artificial functional Group 5 improved the cophenetic correlation between functional groups and phylogeny
 389 (compare Fig. 4c, without Group 5, with Fig. S4, including Group 5, which has a cophenetic correlation of
 390 0.22).

391

392 The distribution of the number of species with most traits measured within functional groups was not
 393 significantly different from the original distribution of all Panamanian species within functional groups (G test,
 394 $G = 9.32$, $P = 0.053$). The only slight difference was the different proportion of species in Group 5, as indicated
 395 previously. On BCI, the distribution of the number of species within functional groups that were not cryptic was
 396 not significantly different from that of all BCI species ($G = 2.71$, $P = 0.609$).

397

398 The COI phylogeny is indicated in Fig. 5 and a pruned phylogeny displaying only Panamanian species for
399 which traits were measured is presented in Fig. S5. Phylogenetic signal was present in some of the analyzed
400 traits. Body length and variation in body surface showed significant phylogenetic signal when calculated with
401 Abouheif's C_{mean} and Pagel's λ , while spatial aggregation showed significant signal when calculated with
402 Abouheif's C_{mean} (Tables S3, S4). The LIPA analysis, based on local Moran's I , indicated the location of the
403 signal along the phylogeny (Fig. S6). Phylogenetic signals were present for a few categorical variables and their
404 states, notably whether the larva lives in soil or insect nests, whether it feeds on roots or has a mixed regime,
405 and whether the adult is pollinator or is absent in decaying wood (Table S4).

406

407 The distribution of the number of species within functional groups was not significantly different when
408 comparing all Panamanian species with BCI species ($G = 1.57$, $P = 0.814$), although there was a relatively low
409 proportion of species included in functional Group 4 (7.1%) on BCI when compared with the original
410 distribution of all Panamanian species (11.6%). The proportion of pollinator species to the total number of
411 species was also similar on BCI to that for the whole country of Panama (Fisher exact test, $P = 0.422$).

412

413 **Discussion**

414

415 We determined 31 traits for the 147 species of Dynastinae known to occur in Panama. Local species richness on
416 BCI, as collected with light traps (32 species), appears similar to local faunas surveyed with the same method in
417 the Neotropics (e.g., Andreezze, 2001; García-López *et al.*, 2012). However, we note a high local alpha
418 diversity when comparing the 1,500 ha BCI to the whole country of Panama (38% of Panamanian species
419 present on BCI). High local diversity has been noted for various insect groups in the tropics, such as butterflies
420 (33%, Borneo, Orr & Haeuser, 1996; 40%, Panama, Basset *et al.*, 2015), Flatidae (22%, Papua New Guinea,
421 Novotny & Missa, 2000), or ants (48%, Costa Rica, Longino *et al.*, 2002).

422

423 After careful selection, we used 11 traits to delineate five functional groups among the Panamanian species. The
424 important traits that influenced the delineation of these groups were number of provinces, body length, seasonal
425 aggregation, larval food and whether the adult may be present in decaying wood. The five functional groups
426 were interpreted as indicated in the results section (section "Importance of traits and functional groups"). We
427 can tentatively link the four first groups to the following ecosystem services: **Group 1**: mostly saprophagous

428 (more rarely rhizophagous) in soil as larvae (soil formation), often pollinators as adults; **Group 2**: mostly
429 saprophagous in soil as larvae (soil formation); **Group 3**: mostly saproxyllic; **Group 4**: decomposers of a variety
430 of substrates. The last group may represent more a convenient category than a formal functional group and we
431 will refrain giving much weight to the ecological interpretation of **Group 5**.

432

433 Only a handful of insect groups are sufficiently well known in Panama so that reasonable matrices of species-
434 traits can be collated, for example Odonata (Donnelly, 1992), Tettigoniidae (Nickle, 1992), Passalidae
435 (Schuster, 2006), Euglossini (Roubik & Hanson, 2004), Formicidae (Antweb, 2021) and Dynastinae (Ratcliffe,
436 2003), the subject of this study. Despite the information available on Dynastinae in Panama (Ratcliffe, 2003),
437 the matrix of 11 selected traits included 31% of missing cells and only 7.5% of Panamanian species had all 11
438 trait values. Thus, a relevant completely filled trait matrix does not exist and it is difficult to discuss cogently the
439 effect of missing traits. Imputation of traits to fill the matrix is possible (Penone *et al.*, 2014), but with unknown
440 effects on the delineation of functional groups in the absence of a reference matrix (but see below the discussion
441 on the relation between functional groups and phylogeny). Measuring intra-specific trait variation (e.g., Didham
442 *et al.* 2016; Raine *et al.*, 2018) represented another difficulty in our study, since many species were rare (a third
443 of species collected at light on BCI included only 5 specimens or less). We deliberately did not include local
444 abundance as trait in our input matrices because we want to summarize elsewhere patterns of Dynastinae
445 population dynamics with specific reference to functional groups and therefore want to avoid circular reasoning.
446 This is a distinct situation than comparing the distribution of functional groups among locations. In this case, it
447 is advisable to include abundance as weight for functional groups (Májeková *et al.*, 2016).

448

449 To answer Question 1, our analyses suggest that variables accounting for geographical distribution (number of
450 Panamanian provinces), body length, seasonal aggregation, larval food and whether the adult may be
451 encountered in decaying wood may represent traits (or ecological preferences) that are important to assign
452 species of Panamanian Dynastinae into functional groups. This is supported by (a) Kruskal-Wallis tests of traits
453 among functional groups; (b) squared correlation coefficients between trait values and constrained axes of the
454 redundancy analysis; and (c) the relatively high proportion of variation in the raw species-trait matrix (> 50%)
455 which is explained by the functional groups delineated by these traits. The first three variables are easy to
456 determine whereas the last two are often missing for many species. Geographical distribution (regional
457 occupancy) represents a surrogate for ecological valence, dispersal ability and commonness (Gaston, 2011). The

458 number of provinces in which the species was collected proved to be an interesting variable, relevant to country-
459 level. A larger and finer scale, encompassing the Neotropics, would be even more informative, but is currently
460 unavailable for Dynastinae, because of poor sampling effort (Ratcliffe, 2003). Insect body size represents a
461 crucial trait, linked to dispersal ability, life span, and the amount and composition of resources used (e.g.,
462 Greenleaf *et al.*, 2007; Stevens *et al.*, 2012; Fountain-Jones *et al.*, 2015; Philpott *et al.*, 2019). Therefore, it is
463 not surprising to observe that body size was important in delineating functional groups, given that there was a
464 huge variation in this trait (e.g., the largest species, *Megasoma elephas*, is 8.3 times larger than the smallest
465 species, *Cyclocephala ovulum*; Appendix S2). Seasonal aggregation is a surrogate for adult seasonal range and
466 seasonality, which are crucial variables affecting adult insect populations in the tropics (Wolda, 1992). Further,
467 many *Cyclocephala* species have evolved flight periods aligned with the flowering periods of their host plants
468 (Maia *et al.*, 2010). Since most monitoring programs need seasonal and spatial replicates to assess the
469 detectability of species (Kéry & Royle, 2008), seasonal aggregation maybe easy to assess. Larval food and
470 whether the adult may be encountered in decaying wood were surprisingly not well correlated (Fig. S2) and
471 were amongst the most difficult variables to determine in this study. We note that the following traits would be
472 interesting for delineating better functional groups in Dynastinae (Fountain-Jones *et al.*, 2015; Moretti *et al.*,
473 2017; Brousseau *et al.*, 2018): clutch size, life span, voltinism and thermal tolerance. However, none of these
474 variables are likely to be quantified for more than a handful of species, emphasizing the poor ecological
475 knowledge of most tropical insects.

476

477 Regarding Question 2, a comparison of dendrograms of functional groups for all Panamanian species (with
478 many missing traits) against species ecologically better known (with most traits determined) indicated that this
479 analysis could be ranked second or third in terms of similarity between all the dendrogram pairs considered.
480 Missing traits do influence the delineation of functional groups, as evidenced by the tanglegram (Fig. 4a). Still,
481 species misclassification was not as severe as in other comparisons (see below). In other words, traits from
482 ecologically well-known and widely distributed species may influence the delineation of functional groups,
483 resulting in a rather dissimilar classification from that obtained with a matrix of many species with only a few
484 traits measured. Which strategy may be best? Inclusion of many or few species? Simply arguing that data should
485 be as representative as possible of the study system, we advise to (a) include as many species as possible
486 (Májeková *et al.*, 2016); (b) use the Gower metric, which handles missing values without the need for
487 imputations (Gower, 1971), to compute the dissimilarity matrix; and (c) identify potential artificial clusters of

488 poorly known species, such as in this study Group 5. These clusters can later be ignored or down weighted when
489 interpreting the results. A variable accounting for the level of ecological knowledge of each species may help
490 identifying artificial clusters. This variable may be qualitative or quantitative (e.g., the number of citations of the
491 species in ecological literature). Since a few traits can nevertheless be easily measured (e.g., body size) and
492 likely to be available for all species, this represents a better strategy than dismissing many species simply
493 because they do not have sufficient traits measured. For analyses considering species abundance (e.g.,
494 community weighted mean) Májeková *et al.*, (2016) suggested including species with measured traits that
495 represent at least 80% of the abundance in the community. Had we followed this rule, we would have excluded
496 more than 75% of all Panamanian species from our analyses (see variable Abundance in Appendix S2).

497

498 With reference to Question 3, cryptic species represented 25% of all known BCI species. If we apply the same
499 ratio to the whole of the Panamanian fauna, then the regional pool size should be at least 184 cryptic and non-
500 cryptic Dynastinae species for Panama. This is without accounting further collecting effort in Panama that
501 doubtlessly may increase the number of species. The high proportion of cryptic species on BCI may to some
502 extent reflect taxonomical efforts and knowledge. For example, on BCI the proportion of cryptic species of
503 butterflies to the local pool of resident species is much lower, 8.7% (Basset *et al.*, 2015). In these conditions it is
504 not surprising to observe that cryptic species do influence the delineation of functional groups in Dynastinae, as
505 evidenced by differences between the two BCI dendrograms (Fig. 4b). Since cryptic species are ecologically
506 poorly known (no binomial name to access the ecological literature), most in this study (79%) were assigned to
507 Group 5. Thus, in line with our preceding recommendation, we advise including cryptic species for the
508 delineation of functional groups, even if many of them may eventually be classified into an artificial cluster.

509

510 Concerning Question 4, we first note that although the COI phylogeny showed strongly supported internal nodes
511 (bootstrap values >65%), the tribal classification and monophyly of many genera was poorly reflected. As
512 evidenced in multi-gene (Moore *et al.* 2015) and morphology-based phylogenetic studies, the tribe
513 Cyclocephalini does not appear to be monophyletic, and in general, phylogenetic placement within the group
514 remains unclear (Clark, 2011; Breeschoten *et al.* 2013). Although our COI phylogeny indicates the inconsistent
515 classification of tribes and that several genera are paraphyletic, a truly robust phylogenetic reconstruction for
516 Dynastinae falls beyond the scope of the present study.

517

518 The similarities between dendrograms of functional groups and phylogeny of all Panamanian species were the
519 lowest of the four tanglegrams that we evaluated. This suggests generally a low correspondence between
520 functional groups and phylogeny, and the difficulty to use phylogeny as a cheap surrogate for functional groups.
521 A few traits were phylogenetically conserved, so that imputation of variables could be guided by phylogeny to
522 improve the species-traits matrix. However, this concerned mostly body length (Gaston, 2011) and variation in
523 body surface, that can be easily measured. Still, for different datasets and groups, testing for trait conservatism
524 and taxonomical imputation may be advisable. For instance, larval habitat preferences appear to be
525 phylogenetically clustered (Table S3) so focusing on a wider range of habitat types captures phylogenetic
526 diversity, as opposed to pollinating adults which are closely related to each other. Similarly, the analysis of local
527 phylogenetic association (LIPA; Fig. S6) suggests a strong signal of body length along the entire phylogeny
528 implying a conserved trait for the whole group, while variation in body surface and spatial aggregation appear to
529 be stronger at specific nodes denoting evolutionary changes specifically along those branches.

530

531 Eventually, relating to Question 5, our results suggest that while differences in the distribution and species
532 assignment to functional groups may exist between Panama and BCI, the overall structure of these groups was
533 conserved in this comparison of regional vs. local data, as evidenced by the relatively high correlations between
534 dendrograms (cophenetic correlation; Fig. 4d). This suggests that functional groups may be relatively well
535 conserved at the local scale for a lowland tropical rainforest when compared to regional scale (country level).
536 We did not observe any loss of functional groups. The proportion of pollinator species to the total number of
537 species was roughly equivalent between BCI and Panama, also suggesting that the pollinating services of
538 Dynastinae may be conserved at the local scale when compared to country level, at least when considering
539 species richness. These observations suggest that for the Dynastinae in this study regional factors may be more
540 important in structuring communities than local factors (Lawton *et al.*, 2003; Galitsky & Lawler, 2015).

541

542 Our results will be invaluable for modelling and forecasting population dynamics of Dynastinae on BCI, using
543 data from the ForestGEO Arthropod Initiative (Lamarre *et al.*, 2020). We are now in a position to consider the
544 population dynamics of functional groups and to evaluate to which functional groups the effective ‘winners or
545 losers’ belong to, in face of climate change (Lamarre *et al.*, 2022). This approach can then be expanded to all
546 Panamanian and tropical Dynastinae, possibly with improved trait matrices building on our original selection.

547

548 In general, the ecological knowledge of tropical insects is very poor, compared to that of plants or vertebrates.
549 This prevents the inclusion of complex traits, limits the delineation of functional groups to only a few clusters
550 with rather broad features, and restricts the scope and interest of subsequent analyses. For example, compare this
551 study (147 species, 5 functional groups) to a bird study in the U.S.A., where 74 species were classified into 20
552 functional groups (Galitsky & Lawler, 2015). Collating species traits for tropical insects is time-consuming and
553 frustrating. In our analyses we used only a third of all traits originally measured. The time and effort used for
554 measuring traits that were eventually not selected could be used instead for documenting well the traits selected
555 a priori to avoid redundancy (Villéger *et al.*, 2008). Alternatively, one may consider investing into field
556 observations or experiments to determine for a few species important but distinct traits that are more difficult to
557 acquire (e.g., clutch size, life span, voltinism and thermal tolerance, as discussed previously). In this context, the
558 inclusion of cryptic species in the analyses is important, so care should be taken to sequence (DNA barcode)
559 representative specimens to recognize these species. This information can then be used to build multigene
560 phylogenies that may help with careful taxonomic imputation (Penone *et al.*, 2014) to complete the species-traits
561 matrices. This may be an arduous but necessary process to improve the ecological knowledge of tropical insects
562 and, ultimately, their conservation.

563

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565

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574

575 **Conflict of interest**

576

577 The authors declare no conflicts of interest in relation to this work.

578

579 Authors' contributions

580 YB, HB and GPAL conceived the study; HB, JAR, FR, RB, YL identified species; GV, HB, RC, PS, AS
581 contributed data; YB, PB, DSV, STS analyzed the data; YB wrote the paper with substantial collaboration from
582 all authors.

583

584 DATA AVAILABILITY STATEMENT

585

586 Data available in article supplementary material.

587

588 Supplementary Information

589

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

592

593 **Appendix S1.** Supplementary methods.

594

595 **Appendix S2.** List of species of Dynastinae reported from Panama and Barro Colorado Island and their species
596 traits.

597

598 **Appendix S3.** Details about the final selection of species traits.

599

600 **Table S1.** Weights used to downweigh the selected traits in Gower similarity matrices.

601

602 **Table S2.** Goodness of fit between traits and constrained axes of the dbRDA.

603 **Table S3.** Phylogenetic signal for continuous traits calculated with various indices.

604 **Table S4.** Standardized effect sizes of mpd and mntd calculated from a phylogenetic distance matrix for
605 categorical traits.

606 **Fig. S1.** Distribution of the number of traits recorded for each of the 147 Panamanian species of Dynastinae.

607

608 **Fig. S2.** Correlation matrix of species trait variables.

609

610 **Fig. S3.** Selection of the number of clusters for all Panamanian species.

611

612 **Fig. S4.** Tanglegram comparing functional groups (including Group 5) vs. phylogenetic tree for Panamanian
613 species.

614

615 **Fig. S5.** Pruned Dynastinae phylogeny to include only Panamanian species, which have available traits.

616

617 **Fig. S6.** Local indicator of phylogenetic association (LIPA) based on Moran's I.

618

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620

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815 **Table 1.** Details of all species trait variables considered, listed by categories. Difficulty: if specimens or data are available, how easy/time consuming it is to measure/estimate this
 816 variable (Easy - Difficult). The suffix “_L” indicates that variables were logarithmically (\log_{10}) transformed for analyses. In this case, they are listed untransformed in Appendix
 817 S2. All variables are further explained in Appendix S1 and detailed in Appendix S2. Variables greyed were selected as final traits for analysis (Appendix S3).

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Category/Trait variable	Code	Units	Proxy of	Measurement/Source	Rationale	Difficulty
1. Spatial distribution						
Geographic distribution	GeoDist	Number	Habitat range	Geographic distribution from Ratcliffe (2003)	Related to commonness and dispersal	Easy
Elevational range	ElevRange	Meters	Thermal range	From Ratcliffe (2003)	Ability to withstand cooler habitats; ecological valence	Easy
No. provinces	NoProvinces_L	Number	Commonness/Rarity	No. provinces collected in Panama (max. 11), from Ratcliffe (2003)	Related to commonness and dispersal	Easy
Spatial aggregation	LloydSpatial_L	Index	Microhabitat use	Aggregation of adults in 10 locations on BCI	Microhabitat specialization (adults)	Easy
2. Temporal distribution						
Seasonal aggregation	SeasonRat	Index	Seasonal range	Aggregation of adults among months. Ratcliffe (2003)	Seasonal aggregation (adults)	Easy
Seasonal distribution	SeasonFG_L	Index	Seasonal range	Variance in the seasonal peak of abundance of adults.	Seasonal distribution (adults)	Easy
3. Adult ecology						
Specialization - genus	AdDBIG_L	Index	Host specialization	Specialization at the genus level	How specialized are species to host plant genus	Difficult
Specialization - family	AdDBIF_L	Index	Host specialization	Specialization at the family level	How specialized are species to host plant family	Difficult
Host growth form	AdHostGF	Categorical	Host specialization	From Ratcliffe (2003); Moore & Jameson (2013)	Preferences depending on growth form of host plant	Difficult
Pollinator	AdPollinator	Binary	Ecosystem service	From Ratcliffe (2003)	Whether pollinator/visiting flower parts or not	Difficult
Decaying wood	AdDecayingWood	Binary	Ecosystem service	From Ratcliffe (2003)	Whether present in decaying wood or not	Difficult
4. Larval ecology						
Larval habitat	LarHabitat	Categorical	Ecosystem service	From Ratcliffe (2003)	Larval substrate	Difficult
Larval food	LarFood	Categorical	Ecosystem service	From Ratcliffe (2003)	Larval food	Difficult
5. Morphometrical traits						

Body length	LengthRat_L ¹	mm	Dispersal	Average between maximum and minimum body length, from Ratcliffe (2003)	Body size and dispersal	Easy
	LengthGer_L	mm	Dispersal	Average body length ²	Body size and dispersal	Easy
Body width	WidthRat_L	mm	Dispersal	Average between maximum and minimum body width, from Ratcliffe (2003)	Body size and dispersal	Easy
	WidthGer_L	mm	Dispersal	Average body width ²	Body size and dispersal	Easy
Body surface	SurfaceRat_L	mm ²	Dispersal	Average length x average width, from Ratcliffe (2003)	Plasticity of larval development. High variation = high plasticity	Easy
Variation in body surface	VarSurfaceRat	%	Dispersal	% of variation in body surface, from Ratcliffe (2003)	Plasticity of larval development. High variation = high plasticity	Easy
Body height	HeightGer_L	mm	Dispersal	Average body height ²	Body size and dispersal. Fossorial habits under bark	Easy
Body volume	VolumeGer_L	mm ³	Dispersal	Average body volume ²	Body size and dispersal. Pollinator foraging (size of flowers visited)	Easy
Variation in body volume	VarVolumeGer	%	Dispersal	% of variation in body volume ²	Plasticity in body volume	Easy
Thorax width	ThoraxWidth_L	mm	Dispersal	Average thorax width ²	Dispersal	Easy
Elytra length	ForewingLength_L	mm	Dispersal	Average elytra length ²	Dispersal	Easy
Wing length	WingLength_L	mm	Dispersal	Average wing length ²	Dispersal	Difficult
Wing width	WingWidth_L	mm	Dispersal	Average wing width ²	Dispersal	Difficult
Wing loading	WingLoad	Ratio	Dispersal	Ratio of wing length to wing width	Dispersal	Difficult
Fore tibia length	ForeTibiaLength_L	mm	Microhabitat use	Average fore tibia length ²	Related to climbing, holding, and the manipulation of flowers and fruits	Easy
Fore tarsi length	ForeTarsiLength_L	mm	Microhabitat use	Average fore tarsi length, measured in ForestGEO collections	Related to climbing, holding, and the manipulation of flowers and fruits	Easy
6. Body lightness						
Average lightness	Lightness	8-bit integers	Heat resistance, thermoregulation	Color measurements of pictures ²	Darker species may capture more heat than lighter species	Difficult
Variation in lightness	LightnessCV	Ratio	Heat resistance	Coefficient of variation of color measurements	Polymorphism in degree of lightness	Difficult

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823¹For cryptic species, the values of this variable were replaced by values of LengthGer_L, which is the average body length measured in the ForestGEO collection.²Measured in the ForestGEO collectio

824 **CAPTION OF FIGURES**

825

826 **Fig. 1.** Cluster dendrogram showing the five functional groups and the Panamanian species (n=147) that belong
827 to them. Species with names in black are present on Barro Colorado Island (n=56).

828

829 **Fig. 2.** Box-plots (median, quartiles, range) and bar-plots showing the distribution of the selected species traits
830 among the five functional groups.

831

832 **Fig. 3.** Plot of the species (dots), species traits (numerical: black vectors; categorical: black dots) and functional
833 groups (95% prediction ellipses) in (a) axes 1,2 and (b) axes 3,4 of the dbRDA. Only traits with >25% of fit to at
834 least one axis were drawn into plots.

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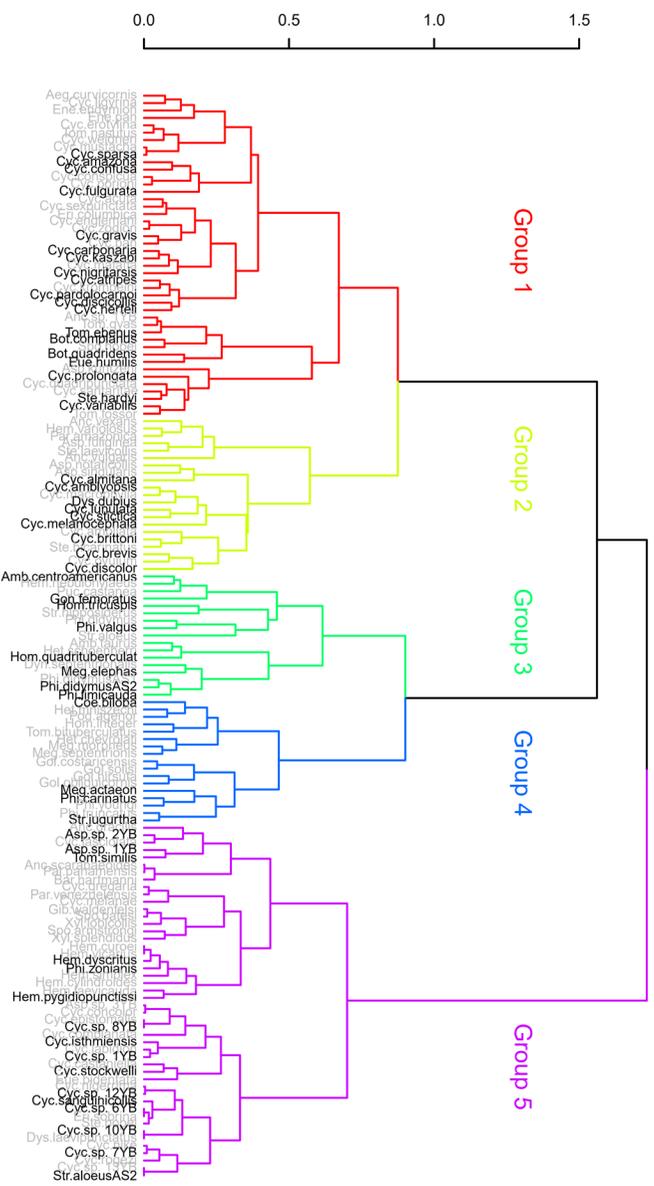
836 **Fig. 4.** Tanglegrams comparing (a) all Panamanian species (with few traits available) with species with most
837 traits available; (b) all BCI species vs. BCI species without cryptic species; (c) functional groups vs.
838 phylogenetic tree for Panamanian species (excluding Group 5); and (d) all Panamanian species vs. BCI species.
839 Species names are colorized according to functional groups based on all Panamanian species, extra species in
840 larger tree were trimmed. The associations between the two dendrograms were measured by cophenetic
841 correlation and Cramer's V.

842

843 **Fig. 5.** Phylogeny for Panamanian Dynastinae. Topology was inferred from COI barcodes by Maximum
844 Likelihood algorithm as implemented in IQ-TREE. Black circles indicate bootstrap support > 70%. Names
845 include BOLD and Genbank Accession numbers when available. Tree visualization and annotation was done
846 using the interactive tree of life (iTOL) online tool. A few Costa Rican and South American species are
847 included, indicated by an asterisk (*). All pictures obtained from the BOLD repository.

FIGURES

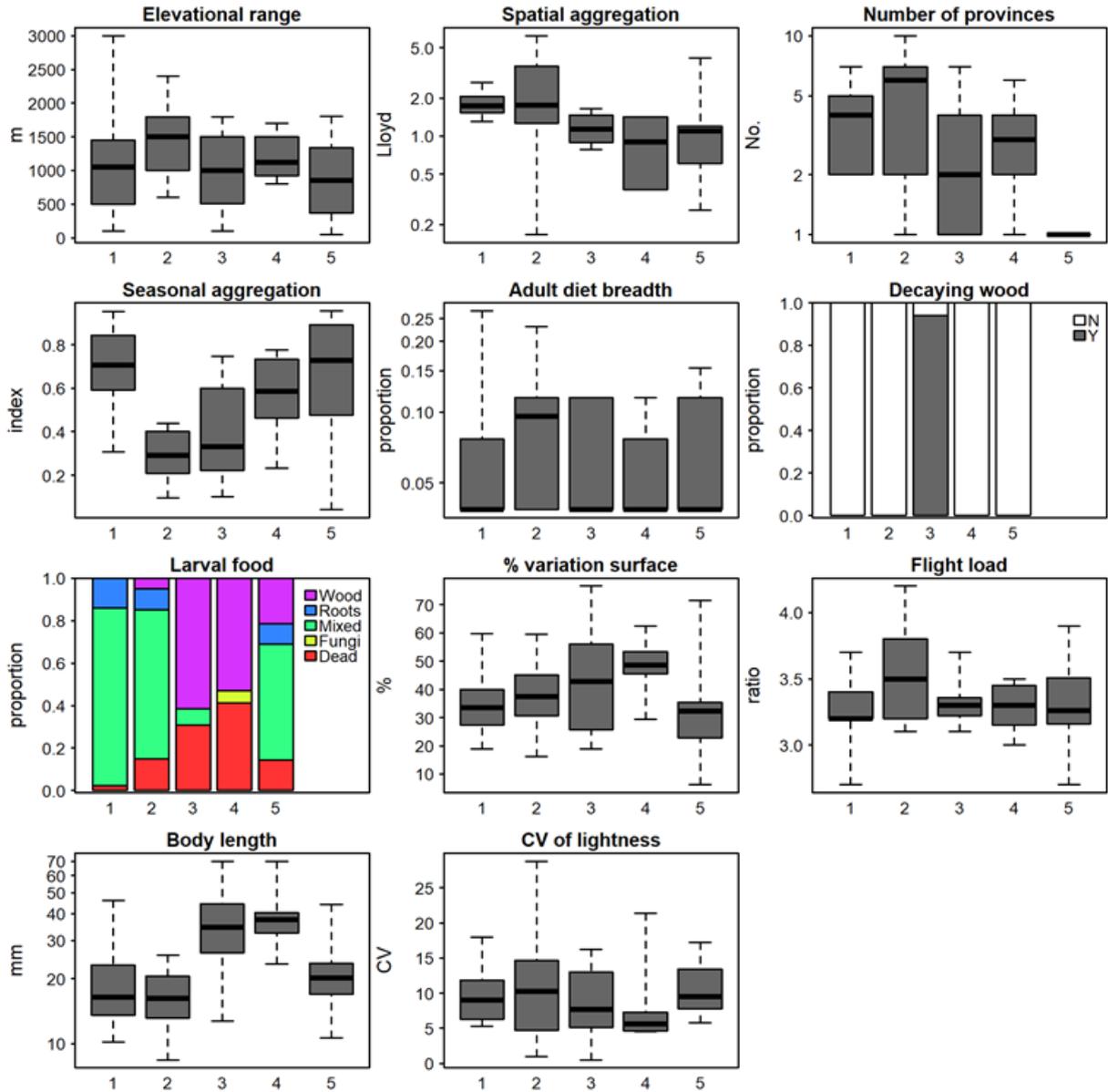
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Fig. 1. Cluster dendrogram showing the five functional groups and the Panamanian species that belong to them. Species with names in black are present on Barro Colorado Island.

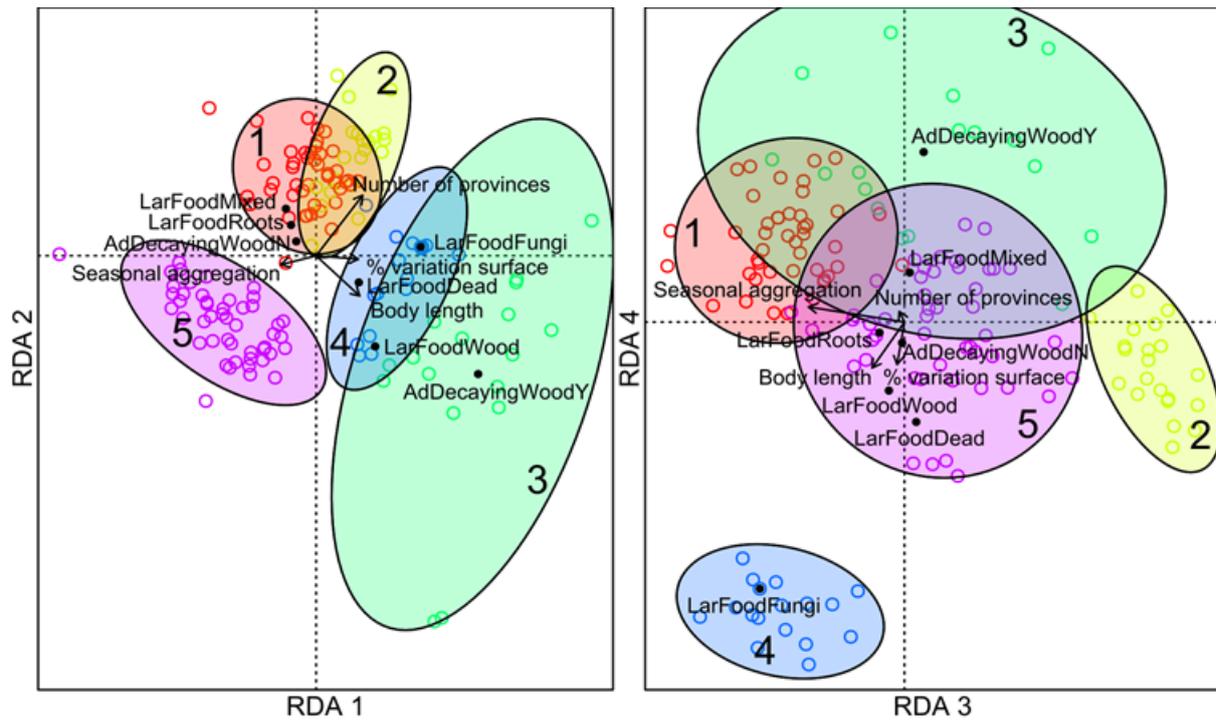
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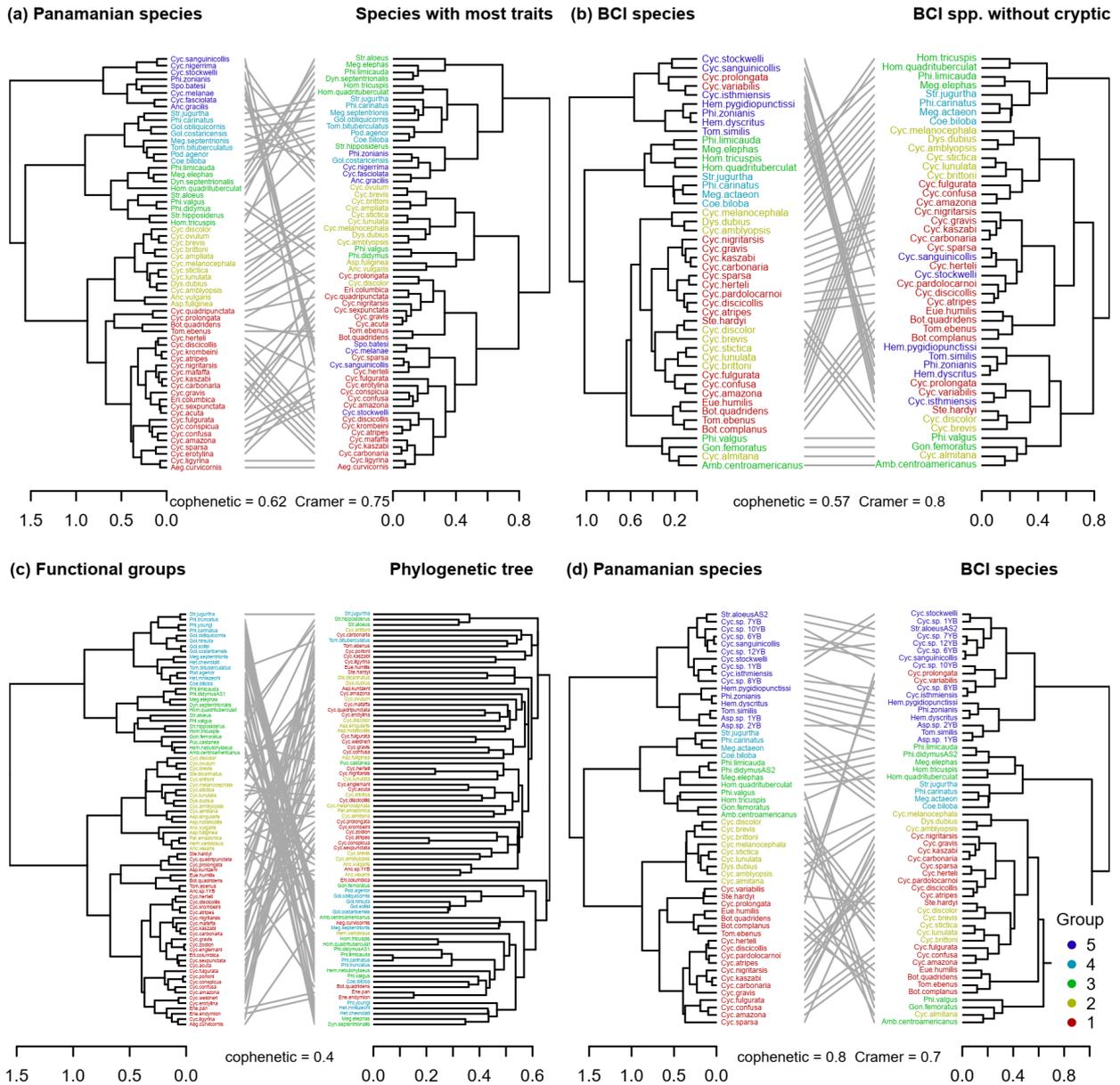
Fig. 2. Box-plots (median, quartiles, range) and bar-plots showing the distribution of the selected species traits among the five functional groups.

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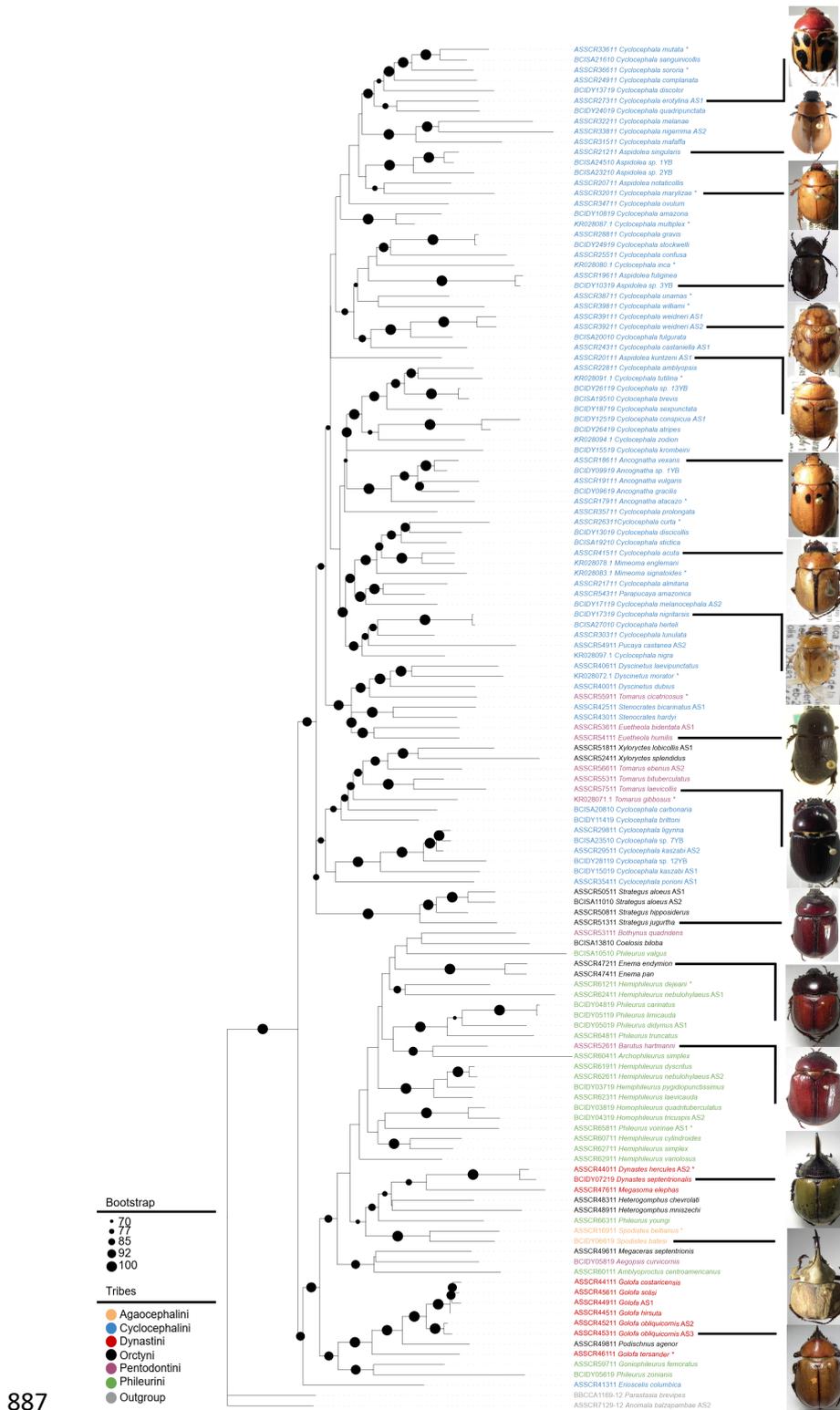
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Fig. 3. Plot of the species (dots), species traits (numerical: black vectors; categorical: black dots) and functional groups (95% prediction ellipses) in (a) axes 1,2 and (b) axes 3,4 of the dbRDA. Only traits with >25% of fit to at least one axis were drawn into plots.



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881 **Fig. 4.** Tanglegrams comparing (a) all Panamanian species (with few traits available) with species with most
 882 traits available; (b) all BCI species vs. BCI species without cryptic species; (c) functional groups vs.
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888 **Fig. 5.** Phylogeny for Panamanian Dynastinae. Topology was inferred from COI barcodes by Maximum
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 891 using the interactive tree of life (iTOL) online tool. A few Costa Rican and South American species are
 892 included, indicated by an asterisk (*). All pictures obtained from the BOLD repository.