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41 LB & JA conceived of project ideas. LB conducted all analyses except for estimating forest loss
42 (AZ) and occupancy (JA). LB wrote the manuscript with feedback from all authors and
43 considerable input from KK. PA, IA, TB, MBH, CG, PAJ, DK, ML, ARM, EHM, TO, JCR,
44 HRS, FR, CHR, DS, CEFS, WRS, and RV contributed TEAM data.

45

46 **ABSTRACT**

47 The conservation of tropical forest carbon stocks offers the opportunity to curb climate
48 change by reducing greenhouse gas emissions from deforestation and simultaneously conserve
49 biodiversity. However, there has been considerable debate about the extent to which carbon
50 storage will provide benefits to biodiversity in part because whether forests that contain high
51 carbon density in their aboveground biomass also contain high animal diversity is unknown.
52 Here, we empirically examined medium to large bodied ground-dwelling mammal and bird
53 (hereafter “ground-dwelling endotherm”) diversity and carbon stock levels within the tropics
54 using camera trap and vegetation data from a pantropical network of sites. Specifically, we tested
55 whether tropical forests that stored more carbon contained higher ground-dwelling endotherm
56 species richness, taxonomic diversity and trait diversity. We found that carbon storage was not a
57 significant predictor for any of these three measures of diversity, which suggests that benefits for
58 ground-dwelling endotherm diversity will not be maximized unless endotherm diversity is
59 explicitly taken into account; prioritizing carbon storage alone will not necessarily meet
60 biodiversity conservation goals. We recommend conservation planning that considers both

61 objectives because there is the potential for more terrestrial endotherm diversity and carbon
62 storage to be achieved for the same total budget if both objectives are pursued in tandem rather
63 than independently. Tropical forests with low elevation variability and low tree density
64 supported significantly higher ground-dwelling endotherm diversity. These tropical forest
65 characteristics may provide more affordable proxies of ground-dwelling endotherm diversity for
66 future multi-objective conservation planning when fine scale data on wildlife are lacking.

67
68 **Key Words:** *Conservation planning, Carbon storage, Biodiversity co-benefit, REDD+, Tropical*
69 *Ecology Assessment and Monitoring Network, camera trapping, wildlife conservation*

70 71 INTRODUCTION

72 Biodiversity loss and climate change are two of the most significant environmental
73 problems of the 21st century (Cardinale et al. 2012, IPCC 2014). Major initiatives to conserve
74 biodiversity include international commitments to expand the extent of protected areas globally
75 and halt the loss of threatened species (Aichi Targets; <http://www.cbd.int/sp/targets>). Programs
76 such as Reducing Emissions from Deforestation and Degradation (REDD+) offer financial
77 incentives for developing countries to reduce their emissions by conserving carbon stocks
78 (FAO/UNDP/UNEP 2010). In practice, however, both biodiversity conservation initiatives and
79 carbon storage programs face limited budgets that are insufficient to achieve their objectives
80 (Eliasch 2008, McCarthy et al. 2012).

81 Multi-objective planning, where, for example, both biodiversity and carbon are
82 considered within the framework of a single analysis, is one way to increase the efficiency of
83 available funds (Venter et al. 2009, Thomas et al. 2013). REDD+ has been identified as having
84 the potential to simultaneously mitigate climate change and conserve biodiversity (e.g.
85 Strassburg et al. 2012). However, REDD+ has yet to be implemented at large geographic scales
86 or with significant budgets in part because a lack of detailed information on site-level carbon and
87 diversity hampers the ability to select REDD+ sites that optimize for both objectives (Anderson
88 et al. 2009, Siikamaki and Newbold 2012). Even though the need to provide deliberate guidance
89 to countries attempting to achieve both objectives has been recognized (Gardner et al. 2012),
90 plans either remain in the developing stage or lack specificity in their definition of biodiversity
91 goals and monitoring indicators (Panfil and Harvey 2014). Site-specific measures of wildlife

92 diversity and carbon are therefore needed to understand to what extent tropical forests with high
93 carbon density also contain high wildlife diversity (Siikamaki and Newbold 2012).

94 Based on ecological theory, a positive correlation between carbon and the abundance and
95 diversity of animals may exist, as both could be related to primary productivity (Wright 1983).
96 One possible mechanism is that high productivity may lead to increased consumer abundances,
97 which may translate into higher species richness because a larger number of species can attain
98 viable population sizes that allow their persistence in the community (Srivastava and Lawton
99 1998). Recent studies have evaluated the relationship between carbon storage and tropical tree
100 diversity and found support for a positive relationship (Cavanaugh et al. 2014, Imai et al. 2014),
101 but information on the fine-grained relationship between carbon storage and tropical wildlife is
102 lacking.

103 The Tropical Ecology Assessment and Monitoring (TEAM) Network was established in
104 2002 and is a partnership between Conservation International, the Smithsonian and the Wildlife
105 Conservation Society. The network includes research sites in 17 tropical forest protected areas
106 that simultaneously monitor plants, animals and climate. TEAM data are uniquely suited for
107 examining relationships between carbon storage and animal diversity for two key reasons. First,
108 ground-dwelling mammals and birds are monitored with camera traps according to a highly
109 standardized protocol (TEAM Network 2011c), forming the largest camera trap network in the
110 world (Jansen et al. 2014). Unlike distribution data extracted from geographic ranges (e.g.
111 Strassburg et al. 2010), which overestimate the occurrence of species (Hurlbert and Jetz 2007),
112 TEAM data capture the real-time co-occurrence of species at the fine-grained local scale at
113 which biotic interactions take place. Moreover, replication of the standardized TEAM protocol
114 throughout the tropics provides fine-grained data collected over a large spatial extent, which is
115 rare but particularly important for understanding diversity (Beck et al. 2012).

116 Secondly, TEAM monitors vegetation plots that overlap spatially with the camera traps
117 and yield ground measurements of carbon storage, which are more accurate than remotely sensed
118 carbon estimates (Mitchard et al. 2014, Rejou-Mechain et al. 2014). The sampling design of the
119 TEAM vegetation plots is optimal for estimating carbon density for two reasons. TEAM
120 vegetation plots are a suitable size (1 ha) for estimating carbon density because this is the plot
121 size at which error rates stabilize (Rejou-Mechain et al. 2014) and the sampling design captures

122 variation in elevation (TEAM Network 2011b, a), which captures heterogeneity in aboveground
123 biomass estimates (Rejou-Mechain et al. 2014).

124 We empirically investigate the relationship between carbon storage, ground-dwelling
125 endotherm diversity and environmental characteristics at a site-level scale throughout the tropics.
126 We use modeling approaches to improve our understanding of predictors of ground-dwelling
127 endotherm diversity. Specifically, we ask 1) to what extent does carbon density predict ground-
128 dwelling endotherm diversity in the tropics and 2) given that the collection of fine-grained
129 endotherm data (i.e., site specific rather than from coarse gridded range maps) at all locations is
130 cost prohibitive (Gardner et al. 2012), what site-level characteristics can be used to predict
131 tropical ground-dwelling endotherm diversity in the absence of high-quality site-specific data?
132 Our goal is to provide quantitative biological results from a pantropical network of sites for
133 consideration in future conservation planning.

134

135

136 **METHODS**

137 **TEAM Network Study Sites**

138 Data on carbon stocks and wildlife were collected at 14 forest sites that are part of the
139 Tropical Ecology Assessment and Monitoring (TEAM) Network, a stratified random selection of
140 active field sites in tropical forests (TEAM Network 2011a) in Latin America, Africa,
141 Madagascar and Southeast Asia (Fig. 1). Sites included Barro Colorado (BCI) in Panama,
142 Caxiuanã (CAX) in Brazil, Cocha Cashu (COU) in Peru, Manaus (MAS) in Brazil, Volcán Barva
143 (VB) in Costa Rica, Yanachaga (YAN) in Peru and Yasuni (YAS) in Ecuador in the Americas;
144 Bwindi (BIF) in Uganda, Korup (KRP) in Cameroon, Nouabalé Ndoki (NNN) in the Republic of
145 the Congo, and Udzungwa (UDZ) in Tanzania in Africa; Bukit Barisan (BBS) in Indonesia and
146 Pasoh Forest (PSH) in Malaysia in Asia and Ranomafana (RNF) in Madagascar (Table 1).

147

148 **TEAM Data Collection**

149 **TERRESTRIAL ENDOTHERM DATA**

150 We restrict our sampling to ground-dwelling and semi- ground-dwelling mammals and
151 birds because these species tend to be a component of vertebrate diversity that (1) is managed

152 locally in protected areas, (2) is important for shaping forest structure through seed dispersal and
153 its effects on tree demography, and (3) constitutes important aspects of ecotourism.

154 Ground-dwelling mammals and birds were surveyed annually at each site, using camera
155 traps, following a standardized protocol (TEAM Network 2011c). Sixty camera traps were
156 deployed per site at a density of 1 camera trap per 2 sq km. The camera traps arrays did not cover
157 the entire protected areas, but provided a core sampling area at each site (Ahumada et al. 2011).
158 Each camera trap was set 30-40 cm from the ground and was active continuously for 30 days
159 during the dry season. While TEAM monitors ground-dwelling endotherms annually at each site,
160 the number of years of camera trap data varies between sites. We therefore used one year of data
161 from each site to control for variation in sampling effort that might otherwise affect diversity
162 estimates.

163 Of the species detected by the camera traps, only those species meeting the following
164 criteria for reliable detection were included: 1) species with average adult body size of 100
165 grams or more (Dunning 2008, Jones et al. 2009) and 2) predominantly ground-dwelling species
166 that spend a large proportion of their time on or near the ground according to species descriptions
167 (IUCN 2014, Myers et al. 2014, Schulenberg 2014). If descriptive data suggested that a species
168 is arboreal, a species was included if there was at least one TEAM site at which the species was
169 detected in five or more events for each year that camera trap data have been collected based on
170 the rationale that TEAM data can be used to increase our understanding of poorly known species.
171 Observed species lists are available in Appendix S1. A single taxonomic authority was used for
172 all sites (IUCN 2014).

173 We used trait data on body mass and guild (carnivore, herbivore, insectivore, or
174 omnivore) (Dunning 2008, Jones et al. 2009, Myers et al. 2014, Schulenberg 2014) for all
175 species, and activity cycle, geographic range size and litter size for mammals (Jones et al. 2009).
176 These traits were selected because they provide information on feeding ecology, life history and
177 behavioral characteristics of the community. Missing trait values were assigned the family mean
178 for continuous traits and family mode for categorical traits. For the 253 mammal species
179 included in the study, family level values were applied to missing values of body mass for 2
180 species (<1%), litter size for 60 species (23.7%), geographic area for 20 species (7.9%), activity
181 cycle for 53 species (20.9%) and guild for 6 species (2.3%). For the 144 bird species included in

182 the study, family level values were applied to missing values of body mass for 2 species (1.3%)
183 and guild for 27 species (18.75%).

184

185 VEGETATION DATA

186 Each TEAM site monitors vegetation in six or more 1-hectare plots in the core study area
187 established following specific guidelines regarding elevation gradients, terrain, soil type and
188 water bodies (TEAM Network 2011a). Trees with diameter at breast height (DBH) of 10 cm or
189 greater were monitored during the dry season following standardized TEAM vegetation
190 protocols (TEAM Network 2011b). We included all TEAM plots for which at least 80% of stems
191 have been identified to the Family level (79 plots total; N=6 plots for each site except NNN
192 (N=4), RNF (N=4), YAN (N=1) and VB (N=10)). All vegetation calculations were conducted at
193 the genus level because this was the highest taxonomic resolution available for some of the stems
194 due to constraints including lack of vouchered specimens for rare tropical species. Site-level
195 values for each variable using vegetation data were calculated as the mean of plots at a site. Data
196 from 2012 were used for four sites (BIF, CAX, PSH, and YAS) and data from 2011 were used
197 for the other ten sites to ensure concurrent camera trap and vegetation data.

198

199 **Model Inputs**

200 For each site, we calculated three measures of ground-dwelling endotherm diversity to
201 use as response variables: species richness, taxonomic diversity and trait diversity. While species
202 richness is a commonly used diversity metric we also used a taxonomic diversity index to
203 account for species commonness or rarity and a trait diversity index to measure variation in
204 species characteristics.

205 We quantified site-level environmental variables to use as predictors of the three
206 measures of ground-dwelling endotherm diversity: 1) carbon density 2) tree density 3) tree
207 diversity 4) protected area size 5) forest loss 6) elevation variability 7) latitude and 8) mean
208 annual rainfall. We used the mean values of all vegetation plots at a TEAM site as site-level
209 predictors. We also examined continent effects.

210

211 RESPONSE VARIABLES: TERRESTRIAL ENDOTHERM DIVERSITY

212 *Species Richness*

213 We estimated ground-dwelling endotherm species richness using a single-season
214 Bayesian model of species richness that accounts for imperfect detection (Dorazio et al. 2006).
215 Each camera trap was a sampling location and each 24-hour period of the 30-day sampling
216 period was a sampling occasion. We executed the models in R version 3.0.1 (R Development
217 Core Team 2014) with the package “rjags”, which implements MCMC methods using the Gibbs
218 sampler JAGS (Plummer and Stukalov 2014). We fit one model for each site using 4 chains with
219 250,000 iterations, a burn-in period of 125,000 iterations and retained every third iteration.
220 Outputs were examined for convergence. Due to the strong positive skew (Appendix S2), we
221 modeled median estimates of terrestrial endotherm species richness.

222

223 *Taxonomic Diversity*

224 We estimated an index of taxonomic diversity based on the occupancy probabilities of
225 observed species. We estimated species and site-specific occupancy using a Bayesian model
226 (Ahumada et al. 2013). The last 1000 iterations from the fully converged single species models
227 formed the posterior distribution of occupancy values for each species. We then computed a
228 distribution of the Shannon index of diversity for each site (Magurran 1988) that consisted of
229 1000 Shannon index values. For each calculation of a site’s Shannon index, we used the
230 occupancy values from the corresponding iteration (i.e. i in 1:1000) for the species at the site as
231 the community composition data with the “diversity” function from the vegan package in R
232 (Oksanen et al. 2013) and modeled the median from this distribution as the taxonomic diversity
233 response variable. The Shannon index increases as species richness and evenness increase
234 (Magurran 1988).

235

236 *Trait Diversity*

237 Trait diversity refers to the values, ranges and abundances of the traits found in a
238 community. We calculated the functional dispersion index (FDis), which is the mean distance in
239 multivariate trait space of individuals to the centroid of all species (Laliberte and Legendre
240 2010). We used the FD package in R (Laliberte and Shipley 2011) and weighted the distances by
241 the posterior distributions of the species-specific occupancy. We modeled the median value from
242 the FDis distribution as the trait diversity response variable. FDis increases as the diversity of
243 traits in the community increases.

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PREDICTOR VARIABLES: SITE-LEVEL ENVIRONMENTAL CHARACTERISTICS

Carbon Storage

We estimated aboveground carbon density for each 1-hectare vegetation plot and used the mean carbon density of all plots a TEAM site as a site-level predictor variable. Specifically, we first estimated aboveground biomass for each plot using the following equation (Chave et al. 2014):

$$AGB_{est} = \exp[-1.803 - 0.976E + 0.976 \ln(W) + 2.673 \ln(D) - 0.0299(\ln(D))^2]$$

where W is the genus wood density (g cm^{-3}), E is a measure of site-level environmental stress and D is the individual stem DBH (Chave et al. 2014). All wood density values were extracted from a publically available database (Zanne et al. 2009). Missing genus values were replaced with the mean family value when available and otherwise were replaced with the plot mean wood density. Genus level wood density values were available for 76% of stems and Family level values were available for 97% of stems. We extracted environmental stress values for the mean latitude and longitude of each site from the E layer provided by Chave et al. (2014), which combines three bioclimatic variables: temperature seasonality, climatic water deficit and precipitation seasonality. We then estimated carbon density per hectare by scaling the aboveground biomass estimate by a factor of 0.5 (Chave et al. 2005) and summing the estimates for all stems in a plot.

Tree Stem Density and Genus Diversity

We calculated the stem density of trees (≥ 10 cm DBH) per hectare and quantified tree genus diversity with the Shannon diversity index (Magurran 1988) using the vegan package in R (Oksanen et al. 2013). All vegetation calculations were at the plot-level.

Protected Area Size

We extracted the polygon of each TEAM site protected area from the World Database on Protected Areas (WDPA) dataset (UNEP-WCMC 2014), and verified each polygon with the appropriate local site manager. We calculated the area in hectares of each protected area after re-projecting the polygons to the appropriate local (UTM) coordinate system.

275 *Forest Loss*

276 TEAM monitors land use and cover change outside of the protected area boundaries of
277 each site using the zone of interaction (ZOI), which is the area that has the potential to strongly
278 influence biodiversity at the site based on systematic quantification of surrounding watersheds,
279 migration corridors and human settlements (DeFries et al. 2010).

280 We estimated the percent of forest area lost within each ZOI using the Global Forest
281 Change (GFC) product (Hansen et al. 2013). The GFC map is a 30m resolution global map of
282 forest change for the 2000-2012 period. To map forest cover in the year 2000, we calculated and
283 applied a 75% canopy cover forest/non-forest threshold to the 2000 percent cover map included
284 in the GFC. The 75% forest cover threshold was selected as a conservative threshold for
285 delineating forested areas. A sensitivity analysis found estimated deforestation rates to be
286 insensitive to variation of this threshold within a range of +/- 10-15%. We used the loss layer
287 included in the GFC to calculate percent forest area lost relative to 2000 forest cover.

288

289 *Elevation, Latitude & Rainfall*

290 Geographic coordinates for each camera trap were collected as GPS waypoints (TEAM
291 Network 2011a). Elevation data were extracted from the NASA STRM digital elevation data
292 (Jarvis et al. 2008). We calculated the coefficient of variation of the elevation and the mean
293 latitude of the camera traps at a site. Mean annual precipitation was extracted at a 2.5 arc-
294 minutes resolution from the Worldclim database (Hijmans et al. 2005) with ArcGIS using the
295 site mean camera trap latitude and longitude.

296

297

298 **Modeling**

299 We began by examining bivariate relationships between ground-dwelling endotherm
300 diversity and carbon using TEAM site-level data. We estimated simple linear regressions with
301 each of the three measures of ground-dwelling endotherm diversity as a dependent variable and
302 mean carbon density per hectare as the independent variable.

303 Next we explored the relationship between ground-dwelling endotherm diversity,
304 vegetation and environmental characteristics in addition to carbon storage by conducting model
305 selection and model averaging (Burnham and Anderson 2002) using the vegetation and

306 environmental variables as potential explanatory variables. We used one of three measures of
307 ground-dwelling endotherm diversity as the response variable and estimated three global linear
308 regression models using ordinary least squares.

309 All three global models included the eight standardized environmental predictor
310 variables, which we selected based on our understanding of tropical vertebrate ecology. For
311 example, we included elevation variability (CV) rather than elevation mean because elevation
312 gradients strongly influence vertebrate species richness and abundance (Gaston 2000). We log
313 transformed protected area size and forest loss because species area relationships are typically
314 linear on a log scale. Because species richness declines with distance from the equator, we used
315 absolute latitude. The global models also included continent fixed effects to account for
316 unmeasured variation between continents.

317 We inspected pairwise correlations between predictor variables (Appendix S3) to ensure
318 there were no excessively correlated predictors. We inspected residuals of the global models for
319 homoscedasticity and normality prior to model selection and averaging. We compared all
320 possible models for each of the three global models using an information theoretic approach
321 based on AICc (Akaike's Information Criterion, corrected for small sample sizes). Models were
322 ranked according to AICc and the confidence set of models was limited to the models that
323 contributed to the top 95% of model weight. The parameter estimates from the models in the
324 confidence set were used to produce estimates of predictors in an averaged model in which
325 model estimates were weighted by their AICc weights. The relative importance of each predictor
326 variable was defined by the sum of the AICc weights over all models in the confidence set in
327 which the variable appeared (Burnham and Anderson 2002). We considered a predictor
328 significant if the 95% confidence interval did not include zero. We conducted all model selection
329 and averaging using the MuMIn package in R (Barton 2013). As a robustness check we repeated
330 the regressions with heteroskedasticity robust standard errors (White, 1980). The robust standard
331 errors did not change our conclusions with regard to which variables were significant in
332 predicting biodiversity.

333

334 **RESULTS**

335 The TEAM Network sites varied considerably in all measured characteristics. Ground-
336 dwelling endotherm species richness estimates ranged widely across sites, from 17 species in

337 Ranomafana to 46 species in Cocha Cashu. Ground-dwelling endotherm taxonomic diversity
338 (Shannon Index) ranged from 2.44 in Ranomafana to 3.30 in Yasuni (Table 1). Functional
339 diversity (FDis Index) ranged from 0.26 in Korup to 0.32 in Pasoh Forest. The network also
340 included large variation in estimated carbon storage, ranging more than two-fold between Barro
341 Colorado (104 Mg C ha⁻¹) and Caxiuanã (233 Mg C ha⁻¹) (Table 1). Stem density ranged from
342 341 stems per hectare in Nouabalé Ndoki to 1169 stems per hectare in Ranomafana. Tree genus
343 richness ranged from 31 genera in Bwindi to 129 genera in Yasuni. Tree genus diversity
344 (Shannon Index) ranged from 2.34 in Udzungwa to 4.15 in Yasuni. Annual rainfall varied from
345 1166 mm/year in Korup to 4368 mm/year in Volcán Barva. Elevation variability of the camera
346 traps ranged from essentially none in Cocha Cashu (0.04 CV) to a linear elevation transect in
347 Volcán Barva (1.01 CV). All sites except Ranomafana were within 12° latitude from the equator.
348 The percent of forest lost in the ZOI between 2000-2012 varied from very little in Nouabalé
349 Ndoki (0.01%) to considerable deforestation near Pasoh Forest (37.9%). Protected area size also
350 varied considerably between Pasoh Forest, the smallest (13,610 ha) and Cocha Cashu (1,704,506
351 ha), the largest protected area (Table 1).

352 Bivariate linear regressions, however, did not yield significant relationships ($\alpha = 0.05$)
353 between carbon storage and three measures of ground-dwelling endotherm diversity at the
354 TEAM sites when examining all sites in a single regression model (Fig. 2). These results were
355 consistent when separated by continent.

356 We also examined the relationship between ground-dwelling endotherm diversity,
357 vegetation and environmental characteristics, as well as carbon. Specifically, we evaluated the
358 significance of the eight predictor variables and continent effects using the model averaged
359 coefficient estimates from the confidence set of models. The AICc comparisons attributed 32%
360 of model weight to the top model of species richness, 10% to the top model of taxonomic
361 diversity and 10% to the top model of trait diversity. A consistent lack of a clear top model (i.e. >
362 90% of model weight) indicated that model averaging was appropriate (Burnham and Anderson
363 2002). Parameter estimates, AICc values and model weights of the confidence sets are available
364 (Appendix S4).

365 In the context of this larger model, we again evaluated the relationship between ground-
366 dwelling endotherm diversity and carbon storage. After controlling for site-specific vegetation

367 and environmental attributes, carbon density was not a significant predictor of any measure of
368 terrestrial endotherm diversity (Fig. 3.).

369 We used the more general model to explore the relationship between ground-dwelling
370 endotherm diversity, vegetation and environmental variables. Elevation variability had
371 significant negative effects for both terrestrial endotherm species richness and taxonomic
372 diversity. Sites with more elevation variability had lower species richness and taxonomic
373 diversity, which suggests that relatively flat areas support more ground-dwelling endotherm
374 diversity. Stem density had a significantly negative effect on species richness and taxonomic
375 diversity. Sites with higher stem densities had lower ground-dwelling endotherm diversity,
376 which suggests that areas with relatively open forest floors support more ground-dwelling
377 endotherm diversity. Additionally, Madagascar had significantly lower species richness than the
378 other regions. None of the environmental predictors produced significant effects on trait
379 diversity, but sites in Africa had significantly lower trait diversity than other continents (Fig. 3).

380 Lastly, we assessed the relative importance of each predictor variable in the confidence
381 set of models. Relative importance is higher for variables in models that have strong support and
382 lower for variables that are only included in models with weak support. In our analysis, the
383 relative importance of all predictor variables was greater than zero (Fig. 4), which indicates that
384 all variables were included in some models in the confidence set and therefore contributed to
385 model averaged predictions. However, carbon consistently had low relative variable importance
386 in comparison with the other predictors of animal diversity (Fig. 4). Elevation variability had
387 high relative importance for the species richness and taxonomic diversity models. The continent
388 effect for Madagascar also had high relative importance for species richness, whereas the
389 continent effect for Africa had high relative importance for trait diversity. Tree diversity, stem
390 density and forest loss had moderate relative importance for taxonomic diversity and trait
391 diversity. The continent effect for Asia, protected area size, latitude and rainfall had low relative
392 importance for all three measures of terrestrial endotherm diversity (Fig. 4).

393

394

395 **DISCUSSION**

396 We evaluated whether tropical conservation stocks that store the greatest carbon
397 simultaneously support the greatest ground-dwelling endotherm diversity in an effort to

398 understand whether conserving carbon rich forests will simultaneously conserve the greatest
399 ground-dwelling mammal and bird diversity. If carbon storage and ground-dwelling endotherm
400 diversity are strongly correlated, then a win-win scenario for climate change and biodiversity
401 conservation would occur by conserving forests with the greatest carbon stocks. Using data from
402 the TEAM Network, the largest combined network of tropical camera traps and vegetation plots
403 in the world, we did not find significant relationships between carbon density and three measures
404 of ground-dwelling endotherm diversity: species richness, taxonomic diversity and trait diversity.
405 Thus, high carbon density and high ground-dwelling endotherm diversity do not necessarily
406 coincide in tropical forests and biodiversity conservation will not necessarily be maximized
407 when only carbon stocks are considered. However, in the absence of a positive relationship
408 between carbon storage and endotherm diversity, win-win scenarios for climate change and
409 biodiversity conservation can be achieved through multi-objective conservation planning in
410 which both carbon and biodiversity are optimized simultaneously. We therefore recommend the
411 explicit inclusion of biodiversity in the planning and implementation of carbon storage programs.

412 We found that elevation variability and the density of trees were significantly related to
413 ground-dwelling endotherm diversity. Sites with less elevation variability had significantly
414 higher species richness and taxonomic diversity than sites with more elevation variability. Sites
415 with fewer trees (≥ 10 cm dbh) had significantly higher ground-dwelling endotherm diversity
416 than sites with more trees. These results broadly suggest that mature tropical forests with
417 relatively even terrain support high diversity of ground-dwelling mammals and birds. Site
418 characteristics such as these may provide useful information in future multi-objective
419 conservation planning by providing affordable proxies of ground-dwelling endotherm diversity
420 when high quality fine-scale data are lacking.

421

422 **Elevation variability**

423 TEAM sites with greater elevation variability had lower estimated richness and
424 taxonomic diversity of ground-dwelling vertebrate species. The opposite result may have been
425 predicted– that sites with more elevation variability might support greater habitat diversity and
426 thus support a higher diversity of species. For example, North American mammal species
427 richness increases with greater elevation variability (Kerr and Packer 1997). Nevertheless, we

428 found that the diversity of tropical ground-dwelling mammals and birds declined as elevation
429 variability increased.

430 One possible explanation is that species richness and diversity are higher at lower and/or
431 mid elevations and decline with increasing elevation, thus a site with more elevation variability
432 may include more sampling of high elevation areas with lower diversity. Given that relatively
433 few mammals and birds specialize on high elevations (Laurance et al. 2011), TEAM sites with
434 more variation in elevation may support fewer species overall because they contain high
435 elevation areas that lack specialist species. In a number of cases, the species richness and
436 abundances of tropical birds and mammals are greatest at low elevations and decline at higher
437 elevations (Terborgh 1977, Marshall et al. 2014), but declining richness with increasing
438 elevation is not a consistent biodiversity pattern (Rahbek 1995). For example, small mammal
439 species richness peaks at intermediate elevations (McCain 2005). Due to the sparseness of
440 tropical endotherm camera trap detections, the data from all camera traps at a TEAM site were
441 utilized to estimate a single measure of species richness per site rather than permitting richness
442 estimates at each camera trap. As a consequence, our analysis does not assess the elevations at
443 which diversity is the greatest, but does suggest that terrestrial vertebrate diversity declines as
444 higher elevation sampling is included.

445

446 **Stem density**

447 We found a significant negative relationship between the density of trees (≥ 10 cm DBH)
448 and both endotherm species richness and taxonomic diversity, which suggests that the diversity
449 of tropical ground-dwelling mammals and birds is higher in forests that have fewer trees. Forests
450 that have fewer trees may have more mature trees. Disturbance in tropical forests typically leads
451 to the growth of many young stems, which thin over time as they reach the canopy. Stem density
452 therefore typically declines as disturbed forests age (Wright 2005). We did not examine mean
453 DBH as a predictor variable because DBH was used in the carbon density calculations. In a post-
454 hoc test, however, mean DBH declined significantly with increasing stem density, which
455 illustrates that TEAM sites with fewer trees contain larger trees (Fig. 5).

456

457 **Continent effects**

458 Ground-dwelling endotherm diversity varied significantly among continents. Species
459 richness was significantly low in Madagascar and trait diversity was significantly low in Africa.
460 The low species richness for the Madagascar TEAM site, Ranomafana, is unsurprising. Because
461 the site is the farthest site from equator, low species richness is expected based on latitudinal
462 gradient of species richness. In addition, Madagascar is unique compared to the other regions in
463 that it is an island with a small geographic area, which supports a smaller regional species pool
464 based on species-area relationships (Gaston 2000). The significantly low trait diversity at African
465 sites may relate to the extinction of many forest specialists over the last thirty million years
466 (Ghazoul and Sheil 2010). The continent effects also include unmeasured variation among
467 regions, such as additional variation in environmental conditions, evolutionary history and
468 anthropogenic impacts, which may have contributed to the low African trait diversity.

469

470 **Tree diversity**

471 The effect of tree diversity on both taxonomic diversity and trait diversity was generally
472 positive with moderately high relative importance for predicting taxonomic and trait diversity.
473 This suggests that tropical forests with more tree genera generally support a greater diversity of
474 ground-dwelling endotherm taxa and traits. The question of whether diversity begets diversity –
475 whether plant diversity is a causal agent of diversity at higher trophic levels – has been of
476 interest to ecologists for decades (Hutchinson 1959). A number of hypotheses have been put
477 forth to explain positive relationships between plant and animal diversity, which have been
478 detected from local to global scales (Jetz et al. 2009). For example, higher plant diversity may
479 supply more resources or more complex vegetation structure and therefore result in niche
480 differentiation and diversification at higher trophic levels. Alternatively, underlying abiotic
481 factors driving overall productivity may enable greater diversity of both plants and animals.

482

483 **Implications for conservation policies**

484 This work demonstrates the value of fine-grain ground-dwelling endotherm data, which
485 are becoming increasingly available as camera trap technology advances and costs decline,
486 because the extent to which carbon storage programs will provide benefits to biodiversity
487 without explicit formalization in REDD+ implementation necessitates understanding
488 relationships between biodiversity and carbon storage (Phelps et al. 2012). While previous

489 studies have found positive relationships between carbon storage and some aspects of tropical
490 diversity, such as trees (Cavanaugh et al. 2014, Imai et al. 2014), we synthesized fine-grained
491 spatial data on vertebrates and vegetation to improve understanding of the spatial congruencies
492 between carbon and tropical terrestrial endotherm diversity, including numerous threatened
493 species (IUCN 2014).

494 The fact that we did not find a significant relationship between carbon storage and
495 ground-dwelling endotherm diversity supports calls for mechanisms that consider both objectives
496 (i.e. carbon storage and diversity) during REDD+ planning and implementation. Specifically, a
497 lack of a significant relationship suggests the potential for more endotherm diversity and carbon
498 storage to be achieved for the same total budget if both objectives are pursued in tandem rather
499 than independently. This finding is in line with prior empirical analyses that anticipate gains
500 from multiple objective planning (as opposed to separate budgets and planning for biodiversity v.
501 carbon storage) that explicitly incorporate biodiversity into carbon storage programs (Venter et
502 al. 2009, Thomas et al. 2013).

503 More broadly, our work provides an example of how fine-scale data can generate inputs
504 to models that inform policy. For example, elevation variability calculated from publically
505 available global elevation data might be used as a proxy for tropical ground-dwelling endotherm
506 diversity in the absence of fine-scale data. Future multiple conservation planning efforts using
507 elevation and stem density as proxies could include reserve site selection approaches used to
508 maximize conservation benefits given a limited budget (e.g. Naidoo et al. 2006) or evaluations
509 and maximization of ecosystem services (e.g. Wendland et al. 2010).

510

511 **Limitations and further research**

512 This study utilized data from the most extensive network of tropical camera traps and
513 vegetation plots available, but we recognize that our sample size of 14 sites is nevertheless small.
514 Expanding the number of sites with comparable data collection could further our understanding
515 of the relationship between carbon storage and ground-dwelling endotherm diversity and would
516 allow for detailed regional analyses (*sensu* Slik et al. 2013) that were not possible in this study.

517 While carbon density was not found to significantly predict ground-dwelling endotherm
518 diversity in this study, the absence of evidence is not necessarily evidence of absence. As with
519 any null result, the finding may be due to sampling design. In addition, our study has focused on

520 only a subset of tropical animal diversity, but carbon density may predict other components of
521 biodiversity. For example, the height of trees in a forest positively predicts the species richness
522 of primates, which are a largely arboreal order. Taller forests may support more primate species
523 through vertical niche stratification (Gouveia et al. 2014). In addition, tree height is an important
524 component of carbon storage estimation (Chave et al. 2014) and differences in tree height among
525 biogeographic regions have been linked to variation in carbon storage (Banin et al. 2014).
526 Additional research is needed to evaluate the relationship between carbon storage and other
527 components of tropical diversity, such as arboreal vertebrate diversity.

528 The measure of carbon density we used considered only the aboveground contributions to
529 carbon storage despite the fact that below ground carbon storage can be both significant and
530 variable across forests (Paoli et al. 2010). Nevertheless, the data necessary for aboveground
531 carbon storage estimates are more readily available and therefore aboveground estimates are
532 more broadly applicable for conservation planning.

533 The TEAM Network sites are uniquely suited for addressing the relationship between
534 terrestrial vertebrate diversity and aboveground carbon storage in the tropics because the sites
535 include vegetation plots that overlap spatially with the camera traps. Nevertheless, the camera
536 traps are deployed across a larger spatial extent than the vegetation plots (TEAM Network
537 2011a). Additional variation in unmeasured vegetation characteristics may influence ground-
538 dwelling endotherm diversity. Lastly, our analysis did not take hunting into account due to a lack
539 of quantitative data, yet hunting can strongly affect wildlife in tropical forests (Wright 2003).
540 The impacts of hunting likely vary among TEAM sites and warrant consideration in future
541 studies.

542

543 **Conclusions**

544 Understanding site-level relationships between carbon storage and aspects of tropical
545 biodiversity has important policy applications because best practices for protecting biodiversity
546 through carbon storage programs have not yet been determined (Panfil and Harvey 2014). The
547 results of our fine-grained, site-level pantropical analysis provide quantitative biological results
548 that suggest a lack of a significant relationship between carbon storage and ground-dwelling
549 mammal and bird diversity. This result is robust to the use of the three diversity metrics: species
550 richness, taxonomic diversity and trait diversity. This finding supports earlier work that suggests

551 the need to develop conservation planning approaches that jointly optimize for carbon storage
552 and biodiversity (Naidoo et al. 2008, Anderson et al. 2009, Siikamaki and Newbold 2012).

553 Collecting fine-grained data at all locations will likely be cost prohibitive (Gardner et al.
554 2012). We therefore examined the relationship between ground-dwelling endotherm diversity
555 and other site characteristics for which data collection may be cheaper. Both elevation variability
556 and stem density were important predictors of terrestrial endotherm diversity. Site characteristics
557 such as terrain and forest maturity can potentially function as proxies of ground-dwelling
558 tropical endotherm diversity in future conservation planning so long as hunting is accounted for.

559

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574

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773

774 **Supplementary Information**

775 **Appendix A.** Posterior distributions of species richness estimates.

776 **Supplement 1.** Species lists for TEAM sites, pairwise correlations and model confidence sets.

777 All code is publicly available on GitHub at github.com/lbeaudrot/Carbon—Endotherm-

778 [Diversity-Paper](https://github.com/lbeaudrot/Carbon—Endotherm-Diversity-Paper).

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Site Code	Site Name	Country	estimate)	Endotherm taxonomic diversity (Shannon Index)	SD	Functional Diversity (FDis)	SD	Stem density (> 10 cm dbh ha-1)	CV	Tree genus richness	CV	Index)	CV	Above ground carbon density (Mg C ha-1)	CV	Annual rainfall mean (mm)	Elevation mean (m)	Elevation CV	Latitude	Forest Loss 2000-2012 ZOI (%)	Protected Area (ha)
BBS	Bukit Barisan	Indonesia	30	2.66	0.11	0.28	0.00	418.8	0.24	66.50	0.18	3.33	0.11	135.70	0.43	2928	123	0.55	-5.660	5.1	331155
BCI	Barro Colorado National Park	Panama	32	2.89	0.06	0.29	0.00	504.2	0.14	71.00	0.11	3.40	0.06	103.93	0.17	2524	94	0.45	9.163	3.0	13800
BIF	Bwindi Impenetrable Forest	Uganda	37	2.56	0.11	0.27	0.00	524.5	0.29	31.17	0.19	2.45	0.19	160.61	0.42	1325	1906	0.17	-1.010	4.7	34276
CAX	Caxiuanã	Brazil	33	3.00	0.05	0.29	0.00	474.0	0.08	87.17	0.12	3.47	0.09	232.93	0.14	2182	38	0.36	-1.770	0.5	35407
COU	Cocha Cashu - Manu National Park	Peru	46	3.22	0.05	0.30	0.00	587.5	0.05	102.33	0.14	3.84	0.07	160.10	0.23	2515	349	0.04	-11.92	0.2	1704506
KRP	Korup National	Cameroon	34	2.94	0.03	0.26	0.00	501.7	0.18	71.67	0.20	3.30	0.09	177.15	0.24	1166	168	0.47	5.044	0.1	130348

	Park																				
MAS	Manaus	Brazil	34	3.00	0.03	0.28	0.01	624.8	0.06	123.17	0.03	4.02	0.02	155.27	0.17	2219	103	0.22	-2.660	2.0	1198944
NNN	Nouabalé Ndoki	Republic of Congo	43	3.14	0.05	0.27	0.00	341.3	0.12	48.75	0.10	3.24	0.07	199.26	0.32	1668	460	0.05	2.498	0.1	411653
PSH	Pasoh Forest Reserve	Malaysia	39	2.82	0.15	0.32	0.01	416.8	0.31	86.17	0.21	3.78	0.07	121.62	0.35	2051	457	0.45	3.082	37.9	13610
RNF	Ranomafana	Madagascar	17	2.44	0.05	0.28	0.01	1169.3	0.18	68.00	0.11	3.26	0.08	133.74	0.19	1738	1083	0.13	-21.24	7.9	40705
UDZ	Udzungwa	Tanzania	42	2.87	0.05	0.27	0.01	536.0	0.17	31.83	0.30	2.34	0.29	166.27	0.26	1377	1144	0.32	-7.771	9.9	209538
VB-	Volcán Barva	Costa Rica	28	2.49	0.14	0.29	0.00	562.8	0.43	59.60	0.50	3.25	0.20	154.54	0.41	4368	705	1.01	10.327	3.8	49317
YAN	Yanachaga Chimillén National Park	Peru	28	2.63	0.08	0.28	0.01	781.0	NA	87.00	NA	3.60	NA	116.33	NA	2554	704	0.31	-10.37	3.5	293234
YAS	Yasuni	Ecuador	44	3.30	0.04	0.30	0.00	683.3	0.07	129.50	0.07	4.15	0.02	118.08	0.07	3135	254	0.08	-0.676	2.1	1040687

1 **Figure Legends**

2

3 Fig. 1. TEAM sites included in this study.

4

5 Fig. 2. Carbon storage density and three terrestrial vertebrate diversity metrics at 14 TEAM sites.

6 Linear regression failed to detect significant relationships ($\alpha = 0.05$) among all sites or within
7 continents.

8

9 Fig. 3. Coefficient plots for averaged models of terrestrial vertebrate diversity based on the
10 confidence set of model for three diversity measures. Standardized coefficients are shown. The
11 filled circles represent the coefficient estimates and the bars represent the 95% confidence
12 intervals around each estimate. Predictor variables are considered to have significant effects if
13 the 95% CI did not contain zero. Continent effects are relative to the Americas.

14

15 Fig. 4. Relative importance of the eight predictor variables and continent effects in the averaged
16 models of three measures of tropical terrestrial vertebrate diversity.

17

18 Fig. 5. Relationship between stem density and mean dbh at the 14 TEAM sites

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21 Figure 1

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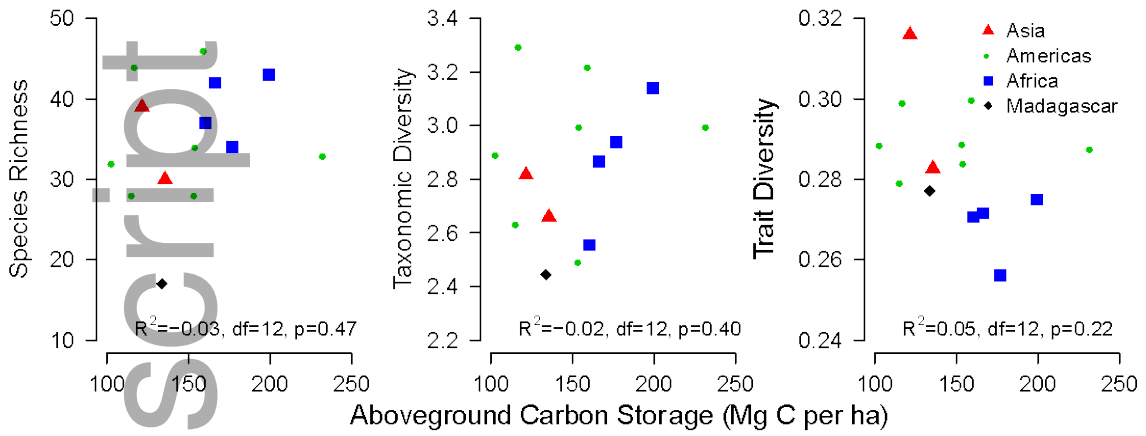
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28 Figure 2

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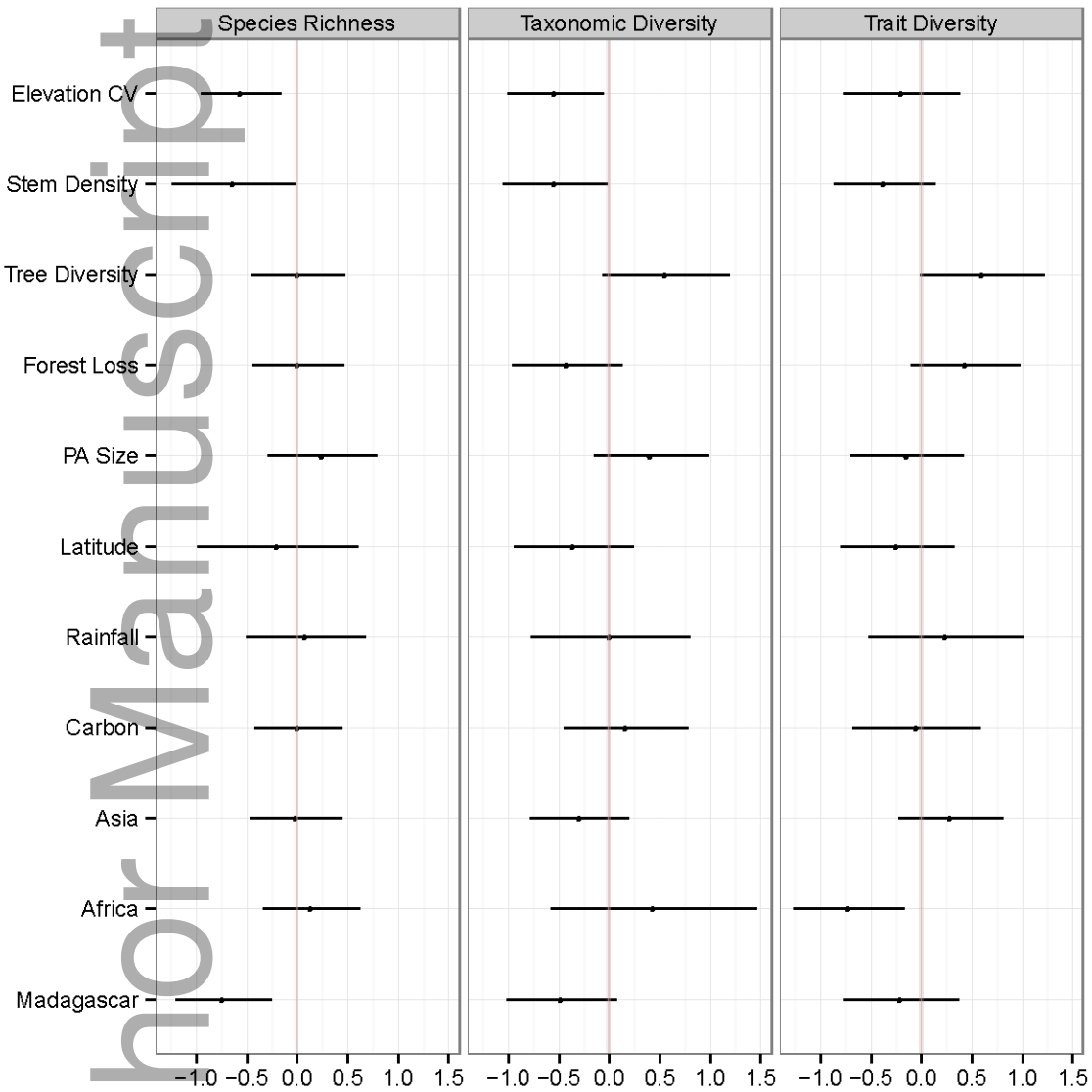
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32 Figure 3

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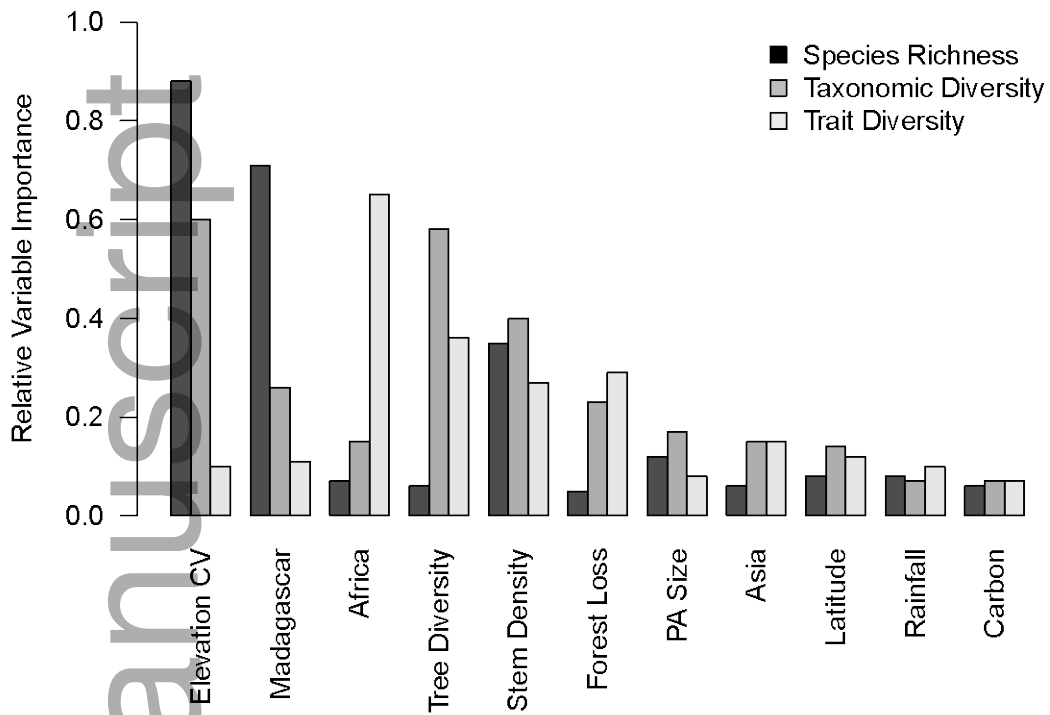
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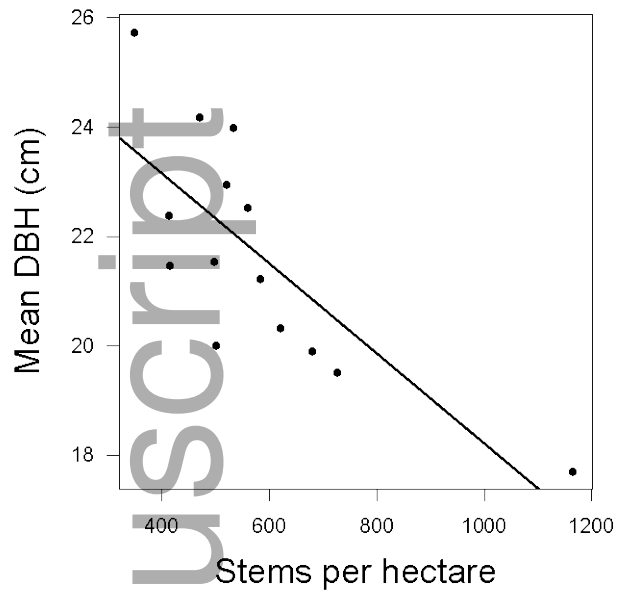
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38 Figure 4



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41 Figure 5



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