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

40

41 **ABSTRACT**

42 The conservation of tropical forest carbon stocks offers the opportunity to curb climate
 43 change by reducing greenhouse gas emissions from deforestation and simultaneously conserve
 44 biodiversity. However, there has been considerable debate about the extent to which carbon
 45 storage will provide benefits to biodiversity in part because whether forests that contain high
 46 carbon density in their aboveground biomass also contain high animal diversity is unknown.
 47 Here, we empirically examined medium to large bodied ground-dwelling mammal and bird
 48 (hereafter “ground-dwelling endotherm”) diversity and carbon stock levels within the tropics
 49 using camera trap and vegetation data from a pantropical network of sites. Specifically, we tested
 50 whether tropical forests that stored more carbon contained higher ground-dwelling endotherm
 51 species richness, taxonomic diversity and trait diversity. We found that carbon storage was not a
 52 significant predictor for any of these three measures of diversity, which suggests that benefits for
 53 ground-dwelling endotherm diversity will not be maximized unless endotherm diversity is
 54 explicitly taken into account; prioritizing carbon storage alone will not necessarily meet
 55 biodiversity conservation goals. We recommend conservation planning that considers both
 56 objectives because there is the potential for more terrestrial endotherm diversity and carbon
 57 storage to be achieved for the same total budget if both objectives are pursued in tandem rather
 58 than independently. Tropical forests with low elevation variability and low tree density
 59 supported significantly higher ground-dwelling endotherm diversity. These tropical forest
 60 characteristics may provide more affordable proxies of ground-dwelling endotherm diversity for
 61 future multi-objective conservation planning when fine scale data on wildlife are lacking.

62

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

65
 66 **INTRODUCTION**

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

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

86 goals and monitoring indicators (Panfil and Harvey 2014). Site-specific measures of wildlife
 87 diversity and carbon are therefore needed to understand to what extent tropical forests with high
 88 carbon density also contain high wildlife diversity (Siikamaki and Newbold 2012).

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

98 The Tropical Ecology Assessment and Monitoring (TEAM) Network was established in
 99 2002 and is a partnership between Conservation International, the Smithsonian and the Wildlife
 100 Conservation Society. The network includes research sites in 17 tropical forest protected areas
 101 that simultaneously monitor plants, animals and climate. TEAM data are uniquely suited for
 102 examining relationships between carbon storage and animal diversity for two key reasons. First,
 103 ground-dwelling mammals and birds are monitored with camera traps according to a highly
 104 standardized protocol (TEAM Network 2011c), forming the largest camera trap network in the
 105 world (Jansen et al. 2014). Unlike distribution data extracted from geographic ranges (e.g.
 106 Strassburg et al. 2010), which overestimate the occurrence of species (Hurlbert and Jetz 2007),
 107 TEAM data capture the real-time co-occurrence of species at the fine-grained local scale at
 108 which biotic interactions take place. Moreover, replication of the standardized TEAM protocol

109 throughout the tropics provides fine-grained data collected over a large spatial extent, which is
 110 rare but particularly important for understanding diversity (Beck et al. 2012).

111 Secondly, TEAM monitors vegetation plots that overlap spatially with the camera traps
 112 and yield ground measurements of carbon storage, which are more accurate than remotely sensed
 113 carbon estimates (Mitchard et al. 2014, Rejou-Mechain et al. 2014). The sampling design of the
 114 TEAM vegetation plots is optimal for estimating carbon density for two reasons. TEAM
 115 vegetation plots are a suitable size (1 ha) for estimating carbon density because this is the plot
 116 size at which error rates stabilize (Rejou-Mechain et al. 2014) and the sampling design captures
 117 variation in elevation (TEAM Network 2011b, a), which captures heterogeneity in aboveground
 118 biomass estimates (Rejou-Mechain et al. 2014).

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

129

130

131 **METHODS**

132 **TEAM Network Study Sites**

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

142
 143 **TEAM Data Collection**

144 TERRESTRIAL ENDOTHERM DATA

145 We restrict our sampling to ground-dwelling and semi- ground-dwelling mammals and
 146 birds because these species tend to be a component of vertebrate diversity that (1) is managed
 147 locally in protected areas, (2) is important for shaping forest structure through seed dispersal and
 148 its effects on tree demography, and (3) constitutes important aspects of ecotourism.

149 Ground-dwelling mammals and birds were surveyed annually at each site, using camera
 150 traps, following a standardized protocol (TEAM Network 2011c). Sixty camera traps were
 151 deployed per site at a density of 1 camera trap per 2 sq km. The camera traps arrays did not cover
 152 the entire protected areas, but provided a core sampling area at each site (Ahumada et al. 2011).
 153 Each camera trap was set 30-40 cm from the ground and was active continuously for 30 days
 154 during the dry season. While TEAM monitors ground-dwelling endotherms annually at each site,

155 the number of years of camera trap data varies between sites. We therefore used one year of data
 156 from each site to control for variation in sampling effort that might otherwise affect diversity
 157 estimates.

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

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

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

179

180 VEGETATION DATA

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

193

194 **Model Inputs**

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

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

205

206 RESPONSE VARIABLES: TERRESTRIAL ENDOTHERM DIVERSITY

207 *Species Richness*

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

217

218 *Taxonomic Diversity*

219 We estimated an index of taxonomic diversity based on the occupancy probabilities of
 220 observed species. We estimated species and site-specific occupancy using a Bayesian model
 221 (Ahumada et al. 2013). The last 1000 iterations from the fully converged single species models
 222 formed the posterior distribution of occupancy values for each species. We then computed a

223 distribution of the Shannon index of diversity for each site (Magurran 1988) that consisted of
 224 1000 Shannon index values. For each calculation of a site’s Shannon index, we used the
 225 occupancy values from the corresponding iteration (i.e. i in 1:1000) for the species at the site as
 226 the community composition data with the “diversity” function from the vegan package in R
 227 (Oksanen et al. 2013) and modeled the median from this distribution as the taxonomic diversity
 228 response variable. The Shannon index increases as species richness and evenness increase
 229 (Magurran 1988).

230

231 *Trait Diversity*

232 Trait diversity refers to the values, ranges and abundances of the traits found in a
 233 community. We calculated the functional dispersion index (FDis), which is the mean distance in
 234 multivariate trait space of individuals to the centroid of all species (Laliberte and Legendre
 235 2010). We used the FD package in R (Laliberte and Shipley 2011) and weighted the distances by
 236 the posterior distributions of the species-specific occupancy. We modeled the median value from
 237 the FDis distribution as the trait diversity response variable. FDis increases as the diversity of
 238 traits in the community increases.

239

240 PREDICTOR VARIABLES: SITE-LEVEL ENVIRONMENTAL CHARACTERISTICS

241 *Carbon Storage*

242 We estimated aboveground carbon density for each 1-hectare vegetation plot and used the
 243 mean carbon density of all plots a TEAM site as a site-level predictor variable. Specifically, we
 244 first estimated aboveground biomass for each plot using the following equation (Chave et al.
 245 2014):

246 $AGB_{est} = \exp[-1.803 - 0.976E + 0.976 \ln(W) + 2.673 \ln(D) - 0.0299(\ln(D))^2]$

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

258
 259 *Tree Stem Density and Genus Diversity*

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

263
 264 *Protected Area Size*

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

269

270 *Forest Loss*

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

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

283

284 *Elevation, Latitude & Rainfall*

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

291

292

293 **Modeling**

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

298 Next we explored the relationship between ground-dwelling endotherm diversity,
299 vegetation and environmental characteristics in addition to carbon storage by conducting model
300 selection and model averaging (Burnham and Anderson 2002) using the vegetation and
301 environmental variables as potential explanatory variables. We used one of three measures of
302 ground-dwelling endotherm diversity as the response variable and estimated three global linear
303 regression models using ordinary least squares.

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

312 We inspected pairwise correlations between predictor variables (Appendix S3) to ensure
313 there were no excessively correlated predictors. We inspected residuals of the global models for
314 homoscedasticity and normality prior to model selection and averaging. We compared all

315 possible models for each of the three global models using an information theoretic approach
 316 based on AICc (Akaike's Information Criterion, corrected for small sample sizes). Models were
 317 ranked according to AICc and the confidence set of models was limited to the models that
 318 contributed to the top 95% of model weight. The parameter estimates from the models in the
 319 confidence set were used to produce estimates of predictors in an averaged model in which
 320 model estimates were weighted by their AICc weights. The relative importance of each predictor
 321 variable was defined by the sum of the AICc weights over all models in the confidence set in
 322 which the variable appeared (Burnham and Anderson 2002). We considered a predictor
 323 significant if the 95% confidence interval did not include zero. We conducted all model selection
 324 and averaging using the MuMIn package in R (Barton 2013). As a robustness check we repeated
 325 the regressions with heteroskedasticity robust standard errors (White, 1980). The robust standard
 326 errors did not change our conclusions with regard to which variables were significant in
 327 predicting biodiversity.

328

329 **RESULTS**

330 The TEAM Network sites varied considerably in all measured characteristics. Ground-
 331 dwelling endotherm species richness estimates ranged widely across sites, from 17 species in
 332 Ranomafana to 46 species in Cocha Cashu. Ground-dwelling endotherm taxonomic diversity
 333 (Shannon Index) ranged from 2.44 in Ranomafana to 3.30 in Yasuni (Table 1). Functional
 334 diversity (FDis Index) ranged from 0.26 in Korup to 0.32 in Pasoh Forest. The network also
 335 included large variation in estimated carbon storage, ranging more than two-fold between Barro
 336 Colorado (104 Mg C ha⁻¹) and Caxiuanã (233 Mg C ha⁻¹) (Table 1). Stem density ranged from
 337 341 stems per hectare in Nouabalé Ndoki to 1169 stems per hectare in Ranomafana. Tree genus

338 richness ranged from 31 genera in Bwindi to 129 genera in Yasuni. Tree genus diversity
 339 (Shannon Index) ranged from 2.34 in Udzungwa to 4.15 in Yasuni. Annual rainfall varied from
 340 1166 mm/year in Korup to 4368 mm/year in Volcán Barva. Elevation variability of the camera
 341 traps ranged from essentially none in Cocha Cashu (0.04 CV) to a linear elevation transect in
 342 Volcán Barva (1.01 CV). All sites except Ranomafana were within 12° latitude from the equator.
 343 The percent of forest lost in the ZOI between 2000-2012 varied from very little in Nouabalé
 344 Ndoki (0.01%) to considerable deforestation near Pasoh Forest (37.9%). Protected area size also
 345 varied considerably between Pasoh Forest, the smallest (13,610 ha) and Cocha Cashu (1,704,506
 346 ha), the largest protected area (Table 1).

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

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

360 In the context of this larger model, we again evaluated the relationship between ground-
 361 dwelling endotherm diversity and carbon storage. After controlling for site-specific vegetation
 362 and environmental attributes, carbon density was not a significant predictor of any measure of
 363 terrestrial endotherm diversity (Fig. 3.).

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

375 Lastly, we assessed the relative importance of each predictor variable in the confidence
 376 set of models. Relative importance is higher for variables in models that have strong support and
 377 lower for variables that are only included in models with weak support. In our analysis, the
 378 relative importance of all predictor variables was greater than zero (Fig. 4), which indicates that
 379 all variables were included in some models in the confidence set and therefore contributed to
 380 model averaged predictions. However, carbon consistently had low relative variable importance
 381 in comparison with the other predictors of animal diversity (Fig. 4). Elevation variability had
 382 high relative importance for the species richness and taxonomic diversity models. The continent

383 effect for Madagascar also had high relative importance for species richness, whereas the
 384 continent effect for Africa had high relative importance for trait diversity. Tree diversity, stem
 385 density and forest loss had moderate relative importance for taxonomic diversity and trait
 386 diversity. The continent effect for Asia, protected area size, latitude and rainfall had low relative
 387 importance for all three measures of terrestrial endotherm diversity (Fig. 4).

388

389

390 **DISCUSSION**

391 We evaluated whether tropical conservation stocks that store the greatest carbon
 392 simultaneously support the greatest ground-dwelling endotherm diversity in an effort to
 393 understand whether conserving carbon rich forests will simultaneously conserve the greatest
 394 ground-dwelling mammal and bird diversity. If carbon storage and ground-dwelling endotherm
 395 diversity are strongly correlated, then a win-win scenario for climate change and biodiversity
 396 conservation would occur by conserving forests with the greatest carbon stocks. Using data from
 397 the TEAM Network, the largest combined network of tropical camera traps and vegetation plots
 398 in the world, we did not find significant relationships between carbon density and three measures
 399 of ground-dwelling endotherm diversity: species richness, taxonomic diversity and trait diversity.
 400 Thus, high carbon density and high ground-dwelling endotherm diversity do not necessarily
 401 coincide in tropical forests and biodiversity conservation will not necessarily be maximized
 402 when only carbon stocks are considered. However, in the absence of a positive relationship
 403 between carbon storage and endotherm diversity, win-win scenarios for climate change and
 404 biodiversity conservation can be achieved through multi-objective conservation planning in

405 which both carbon and biodiversity are optimized simultaneously. We therefore recommend the
 406 explicit inclusion of biodiversity in the planning and implementation of carbon storage programs.

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

416
 417 **Elevation variability**

418 TEAM sites with greater elevation variability had lower estimated richness and
 419 taxonomic diversity of ground-dwelling vertebrate species. The opposite result may have been
 420 predicted– that sites with more elevation variability might support greater habitat diversity and
 421 thus support a higher diversity of species. For example, North American mammal species
 422 richness increases with greater elevation variability (Kerr and Packer 1997). Nevertheless, we
 423 found that the diversity of tropical ground-dwelling mammals and birds declined as elevation
 424 variability increased.

425 One possible explanation is that species richness and diversity are higher at lower and/or
 426 mid elevations and decline with increasing elevation, thus a site with more elevation variability
 427 may include more sampling of high elevation areas with lower diversity. Given that relatively

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

440

441 **Stem density**

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

451

452 **Continent effects**

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

464

465 **Tree diversity**

466 The effect of tree diversity on both taxonomic diversity and trait diversity was generally
 467 positive with moderately high relative importance for predicting taxonomic and trait diversity.
 468 This suggests that tropical forests with more tree genera generally support a greater diversity of
 469 ground-dwelling endotherm taxa and traits. The question of whether diversity begets diversity –
 470 whether plant diversity is a causal agent of diversity at higher trophic levels – has been of
 471 interest to ecologists for decades (Hutchinson 1959). A number of hypotheses have been put
 472 forth to explain positive relationships between plant and animal diversity, which have been
 473 detected from local to global scales (Jetz et al. 2009). For example, higher plant diversity may

474 supply more resources or more complex vegetation structure and therefore result in niche
 475 differentiation and diversification at higher trophic levels. Alternatively, underlying abiotic
 476 factors driving overall productivity may enable greater diversity of both plants and animals.

477

478 **Implications for conservation policies**

479 This work demonstrates the value of fine-grain ground-dwelling endotherm data, which
 480 are becoming increasingly available as camera trap technology advances and costs decline,
 481 because the extent to which carbon storage programs will provide benefits to biodiversity
 482 without explicit formalization in REDD+ implementation necessitates understanding
 483 relationships between biodiversity and carbon storage (Phelps et al. 2012). While previous
 484 studies have found positive relationships between carbon storage and some aspects of tropical
 485 diversity, such as trees (Cavanaugh et al. 2014, Imai et al. 2014), we synthesized fine-grained
 486 spatial data on vertebrates and vegetation to improve understanding of the spatial congruencies
 487 between carbon and tropical terrestrial endotherm diversity, including numerous threatened
 488 species (IUCN 2014).

489 The fact that we did not find a significant relationship between carbon storage and
 490 ground-dwelling endotherm diversity supports calls for mechanisms that consider both objectives
 491 (i.e. carbon storage and diversity) during REDD+ planning and implementation. Specifically, a
 492 lack of a significant relationship suggests the potential for more endotherm diversity and carbon
 493 storage to be achieved for the same total budget if both objectives are pursued in tandem rather
 494 than independently. This finding is in line with prior empirical analyses that anticipate gains
 495 from multiple objective planning (as opposed to separate budgets and planning for biodiversity v.

496 carbon storage) that explicitly incorporate biodiversity into carbon storage programs (Venter et
 497 al. 2009, Thomas et al. 2013).

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

505

506 **Limitations and further research**

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

512 While carbon density was not found to significantly predict ground-dwelling endotherm
 513 diversity in this study, the absence of evidence is not necessarily evidence of absence. As with
 514 any null result, the finding may be due to sampling design. In addition, our study has focused on
 515 only a subset of tropical animal diversity, but carbon density may predict other components of
 516 biodiversity. For example, the height of trees in a forest positively predicts the species richness
 517 of primates, which are a largely arboreal order. Taller forests may support more primate species
 518 through vertical niche stratification (Gouveia et al. 2014). In addition, tree height is an important

519 component of carbon storage estimation (Chave et al. 2014) and differences in tree height among
 520 biogeographic regions have been linked to variation in carbon storage (Banin et al. 2014).
 521 Additional research is needed to evaluate the relationship between carbon storage and other
 522 components of tropical diversity, such as arboreal vertebrate diversity.

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

528 The TEAM Network sites are uniquely suited for addressing the relationship between
 529 terrestrial vertebrate diversity and aboveground carbon storage in the tropics because the sites
 530 include vegetation plots that overlap spatially with the camera traps. Nevertheless, the camera
 531 traps are deployed across a larger spatial extent than the vegetation plots (TEAM Network
 532 2011a). Additional variation in unmeasured vegetation characteristics may influence ground-
 533 dwelling endotherm diversity. Lastly, our analysis did not take hunting into account due to a lack
 534 of quantitative data, yet hunting can strongly affect wildlife in tropical forests (Wright 2003).
 535 The impacts of hunting likely vary among TEAM sites and warrant consideration in future
 536 studies.

537

538 **Conclusions**

539 Understanding site-level relationships between carbon storage and aspects of tropical
 540 biodiversity has important policy applications because best practices for protecting biodiversity
 541 through carbon storage programs have not yet been determined (Panfil and Harvey 2014). The

542 results of our fine-grained, site-level pantropical analysis provide quantitative biological results
 543 that suggest a lack of a significant relationship between carbon storage and ground-dwelling
 544 mammal and bird diversity. This result is robust to the use of the three diversity metrics: species
 545 richness, taxonomic diversity and trait diversity. This finding supports earlier work that suggests
 546 the need to develop conservation planning approaches that jointly optimize for carbon storage
 547 and biodiversity (Naidoo et al. 2008, Anderson et al. 2009, Siikamaki and Newbold 2012).

548 Collecting fine-grained data at all locations will likely be cost prohibitive (Gardner et al.
 549 2012). We therefore examined the relationship between ground-dwelling endotherm diversity
 550 and other site characteristics for which data collection may be cheaper. Both elevation variability
 551 and stem density were important predictors of terrestrial endotherm diversity. Site characteristics
 552 such as terrain and forest maturity can potentially function as proxies of ground-dwelling
 553 tropical endotherm diversity in future conservation planning so long as hunting is accounted for.

554
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569

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769 **Supplementary Information**

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

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

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

773 Diversity-Paper.

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Table 1. Site-level estimates for all model variables.

Site Code	Site Name	Country	Endotherm species richness (median estimate)	Endotherm taxonomic diversity (Shannon Index)	SD	Functional Diversity (FDIs)	SD	Stem density (> 10 cm dbh ha ⁻¹)	CV	Tree genus richness	CV	Tree genus diversity (Shannon 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	Caxiuaná	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 Park	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
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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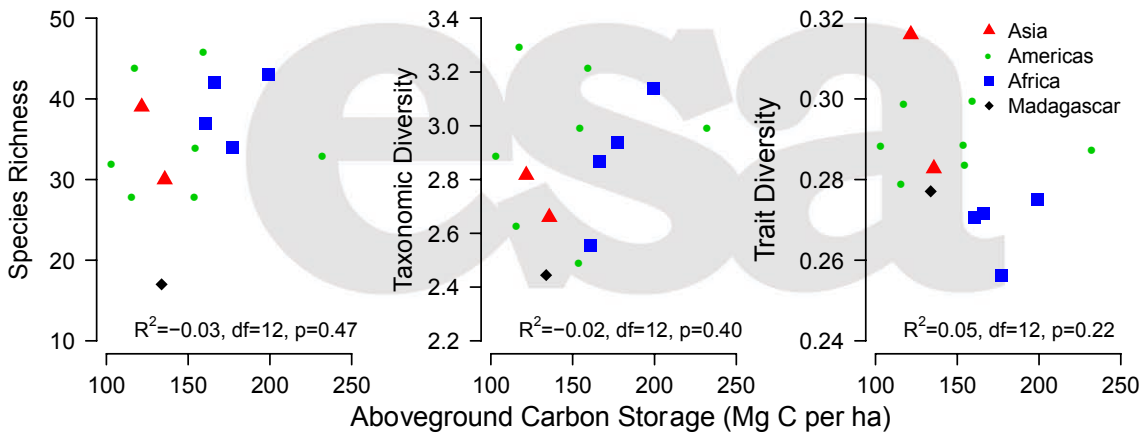
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28 Figure 2

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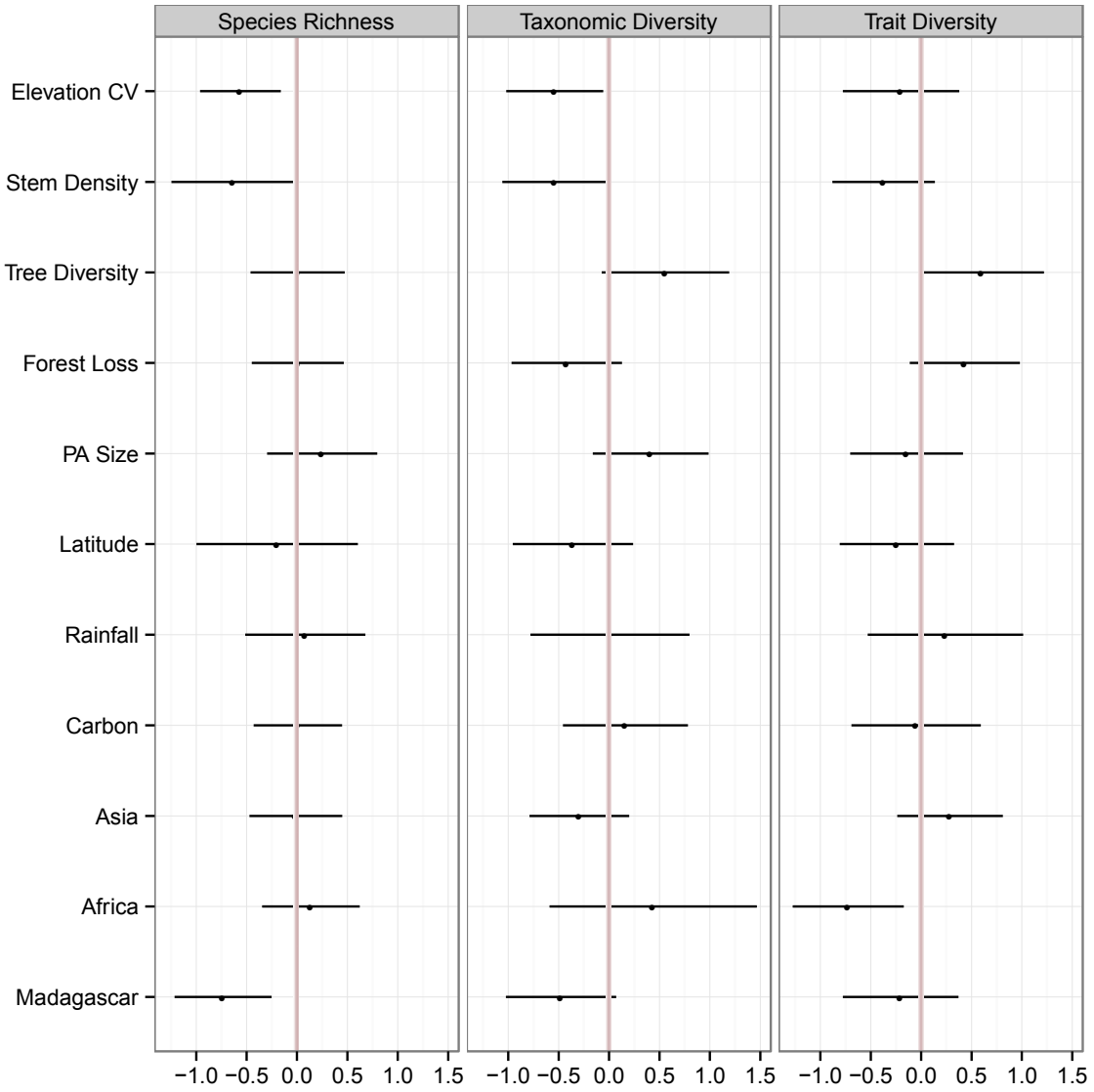
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32 Figure 3

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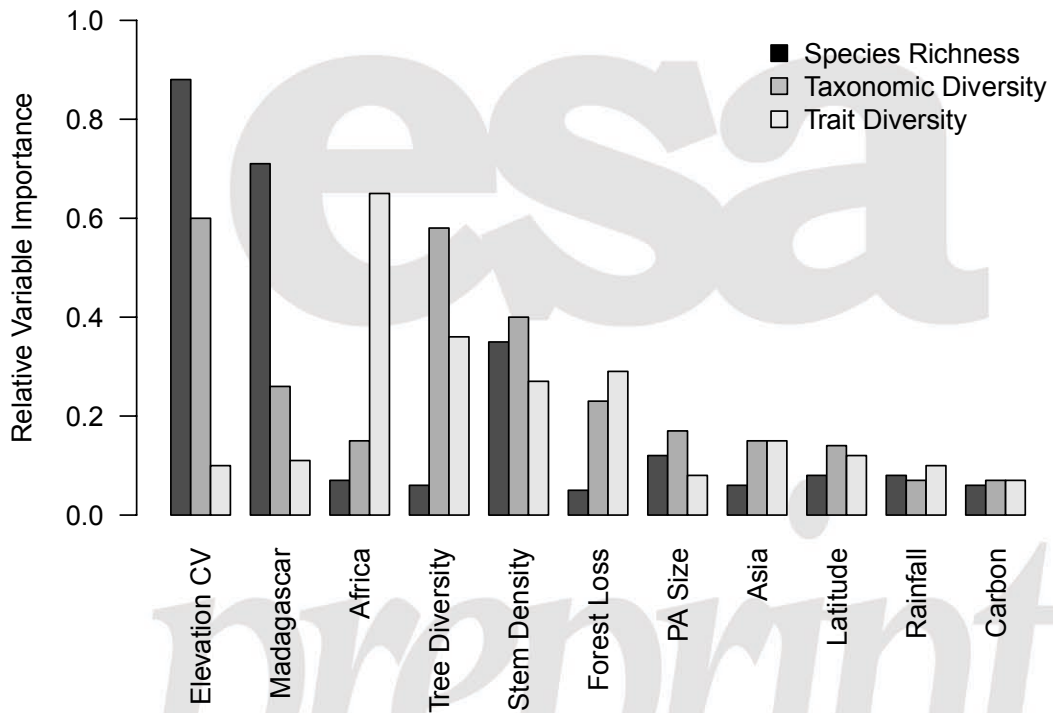
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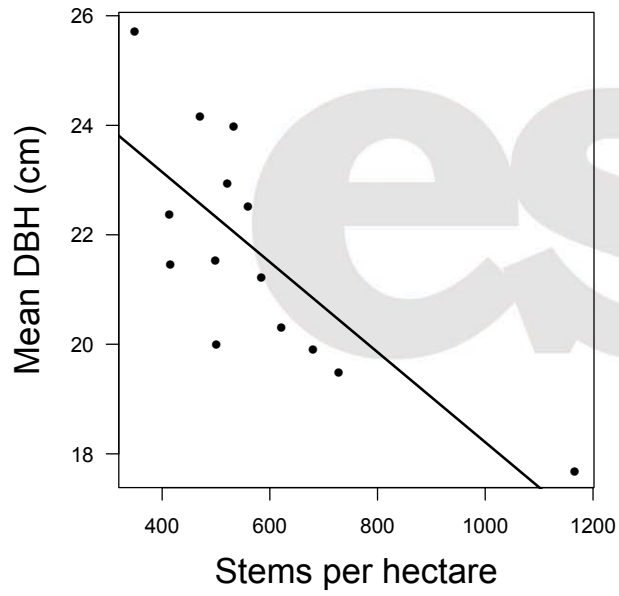
38 Figure 4



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41 Figure 5



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