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Limited carbon and biodiversity co-benefits for tropical forest mammals and birds

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

Key words: biodiversity co-benefit; camera trapping; carbon stocks; conservation planning; REDD+; tropical ecology assessment and monitoring network; wildlife conservation.

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Introduction

Biodiversity loss and climate change are two of the most significant environmental problems of the 21st century (Cardinale et al. 2012, IPCC 2014). Major initiatives to conserve biodiversity include international

commitments to expand the extent of protected areas globally and halt the loss of threatened species (Aichi Targets; Convention on Biological Diversity 2010). Programs such as Reducing Emissions from Deforestation and Forest Degradation (REDD+) offer financial incentives for developing countries to reduce their emissions by conserving carbon stocks (FAO/UNDP/UNEP 2010). In practice, however, both biodiversity conservation initiatives and carbon stock conservation programs face limited budgets that are insufficient to achieve their objectives (Eliasch 2008, McCarthy et al. 2012).

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

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

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

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

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

Methods

TEAM network study sites

Data on carbon stocks and wildlife were collected at 14 forest sites that are part of the Tropical Ecology Assessment and Monitoring (TEAM) Network, a stratified selection of field sites in tropical forests (TEAM Network 2011*a*) in Latin America, Africa, Madagascar, and Southeast Asia (Fig. 1). Sites included Barro Colorado (BCI) in Panama, Caxiuanã (CAX) in Brazil, Cocha Cashu (COU) in Peru, Manaus (MAS) in Brazil, Volcán Barva (VB) in Costa Rica, Yanachaga (YAN) in Peru, and Yasuni (YAS) in Ecuador in the Americas; Bwindi (BIF) in Uganda, Korup (KRP) in Cameroon, Nouabalé Ndoki (NNN) in the Republic of the Congo,

FIG. 1. Geographic location of the 14 TEAM sites included in this study from the Neotropics, Africa, Madagascar and Southeast Asia. Detailed information on each site is available in Table 1.

and Udzungwa (UDZ) in Tanzania in Africa; Bukit Barisan (BBS) in Indonesia and Pasoh Forest (PSH) in Malaysia in Asia, and Ranomafana (RNF) in Madagascar (Table 1).

TEAM data collection

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

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

Of the species detected by the camera traps, only those species meeting the following criteria for reliable detection were included: (1) species with average adult body size of 100 grams or more (Dunning 2008, Jones et al. 2009) and (2) predominantly ground-dwelling species that spend a large proportion of their time on or near the ground according to species descriptions (IUCN 2014, Schulenberg 2014; Animal Diversity Web, *available online*).[19] If descriptive data suggested that a species is arboreal, a species was included if there was at least one TEAM site at which the species was detected in five or more events for each year that camera trap data have been collected based on the rationale that TEAM data can be used to increase our understanding of poorly known species. Observed species lists are available in Data S1. A single taxonomic authority was used for all sites (IUCN 2014).

We used trait data on body mass and guild (carnivore, herbivore, insectivore, or omnivore; Dunning 2008, Jones et al. 2009, Schulenberg 2014; see footnote 1) for all species, and activity cycle, geographic range size, and litter size for mammals (Jones et al. 2009). These traits were selected because they provide information on feeding ecology, life history, and behavioral characteristics of the community. Missing trait values were assigned the family mean for continuous traits and family mode for categorical traits. For the 253 mammal species included in the study, family-level values were applied to missing values of body mass for two species (<1%), litter size for 60 species (23.7%), geographic area for 20 species (7.9%), activity cycle for 53 species (20.9%), and guild for six species (2.3%). For the 144 bird species included in the study, family-level values were applied to missing values of body mass for two species (1.3%) and guild for 27 species (18.75%).

Vegetation data.—At each site, TEAM monitors vegetation in six or more 1-ha plots in the core study area established following specific guidelines regarding elevation gradients, terrain, soil type, and water bodies (TEAM Network 2011*a*). Trees with diameter at breast height (DBH) of 10 cm or greater were monitored during the dry season following standardized TEAM vegetation protocols (TEAM Network 2011*b*). We included all TEAM plots for which at least 80% of stems have been identified to the family level (79 plots total; $N = 6$ plots for each site except NNN, $N = 4$; RNF, $N = 4$; YAN, $N = 1$; and VB, $N = 10$). All vegetation calculations were conducted at the genus level because this was the highest

[19] http://animaldiversity.org/

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

Site code Site name Country	Wildlife species richness (median estimate)	Wildlife taxonomic diversity (Shannon Index)	SD	Functional Diversity (FDis)	Stem density (>10 cm dbh ha^{-1})	CV	Tree genus richness	Tree genus diversity (Shannon Index)	Above ground carbon density (Mg C ha-1)	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, 0.00	0.28	418.8	0.24, 0.18, 0.11, 0.43	66.50	3.33	135.70	2,928	123	0.55	−5.660	5.1	331,155
BCI															
Barro Colorado Nature Monument - Soberania National Park															
Panama	32	2.89	0.06, 0.00	0.29	504.2	0.14, 0.11, 0.06, 0.17	71.00	3.40	103.93	2,524	94	0.45	9.163	3.0	13,800
BIF															
Bwindi Impenetrable Forest															
Uganda	37	2.56	0.11, 0.00	0.27	524.5	0.29, 0.19, 0.19, 0.42	31.17	2.45	160.61	1,325	1906	0.17	−1.010	4.7	34,276
CAX															
Caxiuanã															
Brazil	33	3.00	0.05, 0.00	0.29	474.0	0.08, 0.12, 0.09, 0.14	87.17	3.47	232.93	2,182	38	0.36	−1.770	0.5	35,407
COU															
Cocha Cashu -Manu National Park															
Peru	46	3.22	0.05, 0.00	0.30	587.5	0.05, 0.14, 0.07, 0.23	102.33	3.84	160.10	2,515	349	0.04	−11.92	0.2	1,704,506
KRP															
Korup National Park															
Cameroon	34	2.94	0.03, 0.00	0.26	501.7	0.18, 0.20, 0.09, 0.24	71.67	3.30	177.15	1,166	168	0.47	5.044	0.1	1,30,348

(Continued)

TABLE 1. Continued.

Site code Site name Country	Wildlife species richness (median estimate)	Wildlife taxonomic diversity (Shannon Index)	SD	Functional Diversity (FDis)	Stem density (>10 cm dbh ha^{-1})	CV	Tree genus richness	Tree genus diversity (Shannon Index)	Above ground carbon density (Mg C ha-1)	Annual rainfall mean (mm)	Elevation mean (m)	Elevation CV	Latitude	Forest Loss 2000–2012 ZOI (%)	Protected area (ha)
MAS Manaus Brazil	34	3.00	0.03, 0.01	0.28	624.8	0.06, 0.03, 0.02, 0.17	123.17	4.02	155.27	2,219	103	0.22	−2.660	2.0	1,198,944
NNN Nouabalé Ndoki Republic of Congo	43	3.14	0.05, 0.00	0.27	341.3	0.12, 0.10, 0.07, 0.32	48.75	3.24	199.26	1,668	460	0.05	2.498	0.1	411,653
PSH Pasoh Forest Reserve Malaysia	39	2.82	0.15, 0.01	0.32	416.8	0.31, 0.21, 0.07, 0.35	86.17	3.78	121.62	2,051	457	0.45	3.082	37.9	13,610
RNF Ranomafana Madagascar	17	2.44	0.05, 0.01	0.28	1169.3	0.18, 0.11, 0.08, 0.19	68.00	3.26	133.74	1,738	1083	0.13	−21.24	7.9	40,705
UDZ Udzungwa Tanzania	42	2.87	0.05, 0.01	0.27	536.0	0.17, 0.30, 0.29, 0.26	31.83	2.34	166.27	1,377	1144	0.32	−7.771	9.9	209,538
VB- Volcán Barva Costa Rica	28	2.49	0.14, 0.00	0.29	562.8	0.43, 0.50, 0.20, 0.41	59.60	3.25	154.54	4,368	705	1.01	10.327	3.8	49,317

(Continued)

TABLE 1. Continued.

Site code Site name Country	Wildlife species richness (median estimate)	Wildlife taxonomic diversity (Shannon Index)	SD	Functional Diversity (FDis)	Stem density (>10 cm dbh ha^{-1})	CV	Tree genus richness	Tree genus diversity (Shannon Index)	Above ground carbon density (Mg C ha-1)	Annual rainfall mean (mm)	Elevation mean (m)	Elevation CV	Latitude	Forest Loss 2000–2012 ZOI (%)	Protected area (ha)
YAN															
Yanachaga Chimillén National Park															
Peru	28	2.63	0.08, 0.01	0.28	781.0	NA	87.00	3.60	116.33	2,554	704	0.31	−10.37	3.5	2,93,234
YAS															
Yasuni															
Ecuador	44	3.30	0.04, 0.00	0.30	683.3	0.07, 0.07, 0.02, 0.07	129.50	4.15	118.08	3,135	254	0.08	−0.676	2.1	10,40,687

taxonomic resolution available for some of the stems due to constraints including lack of vouchered specimens for rare tropical species. Site-level values for each variable using vegetation data were calculated as the mean of plots at a site. Data from 2012 were used for four sites (BIF, CAX, PSH, and YAS) and data from 2011 were used for the other 10 sites to ensure concurrent camera trap and vegetation data.

Model inputs

For each site, we calculated three measures of Wildlife diversity to use as response variables: species richness, taxonomic diversity, and trait diversity. While species richness is a commonly used diversity metric, we also used a taxonomic diversity index to account for species commonness or rarity and a trait diversity index to measure variation in species characteristics.

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

Response variables: Wildlife diversity.—Species richness.—We estimated Wildlife species richness using a single-season Bayesian model of species richness that accounts for imperfect detection (Dorazio et al. 2006). Each camera trap was a sampling location and each 24-h period of the 30-d sampling period was a sampling occasion. We executed the models in R version 3.0.1 (R Core Team 2014) with the package rjags, which implements MCMC methods using the Gibbs sampler JAGS (Plummer and Stukalov 2014). We fit one model for each site using four chains with 250000 iterations, a burn-in period of 125000 iterations, and retained every third iteration. Outputs were examined for convergence. Due to the strong positive skew (Appendix S1), we modeled median estimates of species richness.

Taxonomic diversity.—We estimated an index of taxonomic diversity based on the occupancy probabilities of observed species. We estimated species and site-specific occupancy using a Bayesian model (Ahumada et al. 2013). The last 1000 iterations from the fully converged single species models formed the posterior distribution of occupancy values for each species. We then computed a distribution of the Shannon index of diversity for each site (Magurran 1988) that consisted of 1000 Shannon index values. For each calculation of a site's Shannon index, we used the occupancy values from the corresponding iteration (i.e., i in 1:1000) for the species at the site as the community composition data with the diversity function from the vegan package in R (Oksanen et al. 2013) and modeled the median from this

distribution as the taxonomic diversity response variable. The Shannon index increases as species richness and evenness increase (Magurran 1988).

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

Predictor variables: site-level environmental characteristics.—Carbon stocks—We estimated aboveground carbon density for each 1-ha 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):

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

where W is the genus wood density (g/cm), 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/ha 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 (*available online*)[20] 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.

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

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

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

Modeling

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

Next, we explored the relationship between wildlife diversity, vegetation, and environmental characteristics in addition to carbon stocks by conducting model selection and model averaging (Burnham and Anderson 2002) using the vegetation and environmental variables as potential explanatory variables. We used one of three measures of wildlife diversity as the response variable and estimated three global linear regression models using ordinary least squares.

All three global models included the eight standardized environmental predictor variables, which we selected based on our understanding of tropical vertebrate ecology. For example, we included elevation variability (CV) rather than elevation mean because elevation gradients strongly influence vertebrate species richness and abundance

[20] http://www.protectedplanet.net/

(Gaston 2000). We log-transformed protected area size and forest loss because species area relationships are typically linear on a log scale. Because species richness declines with distance from the equator, we used absolute latitude. The global models also included continent fixed effects to account for unmeasured variation between continents.

We inspected pairwise correlations between predictor variables (Data S1) to ensure there were no excessively correlated predictors. We inspected residuals of the global models for homoscedasticity and normality prior to model selection and averaging. We compared all possible models for each of the three global models using an information theoretic approach based on AIC_c (Akaike's information criterion corrected for small sample sizes). Models were ranked according to AIC_c and the confidence set of models was limited to the models that contributed to the top 95% of model weight. The parameter estimates from the models in the confidence set were used to produce estimates of predictors in an averaged model in which model estimates were weighted by their AIC_c weights. The relative importance of each predictor variable was defined by the sum of the AIC_c weights over all models in the confidence set in which the variable appeared (Burnham and Anderson 2002). We considered a predictor significant if the 95% confidence interval did not include zero. We conducted all model selection and averaging using the MuMIn package in R (Barton 2013). As a robustness check we repeated the regressions with heteroskedasticity robust standard errors (White, 1980). The robust standard errors did not change our conclusions with regard to which variables were significant in predicting biodiversity.

Results

The TEAM Network sites varied considerably in all measured characteristics. wildlife species richness estimates ranged widely across sites, from 17 species in Ranomafana to 46 species in Cocha Cashu. Wildlife taxonomic diversity (Shannon Index) ranged from 2.44 in Ranomafana to 3.30 in Yasuni (Table 1). Functional diversity (FDis Index) ranged from 0.26 in Korup to 0.32 in Pasoh Forest. The network also included large variation in estimated carbon stocks, ranging more than twofold between Barro Colorado (104 Mg C/ha) and Caxiuanã (233 Mg C/ha; Table 1). Stem density ranged from 341 stems per hectare in Nouabalé Ndoki to 1169 stems per hectare in Ranomafana. Tree genus richness ranged from 31 genera in Bwindi to 129 genera in Yasuni. Tree genus diversity (Shannon Index) ranged from 2.34 in Udzungwa to 4.15 in Yasuni. Annual rainfall varied from 1166 mm/yr in Korup to 4368 mm/yr in Volcán Barva. Elevation variability of the camera traps ranged from essentially none in Cocha Cashu (0.04 CV) to a linear elevation transect in Volcán Barva (1.01 CV). All sites except Ranomafana were within 12° latitude from the equator. The percent of forest lost in the ZOI between 2000 and 2012 varied from very little in Nouabalé Ndoki (0.01%) to considerable deforestation near Pasoh Forest (37.9%). Protected area size also varied considerably between Pasoh Forest, the smallest (13610 ha) and Cocha Cashu (1704506 ha), the largest protected area (Table 1).

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

We also examined the relationship between wildlife diversity, vegetation, and environmental characteristics, as well as carbon. Specifically, we evaluated the significance of the eight predictor variables and continent effects using the model averaged coefficient estimates from the confidence set of models. The AIC_c comparisons attributed 32% of model weight to the top model of species richness, 10% to the top model of taxonomic diversity, and 10% to the top model of trait diversity. A consistent lack of a clear top model (i.e., > 90% of model weight) indicated that model averaging was appropriate (Burnham and Anderson 2002). Parameter estimates, AIC_c values, and model weights of the confidence sets are available (Data S1).

In the context of this larger model, we again evaluated the relationship between wildlife diversity and carbon stocks. After controlling for site-specific vegetation and environmental attributes, carbon density was not a significant predictor of any measure of wildlife diversity (Fig. 3.).

We used the more general model to explore the relationship between wildlife diversity, vegetation, and environmental variables. Elevation variability had significant negative effects for both wildlife species richness and taxonomic diversity. Sites with more elevation variability had lower species richness and taxonomic diversity, which suggests that relatively flat areas support higher wildlife diversity. Stem density had a significantly negative effect on species richness and taxonomic diversity. Sites with higher stem densities had lower Wildlife diversity, which suggests that areas with relatively open forest floors support higher wildlife diversity. Additionally, Madagascar had significantly lower species richness than the other regions. None of the environmental predictors produced significant effects on trait diversity, but sites in Africa had significantly lower trait diversity than other continents (Fig. 3).

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

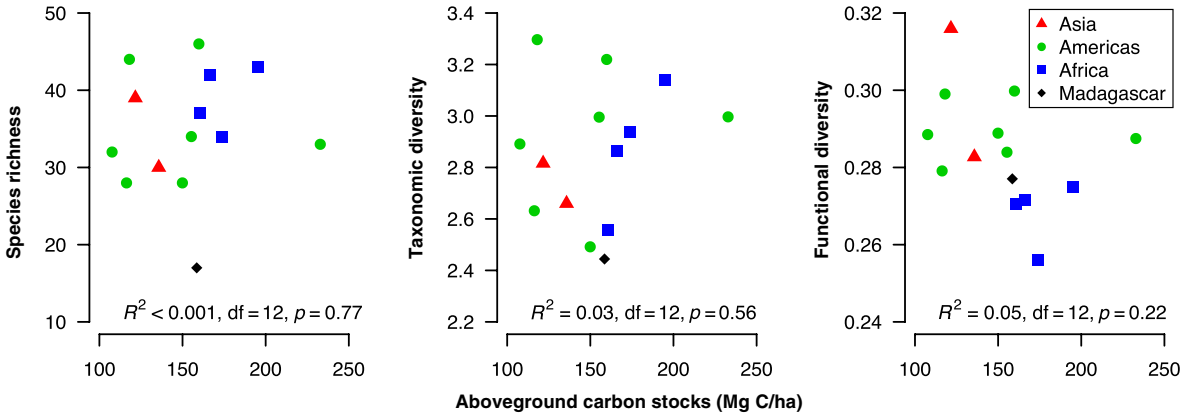

FIG. 2. Carbon density and three terrestrial vertebrate diversity metrics at 14 TEAM sites. Linear regression failed to detect significant relationships ($\alpha = 0.05$) among all sites or within continents.

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

DISCUSSION

We evaluated whether tropical conservation stocks that store the greatest carbon simultaneously support the greatest ground-dwelling mammal and bird diversity in an effort to understand whether conserving carbon rich forests will simultaneously conserve the greatest wildlife diversity. If carbon stocks and wildlife diversity are strongly correlated, then a win–win scenario for climate change and biodiversity conservation would occur by conserving forests with the greatest carbon stocks. Using data from the TEAM Network, the largest combined network of tropical camera traps and vegetation plots in the world, we did not find significant relationships between carbon density and three measures of wildlife diversity: species richness, taxonomic diversity, and trait diversity. Thus, high carbon density and high wildlife diversity do not necessarily coincide in tropical forests and biodiversity conservation will not necessarily be maximized when only carbon stocks are considered. However, in the absence of a positive relationship between carbon stocks and wildlife diversity, win–win scenarios for climate change and biodiversity conservation can be achieved through multi-objective conservation planning in which both carbon and biodiversity are optimized simultaneously. We therefore recommend the explicit inclusion of biodiversity in the planning and implementation of carbon stock conservation programs.

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

Elevation variability

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

One possible explanation is that species richness and diversity are higher at lower and/or mid elevations and decline with increasing elevation, thus a site with more elevation variability may include more sampling of high elevation areas with lower diversity. Given that relatively few mammals and birds specialize on high elevations (Laurance et al. 2011), TEAM sites with more variation in elevation may support fewer species overall because they contain high elevation areas that lack specialist species. In a number of cases, the species richness and abundances of tropical birds and mammals are greatest at low elevations and decline at higher elevations

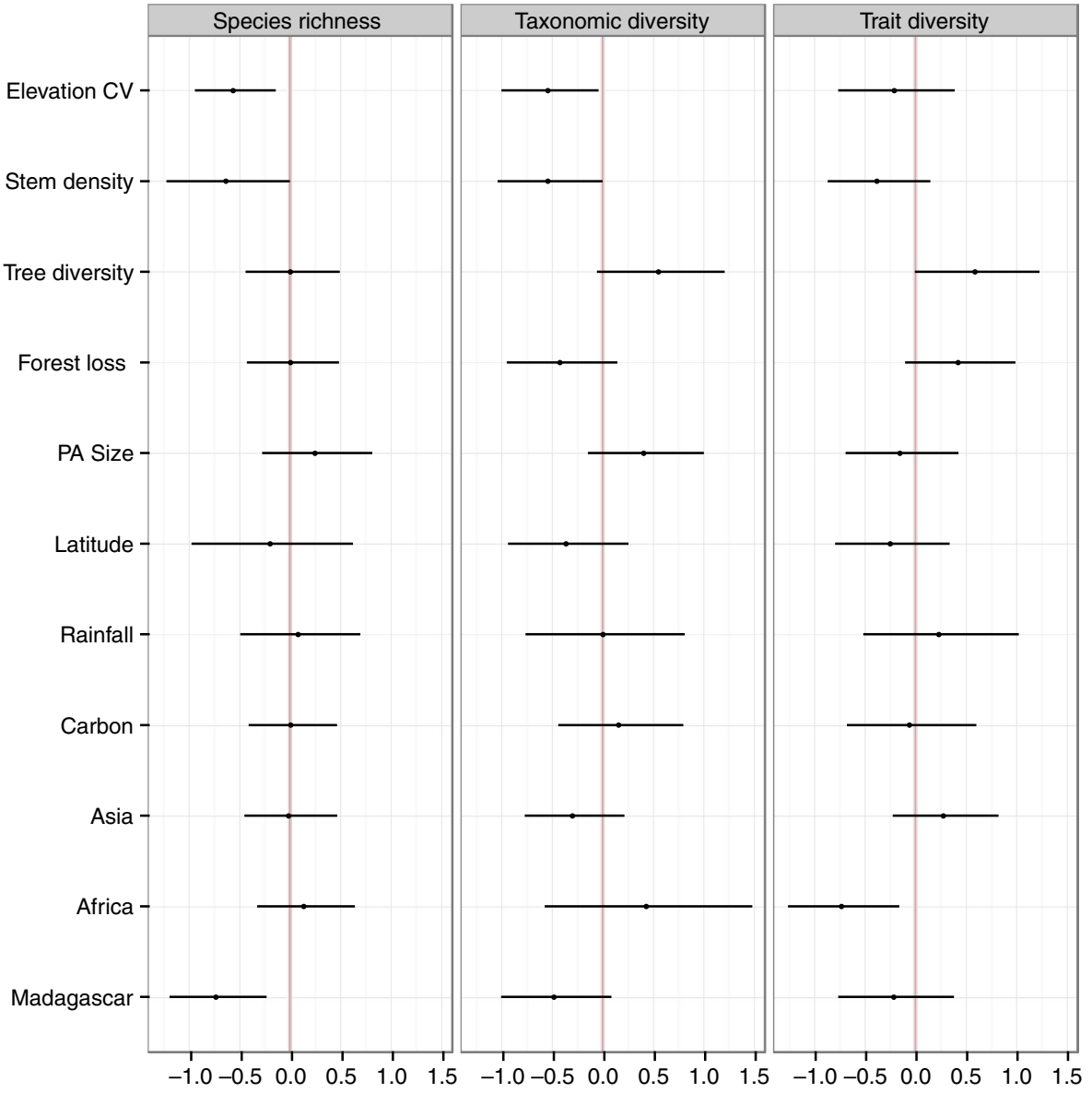

FIG. 3. Coefficient plots for averaged models of terrestrial vertebrate diversity based on the confidence set of models for three diversity measures. Standardized coefficients are shown. The filled circles represent the coefficient estimates and the bars represent the 95% confidence intervals around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

(Terborgh 1977, Marshall et al. 2014), but declining richness with increasing elevation is not a consistent biodiversity pattern (Rahbek 1995). For example, small mammal species richness peaks at intermediate elevations (McCain 2005). Due to the sparseness of tropical wildlife camera trap detections, the data from all camera traps at a TEAM site were utilized to estimate a single measure of species richness per site rather than permitting richness estimates at each camera trap. As a consequence, our analysis does not assess the elevations at which diversity is the greatest but does suggest that terrestrial vertebrate diversity declines as higher elevation sampling is included.

Stem density

We found a significant negative relationship between the density of trees (≥10 cm DBH) and both wildlife species richness and taxonomic diversity, which suggests that the diversity of tropical wildlife is higher in forests that have fewer trees. Forests that have fewer trees may have more mature trees. Disturbance in tropical forests typically leads to the growth of many young stems, which thin over time as they reach the canopy. Stem density therefore typically declines as disturbed forests age (Wright 2005). We did not examine mean DBH as a predictor variable because

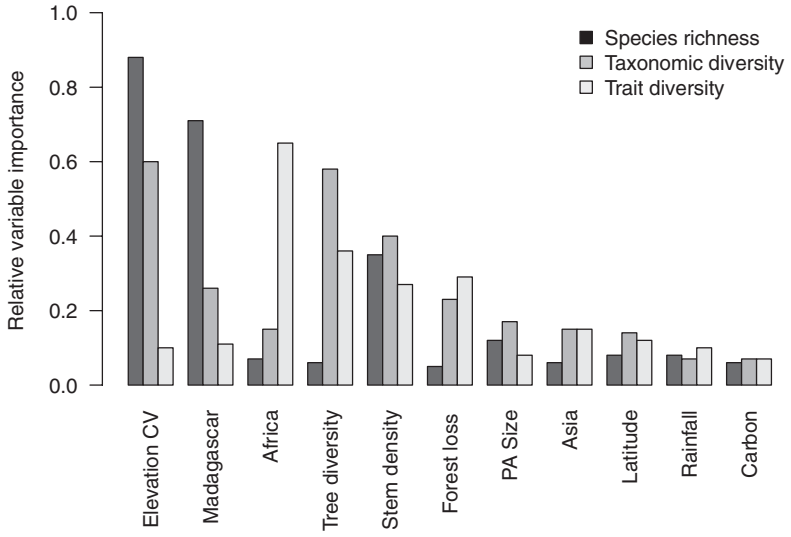

FIG. 4. Relative importance of the eight predictor variables and continent effects in the averaged models of three measures of tropical terrestrial vertebrate diversity.

DBH was used in the carbon density calculations. In a post-hoc test, however, mean DBH declined significantly with increasing stem density, which illustrates that TEAM sites with fewer trees contain larger trees (Fig. 5).

Continent effects

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

Tree diversity

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

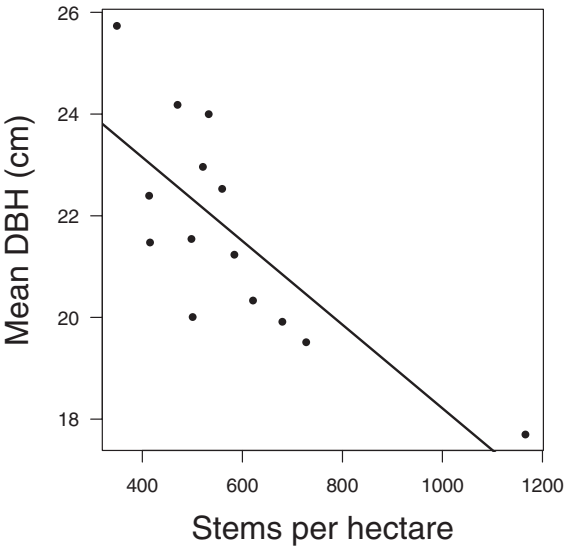

FIG. 5. Relationship between stem density and mean DBH at the 14 TEAM sites.

Implications for conservation policies

The extent to which carbon stock conservation programs will provide benefits to biodiversity without explicit formalization in REDD+ implementation necessitates understanding relationships between biodiversity and carbon stocks (Phelps et al. 2012). While previous studies have found positive relationships between carbon stocks and some aspects of tropical diversity, such as trees (Cavanaugh et al. 2014, Imai et al. 2014), we synthesized fine-grained spatial data on vertebrates and vegetation to improve understanding of the spatial congruencies between carbon and tropical wildlife diversity, including numerous threatened species (IUCN 2014).

The fact that we did not find a significant relationship between carbon stocks and wildlife diversity supports calls for mechanisms that consider both objectives (i.e., carbon stocks and diversity) during REDD+ planning and implementation. Specifically, a lack of a significant relationship suggests the potential for higher wildlife and carbon stocks to be achieved for the same total budget if both objectives are pursued in tandem rather than independently. This finding is in line with prior empirical analyses that anticipate gains from multiple objective planning (as opposed to separate budgets and planning for biodiversity vs. carbon stock conservation) that explicitly incorporate biodiversity into carbon stock conservation programs (Venter et al. 2009, Thomas et al. 2013).

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

Limitations and further research

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

While carbon density was not found to significantly predict ground-dwelling mammal and bird diversity in this study, the absence of evidence is not necessarily evidence of absence. As with any null result, the finding may be due to sampling design. In addition, our study has focused on only a subset of tropical animal diversity, but carbon density may predict other components of biodiversity. For example, the height of trees in a forest positively predicts the species richness of primates, which are a largely arboreal order. Taller forests may support more primate species through vertical niche stratification (Gouveia et al. 2014). In addition, tree height is an important component of carbon stock estimation (Chave et al. 2014) and differences in tree height among biogeographic regions have been linked to variation in carbon stocks (Banin et al. 2014). Additional research is needed to evaluate the relationship between carbon stocks and other components of tropical diversity, such as arboreal vertebrate diversity.

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

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

Conclusions

Understanding site-level relationships between carbon stocks and aspects of tropical biodiversity has important policy applications because best practices for protecting biodiversity through carbon stock conservation programs have not yet been determined (Panfil and Harvey 2014). The results of our fine-grained, site-level pantropical analysis provide quantitative biological results that suggest a lack of a significant relationship between carbon stocks and ground-dwelling mammal and bird diversity. This result is robust to the use of the three diversity metrics: species richness, taxonomic diversity, and trait diversity. This finding supports earlier work that suggests the need to develop conservation planning approaches that jointly optimize for carbon stocks and biodiversity (Naidoo et al. 2008, Anderson et al. 2009, Siikamaki and Newbold 2012).

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

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1890/15-0935.1/suppinfo

Data Availability

Data associated with this paper are available from the Tropical Ecology Assessment and Monitoring (TEAM) Network: teamnetwork.org/data