Received: 26 September 2019 | Revised: 2 December 2019 | Accepted: 17 December 2019
DOI: 10.1111/conl.12699

Conservation Letters
A journal of the Society for Conservation Biology
Open Access
WILEY

LETTER

Tree diversity and carbon storage cobenefits in tropical human-dominated landscapes

Anand M. Osuri[1,2] | **Siddarth Machado**[3,4] | **Jayashree Ratnam**[4] | **Mahesh Sankaran**[4,5] | **N. Ayyappan**[6] | **S. Muthuramkumar**[7] | **N. Parthasarathy**[8] | **Raphaël Pélissier**[6,9] | **B. R. Ramesh**[6] | **Ruth DeFries**[10] | **Shahid Naeem**[10]

[1]The Earth Institute, Columbia University, New York, New York
[2]The Nature Conservancy, Arlington, Virginia
[3]School of Forest Resources and Conservation, University of Florida, Gainesville, Florida
[4]National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, Karnataka, India
[5]School of Biology, University of Leeds, Leeds, UK
[6]Department of Ecology, French Institute of Pondicherry, Puducherry, India
[7]Department of Botany, V. H. N. S. N. College (Autonomous), Virudhunagar, Tamil Nadu, India
[8]Department of Ecology and Environmental Sciences, Pondicherry University, Puducherry, India
[9]AMAP Lab, IRD, CIRAD, CNRS, INRA, University of Montpellier, Montpellier, France
[10]Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York

Correspondence
Anand M. Osuri, Nature Conservation Foundation, 1311, "Amritha," 12th Main, Vijayanagar 1st Stage, Mysore 570 017, India.
Email: moanand@gmail.com

Funding information
Science and Engineering Research Board, Grant/Award Numbers: PDF/2016/000104, SERB/SR/SO/PS/78/2012; Nature Conservancy; Earth Institute, Columbia University

Abstract

A lack of spatial congruence between carbon storage and biodiversity in intact forests suggests limited cobenefits of carbon-focused policies for conserving tropical biodiversity. However, whether the same applies in tropical human-dominated landscapes (HDLs) is unclear. In India's Western Ghats Biodiversity Hotspot, we found that while HDL forests harbor lower tree diversity and aboveground carbon stocks than relatively intact forests, positive diversity–carbon correlations are more prevalent in HDLs. This is because anthropogenic drivers of species loss in HDLs consistently reduce carbon storing biomass volume (lower basal area), and biomass per unit volume (fewer hardwood trees). We further show, using a meta-analysis spanning multiple regions, that these patterns apply to tropical HDLs more generally. Thus, while complementary strategies are needed for securing the irreplaceable biodiversity and carbon values of intact forests, ubiquitous tropical HDLs might hold greater potential for synergizing biodiversity conservation and climate change mitigation.

KEYWORDS

basal area, biodiversity conservation, carbon storage, climate change, forest degradation, meta-analysis, tree density, tropical forests, Western Ghats, wood density

1 | INTRODUCTION

Tropical forest loss and degradation are leading drivers of the global biodiversity decline (Giam, 2017), and constitute a major anthropogenic source of carbon dioxide to the atmosphere (Pan et al., 2011). International climate change mitigation policies such as Reducing Emissions from Deforestation and forest Degradation (REDD+) aim to enhance terrestrial carbon storage by incentivizing forest conservation and restoration (UNFCC, 2018). Such climate-focused policies potentially offer "cobenefits" for biodiversity conservation in tropical forests (Gilroy et al., 2014; Strassburg et al., 2010).

Carbon-biodiversity cobenefits can occur in areas where priority locations for carbon storage overlap with locations of high biodiversity (Phelps, Webb, & Adams, 2012). In tropical (and other) forests, where trees are the primary agents of ecosystem carbon uptake, previous studies have reported a positive tree diversity–carbon relationship at small spatial scales (0.04 ha), and among young forests, potentially driven by "biodiversity" mechanisms such as niche complementarity (Chisholm et al., 2013; Lasky et al., 2014). By contrast, studies in mature and relatively intact forests (i.e., low human footprint) point to the lack of a consistent tree diversity–carbon relationship at larger spatial scales (1.0 ha) (Chisholm et al., 2013; Ferreira et al., 2018; Sullivan et al., 2017). This is because the environmental gradients driving variation in tree diversity in such forests (e.g., soil nutrients, moisture) are not consistently related to attributes of forest structure (e.g., basal area) and species composition (e.g., abundances of hardwood species) that govern the diversity–carbon relationship at larger scales (Chisholm et al., 2013; Sullivan et al., 2017).

While the evidence from relatively intact forests points to a lack of tree diversity–carbon cobenefits, whether the same applies to remnant tropical forests of human-dominated landscapes (HDLs), is unclear. HDLs harbor the majority of Earth's remaining tropical forests (Lewis, Edwards, & Galbraith, 2015; Watson et al., 2018), and are crucial for sustaining biodiversity and carbon storage in many regions (Gardner et al., 2009; Magnago et al., 2015). Chronic anthropogenic disturbances in HDLs such as forest fragmentation, resource extraction, and degradation to secondary forests, are associated with abiotic (e.g., increased light) and biotic (e.g., declines of animal seed dispersal) changes that reduce tree diversity (Letcher & Chazdon, 2009; Santos et al., 2008) and alter forest structure and tree species composition in ways that affect carbon storage (Osuri, Kumar, & Sankaran, 2014). These changes include reduced tree density and basal area (de Paula, Costa, & Tabarelli, 2011), which results in lower biomass volume for storing carbon, and reduced abundances of tree species with high wood density (Laurance et al., 2006), which lowers biomass per unit volume. Further, spatial heterogeneity in fragmentation and disturbance impacts can drive gradients of tree diversity, tree density, basal area, average wood density, and carbon storage, but few studies (e.g., Magnago et al., 2015) have assessed patterns of congruence and implications for diversity–carbon cobenefits in HDLs. Understanding how and why the diversity–carbon relationship differs between HDLs and intact forests can promote conservation strategies based on cobenefits that consider heterogeneity within, and are more representative of, the tropical forest biome as a whole.

This study examines the nature of, and factors underlying, the relationship between tree species richness (TSR) and aboveground carbon storage (ACS) in tropical HDLs. We test the hypothesis that anthropogenic disturbance drives concomitant declines of TSR (all/endemic species), and of attributes related to forest structure (tree density and basal area) and tree species composition (average wood density) that govern ACS, such that diversity–carbon cobenefits are more prevalent among HDL forests than relatively intact forests. We test this hypothesis using small- (0.04 ha) and large- (1.0 ha) scale plot data from HDLs in India's Western Ghats, and examine the generality of our findings using a meta-analysis spanning HDLs in multiple tropical regions.

2 | METHODS

2.1 | Western Ghats data

The Western Ghats Mountains in southern India, along with Sri Lanka, are one of 36 global biodiversity hotspots (https://www.cepf.net/our-work/biodiversity-hotspots). Native tropical forests of the Western Ghats underwent extensive loss (40%) and fragmentation (80% decrease in patch sizes and 400% increase in patch numbers) during 1920–1990, largely due to the expansion of agriculture and coffee plantations (Menon & Bawa, 1997). While around 12% of the Western Ghats is protected by the State as nature reserves, remnant forests with less formal protection situated in surrounding HDLs are crucial for conserving biodiversity (Das et al., 2006), and sustain significant carbon stocks (Osuri et al., 2014).

Our study is based on plot datasets from HDLs in the central Western Ghats (CWG) and the Anamalai Hills (AH) in the southern Western Ghats (Figure 1). Both landscapes comprise fragmented tropical rainforests interspersed among settled agriculture and/or horticulture plantations that date back at least two centuries. Forests in both landscapes range in anthropogenic disturbance from relatively undisturbed areas (e.g., within or abutting State-protected forests) to degraded primary forests that are fragmented and subject to extractive resource use—that is, for fuelwood, and occasionally for timber (Muthuramkumar et al., 2006; Ramesh et al., 2010b).

The CWG dataset comprised sixty-eight 1-ha plots, including 33 plots in structurally and compositionally intact

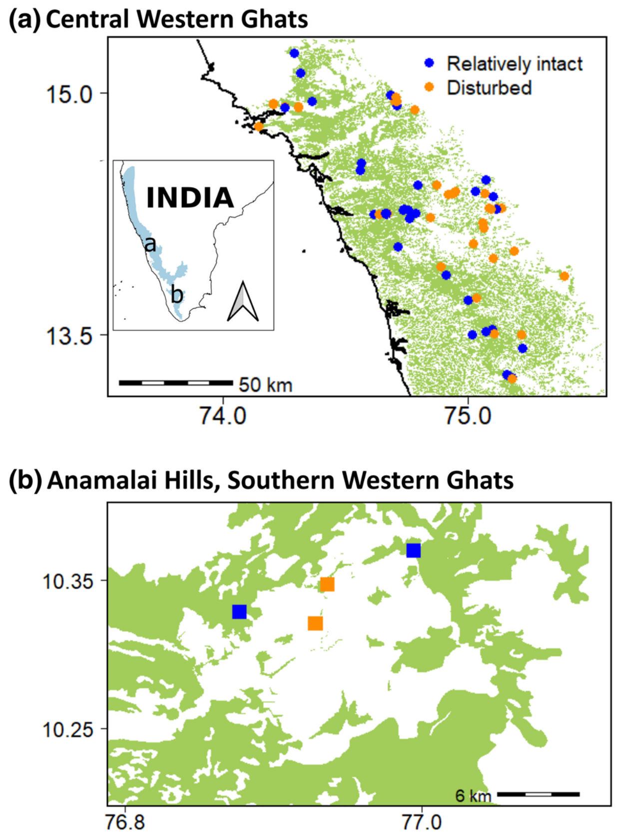

FIGURE 1 The two tropical HDLs in (a) the central Western Ghats and (b) Anamalai Hills of the southern Western Ghats, India. Green shading depicts wet evergreen forest. Points in (a) indicate locations of individual 1-ha plots, and in (b) the locations of sites within which multiple 0.04 ha plots (20–25) were sampled. Forest cover maps were derived from layers generated by French Institute of Pondicherry, available at http://indiabiodiversity.org/

wet-evergreen forests, as classified by the dataset authors, and 35 plots in wet-evergreen forests that were more fragmented, and structurally and/or compositionally degraded. (Ramesh et al., 2010a). Degradation was assessed by the authors of the dataset based on indicators such as decreased canopy cover (structure), and prevalence of deciduous and/or disturbance-adapted species within tree communities (composition) (Ramesh et al., 2010a). The AH dataset comprised ninety 0.04-ha plots, including 50 relatively unfragmented intact forest plots, and 40 plots in more degraded forest fragments (Muthuramkumar et al., 2006; Osuri, Chakravarthy, & Mudappa, 2017).

Plot classification and sampling details are available in Ramesh et al. (2010a) and Muthuramkumar et al. (2006). The former dataset reported species names and girth at breast height (gbh) of all trees over 10 cm gbh (3.18 cm diameter at breast height [dbh]), and was filtered to retain trees ≥10 cm dbh only. The latter recorded species names and gbh of all trees over 30 cm gbh (9.5 cm dbh).

2.2 | Multiregion data

We searched the scientific literature for data on TSR, composition, and forest structure in tropical HDLs. We searched for keywords and phrases such as "tropical forest tree fragment," "tropical forest secondary," and "tropical forest recovery" on the ISI Web of Science (www.webofknowledge.com), within the Dryad data repository (https://datadryad.org/), and the PREDICTS database (Hudson et al., 2017), for relevant datasets. We also examined literature cited by, and citing, studies identified through our primary searches. Given the focus on HDLs, we only considered studies from landscapes featuring sustained human occupation and land use, that is, fragmented primary or secondary forests in landscapes with settled or shifting agriculture, or pastures, were included, but studies in remote logging concessions without sustained human presence were not. Studies from 10 tropical countries reporting plot-level estimates of TSR and/or species composition and/or tree density and/or basal area from disturbed forests (e.g., fragments, secondary forests), or disturbed and relatively intact forests in HDLs, were retained for further analyses (Table S1).

2.3 | Variables assessed

Tree species richness (species/plot), tree density (trees/plot), basal area (m^2/plot), community-weighted average wood density (g/cm^3), and aboveground carbon storage (Mg/plot) were assessed in the Western Ghats datasets. Community-weighted average wood density was estimated at the plot level as $\Sigma R_i . W_i$, where R_i and W_i are relative abundance and wood density, respectively, of each species i. TSR, tree density (TD), basal area (BA) and community-weighted average wood density (WD) were included in the meta-analysis. Species wood densities were obtained from primary sources (AMO, SM, JR, MS and colleagues, unpublished data from the Western Ghats), and from the Global Wood Density Database (Zanne, Lopez-Gonzalez, & Coomes, 2009). In cases of species wood density data being unavailable, genus averages constrained by continent were used (Chave et al., 2006).

Tree height (H, in meters) and aboveground biomass (AGB_{est}, in kg) in the WG plots were estimated using the following general equations for tropical trees:

$$\ln\,(H) = 0.893 - E + 0.760\ln\,(D) - 0.0340[\ln\,(D)]^2,$$

$$AGBest\ = 0.0673 \times \left(\rho D^2 H\right)^{0.976},$$

where D is tree diameter at breast height (cm), ρ is wood density (g/cm^3), and E is a measure of environmental stress (temperature/precipitation) constraining tree diameter–height relationships (Chave et al., 2014). ACS of trees lacking species- or genus-level estimates was estimated by substituting the average wood density across all individuals

TABLE 1 Tree species richness (all and endemic), carbon storage, tree density, basal area, and community-weighted average wood density in relatively intact and disturbed forests in HDLs of the Central Western Ghats and Anamalai Hills in India. Average values across plots and corresponding 95% CIs (in parentheses) are reported

	Central Western Ghats (1.0-ha plots)		Anamalai Hills (0.04-ha plots)	
	Relatively intact ($N = 33$)	Disturbed ($N = 35$)	Relatively intact ($N = 50$)	Disturbed ($N = 40$)
Species richness (species/plot)	46.7 (42.7–50.7)	33.8 (29.5–38.0)	13.0 (12.1–13.9)	8.3 (7.2–9.3)
Endemic species richness (species/plot)	17.4 (15.3–19.6)	5.7 (3.8–7.5)	3.5 (3.0–4.1)	0.7 (0.4–0.9)
Aboveground carbon stocks (Mg/plot)	187.4 (149.5–225.4)	94.6 (77.6–111.6)	18.3 (15.3–21.3)	10.1 (8.1–12.1)
Tree density (trees/plot)	453.9 (392.7–515.0)	242.8 (203.7–282.0)	20.8 (19.4–22.2)	15.8 (14.3–17.4)
Basal area (m^2/plot)	32.7 (29.1–36.4)	19.0 (15.8–22.2)	3.4 (2.9–3.8)	2.1 (1.8–2.4)
Average wood density (g/cm^3)	0.64 (0.62–0.66)	0.63 (0.63–0.64)	0.59 (0.58–0.59)	0.51 (0.49–0.53)

with known wood densities in the respective plots. Carbon stocks were assumed to constitute 47.78% of aboveground biomass, corresponding to estimates for stem carbon content for evergreen trees from Ma et al. (2018).

2.4 | Analysis

2.4.1 | Western Ghats plots

We assessed the relationship of overall TSR, and richness of endemic tree species, with ACS, TD, BA, and WD in the CWG (1.0 ha) and AH (0.04 ha) datasets using Pearson's correlation coefficients. Log transformations were applied to ACS and BA on account of the skewed distributions of these responses.

We used a bootstrapping approach to examine how correlations of TSR with ACS, TD, BA, and WD vary in relation to forest disturbance in the 1.0-ha and 0.04-ha datasets. Starting with the pool of relatively intact forests in each dataset, we iteratively replaced randomly selected intact forest plots with randomly selected disturbed forest plots, such that the total number of plots remained constant (thirty-three 1-ha and forty 0.04-ha plots). At every increasing level of disturbed plot prevalence, we estimated TSR-ACS, TSR-TD, TSR-BA, and TSR-WD correlations. We examined whether correlation coefficients for each relationship (averaged over 100 simulation runs) increased with the percentage of disturbed forest plots.

2.4.2 | Multiregional data

Using data from 15 tropical HDLs, we first estimated Standard Mean Differences (SMDs) in TSR, TD, BA, and WD between relatively intact and disturbed forests of each landscape as:

$$\frac{\bar{X}_D - \bar{X}_I}{SD},$$

where $\bar{X}_D$ and $\bar{X}_I$ denote mean values in disturbed and intact forests, respectively, and SD represents average standard deviation across disturbed and intact forests. As above, we also estimated correlations of TSR with TD, BA, and WD across plots within each HDL.

The meta-analyses of SMD and correlation coefficients were performed using the "metacont" and "metacor" functions of the "meta" package, respectively, with a random effects model specified to take into account heterogeneity in sampling designs and other study characteristics across the different HDLs (Schwarzer, 2015). We interpreted mean and 95% confidence intervals (CI) of the SMD estimates across studies to infer whether disturbance consistently decreases (negative mean and 95% CI range), increases (positive mean and 95% CI range), or does not affect (95% CI range includes zero), the focal responses. Similarly, we interpreted the mean and 95% CI from the meta-analysis of correlation coefficients to infer whether TD, BA and WD are positively (positive mean and 95% CI), negatively (negative mean and 95% CI) or not related to TSR.

All data processing, statistical analyses and preparation of figures were performed using R version 3.6.0 (R Core Team, 2019).

3 | RESULTS

In the Western Ghats, TSR, ACS, TD, and BA were consistently lower in disturbed forests than in intact forests in both landscapes, while disturbed forests in the AH (0.04 ha plots) also had lower WD (Table 1). ACS correlated positively with overall TSR (Pearson's $r = .43$ and .35 [$p < .01$] among 1.0 ha and 0.04 ha plots, respectively), and with endemic species richness (Pearson's $r = .51$ and .59, $p < .01$) in both landscapes (Figure 2). TSR was positively correlated with TD (Pearson's $r = .61$ and .66, $p < .01$) and with BA (Pearson's $r = .50$ and .36, $p < .01$) in both landscapes (Figures 3a, b, d, e), and positively correlated with WD across 0.04 ha plots in AH (Pearson's $r = .43$, $p < .01$; Figure 3f), but not the 1.0 ha CWG plots (Figure 3c). Further, using the unfiltered CWG dataset (all trees ≥ 3.18 cm dbh), we verified that including smaller trees does not alter the above patterns and relationships (Table S2).

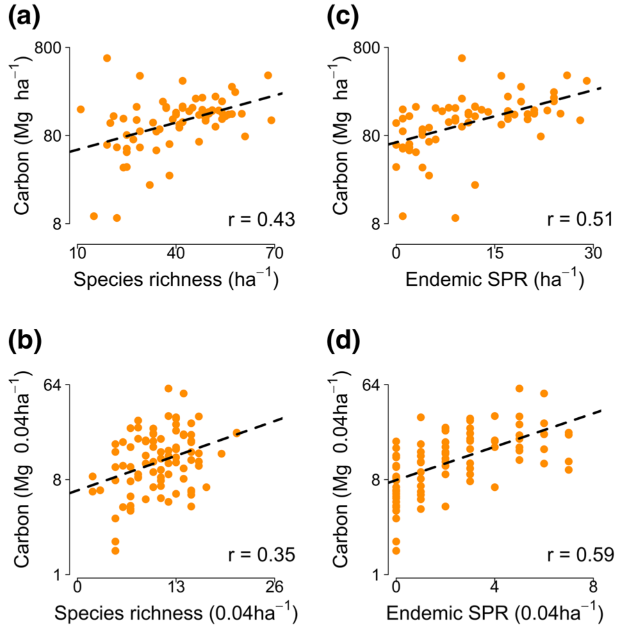

FIGURE 2 Relationships of tree species richness and endemic tree species richness with aboveground carbon storage across relatively intact and disturbed forest plots in the central Western Ghats (a, c), and Anamalai Hills (b, d). Broken lines depict predictions of simple linear regression models. Pearson's correlation coefficients (*r*) are reported

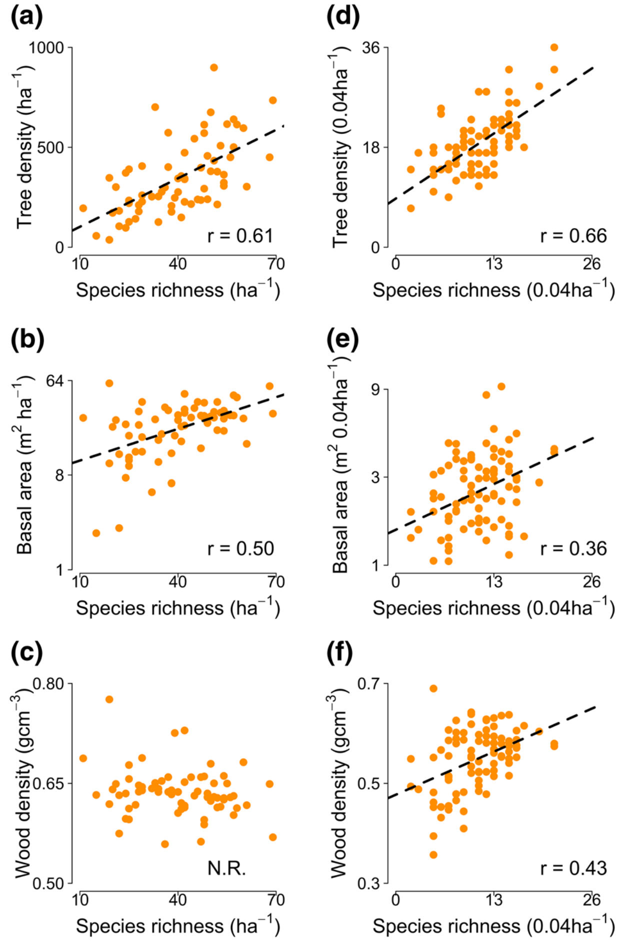

FIGURE 3 Relationships of tree species richness with tree density, basal area, and community-weighted average wood density, across relatively intact and disturbed forest plots in the central Western Ghats (a–c) and the Anamalai Hills (d–f). Broken lines depict predictions of simple linear regression models. Pearson's correlation coefficients (*r*) are reported. N.R. indicates no relationship

In the bootstrapping simulations, higher percentages of disturbed forest plots were associated with a stronger positive correlation between TSR and ACS, on average, in both landscapes (Figures 4a, e). Greater percentages of disturbed forest plots were also associated with stronger positive correlations of TSR with BA and with WD in both landscapes (Figures 4c, d, g, h), and of TSR with TD in the CWG (1.0 ha plots) landscape (Figure 4b). Interestingly, TSR-ACS and TSR-BA correlations (both landscapes), TSR-TD correlations (CWG; 1.0 ha plots), and TSR-WD correlations (AH; 0.04 ha plots) showed a nonmonotonic relationship with the percentage of disturbed forests, with more positive correlations among mixtures of disturbed and intact forest plots (50%–70% disturbed plots), on average, than for either type exclusively (Figures 4a, b, c, e, g, h).

In the multiregional meta-analysis, TSR, BA and WD were consistently lower (38%-74%) in disturbed forests than in remnants of relatively intact tropical forests within HDLs (Figure 5a). Correlations of TSR with TD, BA, and WD were positive (0.26–0.66, on average) across multiple HDLs (Figure 5b).

4 | DISCUSSION

As the anthropogenic footprint in the tropics continues to expand (Lewis et al., 2015), averting losses of the irreplaceable biodiversity and carbon stocks of intact tropical forests (Watson et al., 2018), and securing the conservation and carbon storing potential of forests in ubiquitous human-dominated landscapes (Gardner et al., 2009; Magnago et al., 2015), pose a dual challenge. In intact forests, previous research highlighting the lack of a consistent diversity–carbon relationship underscores the importance of complementary approaches to conservation and climate change mitigation in Earth's most biodiverse and carbon-rich ecosystem (Chisholm et al., 2013; Ferreira et al., 2018; Sullivan et al., 2017).

By contrast, our results from the Western Ghats suggest that although forests in HDLs cannot match intact forests for biodiversity or carbon storage in absolute terms, there is greater congruence between tree diversity (overall and endemic species) and carbon storage across forests in these landscapes at small (0.04 ha) and larger (1.0 ha) scales. This is

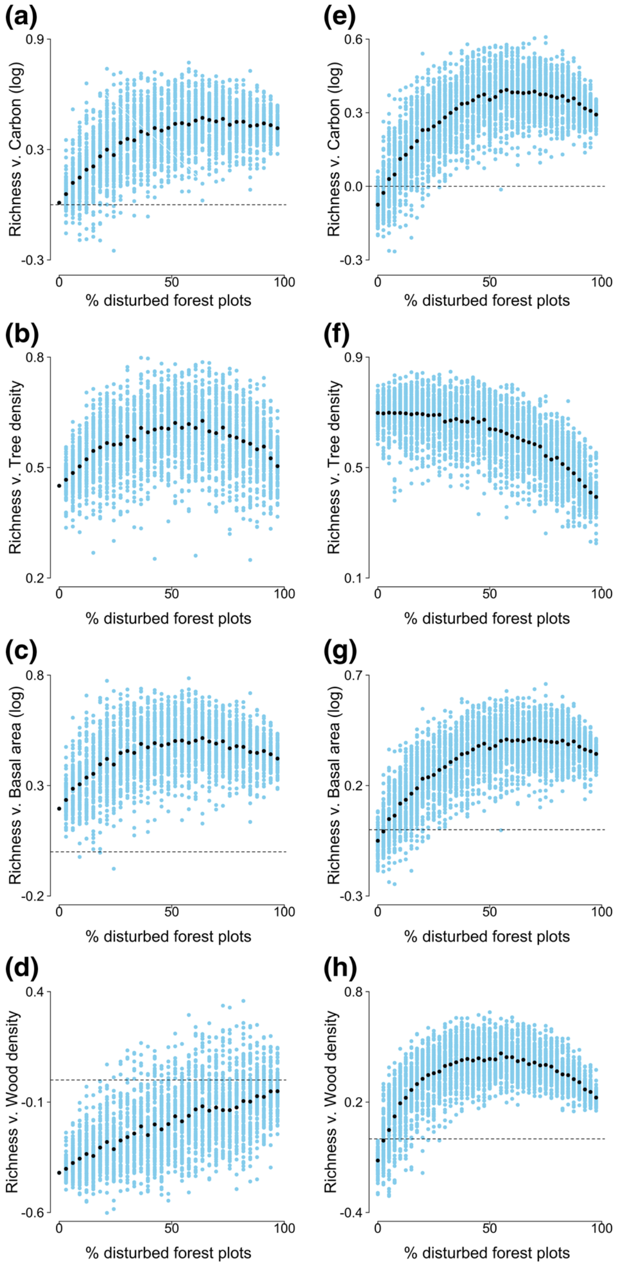

FIGURE 4 Bootstrapped simulation results showing correlations of tree species richness with carbon storage, tree density, basal area, and average wood density at increasing proportions of disturbed forest plots in the central Western Ghats (a–d) and Anamalai Hills (e–h). Blue points represent outcomes of individual simulation runs, and black points represent averages across simulations ($N = 100$), at each level of disturbed plot prevalence

consistent with other studies that have reported tree diversity–carbon cobenefits in HDLs (Magnago et al., 2015; Matos et al., 2019), and with emerging evidence on the diversity of other groups such as mammals and birds, which also appear more congruent with carbon storage over space in HDLs (Deere et al., 2018, Van de Perre et al., 2018) than in intact forests (Beaudrot et al., 2016; Ferreira et al., 2018).

Our findings suggest that the diversity–carbon relationship in HDLs results from anthropogenic disturbances driving convergent responses of tree diversity and attributes of forest structure and tree species composition that govern aboveground carbon storage at small (0.04) and larger (1.0 ha) scales. Consistent with previous findings (Laurance et al., 2006; Osuri et al., 2014; Santos et al., 2008), forest fragmentation and disturbance in the Western Ghats HDLs were associated with tree species loss, reductions in carbon storing biomass volume (fewer trees, lower basal area), and/or reductions in biomass per unit volume (lower average wood density). Important sites for tree diversity, endemic species, and hardwood species—which are often a priority for conservation (Slik et al., 2008)—are therefore more likely to overlap with areas of high carbon storage in HDLs harboring disturbed forests, or a mix of disturbed and relatively intact forests, than in intact forests alone, as suggested by our bootstrapping simulations. The simulations also suggest that the greatest congruence between tree diversity and carbon storage might occur at intermediate levels of disturbed plot prevalence, possibly because intact and disturbed forests together span wider gradients of tree diversity and carbon-related attributes than either type of forest alone (Figure S1).

The results of our meta-analysis suggest that positive correlations between tree diversity and carbon storage potentially occur widely across the human-dominated tropics, mediated by consistency and congruence among the responses of tree diversity, basal area, and average wood density, to forest fragmentation and other disturbances. The strength of such relationships would likely vary with disturbance type and severity (Ferreira et al., 2018), and relationships would potentially be more temporally stable among older forests in fragmented landscapes—because of limited or slow recovery from disturbance in such forests (Tabarelli, Lopes, & Peres, 2008)—compared to younger forests in less fragmented landscapes (Lasky et al., 2014).

Collectively, our findings support the hypothesis that carbon-focused forest policies and management are more likely to align with priorities for tree diversity conservation (i.e., cobenefits) in tropical HDLs than in intact forest landscapes. For example, incentive programs geared towards securing forest carbon stocks from deforestation and degradation are likely to extend protection for species-rich remnants of mature forests, which are crucial for conservation in heavily fragmented and human-dominated biodiversity hotspots such as the Atlantic Forest (Magnago et al., 2015) and the Western Ghats. Restoration of presently degraded forests for future carbon and biodiversity benefits by, for example, promoting spontaneous natural recovery (Matos et al., 2019), or active restoration of degraded forests (Osuri, Kasinathan, Siddhartha, Mudappa, & Raman, 2019), could also offer

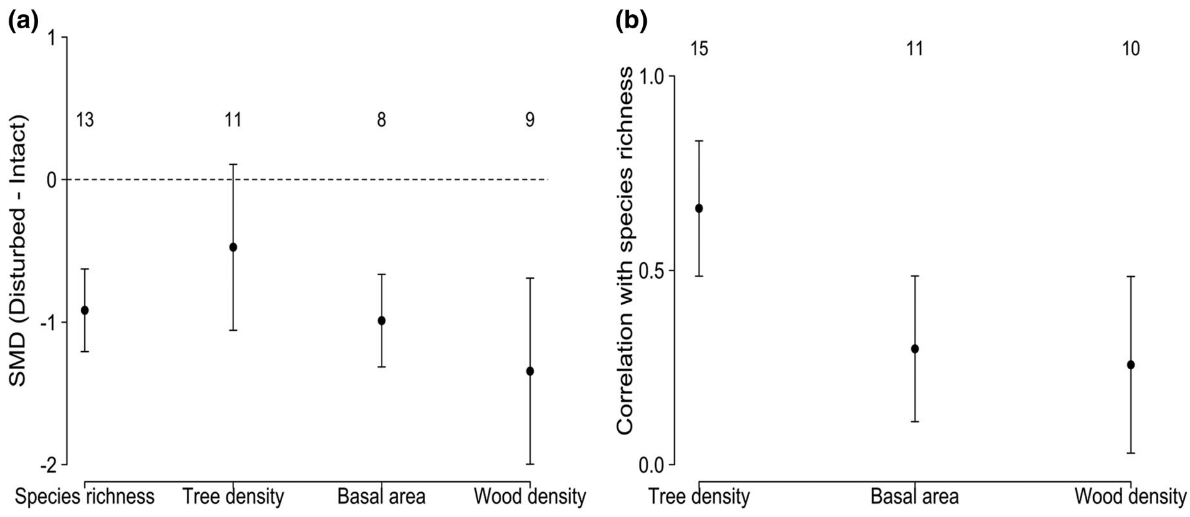

FIGURE 5 Standardized mean differences (SMDs) are consistently negative (i.e., lower in disturbed than intact forests) for tree species richness (TSR), basal area (BA) and community-weighted average wood density (WD), but not tree density (TD), based on the meta-analysis of tropical HDLs (a). Correlations of TSR with TD, BA and WD are consistently positive across tropical HDLs (b). Error bars depict means and 95% CIs of the estimated effect sizes. Sample sizes for each response are reported above bars

synergies for conservation and climate change mitigation in HDLs.

While our study focused on carbon cobenefits for tree diversity conservation, conservation strategies must ultimately be guided by a better understanding of cobenefits and trade-offs involving multiple biodiversity groups (Phelps et al., 2012), and how these potentially differ between HDLs and intact forests. Similarly, potential trade-offs involving other values widely derived by local people from these forests—for example, fuelwood and nontimber forest products—need to be better understood, and are important to address, within programs for biodiversity and carbon conservation in tropical human-dominated landscapes.

ACKNOWLEDGMENTS AND DATA

AMO received fellowships from the Science and Engineering Research Board (SERB) National Postdoctoral Fellowship (PDF/2016/000104), NatureNet Science Fellows and Earth Institute Fellows programs. Fieldwork was funded by a SERB research grant (SERB/SR/SO/PS/78/2012) to MS. We thank Susan Cook-Patton for suggestions that improved the manuscript. All data and the R script are provided in Appendix A.

ORCID

Anand M. Osuri https://orcid.org/0000-0001-9909-5633
Siddarth Machado https://orcid.org/0000-0001-9147-6650
Jayashree Ratnam https://orcid.org/0000-0002-6568-8374
Mahesh Sankaran https://orcid.org/0000-0002-1661-6542
S. Muthuramkumar https://orcid.org/0000-0002-7791-8499
N. Parthasarathy https://orcid.org/0000-0002-3445-1980
Raphaël Pélissier https://orcid.org/0000-0003-4845-5090
Ruth DeFries https://orcid.org/0000-0002-3332-4621
Shahid Naeem https://orcid.org/0000-0002-6569-2648

REFERENCES

Beaudrot, L., Kroetz, K., Alvarez-Loayza, P., Amaral, L., Breuer, T., Fletcher, C. D., … Andelman, S. (2016). Limited carbon and biodiversity co-benefits for tropical forest mammals and birds. *Ecological Applications*, *26*, 1098–1111.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., ter Steege, H., & Webb, C. O. (2006). Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, *16*, 2356–2367.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E. N., Colgan, M. S., Delitti, W. B. C., … Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*, 3177–3190.

Chisholm, R. A., Muller-Landau, H. C., Abdul Rahman, K., Bebber, D. P., Bin, Y., Bohlman, S. A.… Zimmerman, J. K. (2013). Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology*, *101*, 1214–1224.

Das, A., Krishnaswamy, J., Bawa, K. S., Kiran, M. C., Srinivas, V., Samba Kumar, N., & Karanth, K. U. (2006). Prioritisation of conservation areas in the Western Ghats, India. *Biological Conservation*, *133*, 16–31.

de Paula, M. D., Costa, C. P. A., & Tabarelli, M. (2011). Carbon storage in a fragmented landscape of Atlantic Forest: The role played by edge-affected habitats and emergent trees. *Tropical Conservation Science*, *4*, 349–358.

Deere, N. J., Guillera-Arroita, G., Baking, E. L., Bernard, H., Pfeifer, M., Reynolds, G., … Magrach, A. (2018). High carbon stock forests provide co-benefits for tropical biodiversity. *Journal of Applied Ecology*, *55*, 997–1008.

Ferreira, J., Lennox, G. D., Gardner, T. A., Thomson, J. R., Berenguer, E., Lees, A. C., … Barlow, J. (2018). Carbon-focused conservation may fail to protect the most biodiverse tropical forests. *Nature Climate Change*, *8*, 744–749.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, *12*, 561–582.

Giam, X. (2017). Global biodiversity loss from tropical deforestation. *Proceedings of the National Academy of Sciences USA*, *114*, 5775–5777.

Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Baptiste, B. L. G., Uribe, C. A. M., … Edwards, D. P. (2014). Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. *Nature Climate Change*, *4*, 503.

Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., … Purvis, A. (2017). The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. *Ecology and Evolution*, *7*, 145–188.

Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., John Kress, W., & Chazdon, R. L. (2014). The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters*, *17*, 1158–1167.

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo, J. P., … D'Angelo, S. (2006). Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences USA*, *103*, 19010–19014.

Letcher, S. G., & Chazdon, R. L. (2009). Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica*, *41*, 608–617.

Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, *349*, 827–832.

Ma, S., He, F., Tian, D., Zou, D., Yan, Z., Yang, Y., … Fang, J. (2018). Variations and determinants of carbon content in plants: A global synthesis. *Biogeosciences*, *15*, 693–702.

Magnago, L. F. S., Magrach, A., Laurance, W. F., Martins, S. V., Meira-Neto, J. A. A., Simonelli, M., & Edwards, D. P. (2015). Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? *Global Change Biology*, *21*, 3455–3468.

Matos, F. A. R., Magnago, L. F. S., Aquila Chan Miranda, C., de Menezes, L. F. T., Gastauer, M., Safar, N. V. H., … Edwards, D. P. (2019). Secondary forest fragments offer important carbon-biodiversity co-benefits. *Global Change Biology*, https://doi.org/10.1111/gcb.14824.

Menon, S., & Bawa, K. S. (1997). Applications of geographic information systems, remote-sensing, and a landscape ecology approach to biodiversity conservation in the Western Ghats. *Current Science*, *73*, 134–145.

Muthuramkumar, S., Ayyappan, N., Parthasarathy, N., Mudappa, D., Shankar Raman, T. R., Selwyn, M. A., & Pragasan, L. A. (2006). Plant community structure in tropical rain forest fragments of the Western Ghats, India. *Biotropica*, *38*, 143–160.

Osuri, A. M., Chakravarthy, D., & Mudappa, D. (2017). Data from: Successional status, seed dispersal mode and overstorey species influence tree regeneration in tropical rain-forest fragments in Western Ghats, India. Dryad Digital Repository, Retrieved from https://doiorg/105061/dryadvd0nn1

Osuri, A. M., Kasinathan, S., Siddhartha, M. K., Mudappa, D., & Raman, T. R. S. (2019). Effects of restoration on tree communities and carbon storage in rainforest fragments of the Western Ghats, India. *Ecosphere*, *10*, e02860, https://doi.org/10.1002/ecs2.2860.

Osuri, A. M., Kumar, V. S., & Sankaran, M. (2014). Altered stand structure and tree allometry reduce carbon storage in evergreen forest fragments in India's Western Ghats. *Forest Ecology and Management*, *329*, 375–383.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., … Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*, 988–993.

Phelps, J., Webb, E. L., & Adams, W. M. (2012). Biodiversity co-benefits of policies to reduce forest-carbon emissions. *Nature Climate Change*, *2*, 497–503.

Ramesh, B. R., Swaminath, M. H., Patil, S.V., Dasappa, Pélissier, R., Venugopal, P. D., & Ramalingam, S. (2010a). Forest stand structure and composition in 96 sites along environmental gradients in the central Western Ghats of India: Ecological Archives E091-216. *Ecology*, *91*, 3118.

Ramesh, B. R., Venugopal, P. D., Pélissier, R., Patil, S. V., Swaminath, M. H., & Couteron, P. (2010b). Mesoscale patterns in the floristic composition of forests in the Central Western Ghats of Karnataka, India. *Biotropica*, *42*, 435–443.

R Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. URL: Retrieved from https://www.R-project.org/.

Santos, B. A., Peres, C. A., Oliveira, M. A., Grillo, A., Alves-Costa, C. P., & Tabarelli, M. (2008). Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation*, *141*, 249–260.

Schwarzer, G. (2015). meta: General package for meta-analysis. R package version, 4, 3–2. Retrieved from https://CRAN.R-project.org/package=meta

Slik, J. W. F., Bernard, C. S., Breman, F. C., van Beek, M., Salim, A., & Sheil, D. (2008). Wood density as a conservation tool: Quantification of disturbance and identification of conservation-priority areas in tropical forests. *Conservation Biology*, *22*, 1299–1308.

Strassburg, B. B. N., Kelly, A., Balmford, A., Davies, R. G., Gibbs, H. K., Lovett, A., … Rodrigues, A. S. L. (2010). Global congruence of carbon storage and biodiversity in terrestrial ecosystems. *Conservation Letter*, *3*, 98–105.

Sullivan, M. J. P., Talbot, J., Lewis, S. L., Phillips, O. L., Qie, L., Begne, S. K., … Zemagho, L. (2017). Diversity and carbon storage across the tropical forest biome. *Scientific Reports*, *7*, 39102.

Tabarelli, M., Lopes, A. V., & Peres, C. A. (2008). Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica*, *40*, 657–661.

UNFCC. (2018). Reduce emissions from deforestation and forest degradation in developing countries (REDD+) Retrieved from https://redd.unfccc.int/.

Van de Perre, F., Willig, M. R., Presley, S. J., Andemwana, F. B., Beeckman, H., Boeckx, P., … Verheyen, E. (2018). Reconciling biodiversity and carbon stock conservation in an Afrotropical forest landscape. *Science Advances*, *4*, eaar6603.

Watson, J. E. M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., … Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, *2*, 599–610.

Zanne, A. E., Lopez-Gonzalez, G., & Coomes, D. A. (2009). Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository.

SUPPORTING INFORMATION

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

How to cite this article: Osuri AM, Machado S, Ratnam J, et al. Tree diversity and carbon storage cobenefits in tropical human-dominated landscapes. *Conservation Letters*. 2020;13:e12699. https://doi.org/10.1111/conl.12699