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Seeing the wood for the trees: Carbon storage and conservation in temperate forests of the Himalayas

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ABSTRACT

Forests have a prominent role to play in the success of the UN's Agenda 2030, thus actions to halt deforestation are high on the international sustainability agenda. As humans are altering the composition and extent of forest ecosystems, from local to global scales, we are also affecting the provisioning of forest ecosystem goods and services. We tested how measures of biodiversity, structural diversity, forest disturbances and environmental variables affect above ground tree carbon storage as an essential ecosystem service in differing legally protected forest ecosystems in the central Himalayas. This region is part of a biodiversity hotspot as well as a developing country where rural livelihoods are profoundly dependent on forest resources. We analysed drivers of above ground tree carbon in 530 plots, measuring a total of 6879 individual trees across six forests in three regions in legally protected and un-protected forest ecosystems in the Nepalese Himalayas. The aboveground tree carbon was markedly higher in protected forests (164 ± 8 t/ha) compared to in unprotected forests (114 ± 5 t/ha) but varied across regions. Biodiversity matrices were weakly correlated with above ground tree carbon content (hereafter called 'tree carbon') while the matrices of structural diversity were strongly correlated. Tree size inequalities, canopy cover, elevation, management, tree density, ground disturbance and woody species richness had effects on the tree carbon in bivariate regression models. However, in a multiple linear regression model matrices of structural diversity outweighed biodiversity matrices; tree size inequalities have the largest effect size on tree carbon, followed by elevation, management regime and tree richness. Tree size inequality, elevation and management regime show positive effects while tree richness has negative effect on tree carbon when accounting for the random effects of regions. Our analysis gives an evidence-base in support of forest management that retains tree size inequality, with particular emphasis on protecting large trees, as the best strategy to enhance above ground tree carbon storage and their co-benefits in temperate forests of the Himalayas.

1. Introduction

Terrestrial ecosystems, particularly forests and their rich biodiversity and carbon storage capacity, are essential for sustainable development and can advance many of the United Nations Sustainable Development Goals (SDGs) simultaneously, yet the nature-based solutions that forests may provide have not been made explicit in Agenda 2030 (UN, 2015). Forests have the ability to sequester atmospheric carbon into woody biomass and they account for nearly 45% (900 pentagrams) of the terrestrial carbon pool and sequester 2.4 pentagrams of carbon annually (PgC/yr) (Pan et al., 2011). Consequently, maintaining or restoring standing forests is a low-hanging fruit in the way of mitigating anthropogenic greenhouse-gas emissions (Seddon et al., 2020). In addition to working as carbon sinks, forests are important repositories of terrestrial biodiversity, supporting a wide range of organisms including thousands of endangered and endemic plants and animals (FAO and UNEP, 2020). Many people rely on forests for their health, recreational, spiritual and cultural well-being (SDG 3). In the poorest communities, forests serve as a critical safety net providing wild foods and other non-timber forest products (SDG 2), between harvests or in times of drought, flooding, crop failure and other emergencies (DiCarlo et al., 2018; FAO and UNEP, 2020; Shackleton and Shackleton, 2004).

Forests not only act as carbon sinks but also as carbon sources when subjected to deforestation and unsustainable biomass harvest (Pearson

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et al., 2017). Forest ecosystem services have strong interdependencies with climate change (SDG 13) as deforestation is the second largest anthropogenic source of carbon dioxide emission globally (Van Der Werf et al., 2009). With one third of all people (2.5 billion) using biomass fuels (International Energy Agency, 2017), wood is the most important source of bioenergy globally. Recently, deforestation and forest degradation have been associated with outbreaks of zoonotic diseases (White and Razgour, 2020), such as the latest pandemic caused by COVID-19. While forest stands are naturally dynamic, major shifts at a global level is mainly driven by anthropogenic disturbances, resulting in younger forest stands with faster turnover as old-growth forests are dwindling (McDowell et al., 2020). Forests, especially those in tropical and sub-tropical areas, face threats from deforestation, degradation and fragmentation; these threats compromise both the carbon sequestration potential and other ecosystem services dependent on biodiversity (SDG 15). Conserving biodiversity and enhancing carbon sequestration in forests, therefore, are two important strategies for building resilient and sustainable forest ecosystems in the face of the climate- and nature crises.

Recent syntheses and case studies have shown that there is a positive relationship between plant richness and plant productivity (Chen et al., 2018; Grace et al., 2016; Hooper et al., 2012; Liang et al., 2016; Paquette and Messier, 2011). Higher forest ecosystem function and productivity imply higher carbon sequestration, and higher plant richness enhances resource use efficiency through niche portioning (Forrester and Bauhus, 2016; Mensah et al., 2016; Morin et al., 2011). Furthermore, higher diversity also entails higher functional and structural diversity, favouring higher ecosystem production and carbon sequestration. However, empirical studies have documented variable relationships between carbon storage and species diversity (Thompson et al., 2012); some studies show a positive relationship between tree diversity and forest carbon (Arasa-Gisbert et al., 2018; Poorter et al., 2015). But such relationships may vary across taxonomic groups, with only tree diversity showing positive relations with forest carbon (Van De Perre et al., 2018). There may also be trade-offs and synergies between biodiversity and carbon within the same stand (Sabatini et al., 2019).

Above ground tree carbon content (tree carbon) is a major component of forest carbon (DFRS, 2015); its share in the forest carbon pool varies from region to region and from forest to forest (Pan et al., 2011). Tree carbon at larger spatial scale depends on climatic variables like temperature, precipitation, and light availability which in turn determine the net primary productivity. At forest stand level, tree carbon is driven by interactions between climatic, edaphic and topographic factors, and land-use and disturbance related factors (Arasa-Gisbert et al., 2018; Xu et al., 2015; Yuan et al., 2018). In general, protected forests are important carbon sinks. However, not all protected areas are managed equally well and their contribution to carbon sequestration may vary (Collins and Mitchard, 2017). Various metrics related to species diversity, stand structural diversity and functional diversity, along with disturbance and environmental variables, have been used to predict tree carbon (Li et al., 2019; Shen et al., 2016; Yuan et al., 2018). Some studies have found that matrices of structural diversity outperformed metrics of species diversity (Aponte et al., 2020; Yuan et al., 2018); while others report that diversity matrices have relatively stronger predictive power for tree carbon (Liu et al., 2018; Zhang et al., 2017). Among the stand diversity measures, large-sized trees are key structural aspects which overwhelmingly predict forest carbon (Ali et al., 2019; Lutz et al., 2018, Stephenson et al. 2014).

In this study, we analysed how management regime, stand structural attributes, biodiversity metrics, local scale disturbances and environmental variables affect the tree carbon in forests of the central Himalayas while accounting for the potential differences caused by region. We analyzed 530 vegetation plots in six forests, representing two different management regimes; a) under legal protection and b) outside legal protection, in order to answer the following questions (i) Does tree carbon vary between forest management regimes – does legal protection matter?, (ii) What are the relative contributions of management, stand structural attributes, species richness and elevation on tree carbon?, (iii) What attributes of forest biodiversity and structure need to be retained to enhance the carbon storage capacity of the forest? Disentangling the drivers of tree carbon may provide enhanced knowledge to better inform sustainable forest management and to mitigate climate change by maximizing forest carbon storage.

2. Material and methods

2.1. Study area

This study was conducted in three regions of the middle mountains in Nepal, central Himalaya (Fig. 1). The middle mountains are a broad geographical region on the southern slope of the Himalaya, consisting of two mountain ranges; Mahabharata, 1000–3000 m above sea level (masl) and lesser Himalaya, 2000–5000 masl (Upreti, 1999). In these mountains, topography is rugged and heterogeneous. The climate is monsoonal with hot and humid summers and dry and cold winters, with 80% of precipitation falling during the monsoon season in June to September.

Elevations between 2000 and 3000 masl have temperate climate, and the vegetation is mainly composed of oak-rhododendron forests. Oak species (*Quercus semecarpifolia, Q. lamellosa, Q. lanata* and *Q. glauca*) are the dominant structural species. *Rhododendron arboreum*, *Lyonia ovalifolia* and *Daphniphyllum himalayense* are associated species in the canopy layer. *Symplocos ramosissima*, *Lindera pulcherrima* and *Myrsine semiserrata* are common sub-canopy species. The density of sub-canopy tree species is higher than for canopy species in these forests. *Berberis* and *Viburnum* species are common shrubs in the understory (Table 1).

2.2. Land-use and forest management

The middle mountains are one of the most populated physiographic regions of Nepal as nearly 40% of Nepal's population live there, including the largest cities, Kathmandu and Pokhara (CBS, 2012). The mountain slopes are terraced by subsistence farmers for cultivation. Most of the settlements are located below 2000 masl and the forest and patches of semi-natural grasslands located above settlements has since long been used for cattle grazing and biomass extraction; firewood, fodder, timber, and medicinal and edible plants (Måren and Vetaas, 2007; Sharma et al., 2014a,b). Most of this region is inhabited by subsistence farmers who combine farming and livestock grazing. The forests remain an important component of the agro-pastoral production and are subject to chronic disturbance (Måren et al., 2014; Måren and Sharma, 2018; Miehe et al., 2015). In the past, the forests were extensively used

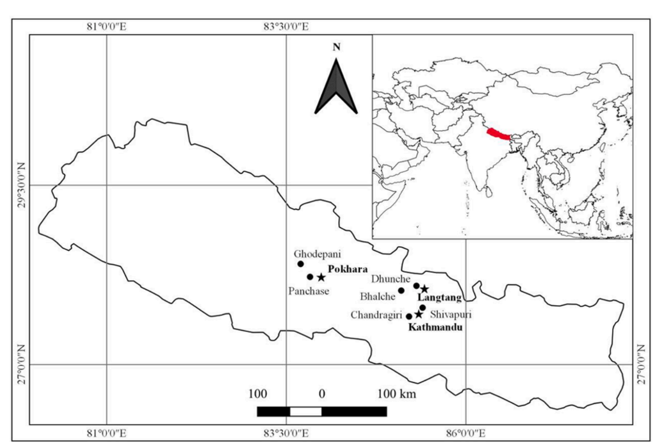

Fig. 1. Map of Nepal showing the three sampled regions (stars) and six forests (filled circles), totaling 530 forest plots.

Table 1
Characteristics of the three study regions in the middle mountains of the Nepalese Himalayas.

Regions	Forests	Major feature/ disturbance	Dominant tree species[#]	Climate
Kathmandu	Shivapuri National Park *Protected*	Forest adjoined with Ktm Valley, urban users for recreation and watershed, no products harvested, relatively long protection history	*Symplocos ramosissima, Myrsine semiserrata, Q. semecarpifolia*	MAT:17.2 MAR:2000
	Chandragiri *Unprotected*	Forest adjoined with Ktm Valley, local people harvest forest products	*Q. lanata, Q. semecarpifolia, R. arboreum, Q glauca*	
Langtang	Langtang National Park *Protected*	Near Dhunche market center, dry firewood collection allowed, heavily disturbed in the past. Established in 1976	*Lindera pulcherrima, Q. semecarpifolia, Lyonia ovalifolia*	MAR: 1610
	Bhalche *Unprotected*	Open access, grazing and tree felling, firewood and fodder harvesting	*S. ramosissima, Q. semecarpifolia, Lyonia ovalifolia*	
Pokhara	Annapurna Conservation Area *Protected*	Forest products used by users under the management of NTNC. Established in 1992	*R. arboreum, S. ramosossima, Neolitsea pallens*	MAR: 3300
	Panchase *Unprotected*	Grazing, tree felling, firewood and fodder harvested, key watershed for Pokhara Valley	*S. ramosissima, Daphniphyllum himalayens, L. ovalifolia, Q. semecarpefoia*	

[#] Listed according to dominance in terms of density, which may not be the structural canopy forming species. Q. = *Quercus, R.* = *Rhododendron,* Ktm = Kathmandu *Weather data comes from the nearest station. MAT = Mean annual temperature (in Celsius) it is similar for the same elevation, MAR = Mean annual rainfall (in millimeters), NTNC-National Trust for Nature Conservation.

for grazing and swidden agriculture, however, peoples' dependence on forests has decreased in recent decades due to urbanization and modernization.

Nepal's mountain forests are subjected to different levels of protection. The National Parks and Wildlife Conservation Act (1973) is the legal basis of protection of National Parks and wildlife reserves, while the Forest Act (1993) is the basis for the management of national forests. These national forests are mostly managed as community forests, where local users can form 'community forest users groups' (CFUGs), to manage their designated forest areas. Although the forests are currently under different management regimes and protection status, they share a more or less similar practice of land use history. Forests are still subject to different levels of disturbance depending on their relative position from settlements, irrespective of protection status, and protected forests are typically less disturbed compared to unprotected forests (Måren and Sharma, 2018).

2.3. Vegetation sampling

Three regions, each represented by a protected and an unprotected forest were selected for this study (Table 1). Vegetation data was collected at two different elevations: 2200 masl and 2500 masl. These two elevations were selected for three reasons: (i) in the middle mountains of Nepal, most of human settlements are located below 2000 masl and patches of temperate forest are located above 2000 masl, (ii) between 2000 and 3000 masl we find the highest tree richness in Nepal (Bhattarai and Vetaas, 2006), and (iii) in the middle mountains, very few peaks are higher than 3000 masl. Sampling above 2500 masl is thus impractical due to the shape of mountains, and below 2200 masl is typically very close to human settlements and agricultural land.

Vegetation data was collected by randomly placing plots of 10 m*10 m (0.01 ha) 20 to 100 m apart along the two elevation lines, i.e. 45 plots at each elevation, making a total of 90 plots per forest and 180 per region, and a total of 540 plots for all three regions combined. Plots were excluded where they: 1) had a greater than 45° slope, and were thus inaccessible; 2) lacked woody vegetation; 3) consisted of more than 50% rock or exposed soil; or 4) contained an established trail. In the final analysis 10 plots (8 from Kathmandu, one from Langtang and one from Pokhara) were removed in the analyses due to missing data, making altogether 530 plots. In each plot, we measured diameter at breast height (DBH = 1,37 m) of all tree individuals (DBH greater than 5 cm, height greater than 2 m). Woody species richness comprised tree species (trees, saplings), shrubs and woody climbers. At the plot center, coordinates, slope, direction of slope and elevation were recorded, along with ocular estimation of overall crown-cover. Approximate walking time in minutes from plots to the nearest settlement was recorded. The cutting of saplings, tree lopping and signs of livestock grazing were estimated in ordinal categories between 0 and 3, with 0 being absence of the disturbance and 3 being highly disturbed, as used by Kumar and Ram (2005).

All woody plant species were identified in the field using standard taxonomic literature (Grierson and Long, 2001), field guides (Polunin and Stainton, 1984) and checklists (Press et al., 2000). Specimens were photographed and unidentified species were collected and later identified at the National Herbarium and Plant Laboratory (KATH) at Godawari, Lalitpur, and Tribhuvan University Central Herbarium (TUCH), Kirtipur (Adhikari et al., 2017).

2.4. Tree carbon calculation

To calculate the above ground tree carbon, firstly the volume and biomass of standing trees were calculated according to National Forest Resources Assessment (DFRS 2015), using the volume equations developed by Sharma and Pukalla (1990). The following allometric equation was used to estimate tree volumes over bark:

$$Vol = exp\ [a + b \times ln(DBH) + c \times ln(h)]$$

Where, a, b and c are species specific coefficients (DFRS 2015), DBH is Diameter at Breast Height (1.37 m above ground), and h = height of tree.

Above ground tree biomass (AGTB) was obtained by using following equation:

$$AGTB = Vol \times wood\ density$$

The air-dried biomass obtained using these equations were converted into oven dried AGTB values using a conversion factor of 0.91 used by National forest assessment (DFRS, 2015). AGTB was converted into carbon, i.e. tree carbon, using a carbon-ratio factor of 0.47 (IPCC, 2006).

2.5. Environmental variables

We used forest stand structural attributes, biodiversity metrics, plot environmental variables and disturbance related variables as predictors of AGTB. We used woody species richness, tree species richness and Shannon Wiener diversity indices as biodiversity variables. Coefficient of variation in DBH (CV_{DBH}), Maximum diameter tree (MAX_{DBH}) in the plot, Basal area (BA) and tree density were used as candidate stand structural attributes. CV_{DBH} was a proxy of tree size inequality. Similarly, we considered disturbance variables as predictors of tree carbon. Relative radiation index (RRI) for each plot was calculated using slope, latitude and the direction of slope (Oke, 1987). Plot disturbance; grazing, cutting, lopping and canopy openness, were standardized to account for the differences in their scale and linearly combined into a disturbance complex by using first axis of a Principal Component Analysis (PCA). Sample score of the first axis was used as the disturbance complex (PCA1). Forest management and elevation were used as predictors of tree carbon in regression modelling.

2.6. Data analysis

Collinearaity among predictor variables were tested and only non-collinear variables (Pearson correlation coefficient < 0.6) were selected for regression analysis. Prior to the regression analysis, tree carbon was natural log transformed. Similarly, each predictor variable was standardized by scaling to obtain a mean 0 and standard deviation 1 to facilitate model convergence and make relative effect size of predictor variables directly comparable (Muscarella et al., 2020; Schielzeth, 2010). First, we analysed the bivariate relationship between forest carbon and each of preselected non-collinear predictor variables (tree density, woody species richness, tree richness, CV_{DBH}, RRI, PCA1, MAX_{DBH}, walking distance, elevation and management categories). Variables which showed a significant relationship with carbon in the bivariate regression were selected for the full model.

Linear mixed effect (LME) was applied to model carbon against the predictor variables. A full model was run where carbon at plot level was used as the response. Biodiversity (woody species richness, tree species richness and Shannon-Wiener diversity index); stand attributes (CV_{DBH}, tree density, and BA), disturbance complex, and environmental variables (elevation, RRI) were used as predictor variables. Elevation and management categories were treated as factors and included as fixed effect variables. The three regions were used as random variables. From the full model, insignificant variables were dropped, and model performance was evaluated using AIC. The model with the lowest AIC values was corroborated. The mixed effect regression model was computed using 'nlme' package in R (R Core Team, 2019).

3. Results

3.1. Tree carbon differ between management and regions

Overall, tree carbon was 138.38 t/ha, and higher in protected forest (mean ± SE; 163.71 ± 8.23 t/ha) than in unprotected forest (114 ± 4.97) (Table 2). Along with the plot mean, the variation in the tree carbon among plots was also markedly higher in protected forests (10–791 t/ha) than in unprotected forests (14–454 t/ha). Across regions, Kathmandu has the highest tree carbon; however, the difference in tree carbon varied between management regimes across regions. Within each region, protected forest had a higher tree carbon (Fig. 2). Tree carbon was higher at upper elevation (2500 masl); 157 t/ha, compared to at lower elevation (2200 masl); 120.19 t/ha, and this difference was consistent across regions and management regimes (Table 2, Fig. 3).

3.2. Correlation among species and structural diversity matrices

Some of the stand structural attributes were highly correlated among themselves and with tree carbon. There was a high and positive correlation between CV_{DBH}, basal area and Max_{DBH}. These in turn were also positively correlated with tree carbon. Tree density showed weak and negative relationship with basal area and large trees (Max_{DBH}), while it did not show any relationship with tree size inequalities, i.e. CV_{DBH} (Supplementary Table 1). Tree density declined linearly along the Max_{DBH} in both protected and unprotected forests (Fig. 4).

Among the diversity matrices, tree species richness and woody richness were positively correlated. Tree richness had a high positive correlation with the Shannon-Weiner diversity index, while woody richness had very low correlation with the index. Diversity matrices showed a weak correlation with tree carbon (Supplementary Table 1).

3.3. Bivariate relationship between tree carbon and predictor variables

We found that tree carbon increased linearly with tree size inequality (CV_{DBH}), Basal area and largest tree in the plot (Max_{DBH}) (Table 3, Fig. 5). Tree carbon also increased linearly with forest canopy cover and woody species richness (Table 3, Fig. 6). Unlike woody species richness,

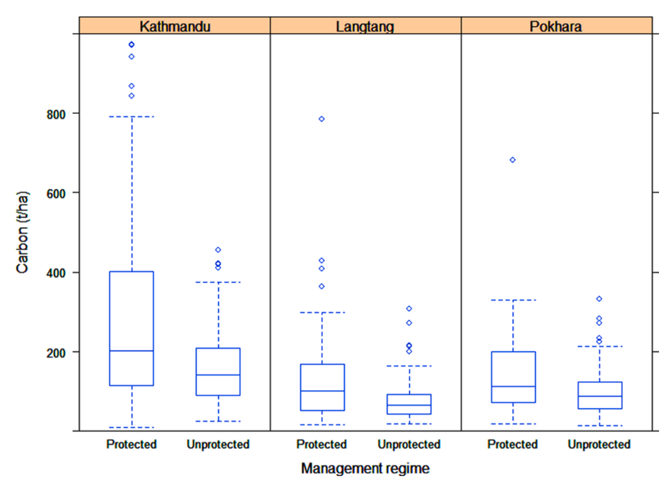

Fig. 2. Box-whisker plot showing the difference in above ground tree carbon (tree carbon) between legally protected and unprotected forests across the three study regions in the Nepalese Himalayas.

Table 2
Above ground tree carbon, species richness and structural diversity metrices across regions and forest management regimes in temperate forests of the Himalaya.

	Regions			Management regime	
Variable	Kathmandu	Langtang	Pokhara	Protected	Unprotected
Carbon (t/ha)	200.14 ± 11.2	100.75 ± 5.76	116.67 ± 5.43***	163.71 ± 8.23	114 ± 4.97***
Tree richness	4.47 ± 0.16	5.77 ± 0.14	4.73 ± 0.12	5.4 ± 0.12	4.61 ± 0.12***
Tree density	10.42 ± 0.27	14.96 ± 0.4	13.46 ± 0.48***	12.25 ± 0.3	13.68 ± 0.37**
Basal area	0.75 ± 0.03	0.61 ± 0.02	0.6 ± 0.02***	0.7 ± 0.02	0.61 ± 0.02***
Max_{DBH}	61.86 ± 1.81	50.56 ± 1.43	52.76 ± 1.33***	59.91 ± 1.43	50.22 ± 1.05***
Woody richness	14.29 ± 0.31	9.8 ± 0.27	15.47 ± 0.28***	14.87 ± 0.26	11.54 ± 0.25***
CV_{DBH}	71.04 ± 2.64	66.96 ± 1.68	71.57 ± 1.52*	78.41 ± 1.73	61.6 ± 1.34***

CV = Coefficient of Variation, DBH = 1.37 m.

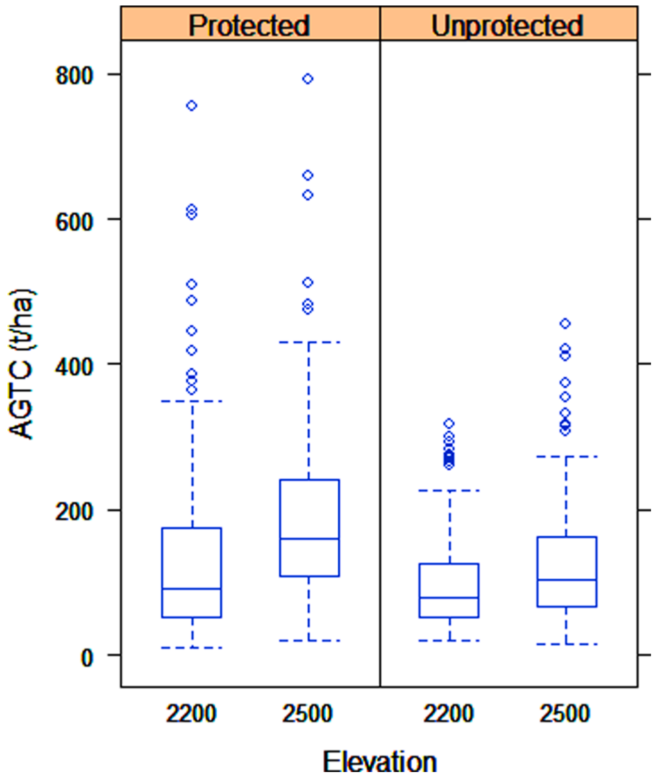

Fig. 3. Box-whisker plot showing the difference in above ground tree carbon (tree carbon) between the two sampled elevation bands (2200 and 2500 masl) in legally protected and unprotected forests in the Nepalese Himalayas.

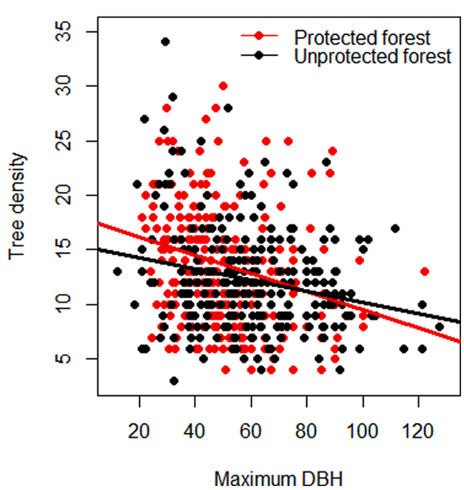

Fig. 4. Relationship between tree density and maximum tree size (Max_{DBH}) in forest plots. DBH = diameter in breast height (137 cm) in centimeters.

there was no relationship between tree richness and tree carbon. Tree carbon increased along the disturbance complex gradient (Fig. 7). Plot level disturbance explained the variation in tree carbon, but it was not related with tree richness. Tree size inequality (CV_{DBH}) explained the largest variation in tree carbon data (r^2 = 0.23) in the bivariate regression by far, as other significant variables were far lower.

3.4. Drivers of tree carbon while accounting for regions

The most parsimonious multiple linear mixed model showed that tree carbon was predicted by tree size inequalities (CV_{DBH}), tree richness, elevation and management category of the forest while accounting

Table 3
Bivariate regression showing relationships of above ground tree carbon (tree carbon) with explanatory variables, in legally protected and unprotected forests of the Himalayas.

	Estimate	Std. error	T value	P
Intercept	4.6504	0.0321	144.7	
Disturbance complex	0.1393	0.02387	5.837	<0.0001
Tree richness	NS			
	4.18777	0.100316	41.746	
Woody richness	0.034975	0.007206	4.853	<0.0001
	5.020472	0.082248	61.04	
Tree density	−0.02866	0.005824	−4.92	0.001
	4.538536	0.060263	75.312	
Walk	0.001594	0.000731	2.181	0.029
	3.679	0.08212	44.8	
CV_{DBH}	0.01388	0.0011	12.62	<0.0001
	3.964357	0.147442	26.888	
Tree cover	0.010641	0.002237	4.757	<0.0001
	4.6485	0.0183	253.32	
Max_{DBH}, 1	14.31591	0.42245	33.888	<0.001
Max_{DBH}, 2	−2.878	0.42245	−6.812	<0.001
RRI	NS			
	4.49689	0.04546	98.918	
factor(Masl) 2500	0.30908	0.06491	4.762	<0.0001
	4.79301	0.04648	103.113	
Unprotected	−0.28365	0.06513	−4.355	<0.0001

Max_{DBH} = maximum tree size, Masl = Meters above sea level, RRI = Relative radiation index, Walk = walking distance in minutes from nearest settlement, Disturbance complex = First axis score of Principal Component Analysis (PCA) combining plot disturbances; grazing, cutting, lopping and canopy openness.

the sites (Table 4). As indicated by Marginal R^2, sites have effect on the tree carbon. Tree density was significant in the bivariate regression but turned out insignificant in the mixed model, while tree richness, which did not show any relationship with tree carbon in bivariate regression, showed negative relationship with the tree carbon in the multiple regressions. Among these predictors, tree size inequalities (CV_{DBH}) have the highest effect size, followed by elevation (Table 4). Tree richness has the lowest effect size and the effect was negative. CV_{DBH} in turn was affected by disturbance (Fig. 8). Tree density did not predict the variation in tree carbon while accounting for the regions. While accounting the variation caused by the regions, it is clear that management has impacts on the tree carbon, showing that forest protection has a positive effect.

4. Discussion

Above ground tree carbon (tree carbon) comprises approximately 60% of the forest carbon pool in forests of Nepal's middle mountains (DFRS, 2015). We demonstrate that the temperate mountain forests store a large quantity of carbon as tree carbon (138.38 ± 4.88 t/ha), considerably higher than the national average (82 t/ha), as documented by Forest Resource Assessment (FRA) Nepal (DFRS 2015). This difference may be explained by the land use/cover categories covered by the National inventory, which covered forest, shrubland and grassland, while we covered only forests. Our results, nevertheless, are not very different from other studies conducted in similar forest types in the Himalayan mountains (Aryal et al., 2018; Singh et al., 1985; Suwal et al., 2015). Here, we highlight how forest carbon is affected by management and other biotic and abiotic factors.

4.1. Forest protection favors carbon storage

Protected areas have been a key strategy to conserve biodiversity and enhance ecosystem functions (Millenium Ecosystem Assessment, 2005; Watson et al., 2016) and they are an important topic in international MEAs such as the Aichi Biodiversity Targets and the UN's SDGs (e.g., SDGs 2, 3, 13, and 15). Protected areas provide dual benefits in carbon storage; protecting trees and reducing emission that would otherwise

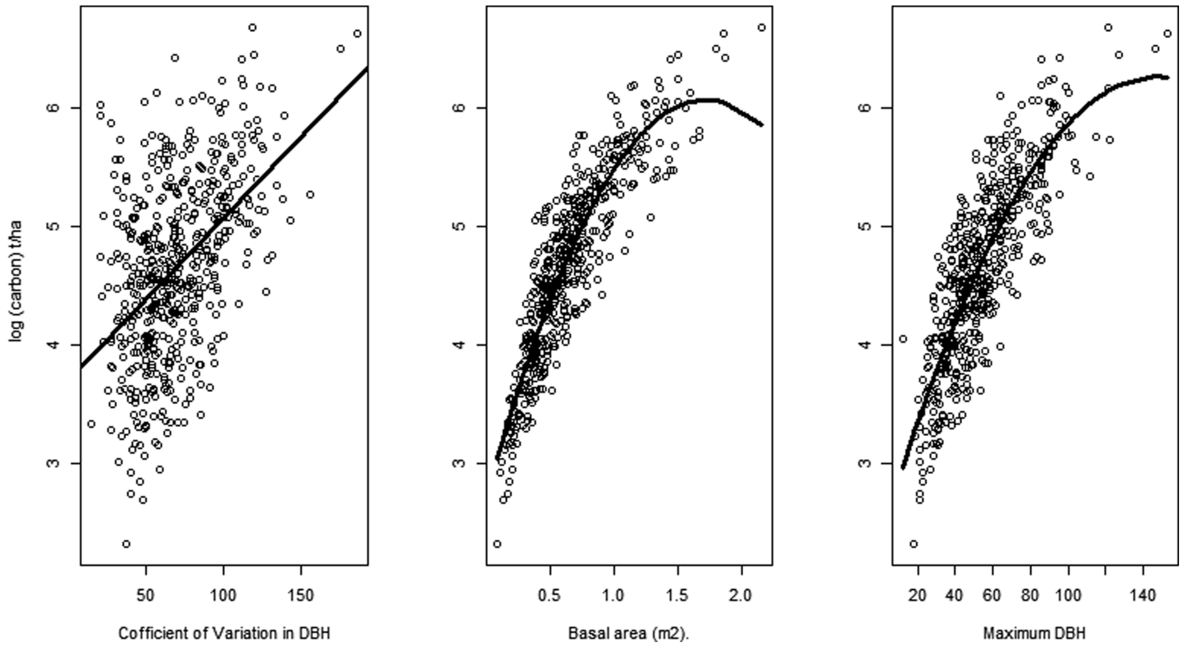

Fig. 5. Relationships between above ground tree carbon (tree carbon) and stand structural attributes; coefficient of variation in DBH-CV_{DBH} (left), basal area (center), and largest diameter tree in the plot (right).

Fig. 6. Relationship between above ground tree carbon (tree carbon) and woody species richness.

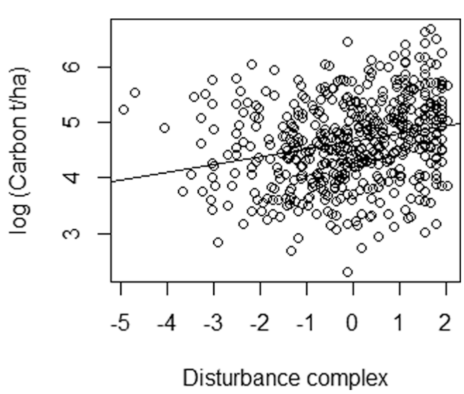

Fig. 7. Relationship between above ground tree carbon (tree carbon) and disturbance complex; negative values of the complex correspond to higher disturbance.

Table 4
Summary statics of the best linear mixed effect model for predicting above ground tree carbon (tree carbon), where the best model was selected using Akaike Information Criteria (AIC).

	Estimate	Std error	t value	p value
Intercept	4.580602	0.145744	31.429036	<0.0001
CV_{DBH}	0.361676	0.029087	12.434107	<0.0001
Tree richness	−0.09935	0.02916	−3.407242	0.0007
Elevation	0.258726	0.052189	4.957449	<0.0001
Unprotected	−0.10731	0.055116	−1.947035	0.0521
Model statics	$R^2_{marginal}$ 0.26	$R^2_{Conditional}$ 0.40	AIC: 976.6	

CV = Coefficient of Variation, DBH = 1.37 m.

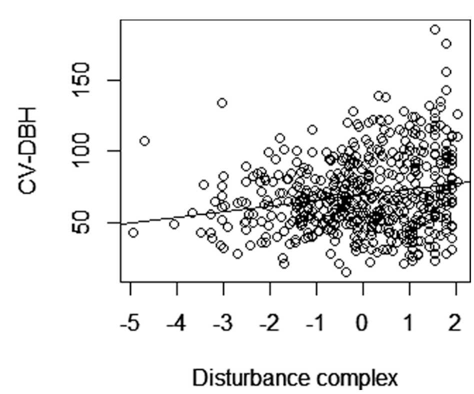

Fig. 8. Relationship between disturbance complex and coefficient of variation (CV_{DBH}) in diameter at breast height (DBH = 1.37 m); Negative values of the complex corresponds to higher disturbance.

originate from forest degradation and deforestation (Naughton-Treves et al., 2005). Forest carbon is generally a function of tree size, tree density and tree richness (Ali et al., 2019; Lecina-Diaz et al., 2018; Van De Perre et al., 2018; Yuan et al., 2018). These attributes, in turn are expected to be better retained in protected forests (Keith et al., 2014). However, land conversion also inside protected areas, particularly in the global south, may be a serious threat to biodiversity and ecosystem services delivery (Collins and Mitchard, 2017; Melillo et al., 2016).

Our analysis confirms that forest protection has positive impacts on carbon storage. We found that protected forests have considerably more tree carbon than the corresponding unprotected forests. There is similarity in the climatic conditions of these study regions so climate may not be an important factor driving differences in tree carbon. Therefore, these differences in tree carbon between management regimes can also be related to the protection history of the sites. Tree carbon also varied across regions, evidenced by the variation explained by the random factors in the mixed effect model. The variation in tree carbon between regions and forests is potentially linked to protection history. The tree carbon was highest in the regions which have a relatively longer history of protection status. Kathmandu has been the capital of Nepal for more than two centuries; therefore, the protected area there has experienced higher attention from the forest department compared to the two other regions. Similar results of higher tree carbon in protected, old-growth and intact forests compared to in unprotected and logged forests have also been found in other empirical studies (e.g., Fongnzossie et al., 2014; Keith et al., 2014; Suwal et al., 2015).

It is generally expected that forest protection reduces disturbance and biomass extraction. Although we found unprotected forests are more disturbed than protected [$t = 3.0837(507.1)$, $p = 0.002$], all of the studied forests are subjected to some form of human pressure in spite of their protection status. Extensive biomass extraction which generally occurs near settlements, alters forest structure and has direct and negative consequences to forest carbon (Sapkota et al., 2018; Vaidyanathan et al., 2010). We found that disturbance in terms of biomass harvest has negative effect on tree carbon. At the upper elevation, tree carbon was higher than at the lower elevation, irrespective of protection status. The upper elevation was further away from settlements and had high canopy cover, bigger trees, high tree size inequalities, and lower disturbances. Large diameter trees and tree size inequalities that better approximate tree carbon were more frequently present in the upper elevation.

4.2. Diversity metrics are a weak proxy of tree carbon

Tree carbon in forests is a function of both biotic and abiotic factors. Various matrices of species diversity have been used to approximate tree carbon (Li et al., 2019). The relative importance of these variables, however, may vary across forest types (Arasa-Gisbert et al., 2018). Our analysis showed that species diversity metrics (woody species richness, tree species richness and Shannon-Wiener diversity index) are weaker variables in explaining the variation in tree carbon. Species diversity (tree species richness and woody species richness) showed different relationships with tree carbon in the bivariate and multiple regression models. Tree richness did not show any relationship with the tree carbon, while woody richness has weak positive relationship with tree carbon in the bivariate regression. Our mixed effect model showed that tree richness has a negative relationship with tree carbon, while woody richness did not show any relationship with it.

This is contrary to a general understanding of species richness and ecosystem function relationships (Poorter et al., 2015; Zhang et al., 2012), as several case studies have documented positive relationships between species richness and forest carbon (Arasa-Gisbert et al., 2018; Emmett Duffy et al., 2017; Fongnzossie et al., 2014; Lecina-Diaz et al., 2018; Liu et al., 2018; Poorter et al., 2015). Synergies between plant diversity and forest carbon have also been reported (Aryal et al., 2018; Gamfeldt et al., 2013; Liu et al., 2018; Van De Perre et al., 2018). In a study in Chinese subtropical forest, tree richness not only explained variation in the tree carbon but also the carbon in soil and underground biomass (Liu et al., 2018). Another study analysing the relationship between tree carbon and different taxa in European forests found very weak relationships between carbon and species richness, however, the relationship was not consistent across taxonomic groups (Sabatini et al., 2019). Analysis of tradeoffs and synergies between carbon and biodiversity goals indicate that the same stand is less likely to demonstrate synergy between these two and suggest dedicating different stands for these interrelated objectives (see Sabatini et al., 2019).

4.3. Stand structural attributes override tree carbon

Structurally diverse forests have higher ecosystem productivity than simpler forests (Ali, 2019). The productivity of a forest stand can be predicted using stand structural attributes (Dănescu et al., 2016). We demonstrated that among the stand structural attributes, tree size inequalities (CV_{DBH}) have direct and positive effect on the tree carbon. CV_{DBH} had high correlation with Max_{DBH} and it co-varied with plot level disturbance and tree density. Plot level disturbance and tree densities both have negative relationships with the CV_{DBH}. Tree density was negatively correlated with the large sized trees, as also reported by Sullivan et al. (2017). Large size trees in turn have the largest effect on the tree carbon. A substantial effect of large sized trees on forest carbon has been commonly observed (Ali et al., 2019; Meyer et al., 2018; Slik et al., 2013). Similarly, tree size inequalities have been reported to have positive effects on forest carbon and diversity (Yuan et al., 2018; Zhang and Chen, 2015). Stands with older trees have lower tree densities but higher variation in tree size inequalities. Relative importance of forest structural diversity measured as variation in diameter class was better than tree richness to explain the variation in forest stand carbon across scales in Mexican (Arasa-Gisbert et al., 2018) and Australian forests (Aponte et al., 2020).

Tree carbon showed strong positive relationship with the largest diameter tree measured (max DBH trees), in congruence with the findings of other studies (Slik et al., 2013, Stephenson et al. 2014). Studies also find that the 1% largest trees override the other 99% of trees and species diversity metrics in explaining the variation in tree carbon in subtropical forests (Ali et al., 2019; Lutz et al., 2018).

4.4. Relative importance of drivers of tree carbon and management implications

Our analysis shows that variation in tree carbon is related to multiple factors like structural diversity, species diversity, elevation and forest management regime. There was also a variation in forest carbon across sites. Our results show that species diversity matrices were weaker than expected in explaining the variation in tree carbon; and this does not support the positive biodiversity and carbon relationship hypothesis. Rather, our results clearly indicate that tree carbon is mainly driven by functional dominance of large-sized individuals and niche complementarity associated with tree-size inequalities. Forest management alters tree carbon through disturbances, nevertheless the relationship between forest disturbance and carbon is not simple (Thornley and Cannell, 2000). Harvest targeting large trees, therefore, reduces forest carbon storage capacity significantly (Lindsell and Klop, 2013). Himalayan temperate forests mainly suffer chronic disturbance associated with biomass harvest. These disturbances have direct consequences for stand structural attributes and species composition (Sapkota et al., 2018). We underscore the need to analyze further how disturbances and management influence stand structural attributes for a range of disturbance gradients and forest types in this important forest region.

Biodiversity conservation and carbon sequestration are two very important international development goals where forests can play an important role in achieving them. There are both tradeoffs and synergies between these two goals at forest stand level (Rana et al., 2017; Sabatini et al., 2019) and management should focus on reducing the tradeoffs and maximizing the synergies, including other ecosystem benefits. We found that structural diversity, rather than species diversity, favours tree carbon with slight tradeoffs as to tree richness. We used one facet of biodiversity, i.e. tree- and woody species diversity, and our results do not say anything about the relationship between forest carbon and metrics of biodiversity based on other taxonomic groups.

5. Conclusions

Using a large dataset from different regions and land management regimes, we demonstrate that stand structural attributes, protection status and environmental variables altogether drive tree carbon in biodiversity rich mountainous forests of the Himalayas. Contrary to the well-known diversity-productivity hypothesis, we found tree species richness to have no relationship with tree carbon, and a negative relationship when accounting for region and land management status. Our results indicate that stand structural attributes, particularly tree-size inequality, have relatively larger effect on tree carbon across regions and management regimes. Tree richness in turn was not correlated with the key structural attributes, i.e. stem-size inequalities and large trees that contribute the most to carbon storage in forest stands. Our results support that niche complementarity, through trees of different sizes, is a mechanism underpinning tree carbon storage in temperate forests. We reiterate that management that retains and enhances tree size inequalities and protects large old trees can help store larger quantities of carbon as live tree biomass and play an important role in climate mitigation while providing other key ecosystem services.

CRediT authorship contribution statement

Inger Elisabeth Måren: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition. **Lila Nath Sharma:** Formal analysis, Writing - review & editing, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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