Environmental correlates of the forest carbon distribution in the Central Himalayas

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In the Central Himalayas, where environmental conditions vary greatly, understanding the biophysical limitations on forest carbon is crucial for accurately determining the region's forest carbon stocks. This study investigates the role of climate and disturbance on the spatial variation of two key forest carbon pools: aboveground carbon (AGC) and soil organic carbon (SOC). Using field-observed plot-level carbon pool estimates from Nepal's national forest inventory and structural equation modeling, we explore the relationship between forest carbon stocks and proxies of environmental constraints. The forest AGC and SOC models explained 25 % and 59 % of the observed spatial variation in forest AGC and SOC, respectively. The climatic availability of water and energy in broad-scale gradients combined with the fine-scale gradients of terrain and disturbance intensity were found to influence forest carbon stocks, but the sign and strength of the statistical relationships differ for forest AGC and SOC. While AGC showed a negative relationship to disturbance, SOC was impacted by the availability of climatic energy. Disturbances such as selective logging and firewood collection result in immediate forest carbon loss, while soil carbon changes take longer to respond. The lower decomposition rates in the high-elevation region, due to lower temperatures, preserve organic matter and contribute to the high SOC stocks observed there. These results have important implications for forest carbon management and conservation in the Central Himalayas.

0.1 Introduction

Early explorers and scientists highlighted the Himalayas' diverse flora (Gould & Gould 1831, Hooker 1854, Smith 1911, Hara 1966), with pronounced variations in geology, relief, and climate contributing to high biological diversity (Vetaas & Grytnes 2002, Oommen & Shanker 2005, Kandel et al. 2016). The Himalayas are a global biodiversity hotspot (Myers et al. 2000) with a high level of endemism and

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priority conservation landscapes (Thompson 2009). Concerns about potential climate change impacts on vulnerable ecosystems have recently brought further attention to the region (Sharma et al. 2009, Shrestha et al. 2012, Dolezal et al. 2016, Gerlitz et al. 2016). The region supports diverse forest types from tropical broadleaved to alpine coniferous forests (Rawat & Lama 2017).

Forest structure, particularly woody plant basal area, height distribution, and wood density, is the primary determinant of carbon stocks (Saatchi et al. 2011), and varies with species distribution and composition (Bohn & Huth 2017). Climate, lithology, and terrain interactions constrain species composition and forest structure by limiting resources. The disturbance regime can alter forest structure and composition (Vlam et al. 2017), affecting carbon stocks (Zhang et al. 2014). Disturbances typically reduce forest carbon density below the climatic/edaphic potential. The environmental control of species richness over large gradients has been well studied worldwide (Sanders 2002, Svenning et al. 2009), including in the Himalayas (Vetaas & Grytnes 2002, Carpenter 2005), but the impact of species composition on forest structure, productivity, and carbon storage is poorly understood. Thus, we hypothesised that the relative importance of environmental controls on forest carbon stocks would vary with species composition, structure, and geographic location within broad temperature and precipitation regimes. Despite a broad understanding of how environmental conditions affect forest productivity, we do not know how the relative importance of different environmental controls varies across large heterogeneous landscapes such as the Central Himalayas (Kohler et al. 2010, Perrigo et al. 2019). A better quantitative understanding of these environmental controls is required to predict the spatial variation in forest carbon stocks across Nepal's highly diverse forest regions.

Broadly, variations in climate, terrain, and parent material set fundamental environmental controls on forest carbon stocks. In high mountain environments, air temperature is widely considered to be the primary control of alpine treeline formation (Körner 2007, Harsch et al. 2009), as low air temperatures and short growing seasons introduce photosynthetic constraints, thus limiting tree growth and survival (Dolezal et al. 2019). The observation of positive influences of both air temperature and precipitation on high-elevation tree growth is thought to be driven by increased moisture availability via snowmelt due to warmer spring temperatures (Wang et al. 2006) and increasing photosynthesis rates (Körner 2012). In the subtropical regions of the lower elevations, we can expect other environmental controls on forest carbon stocks to predominate, as the region has a higher mean annual temperature (Karki et al. 2016), mostly flat topography, and highly fertile alluvium deposits (Carson 1992). The levels of disturbance are also higher in these lower elevation forests because of the relatively high population density and road access (Webb & Sah 2003, Sapkota et al. 2009).

Altitudinal gradients of mean annual air temperature vary with longitude and latitude (Cogbill & White 1991, Champagnac et al. 2012), and affect forest species composition and structure in mountain ranges (Xu et al. 2017b). In the case of the Central Himalayas, the elevational gradient is among the steepest on Earth and is the main cause of strong variations in factors, such as air temperature, precipitation, snow fraction, and solar radiation. These factors are physiologically important for forests, as shown by several dendrochronological studies (Gaire et al. 2014, Sigdel et al. 2020); however, their role in driving spatial variation in forest species composition and structure remains poorly quantified (Rawat & Lama 2017, Bhutia et al. 2019). The NW-SE orientation of the mountain range creates steep elevational gradients from south to north, overwhelming the effects of latitudinal gradients on mean annual air temperature. Thus, there can be a considerable variation in elevation for a given latitude and longitude, and therefore, in the mean annual surface air temperature (Kattel et al. 2013). Similarly, the monsoon rains that originate in the Bay of Bengal gradually move from east to west along the longitudinal gradient of the Central Himalayas (Brunello et al. 2020), causing an east-west gradient in mean annual precipitation and its seasonal timing.

The large-scale climatic gradients that are related to orography, latitude, and longitude do not capture landscape-scale variation in forest site conditions that are influenced by landform, slope, and aspect. There is potential for landscape-scale variation in topoclimatic conditions when the elevational profile does not increase monotonically with latitude (Figure 1). These topographic characteristics result in complex spatial variations in factors such as solar radiation (which depends on aspect and slope orientation), substrate quality, moisture availability, nutrient retention, and local microclimate (Holland & Steyn 1975, Taylor et al. 2015, Yang et al. 2016, Xu et al. 2017a). These topoclimatic variations provide habitats for forests with different species compositions, structures, and carbon densities.

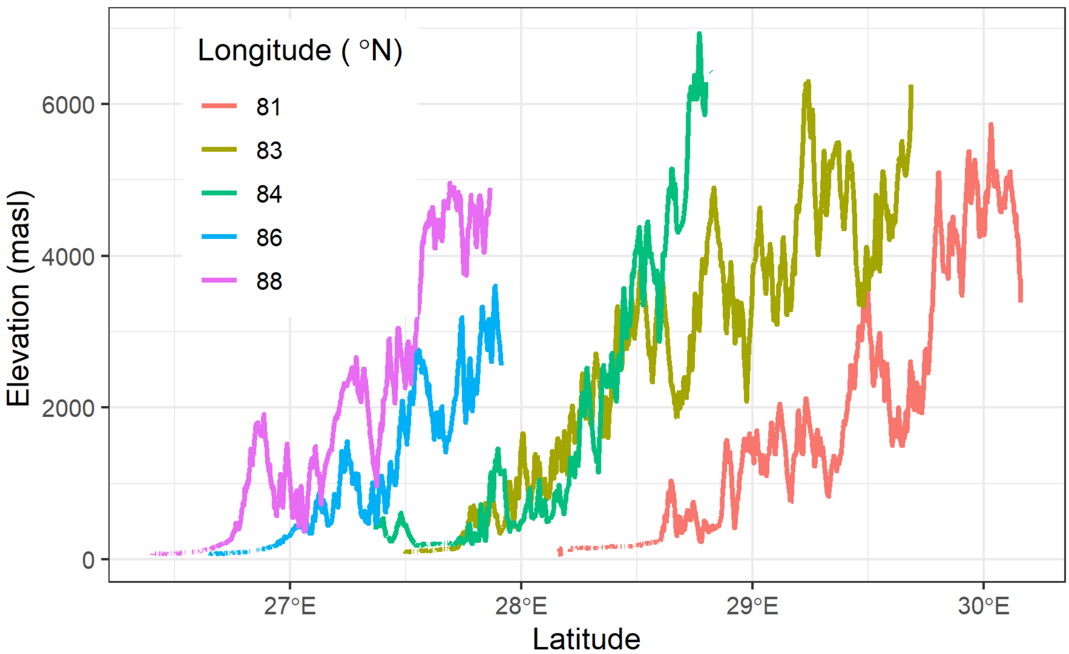

Figure 1: North-south elevational gradient (masl) at different longitudes along the latitudinal gradient in the Central Himalayas derived using ASTER Digital Elevation Model data (NASA et al. 2019).

The local temperature, radiation, and moisture conditions of a forest habitat are influenced by fine-scale topographic features, broadscale orography, and climate. Disturbances, especially those related to human land use, operate at an even finer scale, such as when people access patches to collect forest resources. These factors, operating at different spatial and temporal scales, have significant implications for forest carbon modelling across the Central Himalayas. In Nepal, fine-resolution observations of environmental predictors, such as air temperature, soil moisture, and soil depth, are unavailable. However, fine-resolution digital elevation models (DEMs) can accurately represent topography, which affects air temperature and moisture regimes. Using DEMs, we can derive terrain attributes that indirectly capture the variation in environmental conditions (Wilson 2018). For instance, slope angle and aspect influence solar radiation (Kumar et al. 1997) and temperature (Sheng et al. 2009) regimes. Additionally, slope angle and slope form affect soil depth (Boer et al. 1996, Fan et al. 2020), drainage (Jones 1987), (Schoorl et al. 2002), snow accumulation (Jain et al. 2009), erosion (Mitas & Mitasova 1998), and landslide risks (Pradhan & Kim 2018). By combining fine-resolution terrain attributes with coarse-resolution gridded climate data, we may be able to capture spatial variation in environmental conditions and use that information to predict spatial variation in forest carbon stocks.

The broad and fine-scale environmental gradients expected to affect forest carbon are summarised in a conceptual model (Figure 2). By implementing this conceptual model in the SEM approach, we address the following questions:

a) To what extent can the observed spatial variation in forest carbon stocks be explained by environmental predictors related to climatic water and energy availability, and disturbance?
b) What is the relative contribution of key environmental predictors related to climatic water and energy availability to spatial variation in forest carbon stock? and,
c) Does topography play a mediating role in the relationship between the broad-scale gradients of climatic water, energy availability, and forest carbon stocks?

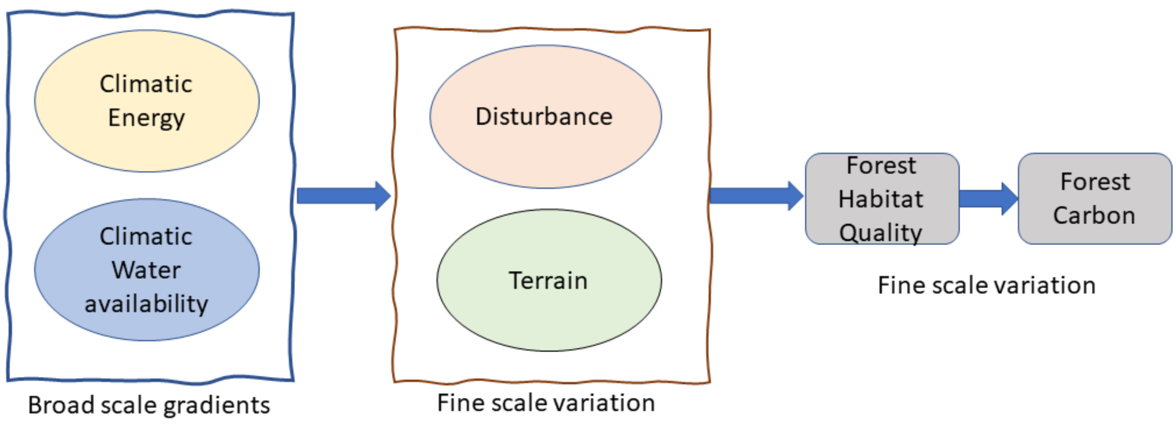

Figure 2: Conceptual model of controls on spatial variation in forest carbon stocks in the Central Himalayas.

0.2 Materials and Methods

0.2.1 Input data

Estimates of forest carbon stocks were obtained from Nepal's national-scale forest inventory, conducted between 2010 and 2014. We used existing field-based estimates of two forest carbon pools: Aboveground Biomass (AGB) and Soil Organic Carbon (SOC) stocks. Estimates of forest AGC and SOC were available for 1,156 and 2,009 plots at the plot level, respectively. A carbon fraction of 0.47 was used to convert forest AGB to AGC (IPCC 2006). Details on the distribution of plot-level field data, study area description, sample plot design, forest attribute measurements, and soil carbon analysis protocols have been submitted as a data paper (Khanal & Boer 2023).

Mean annual precipitation and seasonality are significant indicators of forest habitat quality, as available soil water affects species composition (Miller et al. 2021), tree growth (Eckes-Shephard et al. 2021), and thus, carbon storage (Knapp et al. 2017, Hofhansl et al. 2020). Growing Degree Days (GDD) that exceed a certain temperature threshold indicate the temperature regime and duration of the forest growing season (Hanes & Schwartz 2011, Hankin et al. 2019). In this study, a threshold of 0°C was used to calculate the GDD, given that the study area extends to cold alpine regions. Potential evapotranspiration (PET) measures the availability of climatic energy (Stephenson 1990). Both the GDD and PET are proxies for climatic energy availability.

Terrain and disturbance variables were available at a higher spatial resolution than that of the relatively low-resolution gridded climate datasets. Two terrain variables were used to capture fine-scale variations in potential water and energy availability: the topographic wetness index (TWI) (Beven & Kirkby 1979) and potential incoming solar radiation (PISR) (Lacelle et al. 2016). TWI represents fine-scale variation in potential soil moisture availability (Rodhe & Seibert 1999, Muscarella et al. 2020), whereas PISR represents the potential energy available in the landscape (Stettz et al. 2019).

Human-induced disturbances are related to accessibility, which is particularly important for forest product collection such as tree harvesting. Forested stands closer to the road network were expected to have a higher likelihood of disturbance. In this study, we assumed the likelihood of the disturbance of forest areas to be proportional to the distance to the interface with non-forest areas. Fragmented forests have a large interface with non-forest land use, such as settlements, and hence have high disturbance probabilities. Patch metrics from landscape ecology (McGarigal et al. 2009) were used to quantify the fragmentation of forested landscapes as a measure of the probability of disturbance. The landscape shape index (LSI) (McGarigal 1995) provides a standardised measure of the total edge or edge density relative to the size of the landscape. Forested patches with a longer edge adjacent to non-forest land use were more likely to experience human disturbance than intact stands in the core of forested areas.

The fragmentation of a forest area increases the length of the forest edge and thus the likelihood of disturbance. In mountainous terrain, landslides often occur where slopes are disturbed, such as near roads (Larsen & Parks 1997), and rainfall-triggered landslides on road construction sites are common in Nepal (McAdoo et al. 2018). Using the gridded percentage tree cover data product (Hansen et al. 2013), we computed the landscape openness (LOPEN) for each 30 m grid cell as the percentage of the area within a 1 km buffer that exceeds 10% tree cover. Tree cover of 10% is widely accepted by the United Nations Food and Agriculture Organisation as a criterion for defining forests (FAO 2010). LOPEN is similar to patch percentage metrics, which represents the proportion of the landscape made up of a specific patch type(Liu & Weng 2008) and is used to quantify land-use and land cover changes (Herzog et al. 2001). Unlike the direct use of tree cover, the openness variable represents the proportion of non-forest areas within the surrounding landscape of each grid cell. Forest areas with high landscape openness or low tree cover can be a result of either naturally sparse forests or a reduction in tree cover due to disturbance. However, even stands with naturally low or sparse tree cover are likely to have a larger interface with non-forest land cover, resulting in a higher probability of disturbance.

Predictors were selected to represent latent variables: climatic water availability (mean annual precipitation (Bio12) and seasonality (Bio15)), climatic energy (mean annual potential evapotranspiration (PET), mean annual growing degree days (GDD), and seasonality of mean monthly air temperature (Bio4)), terrain (mean daily potential incoming solar radiation (PISR) and topographic wetness index (TWI)), and intensity of disturbance (landscape shape index (LSI) and landscape openness (LOPEN)) (Table 1). Details on the calculations of LSI, PISR, and TWI can be found in Supporting information S0.3. A summary of the descriptive statistics for input datasets is provided in Table S4, Supporting information.

Table 1: Covariates used for structural equation models (SEMs).

Variable	Description	Units	Spatial Resolution
	Climate Variables		
Bio12	Mean annual precipitation derived using the mean monthly precipitation (Karger et al. 2017)	mm yr^{-1}	1 km
Bio15	Precipitation seasonality derived using the standard deviation of the mean monthly precipitation estimates expressed as a percentage of the annual mean (Karger et al. 2017)	-	1 km
PET	Mean annual potential evapotranspiration (Title & Bemmels 2018). Indicates the potential evaporation when the moisture supply is unlimited.	mm yr^{-1}	1 km

Variable	Description	Units	Spatial Resolution
GDD	Sum of the mean monthly temperature greater than the base temperature (0°C) multiplied by the total number of days. Derived using Chelsa monthly temperature data (Karger et al. 2017) and growingDegDays function in the R package envirem (Title & Bemmels 2018).	-	1 km
Bio4	Temperature seasonality (Standard deviation of the monthly mean air temperatures) (Karger et al. 2017)	-	1 km
	Disturbance Variables		
LSI	Landscape shape index. An aggregation metric representing the ratio of the edge length of forest class to the minimum total edge length of a forest patch. LSI = 1 indicates maximally aggregated patches, while an increase in the index indicates an increase in the edge length, and hence decreasing aggregation. Derived for 1 km buffer using lsm_c_lsi function in R package landscapemetrics (Hesselbarth et al. 2019), and binary forest cover data (DFRS 2015).	-	30 m
LOPEN	Landscape Openness. Using percentage tree cover data (Hansen et al. 2013), LOPEN was calculated as the percentage of grid cells covered by at least 10% tree cover within a circle of 1 km buffer distance. The field sample plot centre was the centre of the buffer.	%	30 m
	Terrain Variables		
PISR	Mean daily potential incoming solar radiation (PISR) was calculated using the SAGA package (Conrad et al. 2015). The function estimates PISR based on a lumped atmospheric transmittance model. The PISR values were calculated at 30-day intervals for a year, and the daily average was derived.	kWh m^{-2}	30 m
TWI	Topographic wetness index indicates potential on where water tends to accumulate in a landscape. A high value indicates a high potential for water accumulation due to a low slope. Derived from 30 m spatial resolution ASTER DEM (NASA et al. 2019) and SAGA package (Conrad et al. 2015)	-	30 m

0.2.2 Statistical Analysis

This study uses structural equation modelling (SEM) to quantify the relative influence of broad and fine-scale environmental predictors on forest carbon stocks. SEM is suitable for examining complex relationships (Grace 2006, Fan et al. 2016) and uses latent variables to capture complex attributes that cannot be directly measured (Bollen 2002). Terrain attributes that determine fine-scale variations in soil moisture availability and potential solar radiation also contribute to the spatial variation in forest carbon. In this case of examining the drivers of forest carbon stocks in heterogeneous landscapes, SEM allows using terrain as a mediator variable (Gana & Broc 2019) that helps explain the relationship between predictor and response.

All statistical analyses were performed using R version 4.0.3 (Team 2020). Two separate SEMs for AGC and SOC were fitted using the lavaan package (Rosseel 2012). The models were fitted using the Maximum Likelihood Estimation with robust standard errors, and the overall model fit was assessed using the Yuan-Bentler test statistic. The model fit was evaluated using the χ^2 test, with a non-significant result indicating a good model fit as it suggests that there is no discrepancy between the model-implied and the original covariance matrix. A commonly used significance cut-off of $p < 0.05$ (Hu & Bentler 1999) was applied. To further evaluate the model fit, commonly used indices such as the comparative fit index (CFI), squared root mean residual (SRMR), and root mean squared error of approximation (RMSEA) were also calculated (Hooper et al. 2008, Fan et al. 2016). The models were compared against the acceptable levels of CFI (>0.95), SRMR (<0.5), and RMSEA (0.05-0.08) (Schumacker & Lomax 2016).

SEM is based on the covariance among variances; therefore, a key assumption of this method is that the data are multivariate normal. If this assumption is violated (e.g. skewness and outliers), it can strongly affect the covariance. To address this, the input variables were rescaled, transformed, and standardised using the DataSetScaleTransformStandardize function (Ryberg 2017) to approximate the multivariate normality. However, some variables still violate these assumptions (Figure S1, Supporting information). To address this, bootstrapping was used (Gana & Broc 2019), with 10,000 bootstraps performed to derive standard errors. The SEM model was designed to examine direct effects (e.g. the path from climatic water availability to forest carbon while controlling for terrain effects), indirect effects (e.g. the path from latent variables to forest carbon considering only terrain effects), and total effects (the sum of direct and indirect effects). Additionally, simple linear models were fitted to visualise the relationships between AGC, SOC, and predictor variables.

0.3 Results

SEM analysis revealed relationships between variables and the observed forest carbon stocks (SOC and AGC) in the Central Himalayas, as depicted in Figure 3. The AGC (Figure 3A) and SOC models (Figure 3B) show that a substantial fraction of the observed spatial variation in forest carbon stocks can be explained by these broad and fine-scale predictors. The AGC model accounted for 25% of the observed spatial variation in forest AGC, while the SOC model accounted for 59% of the observed variation in forest SOC. Among the variables, the latent variable representing disturbance probability was the most influential predictor of forest AGC, with a β coefficient of -0.556 (SE = 0.044, p <.001). Meanwhile, the proxy for climatic energy availability was the most influential predictor of SOC, with a β coefficient of = -0.745(SE = 0.027, p <.001). A summary of the direct and total effects, including standardised coefficients, standard errors, and p-values of SEMs for the AGC and SOC models, is presented in Table S1), Supporting information.

The result of the χ^2 test showed that the estimated covariance matrix significantly differed from the actual covariance matrix for both AGC ($\chi^2(21) = 633.309$, p = 0) and SOC ($\chi^2(21) = 513.863$, p = 0) models. Although a highly significant χ^2 suggests a poor global model fit (Kline 2010), the χ^2 criterion is sensitive to sample size, as it is calculated as a function of the maximum likelihood (F_{ML}) and sample size ($\chi^2 = (n-1)F_{ML}$) (Brown 2015). For example, with more than 200 samples, χ^2 typically indicates a significant probability level (Schumacker & Lomax 2016). The fit indices of both the AGC (CFI = 0.95, SRMR = 0.057, RMSEA = 0.12) and SOC (CFI = 0.961, SRMR = 0.045, RMSEA = 0.107) models indicated a good fit. Thus, the observed range of indices within commonly accepted thresholds provided satisfactory model fits, and the models characterised the data reasonably well.

The SEM fit showed that climatic energy availability was negatively correlated with forest carbon (AGC and SOC). The direct effect size of climatic energy was large, negative, and significant for both forest carbon pools, with a larger impact on forest SOC compared to AGC. Univariate plots and simple linear models revealed that forests with low growing degree days (GDD) may have higher forest carbon stocks than those with high GDD (Figure 4a, j), but the relationship is not strong. However, GDD had a strong negative correlation with SOC. Similarly, SOC had a stronger negative correlation with temperature seasonality (Bio4) and potential evapotranspiration (PET) than with forest AGC (Figure 4k, l).

Variables related to climatic water availability had small but significant indirect effects on forest AGB and SOC. Although marginal, the direct effect size of water availability was positive for forest SOC, whereas it was negative and insignificant for forest AGC. Univariate linear models also showed a significant relationship between forest carbon stocks (both AGC and SOC) and variables representing climatic water availability (mean annual precipitation (Bio12) and precipitation seasonality (Bio15)) (Figure 4d, e, m, n). In contrast to the negative slopes in the linear models, the observed positive direct effect in SEM of SOC and negative effect in SEM of AGC is because SEM is a more complex model that aims to capture causal relationships by taking into account all the relationships among input variables simultaneously.

The significant total effect for the latent variable terrain suggests that it mediates the relationship between water, energy, and disturbance variables and forest AGC and SOC (Figure 3). Although plotting forest carbon stocks (AGC and SOC) directly against terrain attributes did not show pronounced

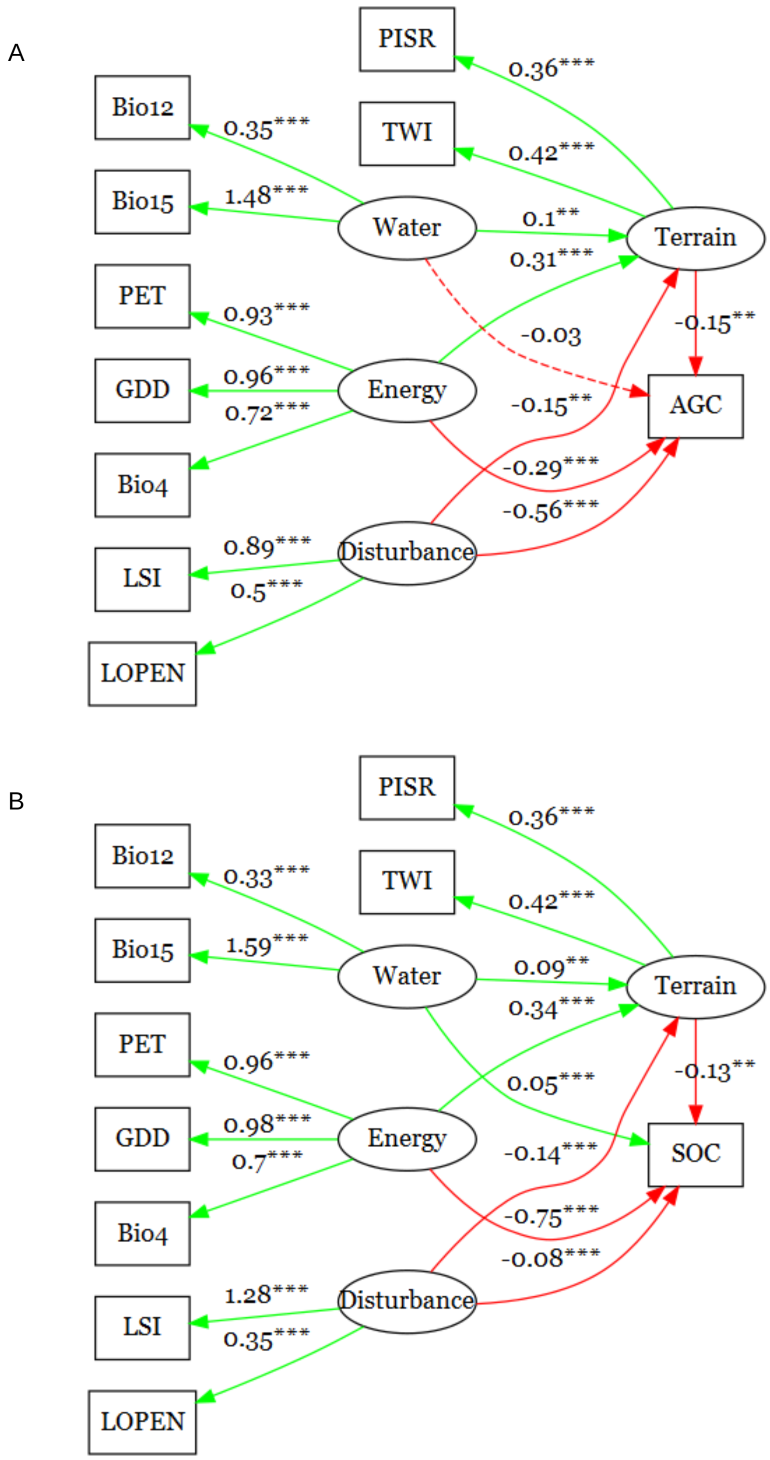

Figure 3: Path diagrams for SEM models of the spatial variation in forest carbon stocks are shown in Panel A (AGC model) and Panel B (SOC model). Latent variables are represented by ovals, while observed variables indicating latent variables are represented by boxes connected to the ovals (variable descriptions can be found in Table 1). The values on arrows pointing from latent variables to observed variables represent the loadings, whereas the values on arrows pointing from latent variables to observed variables indicate path regression coefficients. The significance levels are indicated by asterisks (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$). Positive effects are indicated by green arrows, whereas negative effects are indicated by red arrows. The dashed arrows indicate insignificant path coefficients.

correlations (Figure 4), strong trends were observed in the upper quantiles of forest AGC and SOC for some terrain attributes. For example, despite the weak overall correlations between AGC and mean annual precipitation (Bio12), landscape openness, and TWI, the upper quantiles of forest AGC showed strong trends with these attributes. Similarly, the upper quantiles of forest SOC decreased strongly with TWI, although the overall correlation between the two was weak.

In the SEM output (Figure 3), partial mediation was observed in both the AGC and SOC models, with significant direct and indirect effects (Table S1, Supporting information). Partial mediation indicated that the terrain variable did not fully explain the relationship between climate and forest carbon stocks, as direct effects also played a significant role. The significant total effects, combining direct and indirect effects, further confirm the significance of partial mediation, as stated by (MacKinnon et al. 2007). The partial mediation of terrain attributes on the relationship between forest carbon and climatic factors, such as energy, water, and disturbance (Table S1, Supporting information) highlights the contribution of fine-scale variations due to terrain superimposed on broader controls. More detailed information about the models for AGC and SOC can be found in Tables S2 and S3 in Supporting information, respectively.

The probability of disturbance was found to have the strongest effect on forest AGC compared to water and energy variables (Figure 3A and Table S1, Supporting information). The SEM results showed that forest AGC was strongly related to the forest fragmentation metrics. The univariate linear model also confirmed a strong correlation between disturbance and forest AGC (Figure 4f, g), suggesting that human disturbance, such as wood product collection, plays a significant role in the spatial distribution of forest AGC (Figure 4k, m). Increased forest fragmentation, represented by an increase in the LSI, was associated with a decline in forest carbon. Conversely, forests with relatively low landscape openness, indicating a large proportion of tree cover, had relatively high forest carbon stock.

0.4 Discussion

The SEM findings confirmed that the various environmental factors associated with climatic moisture, energy availability and human disturbances significantly affect the spatial variation in forest carbon stocks in the Central Himalayas. The results of the SEM analysis revealed that a smaller fraction of the variation in forest AGC was explained by the SEM model than by the SEM model for forest SOC (as shown in Figure 3A and Figure 3B). Although the broad controls used in the conceptual model were found to be significantly related to both forest AGC and SOC, their relative importance differed between the two forest carbon pools. Among these controls, the disturbance variable showed the strongest positive correlation with forest AGC. In contrast, the climatic energy variable showed the strongest negative correlation with forest SOC. The significant indirect effects of topography on the spatial variation in forest carbon stocks imply that topography leads to fine-scale variations in forest habitat conditions, which are related to local climate and soil properties.

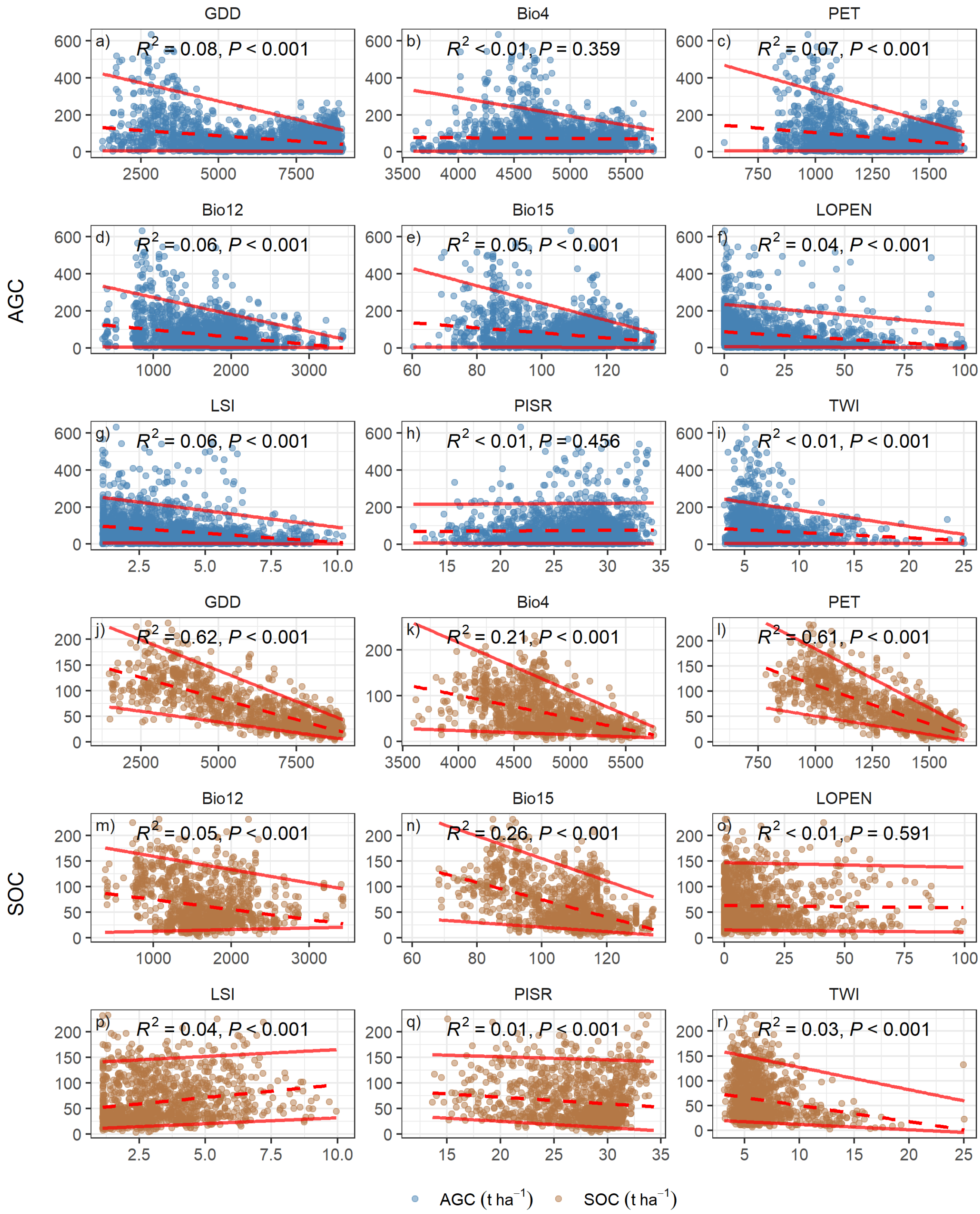

Figure 4: Scatterplots of forest AGC (blue dots) and SOC (brown dots) against each covariate used in the SEM. The solid red lines correspond to the fitted quantiles (0.05 and 0.95), and the dashed red line shows the linear fit. R^2 and p-values in the panels represent linear models. AGC and SOC are on the respective y-axes, and the other variables are on the x-axes. The variables included mean annual growing degree days (GDD), seasonality of mean monthly air temperature (Bio4), mean annual potential evapotranspiration (PET), mean annual precipitation (Bio12), precipitation seasonality (Bio15), landscape openness (LOPEN), landscape shape index (LSI), mean daily potential incoming solar radiation (PISR), and topographic wetness index (TWI).

0.4.1 Broad-scale gradients

The significant negative coefficient between forest carbon stocks and climatic energy availability indicated that areas with higher carbon stocks were located in colder climates with lower growing degree days (GDD) than in warmer climate zones. The mean annual air temperature decreased with elevation, leading to lower plant growth rates at higher elevations. This cold air temperature limits tree growth and survival (Körner 1998) and creates the treeline that defines the upper altitudinal limits of trees. The broad-scale gradients of mean annual temperature and humidity influence tree line elevation and species composition (Schickhoff et al. 2015), and therefore also affect forest carbon. In the Central Himalayas, the treeline elevation ranges between 3400-3600 meters above sea level (masl) (Schickhoff et al. 2015) and can reach even higher in some areas (Stainton 1972). Above the treeline, the forest transitions into low statured shrubs and grasses (Ohsawa et al. 1973, Körner 1998). For instance, at elevations around 3500 masl, the size of common tree species, such as *Juniperus indica* and *Pinus wallichiana*, depends on aspect (Måren et al. 2015), and forest carbon density is lower than at elevations below 3500 masl.

The analysis found that the plots with the highest forest AGC in the country were located at high elevations with relatively cold climates, despite AGC being generally the lowest in the coldest regions (Figure 4a). Similarly, forest SOC was relatively high in cold regions of the high mountain regions, consistent with a negative relationship between GDD and SOC. However, the upper-quantile forest SOC decreased in the coldest region of the study area (Figure 4j). This reflects that soil carbon accumulation is a long-term process influenced by the balance between site productivity and decomposition rates, with decomposition being more sensitive than productivity. On a global scale, mature forest stands with a mean annual temperature (MAT) of approximately 10 °C have the highest carbon density, whereas low carbon density is found in stands with both higher and lower MAT (Liu et al. 2014). Despite the negative relationship in a linear model, the observed maximum forest carbon density stands are towards the middle MAT ranges in the Himalayas, which agrees with earlier findings (Lewis et al. 2013, Reich et al. 2014). The findings of the study agree with earlier research that shows an increase in AGC along the elevational gradient is a result of the combined effects of moisture availability and growth-limiting air temperatures (Yang et al. 2005). Conversely, SOC increases with elevation and is related to a decrease in mean annual air temperature (Liu & Nan 2018).

The results of the analysis showed that the relationship between climatic water availability and forest SOC was significant and positive, whereas the relationship with AGC was negative. In the Central Himalayas, the major sources of soil moisture are the seasonal precipitation during the monsoon and snowpacks (Zobel & Singh 1997). Mean annual precipitation in Nepal varies greatly, with some high-elevation areas receiving as little as 200 mm, while others in the middle mountains receive over 5000 mm (Karki et al. 2016). Despite the limited rainfall, higher elevation areas receive seasonal snow as an additional source of moisture for plant growth (Osmaston 1922, Singh & Singh 1987, Trujillo et al. 2012). The forest AGC was found to have a positive correlation with mean annual precipitation for plots receiving up to approximately 1500 mm year^{-1} (Figure 4d). This pattern is consistent with the dominant effect of water limitation on forest productivity at this precipitation level. These results are in agreement with those of other studies that found a strong positive correlation between forest AGC and precipitation (Swetnam et al. 2017, Fang et al. 2018, Lie et al. 2018-07-12). However, plots receiving more than 1500 mm year^{-1} of precipitation showed a decreasing upper quantile of forest AGC, located in the middle mountains. This region has a history of higher intensity of human disturbances (Smadja 1992, Brown & Shrestha 2000) and frequent natural disasters, such as landslides (Caine & Mool 1982), leading to lower forest AGC along the elevational gradient, as observed when plotted against GDD (Figure 4d).This region has a history of higher intensity of human disturbances (Smadja 1992, Brown & Shrestha 2000) and frequent natural disasters, such as landslides (Caine & Mool 1982), leading to lower forest AGC along the elevational gradient, as observed when plotted against GDD (Figure 4d). It is important to note that the topoclimatic heterogeneity in the study area means that in some areas, rainfall increases with elevation, while in others, it decreases with elevation (Pokharel et al. 2020).

The weaker correlation between climatic water availability and forest carbon compared to climatic energy can be attributed to the effect of temperature in subalpine regions, with snow as the main source of precipitation. In these regions, temperature affects photosynthesis during the colder season but indirectly facilitates tree growth through snowmelt during winter (Huxman et al. 2003). Thus, temperature facilitates tree growth indirectly by increasing moisture availability through snowmelt during winter (Borgaonkar et al. 2011). As a substantial proportion of the Central Himalayan forests are located at elevations exceeding ~2000 masl (DFRS 2015), the snow fraction of precipitation is likely to be a significant determinant of forest habitat quality. The weaker correlation between climatic water availability and forest carbon stocks observed in this study can be attributed to the confounding effects of air temperature. The variables used to represent climatic water availability had only a marginal correlation with forest carbon, except for precipitation seasonality which showed a strong correlation with forest SOC (Figure 4d,e,m,n). Forests with low SOC were located at high elevations with low annual precipitation and low precipitation seasonality (e.g. <80 in Figure 4n). The negative relationship between mean annual precipitation, precipitation seasonality, elevation, and mean annual temperature supports the idea that temperature affects the impact of climatic water availability on vegetation (Morán-Tejeda et al. 2013, Ale et al. 2018). In the higher elevation regions, temperature may limit tree growth and even recruitment despite abundant precipitation as snow. Plants in the alpine region may not have water limitations but can experience a range of atmospheric effects on photosynthesis rates (Wang et al. 2017), including a decrease in the length of the growing season (Barry 2002).

Forest species composition, tree growth, and forest carbon stocks in the lower elevation ranges of the Central Himalayas are expected to respond differently to climate than at higher elevations. For instance, in the subtropical forests of the Central Himalayas, tree species richness increases consistently with water availability and has a parabolic relationship with energy (Bhattarai & Vetaas 2003). Additionally, the growth of Chir pine (*Pinus roxburghii*) in the Himalayan subtropical zone has a strong positive correlation with seasonal precipitation and a negative correlation with mean monthly air temperature (Sigdel et al. 2018, Tiwari et al. 2020). Even in areas with similar elevation and climatic conditions, forest carbon stocks are higher in regions dominated by older trees and nitrogen-fixing trees (Maraseni & Pandey 2014). The study area encompasses diverse ecoregions within the Central Himalayas (Olson et al. 2001), and the relationship between forest carbon stocks and broad climatic gradients highlights the impact of dominant climatic factors on the forests of the entire region.

0.4.2 Fine-scale gradients

The probability of forest disturbance, as represented by the latent variable, was found to have a significant negative correlation with both forest AGC and SOC. As hypothesised, in addition to the broad-scale interaction of climate with topography, the interaction of terrain characteristics with disturbances on a more local scale was also observed. The magnitude of disturbance's effect on forest AGC and SOC varies, with immediate effects on forest AGC after tree removal and soil carbon changes taking longer to respond. In the mountainous environment of the Central Himalayas, terrain constrains human disturbance by limiting forest accessibility. This study found that the spatial and temporal patterns of both natural and human-induced forest disturbance are dependent on topography, as reported by Hadley (1994); Kenderes et al. (2007); Sommerfeld et al. (2018). These results support the observation that topography and human-induced disturbances jointly impact the structure and carbon content of forests in the Himalayas, as noted by Måren et al. (2015); Sharma et al. (2010).

Univariate plots of the indicators of the disturbance also confirmed a significant negative relationship with forest AGC (Figure 4f, g). These findings are consistent with the expectation that the plots with higher disturbance likelihood had lower forest carbon. The level of forest fragmentation, as represented by the LSI, indicates a relatively high likelihood of human disturbance for plots in landscapes that have a relatively high edge density. Similarly, another indicator of forest disturbance, landscape openness, represents the fraction of non-forest area within the buffered region of the forest plots. Although a single or few large-diameter trees sampled in forest inventory plots in forest stands with sparse tree canopy can result in large forest AGC estimates (Vorster et al. 2020-05-14), these have typically low occurrence. Generally, a larger proportion of non-forested areas in a forest patch is thought to result from high-intensity disturbance as opposed to forest patches with a closed canopy (Frolking et al. 2009). Human disturbances such as selective tree removal, which is common in Nepal, would thus reduce tree cover (Shrestha et al. 2013, Aryal et al. 2021) and, therefore, forest carbon stock. In contrast, if these sites naturally have sparse tree cover or only a fraction of the patches with tree cover, we would likely expect these sites to be adjacent to other land uses and have a higher probability of disturbance. Generally, we would expect a forest with a closed canopy to have a higher carbon density. However, in the case of forest SOC, the proxy for forest disturbance showed a weaker relationship compared to forest AGC (Figure 4o,p). The form of the relationships was as expected: the plots with maximum forest SOC occurred in locations with the lowest probability of disturbance, forest SOC declined with the increasing disturbance probability and was smallest for plots in locations with the highest disturbance probability.

The correlation between topographic attributes and forest carbon was significant, reflecting the impact of topography on forest habitat quality through its influence on soil depth, precipitation, water redistribution, and storage capacity in the mountains. Topography modifies the distribution of soil moisture availability and disturbance probabilities across the Central Himalayas (Gerlitz et al. 2016). In mountains, the formation of soil is controlled by slope and aspect, which determine the exposure to sun and wind, erosion potential, and moisture retention (Price & Harden 2013). Topography also affects the spatial variation of soil depths, which in turn controls soil moisture storage and conservation capacity (Boer et al. 1996, Williams et al. 2009). Topography affects the spatiotemporal redistribution of water by altering rainfall, snow accumulation, snowmelt, and meltwater distribution (Gurung et al. 2017). Snow cover duration and other snow-related characteristics, such as the depth and fraction of precipitation, vary depending on topography and wind exposure. The windward slopes in the mountains receive more rainfall than the leeward slopes, creating high spatial variability in moisture availability owing to topographic complexity. Topography also affects the amount of solar radiation received across the mountainous landscape, with significant effects on forest productivity. For instance, the basal area of *Abies pindrow* in sites above 2600 masl can vary by 40% depending on the aspect (Sharma & Baduni 2000). The potential insolation variable used in the models, which is a function of elevation, terrain slope, aspect, and topographic shading (Bohner & Antonic 2009), varies based on topographic position. The significant mediation of the relationship between forest carbon and climate by topography most likely reflects the impact of slope angle and orientation on the spatial distributions of soil moisture (Kopeckỳ & Čížková 2010), solar insolation (Zhang et al. 2017) and evapotranspiration potential (Huang et al. 2019).

Examination of forest carbon density as a function of biophysical constraints, such as water, energy, and disturbance, provided valuable insights into the relative impacts of these constraints across a large heterogeneous study area in the Central Himalayas. Moreover, the significant effect of fine-scale topographic attributes on the relationship between coarse climatic variables and forest carbon density confirmed that the variation in topoclimate determines the variation in forest carbon distribution. By extrapolating these broad-scale gradients and fine-scale variations in forest carbon, forest carbon distribution can be predicted beyond the locations of forest inventory plots.

0.5 Conclusions

Topoclimatic gradients in the Central Himalayas create highly heterogeneous landscapes and influence the species composition, structure, and carbon stock of forests. Structural equation modelling was found to be a useful approach for exploring the relationship between multiple variables and forest carbon stocks. The results indicated that the variation in forest carbon stocks was related to metrics or proxies of forest habitat conditions, such as climatic energy, water availability, and disturbance regimes. Furthermore, the findings showed that topography modified the predominant drivers by adding fine-scale variation in climatic water and energy availability, as well as the likelihood of human disturbances. This provides a better understanding of the relative role of these key drivers in explaining the spatial variation of forest carbon stocks in the Central Himalayas, which is important for improving forest carbon estimates and emission reduction targets such as Reducing Emissions from Deforestation and Forest Degradation (REDD+).

0.6 Author's contribution

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The plot-level estimates of forest AGB and SOC used in this study can be accessed at 10.6084/m9.figshare.21959636.v1.

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