
















## ARTICLE

## Macrosystems Ecology

# Species richness is a strong driver of forest biomass along broad bioclimatic gradients in the Himalayas

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## Abstract

Forest biomass is an important component of terrestrial carbon pools. However, how climate, biodiversity, and structural attributes co-determine spatiotemporal variation in forest biomass remains not well known. We aimed to shed light on these drivers of forest biomass by measuring diversity and structural attributes of tree species in 400-m<sup>2</sup> plots located every 100 m along a 4200-m elevational gradient in the eastern Himalayas. We applied structural equation models to test how climate, species richness, structural attributes, and their interactions influence forest biomass. Importantly, species richness was a stronger driver of biomass than environmental and structural attributes such as annual air temperature or stem density. Integrating the availability of energy and the demand for water, potential evapotranspiration was more strongly correlated with biomass than water availability, likely due to the strong influence of the Indian summer monsoon. Thus, interactions between climate and tree community composition ultimately control how much carbon is stored in woody biomass across bioclimatic gradients. This fundamental understanding will support predictive efforts of the forest carbon sink in this

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hydroclimatically important region and help preserving regional forests as a potent natural solution for climate change mitigation.

#### KEYWORDS

alpine treeline, carbon, climate, diversity, elevation, potential evapotranspiration, tropical forest

## INTRODUCTION

Forest biomass accounts for about 42% of the terrestrial carbon storage (Pan et al., 2011). In particular, woody biomass of a forest constitutes a main component of its lasting carbon stocks, together with soils (DFRS, 2015), contributing substantially to the sequestration of greenhouse gases thus to the mitigation of climate warming (Grassi et al., 2017; Piao et al., 2009; Yu et al., 2019). Standing biomass reflects the net outcome of carbon allocation and disturbance dynamics processes over longer time scales (Dulamsuren et al., 2016; Gao et al., 2022; Måren & Sharma, 2021). As shown by land surface modeling, global warming, drought stress, and deforestation in the past decades have greatly affected the structure and function of forests through change in biomass accumulation, thus altering this crucial natural resource for human well-being (Piao et al., 2009). Therefore, a better understanding of how biomass changes in response to the environment, especially along elevation and climatic gradients in mountainous areas, is vital to inform sustainable forest management (Grassi et al., 2017; Liang et al., 2016) and strengthen natural climate solutions (Fargione et al., 2018).

Forest biomass depends on environmental or climatic variables at the regional scale (Álvarez-Dávila et al., 2017; Wu et al., 2015). At the same time, species composition and vegetation structure govern biomass accumulation in different forest types (Liu et al., 2018; Måren & Sharma, 2021). Tropical forests are known to accumulate higher biomass than temperate and boreal forests (Pan et al., 2011; Poorter et al., 2015). Similarly, biomass is known to decline with elevation in the tropical montane forests (Malhi et al., 2016). Both biotic and abiotic factors affect forest biomass (Fang et al., 2018; Stegen et al., 2011; van der Sande et al., 2017). For example, climatic factors such as available soil moisture (Álvarez-Dávila et al., 2017) and temperature variability (Fei et al., 2018) can influence the accumulation of forest biomass by modifying stand density and forest composition, driving growth rates and phenology, and altering the availability of soil nutrients (Forrester & Bauhus, 2016; Poorter et al., 2015). In addition, diversity is a crucial factor influencing forest biomass (Albrecht et al., 2021; Huang et al., 2018; Liu et al., 2018). For instance, higher functional and species diversity may

enhance productivity by reducing niche overlap and improving resource availability and use (Tilman et al., 1997; Wright et al., 2021). As shown by a series of comprehensive studies, diversity can mediate the sequestration of carbon (C) in subtropical forests (Huang et al., 2018; Liu et al., 2018) and enhance the sequestration of C in soil (Chen et al., 2018). These findings, however, remain controversial for natural forest ecosystems, particularly along elevational and climatic gradients, with positive (Liang et al., 2016; Liu et al., 2018), negative (Ali et al., 2016), or neutral (Måren & Sharma, 2021) relationships reported between species richness and biomass.

Structural attributes (e.g., stem density, tree height, and diameter) are keys for biotic interactions among neighboring trees in a forest stand (Fotis et al., 2018; He et al., 2019), as well as for resource limitation (Chiang et al., 2016; Ouyang et al., 2019). These attributes are tightly coupled with biomass (Ali et al., 2016; Chave et al., 2005; Stegen et al., 2011). The site conditions (e.g., soil type and disturbance) can also influence the structural and diversity attributes of forest stands (Måren & Sharma, 2021; Ouyang et al., 2019; Wu et al., 2015).

Mountains offer heterogeneous environmental and climatic conditions, thus providing habitats for many plant species along wide bioclimatic gradients (Hu et al., 2020; Mittermeier et al., 2011). Most existing studies, however, are limited in geographical scope (Chiang et al., 2016; Fotis et al., 2018), especially in subtropical/tropical forests (Liu et al., 2018; Poorter et al., 2015; van der Sande et al., 2017). A global map of the potential rate of aboveground C accumulation at a resolution of 1 km<sup>2</sup> exists (Cook-Patton et al., 2020), but cannot well represent elevation-dependent biomass and biodiversity gradients (Hu et al., 2020). Indeed, to date, very few field studies have focused on the variability of forest biomass across several bioclimatic zones (Álvarez-Dávila et al., 2017; Stegen et al., 2011; Wu et al., 2015). In addition, most existing studies have considered only one or two factors influencing biomass. In order to gain a better understanding of the complexity of C allocation, it is thus essential to engage in ecological in situ studies across large environmental gradients (Babst et al., 2021; Li et al., 2021), particularly in understudied diversity hotspots such as the Himalayan region.

In the eastern Himalayas, Nepal, the Kangchenjunga Landscape, characterized by a steep environmental gradient, represents one of the most pronounced bioclimatic transitions from lowland tropical forest to alpine vegetation (Chaudhary et al., 2015; Chettri et al., 2007). This mountain range offers a natural laboratory for exploring spatial changes in forest biomass under the simultaneous influences of multiple drivers such as climate, species richness, and structural attributes. A national inventory on biomass is documented based on the physiographical regions across Nepal (DFRS, 2015), while a limited research tried to detect factors governing biomass in tropical and temperate forests (Luintel et al., 2018; Måren & Sharma, 2021). The eastern Himalayan forests are anticipated to experience a severe loss in plant biodiversity as a result of climatic warming (Mittermeier et al., 2011) and increasing anthropogenic pressure (Chaudhary et al., 2015; Chettri et al., 2007; Schickhoff et al., 2016). Thus, an improved understanding of the current stock of forest biomass and its drivers is critical.

The objectives of this study were to shed light on the drivers of forest biomass by combining biotic and abiotic factors in an integrative analysis of their links with forest biomass across the Kangchenjunga Landscape. We hypothesized that (1) climate directly influences forest biomass and also indirectly affects it by mediating diversity and structural attributes, and (2) diversity and forest biomass are positively correlated when the effects of other potentially confounding variables (i.e., climate and structural attributes) are accounted for. To achieve our objectives, we measured diversity and structural attributes of all tree species occurring at every 100-m elevational interval from tropical forests to alpine treeline, and correlated them with climate and biomass.

## METHODS

### Study area and climate

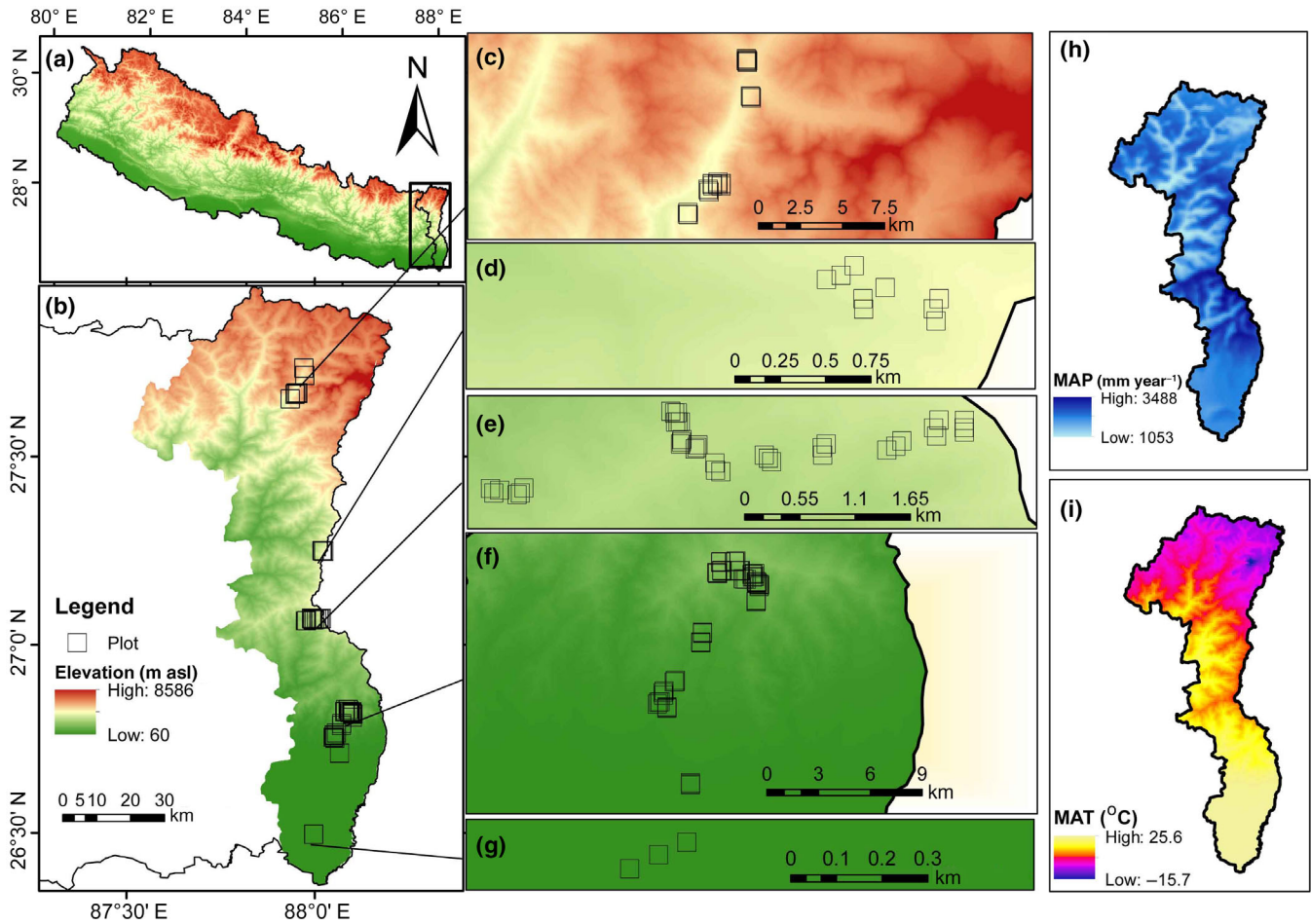
The study was conducted along an elevational transect starting with tropical forests at 80 m above sea level (asl) and extending to the alpine treeline at 4200 m asl in the Kangchenjunga Landscape, Nepal (hereafter KL) (Figure 1). The KL represents one of Earth's most extensive bioclimatic gradients with an array of contrasting vegetation types (Chaudhary et al., 2015; Chettri et al., 2007). It is broadly divided into six zones based on climate and vegetation, representing the major forest types: tropical, subtropical, warm-temperate, cool-temperate, subalpine, and alpine zones (Chaudhary et al., 2015). The tropical zone (60–1000 m asl) is

dominated by tree species such as *Shorea robusta* at lower elevations, followed by *Schima wallichii* at higher elevations. *Schima wallichii* dominates the lower subtropical zone (1000–2000 m asl), whereas *Ostodes paniculata* is abundant at higher elevations. Similarly, *Castanopsis hystrix* and *Quercus glauca* dominate in the warm-temperate zone (2000–2500 m asl), and *Lithocarpus pachyphylla* and *Daphniphyllum himalense* dominate in the cool-temperate zone (2500–3000 m asl). The subalpine zone (3000–4000 m asl) is dominated by the conifers *Abies spectabilis* and *Juniperus recurva*, whereas *Betula utilis* forms the alpine treeline (Appendix S1: Table S1).

The KL is characterized by a monsoon climate, and about 80% of the total annual precipitation occurs during the monsoon season (Chaudhary et al., 2015). It is the moistest transect in comparison with other valleys in the central Himalayas (Liang et al., 2014). The study area covers a wide range of climatic conditions, with mean annual temperature (MAT) ranging from  $-15.7$  to  $25.6^{\circ}\text{C}$  and mean annual precipitation (MAP) ranging from 1053 to 3488 mm (Figure 1). All our sampling plots represented humid forest types with MAP  $>1500$ – $3344$  mm along the elevation gradient (Chave et al., 2005). Potential evapotranspiration (PET) was calculated following Thornthwaite and Mather (1957). It integrates multifaceted climatic variables linked to both the water (evaporation) and energy cycles (energy used for evaporation) (Fisher et al., 2011). MAT and Thornthwaite PET are strongly and negatively correlated with elevation ( $R^2 = 0.98$  and  $0.92$  at  $p < 0.001$ , respectively) (Appendix S2: Figures S1 and S2). By contrast, MAP tends to increase exponentially until about 2000 m asl and then decreases toward the upper treeline ( $R^2 = 0.80$ ,  $p < 0.001$ ) (Appendix S2: Figure S1). Due to a lack of local climate data along the elevational gradient, we used the 30-arcsec gridded climatic database of Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA) from 1979 to 2013 (Karger et al., 2017). The reliability of the climatic data from CHELSA in the central Himalayas has been demonstrated by a recent study (Rai et al., 2020).

### Sampling design and measurements

Two extensive field campaigns were conducted in the KL from September to November in 2017 and 2018. Three plots of  $20 \times 20 \text{ m}^2$  extent were established at each sampling elevation at approximately 100-m intervals between 80 m (tropical forest) and 4200 m asl (alpine treeline). The plots were placed in natural forests with a representative species abundance and composition at each



**FIGURE 1** (a) Overview of the Kangchenjunga Landscape in the eastern Himalayas, Nepal (KL). (b) Map showing the forest plots along the elevational gradient. (c–g) Sampling points from tropical forests to alpine treeline. Changes in (h) mean annual precipitation (MAP) and (i) mean annual temperature (MAT) along the gradient

elevation. Such a sampling design provided a fine resolution of progressive elevational shifts in the composition and structure of the plant communities along the transect (Wu et al., 2015). All living trees in each plot with diameter at breast height (dbh) (measured at 1.3 m)  $\geq 5$  cm were measured using a diameter tape. The height of each tree was measured using a clinometer (Suunto Compass/Clinometer Tandem, SS020420000). We mainly focused on tree species because they comprise a substantial proportion of forest biomass along the broad elevational gradient (DFRS, 2015). A total of 126 plots (42 elevations  $\times$  3 plots) were thus established along the gradient, comprising 4170 trees belonging to 126 species (Appendix S1: Table S2). Tree species were identified following standard literature on plant taxonomy in Nepal (Polunin & Stainton, 1984; Press et al., 2000). Species unidentified in the field were photographed, and their specimens were thereafter identified at the Tribhuvan University Central Herbarium (TUCH), Kirtipur, Nepal.

## Environmental variables, diversity, and structural attributes

We calculated four plot-based attributes of tree diversity: species richness (number of species), the Shannon–Wiener diversity index (number of species and their abundance) (Shannon & Wiener, 1963), dominance, and evenness (similarity of species in terms of their abundances) (Magurran, 2004; Simpson, 1949). We also calculated importance value index to determine dominant and rare tree species in each vegetation zone (Curtis & McIntosh, 1951) (Appendix S1: Table S1). Similarly, stem density (i.e., the total number of tree individuals per plot area; [stems ha<sup>-1</sup>]) was examined in each plot as a structural attribute. Plot coordinates were used to retrieve data for MAT and MAP from the CHELSA database. Climatic variables thus included both energy variables (MAT and PET) and water availability (MAP) for each plot (Appendix S1: Table S3).



## Estimation of stand biomass

We used an allometric equation to estimate stem biomass at the individual level in the moist forest (1500–3500 mm MAP). This allometric equation (1) uses dbh, tree height, and wood density as key predictors of stem biomass (Chave et al., 2005). We chose this equation because it includes wood density, which is an important source of variation in biomass of different tree species (Poorter et al., 2015). In addition, the equation also corresponds to the climate and forest types (i.e., moist forests in our study area), and it is being used as a national guideline for estimating the biomass of tree species along different elevational gradients in Nepal (Luintel et al., 2018; Subedi et al., 2010).

$$\text{Stem biomass} = 0.0509 \times \rho \text{ dbh}^2 \times \text{Ht}, \quad (1)$$

where  $\rho$  is specific wood density (in grams per cubic centimeter), and Ht is tree height (in meters).

Species-specific air-dried wood density obtained from the Nepalese database (MPFS, 1989; Sharma & Pukkala, 1990) was used to calculate stem biomass. In case, species-specific values were unavailable in the database ( $n = 53$  out of 126 species), the genus-level averages were derived from the Nepalese database (MPFS, 1989; Sharma & Pukkala, 1990) or from the Global Wood Density Database (Zanne et al., 2009). The overall regional average from the global dataset was used in case species- or genus-specific data or taxonomic information were unavailable ( $n = 37$  out of 126 species, accounting for <20% of the plot biomass). The air-dried wood density from the Nepalese dataset was converted to oven-dried wood density ( $D_b$ ) using equation (2), assuming a moisture content of 12% for the air-dried density ( $D_{12}$ ) (Vieilledent et al., 2018). We derived wood density at 12% moisture because this level has recently been established as an international standard (Sallenave, 1955; Vieilledent et al., 2018).

$$D_b = 0.828 \times D_{12} \quad (2)$$

Branch and foliage biomasses were estimated using species- or genus-specific branch-to-stem and foliage-to-stem ratios. Acknowledging the strong effect of tree size, the standard dbh-based (<28, 28–53, and >53 cm) ratios as prescribed by MPFS (1989) were used. The recommended branch-to-stem and foliage-to-stem ratios were used for tree species when both the species and genus ratios were unavailable (MPFS, 1989). Similarly, an allometric relationship based on equation (3) was used to estimate root biomass using the shoot biomass (i.e., the sum of stems, branches, and leaves) at the individual level, because the equation captured well the

relationship between root biomass ( $y$ ) and shoot biomass ( $x$ ) in the forests (Mokany et al., 2006).

$$y = 0.489 \times x^{0.890} \quad (3)$$

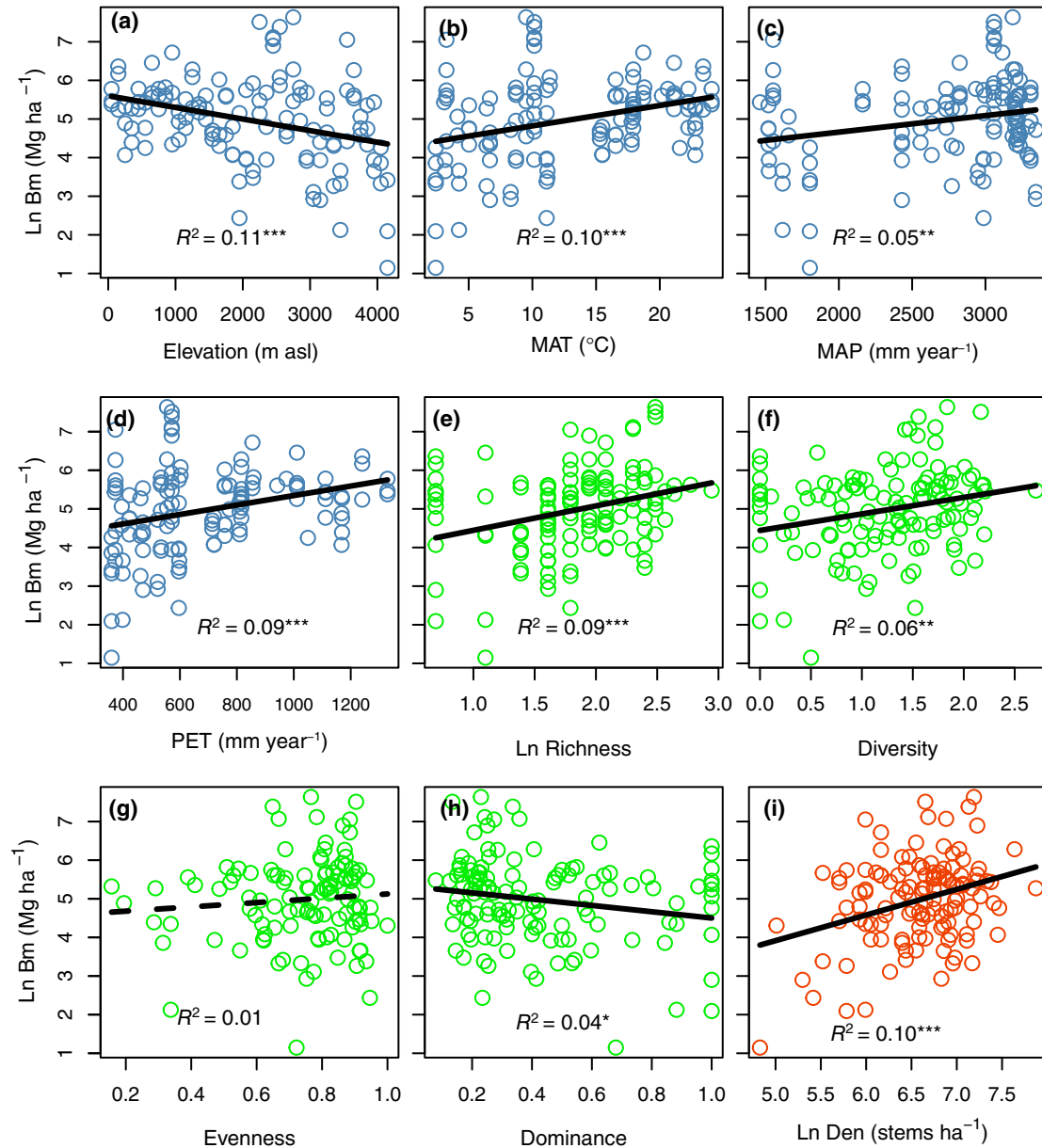
The biomass of each living tree was calculated by summing all above- and belowground biomass components. The plot-level biomass was calculated by summing the biomasses of all trees in a plot. Finally, the plot-based biomass was converted to megagrams per hectare ( $\text{Mg ha}^{-1}$ ).

## Data analysis

We tested the relationships between stand biomass and environmental, diversity, and stand structural attributes using simple linear regressions. Since we used dbh and tree height as predictors of biomass, we only included stem density in our analysis. Given the wide range of climates covered by our transect, the length of the growing season varies substantially with elevation. Thus, we used annual climatic variables in the models. Biomass, species richness, and stem density were log-transformed to achieve normality prior to all analyses. We also used an ANOVA followed by Tukey's honestly significant difference test to identify significant differences in stand biomass among vegetation zones.

## Fitting of structural equation models

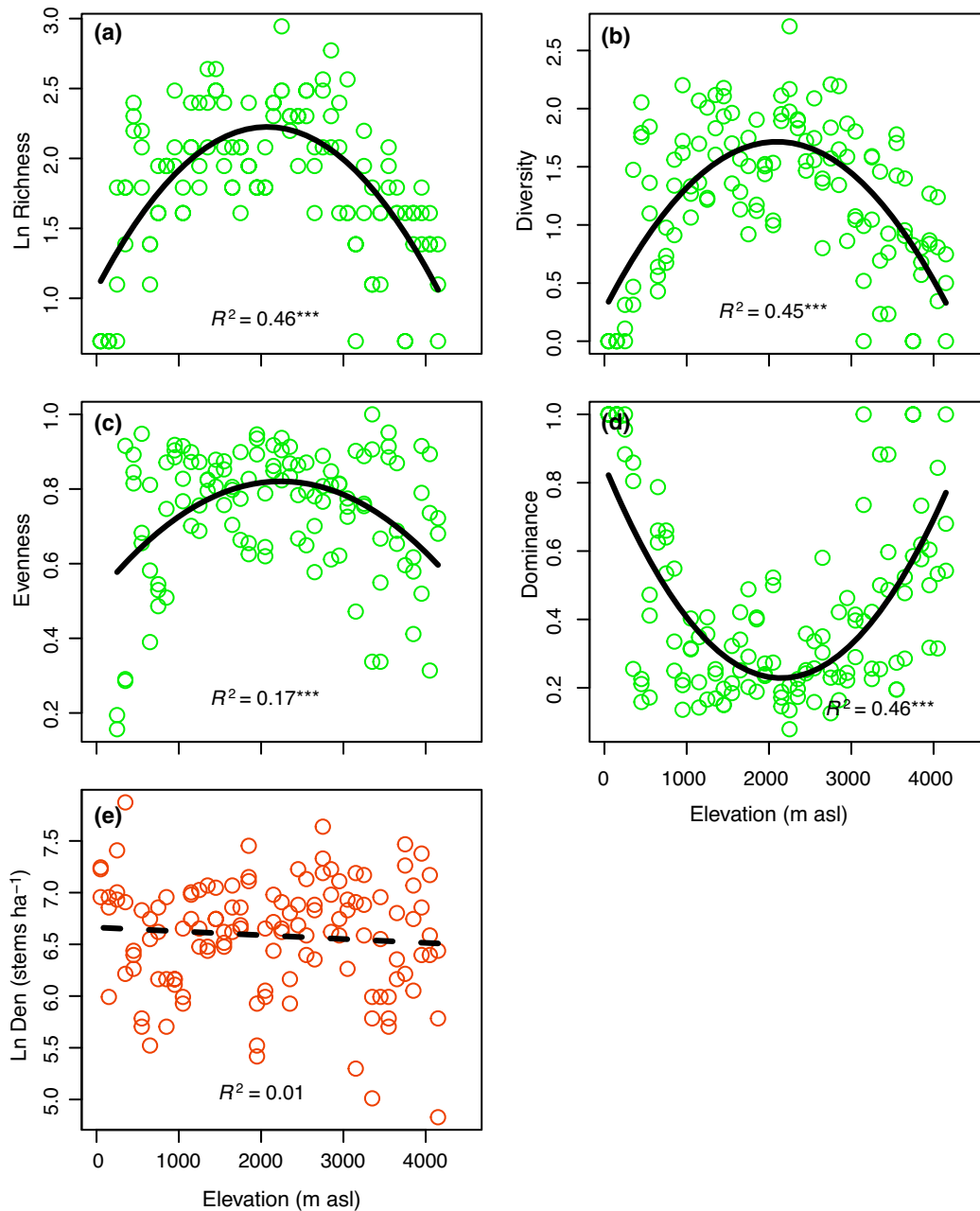
We used structural equation models (SEMs) to test the direct and indirect effects of the environmental variables (elevation and climate), the diversity, and structural attributes on stand biomass using multivariate relationships (Appendix S2: Figure S3). We first calculated the variance inflation factor (VIF) from multiple regression models using the “car” package, version 3.0-13 in R (Fox & Weisberg, 2019) to detect redundant or multicollinear variables. In the best multiple regressions, only significant bivariate relationships and VIFs < 3 were retained for the final SEM to avoid the effects of multicollinearity (Appendix S1: Table S4) (Ouyang et al., 2019). We only included species richness in the SEMs, because the relationship between richness and biomass was the strongest among all diversity attributes (Figure 2). Only those variables that explained most of the variations were thus incorporated into the SEMs (Figures 2 and 3; Appendix S2: Figure S4). Finally, the goodness-of-fit of the SEMs was examined using Fisher's chi-squared test (requiring  $p > 0.05$ ), the Akaike information criterion (AIC), and the Bayesian information criterion (BIC). We



**FIGURE 2** Relationships between forest biomass (Ln Bm) and the environmental variables (blue scatter plots) (a) elevation, (b) mean annual temperature (MAT), (c) mean annual precipitation (MAP), and (d) potential evapotranspiration (PET). Relationships between stand biomass and the diversity attributes (green scatter plots) (e) species richness, (f) Shannon–Weiner diversity index, (g) evenness index, and (h) dominance index. Relationships between stand biomass and the stand structural attributes (orange scatter plot) (i) stem density (Ln Den). The solid and dashed lines represent  $p < 0.05$  and  $p > 0.05$ , respectively. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ . Stand biomass, species richness, and stem density were log transformed.

conducted three different models using the same model structure (Appendix S2: Figure S3) and selected climatic variables that explained the largest variation in biomass, without inflating the AIC and BIC values of the models. We used the lowest AIC to select the best-fitted models. Two models were consequently selected with elevation and PET as environmental variables, species richness as the diversity attribute, and stem density as a structural attribute. We used “aspect” as a random factor in the SEMs to account for other environmental differences

(e.g., leeward and windward side, and level of insolation) (Fotis et al., 2018; Paquette & Messier, 2011). Clearly, all fitted models improved the explanatory power of biomass by including “aspect.” The relative strengths of each predictor were then examined based on standardized coefficient estimates ( $\beta$ ) of SEM to facilitate comparisons between pathways. We determined the total effect of each predictor on stand biomass as the sum of the direct and indirect effects. The piecewise SEM was fitted using the R packages: “piecewiseSEM,” version 2.1.2 (Lefcheck, 2016)



**FIGURE 3** (a) Elevational trend of species richness, (b) Shannon–Weiner diversity index, (c) evenness index, (d) Simpson’s index of dominance, and (e) stem density (Ln Den) (stems ha<sup>-1</sup>). The green and orange points represent the diversity and structural attributes, respectively. The solid and dashed lines represent  $p < 0.05$  and  $p > 0.05$ , respectively. \*\*\* $p < 0.001$ . Tree species richness and stem density were log transformed.

and “nlme,” version 3.1–149 (Pinheiro et al., 2020). All statistical analyses were performed in R version 4.0.0 (R Development Core Team, 2020).

## RESULTS

Forest biomass ranged from 3.15 to 2069.38 Mg ha<sup>-1</sup>, with a mean of 253.79 Mg ha<sup>-1</sup>. Forest biomass was significantly lower in the alpine ( $31.34 \pm 25.17$  Mg ha<sup>-1</sup>)

and subalpine ( $160.10 \pm 219.78$  Mg ha<sup>-1</sup>) zones than in the other zones (Appendix S1: Table S1). Interestingly, mean forest biomass was comparable among the tropical, subtropical, and temperate zones ( $p > 0.05$ ).

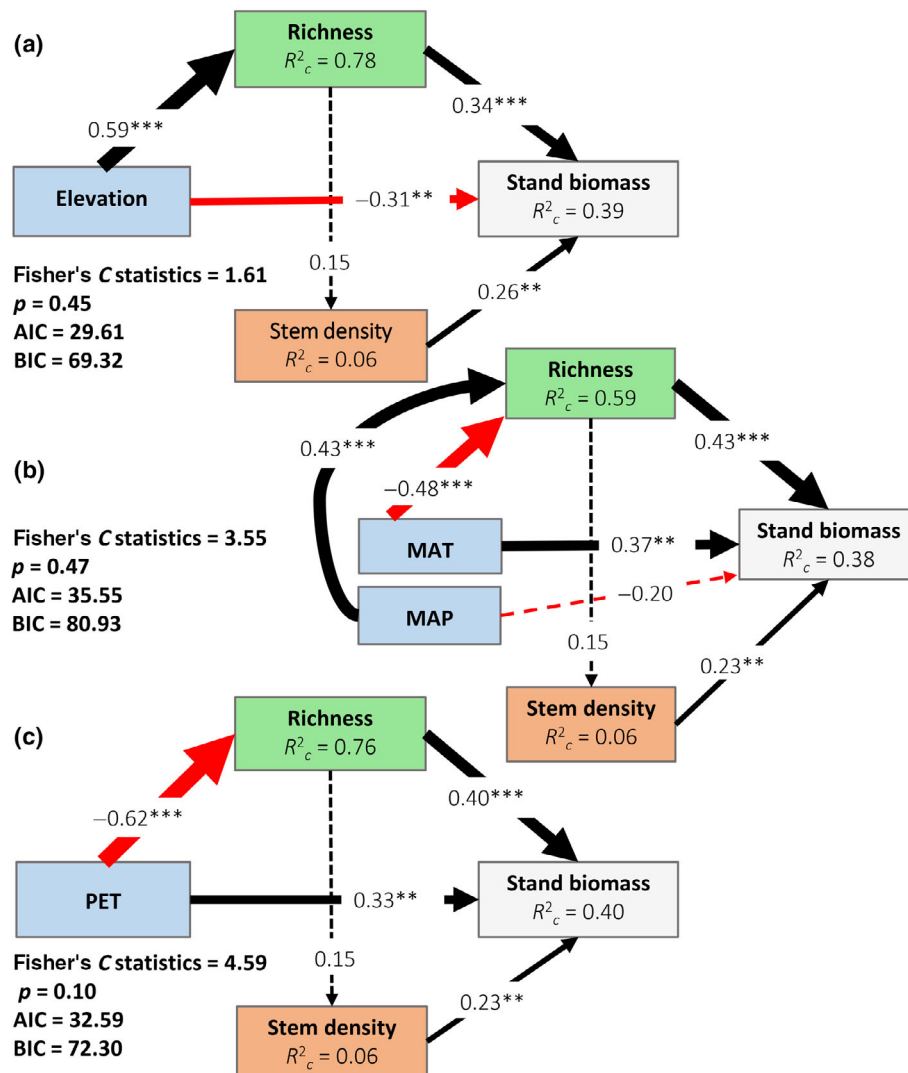
### Drivers of forest stand biomass

The environmental variables, diversity, and structural attributes strongly affected forest biomass (Figure 2). The

variation explained by the environmental variables (i.e., elevation and climate) was comparable, but biomass was only weakly positively correlated with MAP ( $R^2 = 0.05$ ,  $p < 0.01$ ). Elevation ( $R^2 = 0.11$ ,  $p < 0.001$ ), followed by MAT ( $R^2 = 0.10$ ,  $p < 0.001$ ) and PET ( $R^2 = 0.09$ ,  $p < 0.001$ ), explained most of the variation in stand biomass. The area-based measures of diversity (species richness) exhibited the strongest positive correlation with biomass ( $R^2 = 0.09$ ,  $p < 0.001$ ). However, species evenness was not significantly correlated with biomass, whereas biomass was positively correlated with stem density ( $R^2 = 0.10$ ,  $p < 0.001$ ).

## Effects of environmental variables and diversity and structural attributes on stand biomass

The SEMs adequately fit the output from Fisher's chi-squared distribution for the elevation-based model (Figure 4a; Fisher's  $C$  statistic = 1.61,  $p = 0.45$ ; Appendix S1: Table S5), the MAT- and MAP-based model (Figure 4b; Fisher's  $C$  statistic = 3.55,  $p = 0.47$ ; Appendix S1: Table S6), and the PET-based model (Figure 4c; Fisher's  $C$  statistic = 4.59,  $p = 0.10$ ;



**FIGURE 4** Structural equation models (SEMs) based on (a) elevation and (b) mean annual temperature (MAT) and mean annual precipitation (MAP) and (c) potential evapotranspiration (PET), illustrating the hypothesized relationships among the environmental variables (blue boxes), diversity attributes (green box), and structural attributes (orange boxes), where aspect was a random effect.  $R^2_c$  in the boxes is the conditional coefficient of determination. The solid and dashed lines indicate significant ( $p < 0.05$ ) and nonsignificant ( $p > 0.05$ ), respectively, and the red and black lines indicate negative and positive relationships, respectively. \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ . Arrow width is proportional to the standardized regression coefficient ( $\beta$ ), where the numbers accompanying each arrow represent their relative importance. Stand biomass, species richness, and stem density were log transformed. AIC, Akaike information criterion; BIC, Bayesian information criterion



**TABLE 1** Path effects of environmental variables, diversity, and stand structural attributes on biomass based on structural equation models (SEMs)

Predictor	Pathway to biomass	Effect ( $\beta$ )
Elevation-based model		
Elevation	Direct effect	-0.31
	Indirect effect via richness	0.20
	Total effect	-0.11
Richness	Direct effect	0.34
	Indirect effect via density	0.04
	Total effect	0.38
Stem density	Direct effect	0.26
	Indirect effect	—
	Total effect	0.26
MAT- and MAP-based model		
MAT	Direct effect	0.37
	Indirect effect via richness	-0.21
	Total effect	0.16
MAP	Direct effect	-0.20
	Indirect effect via richness	0.18
	Total effect	-0.02
Richness	Direct effect	0.43
	Indirect effect via density	0.03
	Total effect	0.46
Stem density	Direct effect	0.23
	Indirect effect	—
	Total effect	0.23
PET-based model		
PET	Direct effect	0.33
	Indirect effect via richness	-0.25
	Total effect	0.08
Richness	Direct effect	0.40
	Indirect effect via density	0.03
	Total effect	0.43
Stem density	Direct effect	0.23
	Indirect effect	—
	Total effect	0.23

*Note:* The standardized pathway coefficients ( $\beta$ ) indicate the relative magnitude of the relationship between a predictor variable and stand biomass. The indirect effect of each predictor was computed by multiplying the standardized path coefficients from one predictor to mediator and then to stand biomass. The total effect was calculated by summing the standardized direct and indirect effects. The positive and negative values indicate positive and negative relationships, respectively, and “—” represents no significant relationship between the variables. MAT, MAP, and PET represent mean annual temperature, mean annual precipitation, and potential evapotranspiration, respectively.

Appendix S1: Table S7). Elevation- and PET-based models were selected as they showed the lowest AIC values. Both models indicated that all predictors together explained ca. 39%–40% of the variation in biomass, ca. 76%–78% of the variation in richness, and 6% of the variation in stem density (Figure 4). The significant but weak correlation between MAP and biomass (Figure 2) became nonsignificant when accounting for other predictors in the SEM with negligible total MAP effects ( $\beta = -0.02$ ) (Figure 4b, Table 1). The PET model is based on temperature, and both MAT and PET are highly correlated with biomass (Figure 4b,c). The PET-based model has a lower AIC value than the MAT- and MAP-based models.

All environmental variables, diversity, and structural attributes in the best-fit SEMs significantly and directly affected biomass (Figure 4, Table 1). Species richness affected biomass the most, even when covarying climatic conditions and stem density were considered simultaneously. Importantly, PET had a significant and direct effect on biomass ( $\beta = 0.33$ ) and species richness ( $\beta = -0.62$ ), but not on stem density. Potential evapotranspiration had both direct and indirect effects on biomass, partially mediated by diversity (richness,  $\beta = -0.25$ ), rather than the stem density. Despite weak bivariate relationships, the multivariate path analysis in SEM explained substantial variations of biomass (elevation-based model with  $R^2_c = 0.39$  and PET-based model with  $R^2_c = 0.40$ ) in response to environmental, diversity, and structural attributes.

## DISCUSSION

Our research sites included most existing forest types along the broad climatic and elevational gradients in the KL, which encompass the climatic conditions found across most of the tropical land areas worldwide. We found that multiple mechanisms simultaneously determine the variation of forest biomass across bioclimatic zones. Interestingly, species richness in our study outperformed the positive effects of all other variables.

### PET as the main climatic variable associated with forest biomass

The availability of energy and the demand for water, that is, PET, was the most robust climatic predictor of forest biomass along the KL elevational gradient. As reported earlier, PET is a principal control of biodiversity along an elevation gradient in the Himalayas (Vetaas et al., 2019). Our sites represented moist forests (Chave et al., 2005; Poorter et al., 2015) with positive water balances; that is,

PET was always lower than MAP. A weaker limiting role of MAP was also supported by a study across Neotropical forests (Poorter et al., 2015). Our results thus contrast with previous studies reporting that water availability constrained the accumulation of biomass along broad climatic conditions (Álvarez-Dávila et al., 2017). However, such a relationship was not significant in moist/wet forests (Stegen et al., 2011), further supporting our results.

Temperature-mediated processes play important roles in the accumulation of biomass by governing diverse eco-physiological processes that determine C uptake, growth, respiration, and decomposition of organic matter (Bruijnzeel & Veneklaas, 1998). The shift from warm to cool temperatures (with sufficient water availability) may facilitate the pumping of water from the soil to leaves to support photosynthesis and also stimulate soil microbial activity and nutrient uptake, thus increasing the biomass of all plant components (Forrester & Bauhus, 2016). This mechanism can also promote evaporative cooling for maintaining biological activity by fulfilling the demand for water in high-energy zones (Kreft & Jetz, 2007). Forest biomass, thus, was highest in the temperate zones (warm-temperate followed by cool-temperate), as previously reported by Stegen et al. (2011), due to the benefits of favorable environmental conditions. In addition, higher species richness and higher stem density may have considerably promoted biomass accumulation in the temperate zone.

Our findings support a strong limiting effect of climate on forest productivity in the harsh climates at colder sites, for example, compared to the temperate forest (Paquette & Messier, 2011). The significantly lower biomass in the alpine and subalpine zones was linked with the negative effect of PET, likely representing the consequence of limitation in water uptake due to frost at high elevations (Vetaas et al., 2019). The elevation-mediated low temperatures and shorter growing seasons at higher elevations could impair microbial activity and reduce the availability of soil nutrients (Hu et al., 2020), thus further limiting the accumulation of biomass at the highest elevations.

Climate also indirectly affected biomass by regulating elevation-dependent patterns of species richness. The elevational gradient is anticipated to include tree species that are well adapted to the prevailing environmental conditions and thus govern vegetation types in mountains (Read et al., 2014). The hump-shaped relationship between species richness and PET has commonly been described for natural forests (Vetaas et al., 2019). The availability of energy may stimulate species richness up to the optimal PET, and the availability of water may then drive richness in high-energy regions (Kreft & Jetz, 2007). An intermediate PET may notably allow for optimal biological activity, because low temperatures decrease the amount of water available due to soil frost (Vetaas et al., 2019). The

nonsignificant association of stem density with elevation and the climatic variables in our study is consistent with another study in the eastern Indian Himalayas (Acharya et al., 2011). However, minimal stem density was found at the treeline sites in our study area. Microsite conditions (e.g., soil condition and disturbance) also likely affect forest biomass via stand structure (Chaudhary et al., 2015; Ouyang et al., 2019; van der Sande et al., 2017). Thus, climate change can interact with diversity attributes affecting the large-scale production of biomass in the Himalayas. In addition, higher availability of water at our study sites may buffer against negative effects of climate change (principally climate warming) on biomass by reducing the susceptibility of trees to drought and by modulating the biotic interactions among tree species (Chhetri et al., 2020; Schickhoff et al., 2016; Sigdel et al., 2020).

### Species richness as a strong driver of forest biomass

Increasing richness of tree species promotes stand biomass, underlining the importance of species richness as a driver of C sequestration and storage. It is evident that the highest biomass is associated with species richness in the Himalayas (this study; Vetaas et al., 2019; Hu et al., 2020). This concurs well with a recent study carried out at a tropical mountain, Mt Kilimanjaro, Tanzania (Albrecht et al., 2021). A positive relationship between diversity and biomass may be a consequence of complementarity mechanisms (Cardinale et al., 2012; Liu et al., 2018). Coexisting species are required to have different strategies (or attributes) for resource uptake and growth in a diverse community (Cardinale et al., 2012; Wright et al., 2021). Thus, higher species richness, through niche complementarity, can promote a greater use of resource pools and higher biomass production. As shown by epidemiological studies, diversity can also slow down the spread of diseases due to a greater dilution of pathogens (Civitello et al., 2015).

Higher species richness may also promote complementarity through facilitation, particularly at higher elevations (Callaway et al., 2002). The harsh climates and low nutrient concentrations in subalpine and alpine zones tend to favor stress-tolerant species (Read et al., 2014), which can ameliorate the severe stress of neighboring species by favoring facilitation over competition (Callaway et al., 2002). Positive species interactions by facilitation rather than competitive exclusion may consequently be predominant at higher elevations, where environmental conditions are less favorable for tree growth (Sigdel et al., 2020). This diversity–biomass relationship suggests that complementarity may also operate in physically stressful environments where facilitation is the most probable interaction (Callaway et al., 2002).

Biomass or productivity may increase with evenness (Zhang et al., 2012), but our results did not indicate a significant correlation between biomass and evenness. Thus, strong interactions among variables other than evenness contribute to the biomass.

Species richness can also promote packing of tree individuals in a diverse stand (Chiang et al., 2016). The density can, in turn, increase the efficiency of light use by maximizing light interception and usage (Forrester & Bauhus, 2016; Morin, 2015). Consequently, tree species can minimize the competitive interference with the neighboring species by occupying different light niches using different foliar architectures (Yachi & Loreau, 2007) and by occupying different parts of the canopy (Ali et al., 2016; Morin, 2015). The increase in stand biomass with stem density further reinforces the importance of high stem density (Chiang et al., 2016; Ouyang et al., 2019), governing the large-scale forest biomass in mountainous areas. Supporting this idea, the loss of species in the Himalayas could lead to a larger decline in biomass (Liang et al., 2016) due to lower abilities to efficiently use water, nutrients, and light (Chen et al., 2018; Liu et al., 2018). However, structural attributes may not necessarily favor biomass accumulation if changes in climate are accompanied by shifts of tree species (Grytnes et al., 2014; Yan & Tang, 2019) and the loss of species in the eastern Himalayas (Mittermeier et al., 2011).

## Limitations of this study

Our study demonstrates a strong role of species richness in governing broad-scale forest biomass accumulation. However, species richness may also interact with other biotic factors in driving changes in forest biomass at lower elevations with a higher productivity. For instance, higher species richness tends to increase a selection effect through competition (Fotis et al., 2018; Poorter et al., 2015; Zhang et al., 2015). It favors highly productive or large species with a higher capacity to acquire resources (e.g., nutrients and sunlight) that can store a high amount of biomass (Chiang et al., 2016). Future work should consider key functional traits associated with resource uptake and distribution of tree species (Maharjan et al., 2021). Moreover, considering understory plants, animals, and soil can provide deeper insights into the overall ecosystem productivity and ecosystem functioning as it changes with elevation (Albrecht et al., 2021; DFRS, 2015; Dulamsuren et al., 2016). Regardless of these limitations, our findings provide broad empirical evidence for a strong relationship between richness and biomass for tree species. In addition, our study focuses on a humid landscape where precipitation is not limiting. This setting did not allow us to detect how water availability affects forest biomass. Future studies should encompass

different precipitation regimes, particularly in the western Himalayas to better address water effects and gain further insights into how climate, biodiversity, and forest structure co-drive variations in forest biomass.

## CONCLUSIONS

Climate increased forest biomass across a wide Himalayan bioclimatic and elevational gradient through effects of species richness, but not through structural attributes. Our findings have important implications for managing and sequestering C in mountainous forested areas. It provides empirical evidence that protecting tree species richness and managing stem density of major tree species could maximize C storage along broad bioclimatic gradients, thereby supporting natural climate solutions. Such insights from a unique biogeographic extent and a diverse but poorly studied mountainous region are also fundamental for the validation and parameterization of “tree-centered” C models and other studies of C cycling.

## AUTHOR CONTRIBUTIONS

Eryuan Liang planned and designed the research. Nita Dyola and Shalik Ram Sigdel performed the research. Nita Dyola analyzed the data with the assistance of Shalik Ram Sigdel, Eryuan Liang, Flurin Babst, J. Julio Camarero, Sugam Aryal, Shan Gao, and Xiaoming Lu. Nita Dyola wrote the first draft, and all authors substantially contributed to the writing of the manuscript.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Dyola et al., 2022) are available from the National Tibetan Plateau Data Center (TPDC): <https://doi.org/10.11888/Terre.tpdc.272239>.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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