

# Effect of forest chronosequence on ecological stoichiometry, nitrogen and phosphorus stocks in *Alnus nepalensis* forest stands, central Himalaya

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## A B S T R A C T

In the mid and high elevations of the central Himalaya, Nepalese alder (*Alnus nepalensis* D. Don) occurs in areas affected by landslide/slip and is a nitrogen-fixing species; it quickly improves soil physical and chemical properties and facilitates the restoration of degraded forests. In the present study, we evaluated the effect of *A. nepalensis* forest chronosequence on the carbon (C), nitrogen (N), and phosphorus (P) concentrations, N and P stocks, and stoichiometry in the soil, including microbial biomass C (MBC), microbial biomass N (MBN) and microbial biomass P (MBP), and in the plant components. Six naturally occurring forest stands were identified in a chronosequence of *A. nepalensis* (3–270 years old) forest stands, namely alder-early regenerating (AER), alder-late regenerating (ALR), alder young-mixed (AYM), alder mature-oak (*Quercus leucotrichophora*) mixed (AMOM), alder mature-rhododendron (*Rhododendron arboreum*) mixed (AMR), and alder old-oak (*Q. leucotrichophora*) mixed (AOOM) forests. The biomass of tree components was estimated using species-specific allometric equations developed by previous workers for the region. Soil total N and total P stocks of each species were determined by the N and P concentrations and bulk density. Structural equation modeling (SEM) was performed to quantify the contribution of N and P pools to ecosystem nitrogen and phosphorus stock. The results of this study revealed that the stoichiometry (C/N, N/P, and C/P ratios) of tree components, i.e., leaves, litter, twig, and soil and microbial biomass varied widely, and the presence of nitrogen-fixing *A. nepalensis* in different succession stages significantly improved the soil and microbial biomass stoichiometry. Total vegetation (tree, herbs, shrubs, and litter) biomass N stock ranged from 346.77 to 4662.06 kg N ha<sup>-1</sup>, and soil N stock varied from 816.48 to 7334.24 kg N ha<sup>-1</sup>. Total ecosystem N and P stocks were ranged from 1163.26 to 11996.31 kg N ha<sup>-1</sup> and 76.10 to 799.28 kg P ha<sup>-1</sup>, respectively, and positively increased with *A. nepalensis* total biomass. The soil P stock accounting 63.49 to 74.80% of the total P stocks of the forest ecosystems. Overall, our findings suggest that *A. nepalensis* forest chronosequence enhanced the N and P stock, and introducing this species in degraded forests appears to be an option for enhancing forest conservation and rehabilitation actions in central Himalaya.

**Keywords:** Succession; Nitrogen-fixing species; Biomass; Plant-soil nutrient concentrations; Microbial biomass.

## Introduction

Nitrogen-fixing early successional plant species are typically the first to colonize degraded habitats, which fast restore the soil's physical and chemical structure and generally facilitate the establishment of other tree species (Batterman et al., 2013; Menge & Chazdon 2016). The facilitative influence of nitrogen-fixing pioneer trees on forest regrowth and biomass regeneration on nitrogen-limited soil is one of the important consistent influences observed in forest ecosystems (Walker and de Moral, 2003; Callaway, 2007; Bonanomi et al., 2011). This cohesion indicates that nitrogen-fixing pioneer trees function as nurse and keystone species (Power et al. 1996). Nitrogen-fixing trees also play a significant role in the C, N, and P cycles and accelerate cycles of Ca and other rock-derived nutrients in the forests (Menge et al. 2019; Perakis & Pett-Ridge 2019; Joshi and Garkoti 2021b; Pereira et al., 2021). Therefore, changes in the cycles of these elements influence the soil-plant nutrient limitations and may result in altered stoichiometry in the plant-litter-soil system.

The stoichiometry of young ecosystems is controlled by N supply; meanwhile, old ecosystems are governed mainly by the limitation of P supply (Elser et al., 2007; Richardson et al., 2004). Nevertheless, the correlation between soil N and P and the direction of stoichiometry dynamics during successional stages remains controversial (Hooker & Compton, 2003; Yang & Luo, 2011; Yang et al., 2021). It is expected that ecosystem stoichiometry will alter due to changes in biomass production, species composition, and soil properties induced by forest succession (Hooker & Compton, 2003; Yang & Luo, 2011; Ouyang et al., 2017; Yang et al., 2021). Because rapidly growing nitrogen-fixing early successional species and slow-growing late succession species can have substantial variations in C, N, and P concentrations in the above and belowground plant components, stoichiometry and the coupling between C, N, and P in ecosystem components change when species composition changes during forest succession (Hooker, & Compton 2003; McGroddy et al., 2004). Previous studies have analyzed the soil and plant C:N:P stoichiometry in the forest of the central Himalaya (Rawat et al., 2020a; Kumar et al., 2021; Kumar and Garkoti, 2022). Moreover, information on the relationship of C:N:P stoichiometry between soil, plant, and litter and the influence of forest chronosequence on ecosystem C:N:P stoichiometry and nutrient stocks have rarely been evaluated in the central Himalaya forests.

Himalayan forests are subject to many drivers of change, including forest landslide/land slips (due to the natural settings and slopes), forest fire, agricultural expansions, and climate change, which alter both forest and soil health (i.e., structure, productivity, nutrient cycling, and forest successional processes) (Singh 2007; Måren et al., 2014; Verma et al., 2021; Negi 2022). In the central Himalayan mid and high altitudes, forest degradation and soil erosion due to landslide/ slip have been common features (Pandey et al., 2020; Joshi and Garkoti, 2021b). White oak (*Q. leucotrichophora*) is a major forest-forming, late-successional, and keystone tree species in the central Himalayas. It covers approximately a 20,000 km<sup>2</sup> area, and in many sites, it is subjected to natural and anthropogenic disturbances (Pandey et al., 2020; Dhyani et al., 2020). The natural rehabilitation of *Q. leucotrichophora* degraded forest becomes an essential priority for the future forest restoration of the central Himalayan region (Dhyani et al. 2020). Nitrogen-fixing *A. nepalensis* is a fast-growing early successional tree species that often forms pure stands in areas affected by landslide/ slip sites over 1400 m.a.s.l. but also occurs mixed with other late-successional species in the central Himalaya. In addition, being a nurse species, it enhances the ecosystem C, soil C, soil N, improves the physical and chemical properties of the soil, restores the habitat, and facilitates forest succession (Joshi and Garkoti 2021a; Joshi and Garkoti 2021b).

This study investigated the C:N:P stoichiometry in soil and plant components and ecosystem N and P stocks with respect to a chronosequence of *A. nepalensis* forest stands in the central Himalaya. The study also evaluated the influence of *A. nepalensis* chronosequence on soil and microbial biomass stoichiometry. We hypothesized that 1) plant-soil C:N:P stoichiometry and ecosystem N and P stocks change with respect to chronosequence of *A. nepalensis* forest stand 2) different plant components may show different C:N:P stoichiometry. The most active component, i.e., leaves, fine roots, and twigs, has a higher nutrient content than other components. 3) since *A. nepalensis* is a nitrogen-fixing tree, it reveals the change of soil and microbial biomass C:N:P stoichiometry along with the soil depth.

## 2. Material and Methods

## 2.1 study sites

This study area was in Kedarnath Valley (30°31. 44.7” N and 30°58’64.5” N, and 79°6’ 21.1” E, to 79° 02’028.95” E) in the Rudraprayag district of the central Himalaya. The study area has undulating topography with altitudes ranging from 1,335 to 1,609 m.a.s.l. The average annual rainfall was 1971 mm, with the most (70-80%) rainfall occurring during June–September which triggers large numbers of landslides in the area. The area receives medium to massive snowfall during December–February months. The temperature range from 8.32 to 13.15 °C in winter (December to February) months and 27.75 to 32.54 °C in summer (May to July) months. The soil was brown-black, sandy loam, podzolic in nature (Cambisols, USDA Soil Taxonomy), and high organic matter content, low bulk density, and large boulders were common in the area (Joshi & Garkoti 2020; Joshi & Garkoti 2021a). Emergent trees (up to 20 m tall) dominate the forest, which is a mix of evergreen broad-leaved and deciduous, i.e., nitrogen-fixing *Alnus nepalensis* D. Don, *Rhododendron arboreum* Smith, *Lyonia ovalifolia* (Wall.) Drude, *Quercus leucotrichophora* A. Camus, *Pyrus pashia* L., *Myrica esculenta* Buch.- Ham. ex D. Don, *Symplocos paniculata* Miq, *Litsea umbrosa* Nees (Joshi & Garkoti 2021b). The important shrubs are *Berberis aristata* DC, *Rhus parviflora* Roxb, *Pyracantha crenulata* (D. Don), *Carissa congesta* Wight, *Cotoneaster microphyllus* Wall. Ex Lindl, and *Rubus ellipticus* Sm., and the main herbs are *Arthraxon lanceolatus* (Roxb.) Hochst, *Ainsliaea aptera* DC., *Erigeron bellidioides* L., *Craniotome versicolor* Rchb., *Cyperus rotundus* L., and *Eupatorium adenophorum* Spreng.

## 2.2 Experimental design and sampling

After a reconnaissance survey, a series of *A. nepalensis* stands with different ages were selected. Selected forest stands were categorized into six age gradients namely alder-early regeneration (AER, 2-5-year-old) forest, alder-late regeneration (ALR, 7–9-year-old) forest, alder young-mixed (AYM, 20-25-year-old) forest, alder mixed mature oak (AMOM, 80-110-year-old) forest, alder mixed mature-rhododendron (AMR, 85-120-year-old forest) forest, and alder mixed old-oak (AOOM, 250-270-year-old) forest (Joshi & Garkoti 2021b). As the exact details of forest age were not present, we used *A. nepalensis* basal area (a proxy for tree age) and validated it by interviewing elderly local people who had information about the year of landslide and establishment of *A. nepalensis*. We further cross-checked it from the Forest Department.

We evaluated the ecosystem C:N:P stoichiometry and N-P stocks for the following ecosystem components: (i) aboveground components (bole, branch, twigs, and foliage) of trees, (ii) belowground components (fine root, stamp root, and lateral root) of trees species, (iii) aboveground and belowground components of shrubs (stem, leaf, root) (iv) above and belowground parts of herbaceous plants, (v) forest litter and (vi) soil including soil microbial biomass at different soil depths.

In each forest stand, three plots of 0.1 ha were established in August–October 2018. In each plot, ten stratified random quadrats of 10 m x 10 m sizes were laid to evaluate dendrometric attributes (basal area, diameter, density, and important value index (IVI)) and also vegetation biomass and N and P stocks. The biomass of different tree components was estimated using the allometric equations developed by previous workers for the species in the region (Supplementary Table 1). Allometric equations for *A. nepalensis* belowground tree components were not available. Therefore, we used interspecies allometric equations developed by Rawat & Singh (1988).

Understory (shrubs and herbs) biomass was estimated by using the harvest method (Singh & Yadava, 1974). Shrub biomass was estimated by laying three 5m x 5m quadrats, and the same number of 1m x 1m sized quadrats were established to evaluate the litter and herbaceous biomass in each plot (Garkoti & Singh, 1995; Joshi & Garkoti, 2021b). Shrubs were harvested and differentiated into the root, branches, and leaves; herbs were harvested and differentiated into belowground parts and aboveground.

Soil profile varied among the chronosequence of *A. nepalensis* forest stands. Five replicates of soil samples were collected with a stainless-steel corer (diameter, 5 cm) at the four corners and the center of the sampling plots up to the maximum soil depths (0–10 cm in AER, 0–30 cm in AYM, 0–50 cm in ALR, AMOM, AMR, and AOOM plots) and divided in 0–10, 10–20, 20–30, 30–50 cm and then mixed to form one homogenous sample per depth per plot. Each replicate of the soil sample was passed through a 2-mm mesh size sieve

and divided into two parts (1) one part was stored at 4 degC for soil microbial biomass (i.e., soil microbial biomass carbon (MBC), soil microbial biomass nitrogen (MBN), and soil microbial biomass phosphorus (MBP) analysis and (2) second part was air-dried and used for chemical analysis. Soil bulk density of the different soil layers was measured by collecting five replicates of soil in each plot using the same stainless-steel corer as above.

### 2.3. C, N, and P concentrations, ratios, and N and P stocks

The C, N, and P concentrations were estimated for the different aboveground and belowground components (i.e., branch, bole, twigs, foliage, fine root, coarse root, and stump root) of the *A. nepalensis*, *Q. leucotrichophora*, *R. arboreum*, and associated species trees (*P. pashia*, *L. ovalifolia*, *M. esculenta*, *Q. floribunda*, *L. umbrosa*, *A. indica*, *J. regia* and *B. capitata*). In each forest stand, five representative trees of *A. nepalensis*, *Q. leucotrichophora*, *R. arboreum*, and associated species were chosen for the estimation of the tree aboveground and belowground biomass, and nutrient concentrations. From each marked represented tree, mature twigs and fully expanded well illuminated leaves from the middle of the canopy were collected. Five tree ring cores (one from each selected tree) were used to extract bole sampling across the diameter. Tree roots (stump root, coarse root, and fine root) were collected from five soil profiles ranging from 0 to 100 cm and categorized as fine roots (less than 2 mm), coarse roots (more than 2 to 10 mm), and stump roots (greater than 10 mm) (Rawat & Singh, 1988). All samples were brought to the laboratory for chemical analysis. Tree, shrub, and herbaceous components were washed by deionized water and air-dried to constant mass, ground, and sieved through a 0.5 mm screen mesh and kept for chemical analysis.

The vegetation biomass (tree, shrubs, and herbaceous components) and soil C concentrations were determined using the  $K_2Cr_2O_7$  oxidation method (Nelson & Sommers, 1982). Total N was analyzed with the micro-Kjeldahl digestion method (Parkinson & Allen, 1975). Plant and soil samples were digested with  $H_2SO_4-H_2O_2$  and  $H_2SO_4-HClO_4$  separately for total P analysis, and P concentrations were measured using molybdenum antimony colorimetry assays (Parkinson & Allen, 1975). The soil microbial biomass (i.e., MBC, MBN, and MBP) was analyzed by ethanol-free chloroform fumigation-extraction methods (Brookes et al., 1985; Wu et al., 1990). The C, N, and P concentrations of the tree, shrubs, herbaceous components, and soil were defined as  $g\ kg^{-1}$  in dry mass. The stoichiometric ratios (C:N, C:P, and N:P) in the tree, shrub, herbaceous components, and soil were measured using the following formula:

$$C : N = \frac{C_{concentration}}{N_{concentration}}$$

$$N : P = \frac{N_{concentration}}{P_{concentration}}$$

$$C : P = \frac{C_{concentration}}{P_{concentration}}$$

To evaluate the microbial efficiency of SOC, TN, and TP concentrations, the soil microbial quotients MBC:SOC, MBN:TN, and MBP:TP were calculated (Fan et al., 2010). In each plot, N and P stocks in different vegetation components were obtained by multiplying the N and P concentrations of vegetation components by the total biomass of that component. The vegetation components N and P stock were calculated following Tang et al. (2018).

The soil TN and TP stocks for each soil profile were estimated using the following formula:

$$\text{Soil stock (kg ha}^{-1}\text{)} = \frac{\text{TN or TP concentrations (g kg}^{-1}\text{)} \times \text{soil depth (cm)} \times \text{bulk density (g cm}^{-3}\text{)} \times 1000}{10}$$

Soil microbial biomass (MBC, MBP, and MBP) stock were calculated using the equation below:

$$\text{Soil microbial biomass stock (kg ha}^{-1}\text{)} = \frac{\text{soil microbial biomass (MBC or MBN or MBP) concentrations } (\mu\text{g g)} \times}{10}$$

The total ecosystem N and P stock of forest stand were calculated by aggregation of the N and P stock of various components of the ecosystem.

#### 2.4 Statistical analysis

Because the C, N, P concentrations and N and P stock of soil and plant at each sampling plot were average at the stand level, the data were statistically summarized. One-way analyses of variance (ANOVA) were performed to identify the effects of forest stand on various ecosystem components (vegetation biomass, soil, and microbial biomass) C, N, and P concentrations, stoichiometric ratio, microorganism quotient, and stocks. All data were expressed as mean  $\pm$  standard error. All analysis was carried out by R programming language version 4.0 (R core team) based on tukey post hoc test ( $P < 0.05$ ). Further, we used linear relationships to evaluate the relationship between soil and microbial biomass C, N, and P concentrations and their stoichiometry. The responses of soil microbial biomass C, N, and P concentrations and their stoichiometry are defined as dependent on soil C, N, and P and their stoichiometry, defined as the independent variable. We performed structural equation modeling (SEM) with AMOS 21.0 (AMOS IBM, USA) to identify the relationship between vegetation biomass, soil, and microbial biomass variables' effects on ecosystem N and P stocks. Furthermore, in SEM, standardized path coefficients were applied to demonstrate the correlation between factors. The root means the square error of approximation (RMSEA) and the model  $\chi^2$  test was used to evaluate the model fitness. The model fit was considered to be acceptable when RMSEA was close to zero, and the  $\chi^2$  test was not significant ( $P > 0.05$ ) (Schermelleh-Engel et al., 2003).

### 3. Results

#### 3.1. Tree and understory components C, N, and P concentrations and stoichiometry

The C concentrations of boles ranged from  $515.4 \pm 6.2$  to  $461.2 \pm 8.2$  g kg<sup>-1</sup> and were in the following order: *Q. leucotrichophora* > other associated species (*L. ovalifolia*, *P. pashia*, *M. esculenta*, *S. paniculata*, *L. umbrosa*) > *R. arboreum* > *A. nepalensis*, while the N concentrations of leaf ranged from  $33.7 \pm 3.4$  to  $17.3 \pm 4.3$  g kg<sup>-1</sup> and followed the order: *A. nepalensi* > associated species > *Q. leucotrichophora* > *R. arboreum*. P concentrations of *R. arboreum* ( $0.24 \pm 0.02$  g kg<sup>-1</sup>) in leaf and litter were significantly ( $P < 0.05$ ) greater than other plant species (Figure 1). A significant variation in C:N:P ratio was detected among the different tree components. The estimated branch, twig, leaf, fine root, coarse root, and litter C:N:P ratios of *A. nepalensis* were 979:22:1, 760:17.2:1, 578:40:1, 460:17:1, 623:12:1, 494:44:1, respectively and were lower than the other co-occurring tree species (Table 2). The C:N ratios of tree components ranked in the following order: bole > stump root > coarse root > fine root > branch > twig > litter > leaf. The C:N ratios of *Q. leucotrichophora* in bole ( $117 \pm 9.3$ ), stump root ( $98.5 \pm 6.4$ ), and coarse root ( $88.1 \pm 5.3$ ) was significantly greater than the bole, stump root, and coarse root of the other tree species (Figure 1). The C:P ratio of *A. nepalensis* and associated species in bole ( $2254.6 \pm 22.2$  and  $1839.3 \pm 15.2$  respectively) and stump root ( $1646 \pm 21.1$  and  $2213.3 \pm 34$  respectively) were significantly greater than the bole and stump root in comparison to other tree species. The N:P ratio of *A. nepalensis* and associated species in the litter ( $44.2 \pm 3.2$  and  $81.2 \pm 5.4$ , respectively) and leaf ( $44.7 \pm 7.4$  and  $78.3 \pm 8.9$ , respectively) were significantly greater than the litter and leaf of the other tree species ( $P < 0.05$ ).

The C content (g kg<sup>-1</sup>) in different above and below-ground shrub components ranked in the following order: stem > root > leaf, while the shrub N and P concentrations (g kg<sup>-1</sup>) followed order: leaf > stem > root. The highest ( $465.53 \pm 2.06$ ) and the lowest ( $435.68 \pm 2.15$ ) C concentrations were measured in shrub stem and shrub leaf, respectively (Figure 1), while the highest ( $18.98 \pm 3.03$ ) and the lowest ( $12.21 \pm 2.04$ ) N concentrations were found in shrub leaf and shrub root, respectively. The highest ( $3.07 \pm 0.02$ ) P content was found in the leaf and the lowest ( $0.30 \pm 0.02$ ) in the root. The average C, N, and P concentrations (g

kg<sup>-1</sup>) of herb aboveground component ranged from  $448.8 \pm 2.30$  for C,  $15.10 \pm 1.02$  for N, and  $1.21 \pm 0.06$  for P. The concentration of C, N, and P (g kg<sup>-1</sup>) of herb belowground component ranged from  $424.94 \pm 2.34$  for C,  $8.92 \pm 0.49$  for N, and  $0.61 \pm 0.02$  for P. The C:N, N:P and C:P ratio of shrubs ranked in the following order: root > stems > leaf, and the C: N, C:P and N:P ratio of herb ranked in the following order: herbs belowground > herb aboveground. The C:N ratio of herb roots was 1.17 times greater than the shrub roots. However, the C:P ratio of shrub roots was 2.08 times higher than the herb roots. The N:P ratio of shrub roots was 2.87 times greater than herbs roots.

### 3.2. Soil and microbial biomass C, N, and P concentrations and stoichiometry

Results of the one-way ANOVA analysis revealed that forest chronosequence significantly ( $P < 0.05$ ) influenced the soil SOC, TN, and TP concentrations and varied significantly with soil depth ( $P < 0.05$ ). Generally, the SOC, TN, and TP concentrations in the various soil layers increased significantly along with forest chronosequence. Across the forest stands, the highest soil SOC, TN, and TP concentrations were found in the 0-10 cm soil depth, and the lowest was found in the 30-50 cm soil depth (Figure 2). Forest stand, soil depth, and their interaction significantly influenced soil microbial biomass concentrations (MBC, MBN, and MBP) (Figure 3). In the 0-10 cm soil depth, the AOOM stand soil microbial biomass concentrations were significantly greater than the other forest stands (Figure 3). The soil microbial biomass concentrations decreased with an increase in the soil depths in all the forest stands. The ANOVA values for the microbial stoichiometric ratios showed that all variables exhibited a highly significant interaction between forest types and soil depth (Figure 3). The estimated soil C:N:P ratios ranged from 71:12:1 to 269:25:1 and were significantly higher than microbial biomass C:N:P ratios which range from 10:2:1 to 22:2:1 (Table 3). The MBC:MBP and MBC:MBN ratios increased with soil depths and reached the maximum at 20-30 cm or 30-50 cm soil depths. Meanwhile, MBN:MBP ratio did not vary with forest types and soil depth (Figure 3). The microbial quotient, i.e., MBC:SOC ratio, MBN:TN ratio, and MBP:TP ratio decreased with forest chronosequence and increased with soil depths. The overall microbial quotient was higher in early young-aged stands (AER, ALR, and AYM stand) compared to older stands (AMOM, AMR, and AOOM stand).

Along the *A. nepalensis* chronosequence, SOC, TN, and TP concentrations and stoichiometry showed significant relationships with microbial biomass C, N, and P concentrations and stoichiometry. SOC, TN and TP were significantly related MBC ( $R^2 = 0.70$ ,  $P < 0.0001$ ), MBN ( $R^2 = 0.81$ ,  $P < 0.0001$ ), and MBP ( $R^2 = 0.53$ ,  $P < 0.0001$ ), respectively, and soil SOC:TN ratios were positively correlated with the MBC:MBN ratios ( $R^2 = 0.11$ ,  $P < 0.001$ ) while TN:TP and SOC:TP ratios were not related with MBN:MBP and MBC:MBP ratios, respectively (Figure 4). As shown in Figure 5, soil and microbial C, N, and P stocks varied considerably across forest chronosequence and soil depths. Across forest types, soil and microbial C, N, and P stocks showed decreasing trends with soil depths. Across all three soil depths, the highest soil and microbial C, N, and P stocks were noticed at the AOOM stand and the lowest at the AER stand.

### 3.3. Ecosystem N and P stocks

In the present study, tree, shrubs, and herbaceous and litter components N and P stock increased from 346.77 kg ha<sup>-1</sup> in AER (youngest) stand to 4662.06 kg ha<sup>-1</sup> in the AOOM stand (oldest) and 19.17 kg ha<sup>-1</sup> in AER stand to 233.91 kg ha<sup>-1</sup> in AOOM stand, respectively. Across the forest chronosequence, tree bole biomass N and P stock were significantly greater than any other vegetation biomass components. The N and P stocks in different vegetation biomass components follow similar patterns as reported in our previous study (Joshi and Garkoti 2021b) and follow the order: bole > branch > stump root > twig > lateral root > foliage > litter > fine root > shrub aboveground > herbs aboveground > shrubs belowground > herbs belowground and in all vegetation components both N and P stocks increased with forest chronosequence (Table 1). Average total soil N and P varied from 816.44 to 7334.24 kg ha<sup>-1</sup> and 56.95 to 595.36 kg ha<sup>-1</sup>, respectively, and increased along with the forest chronosequence (Figures 5 and 6). Across the forest chronosequence, the contribution of *A. nepalensis* trees to the ecosystem nitrogen and phosphorus stock ranged from 9 % in ALR stand to 23.23 % in AMR stand and 3.31 % in AYM stand to 12.31 % in the AMR stand, respectively (Figure 6 & Figure 7). Of the total ecosystem N stock, the soil contributed from 48.82 % in the ALR stand to 70.18 % in the AER stand. Similarly, the contribution of soil to the total ecosystem P stock ranged from 63.49 % in

the ALR stand to 74.8 % in the AER stand. The soil was the largest P reservoir among all the ecosystem compartments. The understory vegetation (shrubs, herbs) and litter layer added a small fraction to the total N and P stock of the ecosystem. Overall, across the stands, soil and trees were the two largest contributors to the total ecosystem nitrogen and phosphorus stock (Figure 6, and Figure 7).

### 3.4. Driving factors of the ecosystem nitrogen and phosphorus stock

The structural equation model (SEM) revealed that tree biomass (*A. nepalensis*, *R. arboreum*, *Q. leucotrichophora*, and associated species), understory (herbaceous, shrub), litter, and soil (including microbial biomass) was the variable that influenced ecosystem N and P stock (Figure 8). The SEM explained 92.1 % and 92.8 % of the variation in ecosystem N and P stocks, respectively. *A. nepalensis* biomass N stock, soil TN stock, and litter N stock had a significant ( $P < 0.05$ ) direct positive influence on ecosystem nitrogen stocks, in which standardized effects were 0.161, 0.619, and 0.601, respectively. Meanwhile, *Q. leucotrichophora* biomass N stock and associated species biomass N stock had a significant ( $P < 0.05$ ) direct negative influence on ecosystem N stock, in which standardized effects were -0.142 and -0.112. Meanwhile, *R. arboreum* biomass N stock, MBN stock, and understory (herbaceous, shrub biomass) N stock had no direct influence on ecosystem N stock. Similarly, *A. nepalensis* biomass P stock, *Q. leucotrichophora* biomass P stock, associated species biomass P stock, MBP stock, and soil TP stock had a direct positive influence on ecosystem phosphorus stocks in which standardized effects were 0.497, 0.439, 0.112, 0.223 and 0.394, respectively. Meanwhile, *R. arboreum*, *Q. leucotrichophora*, and associated species biomass N and P stock had no direct effects on soil, microbial biomass, and understory (herbaceous, shrub biomass) N and P stock. Furthermore, *R. arboreum*, and associated species biomass N and P stock had a significant ( $P < 0.05$ ) direct positive influence on litter biomass N and P stock. The total influence of each driving factor on the ecosystem N stock in ranked in the following order: 0.61 (soil TN stock) > 0.601 (litter biomass N stock) > 0.161 (*A. nepalensis* biomass N stock) > -0.142 (*Q. leucotrichophora* biomass N stock) > -0.112 (associated species biomass N stock). The standardized total effect of each driving factor on the ecosystem P stock in ranked in the following order: 0.497 (*A. nepalensis* biomass P stock) > 0.439 (*Q. leucotrichophora* biomass P stock) > 0.394 (soil TP stock) > 0.223 (MBP stock) > 0.112 (associated species biomass P stock) > -0.132 (understory biomass P stock). The results of standardized total influence revealed that *A. nepalensis* biomass and soil N and P stocks were the most important direct and indirect driving factors of ecosystem N and P stocks (Figure 8).

## 4. DISCUSSION

### 4.1. Tree and understory components C, N, and P concentrations and stoichiometry

Vegetation components show variations in C, N, and P concentrations and stoichiometry ratios due to the differentiation in their function and structures. The possible explanation for this is that various plant communities and their structural components have different environmental adaptability and nutrient requirements, and conservation strategies (Wright et al., 2004; Laliberté et al., 2014). In the present study, leaf N concentrations in tree species were significantly greater than the shrubs and herbaceous species, while leaf P for shrub and herbaceous species was greater than the tree species. These findings are consistent with the reports of Wright et al. (2004), who found that herbaceous plants have considerably higher leaf P concentrations than tree species. Pan et al. (2011) revealed that N and P concentrations in tree leaves were considerably greater compared to litter, possibly due to resorption strategies.

Variations in C: N: P stoichiometry (C:N, C:P, and N:P ratios) were noticed among the different vegetation components (Niklas, & Cobb 2006; Ågren 2004; Ågren 2008). Our findings revealed that there were significantly different C:N:P ratios among the different components, which tested the second hypothesis. N and P concentrations in leaves, twigs, and litter were higher than other vegetation components and thus showed lower C:P and C:N ratios, which is in agreement with earlier findings (Minden & Kleyer, 2014). Leaf N concentration in tree species was 2 to 4 times greater than other plant components. Tree bole is responsible for support and storage; therefore, it contains more C than other structural components. Because leaves are responsible for photosynthesis, they require a higher amount of N and P to support various biochemical reactions. Present C:N ratios for vegetation components ranged from 8 to 130, and C:P ratios ranged from

138 to 2830 (Fan et al., 2010; Yong et al., 2018). The C:N ratio in bole, branch, and twig was greater than in leaves and roots. Being a nitrogen-fixing tree, *A. nepalensis* showed higher N concentrations in different plant components compared to other plant species. The C:N ratio was lowest in *A. nepalensis* leaf compared to other structural parts and leaves of different plant species. Furthermore, the N:P ratio varies by plant species, growth stage, and study area (Koerselman & Meuleman, 1996; Güsewell, 2004). According to Güsewell (2004), the leaf N/P ratio can be used to evaluate whether the ecosystem is N-limited (N/P ratio < 10) or P-limited (N/P ratio > 20). In the present study, the leaf N/P ratio in *A. nepalensis* and associated species were 44.74 and 78.3, respectively, indicating that their development was P-limited. The leaf N/P ratios in *Q. leucotrichophora* and *R. arboreum* were 19.39 and 16.10, respectively, implying that P limited their growth. The leaf N/P ratios in herbaceous and shrub plants were 6.17 and 9.67, respectively, suggesting that N was limiting their growth. The C : N : P ratios in the bole, branches, and roots were markedly greater than in the leaves, twig, and litter (Table 2), indicating that plants allocate higher nutrients to the leaves to ensure growth (Sardans and Peñuelas 2013). This result aligns with previous conclusions that different components have different demands for nutrients N and P. More dynamic components (e.g., leaves, fine roots, and twigs) have a higher nutrient content to meet the requirements of plant growth (Sterner & Elser, 2002).

#### 4.2 Soil and microbial biomass C, N, and P and C: N: P stoichiometry

Similar to several previous studies, present soil C, N, and P concentrations increased with forest chronosequence (Hooker & Compton, 2003; Guo et al., 2021). These changes could be related to the continuous supply of litter and root exudates that are significantly influenced by the forest chronosequence. Furthermore, along with forest chronosequence, soil microbial activity increases, and soil nutrient concentration and stocks are further increased. Our results revealed that the biomass of vegetation components and litter increased along with the forest chronosequence (Table 1), suggesting that the massive increase in the soil SOC, TN, TP, MBC, MBN, and MBP concentrations because of greater litter accumulation (Deng et al., 2016). SOC, TN, and microbial biomass are mainly driven by the higher quantity of plant residue (rhizodeposition and litter). Nitrogen-rich and fast-decomposing *A. nepalensis* litter seem to have contributed to soil carbon and nutrient enrichment (Binkley et al., 1992; Joshi & Garkoti, 2020). Our results revealed that the improvement in soil nutrient concentrations and microbial biomass corresponded to increases in above and belowground biomass following forest age, particularly in the stands with N-fixing *A. nepalensis*. This suggests that forest chronosequence alters vegetation biomass, improves the soil microenvironment, and promotes soil biological activity, especially MBC, MBN, and MBP (Figure 5). Plant residue (rhizodeposition and litter) accumulation on the soil increases along the forest chronosequence, which in turn, positively enhances the soil microbial activity (Prietzl & Bachmann, 2012; Lucas-Borja et al., 2016). Furthermore, tree biomass and litter of the *A. nepalensis* gradually increased along with forest chronosequence (Table 1). This would cause an increased soil and microbial biomass C, N, and P concentrations because *A. nepalensis* litter and roots are decomposed at a faster rate than other species and provide more raw material for microbial growth (Joshi & Garkoti 2020; Joshi & Garkoti 2021a). Thus our study indicates that *A. nepalensis* forest chronosequence enhances the soil microbial biomass and, as a result, alters soil physicochemical properties (Joshi & Garkoti 2021a).

The significant variations in soil C/P, C/N, and N/P ratios can be believed to be due to shifts in vegetation structure or function impacting the amount and nature of litter production and the degree of degradation of organic matter (McGroddy et al., 2004; Yang and Luo, 2011; Zechmeister-Boltenstern et al., 2015). The significant variations in soil C: N: P stoichiometry (TN/ TP, SOC/TN, and SOC/TP ratios) can be believed to be due to shifts in vegetation structure or function impacting the amount and nature of litter production and the degree of degradation of organic matter (Zechmeister-Boltenstern et al., 2015). The SOC/TN ratio is considered to be an indicator of N mineralization and soil quality. Low SOC/TN ratios show enhanced microbial activity and increased organic N decomposition, whereas high SOC/TN ratios indicate the inverse (Manzoni et al., 2008; Manzoni et al., 2010; Cotrufo et al., 2019). There is a large difference in the SOC/TN ratios among different forest stands and soil layers. The average SOC/TN ratio of the top layer (0-30 cm) in all forest stands is the same as the range of previous findings (8.95 to 10.28) in other studies in the central Himalaya (Kumar et al., 2021). In this study, deeper soil layers (30-50 cm) of old age forest stands had a higher SOC/TN ratio due to low input of N and low mineralization rates of C and N (Bengtsson et al., 2003).

The SOC/ TN ratios revealed substantial variations between forest stands, which may be attributed to the significant effect of the SOC and TN concentrations and their transformation. High SOC/TN, SOC/TP, and TN/TP ratios were found in AYM, AMOM, AMR, and AMOO and varied significantly ( $P < 0.05$ ) along with soil depths and forest age in agreement with the previous reports (McGroddy et al., 2004; Tipping et al., 2016). Present SOC/TP and TN/TP ratios for 0-30 cm soil depths ranged from 49.25 to 172.48 and 1.16 to 20.40, respectively. These estimated values of SOC/TP and SOC/TN are greater than the mean value of 41.94 and 4.30, respectively, reported by Kumar et al. (2021), and are similar to the range 184-299 and 12.9-19.4, respectively reported by Qi et al., (2020) in Chinese mountainous ecosystem. SOC, TN, and TP availability were assumed to be primary driving factors for microbial biomass C, N, and P content dynamics. Higher microbial biomass (MBC, MBN, and MBP concentrations) is generally related to higher litter input, vegetation cover, soil moisture, and soil nutrient concentrations in older forest stands (Joshi & Garkoti 2021b). Moreover, microbial biomass content gradually decreases with increased soil depth across all forest stands (Figure 4 a, b, & c), probably due to a significant reduction in soil SOC, TN, and TP concentrations availability with increasing soil depth. The microbial biomass content was positively correlated with soil SOC, TN, and TP content, indicating that microbial biomass (MBC, MBN, and MBP) concentrations were limited by soil SOC, TN, and TP concentrations across the forest chronosequence. The MBC/MBN ratio in the present study varied from 7.81 to 11.62 across the forest, which is close to the global average for MBC/MBP ratio (Cleveland & Liptzin, 2007; Aponte et al., 2010; Hartman & Richardson, 2013; Xu et al., 2013). We found that the MBC/MBN and MBC/MBP ratios in different forest stands remained relatively homeostatic compared to MBN/MBP ratios. Previous research has illustrated that soil microorganisms have constant C: N: P stoichiometry homeostasis along with forest chronosequence (Yu et al., 2010; Xu et al., 2013).

The microbial quotient, i.e., MBC/SOC, MBN/TN, and MBP/TP ratios were lower in older forest stands (AMR, AMOM, and AMOO stand) compared to the young stands (AER, ALR, and AYM). With the exception of the AER stand, the present MBC/SOC ratios (ranging from 1-7 %) are greater than the values reported for the temperate forests (1.8-2.9 % Vance et al., 1987b). Moreover, MBN/TN and MBP/TP ratios ranging from 1-5 % are also greater than the temperate forest soils (1.6-3%; Zhong & Makeshin 2006), suggesting that microbial biomass contribution was high in soil which indicates microorganisms were found to play a significant role in nutrient cycling. Also, the MBC/SOC, MBN/TN, and MBP/TP ratios are the key indicators of nutrient availability to soil microorganisms (Dilly et al., 2003).

#### 4.3. Distribution of N-P stocks in the different ecosystems

Forest stands varied significantly in the distribution of N and P stocks in different vegetation components and soil layers. The forest structure, vegetation biomass, and nutrient concentrations determined the N and P stock in the vegetative components and different soil layers (Frédéric et al., 2010; Phoenix et al., 2012; Joshi and Garkoti, 2021 b). Present vegetation biomass P (19.19 to 233.91 kg ha<sup>-1</sup>) and N (346.77 to 4662.02 kg ha<sup>-1</sup>) stocks are higher than the values reported (60.5 kg ha<sup>-1</sup> for P and 577 kg ha<sup>-1</sup> for N) by Zhang et al. (2018). Late succession forest stands have higher vegetation biomass and nutrient concentrations and greater litter biomass, which may enhance the forest nutrient dynamics (Joshi & Garkoti 2021b). The high range of C/P and N/P ratio and the low P stock in the soil in young stands (AER, ALR, and AYM) may affect the enzymatic and microbial activities that decompose organic matter, which may, in turn, limit the microbial activities and forest growth during early stages of chronosequence (Richardson et al. 2004). The contribution of soil N and P to the ecosystem N and P stocks ranged from 70.18-48.82 % and 63.49-74.80 %, respectively, which indicate that soil TN and TP stocks (including soil microbial biomass stocks) play a key role in ecosystem N and P stock. Our results reveal the progressive increment in vegetation and soil nitrogen and phosphorus stock along the forest chronosequence. The order of the different N and P stocks in our study sites follows the order: soil > trees > shrubs > herb > litter (Figure 6). Hence, higher litter amount, soil nutrients, and soil microbial biomass (e.g., Deiss et al., 2018) may improve ecosystem N and P stocks. Finally, our findings indicated that there was an interaction between N and P stocks in the plant-soil system.

## 5. CONCLUSIONS

The study revealed that stoichiometric ratios were significantly varied for different soil and plant components, and N and P stocks increased significantly, with *A. nepalensis* forest chronosequence. The C: N: P stoichiometry of vegetation components, soil, and microbial biomass were found to be closely interrelated, indicating that vegetation nutrient content was a critical factor directing soil, microbial biomass nutrient inputs and thus influenced their stoichiometry. Present allocations of N and P concentrations to leaves, twigs, and litter were higher than other ecosystem components, thus reflecting lower C/P and C/N ratios, which support our second hypothesis. Our results revealed that the soil and microbial C, N, and P concentrations increased along with *A. nepalensis* forest chronosequence due to an increase in litter inputs and its subsequent decomposition and mineralization of nutrients. The soil profile stores the highest percentage of the N and P stocks, followed by the trees. The ecosystem N-P stocks were primarily influenced by the biomass of *A. nepalensis*. Overall, present *A. nepalensis* forest chronosequence findings reveal the importance of N-fixing species in the recovery of degraded forest ecosystems and recommend reforestation of broadleaf tree species such as *Q. leucotrichophora*, *R. arboreum*, and other associated species with *A. nepalensis* to rehabilitate the degraded forests.

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## CONFLICT OF INTEREST

The authors declare no competing financial interests.

## DATA AVAILABILITY STATEMENT

The data are available from the corresponding author.

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**Table 1.** Biomass, nitrogen, and phosphorus (kg/ha) poll in different vegetation components across six study sites in the central Himalaya. Values in mean and stander error of three different three plots (n = 3)

Sites/vegetation	Components	Biomass kg/ha	Nitrogen (kg/ha)	Phosphorus (kg/ha)	
<b>AER</b>					
<i>A. nepalensis</i>	Bole	7122.22 ± 471.40	56.97 ± 6.57	1.43 ± 0.10	
	Branch	4396.63 ± 461.50	48.19 ± 5.38	1.54 ± 0.27	
	Twig	1741.04 ± 311.23	32.87 ± 8.60	1.33 ± 0.36	
	Leaf	1067.29 ± 436.10	36.05 ± 14.96	0.80 ± 0.31	
	Stump root	112.66 ± 7.62	0.53 ± 0.05	0.03 ± 0.002	
	Fine root	387.76 ± 280.05	3.73 ± 2.83	0.20 ± 0.14	
	Coarse root	507.60 ± 259.62	2.85 ± 1.65	0.21 ± 0.10	
	Litter	803.33 ± 212.16	19.02 ± 6.36	0.43 ± 0.14	
Herbs	Herbs above	2113.33 ± 202.06	32.77 ± 5.64	2.67 ± 0.51	
	Herbs below	753.33 ± 172.16	6.61 ± 2.18	0.45 ± 0.12	
Shrubs	Shrubs stem	3193.33 ± 272.06	47.15 ± 5.53	2.53 ± 0.26	
	Shrubs root	1313.33 ± 212.10	16.03 ± 5.43	0.40 ± 0.80	
<b>ALR</b>					
<i>A. nepalensis</i>	Bole	129555.48±272.16	1036.44 ± 262.10	26.06 ± 0.09	
	Branch	46736.14 ± 8107.54	512.35 ± 92.02	16.43 ± 1.80	
	Twig	7364.03 ± 1230.74	139.06 ± 24.65	5.66 ± 0.99	
	Leaf	7023.61 ± 1621.60	237.27 ± 55.31	5.31 ± 1.3	
	Stump root	6290 ± 578.12	29.83 ± 3.91	1.73 ± 0.15	
	Fine root	5554.57 ± 577.35	53.56 ± 6.09	2.94 ± 0.30	
	Coarse root	2329.70 ± 507.15	13.12 ± 3.72	0.99 ± 0.24	
	Litter	1560 ± 527.36	36.9 ± 13.44	0.83 ± 0.31	
	<i>Q. leucotrichophora</i>	Bole	17845.01 ± 3458.43	82.29 ± 30.92	7.66 ± 1.8
		Branch	11724.80 ± 3259.74	96.51 ± 38.08	6.07 ± 2.02
		Twig	5566.26 ± 2021.77	60.72 ± 22.99	4.54 ± 1.63
		Leaf	2042.97 ± 486.89	39.51 ± 10.09	2.05 ± 0.38
		Stump root	11911.27 ± 2470.95	56.71 ± 16.84	4.13 ± 0.82
<i>R. arboreum</i>	Fine root	2465.27 ± 1051.09	17.73 ± 9.10	1.53 ± 0.64	
	Coarse root	406.14 ± 157.01	2.11 ± 1.07	0.2 ± 0.08	
	Litter	1100 ± 502.29	14.86 ± 6.78	0.59 ± 0.25	
	Bole	31301.59 ± 5050.68	162.21 ± 28.23	11.12 ± 2.19	
	Branch	12061.06 ± 2516.99	113.27 ± 22.52	5.78 ± 1.74	
	Twig	10262.44 ± 2128.09	99.93 ± 26.58	5.63 ± 0.65	
	Leaf	3079.02 ± 284.23	53.52 ± 4.89	3.32 ± 0.29	
	Stump root	11636.61 ± 2997.30	66.42 ± 16.38	4.65 ± 1.75	
Associated Species	Fine root	5289.60 ± 1239.62	38.89 ± 8.88	3.64 ± 1.28	
	Coarse root	1705.80 ± 472.93	10.89 ± 2.90	0.81 ± 0.31	
	Litter	554 ± 132.79	6.45 ± 196	0.48 ± 0.08	
	Bole	26958.46 ± 1664.32	144.60 ± 15.49	6.1 ± 0.39	
	Branch	17521.89 ± 2654.37	165.65 ± 26.27	5.6 ± 0.85	
	Twig	8213.16 ± 2659.01	111.81 ± 40.83	3.5 ± 1.15	
	Leaf	5487.41 ± 1371.52	105.27 ± 28.37	1.36 ± 0.29	
	Stump root	10900.22 ± 2592.36	55.96 ± 14.56	1.92 ± 0.49	
	Fine root	1108.48 ± 119.79	9.22 ± 1.55	0.5 ± 0.06	
	Coarse root	140.30 ± 17.98	0.75 ± 0.11	0.04 ± 0.005	
Herbs	Litter	975.2 ± 60.18	15.87 ± 0.76	0.13 ± 0.02	
	Herbs above	1840 ± 69.28	28.53 ± 4.86	2.32 ± 0.46	

Sites/vegetation	Components	Biomass kg/ha	Nitrogen (kg/ha)	Phosphorus (kg/ha)
Shrubs	Herbs below	580 ± 79.18	5.09 ± 0.64	0.35 ± 0.03
	Shrubs stem	2340 ± 49.23	34.55 ± 5.46	1.85 ± 1.69
	Shrubs leaf	850 ± 69.28	16.13 ± 5.29	2.6 ± 0.82
	Shrubs root	7040 ± 45.32	11.23 ± 0.45	0.16 ± 0.08
<b>AYM</b>				
<i>A. nepalensis</i>	Bole	17073.57 ± 2450.90	136.58 ± 20.04	3.43 ± 0.09
	Branch	6918.02 ± 1331.78	75.84 ± 15.19	2.43 ± 0.34
	Twig	1597.84 ± 215.82	30.17 ± 4.29	1.22 ± 0.17
	Leaf	1516.56 ± 268.09	51.23 ± 9.15	1.14 ± 0.22
	Stump root	6650 ± 108.24	31.53 ± 1.29	1.8 ± 0.025
	Fine root	5324.57 ± 78.12	51.34 ± 0.67	2.82 ± 0.053
	Coarse root	2099.70 ± 88.42	11.8 ± 0.28	0.89 ± 0.043
	Litter	313 ± 108.42	7.41 ± 2.50	0.16 ± 0.055
<i>Q. leucotrichophora</i>	Bole	39671.14 ± 5162.07	182.94 ± 44.87	17.03 ± 2.40
	Branch	26910.32 ± 5009.18	221.51 ± 50.09	13.95 ± 2.55
	Twig	16150.20 ± 5025.39	176.19 ± 57.78	13.17 ± 4.07
	Leaf	8930.15 ± 3786.54	172.70 ± 77.17	8.9 ± 3.39
	Stump root	14437.75 ± 2564.41	68.74 ± 16.08	5 ± 0.85
	Fine root	9125.57 ± 1515.91	65.64 ± 14.61	5.6 ± 0.92
	Coarse root	1291.17 ± 377.74	6.72 ± 2.52	0.6 ± 0.19
	Litter	1340 ± 461.97	18.11 ± 6.30	0.72 ± 0.26
<i>R. arboreum</i>	Bole	15770.90 ± 1741.85	81.72 ± 9.32	5.6 ± 0.34
	Branch	7250.90 ± 1345.28	68.10 ± 12.68	3.48 ± 0.56
	Twig	4987.73 ± 1082.75	48.57 ± 9.53	2.73 ± 0.76
	Leaf	1480.62 ± 339.06	25.73 ± 5.82	1.5 ± 0.36
	Stump root	8780.94 ± 1285.48	50.12 ± 6.98	3.51 ± 0.38
	Fine root	3407.39 ± 457.44	25.05 ± 3.26	2.35 ± 0.24
	Coarse root	1420.80 ± 3.22.16	9.07 ± 1.97	0.68 ± 0.14
	Litter	490.33 ± 62.59	5.70 ± 0.88	0.42 ± 0.04
Associated Species	Bole	15300.12 ± 783.30	82.06 ± 5.46	3.49 ± 0.17
	Branch	8590.08 ± 193.30	81.21 ± 1.95	2.76 ± 0.06
	Twig	4994.39 ± 323.14	67.9 ± 5.02	2.13 ± 0.14
	Leaf	2624.31 ± 174.91	50.34 ± 3.38	0.65 ± 0.05
	Stump root	7418.83 ± 630.22	38.08 ± 3.66	1.3 ± 0.121
	Fine root	556.02 ± 36.96	4.62 ± 0.30	0.25 ± 0.014
	Coarse root	2967.10 ± 656.60	15.99 ± 3.84	0.91 ± 0.21
	Litter	1821.63 ± 62.59	29.65 ± 1.09	0.24 ± 0.01
Herbs	Herbs above	1657 ± 463.39	25.69 ± 5.23	2 ± 0.49
	Herbs below	1232.33 ± 267.53	10.8 ± 2.60	0.74 ± 0.14
Shrubs	Shrubs stem	2137 ± 463.39	31.55 ± 5.70	1.69 ± 0.38
	Shrubs leaf	1232.3 ± 267.53	23.3 ± 1.29	3.78 ± 0.82
	Shrubs root	1512.33 ± 267.53	18.46 ± 1.06	0.46 ± 0.12
<b>AMOM</b>				
<i>A. nepalensis</i>	Bole	71308.03 ± 7374.07	570.46 ± 78.57	14.34 ± 1.72
	Branch	23905.57 ± 2497.11	262.07 ± 31.46	8.4 ± 0.64
	Twig	2618.03 ± 966.88	49.44 ± 18.69	2 ± 0.76
	Leaf	2828.18 ± 727.19	95.54 ± 25.08	2.1 ± 0.61
	Stump root	2036.66 ± 225.17	9.65 ± 1.45	0.56 ± 0.07
	Fine root	5381.24 ± 235.87	51.88 ± 2.95	2.85 ± 0.15
	Coarse root	2156.37 ± 205.80	12.14 ± 1.69	0.91 ± 0.12

Sites/vegetation	Components	Biomass kg/ha	Nitrogen (kg/ha)	Phosphorus (kg/ha)
<i>Q. leucotrichophora</i>	Litter	772.07 ± 215.17	18.28 ± 7.14	0.41 ± 0.15
	Bole	47477.69 ± 4165.96	218.9 ± 4.56	20.38 ± 1.48
	Branch	29297.79 ± 2348.16	241.16 ± 13.52	15.19 ± 1.23
	Twig	11153.91 ± 1650.18	121.68 ± 16.92	9.09 ± 1.35
	Leaf	5251.43 ± 623.11	101.56 ± 11.16	5.27 ± 0.93
	Stump root	29469.51 ± 2400.87	140.32 ± 6.43	10.22 ± 0.83
	Fine root	5378.75 ± 753.98	38.69 ± 3.94	3.34 ± 0.46
	Coarse root	699.35 ± 299.48	3.64 ± 1.51	0.36 ± 0.15
<i>R. arboreum</i>	Litter	1306.66 ± 338.24	17.66 ± 4.33	0.70 ± 0.17
	Bole	23943.26 ± 2390.19	124.07 ± 14.64	8.5 ± 1.37
	Branch	9609.92 ± 1089.08	90.25 ± 9.69	4.6 ± 0.93
	Twig	8063.82 ± 1021.57	78.52 ± 14.81	4.4 ± 0.19
	Leaf	2695.03 ± 546.09	46.84 ± 9.39	2.9 ± 0.60
	Stump root	9340.42 ± 1035.87	53.3 ± 5.66	3.7 ± 0.73
	Fine root	3914.89 ± 276.85	28.78 ± 2.00	2.7 ± 0.42
	Coarse root	1921.98 ± 703.55	12.27 ± 4.32	0.9 ± 0.45
Associated Species	Litter	877.33 ± 62.27	10.2 ± 0.44	0.7 ± 0.09
	Bole	57210.13 ± 1818.16	306.87 ± 12.74	13.07 ± 0.42
	Branch	30348.84 ± 549.95	286.9 ± 6.82	9.7 ± 0.17
	Twig	23627.44 ± 348.60	321.66 ± 5.53	10.07 ± 0.14
	Leaf	6981.50 ± 474.54	133.93 ± 9.59	1.73 ± 0.109
	Stump root	17596.93 ± 326	90.34 ± 2.58	3.11 ± 0.06
	Fine root	16812.69 ± 46.50	139.88 ± 0.43	7.58 ± 0.02
	Coarse root	7676.94 ± 48.93	41.37 ± 0.344	2.35 ± 0.015
Herbs	Litter	2322.43 ± 76.66	37.80 ± 1.30	0.3 ± 0.005
	Herbs above	949.6 ± 71.01	14.72 ± 1.09	1.19 ± 0.04
Shrubs	Herbs below	149.3 ± 41	1.31 ± 0.39	0.09 ± 0.022
	Shrubs stem	1970.3 ± 61.01	29.09 ± 4.63	1.56 ± 0.08
	Shrubs leaf	1465.2 ± 71.11	27.82 ± 5.67	4.5 ± 0.25
	Shrubs root	442 ± 51.21	5.39 ± 1.07	0.13 ± 0.038
<b>AMR</b>				
<i>A. nepalensis</i>	Bole	176541.57 ± 2057.12	1412.33 ± 99.20	35.51 ± 1.05
	Branch	58302.14 ± 2357.022	639.15 ± 31.02	20.4 ± 0.78
	Twig	4793.08 ± 457.56	90.51 ± 9.76	3.6 ± 0.36
	Leaf	4693.08 ± 578.12	158.54 ± 19.56	3.5 ± 0.49
	Stump root	2882.33 ± 116.27	13.66 ± 0.89	0.79 ± 0.02
	Fine root	2332.04 ± 106.77	22.48 ± 1.22	1.2 ± 0.054
	Coarse root	775.97 ± 146.17	4.37 ± 0.67	0.3 ± 0.044
	Litter	2432.33 ± 106.77	57.6 ± 3.04	1.3 ± 0.06
<i>Q. leucotrichophora</i>	Bole	23033.16 ± 942.80	106.21 ± 15.44	9.8 ± 0.54
	Branch	13384.04 ± 952.83	110.17 ± 11.35	6.9 ± 0.47
	Twig	3310.51 ± 931.110	36.11 ± 10.88	2.7 ± 0.76
	Leaf	1609.68 ± 141.42	31.13 ± 3.11	1.61 ± 0.08
	Stump root	8733.24 ± 942.80	41.58 ± 7.32	3.02 ± 0.31
	Fine root	1442.32 ± 471.40	10.37 ± 4.07	0.89 ± 0.28
	Coarse root	111 ± 4.02	0.57 ± 0.03	0.05 ± 0.002
	Litter	1186.66 ± 182.35	16.03 ± 2.88	0.63 ± 0.09
<i>R. arboreum</i>	Bole	35695.75 ± 912.10	184.98 ± 10.19	12.68 ± 1.17
	Branch	14314.08 ± 952.80	134.44 ± 8.05	6.87 ± 0.88
	Twig	12429.74 ± 852.30	121.04 ± 14.87	6.82 ± 0.16

Sites/vegetation	Components	Biomass kg/ha	Nitrogen (kg/ha)	Phosphorus (kg/ha)	
Associated Species	Leaf	3008.85 ± 122.40	52.30 ± 16.20	3.24 ± 1.03	
	Stump root	14156.61 ± 942.80	80.80 ± 5.17	5.66 ± 0.80	
	Fine root	5855.08 ± 902.50	43.04 ± 6.75	4.0 ± 1.005	
	Coarse root	1921.59 ± 150.07	12.27 ± 0.91	0.92 ± 0.038	
	Litter	1180 ± 181.90	13.73 ± 1.65	1.02 ± 0.19	
	Bole	1477.50 ± 471.40	7.92 ± 3.03	0.33 ± 0.10	
	Branch	916.40 ± 141.42	8.66 ± 1.38	0.29 ± 0.04	
	Twig	401.49 ± 72.08	5.46 ± 1.15	0.17 ± 0.03	
	Leaf	716.31 ± 94.28	13.74 ± 1.93	0.17 ± 0.249	
	Stump root	473.88 ± 188.56	2.43 ± 1.11	0.08 ± 0.036	
	Fine root	3.84 ± 0.94	0.03 ± 0.009	0.0017 ± 0.0004	
	Coarse root	3.74 ± 0.54	0.02 ± 0.007	0.0011 ± 0.000308	
	Herbs	Litter	390 ± 114.40	6.34 ± 1.96	0.05 ± 0.03
Herbs above		2400 ± 56.56	37.21 ± 2.67	3.03 ± 0.11	
Shrubs	Herbs below	960 ± 24.06	8.43 ± 0.911	0.58 ± 0.056	
	Shrubs stem	3440 ± 16.46	50.79 ± 6.62	2.72 ± 0.10	
	Shrubs leaf	1220 ± 55.12	23.16 ± 3.87	3.74 ± 0.20	
	Shrubs root	1440 ± 32.12	17.5 ± 2.72	0.44 ± 0.066	
<b>AOOM</b>					
<i>A. nepalensis</i>	Bole	131461.01 ± 20847	1051.68 ± 173.29	26.44 ± 4.43	
	Branch	42088.13 ± 6056.67	461.40 ± 69.20	14.79 ± 1.20	
	Twig	4084.90 ± 1300.21	77.14 ± 25.01	3.14 ± 1.04	
	Leaf	3441.91 ± 614.69	116.27 ± 21.26	2.6 ± 0.53	
	Stump root	2303.33 ± 176.44	10.92 ± 1.02	0.63 ± 0.043	
	Fine root	1896.75 ± 165.56	18.28 ± 1.70	1 ± 0.08	
	Coarse root	651.94 ± 135.12	3.67 ± 1.00	0.27 ± 0.06	
	Litter	1393.33 ± 165.56	32.99 ± 4.24	0.74 ± 0.08	
	<i>Q. leucotrichophora</i>	Bole	120637.89 ± 8717.49	556.33 ± 113.06	51.80 ± 4.61
		Branch	70943.81 ± 8725.76	583.98 ± 95.60	36.78 ± 4.41
		Twig	20557.50 ± 8734.10	224.27 ± 99.62	16.76 ± 7.06
		Leaf	10337.92 ± 2931.31	199.93 ± 60.74	10.38 ± 2.41
		Stump root	55168.94 ± 11465	262.69 ± 79.32	19.13 ± 3.80
Fine root		10243.32 ± 2959.07	73.69 ± 27.02	6.36 ± 1.80	
Coarse root		577.27 ± 131.11	3 ± 0.77	0.30 ± 0.06	
<i>R. arboreum</i>	Litter	3216.66 ± 138.60	43.47 ± 3.13	1.73 ± 0.08	
	Bole	6239.63 ± 1161.46	32.33 ± 6.34	2.21 ± 0.47	
	Branch	2901.16 ± 1039.39	27.24 ± 9.41	1.3 ± 0.67	
	Twig	2182.53 ± 579.51	21.2 ± 7.19	1.19 ± 0.21	
	Leaf	546.65 ± 204.73	9.5 ± 3.52	0.59 ± 0.22	
	Stump root	2225.52 ± 614.11	12.7 ± 3.35	0.89 ± 0.35	
	Fine root	969.91 ± 413.76	7.13 ± 2.96	0.6 ± 0.38	
	Coarse root	329.47 ± 130.46	2.10 ± 0.80	0.15 ± 0.08	
	Litter	373.33 ± 96.14	4.34 ± 0.97	0.32 ± 0.096	
	Associated Species	Bole	41253.88 ± 136.95	221.28 ± 1.03	9.4 ± 0.03
Branch		21862.49 ± 137.04	206.6 ± 1.85	7.04 ± 0.04	
Twig		6190.30 ± 115.40	84.27 ± 1.78	2.64 ± 0.5	
Leaf		3241.63 ± 57.22	62.18 ± 1.24	0.80 ± 0.006	
Stump root		10848.35 ± 102.93	55.69 ± 0.74	1.9 ± 0.02	
Fine root		4014.20 ± 31.24	33.39 ± 0.288	1.8 ± 0.01	
Coarse root		1367.30 ± 3.07	7.3 ± 0.02	0.41 ± 0.009	

Sites/vegetation	Components	Biomass kg/ha	Nitrogen (kg/ha)	Phosphorus (kg/ha)
Herbs	Litter	2563.33 ± 15.94	41.7 ± 0.26	0.34 ± 0.004
	Herbs above	10262.44 ± 349.09	26.36 ± 7.63	2.1 ± 0.35
	Herbs below	800 ± 312.23	7.0 ± 3.38	0.48 ± 0.23
Shrubs	Shrubs stem	2880 ± 134.12	42.52 ± 12.	2.28 ± 0.18
	Shrubs leaf	1260 ± 221.18	23.9 ± 11.73	3.8 ± 1.10
	Shrubs root	1080 ± 349.09	13.18 ± 6.73	0.33 ± 0.065

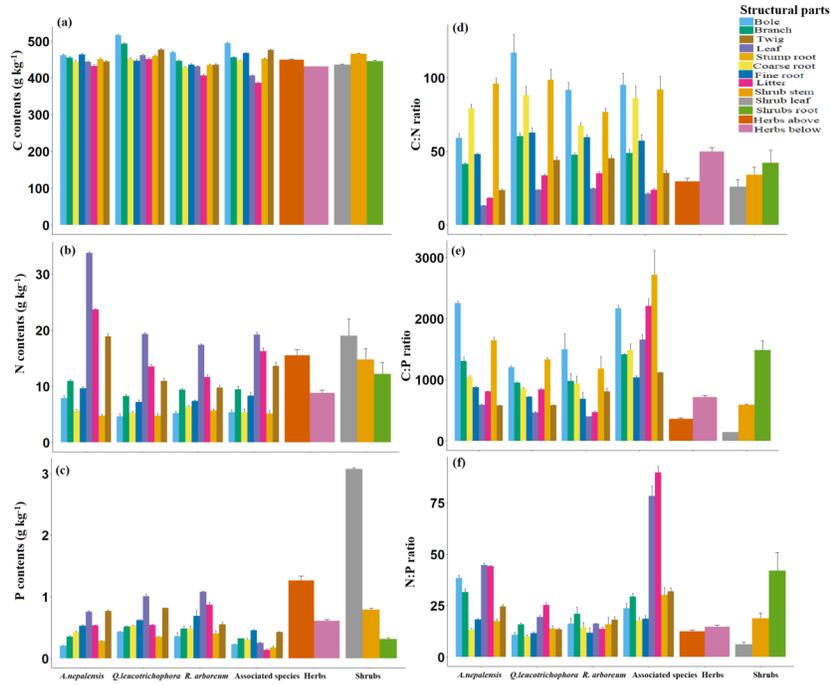
**Table 2.** The C:N:P ratios in vegetation components among the different plant communities.

Tree Species/Components	Bole	Branch	Twig	Leaf	Fine root	Courroot
<i>Alnus nepalensis</i>	2216.98:11.28:1	1279.79:22:1	860.36:17.2:1	578.7:40.2:1	860.36:17.2:1	1023.6:12.4
<i>Quercus leucotrichophora</i>	1113.43:11.16:1	903.4:13.4:1	784.56:9.7:1	460.9:19.7:1	784.56:9.7:1	681.9:11.24
<i>Rhodendron arboreium</i>	1307.38:13.8:1	920.1:18.9:1	882.1:12.8:1	236.9:9.6:1	882.1:12.8:1	623.16:10.4
<i>Pyrus pashia</i>	2166.51:22.98:1	1416.3:29.5:1	1454.21:17.6:1	1637.9:77.3:1	1454.21:17.6:1	1033.34:18
<i>Lyonia ovalifolia</i>	2245.1:25.4:1	1450.98:30.8:1	1420.99:17.9:1	1872.4:90:1	1420.99:17.9:1	1108.49:19
<i>Myrica esculenta</i>	2301.5:9.8:1	1515.69:23.9:1	2096.7:42.2:1	1410.3:77.3:1	2096.7:42.2:1	1094.83:12
<i>Quercus floribunda</i>	1976:26:1	1345.65:28.6:1	1323.4:20.2:1	468.2:22.1:1	1323.4:20.2:1	866.69:17.3
<i>Litsea umbrosa</i>	2252.63:9.8:1	1481.4:24.6:1	2050.2:42.1:1	1416.1:77.1:1	2050.2:42.1:1	1063.89:12
<i>Aesculus indica</i>	2307.68:8.8:1	1520:22:02	2103.1:40.3:1	1476.2:76:1	2103.1:40.3:1	1098.1:11.7
<i>Juglans regia</i>	1635.66:9.5:1	1182.94:14.8:1	2204.7:33.6:1	1293.63:26.5:1	2204.7:33.6:1	848.74:13.6
<i>Benthamidia capitata</i>	1532.18:7.4:1	1147.9:13.7:1	2200.2:11:1	1287.6:34.7:1	2200.2:11:1	849.79:8.6:
Understory						
Herbs above ground	355.2:12.2:1					
Herbs below ground	709.17:14.4:1					
Shrubs stem	587.33:18.6:1					
Shrubs leaf	141.85:6.1:1					
Shrubs root	1438.8:39.4:1					

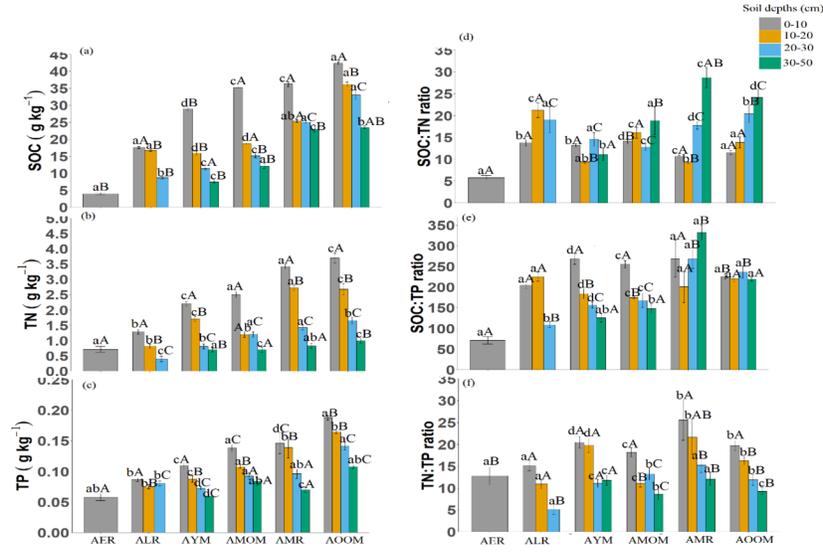
**Table 3.** Soil and microbial biomass C: N: P stoichiometry among different soil depths across six study sites in the central Himalayas

Sites	Soil depth (cm)	Soil C:N:P ratio	Microbial biomass C:N:P ratios
AER	0-10	71.21:12.80:1	14.13:1.90:1
ALR	0-10	204.55:15.07:1	12.91:2.13:1
	10-20	224.82:10.88:1	15.08:2.02:1
	20-30	108.86:5.14:1	22.18:2.07:1
AYM	0-10	268.37:20.44:1	10.89:2.04:1
	10-20	183.83:19.79:1	13.62:1.95:1
	20-30	156.35:11.11:1	17.96:2.00:1
	30-50	125.55:11.77:1	17.89:1.88:1
AMOM	0-10	255.84:18.20:1	14:59:2.03:1
	10-20	174.25:11.07:1	17.97:1.95:1
	20-30	168.04:13.24:1	16.98:1.89:1
	30-50	147.86:8.55:1	19.20:2.02:1
AMR	0-10	269.08:25.57:1	15.83:1.97:1
	10-20	200.51:21.62:1	14.62:1.90:1
	20-30	268.09:15.27:1	19.63:2.20:1

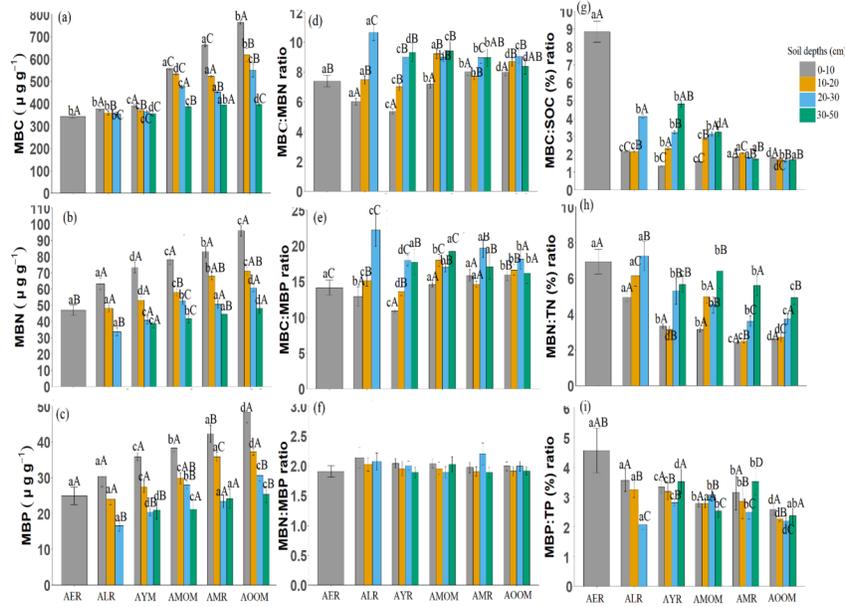
Sites	Soil depth (cm)	Soil C:N:P ratio	Microbial biomass C:N:P ratios
AOOM	30-50	232.22:12.04:1	17.06:1.88:1
	0-10	225.58:19.75:1	15.60:1.99:1
	10-20	220.06:16.21:1	16.60:1.91:1
	20-30	235.47:11.87:1	18.10:1.99:1
	30-50	218.93:9.26:1	16.14:1.91:1



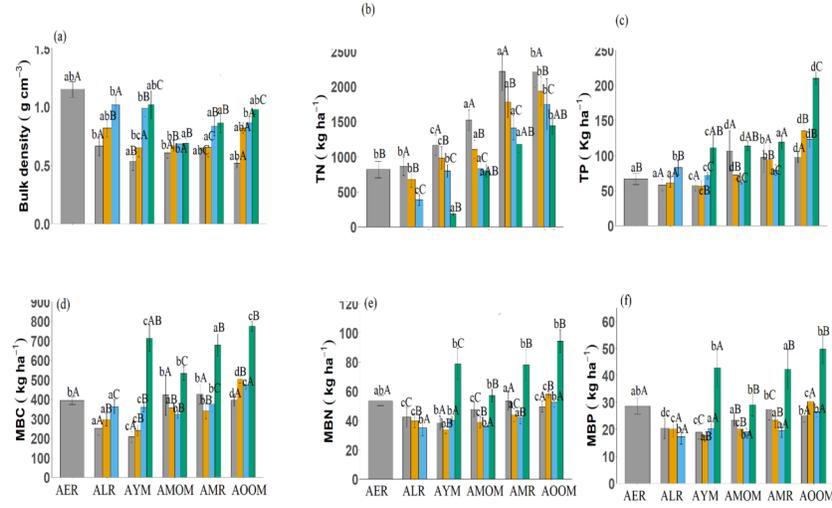
**Figure 1** C, N, and P concentration and ecological stoichiometry in different structural parts among different plant communities.



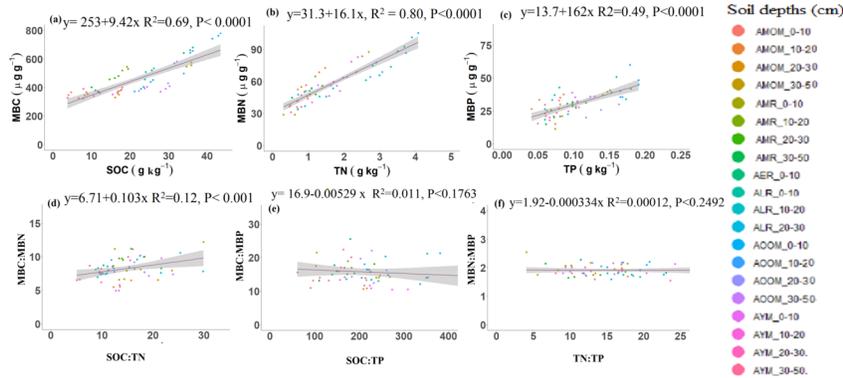
**Figure 2** The vertical distribution of C, N, and P concentration and ecological stoichiometry in the different soil layers (up to maximum soil profile). Vertical bars for each column indicate the standard error of the mean. The means of different layers followed by the lower-case letter or means of the stands followed by the different capital letters are significantly different ( $p < 0.05$ ).



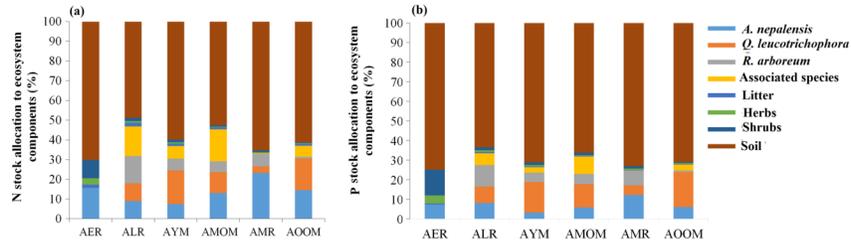
**Figure 3** The vertical distribution of microbial biomass C, N, and P concentration and ecological stoichiometry in the different soil layers (up to maximum soil profile). Vertical bars for each column indicate the standard error of the mean. The means of different layers followed by the lower-case letter or means of the stands followed by the different capital letters are significantly different ( $p < 0.05$ ).



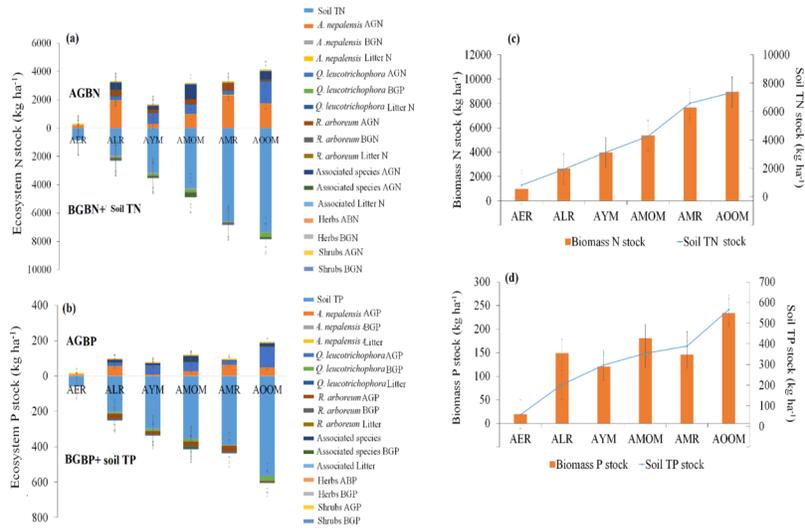
**Figure 4** Soil bulk density, soil nitrogen, and phosphorus stock in the different soil layers (up to maximum soil profile). Vertical bars for each column indicate the standard error of the mean. The means of different layers followed by the lower-case letter or means of the stands followed by the different capital letters are significantly different ( $p < 0.05$ ).



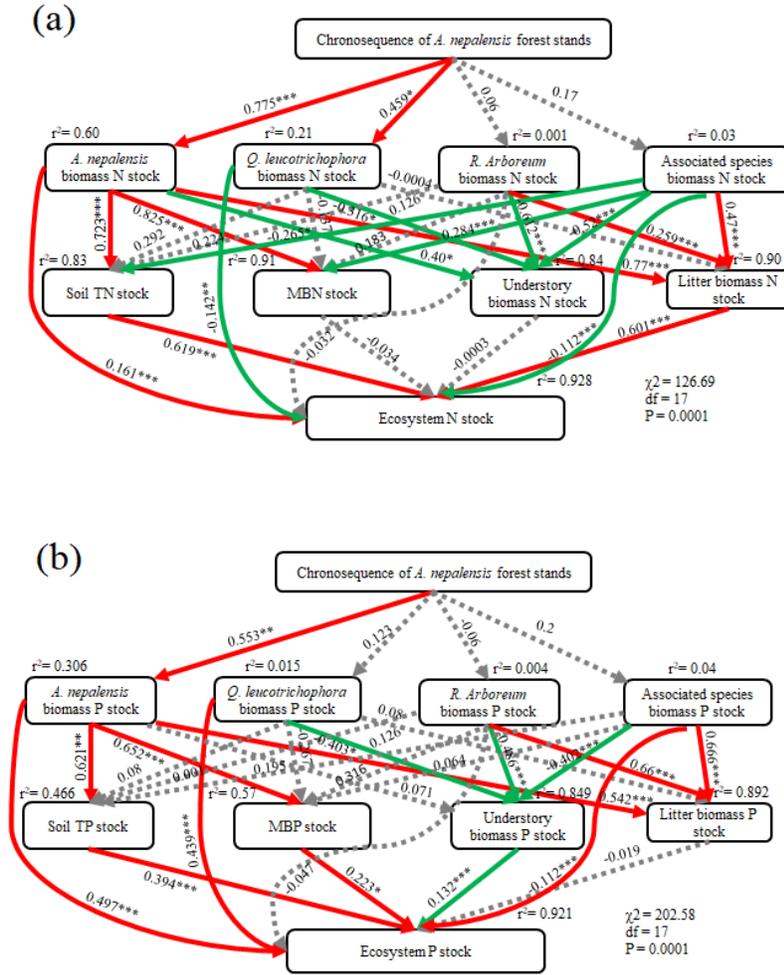
**Figure 5** The relationships between soil C:N:P stoichiometry and microbial biomass C:N:P stoichiometry different *A. nepalensis* occurred forest types: a relationship between the SOC and MBC; b relationship between the TN and MBN; c relationship between the TP and MBP; d relationship between the SOC:TN and MBC:MBN; e relationship between the SOC:TP and MBC:MBP; f relationship between the TN:TP and MBN:MBP.



**Figure 6** Proportion of the nitrogen (a) and phosphorus (b) stock allocation pattern in ecosystem components.



**Figure 7** Total above and below ground nitrogen (a) and phosphorus (b) stocks and the relationship between total biomass N stock to soil TN stock (c), and between total biomass P stock to soil TP stock (d) in different *A. nepalensis* occurred forest types.



**Figure 8** The Structural equation model of ecosystem nitrogen (a) and phosphorus (b) stocks. The number near the arrow are standardized path coefficients. Red arrow denote significant positive (\* < 0.05, \*\* < 0.01, \*\*\* < 0.001) correlation and green arrow denote significant negative (\* < 0.05, \*\* < 0.01, \*\*\* < 0.001) correlations. The solid arrow indicates a positive and negative relationship and the dotted arrow indicates a non-significant relationship. The proportion of variance explained ( $r^2$ ) near endogenous variables represents the proportion of variance explained by the mode.

**Supplementary table 1:** The allometric equations used to estimating the biomass of the tree components (Y, kg per tree) and CBH (circumference at breast height X cm), according to regression equation ( $\ln Y = a + b \ln X$ , where a=intercept, and b= slope) and logarithmic regression relation to biomass of alder tree components dry weight in gram with the function of tree diameter at breast height (DBH, cm).

	<i>Alnus nepalensis</i>	<i>Quercus leucotrichophora</i>	<i>Rhododendron arboreum</i>	Interspecies
Bole	$\log_{10} = 1.532 + 2.461 \log_{10} \text{ DBH}$	$a = -0.523, b = 1.367, r^2 = 0.994$	$a = 1.120, b = 0.704, r^2 = 0.873$	$a = -0.861, b = 1.425, r^2 = 0.915$

	<i>Alnus nepalensis</i>	<i>Quercus leucotrichophora</i>	<i>Rhododendron arboreum</i>	Interspecies
Branch	log10= 1.455 + 2.216 log10 DBH	a= -0.718, b= 1.302, r <sup>2</sup> = 0.973	a= 1.113, b= 0.609, r <sup>2</sup> =0.605	a= -0.908, b= 1.327, r <sup>2</sup> = 0.907
Twig	log10 = 2.963 + 0.628 log10 DBH	a= 0.065, b= 0.895, r <sup>2</sup> = 0.897	a= 1.115, b= 0.373, r <sup>2</sup> = 0.327	a= -0.506, b= 1.028, r <sup>2</sup> = 0.796
Foliage	log10 = 2.963 + 0.628 log10 DBH	a= -0.976, b= 0,954, r <sup>2</sup> = 0.299*	a= 1.194, b= 0.170, r <sup>2</sup> =0.101 n,s	a= -1.106, b= 1.042, r <sup>2</sup> = 0.755
Catkin	log10 = 1.348 + 1 .281 log10 DBH	-	-	-
Stump root	a= 0.098, b= 0.948, r <sup>2</sup> = 0.789	a= 0.982, b= 0,904, r <sup>2</sup> = 0.612	a= -0.119, b= 0.867, r <sup>2</sup> = 0.612	a = 0.098, b= 0.948, r <sup>2</sup> =0.789
Lateral root	a= -2.346, b= 0.997, r <sup>2</sup> = 0.724	a= -0.312, b= 809, r <sup>2</sup> =0.569	a=-1.752, b=0.984, r <sup>2</sup> =0.601	a= -2.346, b= 0.997, r <sup>2</sup> =0.724
Fine root	a= -2.874, b= 0.529, r <sup>2</sup> = 0.722	a= -1.326, b= 0.504, r <sup>2</sup> = 0.487	a= -1.009, b= 0,407, r <sup>2</sup> =0.568	a=-2.874, b=0.529, r <sup>2</sup> =0.722
	<i>Lyonia ovalifolia</i>	<i>Quercus floribunda</i>	<i>Juglans regia</i>	<i>Aesculus indica</i>
Bole	a= -0.6884, b= 1.0865, r <sup>2</sup> = 0.958	a= -1.109, b= 1,518, r <sup>2</sup> = 0.910	a= 1.9626, b= 0.9002, r <sup>2</sup> = 0.91	a=1.9322, b=0.9809, r <sup>2</sup> =0.972
Branch	a= -0.9054, b= 1.0530, r <sup>2</sup> = 0.937	a= -0.987, b= 1,377, r <sup>2</sup> = 0.929	a= 0.0445, b= 0.8730, r <sup>2</sup> = 0.500*	a= 0.7989. b= 0.6836, r <sup>2</sup> = 0.778
Twig	a= -1.5042, b= 1.0496, r <sup>2</sup> = 0.918	a= -1.128, b= 1.268, r <sup>2</sup> = 0.812	a= 0.5687, b= 0.5707, r <sup>2</sup> = 0.526*	a=0.3294, b=0.8008, r <sup>2</sup> =0.848
Foliage	a= -1.6954, b= 0.8085, r <sup>2</sup> = 0.848	a= 1.229, b= 1.384, r <sup>2</sup> = 0.789	a= -2.6355, b= 0.9973, r <sup>2</sup> = 0.752	a=-0.0689, b=0.7308, r <sup>2</sup> =0.752
Stump root	a= -0,1944 b= 0.7920, r <sup>2</sup> = 0.830	a= -0.246, b= 1.106, r <sup>2</sup> = 0.0.798	a=0.9494, b= 0.8010, r <sup>2</sup> = 0.895*	a=2.3831, b=0.6438, r <sup>2</sup> =0.774
Lateral root	a= -2.8928, b= 0.8537, r <sup>2</sup> = 0.899	a= -1.590, b= 1.004, r <sup>2</sup> = 0.712	a= 0.2858, b= 0.7140, r <sup>2</sup> = 0.608*	a=1.0028, b=0.8118, r <sup>2</sup> =0.759
Fine root	a=-1.6587, b=0.4573, r <sup>2</sup> =0.563*	a= -1.048, b= 0.246, r <sup>2</sup> = 0,614	a=-3.2823, b=1.1510, r <sup>2</sup> =0.731	a=0.1808, b=0.7429, r <sup>2</sup> =0.638

Note: The allometric equation were adopted from following published paper:

- (1) Rawat, Y.S., & Singh, J.S. (1988). Structure and function of Oak forest in Central Himalaya. I. dry matter Dynamics. *Annals of Botany*, (62), 397-41 DOI: 10.1093/oxfordjournals.aob.a087673
- (2) Sharma, E. & Ambhasht, R.S. (1991). Biomass, Productivity and Energetics in Himalayan Alder Plantations. *Annals of Botany* (67),285-293.<https://doi.org/10.1093/oxfordjournals.aob.a088138>
- (3) Adhikari, B.S., Rawat, Y.S. and Singh, S.P. (1995). Structure and function of high altitude forests of central Himalaya I. Dry matter dynamics. *Annals of Botany*, 75(3) , 237-248.<https://doi.org/10.1006/anbo.1995.1017>