Relative contribution of plant traits and soil properties to the functioning of a temperate forest ecosystem in the Indian Himalayas

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Abstract.

Plant-soil interactions are a major determinant of changes in forest ecosystem processes and functioning. We conducted a trait-based study to quantify the contribution of plant traits and soil properties to above- and below-ground ecosystem properties in temperate forest in the Indian Himalayas. Nine plant traits (leaf area, specific leaf area, leaf water content, leaf dry matter content, leaf carbon (C), nitrogen (N), phosphorus (P), leaf C/N, and leaf N/P) and eight soil properties (pH, moisture, available N, P, potassium (K), total C, N, P) were selected for determination of their contribution to major ecosystem processes (above-ground biomass C, soil organic C, soil microbial biomass C, N, and P, and soil respiration) in temperate forest. Among the plant traits studied, leaf C, N, P, and leaf N/P ratio proved to be the main contributors to above-ground biomass, explaining 20-27% of variation. Leaf N, P, and leaf N/P were the main contributors to below-ground soil organic C, soil microbial biomass C, N, and P, and soil respiration (explaining 33% of variation). Together, the soil properties pH, available P, total N and C explained 60% of variation in above-ground biomass, while pH and total C explained 56% of variation in soil organic C. Other soil properties (available P, total C and N) also explained much of the variation in soil microbial biomass C (52%) and N (67%), while soil pH explained some of variation in soil microbial biomass N (14%). Available P, total N, and pH explained soil microbial biomass P (81%), while soil respiration was only explained by soil total C (70%). Thus leaf traits and soil characteristics make a significant contribution to explaining variations in above- and below-ground ecosystem processes and functioning in temperate forest in the Indian Himalayas. Consequently, tree species for afforestation, restoration, and commercial forestry should be carefully selected, as they can influence the climate change mitigation potential of forest in terms of C stocks in biomass and soils.

Keywords: Ecosystem services, biomass carbon, leaf nitrogen, specific leaf area, soil microbial carbon, soil organic carbon

1. Introduction

Temperate forests provide various ecological services world-wide (Frelich, 2002; Tateno et al., 2004). They contribute 17% of global net primary productivity, provide 315 Gigatons of carbon (C) storage, are an important source of timber and wood products, and regulate hydrological, nitrogen (N), and C cycles (de Gouvenain and Silander, 2017; Negi, 2018). Temperate forests are characterized by a moderate climate, fertile soils, and high productivity (Singh et al., 2017; Saha et al., 2018). However, they are sensitive to environmental changes such as global climate change (Frelich, 2002; Alexander et al., 2018), and deforestation and degradation activities (Walther et al., 2002; Malik et al., 2016; Negi, 2018). Natural (landslide, wind damage, grazing, etc.) and anthropogenic (forest fire, grazing, logging, lopping, development activities, etc.) disturbances in forest ecosystems can alter forest composition and structure (Frelich, 2002; Dar and Sundarapandian, 2016). As a result, disturbances can lead to loss of biodiversity and altered ecological functioning (Arunachalam et al., 1996; Negi, 2018).

World-wide, many studies have explored the relationship between plant functional traits, soil properties, and ecological functions such as productivity (Eskelinen et al., 2012; Roscher et al., 2012), decomposition (Bakker et al., 2010; Carrillo et al., 2017), nitrification and C storage (Conti and Diaz, 2013), soil fertility (Berner and Law, 2016), above-ground biomass, litter, soil organic matter, N mineralization, and leaching of inorganic N (Grigulis et al., 2013) in different ecosystems. These studies have shown e.g., that 56.7% of variation in microbial properties in semi-arid ecosystems is explained by plant traits, and 63.8% by soil properties (pH, total N, total C, ammonium-N (NH_4-N), nitrate-N (NO_3-N), and phosphate-phosphorus (PO_4-P)) (Chai et al., 2019). Plant traits such as shoot traits (shoot N and C, leaf dry matter content) and root traits (root N, root C/N ratio, root dry matter content) can be used to predict soil properties and ecosystem functions in temperate grasslands (Long et al., 2019). Soil properties and plant functional traits are important for regulating the functioning of tropical cloud forests (Hernández-Vargas et al., 2019), while soil heterogeneity and plant functional traits can predict variation in species distribution in subtropical forests (Zhang et al., 2017).

Studies in Indian Himalayan forests are fewer and have focused solely on variations in biodiversity (Sharma et al., 2010, 2011) and soil characteristics (Gairola et al., 2012; Joshi and Negi, 2015; Dar and Sundarapandian, 2016; Saha et al., 2018). As a result, there is limited understanding of the impact of plant traits and soil properties on ecosystem functioning in temperate forests in the Indian Himalayan region. Under global change, the current understanding is inadequate for determining the mechanisms of ecosystem processes and functioning in temperate forests. The major causes of damage to Himalayan moist temperate forests are forest fires (55.3%), damage to plants due to deforestation/logging activities (87.9%), grazing (91.6%), and other human development activities (85.6%) (http://fsi.nic.in). Himalayan temperate forests are sensitive to disturbance, but in undisturbed form they have great biodiversity and contribute to global biogeochemical and nutrient cycling. There is thus a need to quantify the contribution of plant traits and soil properties to ecosystem functioning in order to manage temperate forests.

In this study, we analyzed the relative contributions of plant traits and soil properties to above- and below-ground ecosystem processes. We hypothesized that above-ground plant traits have stronger effects on above-ground ecosystem processes than on below-ground ecosystem processes. We measured (i) plant functional traits, (ii) soil properties, and (iii) ecosystem properties, including above-ground biomass, soil organic matter, soil microbial biomass C, N, and P, and soil respiration. We then determined the relative effects of plant traits and soil properties on ecosystem properties.

2 Material and methods

2.1. Study site

A forest stand within the temperate central Himalayan region of Uttrakhand, India (30°28'02.6"N; 78°05'47.9"E) was selected as the study area. It is located at an altitude of 2200 m above sea level, in a region with mean annual temperature of 25ºC and mean annual rainfall of 2150 mm. The vegetation in the area is Himalayan moist temperate forest. The soil is acidic and comprises regosols, leptosols, and dolomite (Raina and Gupta, 2009).

2.2 Vegetation analysis

A study plot was randomly selected through grid (cell) selection based on a random number table applied to grids across the study area, and a vegetation survey was carried out in this selected plot using a quadrat method. During the peak plant growing season (March-April), 20 plots (10 m x10 m) were staked out in the forest, using a gridded randomization method in which the plots were selected on a non-replacement basis (Lavrakas, 2008). Three individual trees were selected at random within each plot, for evaluation of plant traits. Therefore, a total of 60 individual trees were studied. The dominance of plant species was determined using importance value index (IVI) and species abundance in a field survey. Next, 10 dominant tree species (seven evergreens, three deciduous) (Table 1) were selected within plots, to cover a variety of plant traits in the forest area (Table 2). Sampling of plants and soils was performed in three different seasons: winter (October-February), summer (May-June), and rainy season (July-September).

2.3 Plant traits

All measurements were taken following an existing protocol (Pérez-Harguindeguy et al., 2013). In each of the 20 plots, three healthy adult specimens of the most dominant woody plant species were selected for leaf trait measurements (Table 2), making a total of 60 individuals. For each selected individual, leaves that were young, fully expanded, and under the highest sunlight exposure were collected. The leaves were placed in plastic bags and transported in a chilled, dark container to the laboratory, where they were stored at 10-15ºC. Leaf area was measured on five fully expanded fresh young leaves per individual tree, by scanning using an LI-3100C instrument (LI-COR, LI-3100C). Specific leaf area was calculated as the area of one side of a leaf divided by its oven-dried weight (at 70ºC for 48 h). Leaf dry matter content was calculated as the ratio between dry and fresh (saturated) leaf weight. Additional leaves (10-20 leaves) were collected from the outer canopy of each tree for chemical analysis. These leaves were separated, oven-dried (at 70ºC for 48 h) and milled using a stainless steel mill (Wiley, Thomas Scientific). Leaf C and N content were determined using an elemental analyzer (CHNS, Euro, EA-3000). Leaf P content was analyzed by the acid digestion method (Pérez-Harguindeguy et al., 2013).

2.4 Soil properties

Each of the 20 selected plots was characterized by analyzing soil samples (three per plot). Standard procedures were followed for soil analysis (Anderson and Ingram, 1994). Soil samples were collected from 0-30 cm depth at randomly selected points, to assess the physicochemical properties of soil under the canopy of the selected dominant tree species. A total of 60 soil samples were taken from each plot in three seasons. The composite soil sample from each sampling point was divided into two equal parts. One part was immediately (within 24 h) sieved (2-mm mesh) and analyzed for pH (digital pH meter), moisture content (gravimetric method), ammonium-N (Kjeldahl method), and available P (molybdenum blue method). The other part was sieved through a 2-mm mesh, air-dried under laboratory conditions, and analyzed for total C and total N, using a CHNS analyzer (CHNS, Euro, EA-3000). Total P was determined by spectrophotometer using the Bray-Kurtz method and soil potassium (K) content was determined using a flame photometer (Systonics, 128).

2.5 Ecosystem properties

The primary ecosystem properties on which the influence of plant traits and soil properties was studied were: above-ground biomass, soil organic C, soil microbial biomass C, N, and P, and soil respiration. Three samples per plot of tree biomass and three samples per plot of soil were taken for the analyses. The height and diameter at breast height (DBH) of all trees with DBH ≥10 cm within each sample plot were measured. The biomass of dominant tree species was taken to represent above-ground biomass (Mg C ha^{-1}). The growing stock volume density (GSVD) of each tree species was estimated using species-specific volume equations developed using multiple regression methods by the Forest Survey of India (FSI, 1996) (Table S1). The estimated GSVD values (m^3 ha^{-1}) were then converted into above-ground biomass by multiplying by an appropriate biomass expansion factor (BEF, Mg m^{-3}):

$$\text{Biomass} = \text{GSVD} \times \text{BEF}$$

where BEF was defined as the ratio of above-ground biomass density of all living trees with DBH ≥2.54cm to GSVD for all trees with DBH ≥12.7 cm.

The equations used for calculation of BEF for hardwood, spruce-fir, and pine tree species were (FSI, 1996):

Hardwood:

$$\text{BEF} = \exp\{1.91\ 0.34 \times \ln(\text{GSVD})\} \text{ (for GSVD <200 m}^3\text{ ha}^{-1}\text{)}$$

$$\text{BEF} = 1.0 \text{ (for GSVD >200 m}^3\text{ ha}^{-1}\text{)}$$

Spruce-fir:

$$\mathrm{BEF} = \exp\{1.77\ 0.34 \times \ln(\mathrm{GSVD})\}\ (\text{for GSVD} < 160\ \mathrm{m^3\ ha^{-1}})$$

$$\mathrm{BEF} = 1.0\ (\text{for GSVD} > 160\ \mathrm{m^3\ ha^{-1}})$$

Pine:

$$\mathrm{BEF} = 1.68\ (\text{for GSVD} < 10\ \mathrm{m^3\ ha^{-1}})$$

$$\mathrm{BEF} = 0.95\ (\text{for GSVD} = 10\ 100\ \mathrm{m^3\ ha^{-1}})$$

$$\mathrm{BEF} = 0.81\ (\text{for GSVD} > 100\ \mathrm{m^3 ha^{-1}})$$

Above-ground biomass C was estimated using the IPCC conversion rate of 0.47 for biomass to carbon:

$$C = 0.47\ \text{Biomass}$$

where C and biomass are in Mg ha^{-1}.

For determination of soil organic C, three soil samples were taken from the top 30 cm of each plot using a soil corer (10 cm diameter) and mixed thoroughly to obtain a composite soil sample. These samples were air-dried, sieved through a 2-mm mesh, and analyzed for organic C using an established procedure (Walkley and Black, 1934).

Soil microbial biomass C and N were estimated by the chloroform fumigation-extraction method (Brookes et al., 1984; Vance et al., 1987). Soil samples were subjected to one of two treatments (chloroform-fumigated and unfumigated), extracted in 0.5 N K_2SO_4 and simultaneously digested and titrated against ferrous ammonium sulfate using 1,10-phenanthroline monohydrate as the indicator (chloroform-fumigated samples) or against N/140 HCl using boric acid as the indicator (unfumigated samples). Soil microbial biomass P was estimated by chloroform fumigation-extraction using 0.5 N $NaHCO_3$(Brookes et al., 1984). In all cases, the values obtained for unfumigated samples were subtracted from those obtained for chloroform-fumigated samples, to obtain microbial C, N, and P content.

Soil respiration was measured as carbon dioxide (CO_2) evolution, using a single-chamber device (LI-8100, LI-COR Biosciences, Lincoln, NE). The closed-chamber method was used to estimate the flux of CO_2 at the soil surface. In this method, a small portion of air is circulated from a chamber to an infrared gas analyzer, and then sent back to the chamber (Madsen et al., 2009). All measurements were programmed using a LICOR 8100 palm-held wireless controller linked with the LI-8100 device. PVC soil collars measuring 20 cm in diameter were inserted to a depth of 3-5 cm and extended approximately 6-10 cm above the soil surface. In total, measurements were made at 60 points.

2.6 Data analysis

Principal component analysis (PCA) and linear mixed modeling with residual maximum likelihood (REML) estimations were carried out with lme4 package R studio (R-3.5.1 version) to quantify the respective contributions of plant traits and soil properties to the variation in selected ecosystem processes. PCA was performed to identify significant contributors among the multivariable components on the basis of their eigenvalue and percentage variance (Orwin et al., 2010). REML is defined as a form of maximum likelihood estimation that uses a likelihood function calculated from a transformed set of data, so that nuisance parameters have no effect. REML provides estimates of parameter effects and variance components for both the fixed and random effects in the model (Grigulis et al., 2013). In this analysis, the response variables were ecosystem processes (above-ground biomass, soil organic C, soil microbial biomass C, N and P, and soil respiration). Fixed effects were plant traits (leaf area, specific leaf area, leaf water content, leaf dry matter content, leaf C content, leaf N content, leaf P content, leaf C/N, and leaf

N/P) and soil properties (pH, soil moisture content, total C, total N, available N, available P, total P, K), with plant species and plot as random effects. All variables were tested for normality and log-transformed before analysis.

3 Results

The average values obtained for plant traits, soil characteristics, and ecosystem properties are presented in Figure S1 in Supplementary Information. Total percentage of variation explained by plant traits was 84% (Figure 1a) and by soil parameters 64% (Figure 1b). Among all plant traits studied, specific leaf area, leaf water content, leaf C, N, and P, and N/P ratio were significant contributors to the variation in ecosystem properties (Table 3a). Among the soil characteristics studied, pH, available P, total C, and total N were significant contributors (Table 3a). These important contributors were considered in model building, to identify their contribution.

3.1 Control of above-ground biomass and leaf traits

Variation in above-ground biomass was best explained (to 20-27%) by functional properties of the leaf, i.e., leaf C, N, and P, and leaf N/P ratio. Variation in soil organic C was best explained (33%) by leaf N and P, and leaf N/P ratio. Above-ground biomass and soil organic C showed a positive correlation with leaf N (Table 3a). Both variables were negatively correlated with leaf P and leaf N/P ratio, while above-ground biomass also showed a negative correlation with leaf C. The effects of random variables (i.e., soil properties, species, and plot) on above-ground biomass and soil organic C were as follows: soil properties (pH, available P, total C and N) explained 60% of variation in above-ground biomass and 56% of variation in soil organic C; species explained 30% of variation in above-ground biomass and 10% of variation in soil organic C; and plot explained 10% of variation in above-ground biomass and 34% of variation in soil organic C (Table 3a).

3.2 Control of below-ground microbial biomass and respiration

Common leaf traits, i.e., leaf N, leaf P, and leaf N/P, explained 33% of the variation in soil microbial biomass C, N, and P, and in soil respiration. These ecosystem processes were positively correlated with leaf P and leaf N/P, and negatively with leaf N (Table 3a). Soil microbial biomass C (52% explained) and N (67% explained) were affected by common soil parameters (available P, total C, and total N) (Table 3a). Soil pH affected soil microbial biomass N (14.5%), but not microbial biomass C (Table 3a). Above-ground species had only a minor effect on soil microbial biomass C (2%) and no effect on soil microbial biomass N (Table 3a). Plot variance made a significant contribution to explaining soil microbial biomass C (45%) and N (33%) (Table 3a). Soil microbial biomass P was highly influenced (81%) by soil properties (available P, total N, and pH) and plant species (19%), while plot had no effect (Table 3a). Soil total C (70%) and plot (30%) explained all of the variation in soil respiration (Table 3a).

The full and null models were estimated and validated based on Akaike Information Criterion (AIC), deviance, and chi-square (Winter, 2013). There model fit was better for some parameters, as indicated e.g., by lower AIC values (Table 3b).

4. Discussion

This study identified the relative contribution of plant traits and soil properties in explaining major ecosystem properties in a temperate forest ecosystem in the Indian Himalayas. In combination, the plant traits and soil properties tested explained 33-70% of the variation in ecosystem properties. In previous studies, the contribution of plant traits and soil properties to explaining variation in above- and below-ground productivity has been within the range 16-38% (Orwin et al., 2010), 60-90% (Grigulis et al., 2013), 36-100% (Legay et al., 2014), and 3-100% (Legay et al., 2016).

4.1 Plant functional traits and ecosystem properties

We found that above-ground biomass and soil organic C were both positively associated with leaf N. The positive association of leaf N with above-ground biomass reflects the exploitative strategy employed by plant species to gain a faster return from nutrient exchange and investment in the ecosystem (Wright et al., 2004; Díaz et al., 2016; Rawat et al., 2019). These results are consistent with previous findings that plant traits explain 60% of variation in above-ground biomass (Becknell and Powers, 2014). Other studies have also found a positive association between leaf traits and biomass increments in forest ecosystems (Finegan et al., 2015 and Bu et al., 2019). Similarly to previous studies (Angst et al., 2019; Bardgett, 2017; Chen et al., 2018; Qiu et al., 2018), we found a significant positive association of leaf traits with soil C. However, the impact of leaf traits on soil C is not straight-forward, as different studies have found contrasting results. For instance, soil organic C has been found to have a positive link with leaf N, as N-rich vegetation contains high soil C stocks (Manning et al., 2015). Other have reported a negative relationship between leaf traits and community-weighted mean leaf N concentration (Ali et al., 2017), or no relationship between leaf traits and C storage (Conti and Diaz, 2013).

Previous studies have indicated a negative relationship between leaf N/P ratio and biomass production (Güsewell, 2004; Wang et al., 2015). Similarly, we found that above-ground biomass and soil organic C were negatively correlated to leaf N/P ratio, and also to leaf P. In contrast, a study across terrestrial biomes in China found an overall positive relationship between leaf P and biomass production (Tang et al., 2018). However, that study also found major fluctuations in the relationship between leaf P and biomass production in different biomes, with no significant relationship in deciduous broadleaf forests and mixed forests, but a negative relationship in evergreen broadleaf forests (Tang et al., 2018). Deciduous trees have a higher leaf P content than evergreen trees (Tang et al., 2018). In addition, plant C and plant P have been shown to decrease with increasing temperature (Reich and Oleksyn, 2004; Tang et al., 2018) and precipitation (Tang et al., 2018). Considering these large variations between biomes and forest types, there is a need for more studies on the relationships between leaf N and P and biomass production in different ecosystems, to get a better understanding of the potential biomass response to the high N and P deposition that is occurring world-wide (Schreeg et al., 2014; Tang et al., 2018).

In the present study, soil microbial biomass C, N, and P, and soil respiration were positively associated with leaf P and leaf N/P ratio, but negatively with leaf N. The negative association of microbial biomass C, N, and P with leaf N might be due to plant-microbe competition for N in temperate forest, as suggested in other studies reporting a negative association of leaf N with bacterial abundance (Pei et al., 2016). However, positive relationships between microbial biomass C or N and leaf N have also been reported (Xue et al., 2014). These contrasting results might be because plants with high leaf N need a rapid nutrient trade-off to fulfil their physiological metabolism. Therefore, leaf N is affected by soil micro-organisms with the ability to compete for soil C and N.

We found a negative association between soil respiration and leaf N, which might be due to differences in litter quality, as suggested by other studies (Jiang et al., 2017; Han et al., 2015).

In contrast, several studies have found a positive relationship between plant diversity, microbial biomass, and respiration (Bardgett et al., 1999; Liu et al., 2017; Chen et al., 2019; Chen and Chen, 2019). Overall, our results indicate that leaf traits are significant drivers of forest above- and below-ground dynamics, as they are the major contributor to acquisition and conservation trade-offs.

4.2 Soil characteristics and ecosystem properties

Soil properties explained in total 60% of the variation in above-ground biomass (pH, available P, total N, total C) and 56% of the variation in soil organic C (pH, total C). This is consistent with previous findings for spruce and pine forests, with global forest data (Paré and Cleve, 1993; Zhou and Dean, 2004; Ordoñez et al., 2009). In other studies, soil, climate, landscape, and space together explained 61% of the variation in above-ground biomass in rain forest and 69.2% in spruce forest (Cao et al., 2019; Santiago-García et al., 2019). Our results also indicated that above-ground species of tree is important for above-ground and soil organic C stocks, explaining 30% and 10% of variation, respectively. This is consistent with previous findings for above-ground biomass in a *Pinus kesiya* forest and soil organic C in pine, oak, conifer, and deciduous forests (Cha et al., 2019; Li et al., 2018). The importance of plant species for soil properties has been shown in several studies. At natural and afforested sites in China, the C, N, and P content in both plants and soils are strongly influenced by plant species (Bai et al., 2019), while in northern Iran, soil C and N vary between forests dominated by different tree species (Kooch et al., 2019). In addition, in the present study, plot explained 10% of variation in above-ground biomass and 34% of variation in soil organic C. Thus, tree species used for afforestation, restoration, and commercial forestry need to be selected with care, as they can influence the climate change mitigation potential of forests in terms of C stocks in biomass and soils.

This study revealed that soil microbial biomass C and N are influenced by available P and soil total C and N, which is consistent with previous findings for Indian *Pinus kesiya* forest and tropical wet evergreen forests (Arunachalam et al., 1996; Barbhuiya et al., 2004). Many previous studies report that microbial biomass C and N show significant correlations with soil total N and pH (Kara and Bolat, 2008; Yang et al., 2010; Ravindran and Yang, 2015; Legay et al., 2016, 2014; Liu et al., 2019). In our case, only soil microbial N was affected by soil pH, while soil microbial biomass C was mainly affected by above-ground tree species. This is consistent with findings for central Himalayan forests (Bargali et al., 2018).

In the present study, soil microbial biomass P was influenced by soil properties (pH, available P, total N). A significant contribution of available soil P to microbial biomass P has also been reported in other studies (Wang et al., 2004; Xue et al., 2014). Soil microbial biomass P was influenced by above-ground tree species in our study. As in previous studies (Chen et al., 2019; Nguyen and Marschner, 2017), the variation in soil respiration was mainly explained by total C.

5. Conclusions

In this study, leaf traits and soil characteristics made a significant contribution to explaining the variation in ecosystem processes and functioning in temperate forest in the Indian Himalayas. While there is considerable variation between biomes globally, the results confirm findings in previous large-scale studies of a general relationship between leaf P and N and biomass production in different forest types. Therefore, use of existing broad-scale patterns of leaf traits for modeling biomass and soil properties in relatively understudied areas, such as the Himalayas, is justified. However, leaf traits had large impacts on biomass production and soil C stocks, so more studies are needed to gain a better understanding of functional trait variations among plants/forest types and the links to soil properties. Choice of tree species used for afforestation, restoration, and commercial forestry also needs to be considered, as it can influence the climate change mitigation potential of forests in terms of C stocks in biomass and soils.

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Additional information

Supplementary material accompanies this paper at (link).

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Table 1. Characteristics of dominant tree species selected for study in temperate forest in the central Himalayan region of Uttrakhand, India

Species	Family	Leaf habit	Leaf type	Tree density (tree ha^{-1})*	DBH (cm)*	IVI
Deciduous						
Aesculus indica, Colebr	Hippocastanaceae	D	B	240	38.99 ± 2.22	27.50
Pyrus pashia, Buch.Hemex D.Don	Rosaceae	D	B	160	25.66 ± 3.33	28.94
Toona ciliata, R.	Meliaceae	D	B	157	33.45 ± 2.98	14.44
Evergreen						
Abies pindrow, Spach Ham	Pinaceae	E	N	220	35.89 ± 3.23	50.82
Cedrus deodara, Loud	Pinaceae	E	N	250	35.78 ± 1.23	41.98
Cupressus torulosa, D. Don	Cupressaceae	E	S	230	29.76 ± 0.12	39.37
Euonymus pendulous, Wall	Celastraceae	E	B	123	23.44 ± 1.11	27.84
Quercus leucotrichophora, A.Comm	Fagaceae	E	B	250	31.12 ± 5.54	31.15
Rhododendron arboreum, Smith	Ericaceae	E	B	260	26.93 ± 6.69	20.62
Pinus wallichiana, Jackson	Pinaceae	E	N	210	34.67 ± 1.45	17.33

*E - Evergreen; D - Deciduous; N – Needle; B - Broadleaf; S - Scaly; DBH – Diameter at breast height *Own survey, IVI -Importance value index.*

Table 2. Description of plant functional traits and related functions, based on the literature*

Trait	Abbreviation	Description	Function
Leaf area	LA (cm^2)	One-sided projected surface area of the leaf	Evapotranspiration, canopy light interception, photosynthetic efficiency, relative growth rate
Specific leaf area	SLA (cm^2 g^{-1})	One-sided area of the fresh leaf divided by its oven-dry mass	Photosynthesis, leaf longevity, relative growth rate
Leaf water content	LWC (%)	Proportion of leaf water content related to the maximum water content that can potentially be achieved by the leaf	Plant water status, flammability, water use efficiency
Leaf dry matter content	LDMC (%)	Oven-dry mass of a leaf divided by its water-saturated fresh mass	Leaf physical resistance, leaf lifespan, stress tolerance
Leaf carbon content	LCC (%)	Total amount of carbon per unit of dry leaf mass	Gas exchange, water use efficiency
Leaf nitrogen content	LNC (%)	Total amount of nitrogen per unit of dry leaf mass	Light capture, photosynthetic rate
Leaf phosphorus content	LPC (%)	Total amount of phosphorus per unit of dry leaf mass	Photosynthesis, nutritional quality
Leaf C/N	LCC/LNC	Ratio between leaf carbon and nitrogen	Life history, availability of carbon and nitrogen
Leaf N/P	LNC/LPC	Ratio between leaf nitrogen and phosphorus	Availability of nitrogen and phosphorus, life history

*Wright et al., 2004; Pérez-Harguindeguy et al., 2013; Díaz et al., 2016.

Table 3 (a). Residual Maximum Likelihood (REML) for each of the ecosystem properties studied in temperate forest in the central Himalayan region of Uttrakhand, India. For trait abbreviations, see Table 2

Linear mixed model

Response variable	Fixed effect (Plant trait)	Estimate	Variation explained (in %)	Random effect (Soil property, species and plot)	Std. dev	% of variation explained
Above-ground biomass	SLA	79.75 (57.47)	0.01	Available P	7.09	16.25
	LWC	52.99 (211.44)	0.12	Total N	1.52	7.50
	LCC	-1632.18 (2743.65)	20.37	Total C	3.67	4.36
	LNC	2113.39 (3119.54)	26.34	Plot	1.74	9.79
	LPC	-2094.89 (3125.86)	26.44	pH	9.97	32.15
	LNC/LPC	-2094.39 (3140.29)	26.69	Species	9.62	29.95
Soil organic carbon	SLA	0.04 (0.11)	0.00	Available P	0.00	0
	LWC	0.11 (0.18)	0.01	Total N	0.00	0
	LCC	-0.25 (0.26)	0.02	Total C	2.70	36.44
	LNC	6.86 (10.42)	33.21	Plot	8.30	34.21
	LPC	-6.76 (10.43)	33.27	pH	6.37	20.18
	LNC/LPC	-6.70 (10.46)	33.47	Species	1.35	9.14
Soil microbial biomass carbon	SLA	262.18 (234.78)	0.00	Available P	55	1.02
	LWC	43.11 (406.18)	0.01	Total N	249.3	20.92
	LCC	-446.36 (571.71)	0.02	Total C	302.77	30.86
	LNC	-3264.85 (22531.64)	33.20	Plot	364.96	44.84
	LPC	3112.5 (22560.71)	33.29	pH	0	0.00
	LNC/LPC	3372.78 (22615.99)	33.45	Species	83.69	2.36
Soil microbial biomass nitrogen	SLA	-2.21 (7.42)	0.00	Available P	7.15	19.17
	LWC	-11.61 (13.45)	0.01	Total N	1.75	11.46
	LCC	28.67 (19.1)	0.02	Total C	7.64	21.86
	LNC	-67.81 (726.21)	33.22	Plot	2.86	32.98
	LPC	51.59 (726.76)	33.27	pH	6.23	14.53
	LNC/LPC	55.5 (728.61)	33.44	Species	0	0.00
Soil microbial biomass phosphorus	SLA	-5.04 (1.98)	0.00	Available P	3.06	49.37
	LWC	2.58 (4.08)	0.01	Total N	1.34	9.47
	LCC	1.7 (5.48)	0.02	Total C	0	0.00
	LNC	-135.79 (222.15)	33.21	Plot	0	0.00
	LPC	136.08 (222.38)	33.28	pH	2.07	22.68
	LNC/LPC	136.05 (222.97)	33.46	Species	1.87	18.47
Soil respiration	SLA	-0.45 (0.93)	0.00	Available P	0	0.00
	LWC	-0.2 (1.69)	0.01	Total N	0	0.00
	LCC	0.28 (2.35)	0.02	Total C	1.65	69.72
	LNC	-39.27 (95.78)	33.19	Plot	1.09	30.28
	LPC	40.86 (95.92)	33.29	pH	0	0.00
	LNC/LPC	39.08 (96.17)	33.47	Species	0	0.00

Values within brackets are the standard error.

Table 3 (b). Model statistics for the null and full models

Model Parameter					
Null Model					
Response variables	df	AIC	log Lik	Deviance	Chi-square (P-value)
Above-ground biomass	8	741.20	-362.60	725.20	
Soil organic carbon	8	291.57	-137.78	275.57	
Soil microbial biomass carbon	8	3079.9	-1532.0	3063.9	
Soil microbial biomass nitrogen	8	1848.1	-916.04	1832.1	
Soil microbial biomass phosphorus	8	1424.8	-704.40	1408.8	
Soil respiration	8	1141.8	-562.91	1125.8	
Full Model					
Above-ground biomass	15	752.43	-361.22	722.43	2.76 (0.90)
Soil organic carbon	17	295.62	-130.81	261.62	13.94 (0.12)
Soil microbial biomass carbon	17	3065.4	-1515.7	3031.4	32.50 (0.00^{***})
Soil microbial biomass nitrogen	17	1827.2	-896.61	1793.2	38.86 (1.21^{***})
Soil microbial biomass phosphorus	17	1391.1	-678.57	1357.1	51.66 (5.23^{***})
Soil respiration	17	1095.6	-530.78	1061.6	64.25 (2.01^{***})

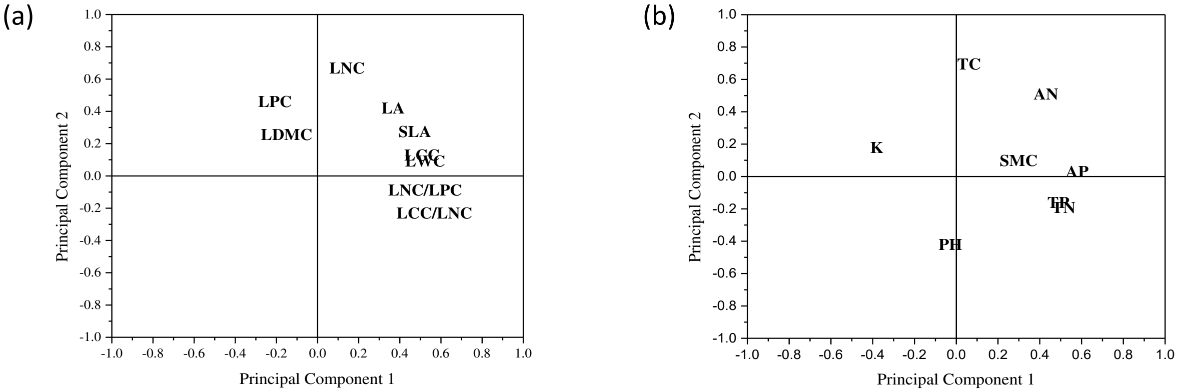

Figure 1. Principal component analysis plot of (a) nine plant traits and (b) eight soil properties studied in temperate forest in the central Himalayan region of Uttrakhand, India.

Plant traits: leaf area (LA), cm^2; specific leaf area (SLA), cm^2 g^{-1}; leaf dry matter content (LDMC), %; leaf water content (LWC), %; leaf carbon content (LCC), %; leaf nitrogen content (LNC), %; leaf phosphorus content (LPC), %; LCC/LNC ratio; LNC/LPC ratio.

Soil properties: pH; soil moisture content (SMC), %; total carbon (TC), %; available nitrogen (AN), µg/g; total nitrogen (TN), %; available phosphorus (AP), µg/g; total phosphorus (TP), %; potassium (K), µg/g.

Supplementary materials: Relative contribution of plant traits and soil properties to the functioning of a temperate forest ecosystem in the Indian Himalayas

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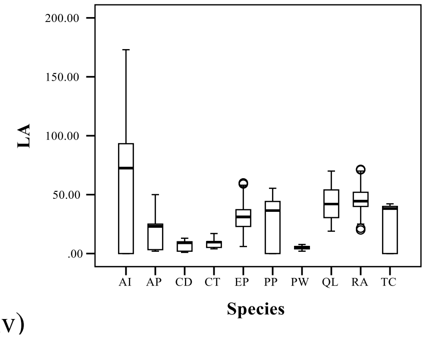
Table S1: Volume equations used for aboveground biomass calculation for different tree species in the temperate forest, central Himalayan region of Uttrakhand, India

S. no	Dominant tree species	Volume equation
	Deciduous	$\sqrt{V} = 0.220191 + 3.923711\ D - 1.117475\ \sqrt{D}$ (L)
1	*Aesculus indica*, Colebr	
2	*Pyrus pashia*, Buch.Hemex D.Don	$V = 0.01284 + 0.2138\ D^2\ H$ (G)
3	*Toona ciliata*, R.	$V = 0.01284 + 0.2138\ D^2\ H$ (G)
	Evergreen	
4	*Abies pindrow*, Spach Ham	$V = 0.17507 + 0.22606\ D^2\ H$ (G))
5	*Cedrus deodara*, Loud	$V = -0.0789 + 0.2836\ D^2\ H$ (G)
6	*Cupressus torulosa*, D. Don	$V = 0.01284 + 0.2138\ D^2\ H$ (G)
7	*Euonymus pendulous*, Wall	$V = 0.01284 + 0.2138\ D^2\ H$ (G)
8	*Quercus leucotrichophora*, A.Comm	$V = 0.014796 + 0.319061\ D^2\ H$ (G)
9	*Rhododendron arboreum*, Smith	$V = 0.06007 - 0.21874V\ D + 3.63428\ D^2$ (L)
10	*Pinus wallichiana*, Jackson	$V = 0.223139 + 2.35096\ D + 11.90669\ D^2$ (L)

Note: L = local volume equations (they have limited application for a forest or small locality and are based only on diameter at breast height); G= general volume equations (they are more broadly based and cover the full distribution of the species); $\sqrt{V}$ or V = volume of tree (Mg ha−1); $\sqrt{D}$ or D= diameter of tree at breast height; H= height of tree. References: FSI (1996)

(i)



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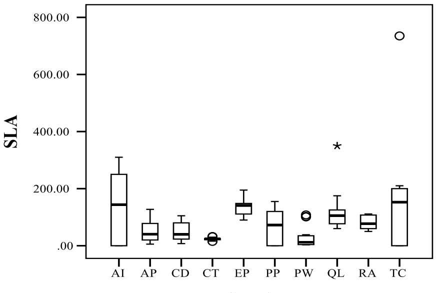

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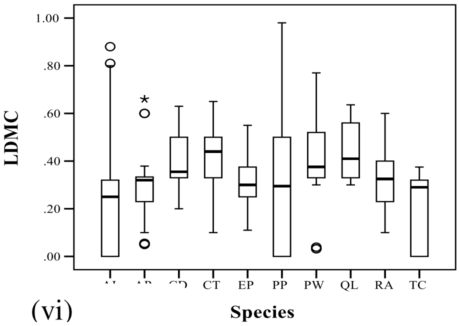

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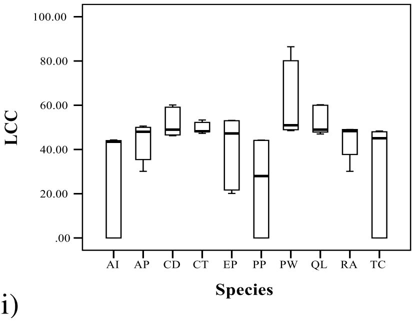

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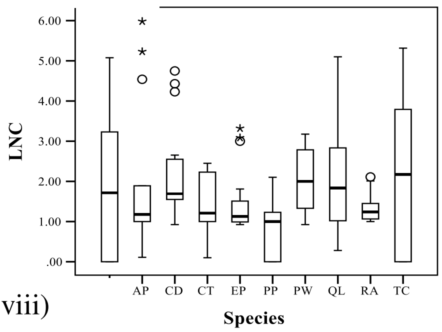

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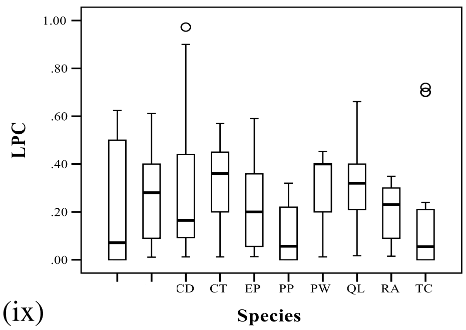

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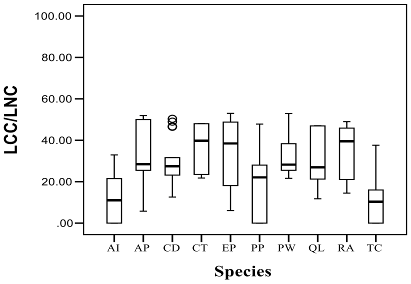

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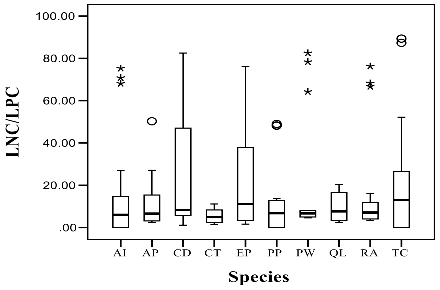

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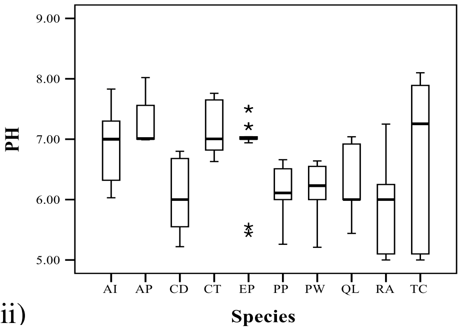

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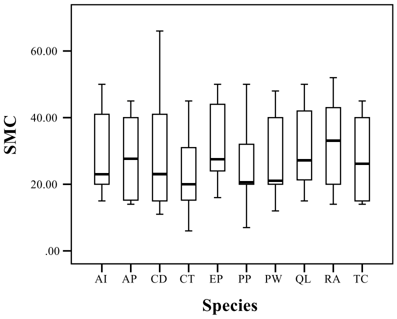

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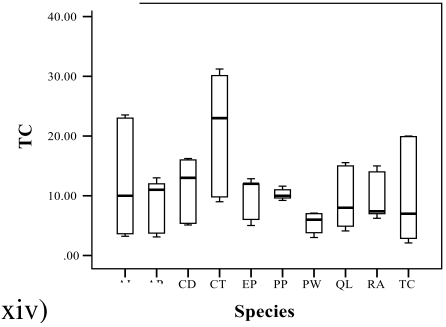

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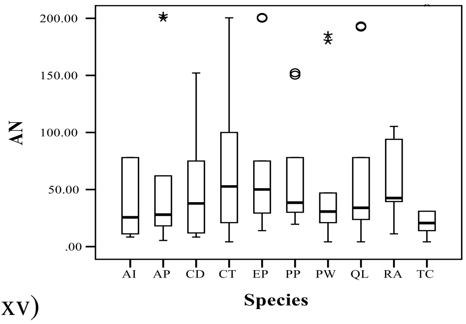

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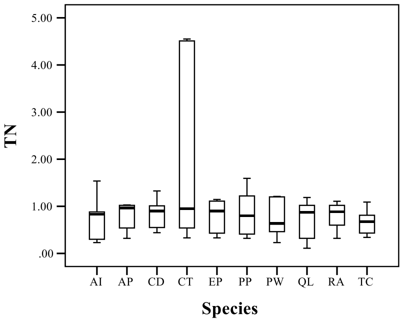

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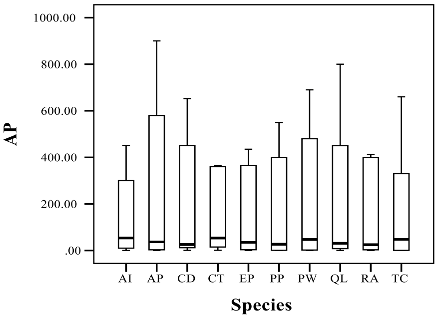

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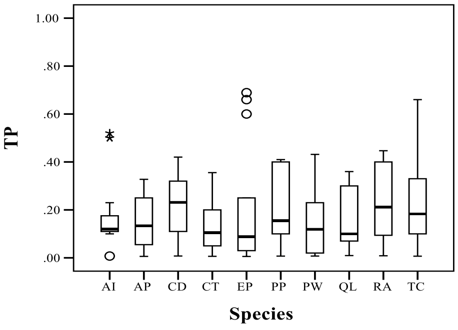

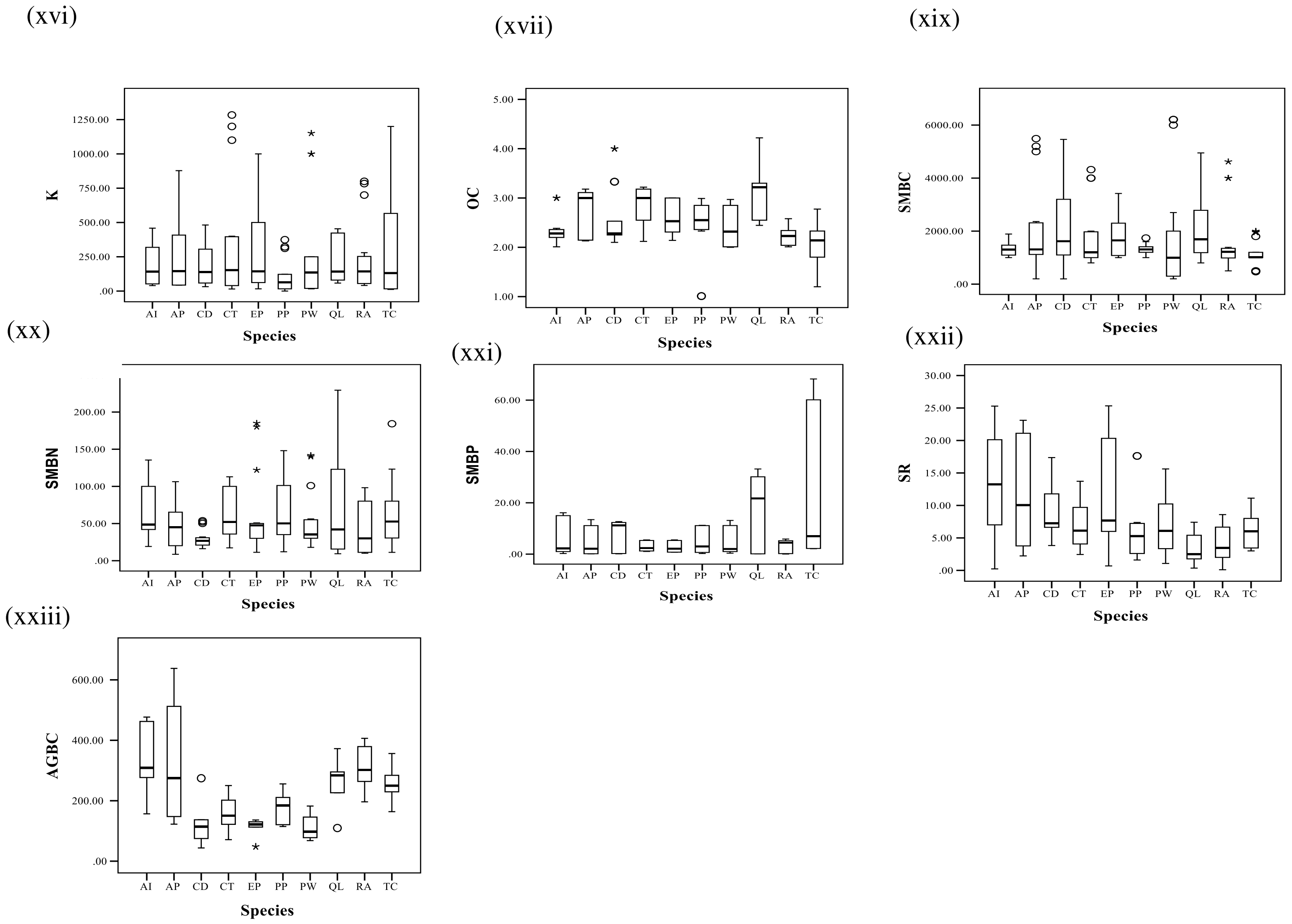
(xvi) (xvii) (xix) (xx) (xxi) (xxii) (xxiii)

Figure S1. Distribution of values of plant traits, soil properties and ecosystem services observed for temperate forest tree species in the temperate forest, central Himalayan region of Uttrakhand, India: *Aesculus indica* (AI), *Abies pindrow* (AP), *Cedrus deodara* (CD), *Cupressus torulosa* (CT), *Euonymys pendulous* (EP), *Purys pashia* (PP), *Pinus wallichiana* (PW), *Quercus leucotrichophora* (QL), *Rhododendron arboretum* (RA), and *Toona ciliata* (TC).

Plant traits: (i) Leaf area (LA), cm^2; (ii) specific leaf area (SLA), cm^2 g^{-1}; (iii) leaf dry matter content (LDMC), %; (iv) leaf water content (LWC), %; (v) leaf carbon content (LCC), %; (vi) leaf nitrogen content (LNC), %; (vii) leaf phosphorus content (LPC), %; (viii) LCC/LNC ratio; (xi) LNC/LPC ratio.

Soil properties: (x) pH; (xi) soil moisture content (SMC), %; (xii) total carbon (TC), %; (xiii) available nitrogen (AN), µg/g; (xiv) total nitrogen (TN), %; (xv)available phosphorus (AP), µg/g; (xvi) total phosphorus (TP), %; (xvii) potassium content (K), µg/g.

Ecosystem services: (xviii) soil organic carbon (OC), %; (xix) soil microbial biomass carbon (SMBC),µg/g; (xx) soil microbial nitrogen (SMBN), µg/g; (xxi)soil microbial phosphorus (SMBP), µg/g; (xxii) soil CO_2 respiration (SR), µmol $mol^{-1}s^{-1}$ and (xxiii) aboveground biomass carbon (AGBC), Mg C ha^{-1}. The centre line in each plot indicates the median and the upper and lower box height indicates the inter-quartile range.