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Interactive climate-soil forces shape the spatial distribution of foliar N:P stoichiometry in *Vaccinium uliginosum* planted in agroforests of Northeast China

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In regions with a ban on forest logging, fruit-bearing shrubs are favored as an alternative source of ecological products over the harvesting of timber. The introduction of cultured shrubs from their habitat to newly developed lands has to be decided according to nutrient availability. Foliar nitrogen (N) and phosphorus (P) stoichiometry is an easily measured and reliable parameter to quickly indicate possible limits in imbalanced N-P availability. When attempting to create a spatial distribution map of the foliar N:P ratio in an objective shrub species, it is helpful to first explore its potential acclimation to the N:P imbalance caused by the joint forces of soil property and regional climate. This study evaluated the cultivated populations of *Vaccinium uliginosum* in northeastern China's agroforests, using *Vaccinium uliginosum* as a model shrub species. A total of 51 populations were selected from 51 managed stands, of which 34 were in forests and 17 on farmlands. Foliar N and P concentrations, soil physical and chemical properties, and topography were investigated in 2018, and regional climatic factors were assessed by averaging previous 5-year records (2013–2018). *V. uliginosum* was determined to have a foliar N:P ratio lower than 4.4, which can be characterized as a limit of N relative to that of P. On forested lands, soil pH negatively impacted regressed foliar N:P, which was also part of the contributions of soil total P content and average temperature to foliar N concentration. On farmlands, low soil pH also resulted in a reduced foliar N:P ratio with joint contributions of ammonium N, nitrate N, and available P contents in soils and air humidity. Spatial interpolation indicated that western forests could benefit from introduced *V. uliginosum* with a higher foliar N concentration, while the introduction to eastern farmlands can lead to a higher foliar N:P ratio up to 14.6. Our study demonstrates recommended locations with expected soil and meteorological conditions by mapping spatial distributions, which can be referred to by other species and regions.

KEYWORDS

nutrient utilization, spatial distribution, non-wood forest product, bog bilberry, stoichiometry, *Vaccinium uliginosum*

Introduction

Climate change may have decoupled the biogeochemical cycles of nitrogen (N) and phosphorus (P), which shift stoichiometry and its ecosystem services (Yu et al., 2018). Foliar N:P stoichiometry refers to a "focus on the balance and a coupling/scaling relationship between main elements and compounds in ecosystems" (Tao et al., 2021). In the terrestrial ecosystem, N:P stoichiometry reveals the state of N-P balance from being subjected to dual N and P availabilities (Penuelas et al., 2013; Song et al., 2014; Ding et al., 2021). Foliar N:P stoichiometry can be gauged by their ratio, which was suggested as a diagnosis of ecosystem limits by N or P availabilities (Zhang et al., 2015; Wei H. et al., 2019). For example, a review of 40 fertilization studies revealed that the foliar N:P ratio changed across ranges of <14, >16, or 14–16, indicating limits by N, P, or a co-limit of N and P, respectively (Koerselman and Meuleman, 1996). Another instance diagnosed ecosystem limits using N:P ratios in a lower range of 10–20 (Goransson et al., 2014). Hence, foliar N:P ratios were screened to detect their critical value as a reliable measure to quickly determine a community's nutritional limits.

Temperate forests in the Northern Hemisphere are probably subjected to an N limit due to a shorter chronicle of soils and a lower cycle rate than other ecosystems located in warmer climates (Reich and Oleksyn, 2004; Suo et al., 2016; Ding et al., 2021). Temperate old-growth forests may have also been suffering co-limits of low N and P availabilities (Yang et al., 2019). When P is supplied sufficiently, the relative N deficit occurs for all botanic life forms in temperate forests (Wang et al., 2018; Yang et al., 2019; Zhang et al., 2020). Given that the foliar N:P ratio of a specific plant species is shaped by changes in its acclimation to a synthesis of dual climate and soil forces, its spatial distribution can be modeled by geographical patterns of driving factors even at the global scale (Gao et al., 2022; Vallicrosa et al., 2022). The variation of N:P ratios in the leaves of forest plants was mapped by modeling distributions of joint soil and climatic factors at the continental scale in the temperate climatic zone (Kang et al., 2011; He et al., 2014; Jiang et al., 2021). Mapping the regional foliar N:P ratios for plants in temperate forests has an academic meaning not only in ecological studies but also in projects forecasting potential locations with good acclimation by objective plants under the combined forces of soil disturbance and climate change.

Shrubs in temperate forests are a part of the undergrowth that suffers from the N limit that is predicted by low foliar N:P ratios (He et al., 2014; Wei H. et al., 2019; Jiang et al., 2021). Shrubs with significant commercial value can be developed and cultured from their habitats in a broad geographical range of agroforest ecosystems (De Clerck and Negreros-Castillo, 2000; Andreu et al., 2013). Commercial shrubs account for an increasing proportion of natural resources in agroforests that provide non-timber forest products (NTFPs) (Guo et al., 2019; Wei H. X. et al., 2019). In northeast China, shrub-product sales are responsible for local household income instead of timber production. Local logging was banned by the policy of natural forest protection (Geng et al., 2021). The understory space for cultivating shrubs as NTFP resources exceeds the natural capacity as demand increases (Marcot et al., 1997; Jiang et al., 2014; Li et al., 2019). Agroforests can provide alternative spaces for cultivating shrubs to harvest their fruits as NTFPs (He et al., 2019; Devagiri et al., 2020). Low nutrition availability and an imbalanced N:P stoichiometry may limit the establishment of introduced shrubs in agroforests. Mapping the spatial distribution of foliar N:P ratios can be used to quickly target locations with proper conditions and nutrition availability.

Vaccinium uliginosum L. (bog bilberry) is a perennial deciduous shrub inhabiting peatlands and moorlands in temperate and boreal tundras (Jiang et al., 2019). Its populations can also be distributed in the understory layer of temperate forests dominated by birch (*Betula nana*) (Ejankowski, 2010) and black spruce (*Picea mariana*) (Rohrs-Richey and Mulder, 2007; Duan et al., 2022). Its fruits have a significant commercial value for extracts containing abundant antioxidants (Kim et al., 2015; Su et al., 2016). Foliar N:P stoichiometry matters for fruits of *V. uliginosum*, which were reported to contain N in the range of 16–84% and P in the range of 20–32% (Rupasova et al., 2007). *V. uliginosum* was developed from natural habitats and introduced to agroforests as a non-timber forest product (NTFP) species in northeast China (Wang et al., 2019). The exploitation, however, has expanded the natural supply to an extra level that stresses the reserves of natural resources. The enlargement of land areas for resources' culture may not always meet the demand for fruits with the desired efficiency if a risk exists due to the low N availability (Duan et al., 2022). Natural *V. uliginosum* populations frequently suffer from low N availability in frozen soils. The inter-species competition and microbial community together generate restrictions in N availability and an imbalanced N-P stoichiometry (Rohrs-Richey and Mulder, 2007; Duan et al., 2022). It is necessary to map the distribution of *V. uliginosum* populations by parameters estimated from combined factors of soil property and regional climate.

This study investigated the cultured resources of *V. uliginosum* populations to detect foliar N and P stoichiometry and soil properties in agroforests. Regional climatic factors were recorded for each location, and all were used to regress the foliar N:P stoichiometry against soil and climatic factors. Model coefficients were used for mapping the potential distribution in agroforests in Jilin and Heilongjiang provinces, where locations will be indicated if desired conditions are met with high N and P availability and balanced N:P stoichiometry. Our goal was to map the theoretical spatial distribution of foliar N:P stoichiometry for *V. uliginosum* in a temperate agroforest ecosystem. The science underpinning these findings will provide references for future studies on mapping natural resources using soil and climate records.

Materials and methods

Study area

This study was conducted in the eastern agroforest regions of Jilin and Heilongjiang provinces (41°38′–48°45′ N, 126°06′–134°15′ E), northeast China. A total of 51 *V. uliginosum* populations were selected as the objectives for investigation, of which 17 were located on farmlands and 34 on forested lands. These populations were originally found on forested lands and established from natural sources at the understory layer. Populations on farmlands were introduced from forests and managed according to the same protocol as those on forested lands. Both types of populations started to be managed in the same period around the year 2013. The county-level areas where *V. uliginosum* populations were located are shown in Figure 1.

Field sampling and chemical analysis

In 2018, when most cultivars were bearing fruits, leaves from *V. uliginosum* individuals in populations with the same characteristics were sampled. Three requirements were needed for investigation and sampling. Firstly, populations for investigation needed to be located in stands with a slope no higher than 9° to avoid the condition of co-limits due to low N and P availability (Wei H. et al., 2019). Selected populations had to be those managed by thinning to leave 40–50 sprouts per square meter. This requirement will result in an even density among populations that can mostly reduce the variation of leaf parameters across sampling stands (Guo et al., 2017; Wei et al., 2021). Thirdly, three plots were randomly set in one stand, and each plot was conducted in a 100 m^2 (10 × 10 m) size. *V. uliginosum* crowds were planted along elevation lines with a width of about 10 m. Each plot was further divided into nine sections, and one crowd was chosen as a sampling unit per section. Ten leaves were randomly collected from the sunlight-exposed sprouts in one crowd at a height of ∼70 cm. Three cores of soil were collected at a depth of 10–15 cm below ground from three sections across a plot. Collected soils were mixed per plot, and three mixed soil samples were assigned as three replicates per stand. Samples of leaves and soils were bulked as sub-samples separately for a plot, and their further results per sub-sample will be averaged for a stand.

Sampled leaves were transported to the laboratory on ice for no longer than 2 days. Leaves were rinsed in distilled water and dried in an oven at 70°C for 72 h. The soils were air-dried to a consistent weight. The leaves were ground to pass a 1 mm filter, soaked in sulfuric acid, then selenium and lithium sulfate solutions catalyzed by hydrogen peroxide were poured onto the leaves (Li T. et al., 2022). Total N concentration (both leaves and soils) was determined by an elemental analyzer (Vario MACRO cube, Elementar-Branch, Shanghai, China). Total P concentration (leaves and soils) was determined by inductively coupled plasma spectroscopy (Model-Thermo Icap-6000 Series, ThermoFisher Scientific Inc., Shanghai, China). Soil organic matter content was determined by the Degtjareff method (Walkley and Black, 1934). Ammonium N and nitrate N concentrations were determined using a flow injection system (Lachat Instrument, Hach Inc., Loveland, CO, USA) (Duan et al., 2022). Soil pH value was measured by the 3020 pH detector (Jenway Inc., Dunmow, United Kingdom). Soil electric conductance (EC) was measured by a Leici DDSJ-308A analyzer (Yidian Sci. Inc., Shanghai, China).

Meteorological data and spatial distribution

Regional climatic conditions were obtained from records at meteorological stations that were close to stands in the national network of the China Meteorological Data Service Center (2022). Climatic conditions were characterized by meteorological factors of rainfall, average temperature,

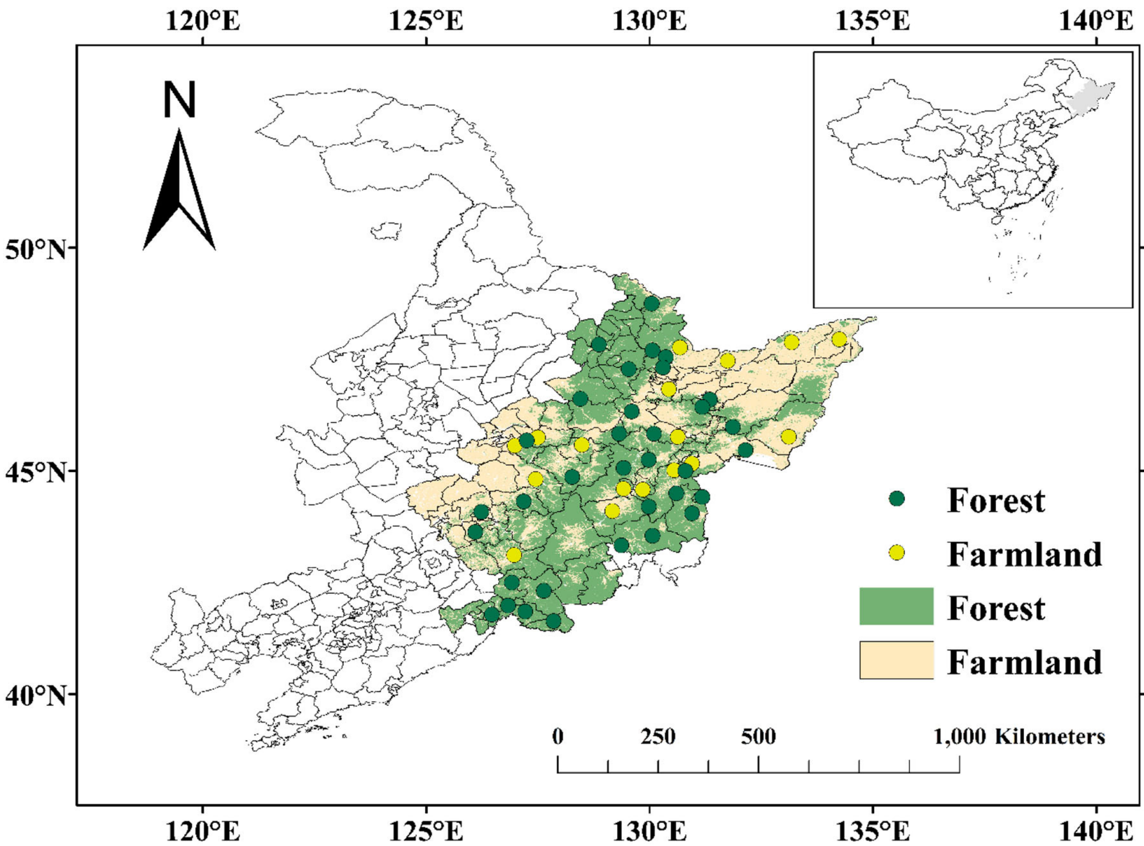

FIGURE 1
Geographical distributions of sampling plots on forested lands and farmlands for *Vaccinium uliginosum* populations in the eastern agroforests of Northeast China.

maximum temperature, minimum temperature, relative humidity, and wind velocity. These weather conditioning factors were found to have close associations with foliar stoichiometry (Gao et al., 2022; Vallicrosa et al., 2022). Meteorological data for each stand were averaged from yearly records from 2013 to 2018. Spatial variation was mapped using ArcGIS (9.3 version, Esri China, Beijing, China) for data about foliar N:P stoichiometry, soil property, and regional climate. A basic map for forest and farmland distributions was employed from 30 m-resolution Landsat 8 OLI satellite imageries. The normalized difference vegetation index (NDVI) was assessed by the model (Huang et al., 2022):

$$\mathrm{NDVI} = \frac{\mathrm{Band8} - \mathrm{Band4}}{\mathrm{Band8} + \mathrm{Band4}} \tag{1}$$

In (1), *Band*8 is the band with near-infrared reflectance, and *Band*4 is the band of reflectance of red light. The digital elevation model (DEM) was extracted from NASA EarthData maps as an Aster GDEM 30 m product (NASA EarthData, 2021). The regional distribution pattern of foliar N:P stoichiometry was mapped by interpolating the data pattern in scattered plots.

Data analysis and statistics

Regional distributions of scattered data in stands were mapped and visualized in subjective areas. Places can distinguish regions with high values with darker colors. All data passed the normal distribution test and were also tested to have a homogeneous variance. Data were pooled for each parameter and split by collection into forested lands and farmlands separately. Independent variables were analyzed for their relationships by Pearson correlations. Multivariate linear regression (MLR) model was conducted to detect the associations of foliar N:P stoichiometry with driving factors of regional climate and soil property. Coefficients for regressed parameters were plotted to reveal the doses of contributions of every independent variable. The regressed foliar N:P

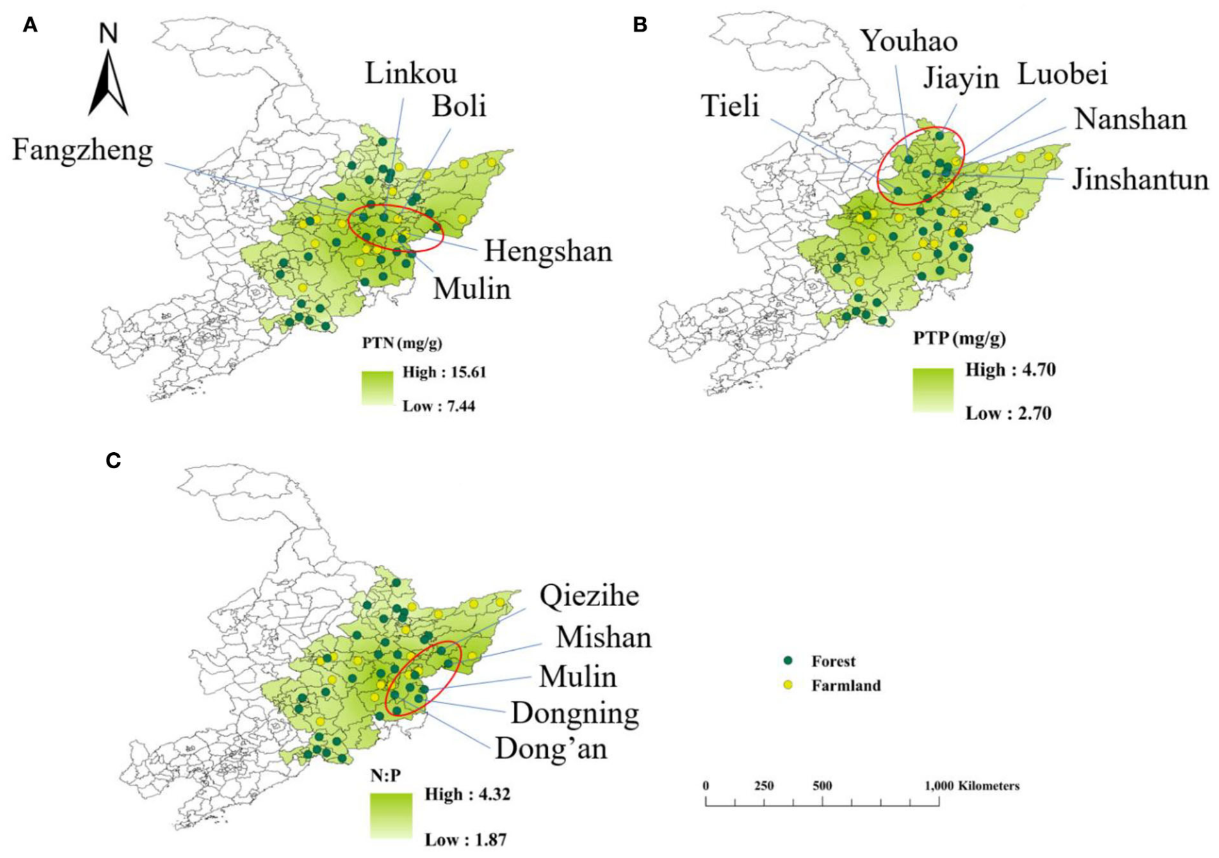

FIGURE 2
Current distributions of total nitrogen (N) **(A)** and phosphorus (N) concentrations (PTN and PTP, respectively) in *Vaccinium uliginosum* plants **(B)** and foliar N:P ratio (N:P) **(C)**.

stoichiometry distribution pattern was mapped by fusing multiple interpolated layers embedded by their coefficients (Li Y. et al., 2022).

Results

Current distribution of foliar N:P stoichiometry

Foliar N concentration was higher on forested lands in the central region of the study area, such as plots in Fangzheng, Linkou, and Mulin (Figure 2A). Foliar N concentration was also higher on Hengshan and Mulin farmlands than on farmlands in other places. Foliar P concentration was higher in the northern part of the study area than in the south. Northern forested lands included regions of Tieli, Youhao, Jiayin, Nanshan, and Jinshantun, and northern farmlands referred to a region called Luobei (Figure 2B). The southern part of the study area was accompanied by populations that generally showed lower foliar N and P concentrations. The foliar N:P ratio was higher in the study area's eastern forests, including regions of Qiezihe, Mishan, Mulin, Dongning, and Dong'an (Figure 2C). The foliar N:P ratio was also higher in regions of farmlands in Hengshan and Mulin than in farmlands in other regions.

Current distributions of geographical characteristics and soil properties

Most regions in the study area had DEMs in a range of 200–255 m, leaving some scattered farmlands with low DEMs in the northern region (Figure 3A). These places included Yanshou, Dongfeng, Tongjiang, Fuyuan, and Sifangtai. As stated before, NDVI was also high in most regions of the area, leaving low levels in scattered places on farmlands in Wuchang, Dongfeng, and Tongjiang and on forested lands in Hengshan (Figure 3B).

Soil ammonium N (SAN) concentration showed alternately high and low levels in the northwestern regions of the study

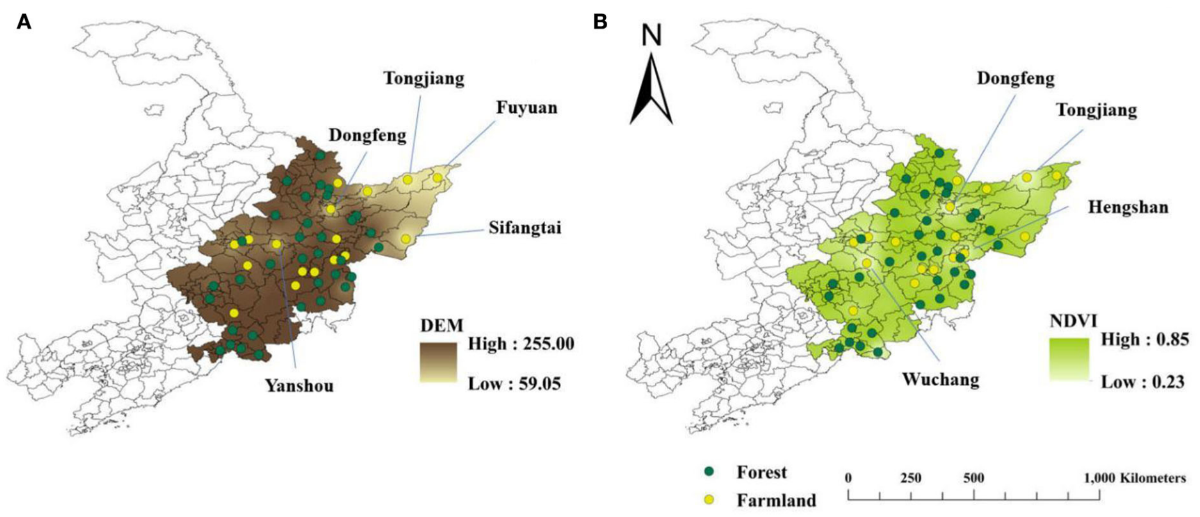

FIGURE 3
Current distributions of digital elevation model (DEM) **(A)** and normalized difference vegetation index (NDVI) **(B)** in *Vaccinium uliginosum* populations distributed on forested lands and farmlands of Northeast China.

area (Figure 4A). High SAN was found on forested land in Youhao, but low SAN was found in the agroforests of Binxian, Acheng, and Luobei counties. Soil nitrate N (SNN) showed a generally decreasing gradient from the north to the south, where high SNN was found on forested lands in Jinshantun and low SNN on forested lands in the western regions of Fusong, Jingyu, Hunjiang, Jiangyuan, Linjiang, and Changbai counties (Figure 4B). Soil total N (STN) concentration was also high on the forested land of Jinshantun, Wangqing, and the western counties of Changbai Mountain (Figure 4C).

Soil available P (SAP) concentration was higher in the central regions of forested lands, such as in Fangzheng and Hailin counties and the agroforests of Boli (Figure 4D). SAP was also higher in the southern forested lands of Hunjiang, Jiangyuan, and Linjiang than in the north. Soil total P (STP) concentration was higher in the northern part and lower in the south (Figure 4E). The regions of the north with high STP included the forested lands of Jiayin, Youhao, Jinshantun, and Luobei, and low STP was found in forests in the counties of the western Changbai Mountain.

Soil pH value (SpH) was higher in the northern and southern parts of the study area and lower in the center (Figure 4F). High SpH was mainly found on Luobei, Dongfeng, and Suibin's farmlands and low SpH on the forested lands of Wangqing. Soil bulk density (SBD) was higher on the eastern farmlands of Hengshan and Lishu and the eastern forested lands of Suifenhe and Dongning (Figure 4G). SBD was also low in forests in the central part, including regions of Jinshantun, Fangzheng, and Hailin. Soil organic matter (SOM) was generally low (<80 g kg^{-1}) in most regions of the study area, but high SOM was mostly found on forested lands in Jinshantun (Figure 4H). As previously stated, soil electric conductance (SEC) was also high on the forested lands in Jinshantun but low on the farmlands of Luobei and Suibin (Figure 4I).

Current distribution of regional climate

Generally, the southern part of the study area had lower temperature records than the north, but spatial distributions were different for different temperature parameters (Figures 5A–C). The average temperature was higher in the forested lands of Changyi, Yongji, and Suifenhe and the farmlands of Ning'an, but it was lower in the agroforests of Jiayin and Luobei (Figure 5A). The maximum temperature was lower than 35°C in most regions of the study area except for higher records on Ning'an and Suifenhe farmlands and on western Changbai Mountain forested lands (Figure 5B). The minimum temperature was found to be higher in the south than in the north due to higher values in the southern regions of farmlands (Hailin and Wangqing) and forests (Changyi and Yongji) (Figure 5C).

Rainfall was generally higher in the north than in the south, especially in the agroforests of Jiayin and Luobei (Figure 5D). In contrast, RH was generally higher in most regions of the study area except in the north and the south around Hunjiang (Figure 5E). Most regions of the study area had a low wind velocity of about 2.0 m s^{-1}, except for the western forests in Changyi and Yongji (Figure 5F).

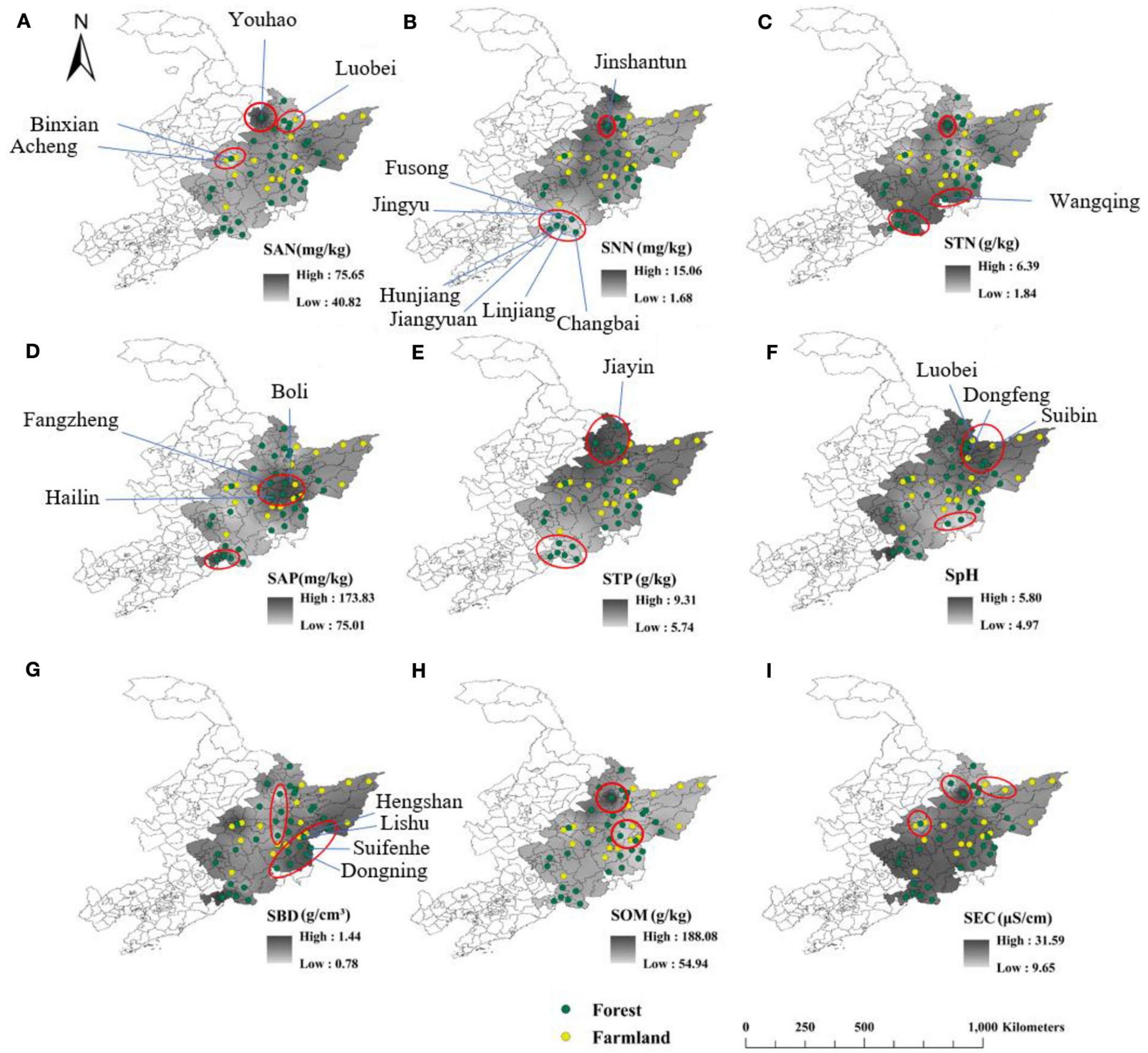

FIGURE 4
Current distributions of soil properties in *Vaccinium uliginosum* populations distributed on forested lands and farmlands of Northeast China. **(A)** SAN, soil ammonium nitrogen content; **(B)** SNN, soil nitrate nitrogen content; **(C)** STN, soil total nitrogen content; **(D)** SAP, soil available phosphorus content; **(E)** STP, soil total phosphorus content; **(F)** SpH, soil pH value; **(G)** SBD, soil bulk density; **(H)** SOM, soil organic matter content; and **(I)** SEC, soil electric conductance.

Correlation analysis

In forests, longitude did not have any correlation with any soil properties except for STP (Figure 6A). Latitude also had a positive correlation with STP and positive correlations with SpH and SNN. Otherwise, latitude is negatively correlated with SBD, SEC, and STN. DEM did not correlate with soil properties, but NDVI positively correlated with SNN. The temperature negatively correlated with STP across maximum, average, and minimum records. Average and minimum temperature records had positive correlations with the SEC. Rainfall had a positive correlation with SOM, STP, and SNN and a negative correlation with SBD and SEC (Figure 6A).

Longitude had no relationship with soil properties on farmlands, and latitude had a negative and a positive correlation with SEC and STP, respectively (Figure 6B). In contrast, DEM had a positive and a negative correlation with SEC and STP, respectively. DEM also had a positive correlation with SNN. Average, maximum, and maximum temperatures had negative correlations with STP and positive correlations with the SEC. Rainfall had a positive correlation with SpH and a negative correlation with SEC. In contrast, RH had

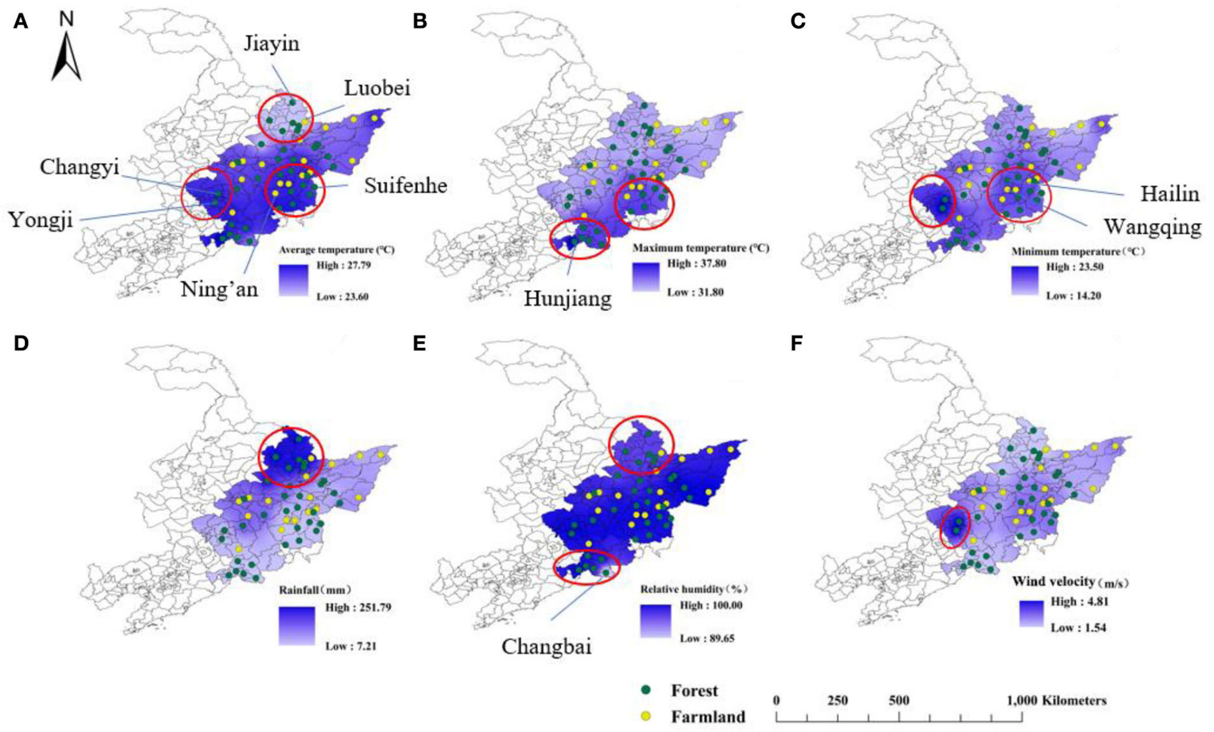

FIGURE 5
Current distributions of meteorological factors in *Vaccinium uliginosum* populations distributed on forested lands and farmlands of Northeast China. **(A)** Average temperature; **(B)** maximum temperature; **(C)** minimum temperature; **(D)** rainfall; **(E)** relative air humidity; and **(F)** wind velocity.

a negative and a positive correlation with SpH and SEC, respectively (Figure 6B).

Multivariate linear regression

In forests, SpH, STP, SAP, and AveT were indicated to have significant coefficients in the MLR model against PTN (Figure 7A). SpH had a negative coefficient with a parameter estimate as low as −5.3, and STP, SAP, and AveT had positive coefficients. On farmland, PTN was regressed against SAN, rainfall, RH, and wind velocity with positive coefficients, while the intercept of the MLR model had a negative coefficient as low as −117 (Figure 7B).

Forest PTP was regressed against SOM, AveT, and rainfall, which all had positive coefficients, and AveT had the highest parameter estimate of ∼0.3 (Figure 7C). On farmlands, only SNN was indicated to contribute to the regressed PTP with a negative coefficient (parameter estimate of −0.14), while the intercept had an extremely high parameter estimate of 4.86 (Figure 7D).

Foliar N:P in forests was regressed against SpH, SAP, and DEM, which had low parameter estimates around the value of zero, but the intercept had a parameter estimate as high as 13.86 (Figure 7E). Foliar N:P on farmland was regressed against SpH with a low parameter estimate of −2.23. Parameters of SEC, SAN, SNN, SAP, and RH had parameter estimates around the value of zero (Figure 7F).

Interpolated distribution of foliar N:P stoichiometry

Based on regressions in Figure 7, foliar N:P stoichiometry was interpolated to distribute as patterns in Figure 8. High PTN values were interpolated to be distributed in agroforests (Figure 8A). For example, a high PTN was interpolated to be distributed in the forests of Changyi and Yongji at the edges of adjacent farmlands. High PTN on forested lands was interpolated in forests close to surrounding segmented farmlands. These forests were mainly distributed in Dongning, Suifenhe, Dong'an, and Wangqing counties.

Again, high PTP values were also interpolated in agroforests (Figure 8B). PTP was interpolated to distribute on western forested lands of the study area, plus other western farmlands in Acheng and forests in Binxian. Northern farmlands were also interpolated to have high PTP in Luobei and Dongfeng and forests attached to adjacent farmlands in Hulin and Lingdong. Forest PTP was interpolated to be high on northern forested lands surrounded by farmlands in Tieli, Youhao, Jinshantun, and Jiayin (Figure 8B).

A Forest

	SBD	SpH	SEC	SOM	STN	STP	SAN	SNN	SAP
Lon	0.0619	-0.1014	-0.3001	-0.0963	-0.1342	0.4786	0.2561	0.1623	0.1225
Lat	-0.3443	0.3701	-0.5085	0.2207	-0.3917	0.8706	0.3063	0.4666	-0.0231
DEM	-0.1612	0.0172	0.2494	0.0894	0.0738	-0.2574	-0.0004	0.1224	0.1930
NDVI	-0.1285	-0.1449	0.2000	0.2416	0.0915	0.1901	0.2883	0.3715	0.0092
AveT	0.3605	-0.3229	0.5071	-0.3529	0.1654	-0.7262	-0.1632	-0.2620	0.2986
MaxT	0.2823	-0.2353	0.2580	-0.2363	0.2283	-0.6587	-0.1748	-0.3185	0.1272
MinT	0.1917	-0.0123	0.3799	-0.2036	0.0226	-0.5366	-0.1336	-0.1592	0.3180
Rain	-0.4216	0.3318	-0.4377	0.4171	-0.2512	0.7788	0.1280	0.4439	-0.2940
RH	0.1657	-0.0603	0.2513	-0.1356	0.0403	-0.1463	0.1968	0.0341	0.2321
Wind	0.1321	-0.0526	0.2724	-0.1843	-0.0716	-0.2351	-0.0532	0.0296	0.2347

B Farmland

	SBD	SpH	SEC	SOM	STN	STP	SAN	SNN	SAP
Lon	0.1476	-0.0666	-0.0848	-0.0742	-0.0430	0.4497	0.1317	0.0707	0.1665
Lat	0.1942	0.4112	-0.5977	-0.2319	-0.2818	0.6863	-0.3304	-0.4609	-0.0587
DEM	-0.2503	-0.1591	0.5764	0.0186	0.0549	-0.8487	0.2321	0.6492	0.2171
NDVI	-0.2618	-0.2943	0.0274	0.2932	0.2150	0.3243	0.2776	0.1877	-0.2309
AveT	-0.1182	-0.4859	0.6968	0.0643	0.1860	-0.5399	0.2656	0.4748	0.2021
MaxT	-0.6111	-0.5932	0.7825	0.4982	0.5551	-0.6153	0.6037	0.7112	0.0506
MinT	-0.1687	-0.2942	0.5592	-0.0092	0.0751	-0.6324	0.1948	0.5240	0.3022
Rain	0.1410	0.5465	-0.6241	-0.1139	-0.3134	0.3630	-0.4346	-0.4047	-0.2041
RH	-0.1354	-0.7091	0.6612	0.3114	0.3821	-0.2639	0.5272	0.5278	0.0209
Wind	-0.0638	-0.2388	0.2923	-0.1712	-0.0776	-0.3331	0.2358	0.4003	0.3500

-1.0 -0.5 0 0.5 1.0

FIGURE 6
Heat map of Pearson correlations between soil properties, topography, and meteorological factors in *Vaccinium uliginosum* populations distributed on forested lands **(A)** and farmlands **(B)** of Northeast China. Values framed by bold-line boxes indicate significant relationships. Colors indicated varied correlation coefficients as positive correlations are marked in red color and negative in blue. SBD, soil bulk density; SpH, soil pH value; SEC, soil electrical conductance; SOM, soil organic matter content; STN, soil total N content; STP, soil total P content; SAN, soil ammonium content; SNN, soil nitrate content; SAP, soil available P content; Lon, longitude; Lat, latitude; DEM, digital elevation model; NDVI, normalized difference vegetation index; AveT, average temperature; MaxT, maximum temperature; MinT, minimum temperature; Rain, rainfall; RH, relative air humidity; and wind, wind velocity.

The foliar N:P ratio was interpolated to be high in agroforests in the middle to eastern regions of the study area (Figure 8C). The foliar N:P ratio was interpolated on the farmlands of Yanshou, Ning'an, Yangming, Sifangtai, Hengshan, and Muling. That was interpolated on the forested lands of Fangzheng, Yilan, and Mishan.

Discussion

N or P limits diagnosed by foliar N:P stoichiometry

Koerselman and Meuleman (1996) reported a critical N:P ratio of 14–16, and Goransson et al. (2014) reported another one of 10–20. Our foliar N:P ratio of *V. uliginosum* was lower than 4.4, which was also lower than that in previous studies (Koerselman and Meuleman, 1996; Goransson et al., 2014). Our N:P ratio was also lower than that in other shrubs in temperate agroforests of northeast China (>6.0) (Wei H. et al., 2019; Yang et al., 2019), grasslands across mainland China (>20.0) (Song et al., 2014), and pine forests in warm temperate climates (>8.0) (Wang et al., 2018). These differences suggest that *V. uliginosum* suffered a relatively higher N limit in the agroforests of northeast China. As suggested by Duan et al. (2022), *V. uliginosum* easily suffered an N deficit due to strong inter-species competition in soils with a microbial community that tends to control N mineralization. *V. uliginosum* populations showed low foliar N:P ratios in most regions of northeast China, except for a small area in eastern agroforests. *V. uliginosum* populations tested in our study managed to raise cultivars to provide fruits to meet the commercial demand. Fertilization is a practical operation in the culture of fruiting *V. uliginosum* populations, but additional practice of competitor removal is needed to further improve N availability.

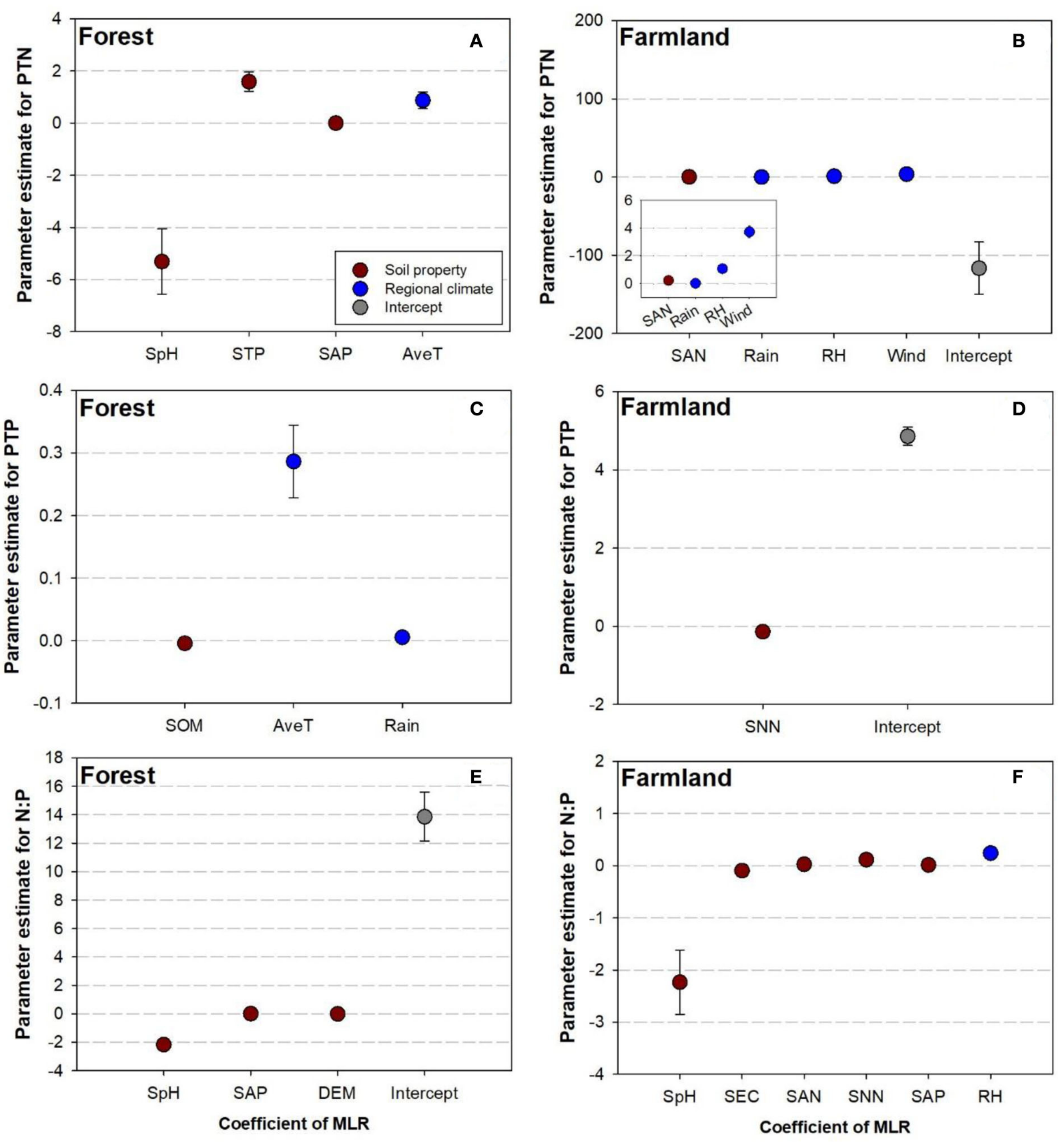

FIGURE 7
Coefficients of multivariate linear regression models in *Vaccinium uliginosum* populations distributed on forested lands **(A,C,E)** and farmlands **(B,D,F)** of Northeast China. SpH, soil pH value; SEC, soil electrical conductance; SOM, soil organic matter content; STP, soil total P content; SAN, soil ammonium content; SNN, soil nitrate content; SAP, soil available P content; DEM, digital elevation model; AveT, average temperature; Rain, rainfall; RH, relative air humidity; and wind, wind velocity.

Soil and meteorological factors determining foliar N:P stoichiometry

Soil properties are the strong drivers that shape spatial distributions of N and P availabilities and may generate a significant limit for foliar N:P stoichiometry (Wei et al., 2017; Ding et al., 2021; He et al., 2021). Soil pH value and available P content were two edaphic parameters that showed significant coefficients for regressing foliar N:P ratios on forested lands and farmlands. Forest soil pH showed a negative contribution to foliar N:P, while available soil P presented a neutral contribution. Soil pH also revealed a negative contribution to foliar N

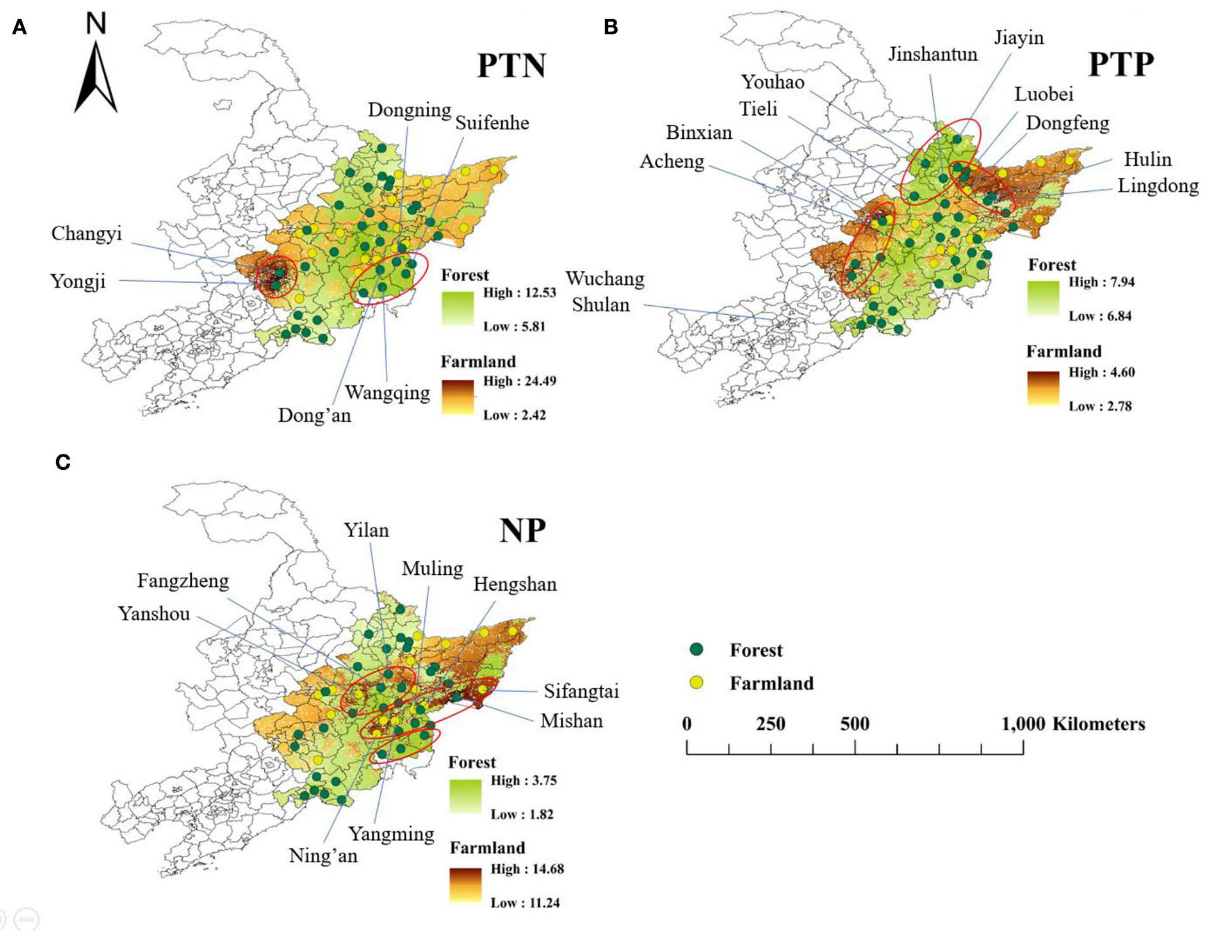

FIGURE 8
Predicted distributions of foliar N concentration (PTN) **(A)**, P concentration (PTP) **(B)**, and foliar N:P ratio (NP) **(C)** in *Vaccinium uliginosum* populations distributed on forested lands and farmlands of Northeast China.

concentration on forested lands, which led to reduced foliar N:P ratios. Low soil pH was found to induce N immobilization by retaining N in microbial communities of soils dominated by competitors, such as *Ledum palustre*, which benefits N uptake by *V. uliginosum* (Duan et al., 2022). The diversity of soil bacteria that retained N used by *V. uliginosum* was maintained at high soil pH (Song et al., 2022). Otherwise, the neutral contribution of soil available P to regressed foliar N:P had a similar coefficient of DEM in forests, where soil total P content generated a stronger contribution than that revealed by average temperature. Because either DEM or soil available P has no relationships with any other soil or meteorological factors in forests, their neutral contributions should be independent of other factors.

Regional climate can shape the nutritional response of forest plants not only as a major driving force but also in combination with soil properties (Guo et al., 2017; Hauer et al., 2021; Tan et al., 2021). Surprisingly, soil total P was negatively associated with local average temperature, but they both generated positive contributions to the foliar N:P ratio in forests. SOM was another soil parameter that had a negative relationship with average temperature, suggesting the high temperature promoted the decomposition of organic matter, further activating the weathering of immobilized P (Zhou et al., 2022). The effects of soil total P and temperature were independent; neither promoted foliar N concentration in either place. For example, the high foliar N found in the forests of Qiezihe and Mishan was also associated with a high soil total P content. The high average temperature found in forests of the central part around Fangzheng and Linkou was also accompanied by high foliar N concentration. Average temperature also strongly contributed to foliar P concentration in combination with little effect of rainfall. The dual promotion of high temperature on both N and P uptake by leaves offsets a further impact of temperature on foliar N:P. Hence, forests in regions with low precipitation but a hot climate can benefit P uptake by *V. uliginosum*. Global warming triggers a sustained demand for P uptake by plants

(Lie et al., 2022). Forests subjected to a climate with little rainfall were associated with high soil total P content, which should be the reason for the high foliar P concentration.

In agroforests, introducing cultured shrubs to a farmland ecosystem may face the challenge of failure due to low nutrient availability (An et al., 2018; He et al., 2019; Cong et al., 2021). On farmlands, soil ammonium N only revealed a tiny contribution to foliar N concentration and foliar N:P ratio. Air humidity is the only meteorological factor that benefited foliar N and N:P. It was revealed that "elevated daytime atmospheric humidity increases the potential for night-time water flux and might also facilitate the uptake of mineral nutrients" (Kupper et al., 2017). Wind velocity also positively contributed to foliar N; however, it had no relationship with any soil properties on farmlands. Therefore, wind velocity was one of the meteorological factors, along with rainfall and humidity, that benefited N uptake. Compared to the coefficient of intercept in the model for foliar N on farmland, those for soil and meteorological parameters were much lower. The driving force was low to form the spatial distribution of foliar N in *V. uliginosum* on farmland. Soil ammonium N had little effect on promoting N uptake, with no driving effects from soil nitrate N content. It was revealed that in the soils of *V. uliginosum* populations, mobile N originated from mineralization mainly in the form of nitrate, but it was ammonium N that was preferred by *V. uliginosum* (Duan et al., 2022). The negative contribution of soil nitrate to foliar P may result from the restraint of P-use efficiency in nitrate-enriched soils (Liu et al., 2022).

Limitations of this study

Firstly, the spatiotemporal scale of data collection in this study was large enough for a regional study on plant distribution, but chronology may still be restricted to a shorter time period. The existing *V. uliginosum* populations were mostly planted in their natural habitats. A new comparison factor between natural and managed populations would account for this to a greater extent in spatial distribution. This can only be achieved in a long-term observation, although we failed to obtain the qualified ability to conduct another longer-term observation in this study.

Secondly, we did not control the criteria of cultural management of *V. uliginosum* populations, which may cause an over-variation of foliar N:P stoichiometry among introduced populations. For example, we exposed the diagnosis of the N limit for all populations, which was concluded to be the lack of operational practice of competitor removal. In populations on forested lands, the understory conditions may vary at different levels of competition and the soil microbial community, which may drive the spatial distribution of soil properties. Further research can specify this field variation to detect more explicit details of the association with soil properties.

Finally, all results in this study can be used to predict the proper places for *V. uliginosum* cultivation that can be distributed in northeast China. We indicated specific locations that may benefit from a high foliar N:P ratio, but all were established based on foliar diagnoses. Our results were still far from the fully expected spatial distribution for the practical introduction of this species because we did not detect fruiting yield. This can only be addressed when the specific cultivars were classified at each site or when the fruiting time varied for different genotypes. Further work can be conducted to detect the relationship between foliar N:P stoichiometry and fruiting load and further predict places that can benefit fruiting. This will make more sense for the industry of *V. uliginosum* cultivation.

Conclusions

The current cultivation of *V. uliginosum* was employed on managed populations in forests or introduced populations on farmlands. Foliar N:P ratios in current populations were found to fall between 1.8 and 4.3, which was diagnosed as the N limit according to current experience. Foliar N:P stoichiometry can be used as a flexible and reliable tool to diagnose the acclimation of the spatial distribution of the newly introduced *V. uliginosum* because it can be regressed jointly against soil properties and meteorological Factors. Therefore, it was also possible to map the spatial distribution of foliar N:P stoichiometry through overlapping distributions of determinants in soil and climate. Finally, we conclude that farmlands will be more suitable for cultivating introduced *V. uliginosum* populations than forested lands because of the higher foliar N:P ratio. Our study demonstrates a probability with the presented results about predicting the potential distribution of foliar N:P stoichiometry in a commercial shrub in Northeast China. The science and methodology can be referred to by testing other NTFP species in other regions.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

Conceptualization and writing—review and editing: YD and HZ. Methodology: JL. Software and data curation: SL. Validation: BG and LZ. Formal analysis and writing—original draft preparation: YD. Investigation: PG, HZ, GY, SZ, CZ, PS, PL, LF, SH, and DS. Resources: HZ. Visualization: WZ. Supervision, project administration, and funding acquisition: PG and HZ. All authors read and agreed to the published version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer HW declared a shared affiliation (different cities) with the author HZ to the handling editor.

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References

An, B. Y., Wei, H. X., Li, L. L., and Guo, P. (2018). Nutrient uptake and utilization and antioxidants of fruits in red raspberry (*Rubus idaeus* L.) cultivar 'autumn bliss' in response to fertilization under extended photoperiod. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 46, 440–448. doi: 10.15835/nbha46211065

Andreu, A., Gonzalez-Dugo, M. P., Kustas, W. P., Polo, M. J., and Anderson, M. C. (2013). "Modelling surface energy fluxes over a dehesa ecosystem using a two-source energy balance model and medium resolution satellite data", in *Conference on Remote Sensing for Agriculture, Ecosystems, and Hydrology XV part of the 20th International Symposium on Remote Sensing. Dresden: Spie-Int Soc Optical Engineering*. doi: 10.1117/12.2029235

China Meteorological Data Service Center (2022). Available online at: https://data.cma.cn/en/?r=site/index (accessed September 21, 2022).

Cong, R. Z., Yu, H. Y., Pei, X. N., and Shen, F. Y. (2021). Above-ground carbon storage in *Pinus pumila* along an alpine altitude in Khingan Mountains, Inner Mongolia of China. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca.* 49, 12389. doi: 10.15835/nbha49312389

De Clerck, F. A. J., and Negreros-Castillo, P. (2000). Plant species of traditional Mayan homegardens of Mexico as analogs for multistrata agroforests. *Agroforestry Syst.* 48, 303–317. doi: 10.1023/A:1006322612362

Devagiri, G. M., Khaple, A. K., Anithraj, H. B., Kushalappa, C. G., Krishnappa, A. K., and Mishra, S. B. (2020). Assessment of tree diversity and above-ground biomass in coffee agroforest dominated tropical landscape of India's Central Western Ghats. *J. For. Res.* 31, 1005–1015. doi: 10.1007/s11676-019-00885-1

Ding, X., Li, X., Qi, Y., Zhao, Z., Sun, D., and Wei, H. (2021). Depth-dependent C-N-P stocks and stoichiometry in ultisols resulting from conversion of secondary forests to plantations and driving forces. *Forests.* 12, 1300. doi: 10.3390/f12101300

Duan, Y., Fu, X., Zhou, X., Gao, D., Zhang, L., and Wu, F. (2022). Removal of dominant species impairs nitrogen utilization in co-existing *Ledum palustre* and *Vaccinium uliginosum* communities subjected to five-year continuous interruptions. *Agronomy-Basel.* 12, 932. doi: 10.3390/agronomy12040932

Ejankowski, W. (2010). Demographic variation of dwarf birch (*Betula nana*) in communities dominated by *Ledum palustre* and *Vaccinium uliginosum*. *Biologia.* 65, 248–253. doi: 10.2478/s11756-010-0007-9

Gao, D. C., Bai, E., Wang, S. Y., Zong, S. W., Liu, Z. P., Fan, X. L., et al. (2022). Three-dimensional mapping of carbon, nitrogen, and phosphorus in soil microbial biomass and their stoichiometry at the global scale. *Glob. Chang. Biol.* 28, 6728–6740. doi: 10.1111/gcb.16374

Geng, Y. D., Sun, S. B., and Yeo-Chang, Y. (2021). Impact of forest logging ban on the welfare of local communities in Northeast China. *Forests.* 12, 3. doi: 10.3390/f12010003

Goransson, H., Edwards, P. J., Perreijn, K., Smittenberg, R. H., and Venterink, H. O. (2014). Rocks create nitrogen hotspots and N:P heterogeneity by funnelling rain. *Biogeochemistry.* 121, 329–338. doi: 10.1007/s10533-014-0031-x

Guo, S. L., Wei, H. X., Li, J. P., Fan, R. F., Xu, M. Y., Chen, X., et al. (2019). Geographical distribution and environmental correlates of eleutherosides and isofraxidin in *Eleutherococcus senticosus* from natural populations in forests at Northeast China. *Forests.* 10, 872. doi: 10.3390/f10100872

Guo, S. L., Zhang, D. H., Wei, H. Y., Zhao, Y. N., Cao, Y. B., Yu, T., et al. (2017). Climatic factors shape the spatial distribution of concentrations of triterpenoids in barks of white birch (*Betula Platyphylla* Suk.) trees in Northeast China. *Forests.* 8, 334. doi: 10.3390/f8090334

Hauer, R. J., Wei, H. X., Koeser, A. K., and Dawson, J. O. (2021). Gas Exchange, Water Use Efficiency, and Biomass Partitioning among Geographic Sources of *Acer saccharum* Subsp. saccharum and Subsp. nigrum Seedlings in Response to Water Stress. *Plants-Basel.* 10, 742. doi: 10.3390/plants10040742

He, C. X., Gao, J., Zhao, Y., and Liu, J. (2021). Root foraging precision of *Pinus pumila* (Pall.) regel subjected to contrasting light spectra. *Plants-Basel* 10, 1482. doi: 10.3390/plants10071482

He, C. X., Zhang, J. S., Meng, P., and Gao, J. (2019). Seasonal dynamics of foliar C-13 and nutrient concentration of Chinese chastetree and spine jujube in foothill rock outcrop habitat of the southern Taihang Mountains, Central China. *Journal of Forestry Research* 30, 45–56. doi: 10.1007/s11676-017-0501-9

He, M. Z., Dijkstra, F. A., Zhang, K., Li, X. R., Tan, H. J., Gao, Y. H., et al. (2014). Leaf nitrogen and phosphorus of temperate desert plants in response to climate and soil nutrient availability. *Sci. Rep.* 4, 6932. doi: 10.1038/srep06932

Huang, S., Zhu, J., Zhai, K., Wang, Y., Wei, H., Xu, Z., et al. (2022). Do emotional perceptions of visible greeneries rely on the largeness of green space? A verification in Nanchang, China. *Forests* 13, 1192. doi: 10.3390/f13081192

Jiang, D. L., Yang, B. L., Cheng, X. L., Chen, H. Y. H., Ruan, H. H., and Xu, X. (2021). The stoichiometry of leaf nitrogen and phosphorus resorption in plantation forests. *For. Ecol. Manage.* 483, 118743. doi: 10.1016/j.foreco.2020.118743

Jiang, J., Wei, J., Yu, H., and He, S. (2019). *"The Developing Blueberry Industry in China," in The Developing Blueberry Industry in China*. United Kindom: IntechOpen. doi: 10.5772/intechopen.88225

Jiang, X. M., Gong, P. C., Bostedt, G., and Xu, J. T. (2014). Impacts of policy measures on the development of state-owned forests in northeast China: theoretical results and empirical evidence. *Environ. Dev. Econ.* 19, 74–91. doi: 10.1017/S1355770X13000363

Kang, H. Z., Zhuang, H. L., Wu, L. L., Liu, Q. L., Shen, G. R., Berg, B., et al. (2011). Variation in leaf nitrogen and phosphorus stoichiometry in Picea abies across Europe: an analysis based on local observations. *For. Ecol. Manage.* 261, 195–202. doi: 10.1016/j.foreco.2010.10.004

Kim, H. M., Ryu, B., Choung, S. Y., and Fang, D. S. (2015). Constituents of the fruits of *Vaccinium uliginosum* (bog bilberry). *Planta Med.* 81, 1460–1460. doi: 10.1055/s-0035-1565503

Koerselman, W., and Meuleman, A. F. M. (1996). The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. Appl. Ecol.* 33, 1441–1450. doi: 10.2307/2404783

Kupper, P., Rohula, G., Inno, L., Ostonen, I., Sellin, A., and Sober, A. (2017). Impact of high daytime air humidity on nutrient uptake and night-time water flux in silver birch, a boreal forest tree species. *Reg. Environ. Change.* 17, 2149–2157. doi: 10.1007/s10113-016-1092-2

Li, T., Yuan, X., Ge, L. M., Cao, C. H., Suo, Y. C., Bu, Z. J., et al. (2022). Weak impact of nutrient enrichment on peat: Evidence from physicochemical properties. *Front. Ecol. Evolut.* 10, 973626. doi: 10.3389/fevo.2022.973626

Li, X. H., Farooqi, T. J. A., Jiang, C., Liu, S. R., and Sun, O. J. (2019). Spatiotemporal variations in productivity and water use efficiency across a temperate forest landscape of Northeast China. *Forest Ecosyst.* 6, 22. doi: 10.1186/s40663-019-0179-x

Li, Y., Sun, Y., Zhao, Y., Wang, Y., and Cheng, S. (2022). Mapping seasonal sentiments of people visiting blue spaces in urban wetlands: a pilot study on inland cities of China. *Front. Ecol. Evolut.* 10, 969538. doi: 10.3389/fevo.2022.969538

Lie, Z. Y., Zhou, G. Y., Huang, W. J., Kadowaki, K., Tissue, D. T., Ya, J. H., et al. (2022). Warming drives sustained plant phosphorus demand in a humid tropical forest. *Glob. Chang. Biol.* 28, 4085–4096. doi: 10.1111/gcb.16194

Liu, S. T., Ranathunge, K., Lambers, H., and Finnegan, P. M. (2022). Nitrate-uptake restraint in Banksia spp. (Proteaceae) and Melaleuca spp. (Myrtaceae) from a severely phosphorus-impoverished environment. *Plant and Soil.* 476, 63–77. doi: 10.1007/s11104-022-05477-3

Marcot, B. G., Ganzei, S. S., Zhang, T. F., and Voronov, B. A. (1997). A sustainable plan for conserving forest biodiversity in Far East Russia and northeast China. *Forestry Chronicle.* 73, 565–571. 73565-5. doi: 10.5558/tfc73565-5

NASA EarthData (2021). *NASA EarthData*. Available online at: https://search.earthdata.nasa.gov/search/?ac=true&m=0.0703125!0!2!1!0!0%2C2 (accessed 7 October 2022).

Penuelas, J., Poulter, B., Sardans, J., Ciais, P., van der Velde, M., Bopp, L., et al. (2013). Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. *Nat. Commun.* 4, 2934. doi: 10.1038/ncomms3934

Reich, P. B., and Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS.* 101, 11001–11006. doi: 10.1073/pnas.0403588101

Rohrs-Richey, J. K., and Mulder, C. P. H. (2007). Effects of local changes in active layer and soil climate on seasonal foliar nitrogen concentrations of three boreal forest shrubs. *Can. J. For. Res.* 37, 383–394. doi: 10.1139/x06-230

Rupasova, Z. A., Morozov, O. V., Vasilevskaya, T. I., and Rudakovskaya, R. N. (2007). *"Species of macroelements compound in fruit of new hybrid forms of ERICACEAE berry plants family under conditions of Belarus", in: Proceedings of the international scientific-practical conference on improvement of fruit, small fruit, nuts and vine assortment under present management conditions*. Matveev, V. A., Grigortsevich, L. N., Dmitrieva, A. M., Ivanyuk, V. G., Kamzolova, O. I., Kapichnikova, N. G., et al. Samokhvalovichi, Belarus: IFG.

Song, Y. Y., Wang, L. L., Ma, X. Y., Shi, F. X., Wang, X. W., Ren, J. S., et al. (2022). Effects of plant community diversity on soil microbial functional groups in permafrost peatlands of Greater Khingan Mountains, Northeast China. *Wetlands Ecol. Manag.* 30, 595–606. doi: 10.1007/s11273-022-09869-1

Song, Z. L., Liu, H. Y., Zhao, F. J., and Xu, C. Y. (2014). Ecological stoichiometry of N:P:Si in China's grasslands. *Plant Soil.* 380, 165–179. doi: 10.1007/s11104-014-2084-y

Su, S., Wang, L., Wu, J., Li, B., Wang, W., and Wang, L. (2016). Chemical compositions and functions of *Vaccinium uliginosum*. *Chin. J. Botany.* 51, 691 (in Chinese with English abstract).

Suo, Y. Y., Yuan, Z. Q., Lin, F., Wang, X. G., Ye, J., Bai, E., et al. (2016). Local-scale determinants of elemental stoichiometry of soil in an old-growth temperate forest. *Plant Soil* 408, 401–414. doi: 10.1007/s11104-016-2939-5

Tan, L., Fan, R. F., Sun, H. F., and Guo, S. L. (2021). Root foraging of birch and larch in heterogeneous soil nutrient patches under water deficit. *PLoS ONE.* 16, e0255848. doi: 10.1371/journal.pone.0255848

Tao, Y., Zhou, X.-B., Zhang, Y.-M., Yin, B.-F., Li, Y.-G., and Zang, Y.-X. (2021). Foliar C:N:P stoichiometric traits of herbaceous synusia and the spatial patterns and drivers in a temperate desert in Central Asia. *Glob. Ecol. Conservat.* 28, e01620. doi: 10.1016/j.gecco.2021.e01620

Vallicrosa, H., Sardans, J., Maspons, J., and Penuelas, J. (2022). Global distribution and drivers of forest biome foliar nitrogen to phosphorus ratios (N:P). *Glob. Ecol. Biogeography.* 31, 861–871. doi: 10.1111/geb.13457

Walkley, A., and Black, I. A. (1934). An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci.* 37, 29–38. doi: 10.1097/00010694-193401000-00003

Wang, N., Fu, F. Z., Wang, B. T., and Wang, R. J. (2018). Carbon, nitrogen and phosphorus stoichiometry in Pinus tabulaeformis forest ecosystems in warm temperate Shanxi Province, north China. *Journal of Forestry Research* 29, 1665–1673. doi: 10.1007/s11676-017-0571-8

Wang, Y., Yang, H. B., Zhong, S., Liu, X., Li, T., and Zong, C. W. (2019). Variations in Sugar and Organic Acid Content of Fruit Harvested from Different Vaccinium uliginosum Populations in the Changbai Mountains of China. *J. Am. Soc. Hortic.* 144, 420–428. doi: 10.21273/JASHS04740-19

Wei, H., Guo, P., Zheng, H., He, X., Wang, P., Ren, Z., et al. (2017). Micro-scale heterogeneity in urban forest soils affects fine root foraging by ornamental seedlings of Buddhist pine and Northeast yew. *Urban Forest. Urban Green.* 28, 63–72. doi: 10.1016/j.ufug.2017.10.006

Wei, H., Zhao, H., and Chen, X. (2019). Foliar N:P stoichiometry in *Aralia elata* distributed on different slope degrees. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca.* 47, 887–895. doi: 10.15835/nbha47311390

Wei, H. X., Chen, G. S., Chen, X., and Zhao, H. T. (2021). Geographical distribution of *Aralia elata* characteristics correlated with topography and forest structure in Heilongjiang and Jilin Provinces, Northeast China. *J. Forest. Res.* 32, 1115–1125. doi: 10.1007/s11676-020-01100-2

Wei, H. X., Chen, X., Chen, G. S., and Zhao, H. T. (2019). Foliar nutrient and carbohydrate in *Aralia elata* can be modified by understory light quality in forests with different structures at Northeast China. *Ann. Forest Res.* 62, 125–137. doi: 10.15287/afr.2019.1395

Yang, D. X., Mao, H. R., and Jin, G. Z. (2019). Divergent responses of foliar N:P stoichiometry during different seasons to nitrogen deposition in an old-growth temperate forest, Northeast China. *Forests* 10, 257. doi: 10.3390/f10030257

Yu, Z. P., Wang, M. H., Huang, Z. Q., Lin, T. C., Vadeboncoeur, M. A., Searle, E. B., et al. (2018). Temporal changes in soil C-N-P stoichiometry over the past 60 years across subtropical China. *Glob. Chang. Biol.* 24, 1308–1320. doi: 10.1111/gcb.13939

Zhang, K., Li, M. M., Su, Y. Z., and Yang, R. (2020). Stoichiometry of leaf carbon, nitrogen, and phosphorus along a geographic, climatic, and soil gradients in temperate desert of Hexi Corridor, northwest China. *J. Plant Ecol.* 13, 114–121. doi: 10.1093/jpe/rtz045

Zhang, W., Zhao, J., Pan, F. J., Li, D. J., Chen, H. S., and Wang, K. L. (2015). Changes in nitrogen and phosphorus limitation during secondary succession in a karst region in southwest China. *Plant Soil.* 391, 77–91. doi: 10.1007/s11104-015-2406-8

Zhou, C. W., Cui, W. J., Yuan, T., Cheng, H. Y., Su, Q., Wei, H. X., et al. (2022). Root foraging behavior of two agronomical herbs subjected to heterogeneous p pattern and high ca stress. *Agronomy-Basel* 12, 624. doi: 10.3390/agronomy12030624