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Plant response to N availability in permafrost-affected alpine wetlands in arid and semi-arid climate zones

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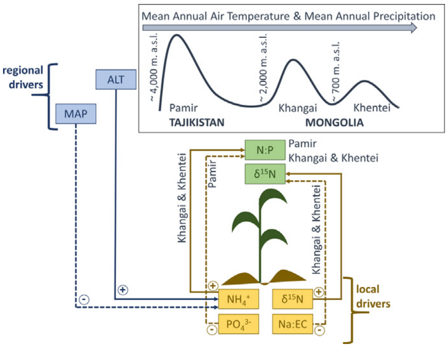
HIGHLIGHTS

- Plant N:P ratio was correlated with regional drivers - altitude and precipitation.
- Vegetation of the Mongolian ranges was more N limited than the Pamir wetlands.
- Vegetation of the Pamir wetlands was influenced by low content of PO_4^{3-} in soil.
- Impact of regional drivers on plant $\delta^{15}N$ was covered by effects of local drivers.
- Plant $\delta^{15}N$ was strongly correlated with soil $\delta^{15}N$ and affected by soil salinity.

GRAPHICAL ABSTRACT



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ABSTRACT

Nutrient cycling in alpine permafrost-affected wetlands remains insufficiently studied, as it is influenced by a complex network of interrelated climatic and environmental factors, at both regional and local scale. Therefore, we applied mathematical models to examine relationship between environmental factors and plant functional traits reflecting N availability in wetland communities developed under locally variable conditions in a geographic and climatic gradient of high-altitude habitats. Moreover, we assessed impact of local differences in soil chemistry on plant fractionation of N isotopes as a response to N availability. Based on environmental data and chemistry of biomass from 192 study sites from the Pamir Mountains (Tajikistan) and Khangai and Khentei Mountains (Mongolia), a matrix of rank correlations was prepared for regional and local factors and community level plant functional traits. For the traits that were highly correlated either with regional or with local drivers (that is plant N:P ratio and plant $\delta^{15}N$), linear models were built, with a limited set of predictors selected according to the Risk Inflation Criterion and the SOS algorithm. The models were fitted for each of the studied regions. Presented regional models indicated significant influence of soil NH_4^+ and/or PO_4^{3-} content on plant N:P ratio, which showed increase with altitude and lowering precipitation. Thus, its values clearly distinguished between the Pamir Mountains (high N:P) and the Mongolian ranges (low N:P). Models for plant $\delta^{15}N$ showed its strong positive correlations with soil $\delta^{15}N$ and soil salinity. Average values of plant $\delta^{15}N$ were comparable for both study areas. The studied plant functional traits showed different response to regional and local drivers. Plant N:P ratio was controlled by regional drivers via their influence on soil NH_4^+ content. Contrastingly, plant $\delta^{15}N$ was significantly affected by local factors, namely soil $\delta^{15}N$ and soil salinity expressed as Na:EC.

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1. Introduction

Even up to 20% of the world permafrost occurs in high mountains located in middle and low latitudes, mostly in Central Asia (Himalayas, Karakorum, Kunlun Shan, Hindukush, Pamirs, and Tien Shan), in southern Siberia and in Mongolia (Altai, Khangai and Khentei) (Bockheim and Munroe, 2014; Lehmkuhl, 1998; Gorbunov, 1978). Such continental (alpine) permafrost covers between 2.5 and 4.9 million km^2 worldwide (Bockheim and Munroe, 2014; Gorbunov, 1978) and is characterized by strong diurnal temperature patterns and high insolation on the surface, which result in a distinct geothermal gradient and deep active layer (Baumann et al., 2009; Bockheim and Munroe, 2014; Gorbunov, 1978). Alpine soils developed on permafrost may support establishment of grassland and wetland communities, and are large stores of organic matter formed due to low temperature and impeded subsurface drainage. Under such conditions, rates of microbial activity and other biogeochemical processes decrease, which results in low rate of decomposition (Baumann et al., 2009; Biskaborn et al., 2019; Bockheim and Munroe, 2014; Koven et al., 2011; Ping et al., 2015; Wang et al., 2013). According to existing estimations, alpine permafrost soils contain 66.3 Pg of soil organic carbon (SOC) to the depth of 100 cm, which comprises 4.5% of the global soil carbon pool (Baumann et al., 2009; Bockheim and Munroe, 2014). Yet, their role as carbon sink will gradually change with ongoing increase in permafrost temperatures worldwide, estimated at 0.29 ± 0.12 °C between 2007 and 2016 (Biskaborn et al., 2019). Potential thaw of permafrost will result in changes in hydrological and thermal regimes of soils, leading to intense decomposition of organic matter and release of greenhouse gases into the atmosphere (Biskaborn et al., 2019; Bockheim and Munroe, 2014; Ping et al., 2015). Alterations in nutrient cycling caused by thaw of alpine permafrost remain hard to predict, as biogeochemistry of alpine permafrost soils is influenced by a complex network of interrelated global and local drivers (Bockheim and Munroe, 2014; Koven et al., 2011; Ping et al., 2015). Nevertheless, thaw-related changes in soil moisture and chemistry will lead to significant structural and functional transformations of high-altitude grasslands and wetlands (Finger et al., 2016; Mętrak et al., 2017; Zhang et al., 2017).

Presently, availability of nutrients, especially nitrogen (N) and phosphorus (P), is a crucial factor influencing development and functioning of these ecosystems (e.g. Makarov et al., 2014; Wang et al., 2013; Xu et al., 2014; Yang et al., 2015). In order to assess it properly, ecological research focuses on N and P contents, N:P ratio and N isotope ratio in biomass at the community level, as these plant functional traits reflect relative nutrient availability in the environment and can be viewed as indicators of complex processes involved in N cycle (e.g. Craine et al., 2015; Gong et al., 2017; Palpurina et al., 2019; Yang et al., 2015). At the community level, values and composition of traits describing plant response to nutrient availability are shaped jointly by local and regional drivers (Fig. 1).

Depending on research scale and individual case, influence of local and regional drivers may vary. At the crude scale usually regional drivers dominate. Thus, at the community level biomass indicators of N availability follow global patterns of broad-scale variability in geography and climatic factors (e.g. Chen et al., 2013; Craine et al., 2015; Gavazov et al., 2016; Reich and Oleksyn, 2004; Saradans et al., 2012). However, at the fine scale their influence can be significantly modified by local drivers (e.g. Fujiyoshi et al., 2019; Ruiz-Navarro et al., 2016; Shtangeeva et al., 2019; Wu et al., 2019; Yang et al., 2015). Therefore, different global-scale drivers can support communities with quite similar trait values and composition, and, contrastingly, under similar global-scale drivers significantly different communities can develop (Bruelheide et al., 2018). We observed such situation during our previous studies in the Eastern Pamir Mountains, where permafrost-affected wetlands were covered by a repetitive mosaic of distinct plant communities, shaped mostly by local differences in water supply and soil salinity (Mętrak et al., 2017). Thus, we hypothesize that in arid and semi-arid

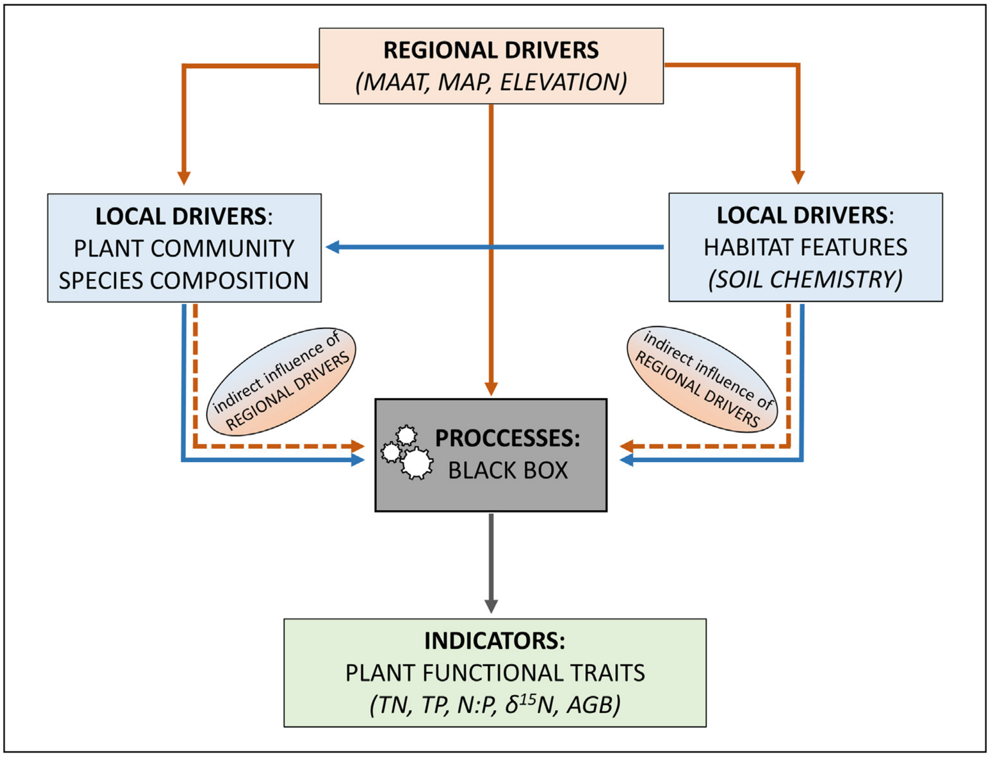


Fig. 1. Conceptual diagram showing influences of regional and local environmental drivers on processes shaping N availability for plants, and thus on indicators of these processes. In brackets - selected parameters that were discussed in this article. MAAT – Mean Annual Air Temperature, MAP – Mean Annual Precipitation, TN – plant total nitrogen, TP – plant total phosphorous, N:P – plant N:P ratio, $\delta^{15}N$ – plant isotopic ratio, AGB – Aboveground Biomass.

mountains of Central Asia, local differences in soil moisture and chemistry are the main factors shaping response of plant functional traits to N availability in alpine wetlands.

These habitats, or cold alpine environments in general, tend to be underrepresented in current models describing controls of biogeochemical cycles and their impact on plant stoichiometry (see e.g. Craine et al., 2015; Reich and Oleksyn, 2004; Saradans et al., 2012). Thus, the drivers and mechanisms of ecosystem N cycling in alpine wetlands, especially in arid and semi-arid climate zones are mostly unknown. Considering vital role of alpine permafrost-affected wetlands as nutrient sinks, this knowledge gap should be bridged, especially with the ongoing climate changes, which are strongly pronounced in high-altitude ecosystems.

Thus, the main objective of this study was to identify regional and local drivers that significantly influence community-level plant response to N availability in alpine permafrost-affected wetlands located in geographic (longitude, altitude) and climatic (Mean Annual Air Temperature, Mean Annual Precipitation) gradient in arid and semi-arid climate zones. In particular, this study had the following aims: (1) to examine influence of selected environmental factors on plant N:P ratio under regionally and locally variable conditions in alpine landscape; (2) to assess impact of local differences in soil chemistry on plant fractionation of N isotopes as a response to N availability. To address these questions we looked for universal and robust linear models describing relationship between regional and local environmental factors and community-level functional traits related to plant response to N availability.

2. Materials and methods

2.1. Study site

Sampling sites were located in the permafrost-affected regions in Mongolia, namely in the Khangai and the Khentei Mountains, and in Tajikistan, namely in the Pamir Mountains (Fig. 2). Basic geographical and climatic characteristics of these areas are presented in Table 1.

In Mongolia permafrost is present in the north, where climatic and topographic conditions are favourable (mostly in mountainous areas). Perennially frozen ground in this region is the southernmost outreach of the Siberian permafrost (Zhao et al., 2008) and covers area of roughly 235,000 km^2 (Glazik, 1995). According to Brown et al. (1998) in more elevated sites in the Khangai and Khentei Mountains dominates continuous permafrost, while in lower sites either sporadic or isolated permafrost is present. Perennially frozen ground develops usually at depths >1 m and in most regions its temperature is close to 0 °C. Hence Mongolian permafrost is very sensitive to climatic changes (Zhao et al., 2008).

In case of the Pamir Mountains both former Russian data and modern modelling confirm presence of permafrost and estimate its area at 54,000 km^2 (Baranov and Klunnikov, 1936; Mergili et al., 2012). According to Brown et al. (1998), our sampling sites are located in the region of discontinuous permafrost. Though the permafrost in this area was reported at the depth of several meters (3–5 m) (Baranov and Klunnikov, 1936), presence of ground ice at a depth of <1 m was confirmed by our observations in 2015 in the Yashilkul and the Rangkul-Shorkul watersheds (Mętrak et al., 2019 and own unpublished data). Such lens-shaped ground ice in these areas was described before by Russian scientists as a result of water freezing in the bottom parts of the active layer (Baranov and Klunnikov, 1936).

Due to significant differences in elevation and high variability of environmental conditions observed at the local scale (mezotopography, water supply, bedrock type etc.), soils developed on the study sites differed in morphology and physiochemical properties. While most soils were of cryogenic origin (Cryosols, Histosols), on several sites, in hollows underlain by impermeable clay layer, strongly saline and alkaline soils developed (Solonchaks).

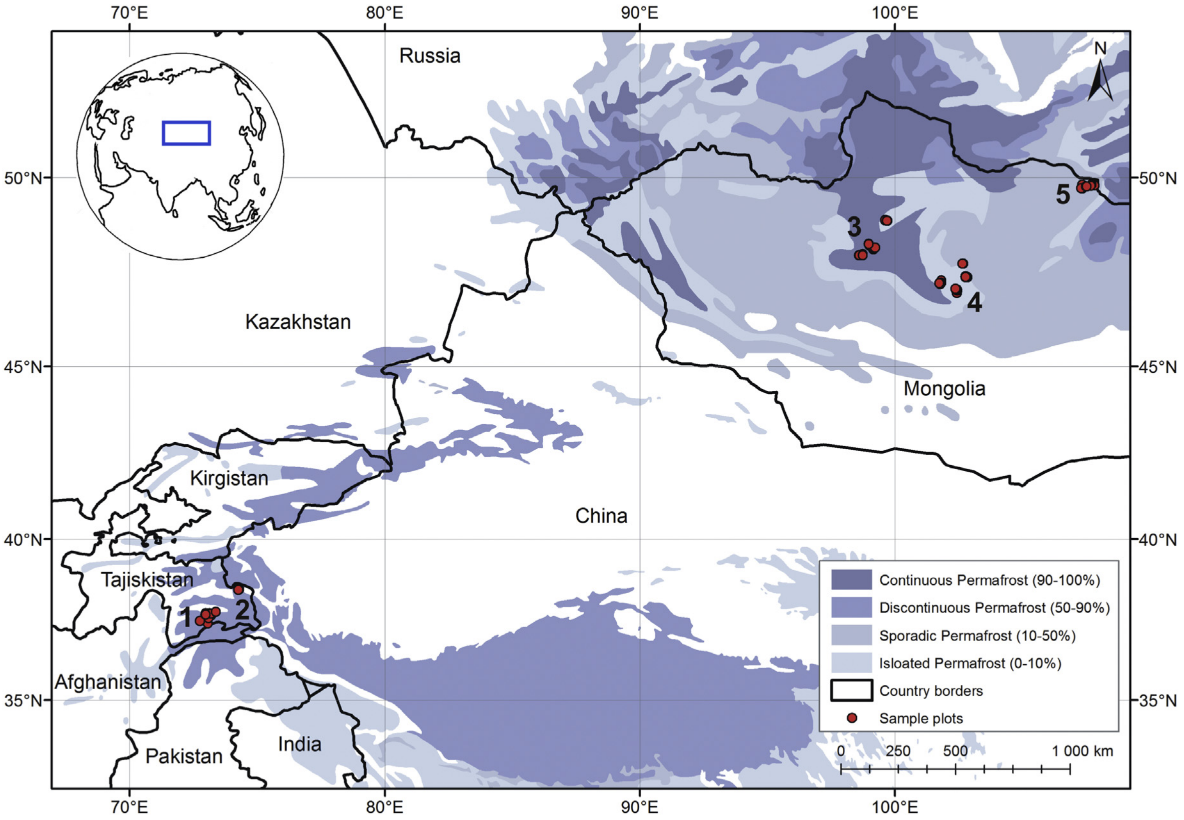


Fig. 2. Distribution of permafrost in Central Asia (from Brown et al., 1998, revised 2001, modified) and location of sampling sites. Pamir Mountains: 1 – Yashilkul watershed, 2 – Rangkul - Shorkul watershed; Mongolian ranges: 3 - West Khagnai Mountains, 4 – East Khangai Mountains, 5 – Khentei Mountains (Selenge River).

Table 1
Basic geographical and climatic characteristics of the sampling sites. MAAT – Mean Annual Air Temperature, MAP – Mean Annual Precipitation. Data for the Yashilkul watershed are given according to unpublished data from the Bulunkul Meteorological Station of the Tajikistan National Agency for Hydrometeorology. Data for the Rangkul-Shorkul watershed are given according to Kayumov (2010) and Williams and Konovalov (2008). Data for the Khangai and Khentei Mountains are given according to climate models for relevant regions in Mongolia accessible at Climate-Data.org.

State	Mountain range	Region	Number of samples	Altitude [m a.s.l.]	MAAT [°C]	MAP [mm]
Tajikistan	Pamir Mts.	Yashilkul watershed (1)	48	3727–4444	(−4.0)	50
		Rangkul - Shorkul watershed (2)	12	3789–3792	(−0.7)	74
Mongolia	Khangai Mts.	West Khangai (3)	48	1510–2535	(−3.1)–(−2.9)	212–218
		East Khangai (4)	60	1285–1768	(−2.9)–(0.5)	218–264
	Khentei Mts.	Selenge River (5)	24	648–794	(−1.0)	305

Observed plant communities reflected soil differentiation and could be classified into two broad categories: (1) mountainous sedge meadows with domination of *Carex* species and different participation of shrubs, forbs and mosses (with floristic similarities to *Halerpestetalia* order as defined by Golub, 1994, and embracing Mongolian moderately saline meadows on permafrost); and (2) salt marshes with domination of *Blysmus* and *Carex* species and different participation of typical hydrophytes (e.g. *Hippuris vulgaris*, *Eleocharis palustris*, *Ranunculus natans*).

2.2. Field research

According to the observed vegetation physiognomy and with the support of historical results from the works by Stanyukovich (1949), we determined the main vegetation types in the study area. In every region we selected ungrazed, homogenous patches of dominating wetland plant communities (in total 192 sites). Within each patch a relevé was performed and a 50 × 50 cm square plot was randomly established, from which soil and biomass samples were collected in June 2014, 2015 or 2016. Soil samples were taken from the effective root penetration zone typical for saturated soils (0–30 cm). Soil moisture (SM) was assessed in the field as the difference in mass between wet (immediately after sampling) and air dried samples. Above ground vascular biomass (AGB) was collected by clipping the vegetation 1 cm above ground level, leaving the moss layer below untouched. Only living biomass was weighted and retained for analysis.

2.3. Laboratory analyses

Soil samples were oven dried at 50 °C, ground manually with a mortar and sieved (1 mm grade). Biomass samples were oven dried at 50 °C and pulverized in an automated mill. In soil samples we measured the following parameters: (1) electrical conductivity (EC) with Hach HQ40d device in water extract (soil:water ratio 1:5) (Shirokova et al., 2000); (2) concentration of exchangeable Na^+, K^+, Mg^{2+} and Ca^{2+} in 0.1 M $BaCl_2$ extract with Flame Atomic Absorption Spectrometer Contraa700 (Ross and Ketterings, 1995); (3) total carbon (TC) and total nitrogen (TN) with a CHNS elemental analyzer FLASH 2000; (4) available phosphorous content (PO_4^{3-}) with the Olsen method. Additionally we measured soil organic carbon (SOC) after carbonates removal with HCl with a CHNS elemental analyzer FLASH 2000, and exchangeable nitrates and ammonium ions in 0.03 M acetic acid extract with Continuous Flow Analyzer SAN++.

In AGB samples we measured the following parameters: (1) total carbon (TC_p) and total nitrogen (TN_p) with a CHNS elemental analyzer FLASH 2000; (2) total phosphorous (P_p) with Continuous Flow Analyzer SAN++ after digestion in HNO_3.

Isotopic signatures (δ^{13}C_p and δ^{15}N_p) of both soil and AGB samples were measured with Thermo Scientific Delta V Plus IR-MS linked with Elemental Analyzer (approximately 1 mg of soil and 0.5 mg of biomass weighted into tin capsule). Calibration curves were calculated using the following standards IAEA 600, USGS 40, USGS 41, UREA 2, UREA 3 (VPDB scale for C and air scale for N). Isotope ratios were calculated according to Hoefs (2009). All parameters measured in AGB are identified throughout the text by a descriptor ‘plant’, e.g. plant N:P ratio, plant δ^{15}N and abbreviated in figures as N:P_p and δ^{15}N_p.

All the above-mentioned analyses were performed at the Laboratory of Biogeochemistry and Environmental Conservation at the Biological and Chemical Research Centre of the University of Warsaw.

2.4. Statistical methods

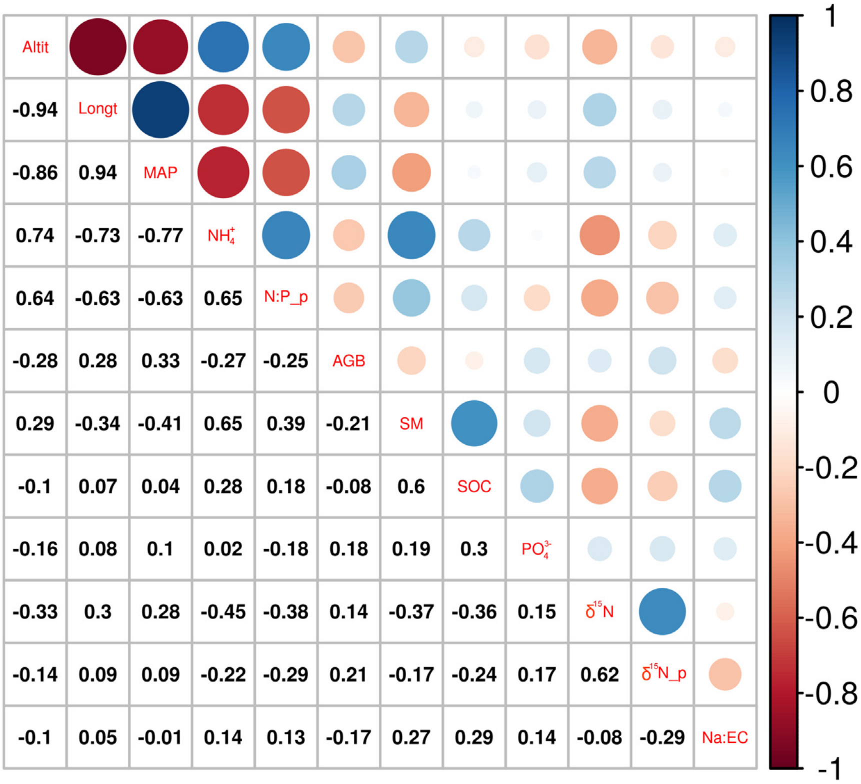
A matrix of robust Spearman rank correlation coefficients ρ was prepared for regional drivers (latitude, longitude, altitude, MAAT and MAP), local drivers (soil moisture, content of TC, SOC, TN, NH_4^+, NO_3^- and PO_4^{3-}, pH, EC, concentrations of exchangeable Na^+, K^+, Mg^{2+} and Ca^{2+}, soil δ^{15}N and δ^{13}C) and community level plant functional traits reflecting nutrient availability (AGB, TN_p, TP_p, TC_p, N:P_p ratio and δ^{15}N_p and δ^{13}C_p). Using this matrix we determined plant functional traits reflecting nutrient availability, that were highly correlated either with regional or with local drivers. For the selected traits and regional and local drivers boxplots were prepared, showing differentiation between studied geographical regions. Finally, linear models were built for plant N:P ratio and plant δ^{15}N. Parameters with asymmetrical distribution and outlying observations were logarithmized to fit in the models. To avoid overfitting of our models, we selected a limited set of predictors using the Risk Inflation Criterion (RIC) (Foster and George, 1994) and the SOS algorithm (Pokarowski and Mielniczuk, 2015) to balance between the complexity of the models and their fitness to plant response in the collected dataset. This method is better suited for models with high number of predictors than the Bayesian or the Akaike Information Criteria (BIC and AIC). Due to significant differentiation of environmental factors and plant functional traits between the studied regions, we decided to fit the models for each region separately. All statistical analyses were prepared in the R environment (R Core Team, 2017).

3. Results

3.1. Relationships between regional-scale environmental factors, local soil chemistry and plant functional traits

Regional drivers used in this study were strongly correlated. MAP values increased from the highest and the most arid Pamir Mountains in Tajikistan (South-West) to the lowest and the least arid Khentei Mountains in Mongolia (North-East), with robust Spearman rank correlation coefficient ρ between Longitude and MAP reaching 0.94. Similar relationship was observed for MAAT, as can be seen in Supplementary materials. Altitude increased in a reversed direction from the North-East to the South-West, with ρ between Longitude and Elevation reaching −0.94 (Fig. 3).

Regional drivers correlated strongly with NH_4^+ content in soil, which increased with altitude to the South-West (ρ between Longitude and NH_4^+ content was −0.73). Simultaneously, NH_4^+ content in soil was correlated with SM ($\rho = 0.65$) and SOC content ($\rho = 0.28$). SM and SOC were in turn positively correlated with $\rho = 0.60$. Considering functional



Altit											
-0.94	Longt										
-0.86	0.94	MAP									
0.74	-0.73	-0.77	NH_4^+								
0.64	-0.63	-0.63	0.65	N:P_p							
-0.28	0.28	0.33	-0.27	-0.25	AGB						
0.29	-0.34	-0.41	0.65	0.39	-0.21	SM					
-0.1	0.07	0.04	0.28	0.18	-0.08	0.6	SOC				
-0.16	0.08	0.1	0.02	-0.18	0.18	0.19	0.3	PO_4^{3-}			
-0.33	0.3	0.28	-0.45	-0.38	0.14	-0.37	-0.36	0.15	$\delta^{15}N$		
-0.14	0.09	0.09	-0.22	-0.29	0.21	-0.17	-0.24	0.17	0.62	$\delta^{15}N$_p	
-0.1	0.05	-0.01	0.14	0.13	-0.17	0.27	0.29	0.14	-0.08	-0.29	Na:EC

Fig. 3. Matrix of Spearman rank correlations for selected regional and local drivers, and community level traits reflecting nutrient availability. In the lower triangular part – numerical values of ρ for each correlation; in the upper triangular part – dots representing ρ values with size and colour intensity. Altit – altitude [m a.s.l.], Longt – longitude [°], MAP – Mean Annual Precipitation [mm], N:P_p – plant N:P ratio, AGB – Aboveground Vascular Biomass [g/m^2], SM – Soil Moisture [%], SOC – Soil Organic Carbon [%], δ^{15}N_p - plant δ^{15}N . For full correlation matrix see Supplementary materials, Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

traits related to plant response to N availability, plant N:P ratio was strongly correlated with regional drivers (ρ between Longitude and N:P ratio was −0.63) and with NH_4^+ content in soil (ρ = 0.65), showing increase to the South-West. Thus, the highest plant N:P values were recorded in samples from the Pamir Mountains. Contrastingly, AGB itself increased to the North-East (ρ between Longitude and AGB was 0.28), with the highest values recorded for samples from the Khentei Mountains. Additionally, plant N:P values were correlated with local drivers, such as SM (ρ = 0.38) and soil δ^{15}N (ρ = −0.37).

Interestingly, plant δ^{15}N showed no significant correlations with regional drivers. However, it was strongly correlated with soil δ^{15}N (ρ = 0.62) and noticeably weaklier correlated with SOC, soil NH_4^+ content and Na:EC ratio (ρ in between 0.22 and 0.29).

Summary of regional distributions of regional factors, soil chemistry parameters (local drivers) and plant functional traits (N:P ratio, δ^{15}N and above ground vascular biomass) reflecting N and P availability in soil is presented in Fig. 4.

Soil parameters and plant functional traits that strongly correlated with regional drivers showed clear distinction between the Pamir Mountains and the Mongolian ranges. Thus, alpine wetland soils from the Pamir Mountains contained 3–4 times more NH_4^+ ions than soils from wetlands located in the Mongolian ranges. Average plant N:P ratio was the highest in samples from the Pamir Mountains (in both regions above 13), and the lowest in the Eastern Khangai and Khentei Mountains (in both regions slightly above 7). N:P values for the Mongolian ranges didn't exceed 15.5, while maximum value for the Pamir Mountains was over 25. Amount of collected AGB was generally higher in the Mongolian ranges than in the Pamir Mountains. In case of SOC, soil content of PO_4^{3-} ions and soil Na:EC ratio, samples from Rangkul – Shorkul watershed showed distinctly lower values and narrower range, while samples from other regions were characterized by higher results and broader ranges (Fig. 4). Considering soil δ^{15}N, samples from the lowest Mongolian range, the Khentei Mountains, were enriched in ^{15}N isotopes in comparison to all other regions. Yet, no regional trends were observed for plant δ^{15}N.

3.2. Response of wetland vegetation to N availability under locally variable conditions in alpine landscape

We selected plant N:P ratio and plant δ^{15}N for construction of linear models, as these functional traits strongly correlated with regional and/or local drivers. The models were fitted using combined data from the Pamir Mountains and the Mongolian ranges, and took the form of the following equations:

$$\mathrm{m\_\ log(N:P\_p)} = a_0 + a_1 \log\left({NH_4}^+\right) + a_2 \log\left({PO_4}^{3-}\right)$$

and

$$\mathrm{m\_}\left(\delta^{15}\mathrm{N\_p}\right) = b_0 + b_1\left(\delta^{15}\mathrm{N}\right) + b_2 \log(\mathrm{Na:EC}).$$

These models were fitted for each region separately, to obtain the best 3-parametric models for regional data. Summary of both linear models is presented in Tables 2 and 3. Regional fitness of the models is shown in Fig. 5.

Due to significant differentiation of environmental factors and plant functional traits between the studied regions, we decided to build regional models for plant N:P ratio and plant δ^{15}N. In line with these models, two main predictors of plant N:P ratio was content of NH_4^+ and of PO_4^{3-} ions in soil (Table 2). According to *p* values of the predictors (Table 2, a_1 for NH_4^+ content and a_2 for PO_4^{3-} content), in samples from the West and East Khangai Mountains positive influence of NH_4^+ content on plant N:P ratio was more significant than negative influence of

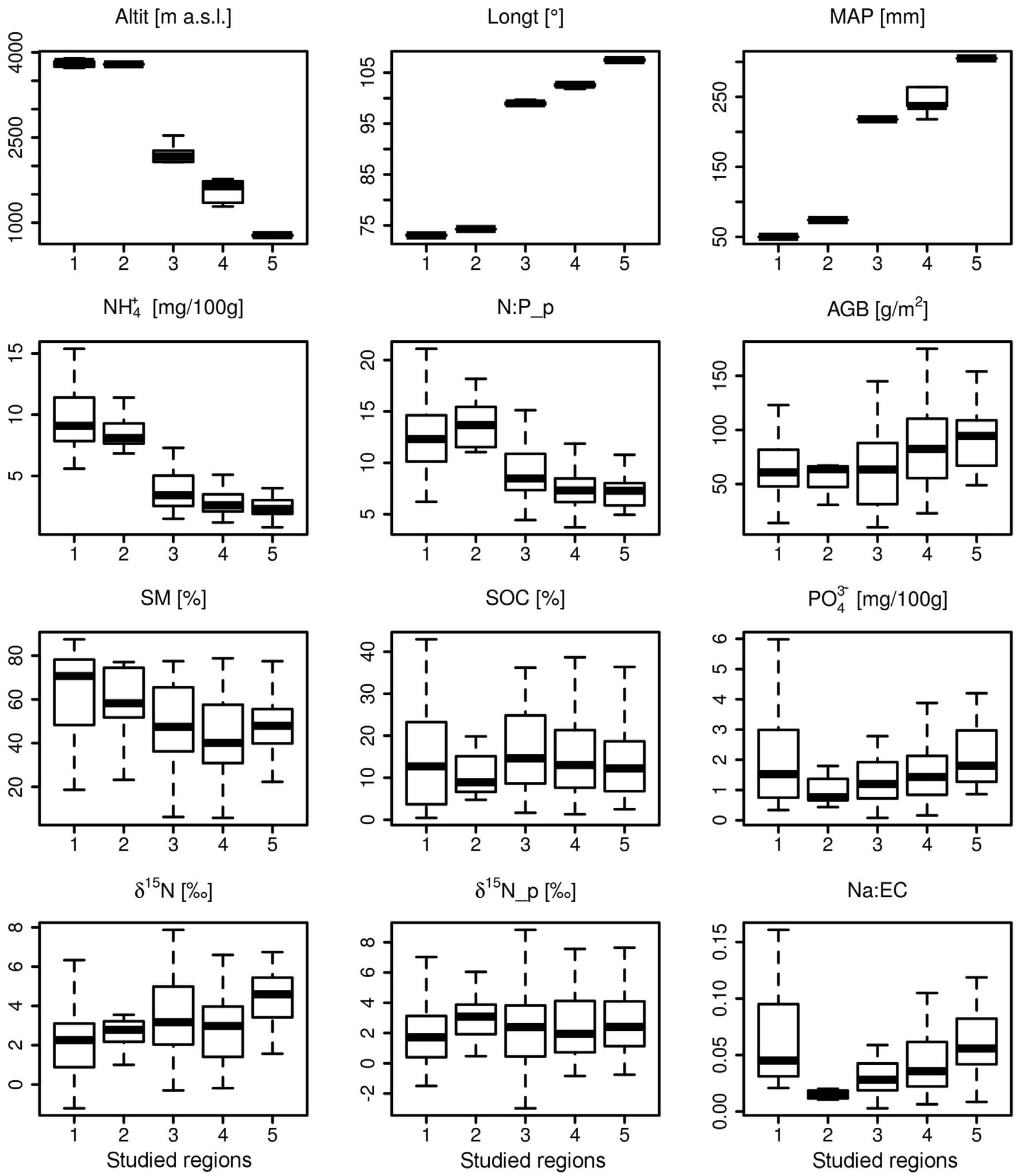


Fig. 4. Distribution of selected regional and local drivers, and community level functional traits for main study sites. Line – median, box – 25–75%, whiskers – range (with outliers excluded). Numbers on X axis denote regions in the Pamir Mountains: 1 – Yashilkul watershed, 2 – Rangkul - Shorkul watershed; and in the Mongolian ranges: 3 – West Khangai Mountains, 4 – East Khangai Mountains, 5 – Khentei Mountains (Selenge River).

Table 2
Basic characteristics of a model for plant N:P ratio: m_log(N:P_p) = $a_0 + a_1\log(NH_4^+) + a_2\log(PO_4^{3-})$. Asterisks denote *p*-values that is levels of significance for estimators of model parameters (***$P < 0.001$; **$P < 0.01$ and *$P < 0.05$). ρ – Spearman rank correlation coefficient.

Estimator	Yashilkul watershed	Rangkul - Shorkul watershed	West Khangai	East Khangai	Khentei (Selenge)
a_0	1.285**	2.836**	1.936***	1.664***	1.932***
a_1	0.581*	−0.116	0.204*	0.331***	−0.012
a_2	−0.174**	−0.235*	−0.013	−0.148**	0.054
ρ	0.402	0.692	0.304	0.517	0.150

Table 3
Basic characteristics of a model for plant δ^{15}N: m_(δ^{15}N_p) = $b_0 + b_1(\delta^{15}N) + b_2\log(Na{:}EC)$. Asterisks denote p-values that is levels of significance for estimators of model parameters (***$P < 0.001$; **$P < 0.01$ and *$P < 0.05$). ρ – Spearman rank correlation coefficient.

Estimator	Yashilkul watershed	Rangkul - Shorkul watershed	West Khangai	East Khangai	Khentei (Selenge)
b_0	0.860	8.477	−4.954***	−3.468**	−5.916**
b_1	0.777***	1.329***	1.215***	0.804***	0.952***
b_2	0.273	2.123	−1.026**	−1.110***	−1.466**
ρ	0.658	0.755	0.806	0.705	0.682

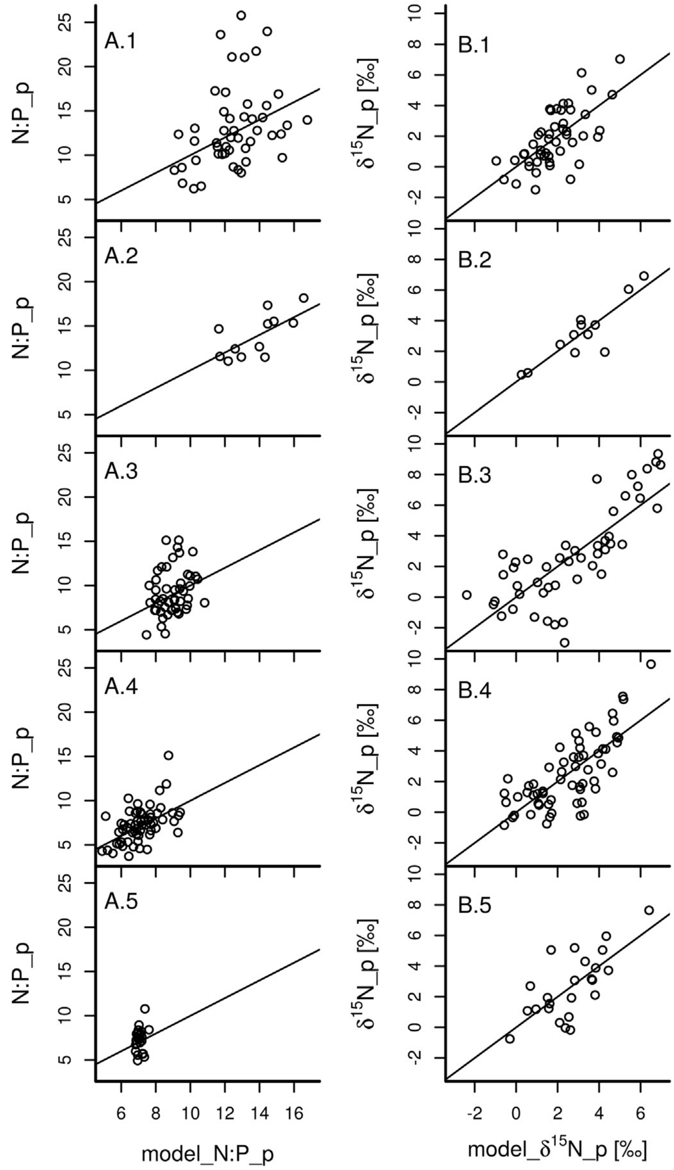


Fig. 5. Relationships between original and modelled values of plant N:P ratio (A) and plant $\delta^{15}N$ (B) for each of the studied regions. Numbers in graphs' titles denote regions in the Pamir Mountains: 1 – Yashilkul watershed, 2 – Rangkul - Shorkul watershed; and in the Mongolian ranges: 3 – West Khangai Mountains, 4 – East Khangai Mountains, 5 – Khentei Mountains (Selenge River).

PO_4^{3-} content. In case of samples from the Pamir Mountains, influence of NH_4^+ content was either insignificant (Rangkul - Shorkul watershed) or less significant than the negative influence of PO_4^{3-} content (Yashilkul watershed). No significant influence of NH_4^+ nor PO_4^{3-} content on plant N:P ratio was observed for samples from the Khentei Mountains, where the correlation between recorded and modelled values of N:P ratio was the lowest. As plant N:P ratio was strongly correlated with regional drivers (altitude, longitude and MAP, see Fig. 3), huge differences in regional correlation coefficients could be observed (ρ values in Table 2).

The main predictor in the model for plant $\delta^{15}N$ was soil $\delta^{15}N$, which was highly significant in all the studied regions (Table 3). In samples from the Mongolian ranges its influence on plant $\delta^{15}N$ was significantly modified by Na:EC ratio in soil. Correlation coefficients calculated between recorded and modelled plant $\delta^{15}N$ for each region separately (ρ values in Table 3) showed far less differentiation than coefficients calculated for N:P values. Thus, potential influence of regional drivers on the variability of plant $\delta^{15}N$ remained indiscernible in our analyses.

4. Discussion

4.1. Influence of selected geographical and climatic factors on plant N:P ratio

Our results showed that N:P ratio increased in plants growing under extreme conditions, namely high altitude combined with low MAP. Simultaneously, such habitats were characterized by less intense biomass production. In the regional models for plant N:P ratio, samples from the Pamir Mountains, having high N:P ratios, were clearly separated from samples from the Mongolian ranges, having low N:P ratios. Such correlations between plant N:P ratio and regional factors are in accordance with the Growth Rate Hypothesis, which states that conservative strategies under stress lead to lower growth rates and higher N:P ratios in biomass (Tan et al., 2018). Under extreme environmental conditions plant productivity decreases, while plant N demands increase to offset various stressors. Extended amounts of N in plant biomass are necessary to compensate for slowing down of temperature-sensitive processes observed in plants. Especially in highly elevated areas, where low partial pressure of CO_2 additionally impairs photosynthetic C assimilation (Reich and Oleksyn, 2004). At high altitudes N can be also used in enzyme-mediated photoprotective mechanisms, necessary in plants exposed to excessive UV irradiation (Solanki et al., 2019). Moreover, vegetation of areas with low MAP values can be subject to periods of draught. To protect cellular organelles from water stress, plants keep an osmotic equilibrium by producing low molecular weight compatible solutes (osmotic adjustment). Most of them contain N atoms and thus further enhance plant N demand (MacTavish and Cohen, 2017; Rajasheker et al., 2019; Wang et al., 2015). However, in our case, plant N content remained uncorrelated with N:P ratios, and was comparable for the Pamir Mountains (mean values of TN 1.47% and 1.75%) and the Mongolian ranges (mean values of TN 1.11%, 1.45% and 1.73%). Thus, the observed discrepancies in plant N:P ratio between the regions resulted mostly from differences in plant P content (on average two times lower in the Pamir Mountains than in the Mongolian ranges) (see Supplementary materials, Fig. 1 and Table 1).

Plant N:P ratio can be used as an indicator of nutrient limitation during vegetation growth, as it reflects relative N and P availability in soil (e.g. Güsewell et al., 2003; Koerselman and Meuleman, 1996; Zhang et al., 2013). The threshold values of plant N:P ratio for ecosystems limited by N were set at below 14 (Koerselman and Meuleman, 1996) or, according to updated results by Güsewell et al. (2003), at below 10. For ecosystems limited by P threshold values were set at above 16 (Koerselman and Meuleman, 1996) or at above 20 (Güsewell et al., 2003). Vast majority of biomass samples from the Khangai and Khentei Mountains was well below the threshold value for N limitation (111 out of 132 with N:P below 10), which is in accordance with several experimental studies that proved N limitation in alpine meadows and wetlands (Gao et al., 2018; Tian et al., 2018; Xu et al., 2014). In case of wetlands in the Pamir Mountains only 11 out of 60 samples N:P ratio was below 10. Thus, we may assume that vegetation of the Pamir wetlands was less limited by soil N availability, which is in agreement with high content of ammonium ions in the Pamir soil samples (soil content of ammonium ions was strongly correlated with regional drivers) and lesser significance of NH_4^+ content in the Pamir models for plant N:P ratio in comparison to the models for samples from the Mongolian ranges. Soil NH_4^+ content was strongly and positively correlated with SM and SOC, probably due to anoxic/suboxic and reductive conditions typical for wetlands. Such conditions affect microbial activity and diminish rate of N and C mineralization in soils. High water saturation (indicated by high SM) decreases decomposition processes and, simultaneously, enhances NO_3^- ammonification (Dissimilatory Nitrate Reduction to Ammonium, DNRA). Thus, it leads to general increase in soil organic matter, characterized by low degree of decomposition, relatively high content of light N isotopes (both mostly due to limited microbial activities), and to accumulation of ammonium ions (due to

DNRA) (Baumann et al., 2009; Bockheim and Munroe, 2014; Finger et al., 2016; Strock, 2008). In our correlation matrix results of these processes were indicated as positive correlations between SM and NH_4^+ content, SM and SOC, and a negative correlation between SM and soil $\delta^{15}N$. In general, ammonium ions accumulation and predominance over NO_3^- is often viewed as an indicative of a conservative, closed nitrogen cycle, with limited gaseous N losses and relatively low soil $\delta^{15}N$, which is considered typical for most permafrost soils (e.g. Baumann et al., 2009; Brearley, 2013).

In several cases from the Pamir Mountains, values of plant N:P ratio indicated P limitation (due to extremely low P content recorded in biomass). These plant communities developed on soils, in which content of PO_4^{3-} ions was well below average value calculated for all the studied soil samples. However, none of our results satisfactorily explained causes of PO_4^{3-} depletion and P limitation, especially well visible in samples from the Rangkul – Shorkul watershed. Soil properties related with P availability, namely organic matter content and its C:N ratio, pH and Ca^{2+} content, in samples from P limited wetlands were differentiated and did not differ significantly from average values calculated for all the studied samples (see Supplementary materials, Table 1). However, amount of plant-available soil P can be influenced by intensity of mechanical rock weathering, as this process releases P bound in minerals, which are its main source in soils (Jiao et al., 2016). Typically, in arid and semi-arid regions, weathering is the most intense during warm and wet periods (Manning et al., 2013; Yang et al., 2013). As MAP values are significantly lower in the Pamir Mountains compared to the Mongolian ranges, we may expect that weathering is also less intense there. Consequently input of PO_4^{3-} with surface and/or ground waters to the studied wetlands will be lower and P limitation more pronounced in plant communities from the Pamir Mountains. Moreover, P availability may be influenced by other interrelated factors affecting its mineralization and immobilization (i.a. soil mineralogical properties, soil moisture and texture, microbial activity), including increasing temperatures and aridity, that can result in soil C-N-P imbalance (e.g. Jiao et al., 2016; Tian et al., 2018).

4.2. Impact of local differences in soil chemistry on plant δ15N

Initially, we expected that plant $\delta^{15}N$ would separate samples from the Pamir Mountains from samples from the Mongolian ranges, reflecting intensity of N-limitation in the studied plant communities. Especially, as in samples from the Pamir Mountains no increase in plant N content was observed, that would confirm elevated plant N intake due to stress compensation processes. Yet, according to the obtained results, plant biomass from the Pamir Mountains and the Mongolian ranges was characterized by comparable $\delta^{15}N$ values, covering slightly broader range for Mongolia (from −2.97‰ to 9.66‰) than for Pamir (from −1.50‰ to 7.03‰) (see Supplementary materials, Table 1). Recorded $\delta^{15}N$ values were noticeably higher than values reported in the literature for similar plant communities (with dominating species from the *Cyperaceae* family) developed in high altitude habitats. According to Yang et al. (2015) values for two *Carex* species (*Carex foetida* and *Carex sempervirens*) in alpine vegetation in Swiss Alps were roughly between −1.5 and 2.5‰. Makarov et al. (2014) reported overall means of −1.47‰ for *Carex sempervirens* and −1.17‰ for *Carex umbrosa* in alpine lichen heath in Northern Caucasus, and Wu et al. (2019) a range between −0.3 and −1.5‰ for alpine meadows in Tibet. Our data, however, remain comparable with our previously published results from the Eastern Pamir (from −0.89‰ to 6.91‰ for communities dominated either by *Blysmus rufus* or *Carex microglochin* and *Carex orbicularis*) (Mętrak et al., 2018) and results of Zech et al. (2011), who gave $\delta^{15}N$ of 9.4‰ for biomass of spring turf under heavy pasturing, also from the Eastern Pamir. Due to high and uniform values of plant $\delta^{15}N$ recorded during our research, statistical analyses showed no significant correlations between plant $\delta^{15}N$ and regional drivers, and as such their potential influence on N fractionation remained indiscernible. Yet, according to our results, plant $\delta^{15}N$ was correlated with local soil features, most importantly with soil $\delta^{15}N$, which was slightly higher for the Mongolian ranges (regional means between 2.80‰ and 4.48‰) than for the Pamir Mountains (regional means between 2.25‰ and 2.69‰). Therefore, plant $\delta^{15}N$ was a good approximation of $\delta^{15}N$ of the available N in soil, even in high-mountain permafrost affected wetlands, where permafrost thawing can significantly influence isotopic composition of soils and vegetation (Finger et al., 2016; Keuper et al., 2012; Koven et al., 2011).

In our models the influence of soil $\delta^{15}N$ on plant $\delta^{15}N$ was modified by soil Na:EC ratio which is a salinity related factor reflecting proportion of Na^+ ions to all ions present in the soil. In soils rich in ions other than Na^+, decrease in Na:EC ratio means increase in overall soil salinity, and as such should be related with common plant response to salt stress. This response, just like plant response to water stress described in the previous chapter, is based upon osmotic adjustment, which can be viewed as a trade-off, where an inefficient N use is exchanged for efficient water use and tolerance of high soil salinity levels (MacTavish and Cohen, 2017; Rajasheker et al., 2019; Wang et al., 2015). Therefore, in saline habitats we can expect less intense N isotopic fractionation during plant uptake and, consequently, higher $\delta^{15}N$ values in plant biomass, especially in N poor soils. Such situation can be observed in samples from the West and East Khangai Mountains and the Khentei Mountains, where decreasing Na:EC values are correlated with increase in plant $\delta^{15}N$. In samples from the Pamir Mountains soil content of Ca^{2+} ions was over two times lower than in soils from the Mongolian ranges (means of 581 and 1523 mg/100 g, respectively, see Supplementary materials, Table 1), while content of other ions (Na^+, K^+ and Mg^{2+}) remained comparable. Therefore, in case of the Pamir Mountains, increase in Na:EC values may better reflect impact of sodium toxicity on the studied ecosystems. As Na^+ ions negatively affect plants, soil fungi and microbes (e.g. Gavazov et al., 2016; Rath et al., 2016; Zhang et al., 2017), they may cause non-directional changes in plant $\delta^{15}N$ at the community level, resulting in lack of trends and correlations between plant $\delta^{15}N$ and local and/or regional drivers.

Despite its significant impact on plant $\delta^{15}N$ at the community level, salinity was absent in our models of plant N:P ratio. A possible explanation can be the fact that plants have rather conservative stoichiometry relative to heterogeneity of their environment (Gong et al., 2017; Miller and Bowman, 2002; Zhang et al., 2013). Thus, N content in the biomass remains stable, while isotopic ratios change, as plant tries to preserve its species-specific stoichiometric equilibrium.

4.3. Limitations and perspectives

One of the main restraints for all studies based on modelling approach is representativeness of used databases, mostly in terms of spatial distribution of sampled material (see e.g. Craine et al., 2015; Reich and Oleksyn, 2004; Saradans et al., 2012 with underrepresented alpine habitats). In our case, more reliable and universal models of plant response to N availability could be probably constructed, if we included other Central Asian ranges in our studies. While due to obvious financial reasons it remains impossible to sample all the ranges ourselves, we see here a potential for collaboration with other scientists working on similar problems in arid and semi-arid mountains, in order to prepare a meta-analysis based on joint data. However, currently there are rather few articles dedicated to plant stoichiometry in arid alpine habitats available - apart from our previous articles, a short study by Zech et al. (2011) and research of Wu et al. (2019) and Gao et al. (2018), both performed on the Tibetan Plateau. Whereas our study focuses on selected habitat features as local drivers of plant response to N availability, there are several up-to-date articles describing connections between plant N management and species composition of the studied communities (e.g. Bruelheide et al., 2018; Gong et al., 2017; Palpurina et al., 2019). Thus, further research on biodiversity and species participation in wetland communities may add more information to the proposed models. Another promising research direction would be exploration of mechanisms behind greater N availability in the Pamir Mountains than in the Mongolian ranges. One of the most plausible processes leading to N enrichment in the permafrost-affected wetlands is permafrost degradation, that speeds-up internal N cycling and induces increase in available N (Keuper et al., 2012; Wang et al., 2013; Zhang et al., 2013). Therefore, current on-site measurements of permafrost depth and distribution, though small-scale and thus random, may give some clues concerning permafrost thawing and potential release of N. On the other hand, N availability may be influenced by microbe-related processes. Under low MAAT combined with high daily amplitudes of air temperature and relatively high soil salinity (conditions typical for the Pamir Mountains), microbes tend to allocate substrate toward maintenance functions (catabolic processes) rather than toward biomass production (anabolic processes). Therefore, their growth will be impaired and potential competition with plants over available N decreased, resulting in bigger pool of N available for plants (Rath et al., 2016; Reich and Oleksyn, 2004). Thus, careful research on microbial activity in the soils from alpine wetlands in arid and semi-arid areas would be beneficial for better understanding of the observed patterns of N limitation.

5. Conclusions

As it is shown by correlations and models based on our data from the Pamir Mountains and the Mongolian ranges, plant response to N availability expressed as plant N:P ratio is affected by geographical and climatic factors, either directly or indirectly, via the influence of regional drivers on soil properties (namely soil NH_4^+ content). According to threshold values of plant N:P ratio, in most of the studied plant communities N limitation was observed. However, due to specific climatic conditions influencing weathering processes, plant communities from the Pamir Mountains were strongly influenced by low soil PO_4^{3-} content and some of them were even P limited. Contrastingly, plant $\delta^{15}N$ showed no significant correlations with regional drivers, probably due to high and uniform values of plant $\delta^{15}N$ recorded in all studied regions. Thus, potential impact of regional drivers on N fractionation was concealed by effects of local drivers, among others N limitation of plant communities located in the Mongolian ranges. As plant $\delta^{15}N$ was strongly correlated with soil $\delta^{15}N$, it can be used as a good approximation of $\delta^{15}N$ of the available N in soil, even in high-mountain soils affected by permafrost. The proper choice of plant functional traits seems to be crucial in any experimental or modelling set-up, as their response to regional drivers can be modified or covered by influence of local factors.

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CRediT authorship contribution statement

Mętrak Monika: Conceptualization, Writing - original draft, Writing - review & editing.**Pokarowski Piotr:**Methodology, Formal analysis. **Sulwiński Marcin:**Methodology, Investigation.**Gantumur Altantsetseg:**Investigation.**Suska-Malawska Małgorzata:**Conceptualization, Writing - original draft, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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