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RESEARCH PAPER

The contribution of intraspecific trait variability to the functional diversity of herbaceous vegetation along a local environmental gradient

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ABSTRACT

Intraspecific trait variability reflects plant acclimation to habitats. In Central Forest Reserve (Tver' Region, Russia) we studied four herbaceous communities with several common species: managed and abandoned mesic meadows, tall-herb subruderal communities and *Filipendula ulmaria* communities. To estimate the contribution of intraspecific variability to community weighted means (CWM) and indices of functional richness, evenness and divergence, we used the data on leaf area, specific leaf area (SLA) and vegetative height, measured per community type and their mean values across communities. Plant height had a positive covariation with CWMs, while SLA mostly had a negative covariation. For CWMs of leaf area, the species turnover was more important than the intraspecific variability. The highest functional richness by all the traits was observed in abandoned meadows. In subruderal communities the intraspecific variability of SLA can compensate for the losses in species and functional richness.

Keywords: plant height, leaf area, specific leaf area, biomass, functional diversity indices

РЕЗЮМЕ

Елумеева Т.Г., Гаврилова Т.М., Чередниченко О.В. Вклад внутривидовой изменчивости признаков в функциональное разнообразие травяных сообществ на локальном экологическом градиенте. Внутривидовая изменчивость признаков отражает акклимацию растений к условиям местообитаний. В Центрально-Лесном заповеднике (Тверская область, Россия) мы исследовали четыре типа травяных сообществ с рядом общих видов: используемые и неиспользуемые мезофитные луга, субрудеральные высокотравные сообщества и таволговые сообщества. Чтобы оценить вклад внутривидовой изменчивости в средневзвешенные значения и индексы функционального богатства, выравненности и дивергенции, мы использовали данные по площади листа, удельной листовой поверхности (УЛП) и высоте вегетативных органов, измеренные в каждом типе сообществ, и их средние значения для всех сообществ. Для высоты растений отмечена положительная ковариация со средневзвешенными значениями, тогда как для УЛП ковариация была в основном отрицательной. Для средневзвешенных значений площади листа изменение видового состава было важнее, чем внутривидовая изменчивость. Наибольшее функциональное богатство по всем признакам отмечено на неиспользуемых лугах. В субрудеральных сообществах внутривидовая изменчивость УЛП может компенсировать потери видового и функционального разнообразия.

Ключевые слова: высота растений, площадь листа, удельная листовая поверхность, биомасса, индексы функционального разнообразия

Current herbaceous vegetation in the forest zone is established and maintained by human management. During millennia of their development, temperate grasslands have accumulated considerable biodiversity and therefore have a high conservation value (Habel et al. 2013, Dengler et al. 2014, 2016). After the management of temperate meadows stops, they often become overgrown with shrub, forest, or subruderal tall-herb vegetation (Valkó et al. 2018). While the changes in species diversity in abandoned meadows are well documented (Wehn et al. 2017), comparatively few studies focused on their functional diversity (Chelli et al. 2019), and even fewer studies were conducted for the European part of Russia (Cherednichenko et al. 2021). We studied the functional diversity of the managed meadows, abandoned meadows and tall-herb communities in Central Forest State Nature Biosphere Reserve (CFSNBR). These communities are spatially close to each other and share a lot of common species, but substantially differ by their productivity (Cherednichenko & Borodulina 2018, Elumeeva et al. 2024).

To study functional diversity the following approaches are often used: 1) the range of functional trait values; 2) the community weighted means (CWM) of traits (Lavorel et al. 2008), which are often strongly influenced by the trait values of dominant species; therefore, CWMs can significantly differ from the means (Onipchenko et al. 2022); 3) the functional diversity (FD) indices (Mason et al. 2005, Schleuter et al. 2010); among them functional

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richness (FRic), functional evenness (FEve) and functional divergence (FDiv) are commonly used. Although the indices can be calculated using both single traits and multiple traits (Laliberté et al. 2014), the single trait indices can be easily explained by environmental gradients (Butterfield & Suding 2013, Dudova et al. 2019, Onipchenko et al. 2022, Wu et al. 2023), while the multitrait FRic can be affected by the number of traits included (Legras et al. 2020). Therefore, interpreting the results and comparing the values of multitrait indices between studies is challenging.

The differences between CWMs and FD indices calculated for different plant communities emerge from the changes in species composition (species turnover) as well as from the intraspecific variability of trait values (Lepš et al. 2011). Intraspecific trait variability is important for between-community estimations (Albert et al. 2010, Siefert et al. 2015, Funk et al. 2017), though its patterns do not always follow those of CWMs (Onipchenko et al. 2020). On the contrary, close CWM values can be obtained in communities with totally different species composition which developed under similar ecological conditions (Elumeeva et al. 2015). The method of Lepš et al. (2011) for decomposing the variance of CWMs caused by species turnover and intraspecific variability was used to evaluate their role in community structure along environmental gradients (Kichenin et al. 2013, Volf et al. 2016, van Zuijlen et al. 2022, Govaert et al. 2024).

Thus, we aimed to reveal the pattern of functional diversity in the range of herbaceous communities in CFSNBR and to evaluate the contribution of intraspecific variability to this pattern.

MATERIAL AND METHODS

Study area

Central Forest State Biosphere Reserve (Tver' Region, Russia) is located in the SW part of the Valdai Upland within the main Caspian-Baltic watershed of the Russian plain (latitude: 56°26'–56°39'N, longitude: 32°29'–33°01'E). The climate is humid continental (Minayeva & Shaposhnikov 1999) with the mean annual temperature of +4.5°C and the mean annual precipitation of 764.9 mm for the period 1963–2020 (Shuyskaya 2022). The reserve area is mostly covered with spruce and mixed secondary forests, while the semi-natural meadows occupy less than 1 % of the territory (Kurayeva et al. 1999). The managed (MMM) and abandoned (AMM) mesic meadows as well as *Filipendula ulmaria* tall-herb communities (FTC) belong to the class Molinio–Arrhenatheretea R. Tx. 1937. The subruderal tall-herb communities (SRC) belong to the class Epilobietea angustifolii Tx. et Preising ex von Rochow 1951 and replace the abandoned meadows over time (Cherednichenko & Borodulina 2018). The productivity of the studied communities increases in a row: AMM, 930 g/m^2 → MMM, 1111 g/m^2 → FTC, 1357 g/m^2 →SRC, 1726 g/m^2. The sites of FTC are moister and richer with labile nitrogen than those of other communities (Elumeeva et al. 2024). The nomenclature of vascular plants is provided according to POWO (2005).

Field sampling

Based on the previous studies (Cherednichenko & Borodulina 2018), we selected four relevés with a typical species composition in each herbaceous vegetation type (MMM, AMM, SRC and FTC, 16 plots in total). In 2019 and 2020 years we sampled 6–8 aboveground phytomass cuts of 0.0625 m^2, in total 59 samples in MMM, 57 samples in AMM, 63 in SRC and 62 in FTC. Then we sorted the biomass by species of vascular plants, dried in the oven until constant mass was achieved and weighed. The biomass of every species per relevé was summarized and expressed as g/m^2.

We measured three functional traits: leaf area (LA), specific leaf area (SLA) of a dry leaf, and plant vegetative height (H) for the most common plant species using the standard protocols (Pérez-Harguindeguy et al. 2013, Dudova et al. 2019). Among these traits, plant height and SLA contributed to the first and the second principal components in the multivariate trait space of temperate grassland species in Europe (Ladouceur et al. 2019).

To consider the intraspecific variability, for some species we measured the traits in two or more communities where they occurred. The data on height was obtained for 91 species, with 12 species measured in all the four communities, 20 species in three communities and 22 species in two communities. Leaf traits were measured for 92 species, where 15 species occurred in all the four communities, 20 species in three communities and 22 species in two communities. The most of species had both height and leaf measurements, while few species lacked one of them, and few species occurred in the biomass samples at low abundance and therefore were not measured. The mean trait values and the mean biomass of species with measured traits are given in Supplementary material.

Data analysis

Prior to the analysis, we compiled two sets of data tables: 1) the tables with biomass and trait values of species, where the mean trait value was calculated using all the samples from the study area (fixed means); 2) the tables with biomass and trait values of species, where the mean trait value was calculated per community type (specific means). In this case we treated the combination "species – community type" as a "species". Few species were present in the biomass samples, but their traits were not measured for the given community. In this case we used fixed means for "species – community type" combinations.

For every trait, we calculated the CWMs in the FD package (Laliberté & Legendre 2010) in two ways: with fixed means (CWMfixed) and with community-specific means (CWMspecific). Then, according to the approach of Lepš et al. (2011), we calculated the difference between CWMspecific and CWMfixed to estimate the contribution of intraspecific variability to the variability of CWMs by communities (CWMintra). We also used the fixed and community-specific trait values to calculate FRic and FEve indices in the FD package, and the FDiv index by the exact formula following Schleuter et al. (2010).

To compare the CWMs and FD indices between the studied communities, we applied one-way analysis of variance

(ANOVA) followed by post-hoc Tukey HSD test. Then we used a paired Student's t-test to assess the significance of the differences between fixed and community-specific values.

To disentangle the effects of species turnover and intraspecific trait variability on CWMs and to estimate the directions of the intraspecific variability, we ran three sets of ANOVAs: 1) with CWMfixed, 2) with CWMspecific, and 3) CWMintra and compared the sums of squares for the residual deviations between the models according to Lepš et al. (2011). When the residual sums of squares SSspecific = SSfixed+SSintra, species turnover and intraspecific variability vary independently, but when SSspecific is higher or lower, there is a positive or negative covariation between them. We conducted this analysis for every pair of communities (MMM vs AMM, MMM vs SRC, MMM vs FTC, AMM vs SRC, AMM vs FTC, and SRC vs FTC).

RESULTS

Plant vegetative height

The CWM height increased in the order: MMM (55 and 54 cm, mean CWMfixed and CWMspecific, correspondingly) → AMM (58 and 55 cm) → SRC (72 and 73 cm) → FTC (94 and 119 cm). The species with the height values close to the CWMs were *Trifolium medium*, *Lolium pratense*, and *Vicia cracca* in both the abandoned and managed meadows, *Lathyrus pratensis* and *Centaurea phrygia* in SRC, and *Lysimachia vulgaris* and *Filipendula ulmaria* in FTC (Fig. 1A). The CWMfixed and CWMspecific differed significantly in MMM and FTC. We observed a positive covariation along the productivity gradient and a high contribution of intraspecific variability for FTC compared with the other communities (Fig. 2A). Thus, besides the tall species increased in abundance, the plant height itself increased in FTC compared with the meadows. The species turnover was important for the pair SRC and MMM (Fig. 2A).

The FRicspecific for the plant height differed significantly in MMM and FTC (Fig. 1D). FEve was rather low and did not differ between the communities; however, in the *Filipendula* community the FEvespecific was lower than the FEvefixed. The functional divergence was the highest in FTC and the lowest in MMM. In SRC the FDivspecific was lower than the FDivfixed in SRC, and in FTC the contrary was observed.

Leaf area

The CWMs of the leaf area increased in the order: MMM (25 and 24 cm^2, mean CWMfixed and CWMspecific, correspondingly) → SRC (34 and 39 см^2) →AMM (83 and 27 cm^2) → FTC (134 and 141 cm^2). The leaf areas close to CWMs were observed for *Knautia arvensis*, *Ranunculus acris*, *Lolium pratense*, *Leontodon hispidus*, *Pimpinella saxifraga* in MMM; for *Geranium palustre* and *Centaurea phrygia* in AMM; for *Knautia arvensis*, *Urtica dioica*, *Alchemilla vulgaris* in SRC; for *Filipendula ulmaria* and *Anthriscus sylvestris* in FTC. The leaves were typically larger in the species of the *Filipendula* community. In AMM the CWMspecific was significantly lower than the CWMfixed (Fig. 1B). The covariation between species turnover and intraspecific variability was positive in the pairs of MMM–SRC, AMM–SRC and AMM–FTC, but negative in the pairs of MMM–AMM and AMM–SRC, where the plants of AMM tended to have larger leaves, and some individual species increased their leaf area in this community. In general, the contribution of intraspecific variability of the leaf area to between-community differences in CWMs was not significant (Fig. 2B).

The FRic of the leaf area did not differ significantly between the communities. AMM and FTC had FRicfixed=1; thus, all the plots contained species with the highest and the lowest leaf area. The maximum FRicspecific occurred in FTC, while in the other communities it was significantly lower (Fig. 1E). The leaf area FEve did not differ between the communities, but in FTC the FEvespecific was lower than the FEvefixed (Fig. 1H). All the communities showed high functional divergence, in SRC it was significantly lower than in FTC. In MMM the FDivspecific was lower than the FDivfixed.

Specific leaf area

The specific leaf area increased in the order: FTC (222 and 241 cm^2/g, mean CWMfixed and CWMspecific, correspondingly) → MMM (254 and 238 cm^2/g) → SRC (272 and 257 cm^2/g) → AMM (279 and 275 cm^2/g). The typical specific leaf areas for the given communities were observed for *Briza media*, *Lathyrus pratensis*, *Leontodon hispidus*, *Trollius europaeus*, and *Vicia cracca* in MMM, *Fragaria vesca*, *Geranium palustre*, and *Potentilla erecta* in AMM, *Cirsium arvense*, *Dactylis glomerata*, and *Hypericum maculatum* in SRC, and *Filipendula ulmaria*, *Cirsium palustre*, *Geum rivale*, and *Succisa pratensis* in FTC. CWMfixed and CWMspecific differed significantly in MMM and FTC (Fig. 1C). The intraspecific variability significantly influenced CWMs; however, in most cases, in contrast to the size traits, there was a negative covariation (Fig. 2C). In FTC, species with a lower SLA increased in abundance, while the SLA of individual species became larger (Fig. 1C). At the same time, we observed a positive covariation between species turnover and intraspecific variability in MMM-AMM communities, where species with a high SLA prevailed in AMM, and the SLA of individual species increased from managed to abandoned meadows.

The specific leaf area FRicfixed was higher in the meadows than in the tall-herb communities, but the FRicspecific did not differ between the communities (Fig. 1F). The FRicspecific was lower than the FRicfixed in all the communities except SRC. Neither FEvespecific nor FEvefixed differed between the communities (Fig. 1I). The FDiv decreased from the meadows to the tall-herb communities (Fig. 1L). In FTC the FDivfixed significantly exceeded the FDivspecific.

DISCUSSION

Intraspecific variability refers to acclimation of individuals to certain habitats, while interspecific variability shows adaptations of species (Dong et al. 2020). Our study confirms the importance of intraspecific trait variability for calculating community weighted means and functional diversity indices along a local environmental gradient, where plant communities share a substantial part of species from the local pool, which are all adapted to macroclimatic and

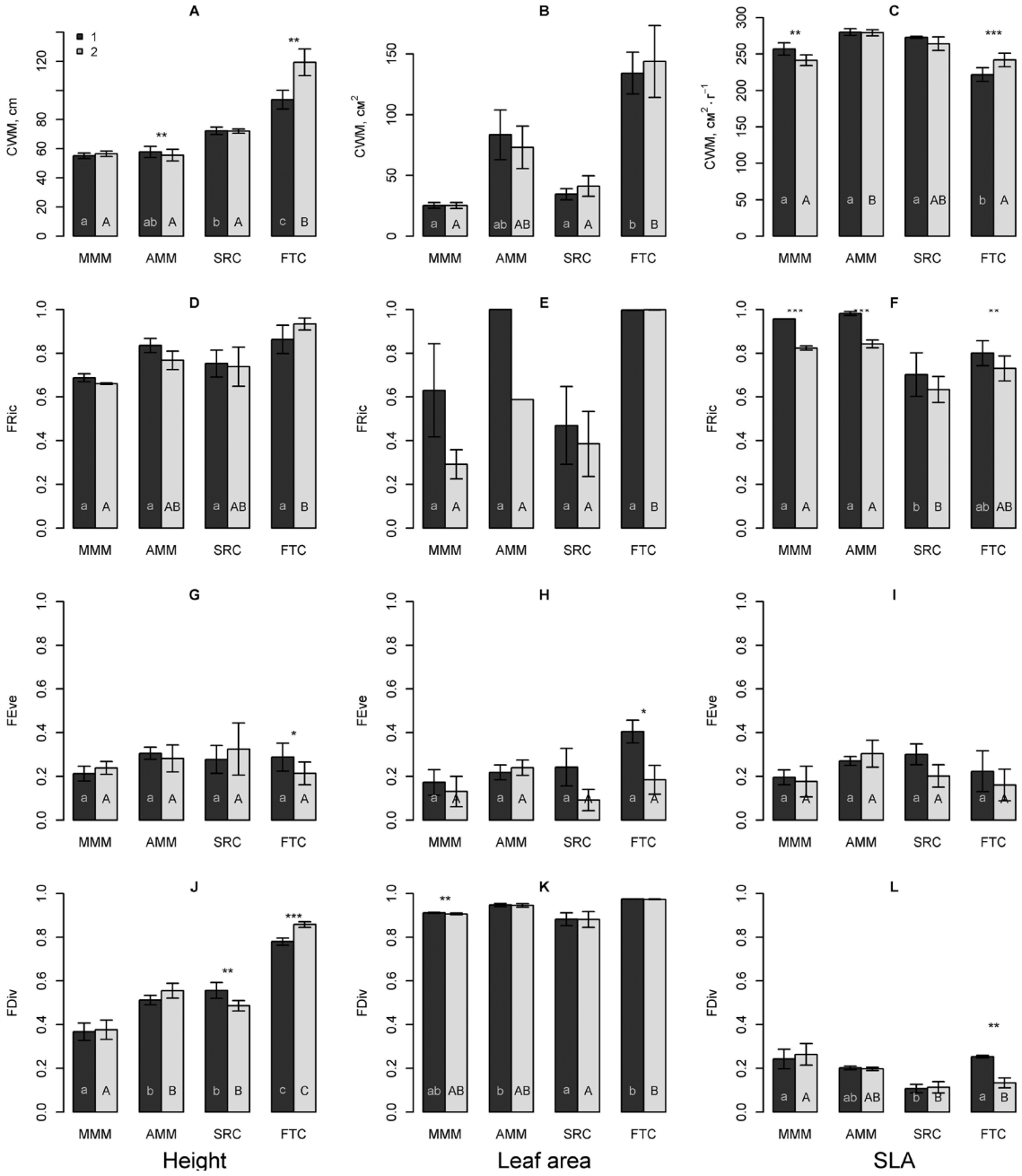

Figure 1 Community weighted means (CWM, A–C) and functional diversity indices (D–L) for plant vegetative height (A, D, G, J), leaf area (B, E, H, K) and specific leaf area (SLA; C, F, I, L). FRic – functional richness, FEve – functional evenness, FDiv – functional divergence. 1 – fixed values. 2 – community specific values. The same letters show communities without significant differences by the results of one-way ANOVA ($p<0.05$). Asterisks show communities, where fixed and specific values differ by the results of a paired Student's t-test. * – $p<0.05$, ** – $p<0.01$, *** – $p<0.001$

geochemical environment, but are to fit in the given conditions of light, moisture, and nutrient availability. Here, the role of species turnover can be relatively low and expressed mostly as the shifts in dominance. The studied traits, namely vegetative height, leaf area, and specific leaf area, showed different patterns of intraspecific variability effects on the functional diversity in the neighboring herbaceous communities.

The positive covariation of plant height inter- and intraspecific variability suggests that if the conditions are favorable for taller species, all species tend to grow taller. This pattern was described for managed grasslands with mowing and nutrient addition (Lepš et al. 2011, Volf et al. 2016), so our data confirmed it for semi-natural herbaceous communities. In contrast to open habitats, negative covariation was reported for the height of understorey herbs (Govaert et al. 2024).

It is interesting to compare the changes in the community weighted means of leaf traits along the productivity gradient of non-managed vegetation. Compared with AMM, plants with a smaller leaf area prevailed in SRC and those with a larger leaf area in FTC. The specific leaf area significantly decreased in FTC compared with AMM but did not change in SRC. SLA is positively correlated with Ellenberg's indicator values of nutrients across a range of boreal species (Dalke et al. 2018), so species of more productive habitats tend to have a higher SLA. On the contrary, the increase in leaf area CWMs in the *Filipendula* communities indicates that

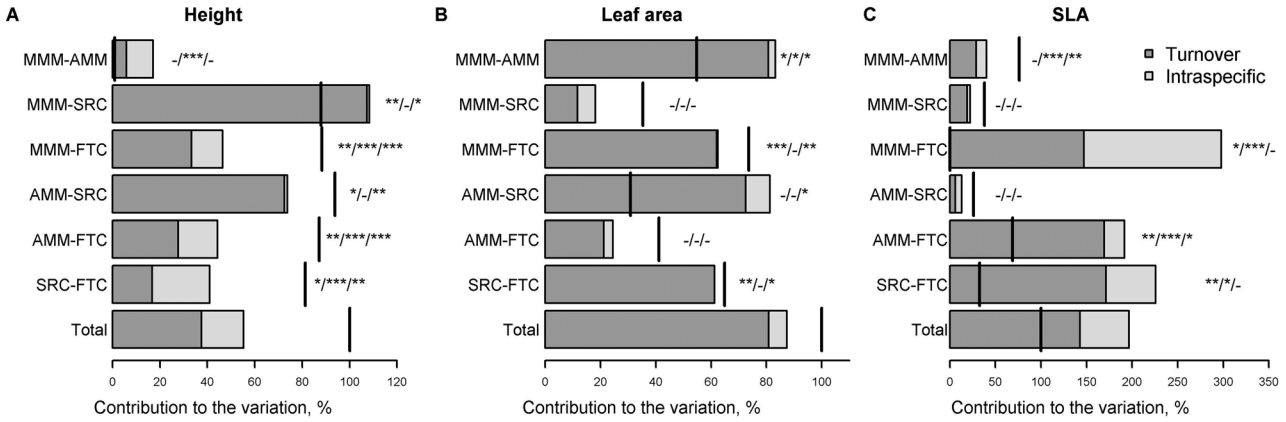

Figure 2 The contribution of species turnover and intraspecific trait variability to explained variance between the pairs of communities, and to the total between-community variability (Total). Dark gray bars show species turnover, light gray bars – intraspecific variability. Vertical lines show the variance, explained by the community factor for the pairs of communities and the total specific variance for the between-community variability. The space between bars and lines indicate positive covariation. If the bars are close to the vertical lines, the species turnover and intraspecific variability are independent of each other. If the bars cross the lines, there is negative covariation. The significance of turnover, intraspecific variability and specific variability are shown by asterisks within -/-/- graphic. * – $p<0.05$, ** – $p<0.01$, *** – $p<0.001$. MMM – managed mesic meadows, AMM – abandoned mesic meadows, SRC – subruderal communities, FTC – *Filipendula* tall-herb communities

plants with larger leaves prevail here, but a larger leaf area at the interspecific level requires more ground tissues and therefore leads to a subsequent decrease in SLA (Milla et al. 2008). Thus, the most productive communities studied showed contrasting patterns of leaf trait CWMs under the relatively dry conditions of SRC and wet conditions of FTC. Interspecific and intraspecific variability of SLA CWMs has a negative covariation along a subalpine-alpine elevation gradient in New Zealand (Kichenin et al. 2013), in temperate forest understorey (Govaert et al. 2024) and in temperate grasslands in response to mowing, but not fertilization (Lepš et al. 2011), and short-term management by mowing and grazing (Volf et al. 2016).

Among the communities of a succession series MMM–AMM–SRC, the abandoned mesic meadows show the highest FRicfixed values calculated using all the three studied traits. The high functional richness of this community type can be explained by its successional status when it contains species of both earlier and later stages. Therefore, the intraspecific variability decreases the ranges of leaf area and SLA values indicating the adaptation of species with generally high and low trait values to a given environment. Our evidence suggests that after abandonment mesic meadows further change to subruderal tall-herb communities. Here the FRicfixed of the leaf traits decreased, but in the case of SLA FRicspecific exceeded FRicfixed and did not differ from that of AMM, so intraspecific variability can compensate for the loss of species with marginal trait values. Therefore, the loss of meadows in the protected area of CFSNBR can result in the decrease in both the species number and the functional diversity. We believe that to protect the abandoned meadows of CFSNBR against overgrowing with subruderal communities low-intensity mowing should be implemented.

Functional evenness was rather low for all the traits and between all the communities. The *Filipendula* community was the only one where the fixed and specific values of vegetative height and leaf area significantly differed. The intraspecific variability reduced the evenness at the high divergence suggesting intensive competition for light in the productive tall-herb community.

Functional divergence varied depending on the traits. The leaf area showed the strongest divergence in all the communities. The FDiv values calculated using the height consistently increased along the productivity gradient indicating the increasing competition for light. The SLA divergence was consistently low, but the most productive SRC and FTC significantly differed by FDivfixed, with SRC being significantly less divergent than FTC. Nevertheless, including intraspecific variability reduced FDiv, so in both communities FDivspecific did not differ.

CONCLUSIONS

Herbaceous vegetation along a local environmental gradient in the forest zone is represented by functionally diverse communities. Thus, calculating CWMs in communities with a number of common species, it is important to consider the intraspecific trait variability. Our data show that in herbaceous communities the intraspecific variability of plant vegetative height and specific leaf area may influence the CWMs and FD indices.

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