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Trait-based numerical classification of mesic and wet grasslands in Poland

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Running title
Trait-based classification of grasslands

Abstract
**Questions:** What vegetation types can be distinguished on the basis of plant functional traits using numerical classification? How do they match syntaxonomical units?

**Location:** Poland

**Methods:** 6985 vegetation plots representing mesic and wet grasslands (*Molinio-Arrhenatheretea, Polygono-Poetea*) were retrieved from the Polish Vegetation Database. Plant functional trait data were assembled from the LEDA and Clo-Pla databases for most species occurring in the data set. Community-weighted mean for five traits were calculated for each plot: specific leaf area, canopy height, seed mass, bud bank index and clonality index. Plots were classified using Ward’s method and iterative relocation based on silhouette widths. The clusters were interpreted and characterized on the basis of species and trait composition, functional diversity, functional redundancy, Ellenberg indicator values, and geographical distribution. The similarity between the trait-based classification and the syntaxonomical assignment of plots is evaluated both statistically and by expert knowledge.

**Results:** Twelve clusters were distinguished. The classification mirrored the main gradients structuring grasslands in Poland, although, some vegetation types with the strong dominance of functionally unique species appeared more distinct than they are treated in syntaxonomy. Clusters did not differ significantly in functional diversity and redundancy. The differences of clusters in species and trait composition and environmental background are discussed.

**Conclusion:** The application of trait data and numerical methods is a promising approach for obtaining vegetation classifications. Such classifications can be in closer relationship with the most important ecosystem processes than floristic classifications because communities comprising different species but similar functional trait distribution are not separated. Trait-based classifications match phytosociological units to a variable degree. Functional uniqueness and variation of abundance determines how individual species influence the delimitation of vegetation types using our approach.

**Keywords**

Introduction

Due to its central role in ecosystem processes, vegetation characteristics are frequently used as general descriptors of ecosystems or habitat types for the purposes of nature conservation, land-use planning, and landscape mapping. Vegetation-plot databases are widely used for establishing classifications, very often with the application of statistical methods (De Cáceres et al., 2015). Such databases contain tens or hundreds of thousands of species by site records collected during the long history of phytosociology, often with additional data on vegetation physiognomy, geographical location and environmental background (Dengler et al., 2011).

These data sources make it possible to answer questions about vegetation variation on scales as broad as countries or continents. As the essential type of data which is recorded in these plots with the highest consistency is species occurrence (and often some form of abundance), most typically these analyses use species as variables and sites as objects. In consequence, the classifications reflect patterns in species composition, together with all the possible mechanisms which influence community assembly, including selection, speciation, dispersal, and drift (Vellend, 2010). However, some of these processes, e.g. random drift, may not be interesting from the viewpoint of the potential user of the classification. Limited dispersal of species has strong consequences on classification results. If the sample includes areas with different site history, which is a common situation, species may not have had enough time to colonise all habitat patches which would have been suitable for them. In this case, a classification based on species composition will reflect not only environmental gradients but differences in regional species pools. When the geographical extent of the study is very large, and the effect of site history is strong, it can become impossible to reach a vegetation classification reflecting environmental gradients, which would be valid over the entire study area. This might be a primary reason for the high level of idiosyncrasy in national vegetation classifications. Patterns of speciation are mainly relevant on biogeographic scales in time and space; although, in specific studies differences in the phylogenetic structure of communities may be important (Lososová et al. 2015). Nevertheless, most vegetation classification studies seek answers for questions about what types of communities exist, and how their occurrence is related to environmental gradients, and ecosystem functions – i.e., the process of selection. However, it is increasingly recognised that patterns in species identities are not always tightly related with ecosystem properties, instead, traits of species are more relevant from this perspective (Díaz & Cabido, 2001; Diaz et al., 2004). Species respond to biotic and abiotic factors by their traits (response traits), as well as they form their environment by them (effect
traits; Lavorel & Garnier, 2002). Species which have similar traits may substitute each other without significantly altering ecosystem functioning – a phenomenon called functional redundancy (Hooper et al., 2005). Integrating the trait-based approach should improve the relevance of vegetation classification with respect to ecosystem functioning, and enhance the generalizability of results. Hérault and Honnay (2007) already presented a classification where instead of species, groups of species sharing similar traits called ‘emergent groups’ were applied as variables. Hence, it was possible to differentiate two types of riverine forests in Luxembourg different in life-form spectra, dispersal modes, and conservation relevance. However, this study restricted its scope on a specific vegetation type of a rather narrow area, while the most typical challenge of recent vegetation classification works is providing relevant and generalizable results over broad sample coverage in space and along ecological gradients.

The functional approach of ecology has been in an intensive research period now for more than a decade, partially shifting the focus away from the study of patterns of species-level composition and diversity (Carlow, 1987; Tilman et al., 1997; McGill, Enquist, Weiher, & Westoby, 2006). A major outcome of this field is the emergence of plant trait databases, which provide trait measurements for thousands of taxa and hundreds of traits (Kattge et al., 2011). Technically they are readily connectable with vegetation-plot databases, providing avenues for the same types of analyses of trait composition which has only appeared at the level of species yet. A fundamental question of trait-based ecology is the distinction between processes which impedes the co-existence of functionally similar organisms (i.e. functional divergence) and those which promotes it (i.e. functional convergence; Lhotsky et al., 2016). Competitive exclusion is known to increase divergence according to the theory of limiting similarity, while environmental (or niche) filtering (and, for traits increasing competitive vigour, also competitive exclusion) supports functional convergence (Weiher & Keddy, 1995). Considering the interest of vegetation classification studies in the response of vegetation to environment, trait convergence should be a key phenomenon in the construction of functionally relevant classifications. Moreover, competitive exclusion is subordinated to environmental filtering according to the filter model of community assembly (Keddy 1992), which is a likely reason why trait convergence is more frequently detected than divergence.

In this paper we present a trial for integrating the functional approach into the context of vegetation classifications using multivariate statistical methods. Our aim is to classify semi-natural grasslands of Poland in a way that resulting groups are relatively similar in their trait
composition with no respect to species composition. We discuss the environmental
background, trait composition, functional diversity, and redundancy of the clusters
distinguished. We assess the similarity between the trait-based classification and the
syntaxonomical system. We expect the resulting classification to be generalizable over the
entire study area, while showing a strong relationship with ecosystem processes.

Materials and Methods

9725 phytosociological relevés representing temperate semi-natural grasslands were retrieved
from the Polish Vegetation Database (Kącki & Śliwiński, 2012; GIVD identifier: EU-PL-
001). In the syntaxonomical system according to Kącki, Czarniecka and Swacha (2013), these
grasslands are classified to *Molinio-Arrhenatheretea* class and comprise three orders, called
*Potentillo-Polygonetalia* (temporarily flooded and heavily grazed and trampled vegetation on
nutrient-rich soils), *Arrhenatheretalia elatioris* (lowland and montane mesic grasslands), and
*Molinietalia caeruleae* (wet grasslands and tall-forb vegetation). We included into the data set
also *Polygono arenastri-Poetea annuae* with one order *Polygono arenastri-Poetalia annuae*
(therophyte-rich dwarf-herb vegetation of trampled habitats) because it strongly resembles
heavily trampled pastures of the *Cynosurion* alliance (*Arrhenatheretalia*). *Polygono-Poetea
annuae* was treated as part of the *Molinio-Arrhenatheretea* in previous syntaxonomical
overviews in Poland. Plot size was restricted to 10 to 100 m². Moss and lichen species were
removed from the data set due to their uneven data availability across plots. Where species
covers were recorded on ordinal scales (e.g. Braun-Blanquet scales, which is ca. 90% of all
plots) cover categories were transformed to their respective mid-point percentages using the
JUICE software (Tichý 2002). Relevés with >5% cover of trees and shrubs were excluded.
The data set was subjected to geographical stratification and heterogeneity constrained
random resampling (Knollová, Chytrý, Tichý, & Hájek, 2005; Lengyel, Chytrý, & Tichý,
2011) using Bray-Curtis index calculated on square-root transformed abundance data. Strata
were 6’×10’ in size. From each stratum the number of plots to select was determined as 5 +
(n-5) × d, where n is the total number of plots in the stratum and d is the mean pairwise
dissimilarity among plots within the stratum. This method down-weighted the contribution of
oversampled areas only if their beta-diversity was low, while intensively sampled but diverse
regions kept their high share (Wiser & De Cáceres 2013). No resampling was done in strata
containing five or less plots. The stratified resampling reduced the data set to 6985 plots.
A key decision in any trait-based study is the selection of traits to involve in the analysis. According to Westoby (1998) and Westoby, Falster, Moles, Vesk, and Wright (2002), the traits of the leaf economics spectrum (Wright et al., 2004), the height, and the seed represent the major dimensions of plant variability along the most typical ecological gradients (the so-called leaf-height-seed or LHS system). Leaf traits, especially specific leaf area (SLA; Cornelissen et al., 2003) are in close connection with resource acquisition and relative growth rate, and thus related to the productivity of the habitat (Wilson & Tilman, 1993; Lhotsky et al., 2016). Canopy height is positively correlated with the ability to outcompete other species in productive habitats, where light is the major limiting factor (e.g. Borer et al., 2014), while seed mass corresponds to reproduction strategy (e.g. Moles & Westoby, 2004). Besides LHS traits, there is growing evidence that clonal growth and bud bank are important in the adaptation of plants to regular disturbance, hence they have central role in the response of herbaceous vegetation to environment (Klimešová, Tackenberg, & Herben, 2016). Clonal growth enables plants to avoid disturbance, while bud bank is key in regeneration after minor damages. Five plant traits were included in the analysis, which can be regarded as the response traits that play the most fundamental role in the adaptation of plants to the environment and management regime. Specific leaf area (SLA), canopy height and seed mass were retrieved from the LEDA database (Kleyer et al., 2008). The ‘bud bank’ and the ‘clonality’ index were introduced according to Johansson, Cousins and Eriksson (2011) and E.-Vojtkó et al. (2016). Bud bank index is the rank sum of above- and belowground bud bank categories, while clonality index is the rank sum of lateral spread and total number of offspring per parent categories. These data were obtained from the Clo-Pla database (Klimešová, Danihelka, Chrtek, de Bello, & Herben, 2017). All measurements were subjected to a semi-automated outlier exclusion and averaging procedure for each species by traits. First, the mean and standard deviation of all measurements from a given species and given trait was calculated. Those measurements which differed by >2*SD from the mean were excluded. The remaining measurements were subjected to averaging weighted by the square-root of the number of replications given for each measurement in the public database (typically, the number of measured individuals for a given record). For species which lacked no more than two out of the five trait values, Bayesian Hierarchical Matrix Factorization (Schrodt et al., 2015) was used to fill the gaps in the trait table. Species with more than two missing trait measurements were rejected from the analysis resulting in 885 species in the final matrix. Plots where the relative cover of such rejected species was higher than 5% were excluded before the stratified resampling. Species-level mean trait values were checked for...
normality by quantile-quantile plots. Since LHS traits proved to be right-skewed, they were log-transformed. Then, all traits were standardized to mean = 0 and standard deviation = 1. These species-level standardized means were used for calculating community-weighted means (CWM; Garnier et al., 2004), which is considered a satisfactory indicator of niche filtering along large-scale environmental gradients (Kleyer et al., 2012; De Bello et al., 2013). The CWM is constrained by the relative dominance of the most dominant trait value in the plot; therefore we expect species forming monodominant vegetation stands to have a high influence on the classification (De Bello, Lepš, Lavorel, & Moretti, 2007). This conforms the mass ratio hypothesis by Grime (1998) stating that ecosystem functioning is mainly determined by traits of the dominant species.

Hierarchical classification was carried out by Ward’s agglomerative method (Podani, 2000) on the matrix of CWM values. Ward’s method relies on Euclidean distances in the trait space between plots. The upper 20 hierarchical levels of the classification were evaluated by several cluster validity indices (see Appendix S1); however, they suggested different numbers of clusters as optimal making it impossible to decide on a single ‘best’ solution. To overcome this, on the one hand, we considered also the biological interpretation of the clusters and the resolution desired typically in such large-scale classifications. Hence, the dendrogram was cut at a particular level and then it was improved using iterative relocation methods (Roberts 2015). Most iterative relocation methods proposed by Roberts (2015) are computationally very demanding; therefore, we applied the REMOS2 algorithm (Lengyel, Roberts, & Botta-Dukát 2019). This procedure uses the silhouette width index (Rousseeuw 1987) to identify misclassified objects, which are then re-assigned to their closest neighbour cluster. After re-assignment, silhouette widths are updated, and misclassified plots are relocated again to their closest neighbour cluster, until the classification cannot be further optimized. This has changed the assignment of 31.58% of all plots. However, we did not change the hierarchical relations of the basic clusters.

Delimited clusters were interpreted as biologically relevant units using expert-based knowledge and we attempted to find correspondence to already known and well-defined vegetation units in the traditional (floristic) syntaxonomical approach (Kącki et al., 2013). For this purpose, phytosociological relevés were assigned to syntaxa at the class, order, and alliance levels using their formal definitions. Relevés were classified to respective syntaxa based on explicit definitions of vegetation units in the way that the relevé matched by the definition of alliance must also match the definitions of the superior syntaxonomical units, i.e.
order and class. This classification system was created using combination of sociological species groups (Bruelheide, 1997), and total cover of individual species or group of species (Kočí, Chytrý, & Tichý, 2003; Dengler et al., 2006; Landucci, Tichý, Šumberová, & Chytrý, 2015), and is part of an ongoing project of vegetation classification in Poland. The outcome of this classification is presented in the shortened synoptic table (Appendix S2). Assignments at order and alliance levels were compared with the trait-based classification using the symmetric version of Goodman and Kruskal’s lambda index (Goodman & Kruskal, 1954). To assess the strength of similarity, the observed lambda values were compared to a reference distribution obtained by re-calculating the index after permuting the trait-based classification 9999 times. In total, five tests were performed: 1) class-level assignment vs. trait-based classification with random permutation; 2) order-level assignment vs. trait-based classification with random permutation; 3) order-level assignment vs. trait-based classification with restricted random permutation using class-level assignment as strata; 4) alliance-level assignment vs. trait-based classification with random permutation; 5) alliance-level assignment vs. trait-based classification with restricted random permutation using order-level assignment as strata. We report the P-values of the null hypothesis stating that the similarity between the trait-based classification and the syntaxonomical assignment is as high as we can observe due to chance. We also show the standardized effect sizes of the observed values calculated by probit transformation (Botta-Dukát, 2018).

For each level of the hierarchical classification until reaching the level of basic clusters and for each trait a Wilcoxon test was carried out to test the difference between the two clusters to be merged in the respective fusion. Two-tailed P-values were calculated by using permutation tests (Hothorn, Hornik, van de Wiel, & Zeileis, 2006). Bonferroni-corrected P-values and standardized test statistics ($W_{st}$) were used for ranking traits by support to the tested fusions.

Distribution of CWMs across clusters are shown on ‘boxes-and-whiskers’ plots. Clusters are also compared on the basis of functional vulnerability measured by Rao Q diversity index (Botta-Dukát, 2005), and functional redundancy (Ricotta et al., 2016). We also provide synoptic tables containing diagnostic, constant and dominant species, Ellenberg indicator values (EIV; Ellenberg et al., 1992), and geographical distribution of the clusters as Appendices S3-S5. Statistical comparison of clusters on the basis of variables dependent on compositional information (e.g. diversity indices, aggregated species attributes) often result in false positive tests due to the so-called ‘similarity issue’ (Zelený & Schaffers, 2012; Zelený, 2018) and other structural biases (Hawkins et al., 2017) if the same occurrence information
had been used for the definition of clusters. To avoid false conclusions we refrain from formal statistical tests in the case of between-cluster comparisons and present only boxes-and-whiskers plots.

To measure the influence of individual species on the trait-based (especially, CWM-based) classification we used a simple formula, that we call ‘influence index’. That species affects CWM of a single community (e.g., a single relevé) the most, which has high abundance and highly different trait value from the other species in the community. If the variation of CWM across several communities is examined, species with highly variable abundance and unique trait values are supposed to be the most influential. Thus, we calculated the influence index for the kth species as follows:

\[ I_k = \sqrt{D_{k} \times SD(a_k)} \]

where \( D_{k} \) is the distance of the kth species from the unweighted mean of trait values of all species in the data set (‘uniqueness’), and \( SD(a_k) \) is the standard deviation of the abundance vector of species k (‘variation of abundance’). Thus, the influence index is the geometric mean of two components, functional uniqueness and variation of abundance. We recommend to re-scale both \( D_{k} \) and \( SD(a_k) \) by division by the maximum, respectively.

Calculations were carried out by the R software (R Core Team, 2017) using vegan (Oksanen et al., 2018), cluster (Maechler, Rousseeuw, Struyf, Hubert, & Horni, 2017), FD (Laliberté, Legendre, & Shipley, 2014), raportools (Blagotić & Daróczki, 2015), and coin (Hothorn, Hornik, van de Wiel, & Zeileis, 2008) packages. Nomenclature of plants follow the Euro+Med PlantBase (last accessed on 27 Sep 2018), syntaxon names are according to Kącki et al. (2013).

**Results**

Most cluster validity measures indicated a peak value between 2 and 5, as well as another peak near 10 clusters (Appendix S1). After considering non-formal criteria, we chose the level of twelve basic clusters for the interpretation because it provided a reasonable compromise between details and conciseness; however, coarser solutions can easily be assembled from this fine-scale classification by merging low-level clusters according to the dendrogram fusions (Fig. 1). Distribution of CWM values across clusters is shown on Fig. 2. Synoptic tables and
textual descriptions of the clusters are presented in Appendix S3, EIVs in Appendix S4, and geographic distributions in Appendix S5.

Clusters 1 to 4 represent different kinds of grazed or frequently cut, often trampled grasslands. Cluster 1 consisted of plots of heavily grazed and trampled, or frequently cut grasslands from various soil types and moisture levels. This cluster is characterised by the lowest canopy among all clusters, high SLA and high clonality index. Cluster 2 represents mostly mesic grasslands on nutrient-poor and acidic soils which are mown or occasionally grazed. In this cluster SLA is slightly above and canopy height is slightly below the sample-wise average, while clonality is similarly high as in Cluster 1. Cluster 3 represents a small and distinct group of relevés dominated by *Agrostis stolonifera* and *Alopecurus geniculatus*. They occur on trampled, sometimes slightly alkaline, irregularly inundated habitats with nutrient-rich soils. In this cluster SLA is highest, canopy is second lowest, seed mass and bud bank are the lowest across all clusters, while clonality is highest among them. Similarly to Cluster 2, Cluster 4 contains plots mostly from extensively grazed mesic grasslands. SLA, seed mass and bud bank values of this cluster are slightly above the average of all clusters, canopy height is below average, clonality is intermediate.

Clusters 5 and 6 are two large, heterogeneous clusters containing several mesic and wet meadow types from lowland to montane sites. They are characterized by above-average seed mass and bud bank. Canopy height is lower in Cluster 5 than in Cluster 6.

Clusters 7 and 8 are two, distinct types with monodominant graminoid species with high canopy. Cluster 7 contains common lowland and montane wet grasslands, mostly with the dominance of *Scirpus sylvaticus*. This cluster has the highest canopy on average, highest bud bank on average, low seed mass and high clonality. Cluster 8 contains mesic meadows of ruderal character with the dominance of *Arrhenatherum elatius* mostly on post-arable lands converted to grasslands. In this cluster SLA, canopy, seed mass and clonality are high.

From Cluster 9 to 12 herbaceous communities of mostly wet habitats are found. Cluster 9 contains a variety of wet and mesic communities including intermittently wet meadows with *Molinia caerulea*, wet tall-forb vegetation, and nutrient-rich mesic meadows. This cluster has high seed mass, high bud bank, low clonality index and intermediate values for the other two traits. Cluster 10 contains montane meadows, and degraded wet meadows with *Deschampsia caespitosa* and to lesser extent *Juncus* species. This cluster was characterised by low SLA and clonality, high bud bank, and intermediate values for the other two traits. Cluster 11 contained
a variety of wet meadows with constant presence of tall forbs. This cluster had low SLA and
clonality, and high values for the other three traits. Cluster 12 comprised relevés dominated
by Juncus species, most frequently Juncus effusus, occasionally J. subnodulosus or J.
conglomeratus. These stands occur mostly on nutrient-poor, waterlogged and acidic soils,
which are sometimes managed by grazing. This cluster has high canopy and low values for all
the other traits.

The cross-tabulation of the trait-based and the syntaxonomical classification is shown on Tab.
1. Permutation tests with Goodman and Kruskal’s lambda index rejected the null hypothesis
stating that trait-based classification and syntaxonomical assignment are as similar as
expected by chance alone. Observed lambda values were higher than any element of the
reference distribution using either the class-level (lambda = 0.007), order-level assignments
(lambda = 0.313) or the alliance-level assignments (lambda = 0.236). In all cases P < 0.001
which gave SES = 3.719 after probit-transformation. However, the matching between
syntaxonomical and trait-based classifications was not perfect. Potentillion anserinae
(Clusters 2 and 3), Juncion effusi (Clusters 10 and 12), and Polygono-Poetalia (Clusters 1 and
4) were the few syntaxa which concentrated on a relatively limited number of trait-based
clusters, while the majority of other units were more broadly dispersed across several clusters.

At the highest hierarchical level (i.e., two clusters), clonality showed a difference between the
merged clusters which was the most extreme not only among all traits at that level but also
across all levels (Wst = 66.56; Table 2). From the three-cluster level onwards, we could found
no difference of this magnitude; although, with <7 clusters all tests showed significant
difference between the merged clusters. The bud bank showed the second largest difference
on absolute scale at the four-cluster level (Wst = -38.04). Apart from those mentioned above,
we could recognize no pattern in the contribution of individual traits to the merging of
clusters.

With some minor inequalities attributable to the unbalanced distribution of relevés, all clusters
were distributed over almost the entire country, none of them was obviously restricted
geo graphically.

In terms of functional diversity, clusters showed high overlap (Fig. 3). The highest median
Rao Q was detected in Cluster 12, while the lowest in Cluster 1. Cluster 12 showed also the
lowest functional redundancy together with Cluster 3. The other clusters resembled each other
very much also in this aspect.
On Fig. 4 we show the distribution of species in the space of $D_k$ and $SD(a_k)$ and Table 3 shows the ten species with the highest scores. Three of the first four species are those, which form monodominant and distinct vegetation types ($Arrhenatherum elatius$, $Scirpus sylvaticus$, $Juncus effusus$), while the rest species also occur as typical dominants of certain clusters (Appendix S3).

**Discussion**

In our paper we present the numerical classification of plots representing semi-natural grasslands of Poland, based on plant trait data, more specifically, on community-weighted trait means of phytosociological relevés. Using the emergent group approach, Hérault and Honnay (2007) showed that the involvement of trait data into classification could provide typologies which reflect certain ecosystem properties better than what would be achieved using only species composition. The main difference between Hérault and Honnay’s approach and ours lays in how we took into account trait information. Hérault and Honnay classified species on the basis of their trait values into ‘emergent groups’, which were used as variables instead of species. The power of the emergent group approach is that it accounts for functionally redundant species explicitly, since emergent groups consist of species possessing the same trait syndrome and thus having very similar ecological functions. On the other hand, classification of species into discrete groups requires subjective decisions from the researcher regarding the clustering algorithm, similarity measure, and number of emergent groups. Moreover, even objective algorithms produce non-intuitive classifications due to methodological constraints, e.g. certain methods tend to prefer clusters with specific size or shape. Our approach avoided this pitfall by using trait information as continuous variables to calculate CWMs which were input for classification. We divided the sample into 12 clusters based on biological interpretability; although, several cluster validity indices had higher values at lower numbers of clusters. It might suggest that the trait-based classification approach recognized coarser vegetation units than we found relevant and well separable. Nevertheless, classification studies are often aimed at providing vegetation typologies at different hierarchical levels, enabling practitioners to choose the most suitable resolution for a given application. The finer cluster resolution discussed here allows a more detailed overview of the whole sample with reduced within-cluster heterogeneity;
however, for specific purposes it is still possible to merge lower-level clusters, e.g., according to the fusions of the dendrogram. Therefore, our view of vegetation classification and typology suggested here is flexible to a degree.

The trait-based classification mirrored the most significant gradients shaping grassland vegetation of Poland, i.e. soil nutrient supply, soil moisture, and management. At the highest classification level, mostly nutrient-rich and mesic types (Clusters 1 to 8, except Clusters 3 and 7) were separated from communities of nutrient-poor and wet habitats (Clusters 9 to 12). Clusters 1 to 4 form a separate group at the four-cluster level. Their separation at high hierarchical level is notable, since these trampled and grazed, highly specialized grasslands include plots which differ in species composition very much but they are rather similar in terms of physiognomy and traits with characteristically low canopy and high SLA.

Goodman and Kruskal’s lambda with a permutation test rejected the independency between the trait-based and the syntaxonomical classification. This is not very surprising given that both formal definitions and CWM values rely on the species composition of relevés; however, we were not able to design a formal test of similarity with higher practical relevance since there is no standard threshold for ‘tolerable difference’ determining whether two classifications can be considered the same or not. With expert-based evaluation of the clusters we could point out several mismatches between the trait-based classification and the syntaxonomical system. A striking example can be seen in form of clusters which were dominated by functionally unique species, e.g. *Scirpus sylvaticus* (Cluster 7), *Arrhenatherum elatius* (Cluster 8), or *Juncus* spp. (Cluster 12). These vegetation types are either differentiated at the association (e.g., *Scirpetum sylvatici*) or alliance level (e.g., *Juncion effusi*), or not differentiated unequivocally (e.g., grasslands dominated by *Arrhenatherum elatius*) in the syntaxonomical system, while in the trait-based classification they appeared as very distinct clusters standing alone sometimes even at high hierarchical levels. Obviously, functionally unique and monodominant types also defined as separate syntaxa increase matching between syntaxonomic and trait-based classification, while syntaxonomically undefined types decrease it. Since monodominant communities are often species-poor, their distinct occurrence in the trait-based classification might be viewed as an artefact attributable to differences in species richness, considering that the more species are selected from the total species pool, the less likely it is to obtain an extreme community-weighted mean. Nevertheless, we consider differences in dominance structure as a relevant aspect of the biological phenomenon we study which mirrors environmental stress, disturbance, or specific
site-history that should not be removed from the analysis. The influence index accurately identified those species which appeared as dominants of certain clusters; therefore, we recommend its application for estimating the influence of individual species on CWM-based classifications. On the other hand, several alliances with more balanced dominance structure, higher species richness, and higher functional similarity between species did not separate well in the trait-based classification. For example, most meadow alliances, including Arrhenatherion and Polygono-Trisetion in the Arrhenatheretalia order, and Calthion, Cnidion, and Molinion in Molinietalia, similarly occurred in Clusters 5, 6, and 9. Considering the five traits we selected for our analysis, there is a high functional overlap between these meadow types despite being assigned to different orders in the syntaxonomical system. Importantly, the inclusion of other traits may explain specific functional differences between these alliances and orders.

Clonality index was the trait having the highest influence on the classification, which is in line with the findings of Klimesová et al. (2008, 2016) and E.-Vojtkó et al. (2016). Bud bank also seemed to have a relatively strong impact. There are several possible reasons for the efficiency of vegetative traits in revealing patterns in herbaceous vegetation. One reason is that grasslands in the temperate zone are usually maintained by some form of biomass removal, typically grazing or mowing. Plants adapt to such disturbances through avoidance or regeneration using clonal and bud bank traits (Klimešová et al., 2016); although, affecting other traits due to developmental trade-offs (Rusch, Wilmann, Klimešová, & Evju, 2011; Herben, Šerá, & Klimešová, 2015). Differences in the form and timing of management may be at least as significant as abiotic variation among the vegetation types included in this analysis (i.e., mesic and wet, semi-natural grasslands without extreme conditions in abiotic environment). Another potential explanation for the high influence of vegetative traits is that the ability of clonal growth as expressed on the relatively coarse scale applied in the Clo-Pla database shows lower levels of intraspecific variation due to stronger phylogenetic constraints and less measurements error. We consider all these explanations similarly likely, and agree that clonal and bud bank traits should be given high attention in the study of functional responses of vegetation to environmental and management gradients.

We did not find striking difference between clusters in terms of functional diversity and redundancy. Only Cluster 12 showed higher functional diversity and lower redundancy than the others in median values, which can be explained also by the functional uniqueness and high dominance of Juncus species. However, this may not be a reliable indication of the
vulnerability or conservation importance of this vegetation type, since *Juncus*-dominated stands, especially with *Juncus effusus*, are very common on nutrient-poor, disturbed or successional wetlands.

We had to apply simplifications during our analyses which could have limited us in revealing certain patterns. We retrieved trait data from LEDA and Clo-Pla database with no respect to the geographical and environmental origin of the records, thus neglecting an amount of variation in trait values attributable to population-level adaptation to local conditions. With the application of community-weighted mean in the description of plot-level trait values, and using their Euclidean distances as dissimilarity measure, we neglected the role of intraspecific variation, despite growing evidence on its significant role in community assembly and response to environmental gradients (Bolnick et al., 2011; Violle et al., 2012; Siefert et al., 2015). Phylogenetic constraints may also bias the relationship between CWM values and an environmental gradient (Duarte, Debastiani, Carlucci, & Diniz-Filho, 2018). Since there is no obvious implementation of phylogenetic correction into a classification framework yet, we neglected this effect. Despite the greatest and honourable efforts of database curators, differences in measurement protocols or technicalities may have caused an amount of variation between data sets coming from different providers. Nevertheless, we believe that these sources of bias do not compromise our results at the scale of the classification discussed here.

In any trait-based study, the choice of the trait determines all the potential results and conclusions. We included LHS, clonal and bud bank traits with equal weight because there is growing evidence of their ability to describe major dimensions of plant variability and response of plants to environmental and management gradients (Westoby et al., 2002; Klimešová et al., 2016). We believe that these five response traits describe the most important vegetation gradients appropriately in the analysed data set. However, different sets of traits, or different weights attributed to them, may have resulted in fundamentally different classifications. For specific studies, it is straightforward to select traits which are relevant for the ecosystem property under study.

**Conclusions**

We prepared a classification system of a broad vegetation unit, semi-natural mesic and wet grasslands of Poland, relying on plot-based numerical classification of community-weighted
means of LHS and vegetative plant traits. The classification mirrors differences in management, moisture, as well as types dominated by functionally unique species (Scirpus sylvaticus, Arrhenatherum elatius, Juncus spp.). Among all traits, clonal index had the strongest influence on the classification. Although, the matching between the trait-based and the syntaxonomical classification was closer than the randomized references applied here, it varied across vegetation types. Syntaxa with high dominance of functionally unique species, typically occurring under more stressed environmental conditions or specific site-history, appeared distinct also in the trait-based classification. In contrast, syntaxa with typically more balanced dominance structure and higher functional overlap between species did not separate well in the trait-based classification. Despite some discrepancies with the traditional species-based classification approach, functional trait-based classification provides biologically interpretable clusters. It must be, however, noted that our classification was performed on a type of vegetation highly dependent on management type and intensity. Classification of less disturbed vegetation types may bring sharper delimitation of vegetation units and different importance of individual traits.

Acknowledgements

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Author contributions

A.L. set the idea, carried out data analysis and led the writing. G.S. and Z.K. prepared the data and added interpretation to the results. Z.B.D. gave suggestions on the methodology. All Authors critically revised the manuscript.

Data accessibility

Vegetation plot data are accessible from the Polish Vegetation Database (Kącki & Śliwiński, 2012; GIVD identifier: EU-PL-001), trait data are available from the LEDA (Kleyer et al., 2008) and Clo-Pla (Klimešová et al., 2017) databases.
References


Supporting information

**Appendix S1:** Evaluation of the hierarchical classification using six validity indices.

**Appendix S2:** Shortened synoptic tables of the syntaxonomic orders and alliances.

**Appendix S3:** Shortened synoptic table and textual description of the discussed clusters.
Appendix S4: Ellenberg indicator values of the discussed clusters.

Appendix S5: Geographical distribution of the discussed clusters.
Figure 1. Dendrogram of the upper 12 clusters in the hierarchy

Figure 2. Boxes-and-whiskers plots comparing community-weighted means of traits across the twelve clusters. Boxes show upper and lower quartiles; whiskers show minimum and maximum values; circles show outliers.
Figure 3. Boxes-and-whiskers plots comparing Rao’s functional diversity and functional redundancy (Ricotta et al., 2016) across the twelve clusters. Boxes show upper and lower quartiles; whiskers show minimum and maximum values; circles show outliers.
**Figure 4.** Distribution of species in dimensions of functional uniqueness and SD of abundance (both divided by maximum). Only names of the ten species with the highest influence index values are shown.
Table 1. Cross-tabulation of the trait-based and the syntaxonomical classification

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Table 2. Standardized test statistic of Wilcoxon tests of CWM-s between clusters to be merged in each fusion level of the hierarchical classification. Significance levels after Bonferroni adjustment (two-tailed tests): *** p<0.001, ** p<0.01, * p<0.05, ns = not significant

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Table 3. Species with the highest influence index

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<td><em>Arrhenatherum elatius</em></td>
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<tr>
<td><em>Juncus effusus</em></td>
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<tr>
<td><em>Agrostis capillaris</em></td>
<td>0.331</td>
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<tr>
<td><em>Scirpus sylvaticus</em></td>
<td>0.322</td>
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<td><em>Festuca rubra</em> s. l.</td>
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<td><em>Molinia caerulea</em> s. l.</td>
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<td><em>Agrostis stolonifera</em></td>
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