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

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22 **Running title**

23 Trait-based classification of grasslands

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25 **Abstract**

26 *Questions*: What vegetation types can be distinguished on the basis of plant functional traits

27 using numerical classification? How do they match syntaxonomical units?

28 *Location*: Poland

29 *Methods*: 6985 vegetation plots representing mesic and wet grasslands (*Molinio-*

30 *Arrhenatheretea, Polygono-Poetea*) were retrieved from the Polish Vegetation Database.

31 Plant functional trait data were assembled from the LEDA and Clo-Pla databases for most

32 species occurring in the data set. Community-weighted mean for five traits were calculated

33 for each plot: specific leaf area, canopy height, seed mass, bud bank index and clonality

34 index. Plots were classified using Ward's method and iterative relocation based on silhouette

35 widths. The clusters were interpreted and characterized on the basis of species and trait

36 composition, functional diversity, functional redundancy, Ellenberg indicator values, and

37 geographical distribution. The similarity between the trait-based classification and the

38 syntaxonomical assignment of plots is evaluated both statistically and by expert knowledge.

39 *Results*: Twelve clusters were distinguished. The classification mirrored the main gradients

40 structuring grasslands in Poland, although, some vegetation types with the strong dominance

41 of functionally unique species appeared more distinct than they are treated in syntaxonomy.

42 Clusters did not differ significantly in functional diversity and redundancy. The differences of

43 clusters in species and trait composition and environmental background are discussed.

44 *Conclusion*: The application of trait data and numerical methods is a promising approach for

45 obtaining vegetation classifications. Such classifications can be in closer relationship with the

46 most important ecosystem processes than floristic classifications because communities

47 comprising different species but similar functional trait distribution are not separated. Trait-

48 based classifications match phytosociological units to a variable degree. Functional

49 uniqueness and variation of abundance determines how individual species influence the

50 delimitation of vegetation types using our approach.

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Keywords

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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; Díaz 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

90 traits; Lavorel & Garnier, 2002). Species which have similar traits may substitute each other
91 without significantly altering ecosystem functioning – a phenomenon called functional
92 redundancy (Hooper et al., 2005). Integrating the trait-based approach should improve the
93 relevance of vegetation classification with respect to ecosystem functioning, and enhance the
94 generalizability of results. Hérault and Honnay (2007) already presented a classification
95 where instead of species, groups of species sharing similar traits called 'emergent groups'
96 were applied as variables. Hence, it was possible to differentiate two types of riverine forests
97 in Luxembourg different in life-form spectra, dispersal modes, and conservation relevance.
98 However, this study restricted its scope on a specific vegetation type of a rather narrow area,
99 while the most typical challenge of recent vegetation classification works is providing
100 relevant and generalizable results over broad sample coverage in space and along ecological
101 gradients.

102 The functional approach of ecology has been in an intensive research period now for more
103 than a decade, partially shifting the focus away from the study of patterns of species-level
104 composition and diversity (Carlow, 1987; Tilman et al., 1997; McGill, Enquist, Weiher, &
105 Westoby, 2006). A major outcome of this field is the emergence of plant trait databases,
106 which provide trait measurements for thousands of taxa and hundreds of traits (Kattge et al.,
107 2011). Technically they are readily connectable with vegetation-plot databases, providing
108 avenues for the same types of analyses of trait composition which has only appeared at the
109 level of species yet. A fundamental question of trait-based ecology is the distinction between
110 processes which impedes the co-existence of functionally similar organisms (i.e. functional
111 divergence) and those which promotes it (i.e. functional convergence; Lhotsky et al., 2016).
112 Competitive exclusion is known to increase divergence according to the theory of limiting
113 similarity, while environmental (or niche) filtering (and, for traits increasing competitive
114 vigour, also competitive exclusion) supports functional convergence (Weiher & Keddy,
115 1995). Considering the interest of vegetation classification studies in the response of
116 vegetation to environment, trait convergence should be a key phenomenon in the construction
117 of functionally relevant classifications. Moreover, competitive exclusion is subordinated to
118 environmental filtering according to the filter model of community assembly (Keddy 1992),
119 which is a likely reason why trait convergence is more frequently detected than divergence.

120 In this paper we present a trial for integrating the functional approach into the context of
121 vegetation classifications using multivariate statistical methods. Our aim is to classify semi-
122 natural grasslands of Poland in a way that resulting groups are relatively similar in their trait

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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 m^2. 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

189 normality by quantile-quantile plots. Since LHS traits proved to be right-skewed, they were

190 log-transformed. Then, all traits were standardized to mean = 0 and standard deviation = 1.

191 These species-level standardized means were used for calculating community-weighted

192 means (CWM; Garnier et al., 2004), which is considered a satisfactory indicator of niche

193 filtering along large-scale environmental gradients (Kleyer et al., 2012; De Bello et al., 2013).

194 The CWM is constrained by the relative dominance of the most dominant trait value in the

195 plot; therefore we expect species forming monodominant vegetation stands to have a high

196 influence on the classification (De Bello, Lepš, Lavorel, & Moretti, 2007). This conforms the

197 mass ratio hypothesis by Grime (1998) stating that ecosystem functioning is mainly

198 determined by traits of the dominant species.

199 Hierarchical classification was carried out by Ward's agglomerative method (Podani, 2000)

200 on the matrix of CWM values. Ward's method relies on Euclidean distances in the trait space

201 between plots. The upper 20 hierarchical levels of the classification were evaluated by several

202 cluster validity indices (see Appendix S1); however, they suggested different numbers of

203 clusters as optimal making it impossible to decide on a single 'best' solution. To overcome

204 this, on the one hand, we considered also the biological interpretation of the clusters and the

205 resolution desired typically in such large-scale classifications. Hence, the dendrogram was cut

206 at a particular level and then it was improved using iterative relocation methods (Roberts

207 2015). Most iterative relocation methods proposed by Roberts (2015) are computationally

208 very demanding; therefore, we applied the REMOS2 algorithm (Lengyel, Roberts, & Botta-

209 Dukát 2019). This procedure uses the silhouette width index (Rousseeuw 1987) to identify

210 misclassified objects, which are then re-assigned to their closest neighbour cluster. After re-

211 assignment, silhouette widths are updated, and misclassified plots are relocated again to their

212 closest neighbour cluster, until the classification cannot be further optimized. This has

213 changed the assignment of 31.58% of all plots. However, we did not change the hierarchical

214 relations of the basic clusters.

215 Delimited clusters were interpreted as biologically relevant units using expert-based

216 knowledge and we attempted to find correspondence to already known and well-defined

217 vegetation units in the traditional (floristic) syntaxonomical approach (Kącki et al., 2013). For

218 this purpose, phytosociological relevés were assigned to syntaxa at the class, order, and

219 alliance levels using their formal definitions. Relevés were classified to respective syntaxa

220 based on explicit definitions of vegetation units in the way that the relevé matched by the

221 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:

$$I_k = \sqrt{D_{.k} \times SD(\mathbf{a_k})}$$

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 $SD(\mathbf{a_k})$ 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 $SD(\mathbf{a_k})$ 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), rapportools (Blagotić & Daróczi, 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 (W_{st} = 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 (W_{st} = -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 geographically.

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.

349   On Fig. 4 we show the distribution of species in the space of $D_{\cdot k}$ and $SD(a_k)$ and Table 3

350   shows the ten species with the highest scores. Three of the first four species are those, which

351   form monodominant and distinct vegetation types (*Arrhenatherum elatius*, *Scirpus sylvaticus*,

352   *Juncus effusus*), while the rest species also occur as typical dominants of certain clusters

353   (Appendix S3).

354

355   **Discussion**

356   In our paper we present the numerical classification of plots representing semi-natural

357   grasslands of Poland, based on plant trait data, more specifically, on community-weighted

358   trait means of phytosociological relevés.

359   Using the emergent group approach, Hérault and Honnay (2007) showed that the involvement

360   of trait data into classification could provide typologies which reflect certain ecosystem

361   properties better than what would be achieved using only species composition. The main

362   difference between Hérault and Honnay's approach and ours lays in how we took into account

363   trait information. Hérault and Honnay classified species on the basis of their trait values into

364   'emergent groups', which were used as variables instead of species. The power of the

365   emergent group approach is that it accounts for functionally redundant species explicitly,

366   since emergent groups consist of species possessing the same trait syndrome and thus having

367   very similar ecological functions. On the other hand, classification of species into discrete

368   groups requires subjective decisions from the researcher regarding the clustering algorithm,

369   similarity measure, and number of emergent groups. Moreover, even objective algorithms

370   produce non-intuitive classifications due to methodological constraints, e.g. certain methods

371   tend to prefer clusters with specific size or shape. Our approach avoided this pitfall by using

372   trait information as continuous variables to calculate CWMs which were input for

373   classification.

374   We divided the sample into 12 clusters based on biological interpretability; although, several

375   cluster validity indices had higher values at lower numbers of clusters. It might suggest that

376   the trait-based classification approach recognized coarser vegetation units than we found

377   relevant and well separable. Nevertheless, classification studies are often aimed at providing

378   vegetation typologies at different hierarchical levels, enabling practitioners to choose the most

379   suitable resolution for a given application. The finer cluster resolution discussed here allows a

380   more detailed overview of the whole sample with reduced within-cluster heterogeneity;

381 however, for specific purposes it is still possible to merge lower-level clusters, e.g., according

382 to the fusions of the dendrogram. Therefore, our view of vegetation classification and

383 typology suggested here is flexible to a degree.

384 The trait-based classification mirrored the most significant gradients shaping grassland

385 vegetation of Poland, i.e. soil nutrient supply, soil moisture, and management. At the highest

386 classification level, mostly nutrient-rich and mesic types (Clusters 1 to 8, except Clusters 3

387 and 7) were separated from communities of nutrient-poor and wet habitats (Clusters 9 to 12).

388 Clusters 1 to 4 form a separate group at the four-cluster level. Their separation at high

389 hierarchical level is notable, since these trampled and grazed, highly specialized grasslands

390 include plots which differ in species composition very much but they are rather similar in

391 terms of physiognomy and traits with characteristically low canopy and high SLA.

392 Goodman and Kruskal's lambda with a permutation test rejected the independency between

393 the trait-based and the syntaxonomical classification. This is not very surprising given that

394 both formal definitions and CWM values rely on the species composition of relevés; however,

395 we were not able to design a formal test of similarity with higher practical relevance since

396 there is no standard threshold for 'tolerable difference' determining whether two

397 classifications can be considered the same or not. With expert-based evaluation of the clusters

398 we could point out several mismatches between the trait-based classification and the

399 syntaxonomical system. A striking example can be seen in form of clusters which were

400 dominated by functionally unique species, e.g. *Scirpus sylvaticus* (Cluster 7), *Arrhenatherum*

401 *elatius* (Cluster 8), or *Juncus* spp. (Cluster 12). These vegetation types are either

402 differentiated at the association (e.g., *Scirpetum sylvatici*) or alliance level (e.g., *Juncion*

403 *effusi*), or not differentiated unequivocally (e.g., grasslands dominated by *Arrhenatherum*

404 *elatius*) in the syntaxonomical system, while in the trait-based classification they appeared as

405 very distinct clusters standing alone sometimes even at high hierarchical levels. Obviously,

406 functionally unique and monodominant types also defined as separate syntaxa increase

407 matching between syntaxonomic and trait-based classification, while syntaxonomically

408 undefined types decrease it. Since monodominant communities are often species-poor, their

409 distinct occurrence in the trait-based classification might be viewed as an artefact attributable

410 to differences in species richness, considering that the more species are selected from the total

411 species pool, the less likely it is to obtain an extreme community-weighted mean.

412 Nevertheless, we consider differences in dominance structure as a relevant aspect of the

413 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

447   vulnerability or conservation importance of this vegetation type, since *Juncus*-dominated

448   stands, especially with *Juncus effusus*, are very common on nutrient-poor, disturbed or

449   successional wetlands.

450   We had to apply simplifications during our analyses which could have limited us in revealing

451   certain patterns. We retrieved trait data from LEDA and Clo-Pla database with no respect to

452   the geographical and environmental origin of the records, thus neglecting an amount of

453   variation in trait values attributable to population-level adaptation to local conditions. With

454   the application of community-weighted mean in the description of plot-level trait values, and

455   using their Euclidean distances as dissimilarity measure, we neglected the role of intraspecific

456   variation, despite growing evidence on its significant role in community assembly and

457   response to environmental gradients (Bolnick et al., 2011; Violle et al., 2012; Siefert et al.,

458   2015). Phylogenetic constraints may also bias the relationship between CWM values and an

459   environmental gradient (Duarte, Debastiani, Carlucci, & Diniz-Filho, 2018). Since there is no

460   obvious implementation of phylogenetic correction into a classification framework yet, we

461   neglected this effect. Despite the greatest and honourable efforts of database curators,

462   differences in measurement protocols or technicalities may have caused an amount of

463   variation between data sets coming from different providers. Nevertheless, we believe that

464   these sources of bias do not compromise our results at the scale of the classification discussed

465   here.

466   In any trait-based study, the choice of the trait determines all the potential results and

467   conclusions. We included LHS, clonal and bud bank traits with equal weight because there is

468   growing evidence of their ability to describe major dimensions of plant variability and

469   response of plants to environmental and management gradients (Westoby et al., 2002;

470   Klimešová et al., 2016). We believe that these five response traits describe the most important

471   vegetation gradients appropriately in the analysed data set. However, different sets of traits, or

472   different weights attributed to them, may have resulted in fundamentally different

473   classifications. For specific studies, it is straightforward to select traits which are relevant for

474   the ecosystem property under study.

475

476   **Conclusions**

477   We prepared a classification system of a broad vegetation unit, semi-natural mesic and wet

478   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.

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.

509

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708

709 **Supporting information**

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

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

712 **Appendix S3:** Shortened synoptic table and textual description of the discussed clusters.

713   **Appendix S4:** Ellenberg indicator values of the discussed clusters.

714   **Appendix S5:** Geographical distribution of the discussed clusters.

715 **Figure 1.** Dendrogram of the upper 12 clusters in the hierarchy
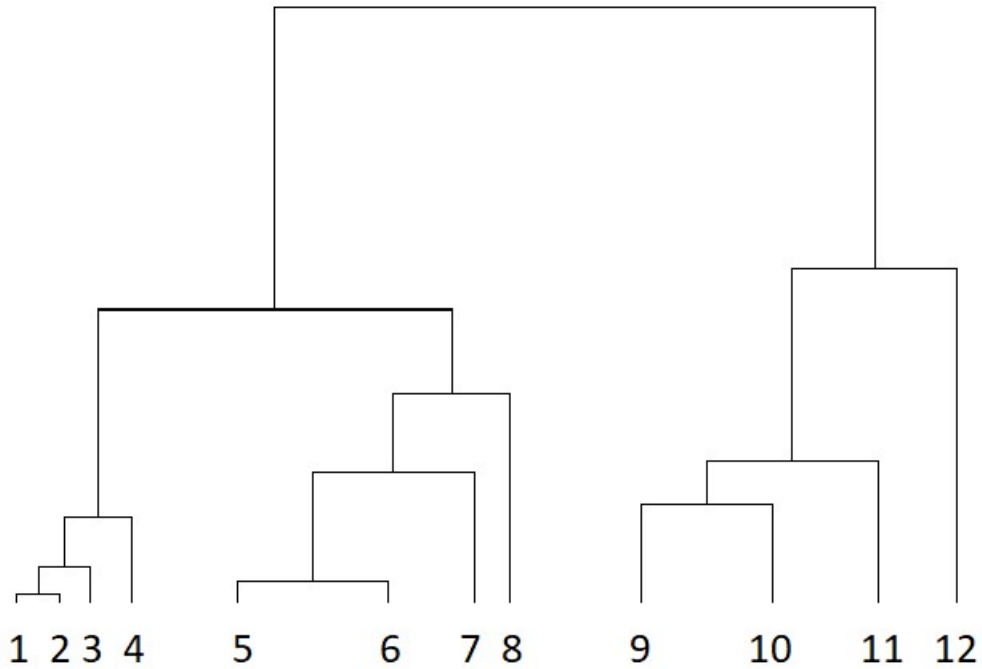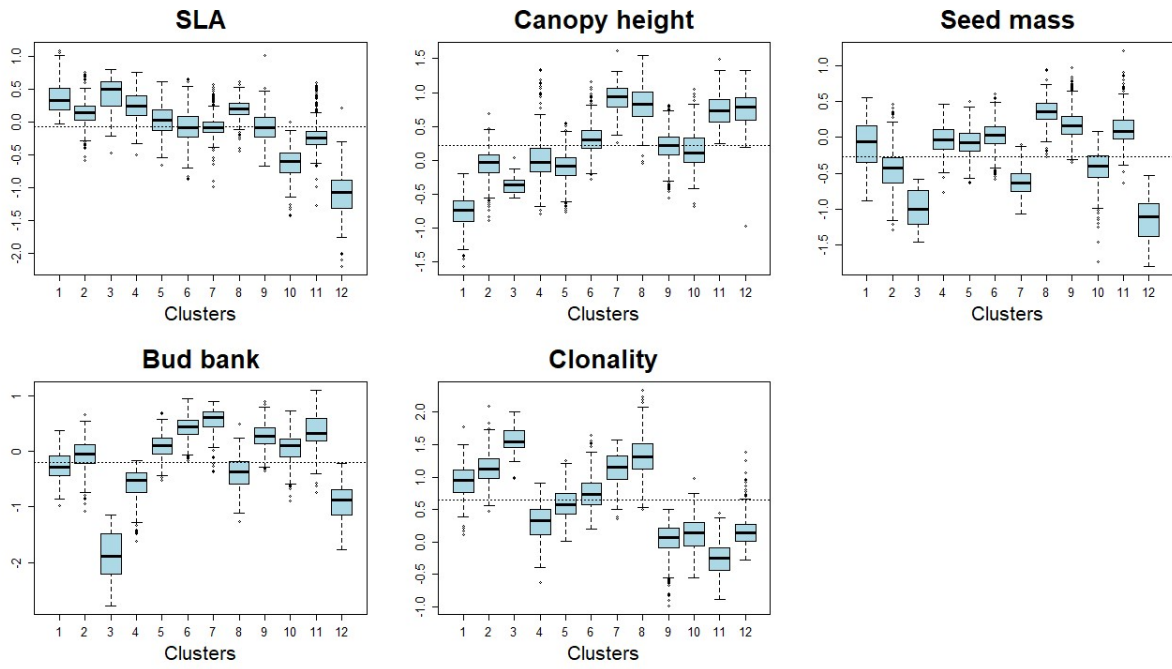

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719 **Figure 2.** Boxes-and-whiskers plots comparing community-weighted means of traits across

720 the twelve clusters. Boxes show upper and lower quartiles; whiskers show minimum and

721 maximum values; circles show outliers

722

723

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

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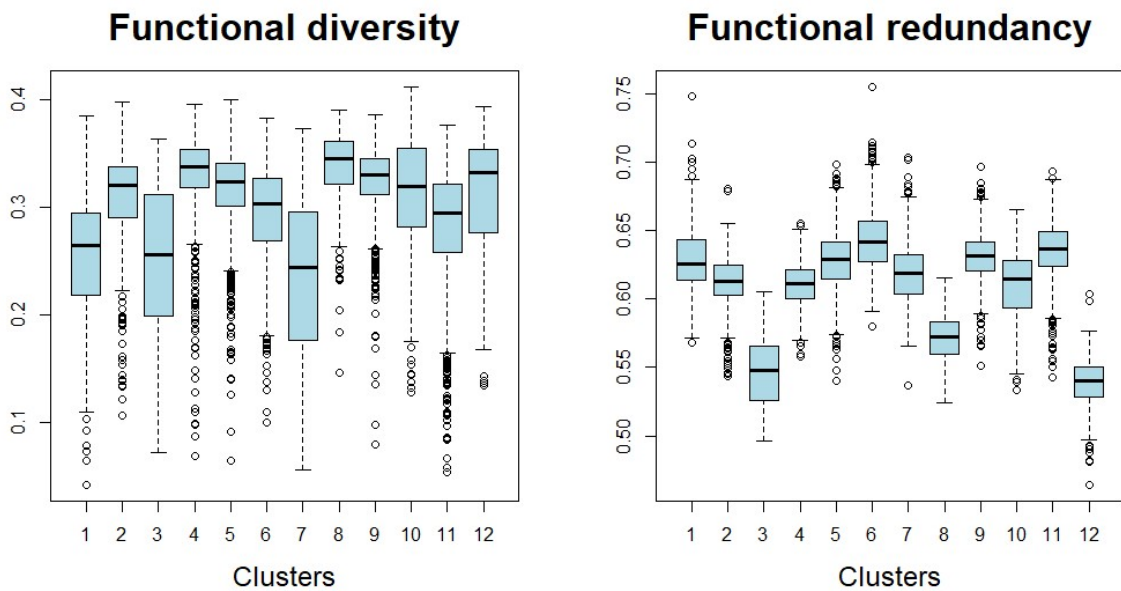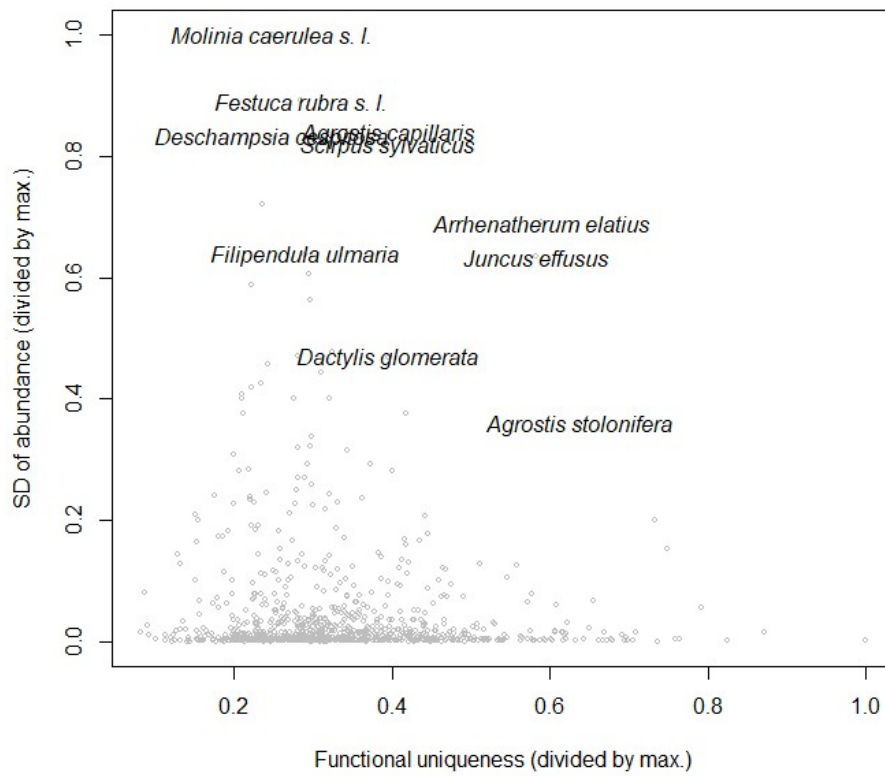**Figure 4.** Distribution of species in dimensions of functional uniqueness and SD of

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

			Clusters of the trait-based classification											
	CLASSES	ORDERS	ALLIANCES	1	2	3	4	5	6	7	8	9	10	11	12
Syntaxonomical classification	Molinio-Arrhenatheretea	Arrhenatheretalia	*Arrhenatherion*	1	70	0	1	120	200	4	251	99	0	8	0
			Cynosurion	83	30	0	127	223	25	0	0	99	2	0	0
			Poion alpinae	0	0	0	1	0	0	0	0	1	0	0	0
			Polygono-Trisetion	0	11	0	0	34	24	0	0	24	1	2	0
			Unidentified at alliance level	9	287	0	39	446	452	1	11	190	7	4	0
		Molinietalia	*Calthion*	0	7	0	41	165	193	203	4	545	92	214	12
			Cnidion	0	0	0	7	35	55	1	0	49	28	4	14
			Juncion effusi	0	2	0	2	0	0	0	0	0	36	0	111
			Molinion	0	0	0	2	23	69	0	0	240	38	320	0
			Unidentified at alliance level	0	9	0	4	112	109	20	12	201	196	113	21
		Potentillo-Polygonetalia	*Potentillion anserinae*	1	11	11	0	1	0	0	0	0	2	0	0
			Unidentified at alliance level	16	13	23	1	7	13	0	1	1	1	0	0
		Unidentified at order level		14	41	0	13	153	260	11	10	33	7	2	2
	Polygono-Poetea	*Polygono-Poetalia*	Unidentified at alliance level	79	7	0	36	10	0	0	0	0	0	0	1
	Dubious assignment			5	0	0	0	1	0	1	0	0	1	0	0

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

No. Clusters	SLA	Canopy height	Seed mass	Bud bank	Clonality
2	34.65***	-19.67***	-17.82***	-9.48***	66.56***
3	20.62***	-15.13***	20.93***	20.81***	-4.74***
4	20.53***	-29.81***	-19.41***	-38.04***	-6.83***
5	-15.69***	-22.37***	-22.22***	25.05***	-20.93***
6	3.37***	-36.72***	-12.05***	-17.44***	25.98***
7	2.22*	-25.42***	23.24***	-15.14***	-17.91***
8	28.88***	2.58**	31.22***	10.05***	-0.74[ns]
9	3.19**	-15.86***	-15.15***	10.13***	24.96***

10	-5.5***	1.43^{ns}	8.52***	9.56***	-8.44***
11	18.81***	-17.4***	-0.79^{ns}	-30.07***	15.83***
12	8.47***	-18.19***	17.84***	-0.63^{ns}	-2.76**

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743 **Table 3.** Species with the highest influence index

Species	Influence index
Arrhenatherum elatius	0.407
Juncus effusus	0.369
Agrostis capillaris	0.331
Scirpus sylvaticus	0.322
Festuca rubra s. l.	0.253
Molinia caerulea s. l.	0.248
Agrostis stolonifera	0.229
Deschampsia cespitosa	0.207
Dactylis glomerata	0.186
Filipendula ulmaria	0.184

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