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Clonal vs leaf-height-seed (LHS) traits: which are filtered more strongly across habitats?

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Abstract Plant functional traits are now frequently used instead of species identity to identify how plant species co-exist in assemblages. One notion is that species inhabiting the same environment have more characteristics in common than species from different habitats, leading to different prevailing dominant traits along environmental gradients, and also to a lesser diversity of traits in habitats that impose a stronger filter on these traits. Though such patterns have been demonstrated for different environmental drivers and different traits, studies using easily available traits connected to above ground processes (i.e. traits of the leaf-height-seed, or LHS, strategy scheme) are largely overrepresented in these analyses. Here we combined data on clonal and bud bank traits, representing the ability to reproduce and spread vegetatively, with LHS trait data and examined how these traits varied in relation to the vegetational composition of 29 Central-European habitat types. Our analysis focused on determining whether clonal/bud bank or LHS traits play an important role for

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environmental filtering along gradients approximated by Ellenberg indicator values (EIV) across these habitats. Our results show that clonal and bud bank traits are at least as – if not more – important for the differentiation of the 29 habitat types. Overall, diversity and dominance of clonal and bud bank traits was more strongly correlated with gradients of light availability, temperature, moisture, soil reaction, and nutrient availability across these habitats than it was the case for traits of the leaf-height-seed scheme. Our results call for a stronger integration of belowground traits into the functional traits approach in plant ecology and for an extension of efforts to collect such data.

Keywords community-weighted mean · Czech Republic · Ellenberg indicator values · environmental filtering · functional diversity · plant strategy

Introduction

One of the oldest questions in plant ecology tackles the processes driving species distributions in response to environmental conditions: Why are some species able to exist in particular habitats or communities, but not in others? This question remains topical today, as multiple processes have been identified to shape species coexistence, and no single mechanism accounts for all observed patterns (Vellend 2010). While species interact with both abiotic and biotic factors, it is generally agreed that environmental conditions 'filter' species with more suitable features (Cornwell and Ackerly 2009).

The pursuit to understand plant-environment relationships has a long history. Schimper (1898) recognized that different plant species thrive in different environmental conditions as they have features enhancing their differential fitness. More recently, such features (coined plant functional traits) have been defined as 'the morphological, physiological and phenological features that represent ecological strategies and determine how plants respond to environmental factors' (Pérez-Harguindeguy et al. 2013). Functional plant traits have proven to be useful tools in understanding ecological processes (e.g. Lavorel and Garnier 2002; Garnier et al. 2004), including the assembly of communities (Cornwell et al. 2006).

The effect of environmental factors on vegetation is widely recognized as 'environmental filtering': Species are filtered from regional to local pools and eventually into local communities based on their traits (Díaz et al. 2004; Cornwell and Ackerly 2009; Götzenberger et al. 2012). Environmental filtering should lead to a reduction of functional diversity (FD) within communities (trait convergence – Grime 2006; de Bello et al. 2013a), because specific traits will be favoured and others selected against. For example, in alpine environments, species without the ability to survive frost will be excluded. Other traits correlated with tolerance of cold, dry conditions would also be favoured resulting in a functionally more homogenous assemblage of species in an alpine community, compared to a more general pool of species (Davis et al. 1999). Strong environmental filtering should result in co-occurring species that are more similar than expected by chance. However, biotic interactions such as competition can limit the similarity of coexisting species (MacArthur and Levins 1967). This would have the opposite effect to that of environmental filtering on trait composition resulting in increased FD (trait divergence – Mason et al. 2013; de Bello et al. 2013b). Though not mutually exclusive (Götzenberger et al. 2012; de Bello et al. 2013b), these two mechanisms are thought to predominate at different scales. At larger spatial scales (e.g. comparisons of habitats), species composition and traits are assumed to be strongly filtered by environmental factors, whereas at smaller scales (e.g. community or plot scale), species interactions and responses to disturbance are assumed to be more influential (de Bello et al. 2013b).

Most studies on plant traits and community composition focus on traits related to plant performance through competitive ability or growth capacity. The most commonly used is the leaf-height-seed (LHS) strategy scheme proposed by Westoby (Westoby 1998; Westoby et al. 2002). This scheme consists of three traits that are associated with principal biological functions: canopy height (competitive ability), seed mass (dispersal and establishment ability) and specific leaf area (rate of resource investment). However, using only LHS traits to characterize species strategies might be insufficient, as these traits do not provide information about below-ground processes (Klimešová and Herben 2015). Alternatively, clonal and bud bank traits can describe clonal growth and spreading (Weiher et al. 1999; Kleyer et al. 2008). The lack of focus on clonal traits in FD studies could be the result of being difficult to measure and not being formed by most trees and annuals (Mudrák et al. 2015; Klimešová and Herben 2015). However, clonal plants are common in temperate, boreal and aquatic vegetation (Klimeš et al. 1997). It has been shown that variation in clonal growth changes between communities (de Bello et al. 2011; Klimešová et al. 2011; 2012), between land use types (Catorci et al. 2011) as well as along large latitudinal, and thus climatic gradients (Ye et al. 2014). Therefore, it is very likely that environmental filters operate on clonal traits (de Bello et al. 2011), as has been shown by Klimešová and Herben (2015) at the community scale.

In this paper our main aim was to study the effect of environmental filtering on LHS vs clonal traits. In particular, we examined patterns of dominant trait values (community-weighted mean, CWM) and functional diversity (FD) in relation to environmental gradients approximated by Ellenberg Indicator Values (EIV). We studied these associations at the habitat type level, because the effect of environmental filtering is assumed to be predominant at such scale and avoids, as much as possible, the potential influence of biotic interactions and hence the effect of limiting similarity.

As both LHS and clonal traits have been demonstrated to respond to environmental conditions, though studied independently from each other, we expected similar response strength for both trait groups. At the same time, LHS and clonal traits should show different responses along particular environmental gradients. A benign environment with sufficient nutrients, light and moisture should provide for a higher diversity regarding above-ground LHS traits, in contrast to more extreme and stressful habitats, where these traits are more strongly filtered. Therefore, we expect FD to be higher in favourable conditions, while in habitats with decreased light, moisture or nutrient availability the FD of LHS traits would be lower. By contrast, clonality as such, as well as a diversity in clonal strategies, could be more beneficial in more stressful and disturbed habitats that are characterized by decreased light and nutrient levels, and increased moisture, in which sexual reproduction might be limited (Herben et al. 2015).

We acknowledge that CWM and FD are likely to be correlated (Ricotta and Moretti 2011; Dias et al. 2013), but we still see value in analysing them independently as no study to date has attempted to quantify their relationship.

Material and methods

Data

Habitats

Species composition in vegetation plots were provided from a standardized and stratified subset (see Herben et al. 2013 for details) of the Czech National Phytosociological Database (Chytrý and Rafajová 2003). Plots were assigned to 32 EUNIS habitats according to Chytrý et al. (2005). These habitats represent major vegetation types found in Central Europe covering terrestrial as well as aquatic vegetation types. We excluded the three strictly aquatic vegetation types dominated by hydrophytes (surface standing waters, surface running waters and littoral zone) but kept bogs, fens and marshes. Aquatic vegetation types are distinctively different from terrestrial systems, therefore presumed not to behave according to expectations for terrestrial habitats. Moreover, certain functional traits, e.g. plant height, are hard to define in the case of hydrophytes. The selection resulted in 15,711 plots in 29 habitats (Table **1**) with occurrence data of 1,812 species. To minimize the effects of interspecific biotic interactions that occur within the plots, we pooled occurrence data at the plot level into frequency data at the habitat level. Finally, the obtained frequencies were transformed into relative frequencies for calculation of CWM and FD indices.

Traits

We obtained two sets of plant functional traits: traits linked to vegetative reproduction (clonal and bud bank traits) and LHS traits. Clonal growth and bud bank traits were extracted from the CLO-PLA database (Klimešová and de Bello 2009, clopla.butbn.cas.cz), whereas LHS traits (specific leaf area, seed mass and plant height) were extracted from the LEDA Traitbase (Kleyer et al. 2008, www.uni-oldenburg.de/en/landeco/research/projects/LEDA). We could retrieve trait data for at least 73% of the species (weighted by their abundance) in the case of all studied traits: SLA 74%, height 75%, seedmass 73%, bud bank traits 95%, and clonal traits 86%. In the following description, trait names and abbreviations used in the remainder of the text are given in brackets.

Table 1 EUNIS habitat types with coding. N plots – number of plots used in the analyses in a certain habitat type. L, T, F, R, N – community-weighted mean of the corresponding Ellenberg values calculated for the habitat types (L – light, T – temperature, F – soil moisture, R – soil reaction, N – soil nutrients).

Code	Habitat type	***N* plots**	L	T	F	R	N
D1	raised bogs	75	7.0	4.3	8.1	2.4	2.1
D2	poor fens and transition mires	375	7.3	5.0	8.2	4.1	3.2
D4	base-rich fens	49	7.3	5.1	7.7	6.2	3.4
D6	brackish marshes	32	7.4	5.8	8.4	7.0	6.2
E1	dry grasslands	2,414	7.5	6.1	3.4	7.1	2.8
E2	mesic grasslands	1,603	7.1	5.4	5.0	5.8	4.4
E3	wet grasslands	2,207	7.0	5.2	6.9	5.4	4.3
E4	alpine grasslands	50	6.3	3.8	5.5	3.1	2.6
E5.2	woodland fringes	369	7.0	5.8	3.8	7.0	3.4
E5.4	wet tall-forb stands	734	6.5	5.2	7.0	6.1	5.6
E5.5	subalpine tall-forb stands	174	5.3	3.9	5.8	5.0	5.0
E5.6	anthropogenic tall-forb stands	799	6.9	5.7	5.2	6.9	6.3
E6	inland saline grassland	151	7.2	5.7	6.7	7.0	5.1
F2	alpine and subalpine scrub	24	5.0	4.0	5.9	4.9	4.8
F3	temperate scrub	87	6.7	5.8	4.0	6.9	4.4
F4	heath lands	200	6.5	5.3	4.2	4.0	2.6
F9.1	riverine willow stands	20	6.3	5.4	7.1	6.6	6.8
F9.2	willow cars	48	6.6	5.2	7.9	5.5	5.2
G1	broad leaved woodland	1,615	4.7	5.4	5.3	6.0	5.2
G1.C	broad leaved plantations	27	5.2	5.5	5.6	6.4	6.2
G3	coniferous woodland	385	5.1	4.6	5.4	3.9	3.7
G3.F	coniferous plantations	163	5.3	5.4	4.8	5.5	4.5
G4	mixed woodland	856	4.6	5.2	5.3	5.6	5.1
G5	forest clearings	448	5.7	5.4	5.4	5.1	5.4
H2	screes	50	7.1	5.8	3.7	6.8	3.7
H3	cliff and outcrops	236	6.5	5.5	4.4	6.1	4.0
H5.6	trampled areas	733	7.3	5.8	5.8	6.2	5.7
I1	arable land	1,397	6.7	5.8	4.9	6.6	6.1
J6	waste deposits	390	7.4	6.0	4.8	6.9	6.4

Traits of the leaf-height-seed (LHS) strategy scheme

Specific leaf area (SLA), defined as the leaf area per dry weight, is positively correlated with the potential growth rate and therefore considered to represent different resource acquisition strategies (Westoby et al. 2002).

Canopy height (Height) describes the mean distance between foliage of a plant and the soil surface. In competitive environments, higher growing plants have an advantage through prior access to light (Westoby et al. 2002). Seed mass is the dry mass without accessories. Heavy seeds have high metabolic reserves which favours the establishment of seeds in productive and competitive environments (Willson and Traveset 2000).

Bud bank traits

Root sprouting capacity (Root spr.) is a binary trait, coding the ability of a plant to resprout from root-derived buds after the destruction of its aboveground biomass. Bud bank size (Sum BB) is defined as the number of vegetative buds per shoot, with these buds residing on belowground stem-derived organs. Bud bank size including buds on roots (Sum BBR) adds the Sum BB and root-derived buds of a plant. Bud bank depth (Depth BB) and bud bank depth including root buds (Depth BBR) describe the depth of buds in relation to the soil surface. The crucial role of the bud bank in regeneration after a disturbance event has been studied in different habitats. Bud banks can increase a plant's distribution by allowing new shoots to be established away from the mother plant; in addition, bud-bearing organs contain carbon reserves used for seasonal regrowth, respiration, flowering and fruiting. Thus, regrowth from reserve meristems is also a successful strategy in severely and repeatedly disturbed habitats (Klimešová and Klimeš 2007; Klimešová and de Bello 2009).

Clonal traits

Multiplication rate (Mult. Rate) is defined as the number of offspring shoots per parent shoot per year (Klimešová and de Bello 2009) and lateral spread (Lat. Spread) is the distance a clonal organism spreads each year. Together, these two traits are combined to give the clonal index (Clo. Index), which is an overall measure of how clonal a plant behaves. For its calculation, lateral spread is assigned to one of four ordinal classes (less than 1 cm, 1–25 cm, more than 25 cm, freely dispersible), multiplication rate to three (less than one offspring, one offspring, more than one offspring), and the clonal index is a summation of the two resulting values for a species. Although clonal growth is achieved through various morphological adaptations and strategies, these three measures of clonality express its main components in terms of function: vegetative reproduction, the exploitation of space and resources, and local persistence (van Groenendael et al. 1996).

Trait combinations

LHS traits (LHS) combine the traits SLA, height and seed mass. Bud bank traits (BB) include the traits root spr., sum BB, sum BBR, depth BB and depth BBR. Clonal traits (Clonal) include the traits Mult. Rate, Lat. Spread and Clo. Index. Clonal and bud bank traits together (Clo. + BB) combine all clonal and bud bank traits.

Community-weighted mean and functional diversity

Traits of the LHS strategy scheme were log-transformed as their values ranged between several orders of magnitude and they had a lognormal distribution. All numeric traits of the clonal and bud bank traits were standardized to zero mean and unit variance. Species that were known to be not clonal received a value of zero for the clonal traits multiplication rate, lateral spread and the clonal index. We used Rao's quadratic entropy (Rao, Botta-Dukát 2005) as index of FD. Rao is an index of functional dissimilarity, expressed as the sum of the abundance-weighted pairwise differences between species of a community

$$Rao = \sum_{i=1}^{n} \sum_{j=1}^{n} d_{ij}\rho_i\rho_j$$

where d_{ij} is the functional distance between species i and j and p_i and p_j are the relative abundances of the i-th and j-th species. The Rao index was calculated for both individual traits as well as for three combinations of ecologically related traits: LHS traits, bud bank traits, clonal traits and the combination of clonal and bud bank traits (see also Table 2). We calculated the community-weighted mean (CWM, Garnier et al. 2004) for the transformed traits, weighted by the relative abundance of species in habitats

$$CWM = \sum_{i=1}^{n} \rho_i x_i$$

where x_i is the mean trait value and p_i is the relative frequency of the i-th species. The CWM for the binary trait root sprouting ranges between 0 and 1, representing the abundance-weighted fraction of species carrying the value 1 (i.e. being capable of root sprouting).

To characterize average environmental conditions in the 29 habitat types, we used the CWM of Ellenberg

Table 2 Expected (Exp.) and observed (Obs.) R^2 values for linear models on community-weighted mean (CWM) and functional diversity (Rao) with linear and quadratic EIV

	CWM		Rao	
	Exp. R^2	Obs. R^2	Exp. R^2	Obs. R^2
Specific leaf area (SLA)	0.33	**0.88**	0.32	0.41
Height	0.33	0.14	0.33	0.39
Seed mass	0.33	0.40	0.33	0.50
LHS traits	NA	NA	0.33	0.29
Root sprouting capacity	0.34	**0.86**	0.35	**0.88**
Bud bank size	0.33	0.46	0.35	**0.75**
Bud bank size including root buds	0.34	0.38	0.35	**0.81**
Bud bank depth	0.31	0.29	0.32	**0.80**
Bud bank depth including root buds	0.34	0.17	0.34	**0.88**
All bud bank traits	NA	NA	0.33	**0.81**
Multiplication rate	0.33	**0.76**	0.34	0.47
Lateral spread	0.35	0.62	0.32	**0.84**
Clonal index	0.33	**0.88**	0.37	**0.84**
All clonal traits	NA	NA	0.32	**0.78**
Clonal + bud bank traits	NA	NA	0.34	**0.79**

Significantly better Obs. than Exp. R2 are shown in bold (SR2 > 1.65, P < 0.05).

Indicator Values (EIV, Ellenberg et al. 1992; Table **1**), calculated the same way as for the traits. EIV are empirical ordinal values of plant species representing their preferences along environmental gradients. We used here EIV of light availability (L), soil moisture (F), soil reaction (R), temperature (T) and soil fertility (N). Each EIV ranges from one (lowest value) to nine (highest value). For example, L1 species occur primarily in shaded habitats, while L9 species are found in habitats with extremely high light availability. Small R values indicate more acidic soils (small pH values), while higher R refers to more basal soils (higher pH values). The EIV for moisture extends the range from one to twelve, with the three highest values indicating the habitat preferences of aquatic plants, which were, however, excluded from this study. In the remainder of the text we use short names or abbreviations for EIVs given above. It is important to note that these gradients reflect species preferences and not direct measures of any environmental variable. Thus, the CWM of L for a habitat type refers to the weighted average preference of species in that habitat not the actual level of light available.

Data analysis

Models

While the literature provides guidance for hypotheses regarding trait-environment relationships, this is less well developed for clonal traits. As a result, in this analysis we took an exploratory approach and thus, to relate CWM and FD to environmental properties (expressed as EIV), we used linear regression with stepwise forward selection to find the most parsimonious model. To counteract the drawbacks of stepwise model selection (see e.g. Mundry and Nunn 2009), stepwise selection was based on Akaike information criterion (Burnham and Anderson 2002), and we reduced the number of our predictors as much as reasonable (see next paragraph).

Initially, using single EIV and their quadratic term as explanatory variables, we tested for the presence of unimodal relationships. Scatterplots of these models, if significant, are depicted in the Electronic Suplementary Material. We found only three non-linear relationships (i.e. only the model including the quadratic terms was significant) of all 100 tested combinations, thus we decided to omit these from further analyses. This exclusion allowed for more reliable results, as stepwise models with high numbers of predictors tend to select irrelevant variables for the minimum adequate model. To further improve the interpretability of predictor variables in terms of their relative importance, they were centred and standardized (Schielzeth 2010). In the following, we refer to the R^2 of these models as the observed R^2 (see also next section).

To analyse the relationship between FD and CWM we used simple linear models, with FD as the response variable and CWM as the predictor, where CWM was entered as a linear and as a quadratic term, as the expected relationship between FD and CWM is unimodal, but can also be linear if the composition of the communities does not include all possible combinations of species (see Dias et al. 2013).

Randomizations

As relating EIV to other metrics derived from species composition can produce confounded results (Zelený and Schaffers 2012), we compared the observed R^2 of final models to the R^2 expected by chance. To derive expected R^2, the stepwise selection method was performed on the same variables, but CWM and FD of traits have been calculated from randomized trait values. Randomization was achieved by shuffling species identities in the species by trait table, thus keeping trait combinations intact, but assigning sets of trait values randomly across all species. Species richness and abundance structure of the habitats are maintained by this procedure. The indices were related to the EIV using the same stepwise regression procedure as on observed species occurrence data, keeping the original centred EIV of habitats. For the R^2 of models on habitats, the mean (referred to as expected R^2) and standard deviation of R^2 were calculated from the distribution of R^2 values from 999 randomizations.

To judge whether the observed models are significantly better than randomized, a standardized R^2 (SR^2) was defined as

$$SR^2 = \frac{\left(\text{Observed}\, R^2 - \text{Mean} \quad \text{Expected}\, R^2\right)}{SD\, \text{Expected}\, R^2}$$

Observed R^2 were considered significantly larger than expected if $SR^2 \geq 1.65$ (based on one-sided t-test with $\alpha = 0.05$).

RDA

Redundancy Analysis (RDA) was used to display the relations between environmental gradients and CWM and FD. For each response group, defined as CWM and Rao of traits in habitats, we performed a single analysis. The standardized response variables were constrained by habitat CWM of EIV light availability (L), temperature (T), soil moisture (F), soil reaction (R) and soil nutrients (N). All analyses except RDA were done in R v. 3.2.2 (R Core Team 2015) and package 'FD' (Laliberté et al. 2014), the RDA's were done with CANOCO v. 5.04 (Microcomputer Power, Ithaca, NY, US).

Results

Comparison of the observed R^2 and the expected R^2 showed that models predicted the observed CWM better than expected by chance in only four out of eleven cases (Table 2). We found at least one trait significantly related to environmental gradients in each group of LHS, bud bank, and clonal traits (SLA, root sprouting capacity, multiplication rate and clonal index, respectively). By contrast, the models on Rao had significantly higher R^2 than expected by chance for almost all clonal and bud bank traits (the only exception being multiplication rate), but for none of the LHS traits.

There was no significant relationship between CWM and FD for any of the LHS traits, but for all clonal and bud bank traits, except multiplication rate. For root sprouting capacity, bud bank size, bud bank size including root buds, and bud bank depth including root buds the relationship was curvilinear, whereas for bud bank depth, lateral spread and clonal index there was a linear relationship of CWM and FD (Fig. S1 in the Electronic Suplementary Material).

The performed RDAs display the links between environmental gradients (expressed as EIV) and CWM and Rao. In both analyses, a substantial amount of variation was explained by the first two axes, with 56.5% in case of CWM and 76.9% in case of Rao, respectively.

The first axis in the RDA on CWM (Fig. 1) is strongly related to soil nutrient content (N). SLA and multiplication rate are also positively correlated with N. The second axis is mainly related to soil moisture (F). Increasing values of F are accompanied by a higher proportion of root sprouting plants, and a higher multiplication rate and clonal index.

Much of the variation in Rao of traits is explained by the first axis (71.1%), with the second axis contributing by only a small amount to the variation explained by the RDA (Fig. 2). The EIV for

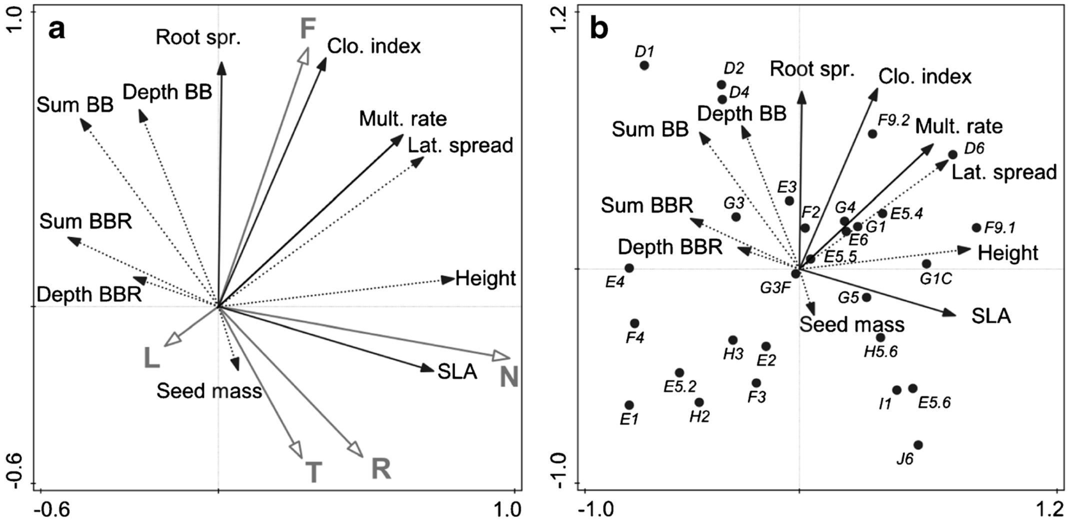

Fig. 1 RDA on CWM for traits using EIV L, T, F, R and N as constraining variables. The first axis explains 32.7%; both axes together explain 56.5% of variance in trait CWM of habitats. When the trait-environment relationship was not different from one expected by chance (i.e. non-significant SR^2), the arrow is dotted. Besides traits, graph **a** displays constraining EIV, and graph **b** displays the 29 habitats. For habitat coding, see Table 1.

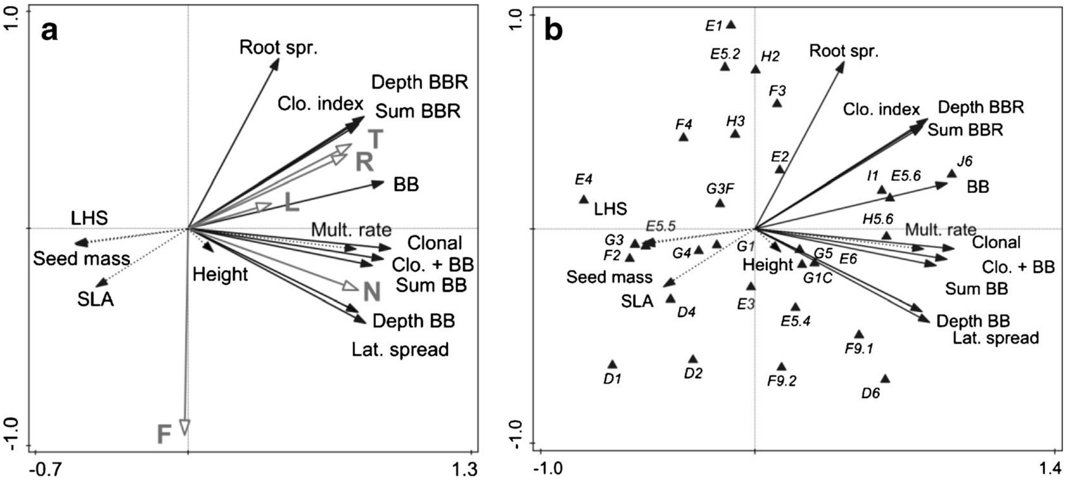

Fig. 2 RDA on Rao for each individual trait and trait combinations using EIV L, T, F, R and N as constraining variables. The first axis explains 71.2%, both axes together explain 76.3% of variance in trait CWM of habitats. For traits that had a non-significant SR^2, the arrow is dotted. Besides traits, graph **a** displays constraining EIV. Graph **b** displays the 29 habitats. For habitat coding, see Table 1.

temperature (T), soil reaction (R), soil nutrients (N) and less pronounced light (L) are positively correlated to the first axis. Rao of clonal and bud bank traits and their trait combinations all (except for multiplication rate) increase in the same direction. Similarly to the RDA on CWM, the second axis mainly represents a moisture gradient (F), to which the Rao of root sprouting is negatively correlated.

In most models that included clonal and bud bank traits' CWM and Rao, the EIV for temperature, moisture and nutrient availability were highly significant predictors (Table 3).

Table 3 Summary of linear models between EIV and CWM and Rao. Cells contain slope estimates for each EIV retained in the most parsimonious model after forward stepwise selection. NA stands for 'not available', as CWM are not meaningful for multiple traits. Highlighted in bold font are the models for which observed R^2 did deviate from expected R^2 (see Table 2). Asterisks indicate the significance of the linear terms. * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$.

Index	CWM					Rao				
EIV	L	T	F	R	N	L	T	F	R	N
Specific leaf area	**−0.37*****			**0.15****	**0.29*****	−0.26*	0.25	0.27**		−0.34**
Height			0.11		0.39***					
Seed mass	−0.26***		−0.12**			−0.19**	0.15		−0.28**	
LHS traits	NA	NA	NA	NA	NA				−0.44**	
Root sprouting capacity		**0.17*****	**−0.2*****				**0.3*****	**−0.44*****		**0.11**
Bud bank size	−0.34**		0.34***	0.14	−0.54***	**0.14***	**0.23***		**−0.13**	**0.36*****
Bud bank size including root taps	−0.14*				−0.25**	**0.15***	**0.31****	**−0.27*****	**−0.12**	**0.34*****
Bud bank depth	−0.26**		0.26***	0.13	−0.32**	**0.11***	**0.21****	**0.11***	**−0.1**	**0.24*****
Bud bank depth including root taps	−0.14*			0.11	−0.18*	**0.15*****	**0.22*****	**−0.23*****	**−0.11***	**0.28*****
All bud bank traits	NA	NA	NA	NA	NA	**0.59****	**0.88****	**−0.39***	**−0.37**	**1.1*****
Multiplication rate	**−0.06**	**0.14***	**0.29*****		**0.08**	0.09**				0.2***
Lateral spread			0.3***		0.25***		**0.47*****	**0.27*****	**−0.16**	**0.51*****
Clonal index	**−0.15*****		**0.35*****			**0.31*****	**0.13**	**−0.3*****	**−0.16***	**0.36*****
All clonal traits	NA	NA	NA	NA	NA	**0.44****	**0.67****		**−0.38***	**1.1*****
Clonal and bud bank traits	NA	NA	NA	NA	NA	**0.71****	**0.91****		**−0.64***	**1.55*****

Discussion

LHS and clonal traits in relation to environmental gradients and habitat types

In this paper we explored the relationship between environmental gradients and LHS and clonal traits across 29 temperate habitat types. We investigated associations for both the dominant trait values (CWM) and functional diversity characterizing those habitat types. The prevailing environmental gradients across habitats were related to soil productivity and moisture. This is consistent with findings of Klimešová and Herben (2015), who used the same data source but analysed trait-environment relationships at the plot level and did not use EIV. Our results suggest that most clonal and bud bank traits are significantly related to all studied environmental gradients. Moreover, these environmental gradients are mostly associated with the diversity of clonal and bud bank traits, but less with the dominant trait values or categories.

By contrast, out of the three LHS traits only CWM of SLA was significantly associated with a single EIV (soil nutrients). These differing results imply that the variation of traits related to vegetative reproduction responds stronger to environmental conditions than the studied aboveground traits.

Use of Ellenberg indicator values

In this study, Ellenberg indicator values were used to characterize environmental conditions of habitats. EIV has been shown to be a useful proxy for environmental variables in several previous studies (see e.g. Schaffers and Sýkora 2000; Tölgyesi et al. 2014). However, EIV are subject to a long debate over whether they are suitable for describing environmental conditions, being derived from empirical experiences about species preferences and distribution patterns rather than based on real measurements (Zelený and Schaffers 2012; Wildi 2016). Exner et al. (2002) discussed that using EIV for habitat characterization based on community composition involves circularity, as species occurrences are involved to generate both, response (community composition) and explanatory (mean EIV) variables. Therefore, we used randomizations to overcome the problem of spurious results. For the discussion, we refer to EIV gradients (obtained by calculating CWM of each indicator value for every habitat type) as environmental gradients: L being light availability, T temperature, F moisture, R soil reaction and N being nutrient availability or productivity of the habitat.

Community-weighted means

Regarding the predominant trait values in different habitats, we found two main gradients in our study, at one end indicating cold and wet conditions (such as bogs, fens and woodlands) while at the other end disturbed, more productive and thermophilous habitats (such as arable lands and trampled areas). Our finding that productive habitats hosted species with higher SLA values is in line with previous studies (e.g. Wilson et al. 1999) indicating higher resource acquisition and a less conservative growth strategy in these habitats (Pérez-Harguindeguy et al. 2013). By contrast, less productive habitats (high F, low T and R) such as bogs and fens, were dominated by species with lower SLA values, indicating that the most abundant species in these more stressful habitats show a more conservative strategy.

Species with clonal growth were more frequent in wet and cold habitats, in accordance with the results of van Groenendael et al. (1996) and Ye et al. (2014). Our results showed increased root sprouting, multiplication rate and clonality, which in general might serve as an alternative to sexual reproduction for several reasons. For instance, in habitats under harsh environmental conditions, as alpine/subalpine and arctic scrublands, clonal growth can ensure reproductive success. At the same time, such habitats expose clonal plants to low levels of disturbance, which favours their establishment and persistence (Callaghan et al., 1992; Klimešová et al. 2011; Klimešová et al. 2012). In woodlands of the temperate regions the time window for pollination and sexual reproduction is often short and limited to early-year unshaded conditions (e.g. Catorci et al. 2012). Also, the recruitment of species without persistent seed banks is supported mostly by clonal organs, allowing establishment in the spatially unpredictable patches of forests (Eriksson 1989).

Considering grasslands among the studied habitats, the clonal index increased from xeric through mesic to wet grasslands, which corroborates a study by Halassy et al. (2005) who found higher proportions of species with short spacers in xeric compared to mesic grasslands. By contrast, Wellstein and Kuss (2011) as well as Klimešová and Herben (2015) found more species with short spreading in relatively wetter, but also considerably colder, high-elevational alpine habitats, which are not represented in our dataset.

Multiplication rate was also positively correlated with productivity. Among others, Klimešová et al. (2011) and Craine et al. (2001) proposed that more fertile habitats favour species with higher competitive ability both above and below ground, leading to species with a higher number of clonal offspring.

Functional diversity

Clonal traits were significantly more diverse in environments that represented high temperature, soil reaction and fertility (Fig. **2**). Despite the tendency for species to be less clonal (see CWM section) in habitats with these conditions (trampled areas, arable lands, waste deposits and anthropogenic tall-forb stands), the species that do form clonal organs and bud banks seem to use different strategies to cope with the unpredictability of occurring disturbances in these habitats.

In rather undisturbed habitats (alpine and subalpine environments, bogs and fens), conditions of low temperature, soil reaction and fertility act as filters that reduce the diversity in clonal traits. In these habitats pollinator availability might be limited, either because of the low temperature at high altitudes, or due to larger open water surfaces (in the case of fens, bogs, wetlands). Even in habitats where pollinators are available, low productivity might lead to a lack of flowering species (Fujita et al. 2014). Therefore, lateral spread might offer an alternative (vegetative) way of reproduction when sexual reproduction is limited (Herben et al. 2015).

Soil moisture constitutes another gradient associated to the diversity of clonal strategy. In moister habitats, species have more diverse lateral spread strategies compared to xeric and rocky habitats (dry grasslands, woodland fringes, cliffs and outcrops). In the latter habitat types, a patchy distribution of nutrients might constitute a filter that can be passed more likely by species with the ability to access nutrients by clonal spreading, a strategy that has been proposed for several systems (reviewed in Liu et al. 2016).

LHS traits were less diverse across the gradients than clonal traits. Moreover, relationships of LHS traits with environmental gradients were not significantly different from patterns expected by chance. In temperate Europe, the three LHS traits show a relatively small range, whereas the divergence in clonal and bud bank traits could allow co-existence of species that are similar above ground but dissimilar below ground e.g. in depth of bud bank, and in shape and size of rhizomes (Klimešová et al. 2011). This adds evidence to the recently expressed view that clonal and bud bank traits could represent an important independent axis of plant strategy (Klimešová et al. 2016).

Theoretically, such a finding could be the result of clonal and bud bank traits usually being recorded more discretely, i.e. with a lower number of unique values along the continuous trait scale, compared to LHS traits. In our dataset, single clonal and bud bank traits are indeed less continuous than LHS traits, leading to a more right-skewed distribution of distances calculated from LHS traits compared to clonal and bud bank traits. While this might in fact contribute to a stronger expression of variation in clonal and bud bank traits, it should not translate into an inability to detect filtering for LHS traits if it would exist, as FD of traits and its association to environmental gradients was investigated in separate models for each trait.

Relationship of CWM and FD for LHS, clonal, and bud bank traits

The finding that clonal and bud bank traits respond more strongly to environmental gradients is also reflected by significant relationships between CWM and FD for these traits. While it has to be noticed that this relationship is based on a mathematical relationship between the two metrics, it is nevertheless possible to refer to this relationship to indicate if a change in one of the metrics is biologically connected to a change in the other.

The whole range of the hypothetical unimodal relationship has been demonstrated by simulated communities (see Dias et al. 2013), whereas the empirical patterns found here all seem to fall on subparts of the entire possible curve. This at least enables us to qualify if observed significant changes in CWM are associated with FD. Thus, there are three different scenarios for the relationship of the two metrics: (i) a change in FD but not in CWM, i.e. there is filtering on trait variation but not on the allowed trait values; (ii) changes in both FD and CWM, i.e. filtering acts on the allowed traits and their variation; (iii) a change only in CWM but not in

FD, indicating that habitat conditions filter out specific trait values, but has no effect on how different these traits are within a habitat.

Our finding that except for SLA, LHS traits are not filtered in the studied habitats are mirrored by the fact that their CWM and FD are unrelated to each other. By contrast, the capacity for root sprouting, and a higher clonal index, bud bank size and bud bank depth coincide with a decreased FD in these traits. This shows that even though CWM for some of these traits was only spuriously correlated with environmental gradients, it is not always straightforward to tease apart if traits respond to gradients by shifts in the trait values of the dominant species or by a reduced variation among the species.

Conclusions

Our analyses revealed more consistent and significant relationships between clonal traits and environmental gradients than between LHS traits and environmental gradients. We therefore propose that there is a stronger filtering on clonal than on LHS traits, as the former tend to be less diverse within habitats that have decreased temperature, pH, nutrient levels and light. These unfertile, harsher environments are all favoured by plant species that are able to spread vegetatively. At the opposite end of these environmental gradients, clonal and bud bank traits are more diverse indicating that the filtering is weaker and more clonal strategies exist in parallel in more fertile habitats.

As such, our results hint at clonal and bud bank traits being an understudied dimension of plant strategy, which are not included in classical strategy schemes as C-S-R (distinguishing competitive, stress-tolerant and ruderal; Grime 2006) or the LHS scheme (Westoby 1998). We propose that clonal and bud bank traits could indeed be added as an independent axis to functional trait space capturing plant form and function (Laughlin 2014).

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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