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Clonal and bud bank traits: patterns across temperate plant communities

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Abstract

Questions: We examine patterns of clonal traits and below-ground bud bank traits in plant communities over a large set of temperate vegetation types. We asked (i) how clonal traits are distributed in different community types and (ii) what are within-community patterns of these traits as an indication of their role in species coexistence and community assembly.

Location: Czech Republic.

Methods: We use a stratified set of more than 20,000 vegetation records from the Czech National Phytosociological Database as a source of species co-occurrence and habitat type data, and combined it with data on clonal and bud bank traits from the CLO-PLA database. We calculated both community trait means and dispersions for all records in the database and used a series of randomization tests to assess effects of environmental filtering and within-community assembly.

Results: Habitat filtering was stronger in bud bank traits than in clonal traits. The key factors driving structure of clonal traits in Central Europe seem to be differences in productivity and in wetness. These gradients are responsible for a major change in clonal growth parameters, from clonal plants with short and persistent connections in dry and unproductive habitats to plants with long- and short-lived connections in wet and productive sites. Size of the bud bank is rather uncorrelated with this gradient: species with small below-ground bud bank size prevail in highly disturbed and in water habitats. None of the traits showed significant overdispersion, either at the level of the whole data set, or at the level of individual habitat types.

Conclusions: Capacity for clonal growth occurs under many different environmental regimes and can give rise to very different growth forms. Therefore, using capacity for clonal growth as a proxy for clonal reproduction, capture of horizontal space or resprouting capacity may hinder understanding of its role. Absence of overdispersion after accounting for habitat filtering means that we found no evidence that clonal traits play a role in niche-based coexistence processes.

Introduction

Use of plant functional traits to formulate and examine hypotheses on processes in plant communities has become firmly established in the past two decades (Lavorel & Garnier 2002; Díaz et al. 2004; McGill et al. 2006). Mean values or ranges of individual traits have proved an excellent tool to identify environmental filters operating on communities (Díaz et al. 2004; Messier et al. 2010), just as various measures of trait variance or spacing have been used to identify non-random patterns of community assembly (Ackerly & Cornwell 2007; Götzenberger et al. 2012).

As plant traits are only proxies for plant functions (Weiher et al. 1999; Lavorel & Garnier 2002), quality of the trait-derived information on community assembly processes always resides in a good choice of traits (Römermann et al. 2008). Trait-based studies have been performed for a wide array of traits intended to capture

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important plant functions, namely dispersal, establishment, persistence and resistance to disturbance (Weiher et al. 1999; Perez-Harguindeguy et al. 2013). However, quality and accessibility of data on individual traits differ, and consequently some easily accessible traits (e.g. seed mass or plant height) have been used much more often than others. Such choice might have biased existing findings by putting more stress on parameters of plant life history that are captured by these traits while neglecting some others. This might be a serious problem if individual plant functions contribute differently to community composition and assembly, or if such contributions change along major environmental gradients. For example, while vertical growth and competition-related traits may be subject to filtering effects, soil foraging traits may underlie niche differentiation (Mayfield & Levine 2010). Further, selection of traits to be used has often been done in a way that would capture differences among a wide array of life forms, from trees to annual plants. This necessarily gave prominence to traits that can be reasonably defined for a majority if not all plant species (see e.g. Westoby 1998). This has necessarily restricted use of traits that are not possessed by all plants, but might still play a key role in some habitats or biomes.

Traits of clonal growth and spreading belong to a group of traits that have been rather neglected in this respect (but see e.g. Klimeš et al. 1997; Craine et al. 2001; Tamm et al. 2001; Song et al. 2002; Sammul et al. 2004; Pakeman 2011; Rusch et al. 2011; Gough et al. 2012; Ye et al. 2014). Although they have been acknowledged as important in several review papers (Weiher et al. 1999; Kleyer et al. 2008), the studies that use them to examine trait–environment relationships or within community differentiation are fairly scarce (but see Klimeš et al. 1997; Craine et al. 2001; Tamm et al. 2001; Sammul et al. 2004; Klimeš 2008; Pakeman 2011; Rusch et al. 2011). There are two reasons for this: clonal growth is rather difficult to capture using traits that are easy to collect, and clonal growth traits, being absent in a number of species (notably many trees and many annuals), have necessarily missing values in these species. Still clonal growth is prevalent in a number of biomes, namely water, temperate and boreal/arctic; it has been estimated that around 70% of species of temperate floras are clonal (Klimeš et al. 1997), and clonal traits have been demonstrated to be important for species performance, both in response to habitat factors and within-community interactions (see e.g. Klimeš et al. 1997; Craine et al. 2001; Gross et al. 2007; De Miguel et al. 2010; Eilts et al. 2011; Gough et al. 2012).

The existing studies examining clonal traits have shown that both capacity for clonal growth and traits of clonal growth organs differ among individual community types (Klimeš 2008; Sosnová et al. 2010, 2011; Benot et al. 2011; De Bello et al. 2011; Klimešová et al. 2011b, 2012; Rusch et al. 2011; Schamp et al. 2011). Proportion of clonal plants is also known to change along long gradients of temperature and precipitation (Song et al. 2002; Ye et al. 2014). This means that parameters of clonal growth confer fitness advantage depending on particular environmental conditions. Clonal growth strongly prevails in wetland and aquatic habitats (Grace 1993; Sosnová et al. 2011). Distance of lateral spread, as another example, is high in wet and nutrient-rich habitats (Klimešová et al. 2011a), whereas it is very much restricted in arctic communities (Klimešová et al. 2012). As a result, clonal traits could be subject to environmental filtering, which is likely to produce underdispersion in distribution of their trait values (De Bello et al. 2011). However, as most of these studies have been done in rather extreme habitats, and studies over large ranges of habitat conditions are rare (but see e.g. Klimeš et al. 1997), we know little about how prevalent such patterns are over large sets of vegetation types.

Even less is known on the potential role of clonal growth traits in community assembly. While studies have shown a wide variety of growth forms coexisting at a single stand (Herben et al. 1993, 1997; Tamm et al. 2001; Sammul et al. 2004; Klimešová et al. 2011b; Benot et al. 2013), it is not clear whether species differing in clonal traits are more likely to coexist, which would show up as trait value overdispersion relative to a random pattern (see Götzenberger et al. 2012). Although such a role of variation in clonal traits for species coexistence in community assembly has been postulated a long time ago (Kull 1995; Gigon & Leutert 1996), more specific data testing within-community patterns of these traits are rare and restricted to a limited range of environmental conditions (De Bello et al. 2011; Schamp et al. 2011). As clonal traits are not directly involved in resource acquisition, they are likely to affect diversity differently from resource competition traits, such as height, or traits correlated with growth rate, such as specific leaf area. While in the latter species interactions are likely to lead to trait clustering due to their role in (asymmetric) competition (Mayfield & Levine 2010; Gerhold et al. 2013; Herben & Goldberg 2014), this is not necessarily true for clonal traits. It has been shown, using a highly parameterized model of a plant community, that variation in clonal growth traits confers species coexistence much more easily than variation in vertical growth and resource acquisition traits (Wildová et al. 2012). Thus, clonal traits might be much more prone to show overdispersion (see also De Bello et al. 2011 for an empirical demonstration).

In this paper, we therefore aim to examine community-wide patterns of clonal traits and below-ground bud bank traits over a large set of temperate vegetation types. We ask

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two questions. First, we aim to assess how clonal traits are distributed in different community types to identify habitat filtering in these traits. Here we extend the existing partial analyses of clonal trait distribution by using a representative set of vegetation records covering temperate vegetation. Specifically, we address whether specific values of individual clonal traits show affinity to certain environmental conditions or habitat types. Second, we examine within-community patterns of these traits as an indication of their role in species coexistence and community assembly. In particular, we examine whether these traits show within-community overdispersion (as a possible indication of limiting similarity) or underdispersion. We use a series of randomization tests to assess potential effects of environmental filtering and within-community assembly (see e.g. De Bello et al. 2011, 2012).

Methods

Data sources

Clonal growth data are taken from the CLOPLA v 3.2 (J. Klimešová, unpublished data). We transformed the data from the database to yield nine traits (Table 1). While these traits express different components of clonal life strategy, they are correlated to some degree (App. S1 and S2).

Species co-occurrence data were taken from the Czech National Phytosociological Database (Chytrý & Rafajová 2003). A stratified subset of the database containing 20,468 plots sampled after 1970 was used (see Chytrý et al. 2005 for the stratification procedure). We refer to these units as ‘plots’ or ‘samples’ (here using these terms interchangeably). These plots contain data on occurrence of 2027 species, out of which 1167 species occur in more than ten plots.

Before stratification, the set was standardized with respect to plot sizes separately for each major vegetation type; plots were 50–500 m^2 for woodland habitats, 10–100 m^2 for scrub, 4–100 m^2 for grassland, wetland and aquatic habitats, and 1–50 m^2 for low-growing vegetation in stressed or disturbed habitats (see Chytrý et al. 2005 for details). These size differences make comparison of trait dispersion across habitats less reliable. On the other hand, as large plots are used for habitats with larger plant individuals, this provides a qualitative correction for different mean sizes of plant individuals. The plot sizes used are too small to include large-scale environmental gradients (e.g. in wetness or productivity) even in large forest plots, while even the smallest ones are large enough to include sufficiently high numbers of plant individuals to avoid data distortion due to constraints on numbers of individuals.

The plots were assigned to 32 EUNIS habitat types (see Chytrý et al. 2005), representing major vegetation types of Central European vegetation. Number of plots in individual EUNIS habitat types varied widely, from wet grasslands, dry grasslands and littoral zone habitats with more than 2000 samples each, to riverine willow stands, alpine and subalpine scrub and brackish marshes, with 20–32 samples each.

Data analysis

First, we calculated mean trait values of individual EUNIS habitat types as ($M = \frac{1}{n}\sum_i \frac{1}{S_i}\sum_j x_{ij}$), where n is the number of plots, S_i is the number of species in plot i, and x_{ij} is the

Table 1. Traits used in the analyses.

Abbreviation	Units	Definition	Number of species for which data are available
Root Sprouting Capacity	Yes/no	Capacity for root sprouting, both spontaneous and triggered by plant injury	1542
Bud Bank Size	Number of buds	Number of stem-derived buds in the soil and at the soil surface	1535
Bud Bank Size (Root Buds Included)	Number of buds	Number of stem- and root-derived buds in the soil and at the soil surface	1535
Mean Bud Bank Depth	cm	Weighted mean depth of stem-derived buds	1484
Mean Bud Bank Depth (Root Buds Included)	cm	Weighted mean depth of stem- and root-derived buds	1484
Capacity for Clonal Growth	Yes/no	Whether the plant possesses organs of clonal growth	1542
Persistence	Yes/no	Whether clonal connections between ramets persist two or more years[1]	814
Multiplication Rate	Number of offspring	Number of offspring shoots per parent shoot per year, including offspring of small size. Small offsprings are defined as those clonal offspring for which it took more years to attain size comparable with other clonal offspring of the plant; they usually resemble seedlings[1]	823
Lateral Spread	Meters	Lateral spreading distance of clonal growth organs[1]	817

[1] Trait defined only for plants with Clonality = 1.

trait value of species *j* in plot *i*. We did not weight species values (x_{ij}) by species cover. This is preferable when plot sizes are not fully consistent (namely across habitat types). Plots in which information was available for less than 80% of the species present were discarded; for traits of clonal growth that are defined for clonal plants only, we discarded plots in which clonal traits information was available for less than 80% of the clonal plants present (for resulting numbers of plots available for analyses see Table 2). Effect size of EUNIS habitat types on distribution of individual traits was expressed using $\eta^2 = SS_{\text{effect}} / SS_{\text{total}}$. Because η^2 may be sensitive to unequal size of individual groups, we calculated it only for the subset of the data with groups with fewer than 100 samples excluded. We further visualized differences among EUNIS habitat types in the structure of clonal trait variables using principal components analysis (PCA) on a correlation matrix. We took each habitat type as one case for the analysis and represented it by averaging individual trait values (which themselves are means over all species in the sample) over all samples in that habitat type. In some analyses, we excluded water habitats (EUNIS types C1 and C2), because they represent very different ecological regimes from terrestrial habitats, and prevailing clonal growth forms there are very different. If they are included in the whole set-level analyses, they bring in very strong habitat filtering effects that tend to hide other effects operating among terrestrial habitats. Unless otherwise stated, results for only non-woody species (herbaceous species and dwarf shrubs) are shown in the paper.

Further, we calculated mean value of the plot-wise SD of each trait in the whole set ($D = \frac{1}{n}\sum_i \sqrt{\frac{1}{S_i-1}\sum_j \left(x_{ij} - \bar{x}_i\right)^2}$), where n is the number of plots, S_i is the number of species in plot *i*, and x_{ij} is the trait value of species *j* in plot *i*. We examined the SD using a randomization procedure in which we randomized clonal traits by randomly assigning each plant species in the data set a value randomly drawn from the pool of all species (without replacement) while keeping the lists of co-occurring species for each plot intact (Stubbs & Wilson 2004; Schamp et al. 2008). We chose this approach because it does not require additional assumptions about how the community structure is generated, and it examines the non-randomness of the trait–species relationship only. Species with missing values were not included in the randomization (i.e. if a plot had information available for less than 100% of its species, only known values were randomized). This randomization process was done 1000 times. We used the randomization procedure to determine the significance of trait dispersion for individual traits by determining the proportion of randomizations with dispersion higher than the empirical dispersion. Further, we used it to calculate standardized effect sizes (SES, defined as $SES = X_{\text{obs}} - X_{\text{exp}}/s_X$, where X_{obs} is the true value of parameter, X_{exp} and s_X are its mean and SD after randomization.

The same analyses were done for each of the EUNIS habitat types separately. In this case, we calculated *D* values by averaging plot-wise values only over plots in each habitat type and using only species from the species pool of the habitat type in which the given plot belongs. The species pool for a habitat type was defined to include any species with at least 1% of all its records occurring in that habitat type. Significance and SES values of trait dispersion within a habitat type were calculated by randomly assigning to each species in each plot a value drawn only from the species pool of that habitat type. Species that

Table 2. Patterns of non-randomness of trait dispersions in EUNIS habitat types; water habitats are excluded. *N* – number of vegetation records with sufficient information used in the analysis; SES – standardized effect size. Significance of dispersion and positive SES were calculated for 30 habitat types.

Trait	*N*	SES of the overall dispersion for the whole data set	Number of habitats showing significant negative sES	Number of habitats showing significant positive SES	Number of positive SES in individual habitat types
Randomization Type Used	–	Whole data set	Each habitat separately	Each habitat separately	Each habitat separately
Root Sprouting Capacity	13027	−0.78	9	1	11
Bud Bank Size	15848	**−6.2****	9	–	6
Bud Bank Size with Roots	15848	**−2.63****	8	–	7
Bud Bank Depth	14459	**−5.52****	8	–	6
Bud Bank Depth with Roots	14459	**−5.37****	13	–	2
Capacity for Clonal Growth	15907	**−13.66****	14	–	1
Persistence	15752	**−7.12****	7	1	5
Multiplication Rate	15905	**−1.96***	5	–	17
Lateral Spread	15895	0.49	0	2	16

$^*P < 0.05$, $^{**}P < 0.01$. Significant values are in bold. SES calculation and significance tests are based on 1000 randomizations.

were missing in the species pool were assigned missing values for their trait data and were not involved in the randomization.

All univariate calculations were done in R v 2.15.1 (R Foundation for Statistical Computing, Vienna, AT); multivariate analyses were performed using CANOCO v 5 (Microcomputer Power, Ithaca, NY, US).

Results

There were strong differences in mean trait values of individual samples among the EUNIS habitat types (Fig. 1). Highest differences among habitats were in bud bank traits, root sprouting capacity and proportion of clonal plants; in contrast, multiplication rate and lateral spread had the

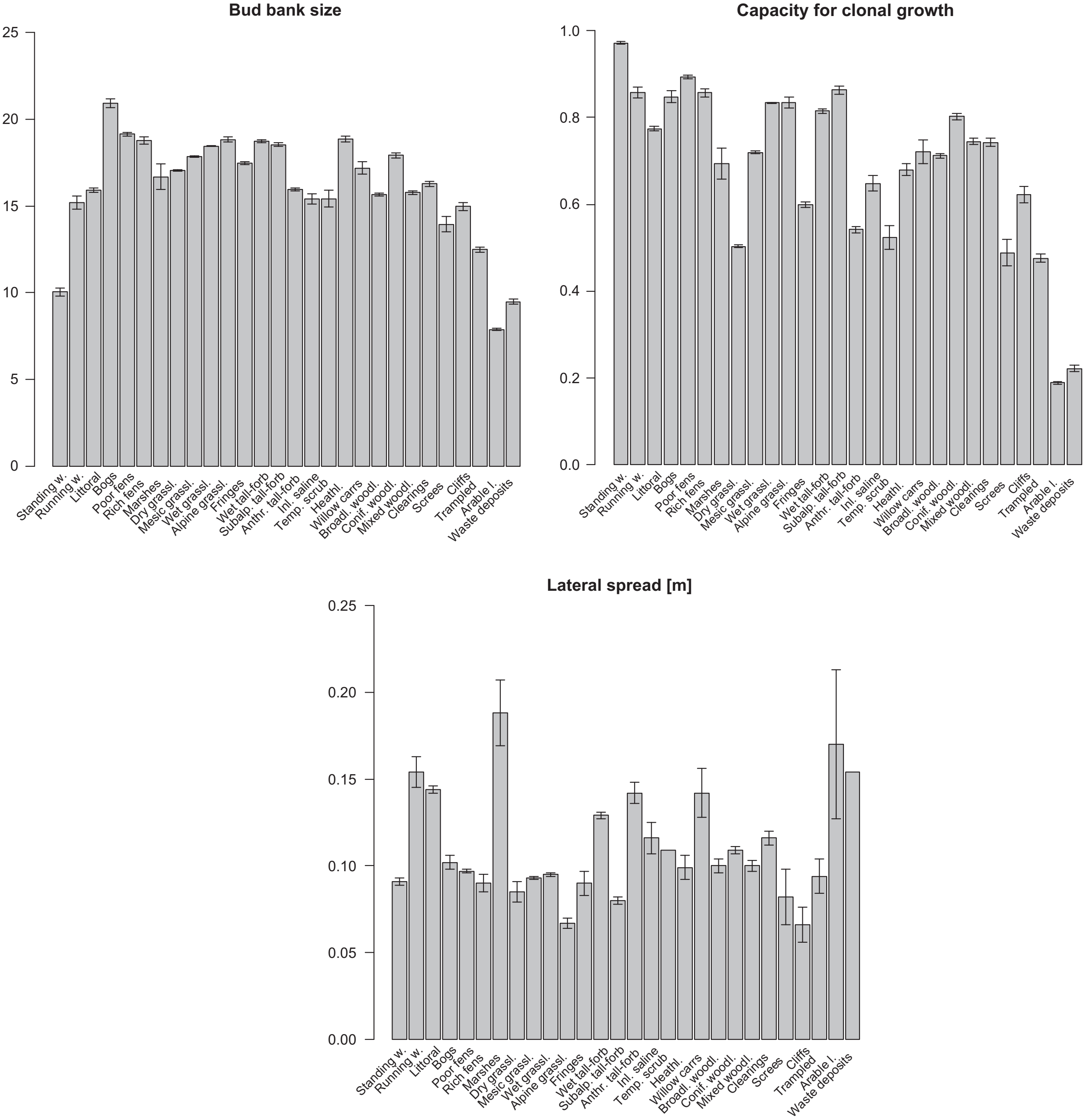

Fig. 1. Community-weighted means of bud bank size (number of buds per mother plant), capacity for clonal growth (proportion of species with this capacity per community) and lateral spread, calculated for the EUNIS habitat types.

lowest amount of variation out of all traits explained by habitat (App. S5).

High proportions of clonally growing plants (over 80% out of the plots for which sufficient data were available) were found in water and mire habitats, a number of grassland types (with an exception of dry grasslands) and tall forb habitats (Fig. 1). Low proportions of clonally growing plants (below 60% out of the plots for which sufficient data were available) were in rocky and anthropogenic habitats, dry grasslands and woodland fringes, and in temperate scrub. Forest habitats typically had average proportions ranging from 60% to 80%, with the highest percentages among these in coniferous forests (Fig. 1). Community mean values of clonal growth traits showed a marked gradient, from habitats with persistent connections among ramets, low multiplication rate (number of clonal offspring per mother plant) and partly also higher proportion of root sprouting (scrub, alpine and dry grasslands, bogs) to habitats with non-persistent connections, high multiplication rate and more extensive lateral spread (water and littoral habitats, marshes, and tall forb habitats etc.; see Figs 1–3).

In bud bank traits, highest numbers of buds were found in several types of mire habitat, in coniferous forests and in scrub; they were low in water and synanthropic habitats (Figs 1 and 4). Forests and forest-related habitats such as fringes and some types of scrub had the deepest bud bank. Mean values of all bud bank traits in individual plots were strongly correlated (all $R^2 > 0.4$; first axis of PCA explains 85% of the variation); habitats with more buds tended to also have higher mean bud bank depth. Overall variation across communities in bud bank size was largely due to variation in stem-derived bud bank, whereas root bud bank contributed relatively little. The R^2 of stem-derived bud bank and total root bank was high (0.705).All traits except root sprouting capacity and lateral spread showed strong underdispersion within samples at the level of the whole data set (Table 2; see also App. S4 and S5). A strong signal of underdispersion remained for a number of traits also at the level of individual habitat types (i.e. when only species belonging to the habitat-specific species pool were used). Significant underdispersion at many habitat types was detected in all bud bank traits, proportion of clonally growing plants, root sprouting capacity and persistence of connection among ramets. In contrast, multiplication rate and lateral spread showed many fewer cases of significant underdispersion (App. S4 and S5). SES values for these traits were often positive (although significant overdispersion was detected in a few habitat types only). In general, the pattern in these traits at the level of habitat types did not differ from the null assumption that positive and negative SES are equally likely: proportion of positive SES is likely under this assumption, and the proportion of significant SES is likely assuming alpha = 0.05.

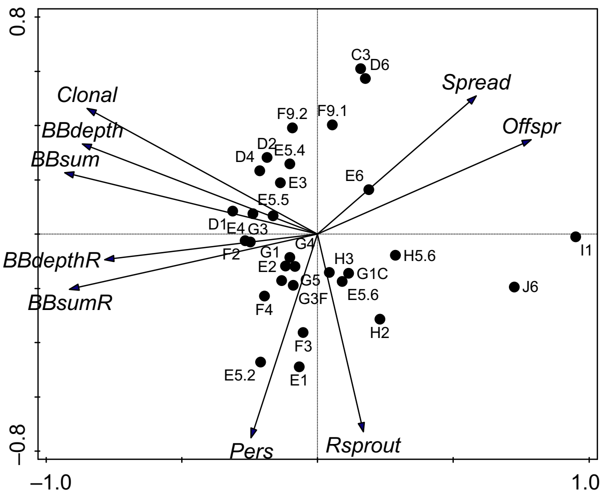

Fig. 2. Principal components ordination of clonal and bud bank traits across individual EUNIS habitat types (water habitats excluded). Rsprout – Root sprouting capacity, BBsum – Bud bank size, BBsumR – Bud bank size with roots, BBdepth – Bud bank depth, BBdepthR – Bud bank depth with roots, Clonal – capacity for clonal growth, Pers – Persistence, Offspr – Multiplication rate, Spread – Lateral spread. Each trait is represented by the mean of sample means in all samples in the given habitat type. The first axis explains 50.7%, the second axis 25.5% of the total variation. C3, Littoral zone; D1, Raised bogs; D2, Poor fens and transition mires; D4, Base-rich fens; D6, Brackish marshes; E1, Dry grasslands; E2, Mesic grasslands; E3, Wet grasslands; E4, Alpine grasslands; E5.2, Woodland fringes; E5.4, Wet tall-forb stands; E5.5, Subalpine tall-forb stands; E5.6, Anthropogenic tall-forb stands; E6, Inland saline grasslands; F2, Alpine and subalpine scrub; F3, Temperate scrub; F4, Heathlands; F9.1, Riverine willow stands; F9.2, Willow carrs; G1, Broad-leaved woodland; G1.C, Broad-leaved plantations; G3, Coniferous woodland; G3.F, Coniferous plantations; G4, Mixed woodland; G5, Forest clearings; H2, Screes; H3, Cliffs and outcrops; H5.6, Trampled areas; I1, Arable land; J6, Waste deposits.

Discussion

Habitat differences and filtering effects in clonal and bud bank traits

Almost all clonal and bud bank traits showed a strong degree of habitat filtering. This confirms that the patterns known from earlier studies done in a narrower range of habitat types (De Bello et al. 2011; Klimešová et al. 2012) can be generalized to a broad range of habitats in temperate vegetation (see also Klimeš et al. 1997; Ye et al. 2014). The strongest differences in clonal traits across habitats are from habitats with plants of bigger stature, such as littoral habitats or tall forb stands, to extreme habitats with smaller plants, such as alpine or dry grasslands. The former are habitats with prevailing low persistence of connection among ramets, high lateral spread and high multiplication rate, while the latter have prevailing high persistence of connection and short lateral spread.

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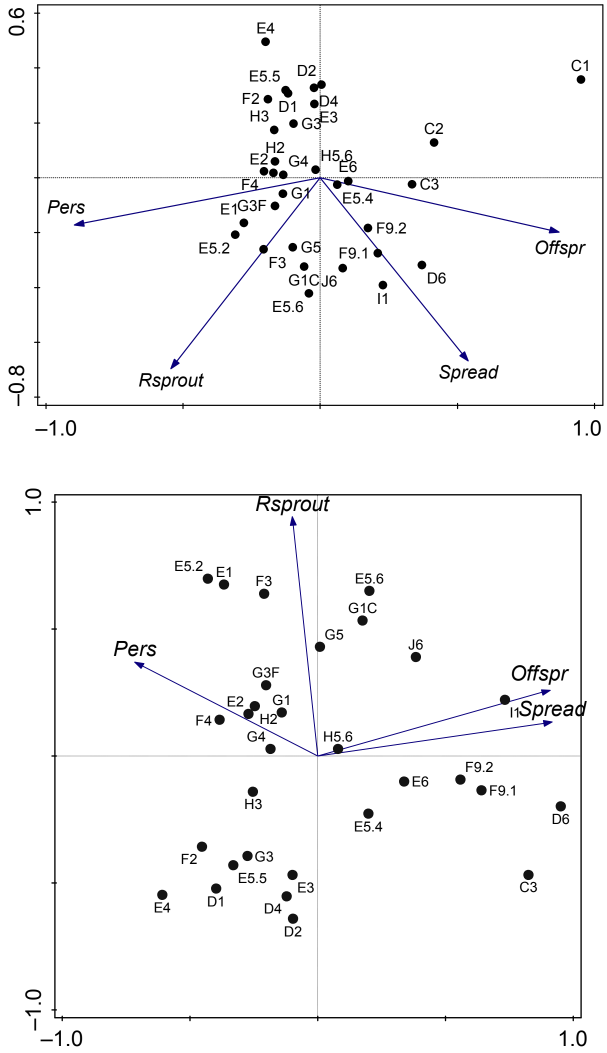

Fig. 3. Principal components ordination of traits of clonal growth across individual EUNIS habitat types. Upper pane: including water habitat types (first axis explains 53.7%, the second axis 25.0% of the total variation); lower pane: without water habitat types C1 and C2 (60.1%, the second axis 27.7% of the total variation). Each trait is represented by the mean of sample means in all samples in the given habitat type. For trait abbreviations see Fig 2. C1 – standing water, C2 – running water; for other habitat type abbreviations, see Fig. 2.

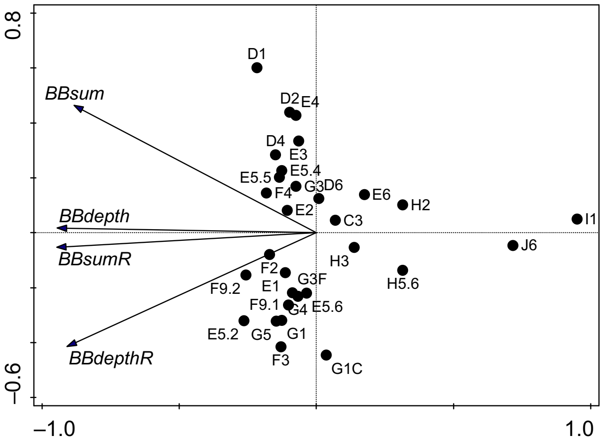

Fig. 4. Principal components ordination of bud bank traits across individual EUNIS habitat types. Each trait is represented by the mean of sample means in all samples in the given habitat type. The first axis explains 84.9%, the second axis 9.8% of the total variation. For trait and habitat type abbreviations, see Fig. 2.

This pattern is likely to be due partly to differences in productivity (as shown by its correlation with plant stature) and partly to differences in disturbance level (as indicated by high lateral spread in anthropogenic habitats and arable fields). Effects of productivity may be related to several non-exclusive causes. First, taller plants in productive habitats will have more extensive lateral spread due to allometric effect of size (taller plants will have longer spacers; see Klimešová et al. 2011a). Second, clonal offspring in more productive habitats with higher competition for light may be more dependent on maternal support early in their life, favouring extensive lateral spread, but maintenance of the connection may be too costly later (Eriksson & Jerling 1990). In contrast, in low productivity stressed habitats offspring may need prolonged maternal support as a safeguard against environmental fluctuations over extended period (Jónsdóttir & Watson 1997; Klimeš 2008), selecting for high persistence of connection among ramets. In addition, the water conduction system in plants in dry habitats (a subset of stressed habitats) must be protected from embolism (Sperry 2003), further requiring stout and hence persistent connections. As asymmetric competition for light is typically weak in such habitats (e.g. Choler et al. 2001), lateral spread can be lower without imposing too much competition burden on the daughter.

High lateral spread in disturbed habitats such as arable fields (Fig. 1) can also have several causes. Disturbance may favour short-lived (monocyclic sensu Klimešová & de Bello 2009) shoots, which are often associated with longer spacers (Craine et al. 2001; Herben et al. 2012). Further, long spacers may be favourable in highly disturbed habitats due to better colonization of temporally varying habitat mosaics (Fahrig et al. 1994) and better survival after spacer fragmentation due to soil disturbance.

It should be pointed out here that the strength of the habitat effects is a function of the range of habitats sampled. While the range of our habitats is fairly representative for temperate vegetation, we necessarily miss patterns that differentiate such vegetation as a whole from other biomes. As a result, it is likely that some traits that are rather habitat-non-specific in Central European vegetation will show a strong environmental signal if broader habitat ranges are compared. For example, lateral spread (one of the least habitat-specific traits in our data set) is strongly constrained in cold habitats, both in the Arctic (Klimešová et al. 2011b) and high alpine habitats (De Bello et al. 2011).

Clonal and bud bank traits, capacity of clonal growth

Our analyses provide the first demonstration of bud bank patterns across a broad range of communities. Bud bank traits seem to carry rather different information from that carried by clonal growth traits (see also Klimešová & Klimeš 2007). They are strongly correlated with capacity for clonal growth as such; size of the bud bank and capacity for clonal growth are essentially manifestations of a single trait and are highly correlated in comparative species sets (J. Klimešová & T. Herben, unpublished data).

Species with small below-ground bud bank size (and non-clonal species) prevail in highly disturbed anthropogenic and arable field habitats, and in water habitats. The likely reason is the prevailing role of seed regeneration in disturbed habitats (for aquatic habitats see discussion below), which is negatively correlated with the size of the bud bank and hence resprouting capacity (Bellingham & Sparrow 2000). In particular, arable fields represent an extreme habitat type in Central Europe, with deep soil disturbance, where seed reproduction may be a better survival strategy than clonal growth, unless species possess clonal growth traits with very long lateral spread and capacity to resprout from fragments (see above). While existence and size of the bud bank act as a buffer against disturbance (see Dalgleish & Hartnett 2009; Clarke et al. 2013), clonal plants are not able to build sufficient storage of carbohydrates for resprouting if severe disturbance is too frequent (Iwasa & Kubo 1997). In contrast to studies in American prairies (Dalgleish & Hartnett 2006; Cleland et al. 2013), our data do not support strong differences in the size of the bud bank along a wetness/productivity gradient. This is clearly due to the absence of the extreme dry habitats relative to North American prairies.

In addition to bud bank size, bud bank depth in the soil may act as a measure of bud bank protection from disturbance acting from above the ground (Vesk & Westoby 2004; Dalgleish & Hartnett 2009; Clarke et al. 2013) or as simple effect of plant size, as bigger plants have their below-ground organs placed deeper due to biomechanical and allometric constraints. In our data set, bud bank size is largely correlated with bud bank depth. This is because plants having bud banks deep in soil usually have some buds also in more shallow soil layers. However, there are some interesting deviations from this rule. Bud banks are shallow (relative to their size) in grassland habitats, whereas they are deep in scrub, fringe and forest habitats (in herb species only; woody species are excluded from the analyses). This also makes grassland habitats rather vulnerable to soil disturbance (see Dalgleish & Hartnett 2009); in contrast, herbaceous plants of forest fringes and forests may survive and even spread after fires, windthrow or logging, i.e. disturbances that also affect the soil surface.

Bud bank size is determined primarily via stem-borne buds, with root buds playing a minor role. Nevertheless, root buds themselves show some specific patterns. In several habitat types (namely dry grasslands, woodland fringes and temperate scrub), sprouting from roots seems to be a fairly common strategy, possessed by close to 30% of species present. These habitats are characterized as having a low proportion of species with the capacity for (stem-based) clonal growth and also rather low lateral spread. Root sprouting constitutes here an alternative strategy to clonal growth involving stem-derived buds (see Klimešová & Klimeš 2007).

Water habitats are fairly specific in terms of participation of clonal plants and their bud banks. Plants in water habitats are much more likely to be clonal than in any other habitat (see also Grace 1993; Sosnová et al. 2010, 2011), however, they show low bud bank sizes. This is in contradiction to other habitats where capacity for clonal growth and bud bank size are closely linked. This is clearly due to low persistence of connections among ramets in wetland and aquatic habitats, which lead to a loss of structures that would otherwise bear the buds. In addition, the below-ground bud bank is not of much importance in water habitats, as many regenerative and overwintering buds (e.g. turions) are produced above the ground and rely on protection by the water column and dispersal by water currents.

Clonal traits and community assembly

None of the traits examined showed strong overdispersion, either for the whole data set or when the data set was analysed at the level of individual habitat types. This means that for none of the clonal traits do we possess an unequivocal indication of their role in some niche-based coexistence processes (Mayfield & Levine 2010). This does not rule out that clonal traits are involved in niche differentiation, but it must take place at scales finer that the plot sizes used for vegetation data collection (several metres for most of habitat types).

There are strong differences among the individual traits at the level of individual habitat types. Traits of clonal growth (namely lateral spread, to a lesser degree, multiplication rate) have essentially random dispersion (see also Schamp et al. 2011), i.e. show no indication of habitat filtering or involvement in niche differentiation. In the remaining traits, there is strong underdispersion even at the level of individual habitat types. This could be due to two non-exclusive causes: (i) either there is strong habitat filtering at a finer level that is not captured by classification of habitats into the EUNIS habitat types used, or (ii) coexistence is favoured by similarity in these traits due to the equalizing forces in competition (Ågren & Fagerström 1984; Mayfield & Levine 2010). Both options are theoretically possible and cannot be unequivocally separated from each other. Traits such as bud bank size or multiplication rate can be involved in competition, for example by determining the rate of habitat occupation after a disturbance event. Therefore, in disturbed habitats, there could be an equalizing selection on the bud bank that could theoretically lead to trait underdispersion. A similar process can operate on multiplication rate in productive habitats. Persistence of connection is underdispersed mainly in extreme (namely dry) habitats, where differences in this trait may affect plant success due to both abiotic and biotic interactions (Jónsdóttir & Watson 1997; Klimeš 2008).

Conclusions

The key factors driving distribution of clonal growth traits in habitats of Central Europe seem to be differences in productivity and in wetness. These gradients underlie the major shift in clonal growth parameters, from clonal plants with short and persistent connections among ramets, to plants with long- and short-lived connections. Importantly, the proportion of plants having the capacity for clonal growth and size of their below-ground bud bank do not change strongly along these gradients. Capacity for clonal growth occurs under many different environmental regimes and can give rise to very different growth forms, from tightly clumped tussocks with persistent connections to fast spreading plants (Klimeš et al. 1997; Klimešová & de Bello 2009); each of these growth forms may be successful in different community types. Therefore, using capacity for clonal growth as such over longer ecological gradients as a proxy for clonal reproduction, capture of horizontal space or resprouting capacity may hinder understanding of its true role, either in species or community analyses.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Correlation matrix of clonal traits.

Appendix S2. Correlation matrix of clonal traits in text format.

Appendix S3. Non-randomness of trait dispersions in the EUNIS habitat types.

Appendix S4. Non-randomness of trait dispersions in the EUNIS habitat types in text format.

Appendix S5. Effect sizes of individual clonal and bud bank traits.