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Reproduction by seed and clonality in plants: correlated syndromes or independent strategies?

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Summary

1. We examine the relationships of traits of seed reproduction to traits of clonal growth and bud banks. Although there are a number of functional differences between these sets of traits underlying two different modes of reproduction, they both constitute a response to ecological gradients, which makes them potentially interdependent.

2. We performed phylogenetic regressions of seed traits and traits of bud banks and clonal growth across the Central European flora. We took Ellenberg indicator values and indices of responses to disturbance as information on the positions of species optima along important ecological gradients.

3. The analyses show that there are almost no relationships between these two groups of traits. This contrasts with the existence of strong correlations *within* these groups of traits which indicate specific syndromes of seed reproduction and of clonality. Both seed traits and traits of bud banks and clonal growth show fairly strong phylogenetic conservatism.

4. The absence of correlations between individual groups of traits is at least partly due to the fact that each trait group shows relationships to different parameters of species' niches. Bud bank traits are determined by the disturbance niche of the species, clonal traits by soil and climatic factors, while seed traits show only weak correlations with the examined environmental factors if phylogeny is taken into account.

5. *Synthesis*. The absence of integrated syndromes that would cover both seed reproduction and clonality across the flora implies that there are no selective forces that would affect both trait groups simultaneously. Clonal and bud bank traits are more tightly linked to species' niches, presumably because they are selected by local population processes only, in contrast to seed traits, which play a role also in dispersal. As the phylogenetic conservatism of clonal traits is almost as strong as the phylogenetic conservatism of seed traits, these traits do not serve as an evolutionarily more flexible alternative to seed reproduction.

Key-words: bud bank traits, clonal traits, CLOPLA data base, D3 data base, dispersal, phylogenetic regressions, reproductive ecology

Introduction

The capacity to reproduce is one of the key components of any organism's survival and ecological success. From the point of view of population dynamics, reproduction (i) drives local population dynamics by determining natality within populations, and (ii) is involved in regional dispersal, that is spreading to hitherto unoccupied sites within a region (Horwitz & Schemske 1988). Almost all plants reproduce by sexually formed seeds, but they often complement reproduction by seed with clonal (asexual) reproduction, most often by stolons, rhizomes or similar organs capable of rooting and/or resprouting and forming new fully functional individuals (Mogie & Hutchings 1990; Aarssen 2008). While clonal growth does not necessarily result in the formation of new functionally independent individuals, it often does so, producing asexual offspring with large maternal investment dispersed only over short distances. This contrasts with seeds, which have much less maternal support and can disperse over large distances. Therefore, they are involved both in local (population persistence) and regional processes (dispersal), in contrast to clonally formed offspring, which contribute to local population processes only.

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Each of these processes is determined by a specific set of life-history traits, such as seed mass and dispersal potential for sexual reproduction, and lateral spreading distance and persistence of clonal connections for clonal growth. Various costs involved in the reproductive and dispersal processes typically result in correlations of such traits, which may be further strengthened due to selection that operates on them (Bonte *et al.* 2012). For example, there are relationships between different modes of dispersal (e.g. wind dispersal vs. fleshy fruit, Eriksson & Jakobsson 1999) or trade-offs of dormancy and seed mass (Thompson, Band & Hodgson 1993; Thompson *et al.* 1998; but see Saatkamp *et al.* 2009), ultimately leading to a limited number of dispersal syndromes (Ronce & Clobert 2012; Stevens *et al.* 2013; Buoro & Carlson 2014). Correlations among clonal traits are much less documented, but exist as well, for example between persistence of a clonal connection and its length (Klimeš *et al.* 1997; Klimešová & Herben 2015). As the ability to grow clonally can serve a number of purposes (resource storage and sharing, insurance strategy; Hutchings & De Kroon 1994; Vallejo-Marín, Dorken & Barrett 2010) in addition to reproduction, correlation of its traits can be also due a multiplicity of selection forces that act on all these functions.

Seed traits and their syndromes are selected both by processes of local population dynamics and regional dispersal (Bonte *et al.* 2012). They are also known to be highly phylogenetically conserved (Eriksson 2008) and thus offer their bearers only limited chance for a fast response to these selective forces. By contrast, clonal reproduction and its traits are selected by local population dynamics only (Eriksson 1992). Limited analyses of conservatism of traits of clonal reproduction show them to be less conservative (see, e.g. Eriksson 1992; Klimeš *et al.* 1997; Bond & Midgley 2003). It has therefore been suggested to serve as a more flexible life strategy trait, albeit affecting only local population dynamics.

Surprisingly, we know little about the interrelationships between traits of reproduction by seed and clonal traits. The key argument for their correlation arises because of the simultaneous response of both of them to underlying environmental factors. Indeed, it has been argued that plants show ‘remarkably stereotypical avenues of specialization in life history’ (Grime 2001), that is a few main niche axes that drive plant specialization, namely gradients of productivity and disturbance. These gradients are also likely to underlie important differences both in seed traits and traits of clonality. For example, the importance of long-distance dispersal increases in frequently disturbed habitats with frequent disturbance (Grime 1979; Glenn-Lewin, Peet & Veblen 1992; Hill, Roy & Thompson 2002). Clonal growth has been hypothesized to show a nonlinear response to disturbance, with the highest values for intermediate disturbances (Bellingham & Sparrow 2000; Pausas & Verdú 2005). Productivity gradients can affect both reproduction by seed (decrease in low productive habitats; Eckert 2001; see also Moles *et al.* 2007) and clonal traits (Klimeš *et al.* 1997; Ye *et al.* 2014). Further, there are known correlations between sexual reproductive traits and environment-related plant traits such as plant size or specific leaf area (Aarssen 2005; Moles & Westoby 2006; Pierce *et al.* 2014), which also determine traits of clonal growth to some extent (Klimešová, Tackenberg & Herben 2016). Correlation between traits of reproduction by seed and of clonal growth may arise because different species may use different avenues to reach a specific goal. In his pioneering work, Eriksson (1989, 1992) showed that in many clonal plants, seeds do not contribute much to local population dynamics (see also Ozinga *et al.* 2007; Johansson, Cousins & Eriksson 2011). By contrast, local population dynamics of non-clonal plants must rely on reproduction by seed. Clonality and seed reproduction by seed thus constitute two different strategies for colonizing a site, possibly resulting in a negative correlation between them.

Still data on correlations between (traits of) seed and clonal reproduction are sparse. There are documented cases of negative relationships between them over sets of species in the field (Rees 1996; Boedeltje, Ozinga & Prinzing 2008), but without a clear demonstration of the processes that lead to these correlations. Further, simple energetic costs of sexual reproduction may affect growth in size, including clonal growth and reproduction (Obeso 2002). However, as clonal growth covers a large range of behaviours, the borderline between simple growth/survival and asexual reproduction is rather fuzzy, so costs to asexual reproduction due to sexual reproduction are often included in overall survival costs of reproduction, and no specific data are available on it (Obeso 2002).

In this paper, we examine the relationships between traits of reproduction by seed and of clonal growth and search for patterns that would be indicative of selection by common factors. In doing so, we are not interested in resource-based trade-off relationships such as with seed number and size (Harper, Lovell & Moore 1970; Shipley & Dion 1992; Westoby, Leishman & Lord 1996), but primarily in relationships that arise over evolutionary time-scales and that may involve traits underlying both types of reproduction.

We use the term ‘clonal reproduction’ to denote the formation of functionally independent individuals by clonal growth. From a morphological point of view, clonal *reproduction* depends on two major trait groups: the ability to spread by horizontal spacers (stolons, rhizomes, etc.), which are determined by traits of clonal growth, and by the ability to resprout from below-ground plant parts, which is determined by traits of the (below-ground) bud bank. We therefore distinguish these two groups within traits of clonal (asexual) reproduction (Klimešová & Herben 2015) and in most cases perform separate analyses on each of these groups. Further, we use the term ‘sexual reproduction’ for reproduction by seeds (in spite of the fact that apomictic plants can produce seeds asexually) and refer to its traits as seed traits or traits of seed/sexual reproduction. We do not deal with reproduction by dispersible clonally formed organs (bulbils), as these concern only a tiny fraction of plant species.

We proceed in three steps. First, we examine correlations of traits of seed and clonal reproduction in a large set of herbaceous species of the Central European flora and compare them with correlations found within each of these groups of traits. Consequently, we use correlations within seed traits, clonal growth traits and bud bank traits to identify trait ‘syndromes’ and use correlations among them to see whether they form syndromes that involve both traits of sexual and asexual (clonal growth and bud bank) reproduction. To account for effects due to differences in plant size (Thompson & Rabinowitz 1989; Moles & Westoby 2006), we also fit partial models taking account of height at maturity as a proxy for plant size. Secondly, we compare phylogenetic conservatism across these traits and assess how their relationships (both within each group and between them) change when phylogeny is taken into account. We assume that if a correlation between two traits decreases in phylogenetic regression, it is primarily due to evolutionary contingency; by contrast, correlations that remain strong when phylogeny is taken into account are indicative of functional relationships. Thirdly, we examine relationships of individual traits and of correlated trait suites to positions of species' optima along key environmental gradients, namely soil and climatic parameters and disturbance. We use Ellenberg indicator values (Ellenberg *et al.* 1992) to assess species optima along the soil and climatic gradients (primarily corresponding to site productivity). Species responses to disturbance are assessed using disturbance indicator values of Herben, Chytrý & Klimešová (2016).

Materials and methods

TRAIT DATA

Seed traits were generally taken from the D3 data base (Hintze *et al.* 2013), with some additional data taken from other sources, mainly LEDA and BIOLFLOR (see Table 1). In addition to measured traits such as seed mass or length, the D3 data base contains traits expressed as species ranks (anemochory or hydrochory rank). They have been derived from numerical values of one or several indicators, that is dispersal traits or experimental assessments and have been calculated as the percentile rank of the indicator(s) of the species relative to all species in D^3. Consequently, their values range from 0 to 1, with 0 indicating species with the lowest and 1 indicating species with the highest dispersal potential for the given dispersal agent (for details, see Table 1). For numerical traits, generally the mean of all available data sets is used to characterize the species with a single value. Further details on seed dispersal traits can be found at www.seed-dispersal.info and in Hintze *et al.* (2013).

Clonal growth traits were taken from the CLOPLA data base version 3.2 (Klimešová & de Bello 2009). We transformed the data from the data base to yield eight traits (see Table 2). Following Johansson, Cousins & Eriksson (2011), we used the sum of ordinal values of multiplication rate and lateral spread as a synthetic measure of the capacity for clonal growth (further referred to as the clonal index). Ordinal values for this purpose are defined using the following cutpoints: number of offspring shoots per mother shoot per year: <1, 1, >1, and lateral spread (<0.01, 0.01–0.25, >0.25 m, dispersible). Data on plant height at maturity were taken from the D3 data base (Hintze *et al.* 2013), with additional data taken from Kubát *et al.* (2002).

Phylogenetic data were taken from Durka & Michalski (2012), with dated branch lengths. If no data were available for a given species in Durka & Michalski (2012), the species were excluded from phylogenetic analyses.

Two sources of information were used to characterize species' niches: (i) Ellenberg indicator values (Ellenberg *et al.* 1992), which assess species optima in terms of major soil and climatic factors (temperature, light, continentality, nutrients, soil pH and soil moisture), and (ii) species response to disturbance, which was expressed by four indices following Herben, Chytrý & Klimešová (2016). These indices

Table 1. Seed dispersal traits used in the analyses

Column_code	Short description	Data sources
Anemochory index	Anemochory ranking index, an index that ranges from 0 to 1, with 0 addressing species with the lowest and 1 addressing species with the highest potential for anemochory.	D3
Diaspore mass	Diaspore mass is the fresh weight (in mg) of one diaspore including all appendages.	D3, LEDA, BIOLFLOR
Diaspore length	Length of the diaspore, that is the longest axis, which is measured including all appendages.	D3, LEDA
Diaspore shape index	Diaspore shape is a dimensionless index ranging from 0 to 0.23. It describes the deviation of a diaspore's shape from a sphere in three dimensions. Zero addresses a perfect sphere, whereas values > 0 means flat or elongated diaspores.	D3
Epizoochory index	Epizoochory ranking index, an index that ranges from 0 to 1, with 0 addressing species with the lowest and 1 addressing species with the highest potential for epizoochory. It is based on a combination of attachment potential (ATP; Will, Maussner & Tackenberg 2007) and retention potential (RTP; Römermann, Tackenberg & Poschlod 2005; Tackenberg *et al.* 2006) and is calculated as the percentile rank of (ascending) ATP*RTP of the respective species in relation to the values of all species for which data were available. This potential can be interpreted as the proportion of seeds that are transported by an animal over a longer time period that principally allows long-distance dispersal. The index was computed for the transport in woolly hair.	D3
Hydrochory index	Hydrochory ranking index, an index that ranges from 0 to 1, with 0 addressing species with the lowest and 1 addressing species with the highest potential for hydrochory. We use the proportion of floating seeds measured in a standardized laboratory experiment (Römermann, Tackenberg & Poschlod 2005 and O. Tackenberg, unpubl. data) as an indicator of hydrochory potential. It is calculated as the percentile rank of the proportion of the respective species still floating after 1 week in relation to all species for which data were available.	D3
Endozoochory index	Endozoochory ranking index, an index that ranges from 0 to 1, with 0 addressing species with the lowest and 1 addressing species with the highest potential for endozoochory, based on digestibility experiments.	D3
LDD index	Combined potential for long-distance dispersal.	D3

Table 2. Clonal growth and bud bank traits used in the analyses

Abbreviation	Unit	Definition
Bud bank size	Number of buds	Number of stem-derived buds in the soil and at the soil surface.
Bud bank size (w root buds)	Number of buds	Number of stem- and root-derived buds in the soil and at the soil surface.
Mean bud bank depth	Centimetres	Weighted mean depth of stem-derived buds.
Mean bud bank depth (w root buds)	Centimetres	Weighted mean depth of stem- and root-derived buds.
Number of clonal offspring	Number of individuals	Number of offspring shoots per parent shoot per year including offspring of small size. Small offspring 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.*
Spreading distance	Metres	Lateral spreading distance of clonal growth organs.*
Clonal index	Ordinal	Defined following Johansson, Cousins & Eriksson 2011 (sum of ordinal values of number of offspring and spreading distance).*
Persistence	Years	Number of years over which clonal connections between ramets persist.*

*Trait defined only for plants with clonal growth.

express the mean value of frequency and severity of disturbance over the range of habitats where the species occurs and is assessed separately for disturbance of the whole community and of the herb layer only (for shrublands and forests). Ellenberg indicator values (EIV) and disturbance indices are further collectively referred to as species niche parameters.

DATA ANALYSIS

Pairwise trait correlations

Incomplete cases were excluded (actual number of species/cases is reported for each analysis). For each trait pair *y* and *x*, we fitted two linear statistical models: $y \sim x$, and $y \sim x$ conditioned by log(height), and estimated R^2 of each of them. To deal with phylogenetic trait correlations, we first estimated phylogenetic signal of each trait using Pagel's λ (Freckleton, Harvey & Pagel 2002). We fitted λ using the maximum likelihood approach as implemented in the function PGLS from the package CAPER for R (Orme 2012) and calculated its upper and lower confidence limits for each trait. In cases of traits that had strongly skewed distributions (diaspore mass and diaspore length), we log-transformed their values prior the analysis, that is assumed multiplicative process in their evolution. Then, we fitted phylogenetic least squares regressions assuming the Brownian motion model of trait evolution; to express different degree of phylogenetic conservatism, we used Pagel's λ transformation of the phylogenetic tree by the value of λ for the given dependent variable. All phylogenetic regressions were calculated using the function PGLS from the package CAPER for R (Orme 2012).

Multivariate trait relationships

Multivariate trait relationships were examined using principal component analyses (PCA). All multivariate analyses were done on standardized variables. Incomplete cases were excluded (actual number of species/cases is reported for each analysis). We did not include the hydrochory index and endozoochory index into the multivariate analyses due to the low number of species for which such data were available. All these multivariate analyses of traits were calculated using the VEGAN R package (Oksanen *et al.* 2013). To visualize individual syndromes of correlated traits, we used a K-means classification to assign species to clusters. We used Euclidean distance on standardized data and the Hartigan & Wong (1979) algorithm as implemented in the function KMEANS (R Core Team 2012) and identified the optimum number of clusters using proportion of intracluster variation.

To address possible phylogenetic dependence of trait values among species from multivariate analyses, we used the approach of Diniz-Filho, de Sant'Ana & Bini (1998; see also Desdevises *et al.* 2003). We summarized the matrix of phylogenetic distances using non-standardized principal coordinates analysis (PCoA) using the function DUDI.PCO from the ADE4 package for R (Dray & Dufour 2007). The first sixty axes from this PCoA account for 90% of the total phylogenetic variation. These axes were used as covariates in phylogenetic analyses. Separate analyses were done for seed, clonal and bud bank traits, and for all traits together.

For concurrent analysis of two variable sets and identification of intercorrelations between them, we used redundancy analysis (a form of multivariate regression analysis). Adjusted R^2 of relationships of trait groups were calculated on standardized variables using the function RDA from the R package VEGAN (Oksanen *et al.* 2013). Phylogenetic adjusted R^2 were calculated by conditioning the whole analysis on the values of the same phylogenetic PCoA axes as above.

Summary scores

As preliminary analyses showed that individual seed, bud bank and clonal traits were highly correlated within each group, we summarized their values using scores based on PCA of standardized trait values. We used three summary scores: (i) the **seed dispersal score**, that is score on the first PCA axis based on anemochory rank, diaspore mass, diaspore length, diaspore shape index, epizoochory rank and LDD rank (see Table 1), accounting for 38.9% of the total variation of these variables; this score primarily separates plants on the combination of anemochory and epizoochory traits, with high score values indicating species with heavy seeds and bad capability for anemochory and epizoochory, (ii) the **bud bank score**, that is score on the first PCA axis based on bud bank size and depth, both stem-based only and with roots included, accounting for 77.5% of the total variation of these variables; this score separates plants with large and deep below-ground bud banks from plants with small bud banks with high score values for species with large bud banks, and (iii) the **clonal spread score** (for clonal plants only), that is score on the first PCA axis based on persistence, the number of offspring, spreading distance and the clonal index, accounting for 49.0% of the total variation of these variables; this score separates plants with extensive clonal spacers, numerous clonal offspring and temporary connections (high scores) from plants with short clonal spacers, but often persistent clonal connections. All scores are essentially uncorrelated; the highest correlation is between seed dispersal score and clonal spread score ($R^2 = 0.032$).

Traits and species niche parameters

We examined how values of individual traits and species summary scores are related to species niche parameters by linear correlations; in all cases, we examined potential nonlinearity in data by testing also the quadratic term. Further, we examined how these relationships change with phylogenetic axes taken as covariates. For each trait, we searched for the best combination of predictors among species niche parameters using stepwise regressions based on AIC, beginning with the full model. As in many cases, the relationships were strongly nonlinear, and we considered both linear and quadratic terms for each parameter to account for potential nonlinearity. When a quadratic term of a model was included, we kept also the linear term irrespective of its explanatory power.

Results

TRAIT CORRELATIONS

There were a number of strong correlations within the group of seed traits (Table S1 in Supporting Information, Fig. 1). The relationships between most traits were not due to correlations with height; in very few trait pairs, there was any noticeable change in R^2 after height was partialled out. Multivariate analysis of seed traits identified a combined anemochory-epizoochory axis as the dominant direction of variation of seed traits (accounting for slightly <40% of the total variation in six seed traits; Fig. S1). Consequently, there were three main clusters of species based on their seed traits: (i) species that are both anemochorous and epizoochorous, with non-isodiametric diaspores and/or pappus, (ii) predominantly anemochorous species, with isodiametric small diaspores, and (iii) species not dispersed by wind and animal fur/feathers, with isodiametric large diaspores, including fleshy fruit (Fig. S3).

In a similar fashion, there were a number of correlations within clonal and within bud bank traits. The four bud bank traits formed a very tightly correlated group (dominant eigenvalue in PCA accounting or 77% of the total variation), separating species into two groups depending on the number of below-ground buds and their depth. Clonal traits were correlated less strongly (49% accounted for by the first axis). Clonal growth traits and bud bank traits represented two rather separate dimensions (Table 3; Figs S1 and S2). The combination of clonal and bud bank traits can be used to delimit four main clusters of species (Fig. S3): (i) slowly spreading clonal species with highly persistent stem-derived organs of clonal growth and with well-developed bud banks (but no root buds; e.g. *Nardus stricta, Primula elatior, Luzula campestris, Leontodon hispidus*), (ii) fast spreading clonal species with strongly developed bud banks deep in the soil, often with root sprouting (e.g. *Elymus repens, Vaccinium myrtillus, Rumex acetosella*), (iii) species with small bud banks and slow clonal

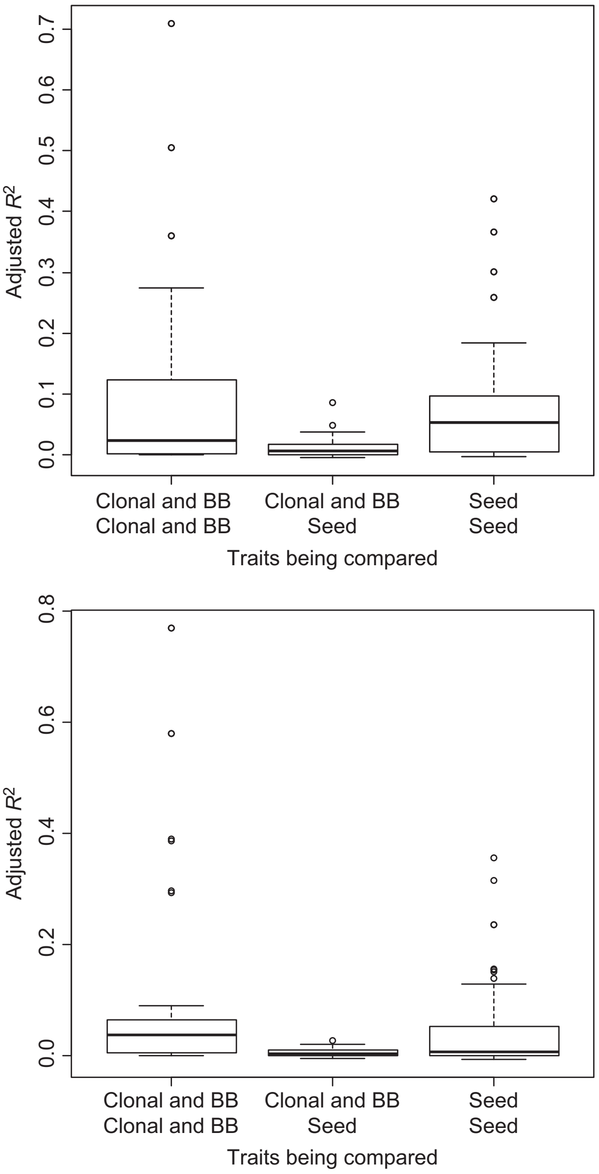

Fig. 1. Adjusted R^2 of pairwise correlations between traits of clonal growth (left), traits of seed reproduction (right) and between traits from different groups (centre). Upper plot – simple regression, lower plot – phylogenetic regression. Correlations of traits that are linked by their definition (e.g. bud bank size and bud bank size with root buds) are not included. Clonal and BB – traits of bud bank and clonal growth; Seed – traits of seed dispersal.

Table 3. Relationships between groups of traits. Values in the table are adjusted R^2 from redundancy analyses

	Analysis	Simple	Phylogenetic	*N*
Bud bank traits vs. seed traits	BB~seed	0.056	0.041	795
	Seed~BB	0.027	0.004	795
Bud bank+clonal traits vs. seed traits	Clonal+BB~seed	0.050	0.027	338
	Seed~clonal+BB	0.091	0.022	338
Bud bank traits vs. clonal traits	Clonal~BB	0.096	0.038	976
	BB~clonal	0.171	0.080	976

spreading (e.g. *Gagea lutea, Ranunculus lanuginosus, Epilobium montanum*), and (iv) reasonably fast spreading clonal species with short-lived stem-derived organs of clonal growth close to the soil surface and with well-developed bud banks (but no root buds; e.g. *Achillea millefolium, Carex brizoides, Fragaria vesca, Prunella vulgaris*).

By contrast, there were only few noticeable correlations between any of the seed traits and a trait of clonal growth or the bud bank (Fig. 1). Most of the stronger ones disappeared in phylogenetic regressions, implying that they were due to shared phylogenetic history, not a functional relationship (e.g. positive correlation between connection persistence and diaspore mass). An exception was positive correlation between mean bud bank depth and diaspore length which appeared also in phylogenetic regression, indicating possible, albeit fairly weak (R^2~0.02), functional relationship. Multivariate analysis of relationships between whole groups of traits captured only a minor (but statistically significant) portion of the total variation (Table 3). Separation of individual groups of traits (e.g. clonal vs. bud bank) was even stronger in phylogenetic analyses (Table 3).

There were marked differences among traits in the degree of their phylogenetic conservatism (Fig. 2). Seed traits had generally very high conservatism corresponding to the Brownian motion model of trait evolution (with the exception of endozoochory potential and long-distance dispersal potential). Bud bank traits had lower phylogenetic conservatism (namely if root buds were included). The lowest phylogenetic conservatism was exhibited by certain clonal growth traits (namely number of clonal offspring and clonal index). There was a significant difference between the estimated lambda of seed dispersal score and both the bud bank and clonal score; the latter two were smaller and not significantly different from each other (Fig. 2).

RELATIONSHIPS OF TRAITS TO SPECIES NICHE PARAMETERS

A number of seed, bud bank and clonal growth traits showed correlations with individual species niche parameters, that is Ellenberg indicator values (EIV) and disturbance indices (Table S2). Bud bank traits were predicted best by species niche data; by contrast, the long-distance dispersal index, endozoochory index and diaspore traits (size and shape) were predicted worst. The hydrochory index showed the highest predictive power among the seed traits due to its high correlation with the Ellenberg value for moisture.

Ellenberg indicator values (including the proxy for habitat productivity) and disturbance parameters had very different effects on individual groups of traits (Figs 3 and 4). Disturbance parameters primarily predicted bud bank traits, often with nonlinear (unimodal) relationships (Table 4, quadratic effects of disturbance severity). By contrast, clonal traits were (with the exception of Number of offspring) better predicted by Ellenberg values and showed weaker relationships to

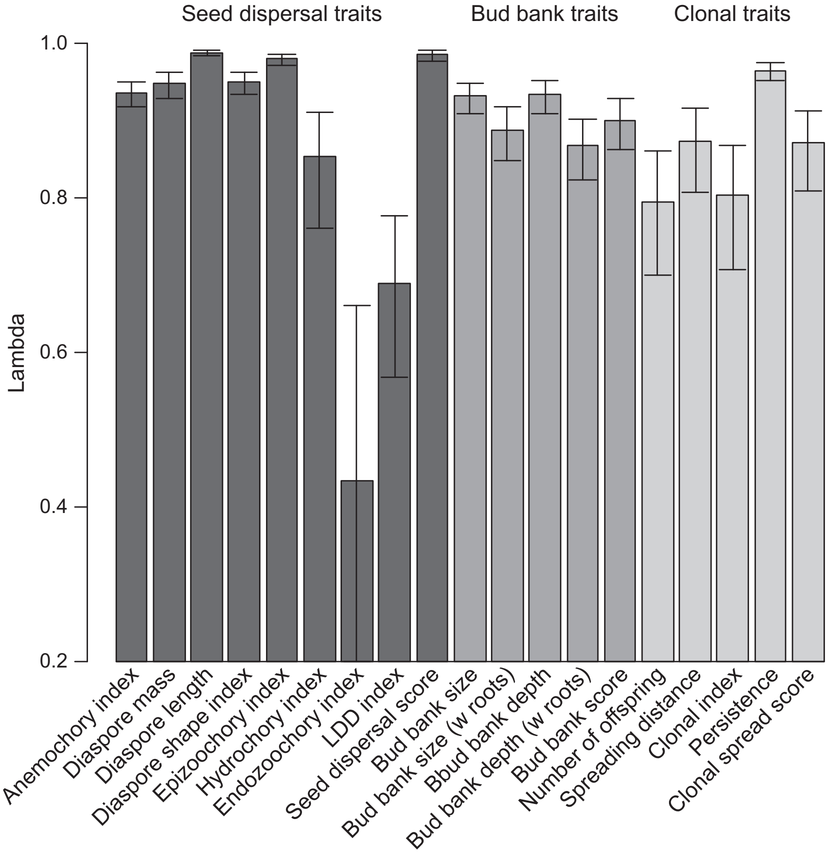

Fig. 2. Phylogenetic conservatism of traits of seed reproduction and clonality (including summary scores) assessed by Pagel's lambda. Bars indicate standard errors.

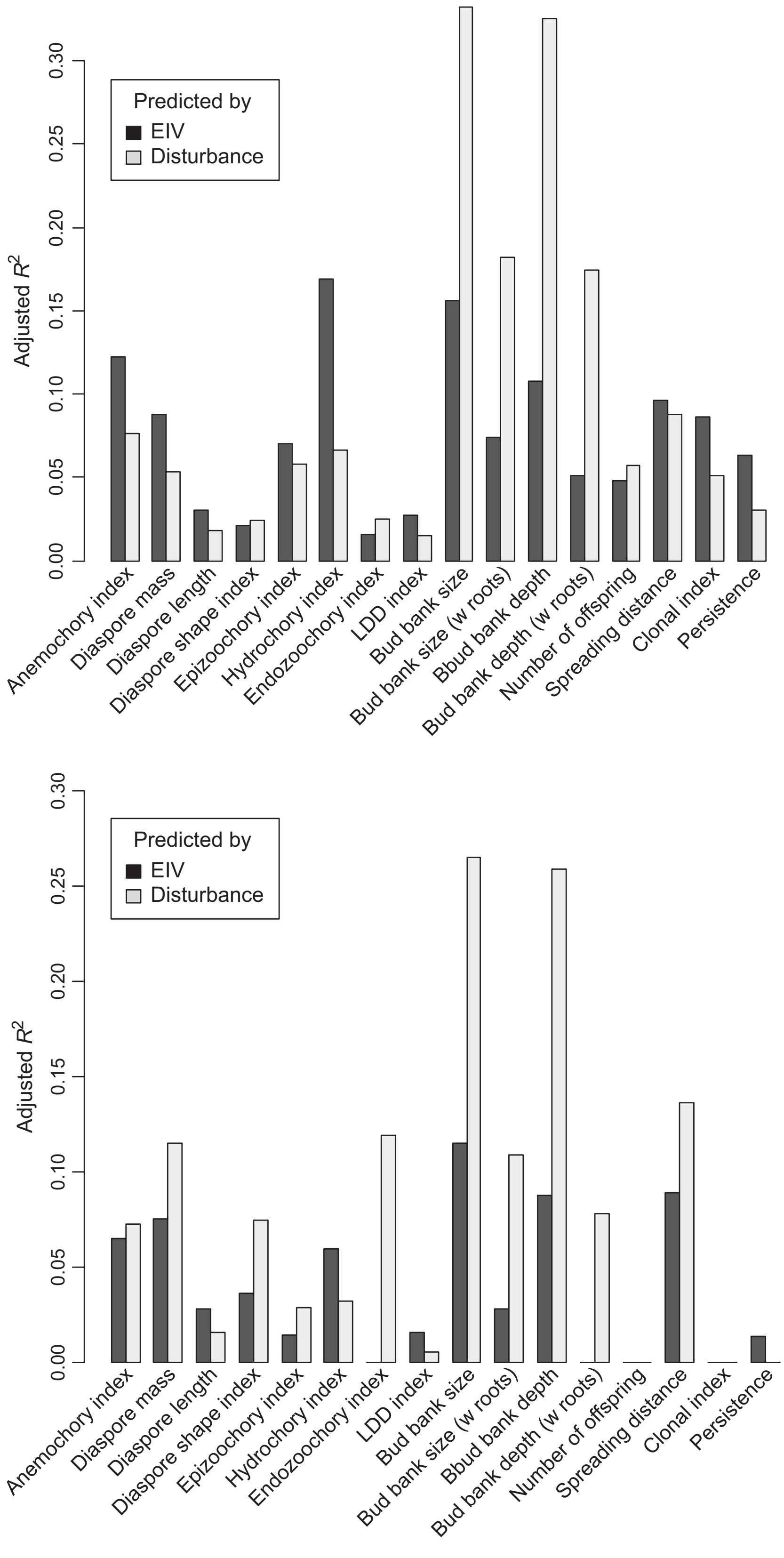

Fig. 3. Prediction of individual traits by species niche parameters, grouped to soil and climatic parameters (expressed by Ellenberg indicator values for each species), and disturbance parameters (expressed by disturbance indicator values). Upper pane: non-phylogenetic regression; lower pane: correlation due to shared phylogenetic history removed. Adjusted R^2 of the best model built from predictors from the given group are shown. Nonlinear (quadratic) prediction is used in all cases.

disturbance indices. Seed traits generally showed stronger relationship to Ellenberg values (anemochory index, hydrochory index), but many of them showed very weak relationship to either group (LDD index, diaspore length).

These results were well summarized using species summary scores (Table 4, Fig. 4, Table S3). The seed dispersal score was mainly related to soil variables (pH, nutrients and moisture) and to disturbance frequency (unimodal relationship).

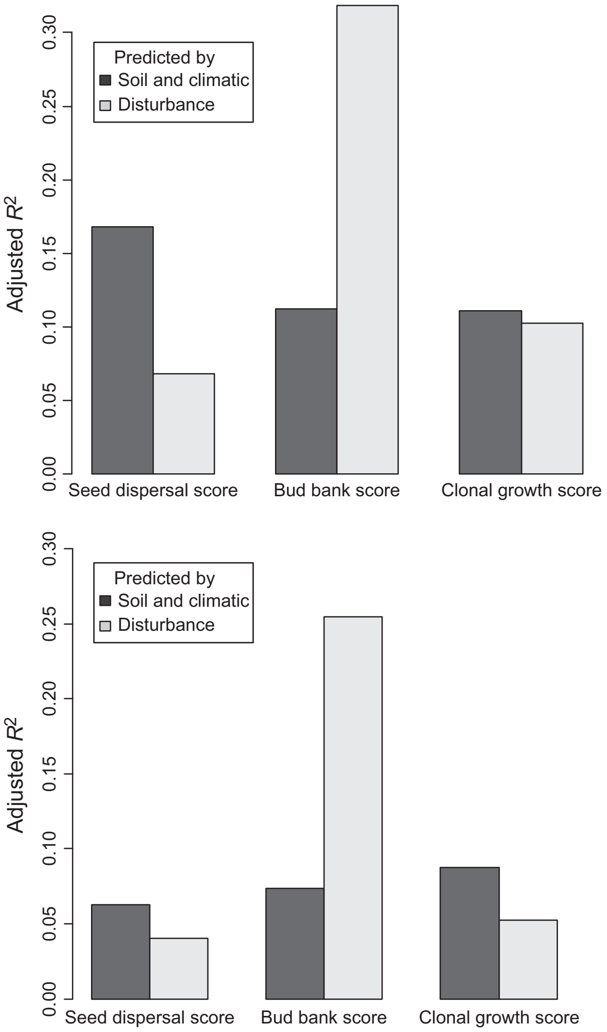

Fig. 4. Prediction of the scores summarizing trait values in the three trait groups (seed traits, bud bank traits and clonal growth traits) by soil and climatic parameters (expressed by Ellenberg indicator values for each species), and disturbance parameters (expressed by disturbance indicator values). Upper pane: non-phylogenetic regression; lower pane: correlation due to shared phylogenetic history removed. Adjusted R^2 of the best model built from predictors from the given group are shown. Nonlinear (quadratic) prediction is used in all cases.

Some relationships of the seed dispersal score disappeared or became weaker when species phylogenetic history was taken into account (disturbance frequency, temperature, light). The bud bank score was strongly predicted by all disturbance parameters (namely disturbance intensities) and several soil and climatic parameters. Their relationship to disturbance frequency was nonlinear (unimodal; see quadratic effects in the Table 4). Most relationships between the bud bank score and species niche parameters did not change when species phylogeny was taken into account. The clonal spread score was predicted by disturbance parameters (negative by disturbance frequency and positive by severity of disturbance of the herb layer) with no significant nonlinearity. Further, they were predicted by light and pH (negative relationship), temperature, nutrients and moisture (positive relationship); with the exception of pH, these relationships changed little after phylogeny was taken into account.

Discussion

We used phylogenetically informed analyses to examine the relationships between traits of seed reproduction and of clonal growth and bud banks and searched for systematic correlations that would be indicative of selection by common factors. Our analyses show rather convincingly that these groups of traits are essentially unrelated to each other that and different types of reproduction combine almost freely across the herbaceous flora of Central Europe. Moreover, the few existing correlations between these two groups of traits disappear in phylogenetic regressions (e.g. between connection persistence and diaspore length), implying that they are due to evolutionary contingencies and are not indicative of a functional relationship. The almost complete absence of correlated trait groups that would cover both trait groups contrasts with the existence of rather strong correlations *within* each of these group of traits, which implies the existence of specific syndromes of reproduction by seed and by clonal growth. These arose either due to selection acting on several traits within each group simultaneously, or common trade-offs that affect several traits.

The absence of integrated syndromes that would cover both groups of traits indicates there are no selective forces or common constraints that would affect these groups of traits simultaneously. While traits of both groups have been shown to be correlated with general plant traits, such as plant stature or specific leaf area (Aarssen 2005; Moles & Westoby 2006 Pierce *et al.* 2014), these relationships are clearly not sufficient to constitute a broad spectrum that would involve both types of reproductive traits.

First, this absence of correlations between individual groups of traits and syndromes can be due to the fact that these trait groups are related to different aspects of species' environmental niches. This is fairly well supported by our data. Bud bank traits show by far the strongest correlation with parameters of the species niche, in particular with species responses to disturbance. By contrast, traits of clonal growth proper show only weaker relationships (in relative terms) to disturbance, namely in phylogenetic analyses, and stronger relationships to habitat factors. Specifically, plants have shorter lateral spread, fewer clonal offspring and more persistent connections with increasing light and decreasing temperature and moisture (see also Eckert 2001; Ye *et al.* 2014; Klimešová & Herben 2015). This supports the notion that clonal spreading is particularly important in shaded and moist conditions (Eckert 2001; Herben, Šerá & Klimešová 2015). Seed traits show weak relationships to disturbance parameters (but see below), while their relationships to habitat parameters (light, temperature and moisture) largely disappear in phylogenetic analyses. This implies that seed traits do not respond substantially to the niche parameters that we were able to use. There are a few specific cases of strong relationships (e.g. good prediction of the hydrochory index by the Ellenberg value for moisture), but these are more exceptions to the general pattern.

Table 4. Relationships of the three species summary scores to niche parameters. Each column corresponds to the best model selected by stepwise procedure using AIC. Significances are based on F statistics testing deletion of individual terms. Values in the table are standardized regression coefficients. Parameter names followed by ‘2’ indicate quadratic terms; simple – non-phylogenetic regression, phylog. – phylogenetic regression

	Seed dispersal score		Bud bank score		Clonal spread score	
	Simple	Phylog.	Simple	Phylog.	Simple	Phylog.
Adjusted R^2	0.201	0.078	0.336	0.260	0.143	0.161
d.f. residual	442	384	862	802	460	402
Soil and climatic parameters of the species niche						
Light	−0.462	0.102*	0.470*	0.455*	−0.512*	−0.511*
Light2	0.676*		−0.456*	−0.471*	0.601*	0.628**
Temperature	0.759		0.332	0.341	0.347***	0.276***
Temperature2	−0.764		−0.417	−0.432		
Continentality						
Continentality2						
Moisture	0.187**	−0.19	−0.081	−0.077	0.184**	0.246**
Moisture2		0.41				
pH	−0.229***	−0.168***	0.089*	0.148***	−0.136*	0.677*
pH2						−0.740*
Nutrients	0.21	0.251	0.355*	0.407**	0.104	
Nutrients2	−0.382	−0.346	−0.263	−0.357*		
Disturbance parameters of the species niche						
Disturbance frequency (whole community)	−0.368*		−0.338***	−0.456***		
Disturbance frequency (whole community)2	−0.406**			−0.309		
Disturbance severity (whole community)	0.119	−0.135	0.14	0.615		
Disturbance severity (whole community)2		−0.263	−3.191**	−2.980**		
Disturbance frequency (herb layer)					−0.417*	−0.168
Disturbance frequency (herb layer)2					−0.194	
Disturbance severity (herb layer)		0.423	−0.367	−0.891	0.594***	0.396
Disturbance severity (herb layer)2			3.031**	2.823**		

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

This differential response to environmental drivers would make the trait groups independent only if there is low correspondence of their drivers in the field. While there are surprisingly few analyses of such relationships, existing data show generally weak correlations among habitat parameters estimated by Ellenberg indicator values (Cornwell & Grubb 2003; Wagner *et al.* 2007; Szymura, Szymura & Macioł 2014). Our data show that disturbance indices are only weakly correlated with Ellenberg indicator values (T. Herben & J. Klimesova, unpubl. data; compare also Douma *et al.* 2012), giving strong support to the idea that these environmental factors are essentially independent, and traits associated with them can therefore vary independently of each other.

Secondly, low correlations between these groups can be due to different selective forces (unrelated to the environmental factors above) that affect them. In contrast to clonal and bud bank traits, seeds are subject to multiple selective forces due to their role both in local population dynamics and regional dispersal. While local processes (that involve the highest number of propagules) are likely to have the strongest selection pressure (see, e.g. Carlquist 1966), they are likely to be less important in highly dynamic landscapes, where long-term survival and species overall abundance depend on the capacity to disperse (Soons & Ozinga 2005; Ozinga *et al.* 2009; Herben, Nováková & Klimešová 2014; Baeten *et al.* 2015; Riibak *et al.* 2015). Indeed, the seed dispersal score (which is primarily the anemochory/epizoochory syndrome) shows a unimodal relationship to disturbance frequency; that is, easily dispersed seeds are found both in frequently disturbed communities and in non-disturbed communities. In the similar vein, the low selective effect (due to the low frequency of events it affects) of long-distance dispersal explains that the ability of long-distance dispersal is essentially uncorrelated with any predictor.

Similarly, clonal growth is a highly diverse phenomenon involving morphologically very different structures (stolons, root buds, different rhizome types; see Klimeš *et al.* 1997; Klimešová & de Bello 2009), each of which serves a number of functions such as storage and resource sharing, with clonal reproduction being only one of them. Correlation of its traits is likely due to the multiplicity of selection forces that act on all these functions, which may be very different from selection that operates on seed dispersal. Both types of analyses done (correlations of traits and relationship to environmental variables) support out initial hypothesis that traits of clonal *reproduction* fall into two almost independent groups of traits, that is traits of clonal *growth* and traits of bud banks, underscoring the richness of clonal strategies that individual species may have (Klimeš *et al.* 1997). Whereas traits of clonal growth determine encroachment of space and can significantly contribute to local population dynamics, traits of bud banks determine primarily response of species to disturbance. This relationship is nonlinear, supporting the prediction of

Bellingham & Sparrow (2000; see also Klimešová & Klimeš 2003) that resprouting is favoured under moderate disturbance, which is survived by below-ground plant organs.

While we did not identify syndromes that would cover traits of reproduction by seed and by clonal growth, this finding does not imply that plants in the field do not rely differently on different types of reproduction (see, e.g. Boedeltje, Ozinga & Prinzing 2008; Herben, Šerá & Klimešová 2015). Shifts between seed and clonal reproduction may occur both at intraspecific and interspecific levels (Eckert 2001; Aarssen 2008). Similarly, it does not necessarily imply that such correlations could not be found for specific community types, where such correlations may arise due to constrained sampling in a limited range of environments (see, e.g. Funk & Cornwell 2013).

Finally, our analyses show strong phylogenetic conservatism in both seed traits and traits of clonal reproduction (bud bank/clonal traits). While clonal and bud bank traits show slightly weaker phylogenetic conservatism (with the exception of connection persistence, which shows similar phylogenetic conservatism as most seed traits), the difference does not seem to be strong enough to view clonal traits as a group that is the evolutionarily more flexible part of the life strategy (see, e.g. Eriksson 1992). However, there are a few clonal traits that are less conservative, namely the number of clonal offspring and bud bank traits involving root buds. Specifically, the ability to form root buds has been proposed to act as a substitute for phylogenetically much more conservative traits of stem buds, and existing data on distribution of root buds support it (Klimešová & Martínková 2004).

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Data accessibility

All trait and environmental data are included in Table S4 as a semicolon-separated CSV file.

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Supporting Information

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

Figure S1. Variable loadings in principal components analysis (PCA) of seed traits.

Figure S2. Variable loadings in principal components analysis of traits of bud bank and clonal growth (for clonal plants only).

Figure S3. Species clusters corresponding to individual syndromes of dispersal by seeds and by clonal growth.

Table S1. Pairwise Pearson correlations between traits. Boxes indicate seed traits vs. clonal and bud bank correlations.

Table S2. Best models predicting values of individual seed, clonal and bud bank traits using species niche parameters, that is Ellenberg indicator values (EIV) and disturbance parameters.

Table S3. Pairwise tests of effects of individual species niche parameters, that is Ellenberg indicator values (EIV) and disturbance parameters on seed, clonal and bud bank scores.

Table S4. Data used for the analyses.