

RESEARCH ARTICLE

Unravelling the clonal trait space: Beyond above-ground and fine-root traits

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Abstract

1. Plant trait variation is constrained by mechanical and energetic trade-offs as attested by the global spectrum of plant form and function and the fine-root economics space for above- and below-ground traits. However, traits that are key for fitness maintenance in some plant groups, such as clonal and bud bank traits, have not yet been integrated within the frameworks provided by the above-ground and the fine-root economics space.
2. By using an extensive dataset encompassing above-ground, fine-root, clonal and bud bank traits of 2000 species of Central European herbs, we asked whether clonal and bud bank traits correspond to the placement of species in the above-ground or fine-root trait space.
3. Perennial clonal and non-clonal herbs show indistinct positioning within the above-ground and fine-root trait spaces. This extends and reinforces previous fragmentary evidence of weak correlations between clonal and bud bank traits and above-ground trait dimensions. Additionally, we identify for the first time a limited correlation between clonal and fine-root traits as well. This disconnection suggests that clonal traits operate independently from other trait spectra. For this reason, we introduce the concept of a 'clonal trait space' for clonal herbs. The first dimension of this space is defined by bud bank size and the persistence of clonal connection, reflecting a gradient of species specialisation for on-spot persistence and tolerance to disturbance (*persistence* dimension). The second dimension, defined by multiplication rate and lateral spread, reflects a specialisation axis for clonal multiplication and horizontal size dimension (*clonal multiplication* dimension). Clonal trait dimensions add non-redundant information to the above-ground or fine-roots trait space.
4. *Synthesis:* We champion the integration of the *persistence* and *clonal multiplication* dimensions from the 'clonal trait space' into the frameworks provided by the above-ground trait and the fine-root economics spaces, thereby enhancing our comprehension of the multifaceted trait strategies exhibited by plants.

KEYWORDS

bud bank, functional strategy, functional trait space, life history traits, perennial herbs, plant clonality, trait coordination

1 | INTRODUCTION

Plants continuously acquire, use and store above- (i.e. carbon) and below-ground (i.e. water and nutrients) resources to serve multiple functions related to growth, survival and reproduction (Weiher et al., 1999). Different functional traits (sensu Violle et al., 2007) are tightly related to these functions and have been extensively used across the Tree of Life to describe the adaptive strategies of many organisms, including plants (e.g. Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004). This trait-based approach (sensu Westoby & Wright, 2006) identified a limited set of trait combinations summarising leading and independent dimensions of trait variation (Díaz et al., 2016). These dimensions reflect evolutionary, mechanical and energetic constraints over functional differentiation in all major groups of vascular plants. However, the precise number of independent dimensions of ecological specialisation required to describe plant strategies comprehensively remains an open question (Laughlin, 2023).

At the global scale, aboveground functional differentiation among vascular plants is summarised by two independent trait dimensions defining the so-called global spectrum of plant form and function (Díaz et al., 2016; referred to as above-ground trait space). This trait space is defined by six traits—plant height, specific stem density, seed mass, individual leaf size, specific leaf area and leaf nitrogen content on a mass basis—that are known to reflect key mechanical and energetic trade-offs underlying the above-ground vascular plant trait strategies (Díaz et al., 2016; but see also Westoby et al., 2002; Wright et al., 2004). The above-ground trait space summarises how the independent plant economics and size-related trait dimensions define plant resource acquisition and use strategies related to species' growth, survival and reproduction. Since its formulation, the above-ground trait space represents a leading trait framework for describing and comparing above-ground vascular plant functional strategies across all levels of biological organisation and spatial scales (Bruehlheide et al., 2018; Joswig et al., 2022; Pavanetto et al., 2023; Thomas et al., 2020).

The definition of the above-ground trait space raised the question of whether below-ground traits could add independent trait dimensions to the spectrum of plant form and function. Bergmann et al. (2021) and Carmona et al. (2021) identified two main axes summarising the variation in fine-root traits: (i) a trade-off-specific root length versus root diameter that represents a 'fungal collaboration gradient' from plants outsourcing nutrient acquisition to mycorrhizal fungi (greater root diameter) to those that build an extensive network of fine roots (large specific root length) and (ii) the second dimension is a trade-off root tissue density versus root nitrogen content reflecting root economics, and thus a gradient from more acquisitive and cheap roots (greater root nitrogen content) to more conservative and expensive roots (greater root tissue density). Bergmann et al.'s (2021) 'fungal collaboration gradient' adds an independent dimension to the spectrum of plant form and function (see Weigelt et al., 2021). Whether the root economic dimension aligns with the leaf economics dimension, thus defining a

single economics dimension, remains debated (Bueno et al., 2023; Carmona et al., 2021; Weigelt et al., 2021, 2023). Indeed, other studies (e.g. E-Vojtkó et al., 2022; Laughlin, 2023) have already suggested that the potential number of trait dimensions might surpass what is predicted by the proposal of a single whole-plant economics spectrum (Reich, 2014) governing the combination of both above-ground and fine-root traits.

The above-ground and fine-root trait spaces have simplified the ecological complexity of 10 functional traits (six from the above-ground trait space and four from the fine-root trait space) into a handful of axes of trait variation. However, these frameworks might have missed important traits that capture other functions, that is, traits linked to on-spot persistence, horizontal space occupancy, resource storage and sharing among ramets, as well as clonal multiplication (Klimešová et al., 2018; Ottaviani et al., 2017). These functions are performed by below-ground organs such as rhizomes, tubers and bulbs (Klimešová et al., 2019). They occur in approximately 60% of European perennial herbs (Van Drunen & Husband, 2019). Perennial herbs can rely on these organs to reproduce clonally as an alternative to sexual reproduction (Aarssen, 2008). In addition, clonal reproduction for these plant groups is essential for their spatial organisation within communities and their competitive ability in horizontal dimension and resilience after biomass removal (e.g. after grazing, mowing, and fire; Pausas et al., 2018). These functions are influenced by clonal and bud bank traits (Klimešová et al., 2017). Hence, in perennial clonal herbs, these traits promote fitness and long-term population persistence (e.g. Mogie & Hutchings, 1990). As such, clonal and bud bank traits (hereafter broadly defined as clonality-related traits) are considered one of the most prominent axes of variation in the ecological strategies of many perennial herbs (Aarssen, 2008; Klimešová et al., 2017).

The integration of clonality-related traits with other major axes of ecological differentiation in perennial herbs remains unclear. Studies relating these traits with above-ground traits are sparse, focused on a limited set of traits (i.e. the ones defining the leaf-height-seed [LHS] scheme, Westoby, 1998) and on a reduced number of species within a given habitat type (e.g. temperate grasslands; Ladouceur et al., 2019). Consequently, the outcomes of previous studies are inconclusive (Herben et al., 2012, 2016, 2018; Klimešová et al., 2016; Ladouceur et al., 2019; Lubbe et al., 2021). Similarly, the relationship between clonality-related traits and root economics traits is not well-explored. In this respect, only one study has investigated the distribution of fine-root traits among clonal growth forms (Klimešová & Herben, 2023). Given the widespread importance of clonality in plants (Klimešová et al., 2018; Laughlin, 2023), integrating clonality-related traits into existing above-ground and fine-root trait spaces remains a priority (Laughlin, 2023), poised to reveal previously overlooked facets of plant ecological strategies.

We conducted an extensive study using a wide range of European perennial herbs and their traits to investigate the relationship between clonal and bud bank traits and the above-ground and fine-root trait spaces. To this end, we combined the largest dataset of plant clonal and bud bank traits, the CloPla database (Klimešová

et al., 2017), with the above-ground and fine-root trait frameworks provided by the above-ground (Díaz et al., 2016) and the fine-root (Bergmann et al., 2021; Carmona et al., 2021) trait space. First, we analysed whether perennial clonal herbs differ regarding above-ground and fine-root traits from perennial non-clonal herbs. Similar trait combinations would suggest that being clonal does not necessarily correspond to peculiar trait syndromes, hinting that clonality might add a function not captured by the above-ground and fine-root trait combinations alone. Next, we explored the multivariate relationships between clonal and bud bank traits with the above-ground and fine-root trait combinations. We analysed how single clonal and bud bank traits, and their combinations in multivariate space, relate to above-ground and fine-root trait combinations for perennial clonal herbs. The degree of coordination between clonality-related traits and both above-ground and fine-root trait spectra could finally clarify whether clonality-related traits can capture information on plant strategies beyond the current trait frameworks.

2 | METHODS

2.1 | Dataset construction

2.1.1 | Clonal and bud bank traits

We obtained clonal and bud bank data from the CloPla database (Klimešová et al., 2017). CloPla contains data for 2909 clonal and non-clonal vascular plant species that are common across Central Europe. For our analysis, we selected the following traits (Table S1): (i) The *total bud bank size*, expressed as the total number of buds per shoot, including stem buds at the soil level and root buds at different depths. (ii) The *multiplication rate*, calculated as the number of offspring shoots/parent shoot. (iii) The *lateral spread*, defined as the lateral spreading distance of clonal growth organs. (iv) The *persistence of clonal connection*, expressed as the lifespan of connection between offspring and parental rooting units. We focused our analysis on these clonal traits because: (a) they reflect meaningful aspects of clonal plants ecological strategies along environmental gradients (e.g. Herben et al., 2018; Chelli et al., 2019; Table S1); (b) they have been recently included in a robust conceptual framework with the availability of standard protocols for field measurements (Klimešová et al., 2019); (c) they synthesise the main functions provided by the vast array of clonal and bud bank traits (see Section 1 and Ottaviani et al., 2017). Species-specific values in CloPla are mean values of all the available information per each species, and no information at the intraspecific level is available (Klimešová et al., 2017).

2.1.2 | Above-ground and fine-root functional trait data

We combined CloPla with the above-ground and the fine-root economics traits information obtained from Carmona et al. (2021)

(Table S1). Before merging the datasets, taxonomic information was homogenised following The Plant List v.1.1 using the 'Taxonstand' R package (Cayuela et al., 2012). We acknowledge that newer sources of nomenclature exist and have opted to use this version as it allows seamless connectivity between existing trait and phylogenetic databases amenable to further investigation. Above-ground traits included: plant height (ph), specific stem density (ssd), seed mass (sm), individual leaf size (la), specific leaf area (sla) and leaf nitrogen content on a mass basis (ln). Trait information was available for 2674 species also included in CloPla (completeness: ph=97%, ssd=66%, sm=78%, la=72%, sla=70%, ln=43%). Fine-root economics traits included: specific root length (SRL), root tissue density (RTD), root nitrogen content (N) and root diameter (D). This trait information was available only for 474 species also included in CloPla (completeness: SRL=82%, RTD=68%, N=50%, D=83%). For both above-ground and fine-roots traits, each species-specific trait value was obtained in Carmona et al. (2021) as an average (after exclusion of observations exceeding the threshold of 3SD) calculated first within individuals (if within-individual measurements were available), then aggregated at the dataset level (i.e. multiple individuals were measured in the same location) and finally at the species level (i.e. across individuals measured in various locations). We analysed the above-ground and fine-root datasets separately due to the dramatic difference in the number of species and because there is an unresolved debate on how to integrate these two trait spaces into a single framework (Bueno et al., 2023; Carmona et al., 2021; Weigelt et al., 2021, 2023).

2.2 | Data analysis

2.2.1 | Trait differences between clonal and non-clonal perennial herbs

We first defined the above-ground and fine-root trait spaces using principal component analysis (PCA) on imputed trait data (i.e. with completeness of 100% for all the considered traits) by using the 'fun-space' R package (Carmona et al., 2023). Overall, the imputation procedure did not alter the definition of the above-ground and fine-root trait spaces (see Appendix S1; Figures S1 and S2). To test how clonality affects above-ground and fine-root trait combinations, we classified the species in our dataset as perennial clonal herbs ($n=1323$ and 195, in the above- and below-ground datasets, respectively) and perennial non-clonal herbs (603 and 79) using all the metadata available in CloPla. We did not consider woody or annual species because clonality is rare for these growth forms. We used overlap-based dissimilarity (Carmona et al., 2016) to quantify the extent of the shared portion of the trait space between clonal and non-clonal perennial herbs. The trait space was defined at the 0.99 quantile of the multivariate probability distribution of either above-ground or fine-roots trait combinations using the 'TPD' R package (Carmona et al., 2019). The results were visualised using the 'fun-space' R package (Carmona et al., 2023). To account for the different sample size between clonal

and non-clonal perennial herbs either in the above-ground or in the fine-root trait dataset, we assessed the overlap-based dissimilarity using an equally sized random sample of species in each group ($n=50$ for each group) across 500 iterations. PERMANOVA was also used to quantify how much of the trait variation along PC1 and PC2 of the above-ground or the fine-root trait space was explained by the group (Carmona et al., 2021).

2.2.2 | Linking clonal and bud bank traits to above-ground and fine-root trait combinations

To analyse the linkage between above-ground and fine-root traits and clonality-related traits, we calculated Pearson's correlation coefficients between clonal traits and above-ground and fine-root traits, and we visualised them using the 'corrplot' R package (Wei & Simko, 2021). Then, we mapped the clonal and bud bank traits within the trait spaces defined by the above-ground and fine-root traits. For this analysis, since clonality-related traits were available primarily for clonal plants, we redefined the above-ground and fine-root trait spaces using clonal plants only (i.e. perennial clonal herbs; Figures S3 and S4). Our final datasets for this analysis included information for 1257 and 195 species for the above-ground and the fine-root datasets, respectively. Generalised additive models (GAMs) with a bivariate smoother were used to draw patterns of variation of clonality-related traits within the above-ground and fine-root trait spaces in clonal plants. We ran GAMs using the 'funspace' R package (Carmona et al., 2023) by setting a clonal trait as the response variable and the trait space axes defining either the above-ground or the fine-root trait space of clonal plants as the bivariate explanatory variable. We also repeated the GAM analysis using the non-imputed version of the datasets (Figures S5 and S6; Table S2). Finally, to test the consistency of the target relationships within functionally and ecologically distinct groups, clonal species were classified as ferns, forbs and graminoids. Unfortunately, the fine-root trait dataset did not include ferns ($n=68$). Consequently, we restricted all the analysis to forbs and graminoids to ensure comparability between the above-ground and fine-root analyses (Figure S7–S17). The above-ground dataset included 919 forbs and 338 graminoids. The fine-root dataset included 110 forbs and 85 graminoids. For this test, we ran GAMs and mapped their predictions only within the specific regions of the trait space occupied by each functional group.

To further test the relationship between clonality-related traits and above-ground and fine-root trait combinations, we used the following approaches: (i) we characterised the clonal trait space using the species with complete trait information for total bud bank size, multiplication rate, lateral spread and persistence of clonal connections ($n=1181$ species) via PCA. (ii) We tested for the correlation between the clonal trait space and its above-ground or fine-root counterpart using Procrustes analysis run via 'protest' function included in the vegan R package (Dray & Dufour, 2007). This analysis rotates one configuration (the observed clonal trait space) to maximum similarity with a target one (above-ground or fine-root trait

space). It tests the non-randomness of the similarity via permutation (999 randomisations) based on Monte Carlo simulations.

Finally, to test whether clonality-related traits add non-redundant information to the above-ground or fine-root trait space, we first performed a PCA with varimax rotation including either above- or fine-root traits together with clonality-related traits. Then, we tested the dimensionality of the generated space using 'funspace' R package that tests trait space dimensionality through the paran test function from the 'paran' R package (Dinno, 2018). We performed all analyses with R 4.2.0 (R Core Team, 2022).

3 | RESULTS

3.1 | Trait differences between clonal and non-clonal perennial herbs

In terms of both above-ground and fine-root trait combinations, perennial clonal and non-clonal herbs were similar (for above-ground traits, $\text{overlap}=0.89\pm 0.07$; for fine-root traits, $\text{overlap}=0.88\pm 0.08$ Figure 1). Overall, in the above-ground trait space, the main differentiation between perennial clonal and non-clonal plants was along PC1 (Figure 1a,b), since the PERMANOVA analysis showed that the grouping variable explained 18% of trait variation along PC1 of the above-ground trait space and only 3% along PC2. Concerning the fine-root trait space, there was little differentiation between perennial clonal and non-clonal plants (Figure 1c,d), and the grouping variable explained only 3.1% and 2.8% of trait variation along PC1 and PC2 of the fine-root trait space, respectively.

3.2 | Linking clonal and bud bank traits to above-ground and fine-root trait combinations

The correlation analysis showed a weak relationship between clonality-related traits and above-ground and fine-root traits (Figure 2a,b). Correlation coefficients between clonal and above-ground traits ranged between -0.33 and 0.46 , and they were significant only in 15 out of 24 tests (Figure 2a). The correlation of clonality-related traits with fine-root traits was weaker compared with that in above-ground traits, and correlation coefficients ranged between 0.20 and 0.27 and they were only significant in 7 out of 16 tests (Figure 2b).

The GAM analysis confirmed that the relationship between clonal and above-ground and fine-root traits was weak also in the multivariate case (Figures 2 and 3). Clonal and bud bank traits were significantly associated with above-ground trait combinations (Figure 2a–d, p always <0.05 , full model statistics in Tables S2 and S3), but the patterns differed among clonal traits and the relationships had a low explanatory power ($R^2=4\%–22\%$). For all data pooled, total bud bank size and lateral spread were associated with the greatest plant height, seed mass and leaf area (see hot spots in Figure 3a,c). The multiplication rate increased

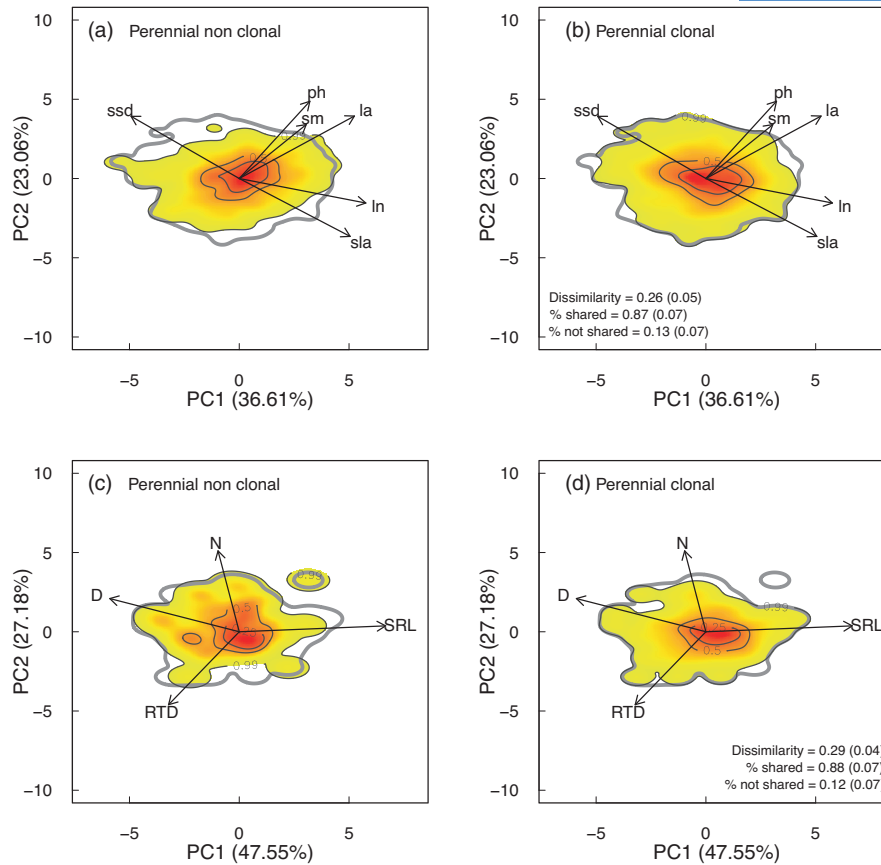


FIGURE 1 Comparing the trait spaces of perennial clonal and non-clonal plants. The upper panels (a, b) display the above-ground trait space, while the lower panels illustrate the fine-root trait space (c, d). Coloured areas represent the probability of encountering specific trait combinations within these spaces (red area = high probability). Contour lines delineate the 0.99, 0.50 and 0.25 quantiles of the multivariate probability distribution of trait combinations. The values (means and standard deviations across 500 replicates) of dissimilarity and the proportion of the trait space that is shared/not shared refer to the comparison between perennial clonal and non-clonal herbs in either above-ground or fine-root trait space (see Section 2.2 for details). The thick grey line indicates the trait space defined by pooling together clonal and non-clonal perennial herbs. ssd, specific stem density; ph, plant height; sm, seed mass; la, leaf area; ln, leaf nitrogen content (mass basis); sla, specific leaf area; D, mean root diameter; N, root nitrogen content (mass basis); SRL, specific root length; RTD, root tissue density.

towards lower values of plant height, seed mass and leaf area and greater values of specific leaf area and leaf nitrogen content (see hot spot in Figure 3b). However, this pattern was weak overall. The persistence of clonal connections increased with specific stem density (hot spots in Figure 3a,b,d). Belowground (Figure 4a–d, Table S3), we found two significant relationships: lateral spread weakly increased with the N content in fine roots (hot spot in Figure 4c, $R^2=5\%$, $p=0.004$) and persistence of clonal connection increased with root tissue density (a hot spot in Figure 4d, $R^2=10\%$, $p=0.002$). Imputing trait data did not influence the patterns observed on pooled data (Figures S5 and S6; Table S2). However, the patterns of how clonal-related traits varied within the above-ground and fine-root trait spaces sometimes differed between functional groups (Figures S10–S17, Table S3).

In addition, we found a significant but overall weak correlation between clonal-trait combinations (i.e. PCA run on clonality-related traits) and the above-ground or fine-root trait space of clonal plants. In detail, the correlation between the clonal trait space and the above-ground trait space was 0.26 (Procrustes sum

of squares = 0.93, $p=0.001$), while that of clonality-trait space and the fine-root trait space was 0.20 (Procrustes sum of squares = 0.96, $p=0.003$). The clonal trait space that we formalised spans two dimensions (Figure 5). The first dimension explained 38.9% of the total variance in clonal trait data and total bud bank size and persistence were positively loaded on this axis (loading = 0.71 and 0.64, respectively). The second dimension explained 32% of the total variance in clonal traits and multiplication rate and lateral spread were positively loaded on this dimension (0.67 and 0.66).

When building a trait space including clonal traits and either above-ground or fine-root traits, we found that clonal traits add non-redundant information to the current trait frameworks. In particular, the two-dimensional above-ground trait space expands to four dimensions (Table 1). The first and second dimensions reflect an economic axis and size-related axes, respectively. The third and the fourth dimensions correspond to the dimensions of the clonal trait space (Table 1, Figure 5). For fine-root trait space, we found that it expands to three dimensions when including clonal traits (Table 1). The first dimension corresponds to a trade-off between specific root

length and root diameter, the second axis corresponds to the first dimension of the clonal trait space, and the third axis was positively related to bud bank size and lateral spread.

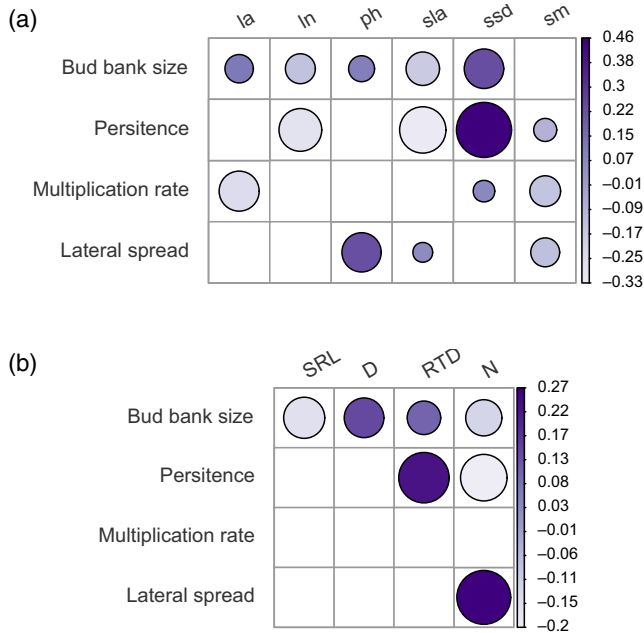


FIGURE 2 Correlation between the selected trait sets. (a) Correlation between clonal traits and above-ground traits. la, leaf area; ln, leaf nitrogen content (mass basis); ph, plant height; sla, specific leaf area; ssd, specific stem density; sm, seed mass. (b) Correlation between clonal traits and fine-root traits. SRL, specific root length; D, mean root diameter; RTD, root tissue density; N, root nitrogen content (mass basis). Only significant correlation coefficients ($p \leq 0.05$) are shown. The size and the colour of a circle reflects the magnitude and the sign of the correlation coefficient.

Aboveground trait space

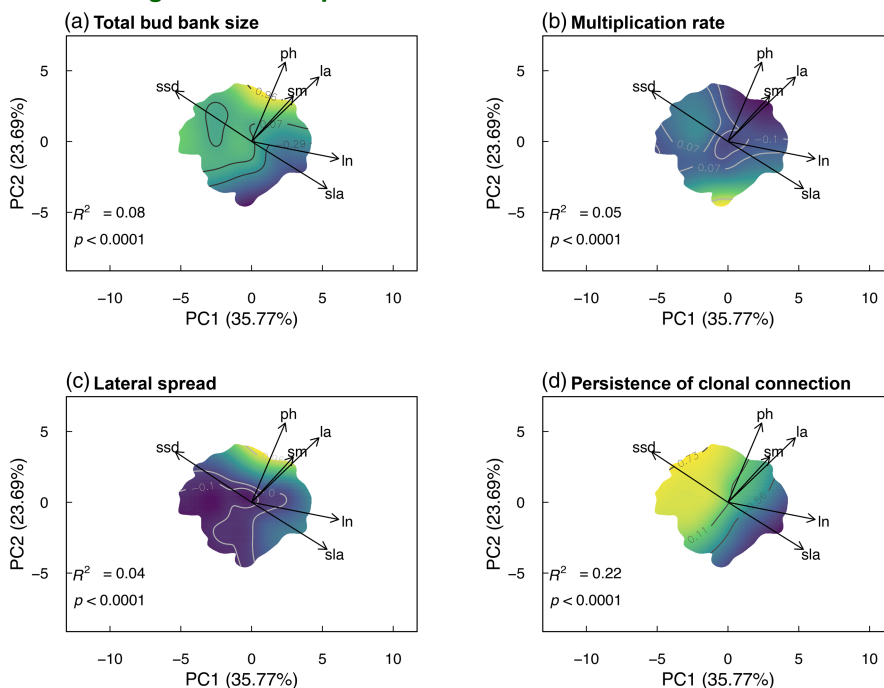


FIGURE 3 Mapping clonality-related traits in the above-ground trait space. (a) Total bud bank size; (b) multiplication rate; (c) lateral spread; (d) persistence of clonal connection. High values of the trait being mapped are shown in yellow. ssd, specific stem density; ph, plant height; sm, seed mass; la, leaf area; ln, leaf nitrogen content (mass basis); sla, specific leaf area. Details of the considered traits are shown in Table S1. Contour lines within the map correspond to quantiles of GAM predictions. Note that the response variable was scaled before the analysis. Only the R^2 and the p -value of each relationship are shown. Full GAM statistics are reported in Table S3. n.s., not significant.

4 | DISCUSSION

We present the most comprehensive analysis combining clonal and bud bank traits within current above-ground (Díaz et al., 2016) and fine-root (Bergmann et al., 2021; Carmona et al., 2021) trait frameworks. Our findings reveal that the traits associated with above-ground or fine-root compartments fail to distinguish between clonal and non-clonal Central European herbs. Furthermore, we observed a limited correlation between clonality-related traits and combinations of above-ground and fine-root traits in perennial clonal herbs. Our results underscore that clonality is a strategic axis for perennial herbs, a dimension only minimally reflected by other traits. Consequently, we advocate for a clonal trait framework that encapsulates the potential independent dimensions of specialisation of perennial herbs linked to space-holding ability (represented by persistence and bud bank size) and clonal multiplication (represented by lateral spread and multiplication rate).

4.1 | Above-ground and fine-root trait dimensions do not distinguish clonal from non-clonal herbs

Although visual and functional distinctions exist between clonal and non-clonal perennial herbs, effectively delineating these groups within multivariate trait spaces using existing above-ground and fine-root frameworks has posed a challenge. By integrating clonal trait data into the frameworks of the above-ground trait space and fine-root trait space, we found that perennial clonal and non-clonal herbs were indistinguishable. This means that being clonal does not constrain above-ground or fine-root functional differentiation in perennial herbs, hinting that clonality might add functions not captured by both the above-ground and fine-root trait spaces. These

FIGURE 4 Mapping clonality-related traits in the fine-root trait space. (a) Total bud bank size; (b) multiplication rate; (c) lateral spread; (d) persistence of the trait being mapped are shown in yellow. D, mean root diameter; N, root nitrogen content (mass basis); SRL, specific root length; RTD, root tissue density. Details of the considered traits are shown in Table S1. Contour lines within the map correspond to quantiles of GAM predictions. Note that the response variable was scaled before the analysis. Only the R^2 and the p -value of each relationship are shown. Full GAM statistics are reported in Table S3. n.s., not significant.

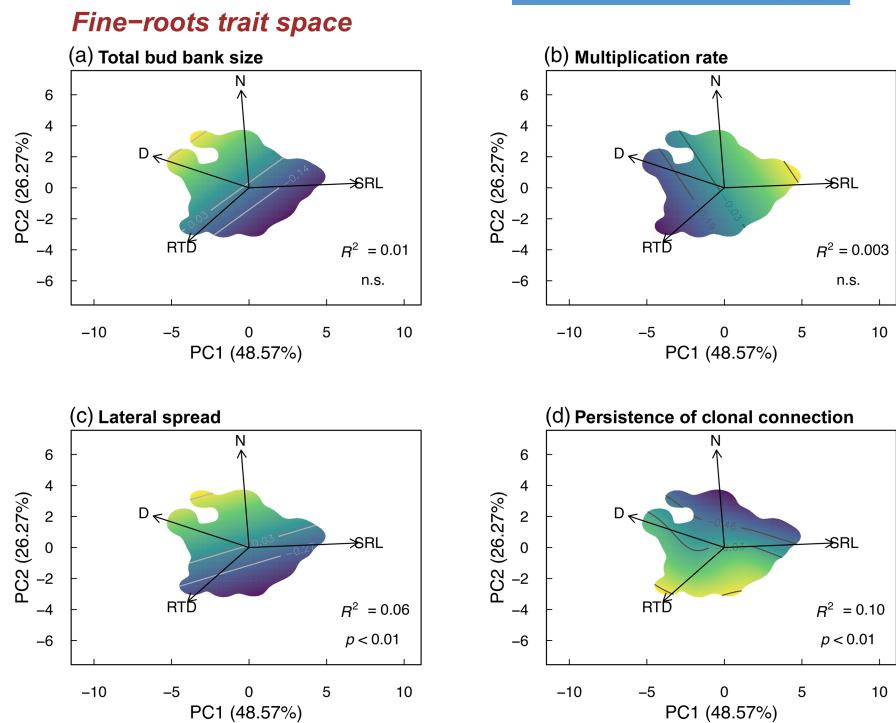
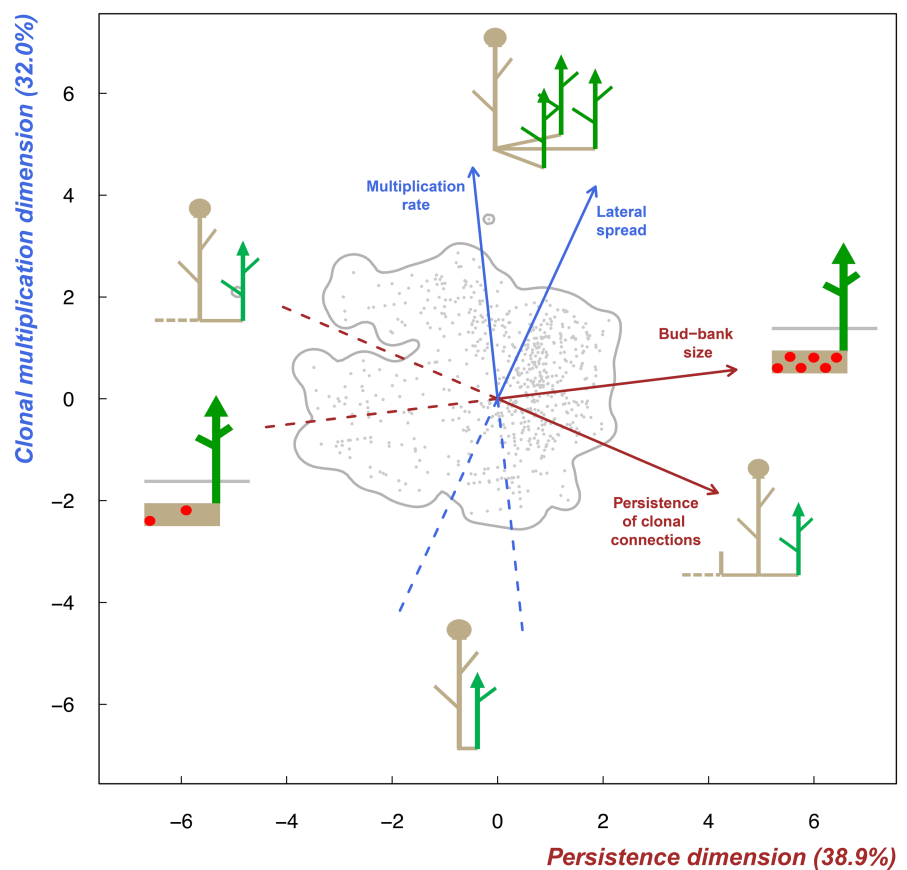


FIGURE 5 The clonal trait space. The trait space defined by a PCA on clonal and bud bank trait data for 1181 clonal species with complete trait information. The first component is interpreted as a 'persistence dimension' running from splitting clones with short persistence of clonal connections (P) and small bud bank size (BBS) to integrated clones with longer P and larger BBS. The second component is interpreted as a 'clonal multiplication axis,' a spectrum from low to high rates of clonal multiplication (MR) and lateral spread (LS). The variance percentage in the data explained by each axis is shown. The grey line represents the 0.99 quantile of the multivariate kernel density function. Drawings from Klimešová et al. (2016).



functions are: on-spot persistence; horizontal space occupancy and competition; resource storage and sharing among ramets; and clonal multiplication. The idea that clonality may play a distinct functional role in plant ecology, differing from established paradigms (above-ground and fine-root trait spaces), has been suggested by previous

authors (e.g. Klimešová et al., 2018, 2021; Ottaviani et al., 2017), our study provides the first empirical evidence on a broad taxonomic scale.

The reasons why clonal and non-clonal herbs are similar in terms of above-ground and fine-root traits are speculative. First, there

TABLE 1 Loadings from principal component analysis ran by combining clonal with either above-ground ($n = 1181$) or fine-root traits ($n = 195$). The colour code distinguishes the traits that define each principal component (PC), which we considered to be those traits with a loading ≥ 0.60 . Loadings with a value comprised between 0.40 and 0.50 are shown in grey. Loadings below 0.40 are not reported for clarity. The number of retained PCs is based on the results of a paran test (see Section 2.2). The variance explained by each PC is shown in parenthesis.

	Clonal traits in the above-ground trait space				Clonal traits in the fine-root trait space			
	PC1 (20.5%)	PC2 (16.5%)	PC3 (16.0%)	PC4 (15.7%)		PC1 (24.0%)	PC2 (19.4%)	PC3 (18.2%)
ln	0.72				SRL	-0.96		
sla	0.79				D	0.89		
ssd	-0.79				RTD	0.47	0.43	
la		0.80			N			0.565
ph		0.74		0.43	Bud bank size		0.62	
sm		0.61			Persistence		0.84	
Bud bank size			0.86		Bud bank size			0.62
Persistence	-0.42		0.72		Lateral spread			0.84
Multiplication rate				0.76				
Lateral spread				0.69				

could be underlying evolutionary forces at play—for instance, we know that clonal traits are relatively evolvable, and that angiosperms can transition between clonal and non-clonal forms relatively easily (Herben & Klimešová, 2020; Klimešová et al., 2021); whether other traits are equally evolvable remains an open question (Opedal, 2019 for vegetative and floral traits). Second, having different suites of traits simply offers more pathways to promote plant survival. For instance, clonal plants may cope with limiting resources not only by modulating above- (i.e. leaves) and/or below-ground (i.e. roots) acquisitive organs but also by sharing resources horizontally between distinct parts of a clone, thus equalising conditions over heterogeneous environments (Jonsdottir & Watson, 1997; Klimešová et al., 2021). Third, having different regenerative traits (including traits of both vegetative and generative regeneration) is typical for co-existing species and may be considered as a mechanism allowing coexistence (Ladouceur et al., 2019).

4.2 | Clonal and bud bank traits are decoupled from above-ground and fine-root trait spectra: Towards a clonal trait space

When examining perennial clonal herbs explicitly, we observed a limited correlation between clonality-related traits and the above-ground and fine-root trait spectra. This indicates that the investment in clonal growth only partly depends on resource acquisition strategies and plant size. Consequently, species located within the clonal trait space exhibit minimal correlations with their position in the above-ground or fine-root trait space, substantiating previous findings from smaller species datasets (Herben et al., 2012, 2016, 2018; Klimešová et al., 2016). Finally, we demonstrated for the first time that clonal traits add non-redundant information to current trait frameworks (Table 1). Given a larger dataset, the next endeavours

should combine above-ground, fine-roots and clonal traits into a single trait space to provide an integrated picture of the form and function of herbs.

The analysis of the clonal trait space identified two primary dimensions summarising clonal and bud bank trait combinations in clonal perennial herbs (Figure 5). We interpreted the first dimension of the clonal trait space as a 'persistence' dimension that might reflect a spectrum of strategies from splitting clones with small bud bank in shaded and undisturbed habitats to integrated clones with large bud banks typical for open and disturbed habitats. The connection between small bud banks and rare disturbance was proposed by Bellingham and Sparrow (2000) and more recently by Herben et al. (2018). Both papers, however, indicate small investments to bud bank also under the most severe and frequent disturbances—both, however, include annual plants for their evaluation while we focused only on clonal perennial herbs. Open and closed canopy ecosystems not only differ by disturbance regime in Central Europe but also provide contrasting habitats concerning resource limitation. In open habitats, plant growth is often constrained by nutrients (e.g. P, N), whereas in forest understorey, plant growth is limited by carbon, and the construction and maintenance of persistent below-ground organs may be too costly for plants. This result is in line with clonal research that traditionally distinguishes the gradient of strategies known as splitter-integrator continuum (Jonsdottir & Watson, 1997) along a productivity gradient.

Above-ground, the persistence of clonal connection exhibited a positive association with specific stem density, revealing a consistent relationship across pooled data for both forbs and graminoids. Below-ground, the persistence of clonal connections showed a slight positive relationship with fine-root tissue density. These patterns suggest that the persistence of clonal connections serves as an economic trait for clonal plants coordinated over whole plants growing in resource-limited environments. In such conditions, all

plants adopt conservative strategies with prolonged longevity of all organs but, in the case of clonal plants, this strategy facilitates unique functions like resource sharing among parts of the clone or harvesting soil resources from large areas (Craine et al., 2001; Jonsdottir & Watson, 1997; Klimešová et al., 2016) through clonal growth organs like rhizomes. Regarding the bud bank size, we observed only a weak positive correlation with the above-ground traits of plant height, seed mass and leaf area, mirroring the size-related dimension of the above-ground trait space. Unsurprisingly, plants with larger bud banks were larger with bigger-sized above-ground organs.

The second dimension of the clonal trait space is a 'clonal multiplication' dimension that mirrors the capacity to occupy new space by growing clonally and represents a trade-off between competitive ability and stress tolerance. Consequently, it can be related to resource availability, which is higher where we find higher lateral spread and multiplication rates and lower at the other hand of the axis. The fast growth necessary to produce both long spacers (annual increment of clonal growth organs) and numerous clonal offspring requires enough resources and is concentrated in nutrient-rich, open habitats like grasslands (Craine et al., 2001; Klimešová et al., 2016). The most considerable lateral spread and multiplication rate can be found in wetlands or aquatic habitats, but only when enough nutrients are available (Klimešová & Herben, 2015). On the other hand, in nutrient-poor or cold places, clonal plants with low lateral spread and low multiplication rate prevail (Klimešová & Herben, 2015). The 'clonal multiplication' dimension can be seen as a strategy to gain a competitive advantage in conditions where vertical growth is not possible, that is, in open habitats in central Europe that are also under regular disturbance regimes. This points to the likelihood that the mechanisms governing the clonal multiplication axis, potentially associated with genetic or physiological factors, have limited ties to resource acquisition or allocation strategies and may be governed by their role in the demography of plants or response to disturbance.

5 | CONCLUSIONS

We provide the first evidence at a large taxonomic scale that clonality-related traits add independent trait dimensions to the above-ground and fine-root trait spaces. It suggests that clonal trait combinations might provide alternative ways to endure stress and disturbance through different mechanisms than those provided by other above- and below-ground traits. The advantages that such alternative strategies might bring under multiple ecological contexts compared to above-ground and fine-root trait combinations need further investigation. However, despite the eco-evolutionary relevance of clonal and bud bank traits and the availability of standard protocols for their sampling (see Klimešová et al., 2019), there is still a huge data gap for species outside Europe (Klimešová et al., 2017). This potential geographical and functional limitation of our study—which is indeed limited to perennial herbs from Central Europe—can, however, turn into an advantage as our results can be considered

spurious of many potential confounding effects typical of large cross-species studies (e.g. species distribution across disparate biomes, broad latitudinal gradients and many functional types). Finally, as a natural next step towards reinforcing the concept of a clonal trait space and its integration with current strategy schemes, we need a global assessment of the patterns highlighted in this study.

AUTHOR CONTRIBUTIONS

Stefano Chelli and Giacomo Puglielli conceived the idea and led the writing of the paper with inputs from Jitka Klimešová and James Lee Tsakalos. Stefano Chelli, Jitka Klimešová and Giacomo Puglielli conceptualised the study. Giacomo Puglielli and James Lee Tsakalos performed statistical analyses. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14265>.

DATA AVAILABILITY STATEMENT

Data and code to reproduce the analyses are available at: <https://doi.org/doi:10.5061/dryad.bzkh189h0> (Chelli et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Building aboveground and fine-root trait spaces and testing the effect of trait data imputation.

Figure S1. Trait space defined by above-ground traits for the clonal species in the not imputed versus imputed dataset.

Figure S2. Trait space defined by below-ground traits for the clonal species in the not imputed versus imputed dataset.

Figure S3. Trait space defined by above-ground traits for the clonal species in the dataset.

Figure S4. Trait space defined by fine-root traits for the clonal species in the dataset.

Figure S5. Mapping clonality-related traits in the above-ground trait space using not imputed data.

Figure S6. Mapping clonality-related traits in the below-ground trait space using not imputed data.

Figure S7. Distribution of clonal forbs and graminoids in the above-ground trait space.

Figure S8. Distribution of clonal forbs and graminoids in the fine-root trait space.

Figure S9. Comparing functional diversity between clonal forbs and graminoids.

Figure S10. Mapping total bud-bank size in the above-ground trait space for forbs (left column) and graminoids (right column).

Figure S11. Mapping multiplication rate in the above-ground trait space for forbs (left column) and graminoids (right column).

Figure S12. Mapping lateral spread in the above-ground trait space for forbs (left column) and graminoids (right column).

Figure S13. Mapping persistence in the above-ground trait space for forbs (left column) and graminoids (right column).

Figure S14. Mapping total bud-bank size in the fine-root trait space for forbs (left column) and graminoids (right column).

Figure S15. Mapping multiplication rate in the fine-root trait space for forbs (left column) and graminoids (right column).

Figure S16. Mapping lateral spread in the fine-root trait space for forbs (left column) and graminoids (right column).

Figure S17. Mapping persistence in the fine-root trait space for forbs (left column) and graminoids (right column).

Table S1. List of traits used, their abbreviation (in parenthesis), description and related function.

Table S2. GAM statistics.

Table S3. Full GAM statistics.

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