Letters

Herbs are different: clonal and bud bank traits can matter more than leaf–height–seed traits

Introduction

Current understanding of functional differences among plant species is based on several key axes of specialization in response to environmental gradients, namely of productivity and disturbance. These axes include leaf economy spectrum, plant size and dispersal ability (Westoby, 1998; Westoby *et al.*, 2002; Wright *et al.*, 2004). These axes are typically proxied by easily measurable traits, namely specific leaf area, height at maturity and seed mass (leaf–height–seed (LHS) traits of Westoby, 1998) which capture well variation in a number of correlated plant characteristics (Westoby & Wright, 2006; Laughlin *et al.*, 2010).

While the first comprehensive trait-based analysis was dealing primarily with herbs (Grime, 1977), LHS-based analyses turned out to be particularly powerful to describe ecological differentiation of woody plants. In spite of the fact that woody species constitute less than a half of existing plant species (FitzJohn *et al.*, 2014), much current understanding of plant functional tradeoffs is based on species sets that contain primarily woody species (Verdu, 2002; Kerkhoff *et al.*, 2014; Lamanna *et al.*, 2014).

However, differentiation of herbaceous plants is likely to be shaped by factors different from woody species. They do not possess permanent aboveground structures which permits entirely different response to disturbance (Aarssen *et al.*, 2006; Aarssen, 2008; Zanne *et al.*, 2014), but also to other factors, such as drought (Bennett *et al.*, 2015). While strong and infrequent disturbance kills whole plants and generates a long gradient of time-since-disturbance which favours woody species (Meiners *et al.*, 2015), weaker and regular disturbance events leave belowground regenerative organs intact, favouring plants which can resprout from them (Bellingham & Sparrow, 2000; Mackey & Currie, 2001; Buoro & Carlson, 2014). Such disturbances preclude plants from developing long-lived structures aboveground found in trees and favour resprouting from permanent belowground structures (Bellingham & Sparrow, 2000; Vesk *et al.*, 2004; Dietze & Clark, 2008) as found in shrubs (Bond & Midgley, 2001; Vesk *et al.*, 2004; Dietze & Clark, 2008; Clarke *et al.*, 2013) and herbs (Klimešová & Klimeš, 2007; Meiners *et al.*, 2015). Further, short disturbance intervals (such as winter frost in temperate climates, regular drought or grazing) require rapid resprouting and therefore cheap aboveground tissues that are non-woody (Vesk, 2006; Zanne *et al.*, 2014) and thus largely eliminate selective advantage provided by vertical growth and favour expansion in a horizontal dimension by clonal spread.

Selective forces operating on resprouting plants are thus fairly different from those operating on trees. As a result, tradeoffs and correlations of their traits should be different from those known from woody species (Meiners *et al.*, 2015). Still we do not know to what extent the key role of the LHS-differentiation applies to herbs as it does to woody species, and trees in particular. We also do not know whether and how traits that determine ability to resprout and spread horizontally in space (namely traits of belowground bud banks and traits of clonal growth) fit into this differentiation or whether they constitute an axis of specialization independent of the LHS traits.

Clonal and belowground bud bank traits and their relationship to the LHS scheme

We examined relationships between LHS traits and traits of bud bank (size and depth) and of clonal growth (extension of lateral spread, multiplication rate and persistence of clonal connections; for an illustration see Fig. 1) of Central European species (*c.* 2000 species). Analysis of this data set shows that almost all relationships between LHS traits, bud bank and clonal traits are very weak (Table 1; for methodological details see Supporting Information Methods S1 and Tables S1 and S2). With the exception of bud bank depth and connection persistence, LHS traits explain < 5% of the variation in clonal and bud bank traits (and often much less). This means that the variation on traits that determine resprouting and clonal spread do not fit well into the syndromes of the LHS traits.

The few significant cases of correlation of clonal and bud bank traits with the LHS traits (see Table S3; Fig. S1) are likely to be due to two different reasons. First, bud bank depth, and to a much lesser extent bud bank size and lateral spread, are positively correlated with plant height at maturity. These relationships are likely to be due to allometric effects of plant size (Enquist & Niklas, 2001; Schenk & Jackson, 2002). Tall plants are likely to have more extensive root and rhizome systems, bear more buds than short roots and rhizomes (VanderWeide & Hartnett, 2015) and are more likely to spread farther away from the mother plants. Second, negative correlation of specific leaf area with connection persistence implies that clonal plants are also differentiated in terms of leaf economics, and faster growing plants of more productive conditions tend to have short-lived connections between ramets and longer rhizome increments relative to plants that grow slower (see also Jónsdóttir & Watson, 1997; Craine *et al.*, 2001).

Clonal and belowground bud bank traits as predictors of herb distribution along ecological gradients

An independent axis of plant specialization is not characterized only by a trait which is not correlated with LHS traits, but, at the same
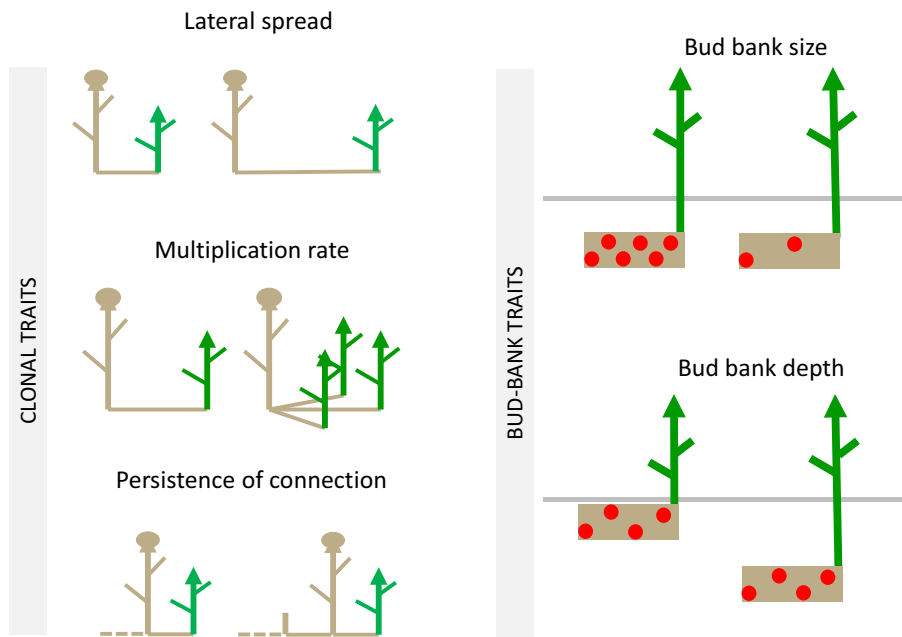
Lateral spread

Bud bank size

CLONAL TRAITS

BUD-BANK TRAITS

Multiplication rate

Bud bank depth

Persistence of connection

Fig. 1 A schematic representation of clonal and bud bank traits. Each trait is illustrated by a pair of species that differ in the value of that trait. Red dots, buds. Full horizontal line, living spacer (rhizome or stolon); dashed horizontal line, dead spacer. For further details see Supporting Information Table S1.

Table 1 Prediction of clonal and bud bank traits with leaf–height–seed (LHS) traits in a set of herbs of the Central European flora

Predictor		Bud bank size	Mean bud bank depth	Multiplication rate[1]	Lateral spread[1]	Persistence of connections[1]
Height	phylogenetic adjusted R^2	0.017*** (+)	0.047*** (+)	0.007* (−)	0.008** (+)	−0.001
	adjusted R^2	0.010*** (+)	0.030*** (+)	0.021*** (−)	0.018*** (+)	0.024*** (+)
	n	1359	1316	718	715	711
SLA	phylogenetic adjusted R^2	0.009*** (−)	0.009** (−)	0	−0.001	0.028*** (−)
	adjusted R^2	0.017*** (−)	0.018*** (−)	0.001	0.008* (+)	**0.101*** (−)**
	n	1078	1039	577	572	568
Seed mass	phylogenetic adjusted R^2	0.003* (+)	0.009** (+)	0.008* (−)	0.004	0.007* (+)
	adjusted R^2	−0.001	0.022*** (+)	0.022*** (−)	0.004	0.001
	n	990	957	519	517	513
All three	phylogenetic adjusted R^2	0.032***	**0.065***	0.003	0.007	0.026***
	adjusted R^2	0.030***	**0.062***	0.009	0.016**	**0.071***
	n	877	848	462	460	457

Phylogenetic adjusted R^2 is based on the value of Pagel's λ estimated by maximum likelihood; adjusted R^2, adjusted R^2 assuming independence of phylogenetic histories of species; n, number of cases; SLA, specific leaf area. R^2 values > 0.05 are indicated in bold. Sign of the relationship (if significant) is in parentheses. Asterisks indicate uncorrected significance values: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
[1]Defined for clonal plants only. For further details see Supporting Information Methods S1 and Table S1. For further information on individual clonal and bud bank traits, see Fig. 1.

time, it must improve substantially the predictive power of LHS traits for plant distribution in the field. Existing data show that traits of clonal growth and belowground bud bank (namely bud bank size and connection persistence) predict species distribution along ecological gradients in Central European vegetation at least as well as the LHS traits. Their net predictive power is similar to that of the LHS traits combined (Fig. 2; Table 2) and is not due to the (small but existing) covariation of these traits with the LHS traits. This leads to a conclusion that clonal and bud bank traits, that is, traits that determine resprouting and clonal multiplication, indeed form axes of specialization of temperate herbs fairly independent of the LHS traits. However, it should be noted that the combined predictive power of both groups of traits reaches only *c.* 10% of the total variation in the species habitat distribution in the field.

First, the distribution along ecological gradients is best predicted by bud bank size and connection persistence. In contrast to the LHS traits, which (namely leaf traits) capture the role of physiological performance and the pace of life, the bud bank size and clonality per se expresses primarily morphological/developmental constraints on the potential to resprout. Although the herbaceous habit probably did not evolve in temperate regions (Zanne *et al.*, 2014), prevalence of resprouting and/or clonally growing herbs is the determining feature of temperate vegetation, both in (semi-)natural habitats and in communities regularly disturbed by human activities such as arable fields, mown and pastured grasslands, and ruderal places (Klimešová & Herben, 2015). The resprouting ability in herbs is likely to have evolved under a number of disturbance regimes, such as large ungulate grazing, fire, flooding and avalanches (Klimeš
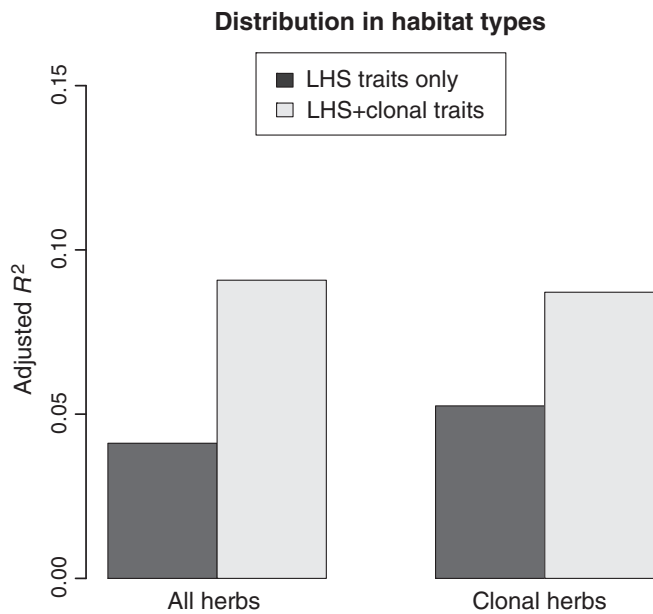
Distribution in habitat types

Fig. 2 Predictive power of bud bank and clonal traits as a group for species distribution across habitat types compared with the predictive power of leaf–height–seed (LHS) traits. Models for all herbs use bud bank traits only, while models for clonal plants use all clonal traits. For further details see Table 2 and Supporting Information Table S1.

et al., 1997; Bellingham & Sparrow, 2000; Klimešová & Klimeš, 2007).

Second, the differences due to connection persistence and correlated clonal traits are likely to reflect the gradient of stress/productivity as clonal plants with persistent connections are known to occur in stressed and unproductive conditions (Jónsdóttir & Watson, 1997; Klimešová & Herben, 2015). Slow growing clonal plants tend to have long-lived connections between ramets and shorter rhizome increments relative to plants that grow faster (see definition of different clonal growth strategies in de Kroon & Schieving, 1990; Jónsdóttir & Watson, 1997; Craine *et al.*, 2001). This parallels development of costly, but long-lived leaf tissues in slowly growing plants in stressed conditions and cheap short-lived tissues in fast growing species under productive conditions (Reich *et al.,* 1992; Westoby & Wright, 2006).

Implications

Our analyses support the hypothesis that functional differentiation within herbaceous plants thus is based, to an important extent, on dimensions different from those that are used in large-scale studies that include primarily woody species. This is due to the two fundamentally different strategies that plants use to cope with disturbance: tolerance (resprouting) and avoidance (by dispersing to disturbed habitats by seeds, either in time or in space). The LHS system captures seed and growth-related traits that are primarily important for disturbance avoidance, whereas milder and more frequent disturbances select for the second strategy, which is associated with clonal and bud bank traits that supply reserve meristems for survival.

Further, it should be noted here that while the predictive power of clonal and bud bank traits relative to that of the LHS trait is high, neither of them is a very strong predictor of species habitat distribution. This may be partly due to the restricted range of plants studied here, as traits of temperate herbs have smaller ranges relative to what is found across the plant kingdom, namely in height, but also in seed size (see e.g. Thompson & Rabinowitz, 1989; Moles *et al.*, 2007). However, we would like to point out here the low predictive power of *all* commonly collected traits for species distribution along ecological gradients which is often not paid sufficient attention (but see e.g. Coyle *et al.*, 2014; Moles *et al.*, 2014).

Finally, we would like to point out that clonal and bud bank traits should be given more prominence in trait-based analyses of species habitat distribution and coexistence. Clonality is a key potential of plant bodies (Mogie & Hutchings, 1990; Klimešová *et al.*, 2015) with deep interspecific differences in the way in which it is expressed (Klimeš *et al.*, 1997), but we are only beginning to appreciate its full ecological implications. Temperate herbs show rather a broad range of clonal growth types (J. Klimešová, 2015, unpublished data), but clonal growth is also found in trees and woody species, albeit in lower proportions (Aarssen, 2008). While collecting data on its traits is often more difficult than collecting data on LHS traits, it is feasible and has been done both for herbs and woody species (Bond & Midgley, 2001; Klimešová & de Bello, 2009; Clarke *et al.*, 2013; VanderWeide & Hartnett, 2015). Comparative analyses of their role relative to other traits, and their mutual relationships across different biomes and different floras

Table 2 Predictive power of individual clonal and bud bank traits for occurrence of herb species in habitat types of Central European vegetation

	Adjusted R^2 LHS	Adjusted R^2 LHS+trait	Partial adjusted R^2 trait	*n*
Bud bank size	0.061***	0.113***	0.055***	757
Mean bud bank depth	0.066***	0.115***	0.052***	730
Multiplication rate[1]	0.087***	0.094***	0.007**	413
Lateral spread[1]	0.088***	0.099***	0.012***	411
Persistence of connections[1]	0.088***	0.122***	0.037***	409

Relative number of occurrences in major habitat types are taken as dependent variables, and their prediction by leaf–height–seed (LHS) traits (first column) and individual clonal and bud bank traits (second and third columns) is examined by multivariate extension of multiple regression (redundancy analysis). Phylogenetic non-independence of traits is removed using phylogenetic eigenvectors (Diniz-Filho *et al.*, 1998). Differences among rows in the first column (the model with LHS traits only) is due to different number of cases included. Significances are based on randomization tests. **, $P < 0.01$; ***, $P < 0.001$.
[1]Defined for clonal plants only. For further details see Supporting Information Methods S1 and Table S1.

would provide better understanding about how plants respond to a number of factors, namely disturbance. Comparison of the role of clonal growth and bud banks in herbs and woody species would also shed more light on differences between these two fundamental ecological strategies in the plant kingdom.

Acknowledgements

Author contributions

J.K. and T.H. planned and designed the research, J.K. and O.T. assembled data, T.H. analysed data, T.H. wrote the manuscript with contributions of J.K. and O.T.

Jitka Klimešová[1], Oliver Tackenberg[2] and Tomáš Herben[3,4]*

[1]Institute of Botany, Academy of Sciences of the Czech Republic, CZ-379 82, Třeboň, Czech Republic;
[2]Institute of Ecology, Evolution and Diversity, Goethe-University Frankfurt, Max-von-Laue-Straße 13, D-60438, Frankfurt, Germany;
[3]Institute of Botany, Academy of Science of the Czech Republic, CZ-252 43, Průhonice, Czech Republic;
[4]Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01, Praha 2, Czech Republic
(*Author for correspondence: tel +420 221951653;
email herben@site.cas.cz)

References

Aarssen LW. 2008. Death without sex - the 'problem of the small' and selection for reproductive economy in flowering plants. *Evolutionary Ecology* 22: 279–298.

Aarssen LW, Schamp BS, Pither J. 2006. Why are there so many small plants? Implications for species coexistence. *Journal of Ecology* 94: 569–580.

Bellingham PJ, Sparrow AD. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409–416.

Bennett AC, McDowell NG, Anderson-Teixeira KJ. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* 1: 15139.

Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16: 45–51.

Buoro M, Carlson SM. 2014. Life-history syndromes: integrating dispersal through space and time. *Ecology Letters* 17: 756–767.

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197: 19–35.

Coyle JR, Halliday FW, Lopez BE, Palmquist KA, Wilfahrt PA. 2014. Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. *Ecography* 37: 814–826.

Craine JM, Froehle J, Tilman GD, Wedin DA, Chapin FS. 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* 93: 274–285.

Dietze MC, Clark JS. 2008. Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecological Monographs* 78: 331–347.

Diniz-Filho JAF, de Sant'Ana CER, Bini LM. 1998. An eigenvector method for estimating phylogenetic inertia. *Evolution* 52: 1247–1262.

Enquist BJ, Niklas KJ. 2001. Invariant scaling relations across tree-dominated communities. *Nature* 410: 655–660.

FitzJohn RG, Pennell MW, Zanne AE, Stevens PF, Tank DC, Cornwell WK. 2014. How much of the world is woody? *Journal of Ecology* 102: 1266–1272.

Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.

Jónsdóttir IS, Watson MA. 1997. Extensive physiological integration: an adaptive trait in resource-poor environments. In: de Kroon H, van Groenendael JM, eds. *The ecology and evolution of clonal plants*. Leiden, the Netherlands: Backhuys Publishers, 109–136.

Kerkhoff AJ, Moriarty PE, Weiser MD. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proceedings of the National Academy of Sciences, USA* 111: 8125–8130.

Klimeš L, Klimešová J, Hendriks RJJ, van Groenendael JM. 1997. Clonal plant architecture: a comparative analysis of form and function. In: de Kroon H, van Groenendael JM, eds. *The ecology and evolution of clonal plants*. Leiden, the Netherlands: Backhuys Publishers, 1–29.

Klimešová J, de Bello F. 2009. CLO-PLA: the database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science* 20: 511–516.

Klimešová J, Herben T. 2015. Clonal and bud bank traits: patterns across temperate plant communities. *Journal of Vegetation Science* 26: 243–253.

Klimešová J, Klimeš L. 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 115–129.

Klimešová J, Nobis MP, Herben T. 2015. Senescence, ageing and death of the whole plant: morphological prerequisites and constraints of plant immortality. *New Phytologist* 206: 14–18.

de Kroon H, Schieving F. 1990. Resource partitioning in relation to clonal growth strategy. In: van Groenendael J, de Kroon H, eds. *Clonal growth in plants: regulation and function*. The Hague, the Netherlands: SPB Academic Publishing, 113–130.

Lamanna C, Blonder B, Violle C, Kraft NJB, Sandel B, Simova I, Donoghue JC, Svenning JC, McGill BJ, Boyle B et al. 2014. Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences, USA* 111: 13745–13750.

Laughlin DC, Leppert JJ, Moore MM, Sieg CH. 2010. A multi-trait test of the leaf–height–seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* 24: 493–501.

Mackey RL, Currie DJ. 2001. The diversity–disturbance relationship: is it generally strong and peaked? *Ecology* 82: 3479–3492.

Meiners SJ, Cadenasso ML, Pickett STA, Morin P. 2015. *An integrative approach to successional dynamics*. Cambridge, UK: Cambridge University Press.

Mogie M, Hutchings MJ. 1990. Phylogeny, ontogeny and clonal growth in vascular plants. In: van Groenendael J, de Kroon H, eds. *Clonal growth in plants: regulation and function*. The Hague, the Netherlands: SPB Academic Publishing, 3–22.

Moles AT, Ackerly DD, Tweddle JC, Dickie JB, Smith R, Leishman MR, Mayfield MM, Pitman A, Wood JT, Westoby M. 2007. Global patterns in seed size. *Global Ecology and Biogeography* 16: 109–116.

Moles AT, Perkins SE, Laffan SW, Flores-Moreno H, Awasthy M, Tindall ML, Sack L, Pitman A, Kattge J, Aarssen LW et al. 2014. Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* 25: 1167–1180.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* 62: 365–392.

Schenk HJ, Jackson RB. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90: 480–494.

Thompson K, Rabinowitz D. 1989. Do big plants have big seeds? *American Naturalist* 133: 722–728.

VanderWeide BL, Hartnett DC. 2015. Belowground bud bank response to grazing under severe, short-term drought. *Oecologia* **178**: 795–806.

Verdu M. 2002. Age at maturity and diversification in woody angiosperms. *Evolution* **56**: 1352–1361.

Vesk PA. 2006. Plant size and resprouting ability: trading tolerance and avoidance of damage? *Journal of Ecology* **94**: 1027–1034.

Vesk PA, Warton DI, Westoby M. 2004. Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos* **107**: 72–89.

Westoby M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**: 213–227.

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**: 125–159.

Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* **21**: 261–268.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M et al. 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlinn DJ, O'Meara BC, Moles AT, Reich PB et al. 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* **514**: 394.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Pairwise plots of leaf–height–seed (LHS) traits and clonal traits.

Table S1 Bud bank and clonal growth traits used in the analyses

Table S2 Values of individual species traits, and their distribution in the EUNIS habitat types

Table S3 Pearson correlation coefficients of leaf–height–seed (LHS) traits and clonal traits

Methods S1 Data sources and data analysis.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.