The functional trait spectrum of European temperate grasslands

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Citation

Ladouceur, E., Bonomi, C., Bruelheide, H., Klimesova, J., Burrascano, S., Poschlod, P., ... Jimenez-Alfaro, B. (2019). The functional trait spectrum of European temperate grasslands. *Journal Of Vegetation Science*, *30*(5), 777-788. doi:10.1111/jvs.12784

Ladouceur E., Bonomi C., Bruelheide H., Klimešová J., Burrascano S., Poschlod P., Tudela-Isanta M., Iannetta P., Mondoni A., Amiaud B., Cerabolini B.E.L., Cornelissen J.H., Craine J., Louault F., Minden V., Öllerer K., Onipchenko V., Soudzilovskaia N.A., Jiménez-Alfaro B. 2019. The functional trait spectrum of European temperate grasslands. Journal of Vegetation Science 30: 777-788. https://doi.org/10.1111/jvs.12784

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Printed Journal page estimate: 5822 words (7.2 pages), Figures 3 pages, Tables 1.5 pages, Data sources 3288 words (1 table & second references list, 3.8 pages).

Keywords: clonality, functional traits, germination, grasslands, regeneration niche, seed traits, specialist species, species pool, trait spectrum

Nomenclature: The Plant List (http://www.theplantlist.org/, accessed on 22 June, 2015).

Funding Statement: EL, BJA, MTI, AM, PI and CB acknowledge the research leading to these results has received funding from the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme FP7/2007-2013/ under REA grant agreement n°607785- as a part of the NAtive Seed Science TEchnology and Conservation (NASSTEC) Initial Training Network (ITN). BJA was further funded by the Marie Curie Clarín-COFUND program of the Principality of Asturias and the European Union (ACB17-26). BJA, and HB acknowledge support from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (DFTG FZT 118) through the sPlot research platform. PI acknowledges support from the Rural & Environment Science & Analytical Services Division of the Scottish Government. KÖ thanks RO1567-IBB03/2018 for financial support.

eTOC: In specialist species of alpine grassland habitat types of continental Europe, non-regeneration traits seem to be filtered across habitat gradients, and most regeneration traits demonstrate multiple strategies within each habitat type, indicating possible variable trait strategies with trait groups associated with different processes.

Abstract

Questions: What is the functional trait variation of European temperate grasslands and how does this reflect global patterns of plant form and function? Do habitat specialists show trait differentiation across habitat types?

Location: Europe.

Methods: We compiled 18 regeneration and non-regeneration traits for a continental species pool consisting of 645 species frequent in five grassland types. These grassland types are widely distributed in Europe but differentiated by altitude, soil bedrock and traditional long-term management and disturbance regimes. We evaluated the multivariate trait space of this entire species pool and compared multi-trait variation and mean trait values of habitat specialists grouped by grassland type.

Results: The first dimension of the trait space accounted for 23% of variation and reflected a gradient between fast-growing and slow-growing plants. Plant height and SLA contributed to both the first and second ordination axes. Regeneration traits mainly contributed to the second and following dimensions to explain 56% of variation across the first five axes. Habitat specialists showed functional differences between grassland types mainly through non-regeneration traits.

Conclusions: The trait spectrum of plants dominating European temperate grasslands is primarily explained by growth strategies which are analogous to the trait variation observed at the global scale, and secondly by regeneration strategies. Functional differentiation of habitat specialists across grassland types is mainly related to environmental filtering linked with altitude and disturbance. This filtering pattern is mainly observed in non-regeneration traits, while most regeneration traits demonstrate multiple strategies within the same habitat type.

INTRODUCTION

At the global scale, the variation in plant functional traits in multidimensional trait-space is determined by two axes related to plant size and leaf area (Diaz et al. 2016). These two dimensions are mainly linked with ecological trade-offs on a uniformly fast, medium, or slow growth strategy gradient (Reich 2014; Salguero-Gómez et al. 2016); and along a leaf construction economics spectrum (Wright, Reich, Westoby, Ackerly & Baruch 2004). The multidimensional trait perspective helps to understand evolutionary constraints of functional diversity for plant species, but linking this trait variation with ecological drivers is still needed (Bruelheide et al. 2018). Functional plant strategies can be explained by traits filtered in biogeographic regions and in local ecological communities as a response to historical and environmental conditions (de Bello et al. 2006; de Bello et al. 2012; Poschlod et al. 2013). However, linking local filtering with regional and continental processes remains a major challenge (Pärtel et al. 2016), and new approaches in functional-trait ecology are needed to better understand these patterns and processes in plant community ecology.

Within different historical and environmental contexts, some species are more influenced by ecological filters than others, resulting in some level of species sorting in different habitats (Leibold & Chase 2018). While some species may be restricted to one habitat as specialists (Fridley et al. 2007), other species can plastically respond to different environmental conditions (Vellend 2016) and occur commonly across environmental gradients as generalists. The presence of generalists in local communities weakens the importance of environmental filtering within habitat types, and the predictability of environment-trait relationships in favour of non-niche processes such-as dispersal limitation (Fridley et al. 2007). In contrast, plant specialists consistently associated with local environmental conditions are expected to present specific traits that make these species a strong competitor in a given habitat. Studying the trait variation of plant specialists may therefore help to detect environmental filtering within the species pool, or the species which can potentially occur at a site (Pärtel et al. 2011). Identification of functional species pools is a pre-requisite to differentiate functional patterns produced by abiotic filters (de Bello et al. 2012), and separating specialists from generalists within species pools could perhaps strengthen this approach.

Plant species may be particularly sensitive to environmental filtering at the regeneration stage and this might be more important than other life-history stages as species could be totally excluded from a habitat due to inappropriate environmental conditions for germination or successful establishment (Grub 1977). However, our knowledge of plant trait ecology is largely focused on few traits concerning aboveground vegetative growth and morphology, and very few studies have assessed the potential role of regeneration traits (Poschlod et al. 2013; Jiménez-Alfaro et al. 2016; Larson & Funk 2016; Saatkamp et al. 2018). Regeneration traits have been long acknowledged as relevant to the natural maintenance of biodiversity (Grubb 1977), and have been found to be important for both species coexistence and species sorting (Bernard-Verdier et al. 2012; Pierce et al. 2014; Fernández-Pascual et al. 2017). Processes captured by regeneration traits including flowering, seed production, clonal growth, dispersal, germination, and growth rates are relevant to community assembly, species turnover, survival and persistence (Pohl et al. 2011; Poschlod et al. 2013; Klimešová et al. 2016). When combined with non-regeneration traits, regeneration traits might add new dimensions to the plant trait spectrum (Laughlin 2013; Pierce et al. 2014; Salguero-Gómez et al. 2016; Herben et al. 2016), providing a better understanding of the role of environmental filtering in plant communities and on different types of traits.

Here, we study the functional trait variation of a species pool representative of European temperate grasslands. Our case study consists of the most frequent and dominant species occurring in widely distributed grasslands types, with similar growth and life forms but differing in species composition and environmental conditions along gradients of altitude and traditional long-term disturbance regimes (Ellenberg 2009; Körner 2003; Nagy et al. 2003; Dainese et al. 2012). By combining non-regeneration traits and less commonly studied regeneration traits, our first aim was to describe the trait spectrum of the species pool of European temperate grasslands, and to test whether this spectrum reflects the main dimensions observed at the global scale. Our second aim was to test whether habitat specialists of each grassland type show trait differentiation that might explain environmental filtering. Despite the marked dominance of few life- and growth- forms in European grasslands, we expect habitat specialists to exhibit trait combinations that may allow us to functionally characterize vegetation types, possibly with more subtle detail than at a global scale across disparate biomes.

METHODS

Species data

We focused on five grassland types representing wide ecological variation in altitude, soil and disturbance (Table 1) as described in the classification of European habitats (Galvanek & Janak 2008; Garcia-Gonzalez 2008; Calaciura & Spinelli 2008; European Environment Agency 2012). We obtained the species list of constituent species from a continental review (Schaminée et al. 2016) based on the European Vegetation Archive (Chytrý et al. 2015) and over 1 million field surveys to report species frequencies in these European habitat types. We removed rare species with <5% frequency of occurrence in each grassland type at the continental scale. We identified as specialists those species with a significantly ($P < 0.05$) higher frequency of occurrence in one grassland type than any other using a Fisher's exact test (Agresti 2002). Most of these specialists are generally described as characteristic or dominant species of the study grassland types in Europe (see habitat descriptions and references in Table 1). All other species were labelled as generalists. We note that our definition of specialists applies exclusively to the five grassland types compared here, assuming the association of species with one grassland type is mainly due to ecological preferences.

Traits selection and data collection

The majority of trait data was compiled from existing datasets contributed to the TRY Plant Trait Database (see Data Use and Table 2) (Kattge et al. 2011). A request to TRY for relevant datasets returned 8,655,033 records and 96,493 unique species names across 95 trait categories in 104 datasets. Taxonomic synonyms were made consistent using the Plant List Project (Missouri Botanical Gardens & Royal Botanic Gardens Kew 2013). Traits were selected to represent different aspects of plant organs or whole plant properties and their functional significance and life history (Laughlin 2013; Jiménez-

Alfaro et al. 2016). Data were then extracted by matching accepted plant names and known synonyms from the target species list into subsets. Eleven traits were used from TRY, across 47 TRY datasets, and 10 from other sources (Table 2), selected from a larger list of traits of interest. A trait was used as long as there were at least three data points for each grassland type. Trait units of measurement were standardised across datasets, and where multiple values existed, we used the mean of all individual traits of each species. While this approach does not account for intraspecific trait variation, it is expected that the influence of this variation takes place mostly within each grassland type, representing less than 20% of total variation (Siefert et al. 2015).

Data Analysis

All statistical analyses and plotting were conducted using the R Studio language and environment for statistical computing and graphics (version 3.4.0). Each R package used is referenced as each approach is explained.

We used a Principal Component Analysis (PCA) to describe the multivariate trait spectrum and to identify the contribution of individual traits. We used the R package missMDA (Husson & Josse 2018) to replace missing values in the numerical traits for the PCA and to estimate parameters based on existing values within the dataset (Josse & Husson 2012; Josse & Husson 2016). Out of 9,002 (643 rows of numerical trait data x 14 columns) possible records in the PCA, 48.5% of data was missing and replaced with predicted values from the observed data. Categorical traits were excluded from the multivariate analysis. Missing data was unevenly distributed across traits, with less-commonly studied regeneration traits missing more data than others, but averages between non-regeneration and regeneration traits overall were the same, and all traits were considered regardless (Data Quality, Table S1). The implication of this gap-filling method is that the variance in the estimators is underestimated (Josse & Husson 2012; Josse & Husson 2016). The gap-filled data was then log transformed as data were not normally distributed. The loadings of each trait and the scores of each species were extracted for the first five axes. Results were plotted using ggplot2 (Wickham 2009), FactoMineR (Husson, Josse & Mazet 2018), and factoextra (Kassambara & Mundt 2017). The collinearity of traits in the PCA was evaluated in a correlation matrix using the package corrplot (Wei & Simko 2017).

We examined the distribution of specialists and generalists in the trait space by plotting the PCA scores of both species groups for each grassland type. The PCA results were used to compare the trait space of different grassland types, plotted using packages ade4 (Dray, Dufour & Thioulouse 2018) and adegraphics (Dray & Siberchiot 2018). Differences in PCA scores between grassland types were tested with a permutational analysis of variance (PERMANOVA) using vegan (Oksansen et al. 2018) and with a post-hoc pairwise PERMANOVA statistical tests using RVAideMemoire (Hervé 2018). Both tests were based on 999 permutations. To identify the traits that best separated the different grassland types, we employed discriminant analysis using the gap-filled data. A stepwise forward variable model selection was performed based on Wilk's Lambda criterion using the packages klaR (Roever 2018), and mda (Hastie et al. 2017), which minimizes within-class distances and contextually maximises class discrimination (Bianco et al. 2016).

We tested for differences in mean trait values among grassland types using a post-hoc pairwise Kruskal-Wallis χ^2 test from the package PMCMR (Pohlert 2018). Raw data were plotted for single traits, with no gap-filling or transformation taking place. Categorical traits were plotted in the package ggplot2 (Wickham 2018). The numerical traits and individually plotted PCA axis coordinates were visualized as RDI plots (Raw data, descriptive and inference statistics) created using the package yarrr (Phillips 2017), to effectively visualise the breadth of each trait within categories, as well as for visual comparison between them. This allowed for individual investigation of trait patterns found in the multivariate space without gap-filling.

RESULTS

We compiled a list of 645 species in total (excluding 44 species with missing data), including 257 generalists and 388 specialists, 52 taxonomic families and 244 genera (Table S1, Supporting Information). Overall, we identified 56 specialists in meadows, 75 in dry grasslands, 77 in *Nardus*-dominated grasslands, 133 in calcareous alpine grasslands, and 47 in acidic alpine grasslands for which there was available trait data (Table S1). Both the specialists and generalists represent > 83% of the species detected in the study habitats and in the context of this study we refer to them as the continental species pool.

Multivariate trait spectrum

The first, second and third axis of the PCA based on 14 numerical traits explained 23%, 9.2 % and 9.1% of the total variance, respectively (Fig. 1). All non-regeneration traits, including radial growth rate, SLA and plant height had relatively high loadings on the first axis of the PCA (Fig. 1a, Table 3). The regeneration traits with the highest contribution with the first axis were T_{max}, soil seed bank longevity, flowering duration and flowering onset. Plant height and SLA also contributed to the second axis, together with flowering onset, seed mass, seed number per ramet, and flowering duration (Fig. 1a, b, Table 3, Table S2). On the third axis, regeneration traits (T_o, seed mass, clonal index, flowering onset and T_{min}) contributed the most variation (Fig. 1 b, Table 3).

Most of the traits (85%) were significantly correlated among each other (Table S4). The strongest correlations were between flowering onset and flowering duration (Pearson r = -0.463); between T_{max} and duration of seed bank longevity (0.358); and between plant height and seed number (0.345). T_o was negatively correlated with plant height and seed number per ramet T_{min}, clonal shoot cyclicity and flowering onset were negatively correlated with all traits except T_o, seed mass and each other. Seed mass was negatively correlated with seed number per ramet and clonal index, and positively correlated with all other traits except T_o. The other traits had positive correlations.

Trait variation of habitat specialists

The groups of habitat specialists were differentiated among each other in the trait space (PERMANOVA F=13.43, R2=0.095, P=<0.001, Fig. 2 a, Table S6b,c). Main differences between habitats were related to the first axis of variation (Fig. S1 b, Kruskal-Wallis s^2= 127.4, P= <0.001, Table S5). On axis 2, only acidic alpine grasslands were differentiated from *Nardus*-dominated grasslands (Fig. S1 b, s^2= 12.029, P= 0.03, Table S5). The variability between group means (F-value) was larger for regeneration (F= 13.77, R2 0.098, P=<0.001, Table S6f) than for non-regeneration traits (F= 10.071, R2= 0.073, P=<0.001, Table S6e). The most important traits in differentiating specialist groups according to the discriminant analyses were plant height, flowering duration, seed bank longevity, SLA, and flowering onset (Table 3,I; Table S7; Fig. S2). There was an overall misclassification error of 51%, which was mainly brought about by a strong overlap in predictions for *Nardus*-dominated grasslands with calcareous and acidic alpine grasslands (Table S8a). Predictions were similar when non-regeneration traits were analysed separately, better characterising certain grassland specialists, while other specialists were better characterised by regeneration traits (Table S8bc). However, the discriminative power was more accurate when all traits were used together, rather than separately (Table S8).

Acidic alpine grasslands had the lowest SLA (Kruskal-Wallis s^2= 73.28, P= <0.001, Table S1), shortest plant height (s^2= 95.59, P= <0.001, Table S10), and a slow radial growth rate (s^2= 28.56, P= <0.001, Table S10) with a late (s^2= 51.38, P= <0.001, Table S10) and short flowering duration (s^2= 74.87, P= <0.001, Table S10) (Fig. 3, Fig. 4). *Sempervivum arachnoideum,* with its far-reaching runners was the only acidic alpine specialist with a high clonal spread rate. Human assisted dispersal was proportionally less present in calcareous alpine and acidic alpine grassland specialists than in other grassland types (Fig. S3 d). The traits of *Nardus*-dominated grassland specialists were similar to alpine specialists in terms of their non-regeneration traits, i.e. short height, low SLA and slow radial growth. They start flowering at a similar time to acidic, calcareous alpine, dry grasslands and generalists, but flowering for a similarly short length as both alpine grassland types, and much shorter time than dry grassland specialists (Table S9, P=0.01).

Nardus grassland specialists had the smallest seed mass by a large margin (s^2= 28.30, P= <0.001, Table S10); a soil seed bank characterised by short-term persistent seeds (Table 2); and a high T_{min}, but only differentiated from the very low T_{min} of meadows (P=0.03, Table S11). There was higher proportion of seed shedding in late summer in *Nardus*-dominated (70%), calcareous alpine (79%) acidic alpine grasslands

(79%) (Fig. S3 c), which was consistent with the marginally narrower window of germination temperatures available to specialists of these grassland types (Fig. 4 g-i). Finally, both meadows and dry grasslands had the highest SLA, tallest plants, the fastest radial growth rates, and the earliest flowering onset and longest flowering duration compared to the other three, high-altitude habitats. Meadows also had a faster clonal lateral spread rate than calcareous alpine specialists (s^2= 13.53, P= 0.018, Table S11). Specialists of dry grasslands had a notably larger presence of physical dormancy (PY) (24%, Fig. S3 a) than other habitat types.

DISCUSSION

The trait spectrum of European temperate grasslands

The main trait dimension of the temperate grasslands analyzed in this study is similar to the 'fast-slow' continuum described globally (Reich 2014; Salguero-Gómez et al. 2016) and to the latitude-driven first dimension of the global spectrum of vascular plants (Westoby 1998; Diaz et al. 2016). The main gradient between fast-growing plants with high regeneration rates (on the right side of the PCA) and slow-growing plants with shorter flowering duration (on the left side) is likely driven by ecological differences in seasonal length and climate along the altitudinal range in which these species occur. We further found that regeneration traits including annual radial growth rate, clonal lateral spread, T_{max}, and seed bank longevity also contribute to the fast-slow strategy.

The second axis of trait variation of European temperate grasslands suggests a leaf economic spectrum driven by environmental gradients, which is mainly explained by the contribution of SLA. Plant height, flowering onset and seed mass also contributed largely to the second axis, while on the third, fourth and fifth axes major contributions were related to regeneration traits such as T_o, T_{min}, flowering duration, clonal shoot cyclicity, clonal index, clonal spread, and seed number. Similarly, Pierce et al. (2014) found that reproduction traits affect plant survival independently from primary strategies, while Salguero-Gómez (2016) found that regeneration traits, such as degree of iteroparity and net reproductive rate, were perpendicular to the leaf economics spectrum. Other studies found weak correlation or even a lack of correlation between seed and clonal traits across a whole flora (Herben et al. 2012; Herben et al. 2016). Our results therefore suggest that reducing the species pool to a unique formation (temperate grasslands) removes functional variation of distinct habitat types (such as forests, wetlands, etc.) that may confound the interpretation of habitat-specific trait dimensions. In addition, the use of traits representing different life-stage processes (regeneration and non-regeneration traits) provides a more comprehensive explanation of the observed functional patterns.

Trait differences between habitat specialists

Our results support the idea that environmental filtering and disturbance governs the functional composition of plant specialists related to temperate grassland types in Europe. Specialists of low-altitude disturbed and managed habitats are characterised by 'fast' traits such as greater height, SLA, longer flowering duration and increased radial growth rate. In contrast, the 'slow' traits stand out in specialists of harsh alpine habitats with less disturbance. The combination of all available traits discriminated grassland types better than considering non-regeneration or regeneration traits separately, supporting the multidimensional nature of plant traits for understanding environmental relationships (Laughlin 2013). Nevertheless, we found weak functional differentiation between the high-altitude acidic and calcareous alpine grasslands, despite having distinct differences in soil conditions and species composition. Trait-based differences between these habitats have been found in germination traits related specifically to pH and water availability that require more experimental data (Tudela-Isanta et al. 2017) than is currently available for this entire species pool. Despite the comprehensive set of traits used in this study, the lack of more specific traits, reflecting e.g. physiological species responses, makes it possible to differentiate up to three major functional groups: (i) high-altitude grasslands (both acidic and calcareous grasslands); (ii) low-altitude grasslands from disturbed habitats (dry grasslands and meadows); and (iii) mid-altitude *Nardus*-dominated grasslands (differentiated from (i) or (ii) depending on which trait is being examined).

The explanatory power of traits for differentiating habitat types was mainly related to non-regeneration traits and flowering, which are in general more under-dispersed than would be expected randomly within each habitat, suggesting environmental filtering may be taking place on these traits. The regeneration traits of specialists showed more over-dispersion than expected randomly, varying more within than among grassland types, supporting the idea that a multitude of regeneration niches may coexist within the same grassland type (Grubb 1977). This suggests that regeneration traits may have a different ecological role than non-regeneration traits, such as the competitive niches of species, or coexistence mechanisms (Mayfield & Levine 2010; HilleRisLambers et al. 2012). However, we found differentiation of soil seedbank longevity across habitats, which is likely influenced by traditional long-term-management practices such as regular mowing or grazing in meadows (Bekker et al. 1998; Fenner & Thompson 2005). In addition, human dispersed seeds are less represented among alpine grassland specialists, demonstrating the importance of traditional management for seed dispersal (Poschlod et al. 1998; Auffret 2011) and the possible complementary effect of long-term disturbance regimes for understanding functional differentiation in these habitats (Louault et al. 2005; Kahmen & Poschlod 2008). Our results also suggest that clonal traits could be affected by abiotic and biotic filters such as disturbance and soil, which perhaps are clearer in wider gradients than explored here (Fujita et al. 2013), so the extent of environmental filtering at different scales and gradients on these traits (Klimešová et al. 2013; Klimešová & Herben 2014) is worth investigating further.

CONCLUSION

This study is, to our knowledge, the first attempt to investigate the trait variation of a continental species pool within a particular vegetation type. We found that the trait spectrum of European temperate grasslands is related to the main trade-offs observed at the global scale. However, our analyses also reveal new contributions of traits with a functional role in our study system, details that might be lost when analyzing the functional variation across distinct vegetation types. Since temperate grasslands are by definition dominated by grasses and forbs, the analysis of functional variation within this relatively homogeneous system allows us to focus on patterns and drivers linked with the specific differentiation of grassland types. Non-regeneration traits related to plant growth were mainly related to environmental gradients and disturbance across grasslands, while regeneration traits demonstrated a multitude of regeneration strategies existing within grassland types. We conclude that functional characterization of habitat specialists within species pools may be a promising approach for understanding the role of environmental filtering on trait-based ecology and vegetation diversity across large scales. However, this approach is also limited by the quality of plant traits available. Besides the integration of regeneration and non-regeneration traits, future research will need to explore traits with a stronger physiological impact on species ecological responses.

Author Contributions

BJA conceived the idea. EL, CB and BJA designed the methodology, and arranged acquisition of data. BA, SB, BC, JHC, JC, JK, FL, VM, AM, KÖ, VO, PP, NS, MTI, donated substantial amounts of data. EL lead data analysis and writing of the manuscript. BJA, HB, JK, SB, PP, MTI, PI, AM and CB contributed critical feedback to data interpretation and initial drafting of the manuscript. All authors made intellectual contributions and provided essential feedback. The first nine authors, and last author are ordered by their relative contribution, the others are ordered alphabetically.

Acknowledgements

EL, BJA, MTI, AM, PI and CB acknowledge the research leading to these results has received funding from the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme FP7/2007-2013/ under REA grant agreement n°607785- as a part of the NAtive Seed Science TEchnology and Conservation (NASSTEC) Initial Training Network (ITN). BJA was further funded by the Marie Curie Clarín-COFUND program of the Principality of Asturias and the European Union (ACB17-26). BJA, and HB acknowledge support from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (DFTG FZT 118) through the sPlot research platform. PI acknowledges support from the Rural & Environment Science & Analytical Services Division of the Scottish Government. KÖ thanks RO1567-IBB03/2018 for financial support.

Data Accessibility

Most data were collected from donated existing databases within the TRY Global Plant Trait Database (Table 2, & Supporting Information Appendix S2). Mean values of all trait data are detailed in Supporting Information Appendix S3 Table S1. Each individual dataset which was used to calculate the mean value of each trait is referenced individually in the extended version of Table 2, in Supporting Information Appendix S2.

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Supporting Information

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

https://onlinelibrary.wiley.com/doi/abs/10.1111/jvs.12784

Table 1: Description of the five grassland types investigated. Altitude shows estimated ranges above the sea level. Number of specialist species describes the total number of specialists identified for each grassland type. EUNIS and ANNEX I habitats and their management practices according to www.eunis.eea.europa.eu/habitats. Soil pH and moisture values are derived from the Ellenberg indicator values of each species (Fitter & Peat 1994; Sanda et al. 2003; Ciocârlan 2009; Moretti & Legg 2009; Ellenberg 2010; Hill et al.; Kattge; Öllerer), expressed as the mean of those specialists (Table 2). VPL= vegetation period length (Aeschimann et al. 2004). Data sources listed in Appendix S2.

Grassland type	Altitude	# of specialist species	European Nature Information System (EUNIS) habitat classification	ANNEX I habitats of EU Habitat Directive	Traditional management practice	Soil pH	Soil moisture	VPL
Meadows	0-1000m	57	E2.2 Low & Medium altitude meadow E2.3 Mountain hay meadows	Lowland Hay Meadows 6510 + High Altitude Hay Meadows 6520	Mowing, (Grazing)	6.9 (neutral)	4.78	March-October (8 months)
Dry Grasslands	500-1400m	77	E1.2 Perennial calcareous grassland and basic steppes	Semi-natural Dry Grasslands (Festuco-Brometalia) 6210	Mowing & Grazing	7.3 (calcareous)	3.2	March-October (8 months)
Nardus-dominated	1400-1800m	81	e1.7 Closed non-Mediterranean dry acid & neutral grassland	Mountain acid grassland Species Rich Nardus Grasslands 6230	Grazing	4.39 (acidic)	5.8	May-September (5 months)
Calcareous Alpine	1800-2700m	149	E4.4 Calcareous alpine and subalpine grassland	Alpine & subalpine calcareous grasslands 6170	None	7.7 (calcareous)	4.68	June-August (3 months)
Acidic Alpine	>2700m	52	4.3 Acid alpine and subalpine grassland	Acidic Alpine grasslands 6150	None	2.3 (acidic)	4.5	June-August (3 months)

Table 2: Loadings of the plant trait values for the first three axes of the PCA for: all traits and all species. Bold numbers indicate the top three (3)- five (5) highest loadings on each axis.

a) All Traits	i) All species (Main Analysis)				
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Variance Explained	23.1	9.15	9.08	7.84	6.83
Eigenvalue	3.23	1.28	1.27	1.1	0.96
SLA	**0.29**	**-0.30**	0.05	0.07	0.06
Plant height	0.27	**0.49**	0.09	0.19	0.25
Radial growth rate	**0.30**	-0.04	0.07	0.1	-0.07
Flowering onset	**-0.29**	**0.36**	**0.33**	0.05	-0.06
Flowering duration	**0.31**	**-0.32**	-0.24	**-0.27**	0.25
Clonal spread	0.28	0.18	0.26	-0.19	**-0.40**
Clonal index	0.26	-0.07	**0.38**	-0.19	**-0.46**
Clonal cyclicity	-0.25	0.1	0.22	**-0.37**	0.08
Seed mass	0.16	**0.34**	**-0.4**	0.5	-0.2
Seed # /ramet	0.24	**0.34**	0.27	-0.17	**0.51**
Soil seed bank longevity	**0.33**	-0.04	0.08	-0.01	0.11
T_{min}	-0.18	-0.23	**0.33**	**0.41**	-0.15
T_o	-0.05	**-0.3**	**0.43**	**0.43**	**0.37**
T_{max}	**0.37**	-0.04	0.13	0.18	-0.12

Figures

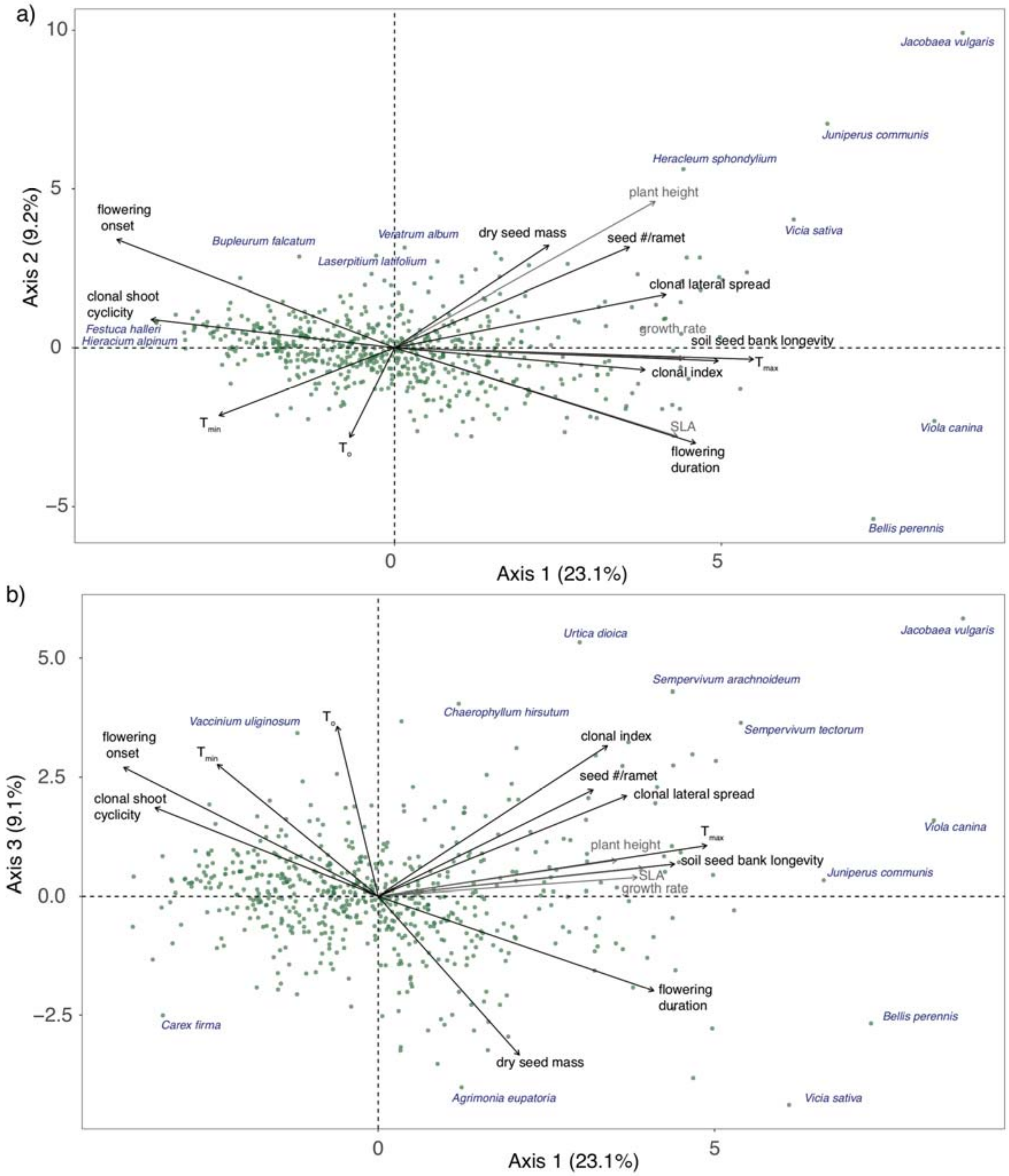


Figure 1: Trait space of the functional species pool of European temperate grasslands. Sample scores representing 645 plant species in a Principal Component Analysis (PCA) based on numerical plant traits and a correlation matrix. Each point represents a species, arrows represent the visualisation of the contributing variables (See Table 2 for trait abbreviations). Grey arrows/labels represent non-regeneration traits and black arrows/labels regeneration traits. The five species that contribute the most variation to each axis are labelled in blue and detailed in Table S3. Percentages for the three main axes represent the explained variance.

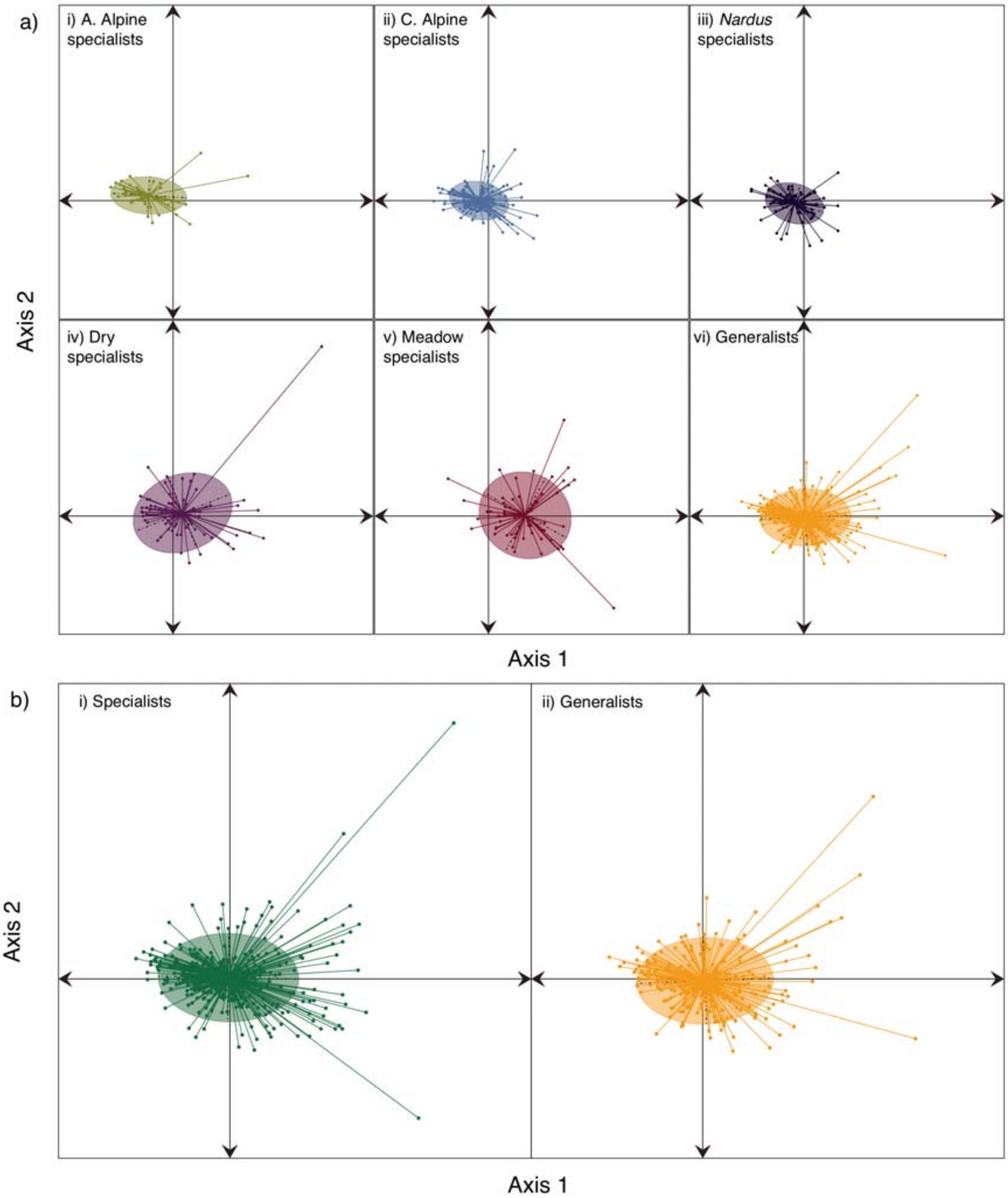


Figure 2: Trait space of habitat specialists grouped in five grassland types and generalists. Sample scores representing 645 plant species in a Principal Component Analysis (PCA) for axis 1 & 2 based on numerical plant traits and a correlation matrix. Each point represents a species, and each line shows its distance from the centre point of the data for each species group. a) Colored ellipses representing species belonging to each specialist group are separated by facets, detailed in the key; b) pooled specialists vs. generalists (See Table 1 for grassland type abbreviations). Degrees of freedom=5.

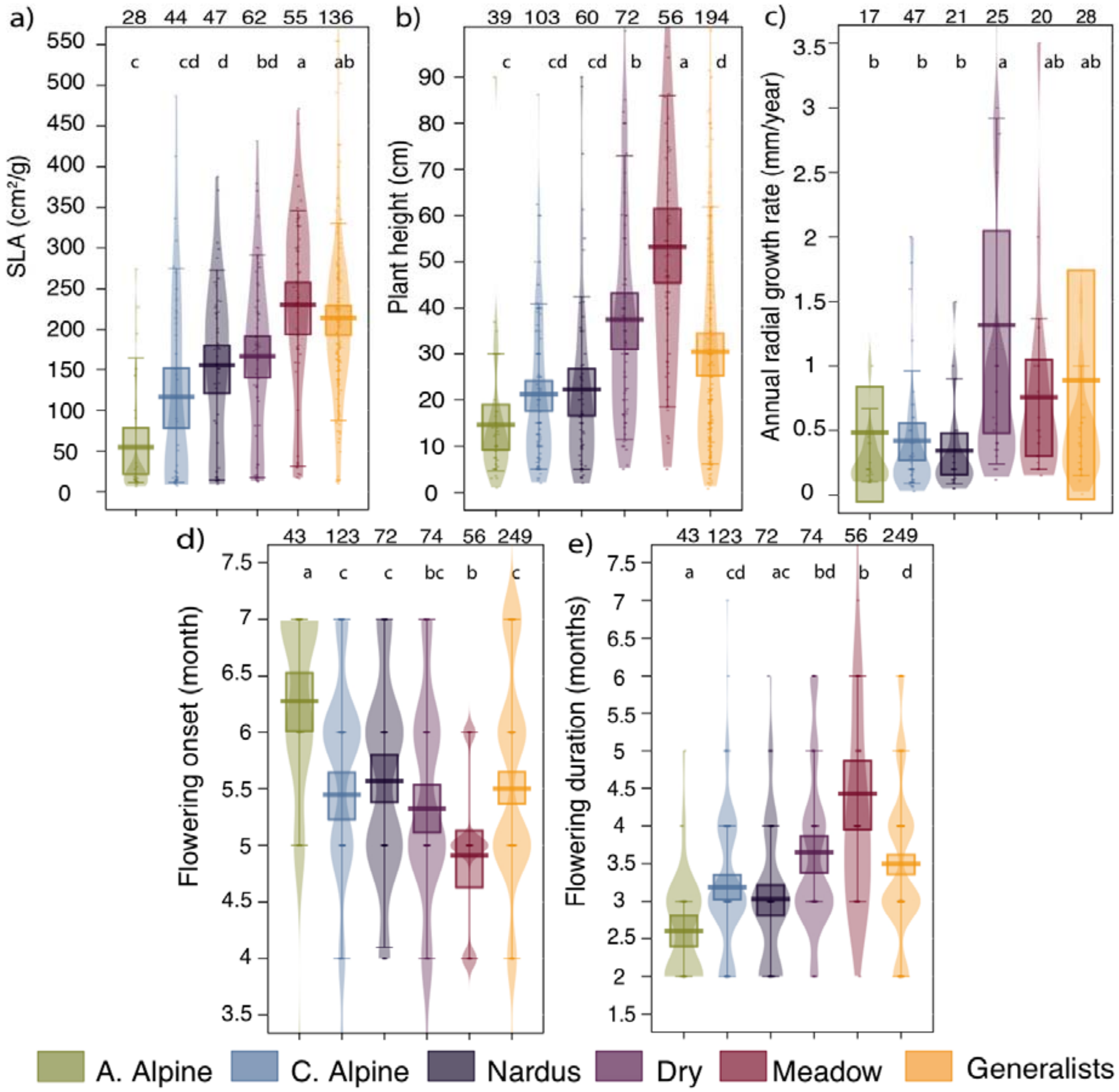
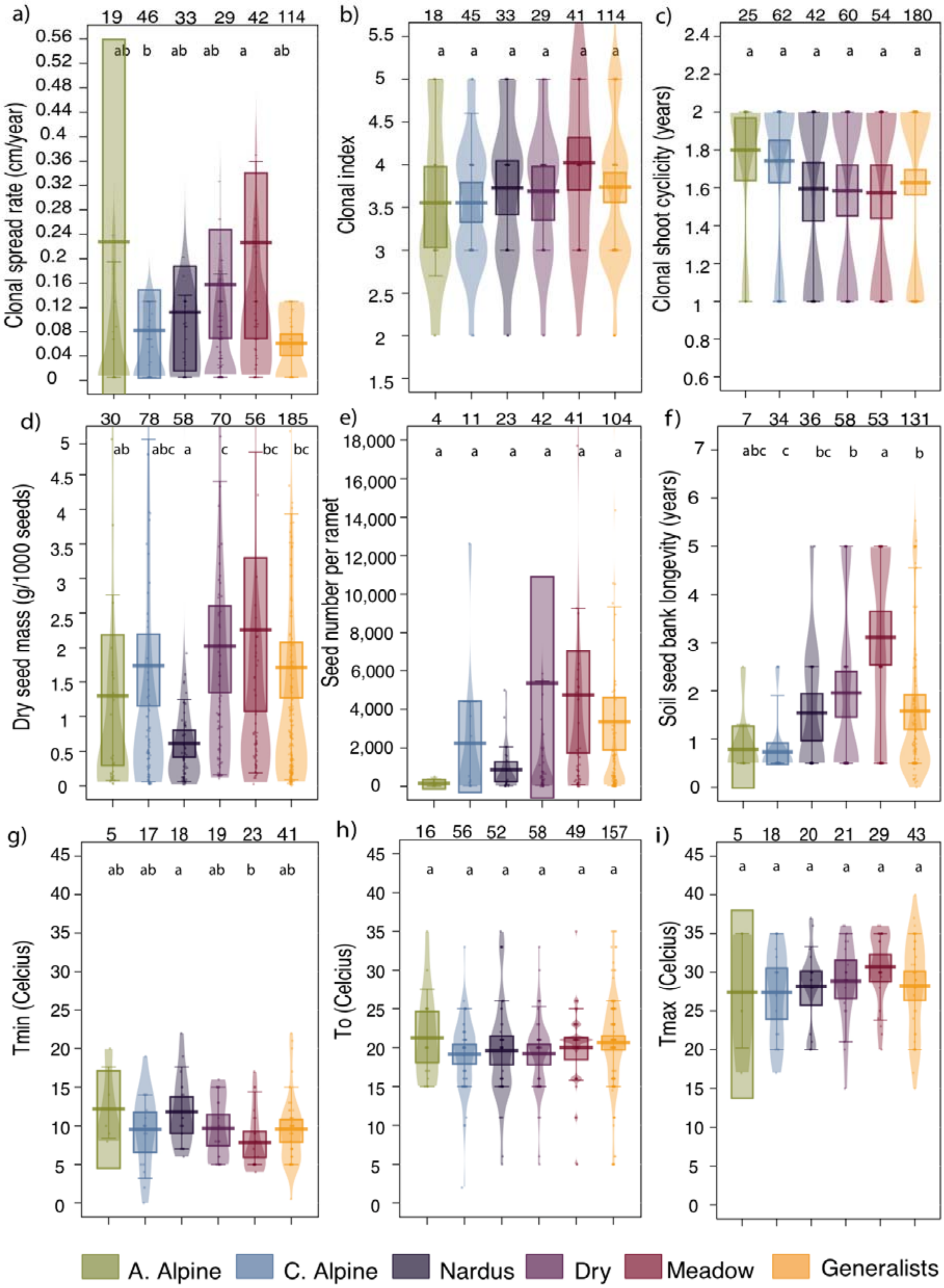


Figure 3: Non-regeneration traits across habitats. a) SLA, b) plant height, c) annual radial growth rate, d) flowering onset, e) flowering duration. RDI plots (Raw data, Descriptive and Inference statistics) show jittered points of raw data, centre bars indicate the mean of the data, beans outline the smoothed density of the data, whiskers mark the 10% and 90% quartiles of the data, and inference bands show the Bayesian 95% High Density Interval inferential statistics for each group. Numbers at the top of each group indicates the number of data points for each trait, and letters show statistical differences between groups.


a)
19 46 33 29 42 114
ab b ab ab a ab
Clonal spread rate (cm/year)
0.56
0.52
0.48
0.44
0.4
0.36
0.32
0.28
0.24
0.2
0.16
0.12
0.08
0.04
0
b)
18 45 33 29 41 114
a a a a a a
Clonal index
5.5
5
4.5
4
3.5
3
2.5
2
1.5
c)
25 62 42 60 54 180
a a a a a a
Clonal shoot cyclicity (years)
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
d)
30 78 58 70 56 185
ab abc a c bc bc
Dry seed mass (g/1000 seeds)
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
e)
4 11 23 42 41 104
a a a a a a
Seed number per ramet
18,000
16,000
14,000
12,000
10,000
8,000
6,000
4,000
2,000
0
f)
7 34 36 58 53 131
abc c bc b a b
Soil seed bank longevity (years)
7
6
5
4
3
2
1
0
g)
5 17 18 19 23 41
ab ab a ab b ab
Tmin (Celcius)
45
40
35
30
25
20
15
10
5
0
h)
16 56 52 58 49 157
a a a a a a
To (Celcius)
45
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5 18 20 21 29 43
a a a a a a
Tmax (Celcius)
45
40
35
30
25
20
15
10
5
0
A. Alpine
C. Alpine
Nardus
Dry
Meadow
Generalists

Figure 4: Regeneration traits across habitats. a) clonal lateral spread, b) clonal index (number of offspring + spread) and c) clonal shoot cyclicity, d) dry seed mass, e) seed number per ramet/plant, f) soil seed bank longevity, and seed germination traits g) minimum germination temperature, h) optimal germination temperature and i) maximum germination temperature. RDI plots as in Fig.3.