





# The functional trait spectrum of European temperate grasslands

Emma Ladouceur<sup>1,2,3</sup>  | Costantino Bonomi<sup>2</sup> | Helge Bruelheide<sup>1,4</sup>  |  
 Jitka Klimešová<sup>5</sup> | Sabina Burrascano<sup>6</sup>  | Peter Poschlod<sup>7</sup> | Maria Tudela-Isanta<sup>3</sup> |  
 Pietro Iannetta<sup>8</sup> | Andrea Mondoni<sup>3</sup> | Bernard Amiaud<sup>9†</sup> | Bruno E. L. Cerabolini<sup>10</sup> |  
 Johannes Hans C. Cornelissen<sup>11</sup> | Joseph Craine<sup>12</sup> | Frédérique Louault<sup>13</sup> |  
 Vanessa Minden<sup>14,15</sup> | Kinga Öllerer<sup>16,17</sup> | Vladimir Onipchenko<sup>18</sup> |  
 Nadejda A. Soudzilovskaia<sup>19</sup> | Borja Jiménez-Alfaro<sup>20</sup> 

<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

<sup>2</sup>Botany Department, Museo delle Scienze (MUSE), Trento, Italy

<sup>3</sup>Department of Earth and Environmental Sciences, University of Pavia, Pavia, Italy

<sup>4</sup>Geobotany and Botanical Garden, Institute of Biology, Martin Luther University, Halle-Wittenberg, Halle, Germany

<sup>5</sup>Institute of Botany, Academy of Sciences of the Czech Republic, Třeboň, Czech Republic

<sup>6</sup>Department of Environmental Biology, Sapienza University of Rome, Rome, Italy

<sup>7</sup>Department of Ecology and Conservation Biology, University of Regensburg, Regensburg, Germany

<sup>8</sup>Ecological Sciences, James Hutton Institute, Dundee, UK

<sup>9</sup>Department of Forest Ecology and Ecophysiology, UMR 1137, University of Lorraine-INRA, Lorraine, France

<sup>10</sup>Department of Theoretical and Applied Sciences, University of Insubria, Varese, Italy

<sup>11</sup>Department of Ecological Science, Faculty of Earth and Life Sciences, Vrije Universiteit, Amsterdam, The Netherlands

<sup>12</sup>Jonah Ventures, Boulder, CO, USA

<sup>13</sup>UCA, INRA, VetAgro Sup, UREP, Clermont-Ferrand, France

<sup>14</sup>Institute of Biology and Environmental Sciences, Carl von Ossietzky-University of Oldenburg, Oldenburg, Germany

<sup>15</sup>Department of Biology, Ecology and Biodiversity, Vrije Universiteit Brussel, Brussels, Belgium

<sup>16</sup>Institute of Biology Bucharest, Romanian Academy, Bucharest, Romania

<sup>17</sup>Institute of Ecology and Botany, MTA Centre for Ecological Research, Vácrátót, Hungary

<sup>18</sup>Faculty of Biology, Moscow State University, Moscow, Russia

<sup>19</sup>Department of Ecology and Environmental Sciences, Leiden University, Leiden, The Netherlands

<sup>20</sup>Research Unit of Biodiversity (CSIC/UO/PA), González Gutiérrez Quirós, Universidad de Oviedo, Mieres, Spain

## Correspondence

Emma Ladouceur, Biodiversity Synthesis,  
 German Centre for Integrative Biodiversity  
 Research (iDiv) Halle-Jena-Leipzig,  
 Deutscher Platz 5e, 04103 Leipzig, Germany.  
 Email: emma.ladouceur@div.de

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## 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

<sup>†</sup>Deceased



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.

#### KEYWORDS

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

## 1 | 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 (Díaz 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 et al., 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 (Bruehlheide 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, Lepš, & Sebastià, 2006; de Bello et al., 2012; Poschlod et al., 2013). However, linking local filtering with regional and continental processes remains a major challenge (Pärtel, Bennett, & Zobel, 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, Vandermaast, Kuppinger, Manthey, & Peet, 2007), other species can plastically respond to different environmental conditions (Velland, 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 that can potentially occur at a site (Pärtel, Szava-Kovats, & Zobel, 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 (Grubb, 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 (Jiménez-Alfaro, Silveira, Fidelis, Poschlod, & Commander, 2016; Larson & Funk, 2016; Poschlod et al., 2013; Saatkamp et al., 2019). 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; Fernández-Pascual, Pérez-Arcoiza, Prieto, & Díaz, 2017; Pierce, Bottinelli, Bassani, Ceriani, & Cerabolini,

**TABLE 1** Description of the five grassland types investigated

Grassland type	Altitude	No. 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	0–1,000 m	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	500–1,400 m	77	E1.2 Perennial calcareous grassland and basic steppes	Semi-natural dry grasslands ( <i>Festuco-Brometalia</i> ) 6210	Mowing & grazing	7.3 (calcareous)	3.2	March–October (8 months)
<i>Nardus</i> -dominated	1,400–1,800 m	81	e1.7 Closed non-mediterranean dry acid & neutral grassland	Mountain acid grassland Species-rich <i>Nardus</i> grasslands 6230	Grazing	4.39 (acidic)	5.8	May–September (5 months)
Calcareous alpine	1,800–2,700 m	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	>2,700 m	52	4.3 Acid alpine and subalpine grassland	Acidic alpine grasslands 6150	None	2.3 (acidic)	4.5	June–August (3 months)

Note: Altitude shows estimated ranges above 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](http://www.eunis.eea.europa.eu/habitats). Soil pH and moisture values are derived from the Ellenberg indicator values of each species (sourced from Ciocărian, 2009; Ellenberg, 2010; Fitter & Peat, 1994; Hill et al.; Kattge; Moretti & Legg, 2009; Öllner; Sanda et al., 2003), expressed as the mean of those specialists (Table S2). Data sources listed in Appendix S2. Abbreviation: VPL, vegetation period length (sourced from Aeschmann, Lauber, Martin Moser, & Theurillat, 2004).

2014). 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 (Klimešová, Tackenberg, & Herben, 2016; Pohl, Stroude, Buttler, & Rixen, 2011; Poschlod et al., 2013). When combined with non-regeneration traits, regeneration traits might add new dimensions to the plant trait spectrum (Herben, Tackenberg, & Klimešová, 2016; 2014; Pierce et al., 2014; Salguero-Gómez 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 (Dainese, Scotton, Clementel, Pecile, & Leps, 2012; Ellenberg, 2009; Körner, 2003; Nagy, Grabherr, Körner, & Thompson, 2003). 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.

## 2 | METHODS

### 2.1 | 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 (Calaciura & Spinelli, 2008; 2009; Galvanek & Janak, 2008; Garcia-Gonzalez, 2008). We obtained the species list of constituent species from a continental review (Schaminée et al., 2016) based on the European Vegetation Archive (2016) and over one million field surveys to report species frequencies in these European habitat types (Appendix S1). 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.



## 2.2 | Traits selection and data collection

The majority of trait data was compiled from existing datasets contributed to the TRY Plant Trait Database (see Data Accessibility and Table S2; 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 (Jiménez-Alfaro et al., 2016; Laughlin, 2014). 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 S2), 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 <20% of total variation (Siefert et al., 2015).

## 2.3 | 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; R Core Team, R Foundation for Statistical Computing, Vienna, Austria). Each R package used is referenced as each approach is explained.

We used a Principal Components 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, 2016). Out of 9,002 (643 rows of numerical trait data  $\times$  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, Appendix S1). The implication of this gap-filling method is that the variance in the estimators is underestimated (Josse & Husson, 2012, 2016). The gap-filled data were 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 2018), FactoMineR (Husson, Josse, Le, & Mazet, 2018), and factoextra (Kassambara & Mundt, 2017). The collinearity of traits in the PCA was evaluated in a correlation matrix using the package corplot (Wei et al., 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 & Siberchicot, 2018). Differences in PCA scores between grassland types were tested with a permutational analysis of variance (PERMANOVA) using vegan (R Core Team, R Foundation for Statistical Computing, Vienna, Austria) and with a post-hoc pairwise PERMANOVA statistical test 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 (Roeve et al., 2018), and mda (Hastie, Tibshirani, Leisch, Hornik, & Ripley, 2017), which minimizes within-class distances and contextually maximises class discrimination (Lo Bianco et al., 2017).

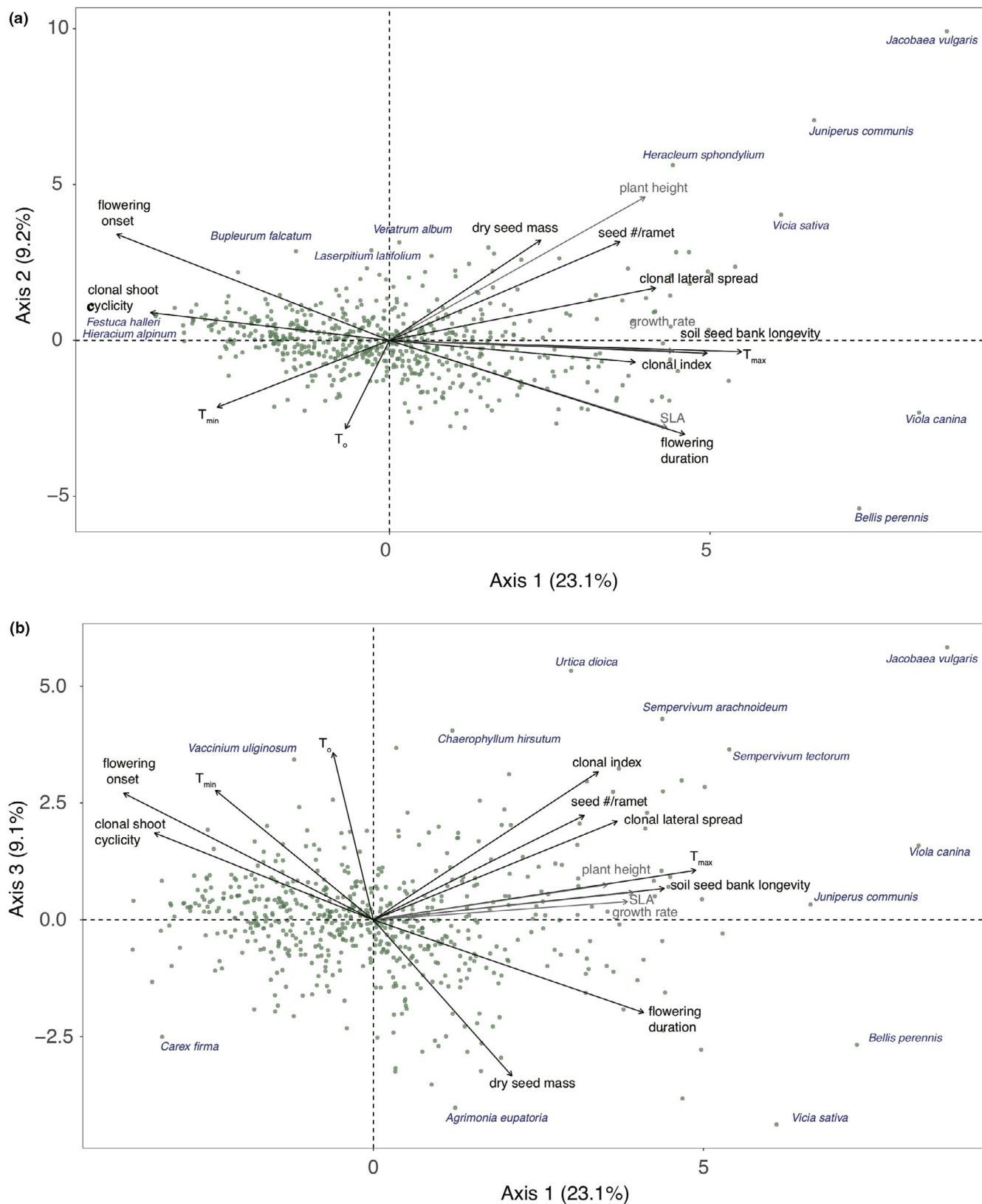
We tested for differences in mean trait values among grassland types using a post-hoc pairwise Kruskal-Wallis  $\chi^2$  test from the package PMCMR (Pohlert 2018). Raw data were plotted for single traits, with no gap filling or transformation taking place. Categorical traits were plotted in the package ggplot2 (Wickham et al., 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 yarr (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.

## 3 | 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 (Appendix S1). 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 (Appendix 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.

### 3.1 | 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 (Figure 1). All non-regeneration traits, including radial growth rate, SLA and plant height had relatively high loadings on the first axis of the PCA (Figure 1a, Table 2). 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



**FIGURE 1** Trait space of the functional species pool of European temperate grasslands. Sample scores representing 645 plant species in a Principal Components 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 S2 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 Appendix S4. Percentages for the three main axes represent the explained variance [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**TABLE 2** Loadings of the plant trait values for the first three axes of the PCA for: all traits and all species

(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	<b>0.29</b>	<b>-0.30</b>	0.05	0.07	0.06
Plant height	0.27	<b>0.49</b>	0.09	0.19	0.25
Radial growth rate	<b>0.30</b>	-0.04	0.07	0.1	-0.07
Flowering onset	<b>-0.29</b>	<b>0.36</b>	<b>0.33</b>	0.05	-0.06
Flowering duration	<b>0.31</b>	<b>-0.32</b>	-0.24	<b>-0.27</b>	0.25
Clonal spread	0.28	0.18	0.26	-0.19	<b>-0.40</b>
Clonal index	0.26	-0.07	<b>0.38</b>	-0.19	<b>-0.46</b>
Clonal cyclicity	-0.25	0.1	0.22	<b>-0.37</b>	0.08
Seed mass	0.16	<b>0.34</b>	<b>-0.4</b>	0.5	-0.2
Seed no./ramet	0.24	<b>0.34</b>	0.27	-0.17	<b>0.51</b>
Soil seed bank longevity	<b>0.33</b>	-0.04	0.08	-0.01	0.11
$T_{\min}$	-0.18	-0.23	<b>0.33</b>	<b>0.41</b>	-0.15
$T_o$	-0.05	<b>-0.3</b>	<b>0.43</b>	<b>0.43</b>	<b>0.37</b>
$T_{\max}$	<b>0.37</b>	-0.04	0.13	0.18	-0.12

Note: Bold numbers indicate the top three (3)–five (5) highest loadings on each axis.

SLA also contributed to the second axis, together with flowering onset, seed mass, seed number per ramet, and flowering duration (Figure 1a, b; Table 2; Appendix S3). On the third axis, regeneration traits ( $T_o$ , seed mass, clonal index, flowering onset and  $T_{\min}$ ) contributed the most variation (Figure 1b; Table 2).

Most of the traits (85%) were significantly correlated among each other (Appendix S5). 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.

### 3.2 | Trait variation of habitat specialists

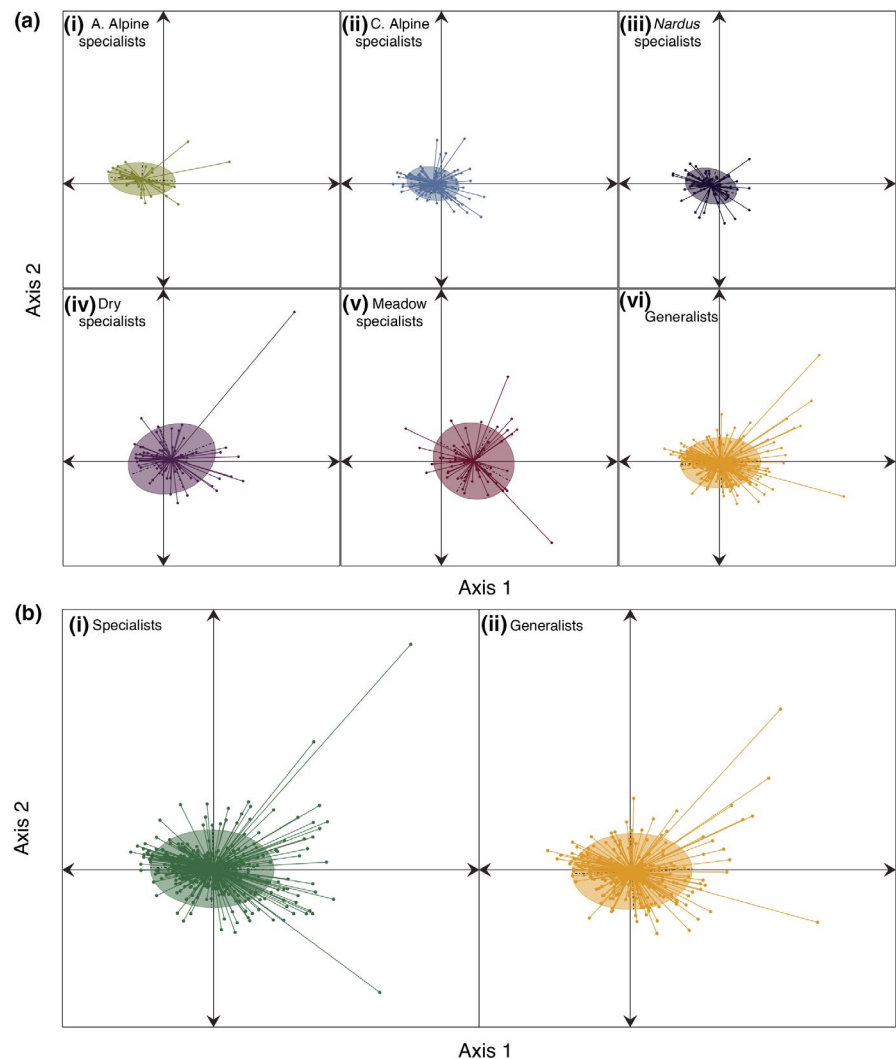
The groups of habitat specialists were differentiated among each other in the trait space (PERMANOVA  $F = 13.43$ ,  $R^2 = 0.095$ ,

$p < 0.001$ ; Figure 2a; Appendix S6b,c). Main differences between habitats were related to the first axis of variation (Kruskal–Wallis  $s^2 = 127.4$ ,  $p < 0.001$ ; Appendix S7, Appendix S8). On axis 2, only acidic alpine grasslands were differentiated from *Nardus*-dominated grasslands ( $s^2 = 12.029$ ,  $p = 0.03$ ; Appendix S7, Appendix S8). The variability between group means (F-value) was larger for regeneration ( $F = 13.77$ ,  $R^2 = 0.098$ ,  $p < 0.001$ ; Appendix S6f) than for non-regeneration traits ( $F = 10.071$ ,  $R^2 = 0.073$ ,  $p < 0.001$ ; Appendix 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 2; Appendix S9, Appendix S10). 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 (Appendix S11a). Predictions were similar when non-regeneration traits were analysed separately, better characterising certain grassland specialists, while other specialists were better characterised by regeneration traits (Appendix S11b, c). However, the discriminative power was more accurate when all traits were used together, rather than separately (Appendix S11).

Acidic alpine grasslands had the lowest SLA (Kruskal–Wallis  $s^2 = 73.28$ ,  $p < 0.001$ ; Appendix S12), shortest plant height ( $s^2 = 95.59$ ,  $p < 0.001$ ; Appendix S12), and a slow radial growth rate ( $s^2 = 28.56$ ,  $p < 0.001$ ; Appendix S12) with a late ( $s^2 = 51.38$ ,  $p < 0.001$ ; Appendix S12) and short flowering duration ( $s^2 = 74.87$ ,  $p < 0.001$ ; Figures 3 and 4; Appendix S12). *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 (Appendix S13d). 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. These specialists begin flowering at a similar time to acidic, calcareous alpine, dry grasslands and generalists, but are flowering for a similarly short length as both high-alpine grassland types, and for a much shorter time than dry grassland specialists ( $p = 0.01$ ; Appendix S14).

*Nardus* grassland specialists had the smallest seed mass by a large margin ( $s^2 = 28.30$ ,  $p < 0.001$ ; Appendix S14); a soil seed bank characterised by short-term persistent seeds (Table S2); and a high  $T_{\min}$ , but only differentiated from the very low  $T_{\min}$  of meadows ( $p = 0.03$ ; Appendix S14). Proportion of seed dispersal was higher in late summer in *Nardus*-dominated (70%), calcareous alpine (79%) and acidic alpine grasslands (79%) (Appendix S13c), which was consistent with the marginally narrower window of germination temperatures available to specialists of these grassland types (Figure 4g–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 ( $s^2 = 13.53$ ,  $p = 0.018$ ; Appendix S14). Specialists of dry grasslands had a notably larger presence of physical dormancy (PY, 24%; Appendix S13a) than other habitat types.

**FIGURE 2** Trait space of habitat specialists grouped in five grassland types and generalists. Sample scores representing 645 plant species in a Principal Components Analysis (PCA) for axes 1 and 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 versus generalists (See Table 1 for grassland type abbreviations). Degrees of freedom = 5 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



## 4 | DISCUSSION

### 4.1 | The trait spectrum of European temperate grasslands

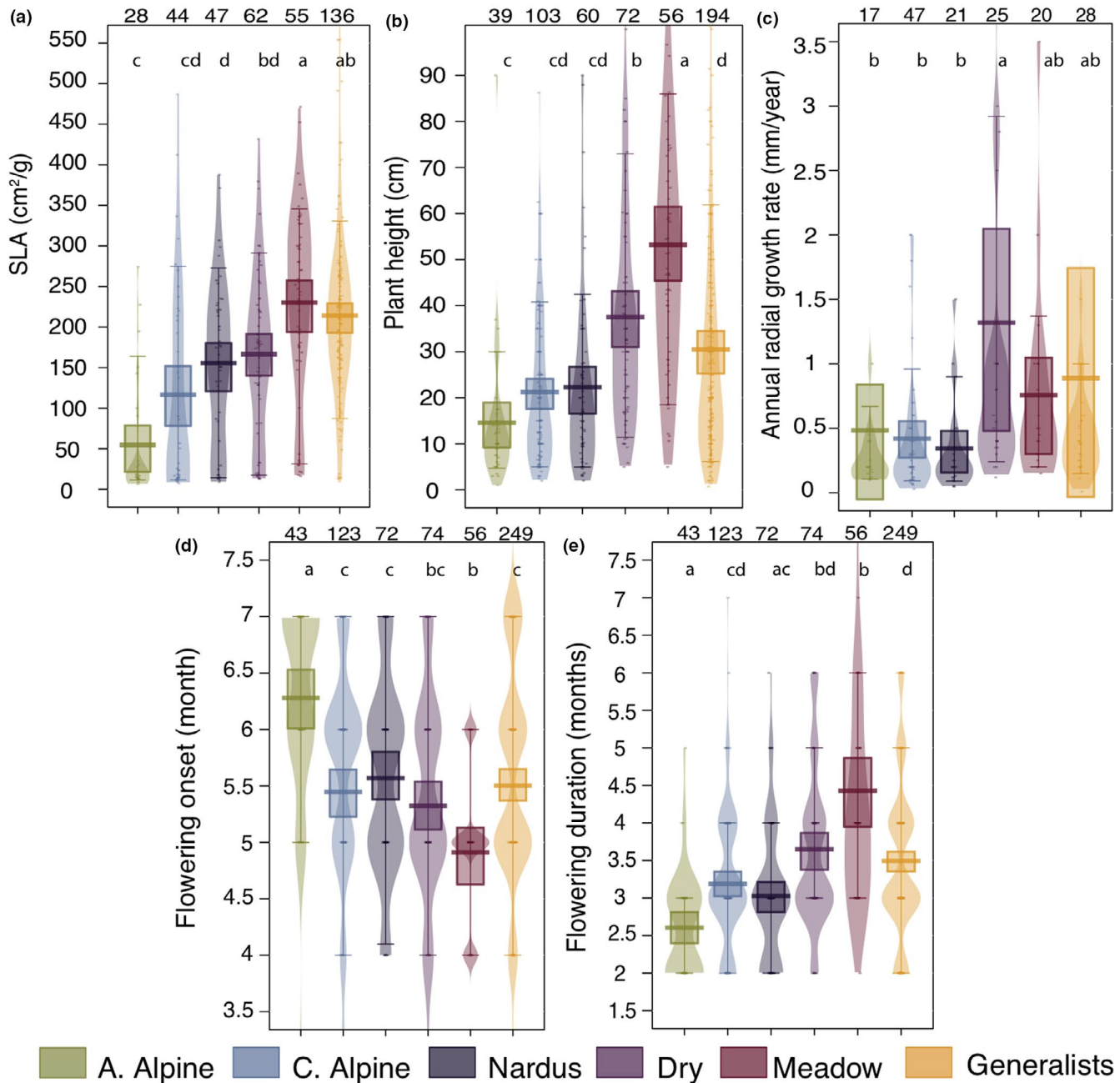
The main trait dimension of the temperate grasslands analysed in this study is similar to the “fast-slow” continuum described globally (Reich, 2014; Salguero-Gómez et al., 2016) and to the latitude-driven first dimension of the global spectrum of vascular plants (Díaz et al., 2016; Westoby, 1998). The 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, Nováková, Klimešová, & Hrouda, 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.

### 4.2 | Trait differences between habitat specialists

Our results support the idea that environmental filtering and disturbance governs the functional composition of plant specialists related



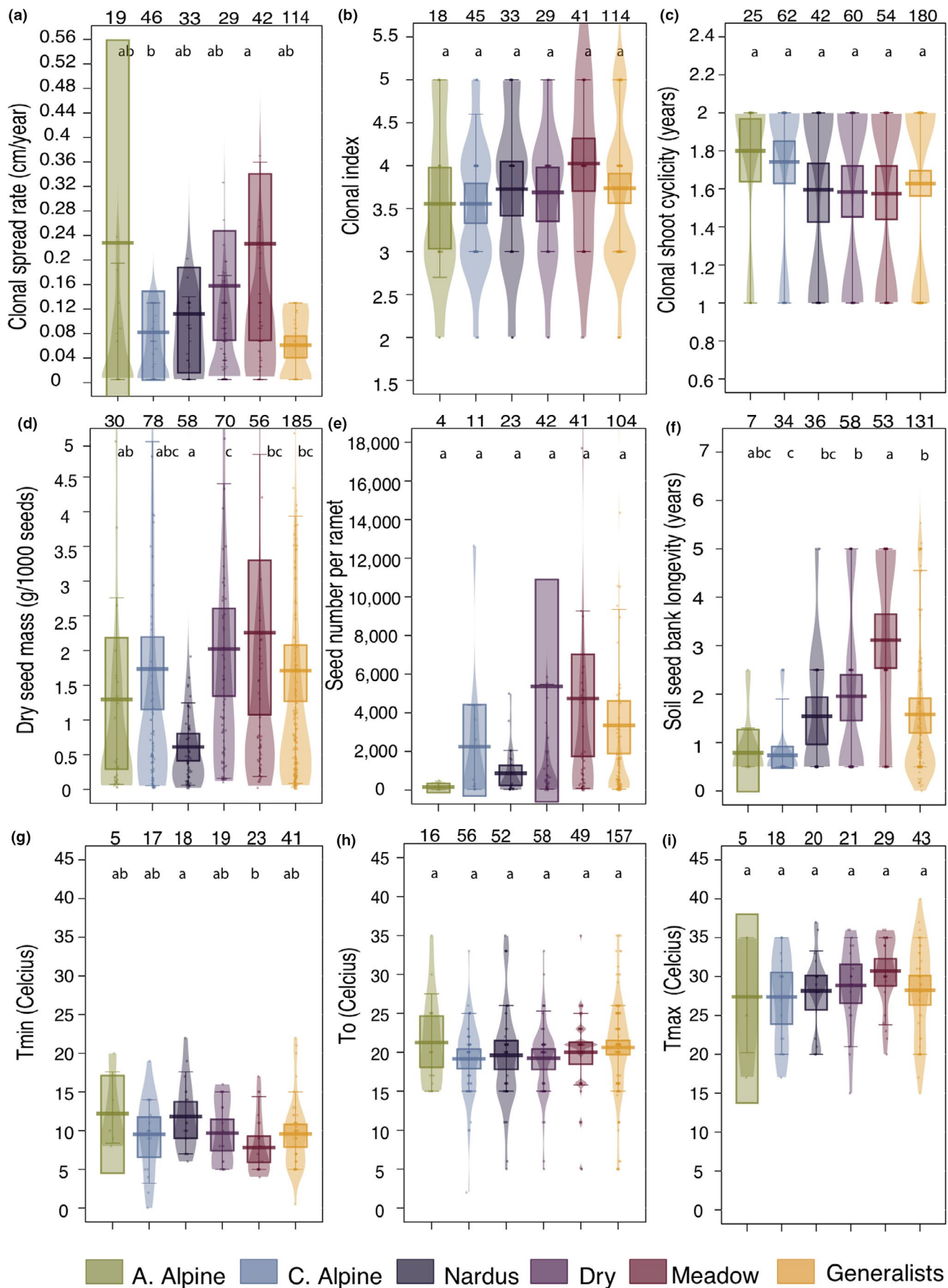
**FIGURE 3** Non-regeneration traits across habitats. (a) SLA, (b) plant height, (c) annual radial growth rate, (d) flowering onset, (e) flowering duration. RDI plots (Raw data, Descriptive and Inference statistics) show jittered points of raw data, centre bars indicate the mean of the data, beans outline 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 indicate the number of data points for each trait, and letters show statistical differences between groups [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

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

**FIGURE 4** Regeneration traits across habitats. (a) Clonal lateral spread, (b) clonal index (number of offspring + spread), (c) clonal shoot cyclicity, (d) dry seed mass, (e) seed number per ramet/plant, and (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 Figure 3 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]







relationships (Laughlin, 2014). 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., 2018) than are 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: (a) high-altitude grasslands (both acidic and calcareous grasslands); (b) low-altitude grasslands from disturbed habitats (dry grasslands and meadows); and (c) mid-altitude *Nardus*-dominated grasslands (differentiated from (a) or (b) 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 (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Mayfield & Levine, 2010). 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, Schaminee, Bakker, & Thompson, 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 (Auffret, 2011; Poschlod, Kiefer, Tränkle, Fischer, & Bonn, 1998) and the possible complementary effect of long-term disturbance regimes for understanding functional differentiation in these habitats (Kahmen & Poschlod, 2008; Louault, Pillar, Aufrère, Garnier, & Soussana, 2005). 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 (2018), so the extent of environmental filtering at different scales and gradients on these traits (2012; 2015) is worth investigating further.

## 5 | 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 distinct functional role in our study system, details that might be

lost when analysing the functional variation across, rather than within 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.

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## 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 led 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.

## DATA AVAILABILITY STATEMENT

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



## ORCID

Emma Ladouceur  <https://orcid.org/0000-0002-4943-4358>  
 Helge Bruelheide  <https://orcid.org/0000-0003-3135-0356>  
 Sabina Burrascano  <https://orcid.org/0000-0002-6537-3313>  
 Borja Jiménez-Alfaro  <https://orcid.org/0000-0001-6601-9597>

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## SUPPORTING INFORMATION

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

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