Calcareous grassland restored by clearance and subsequent sheep grazing show fast recovery of plant functional traits – Results from a 25-year-long experiment

Patricia Krickl [*], Peter Poschlod

Ecology and Conservation Biology, Institute of Plant Sciences, University of Regensburg, Universitaetsstrasse 31, D-93053 Regensburg, Germany

A B S T R A C T

In this study, the long-term restoration success of calcareous grasslands was investigated using a functional trait approach. The study site is located in the Swabian Alb, Germany, where a former calcareous grassland patch was restored in the 1990s by clearance of a spruce (*Picea abies (L.) H. Karst.*) afforestation and subsequent reintroduction of sheep grazing as mobile dispersal vector. Vegetation development was monitored over a period of 25 years, both on the restored and an adjacent never afforested ancient grassland which is still managed by traditional sheep grazing. Changes in the functional composition of fifteen ecological meaningful traits were investigated by comparing the respective attribute expressions of the restored with the ancient reference grassland for each year of observation. A RLQ-analysis was conducted in order to identify plant functional groups. The comparison of attribute expressions showed that differences between restored and ancient grassland decreased rapidly over time. The greatest differences were found in persistence-related traits (e.g., life span and growth form) while dispersal- and establishment-related traits recovered faster. The clustering of plant functional groups showed similarities with Grime's CSR-strategy, as cluster analysis grouped species with either ruderal, competitive or stress-tolerant trait attributes. 20 years after restoration, stress-tolerators dominated, while the ruderal cluster could not longer be detected and only a small group of competitive, mostly woody species remained. In 2018, RLQ analysis revealed no differences in the functional composition between restored and ancient grassland. The quick functional recovery is most likely attributed to the reestablishment of the traditional low-intensive grazing management but also to the close vicinity of the ancient grassland as no spatial isolation prevented dispersal of plant species. Hence, the functional trait approach showed that restoration by clearance and subsequent sheep grazing was a suitable management in our study.

1. Introduction

The concept of plant functional traits is an important tool for answering many crucial ecological questions (McGill et al., 2006; Pérez-Harguindeguy et al., 2013) especially in the context of restoration ecology (Clark et al., 2012; Hedberg et al., 2013; Laughlin, 2014; Sandel et al., 2011). Thereby, functional traits are generally defined as environment-responsive plant-specific characteristics (Lavorel et al., 1997) following the idea that species having a similar trait composition respond similarly to changes in the

environment, including climate change (Bjorkman et al., 2018; De Bello et al., 2005; Soudzilovskaia et al., 2013), land-use change (Díaz et al., 2007; Kahmen and Poschlod, 2008, 2004; Purschke et al., 2014; Vandewalle et al., 2014) or the arrival of invasive species (Loiola et al., 2018). Additionally, underlying processes (e.g. the impact of different filtering mechanisms (Zobel, 1997)) can be identified more accurately when the functional compositions of plant communities are compared rather than species compositions (McGill et al., 2006), especially for gaining knowledge on the ecosystem services a certain habitat may provide (Rusch et al., 2003; Zirbel et al., 2017). This is particularly true if some habitat-specific plant species are absent from the vegetation due to dispersal limitations (Öster et al., 2009; Ozinga et al., 2005) but can be substituted by other species which are characterised by a similar trait composition. Therefore, it can be suspected that estimating restoration success based on species composition may lead to misleading or incomplete conclusions (Derhé et al., 2016; Engst et al., 2016) which is not the case when a functional analysis is additionally applied (Engst et al., 2016).

The concept of analysing plant functional groups is particularly useful for understanding vegetation changes, which has therefore been applied for estimating responses to changes in land-use managements in a variety of habitat types (Drobnik et al., 2011; Gondard et al., 2003; Kahmen and Poschlod, 2008; Römermann et al., 2009; Tozer et al., 2012; Zirbel et al., 2017). Thereby, species are grouped according to their functional trait composition and thus species, which are allocated to the same functional group, are expected to similarly respond to changes in the environmental conditions (Lavorel et al., 1999).

In the present study, we used such a functional trait approach to gain knowledge on the vegetation development following the implementation of restoration management on calcareous grasslands, which are protected by European Law (EU-Code: 6210(*), European Commission 1992). Typical calcareous grassland species have adapted to the constant pressure caused by grazing and nutrient-poor, dry habitat conditions over the duration of several centuries or even millennia (Poschlod and Baumann, 2010; Poschlod and WallisDeVries, 2002). Due to major changes in the traditional land-use practices over the past 150 years, these species-rich habitats have rapidly declined in area and number throughout Europe (Poschlod, 2017; Poschlod and WallisDeVries, 2002). Main drivers for the substantial area loss were abandonment, afforestation and amelioration. These threats continue to negatively affect the occurrence of calcareous grasslands until today. Consequently, calcareous grasslands are still a main issue in restoration and conservation ecology (Poschlod and WallisDeVries, 2002) and information on which restoration measures show a reliable long-term success is more important than ever.

The current study investigated a grassland patch that was afforested with spruce (*Picea abies*) in the 1960s and restored by clearing in the early 1990s. Subsequently, sheep grazing was reintroduced, which was the traditional management before the patch was afforested. The reintroduction of the extensive grazing regime has the added advantage that the restored grassland has been reconnected to the directly adjacent ancient calcareous grassland.

It has previously been stressed that there is a gap in evaluating restoration measures in regard to long-term data on permanent observation plots, as on the one hand restoration of grazed grassland is assumed to proceed slowly and on the other hand chronosequence studies are vulnerable to site-specific influences (Bullock et al., 2001; Helsen et al., 2013). However, most restoration studies used indirect methods to follow vegetation development after restoration, e.g. by comparing different temporal stages of succession ("time-for-space substitutes" or chronosequences, (Bakker et al., 1996b); Kalamees and Zobel, 1997; Pickett, 1989) or restoration (Lindborg and Eriksson, 2004; Piqueray et al., 2015) or by recorded changes in vegetation composition for few years at one particular study site (Barbaro et al., 2001; Bistea and Mahy, 2005; Dzwonko and Loster, 1998). The disadvantage of these study designs is that site-specific characteristics can lead to misleading conclusions or that the long-term direction of the vegetation development might be predicted inaccurately (Helsen et al., 2013). Moreover, Cusser et al. (2021) just recently reported that study durations of more than 20 years are needed to achieve consistent results.

To fill this gap, we used vegetation data derived from continuously conducted vegetation surveys on permanent plots on both, the restored and the ancient reference grassland, covering in total a time span of 25 years. Given the long-term data set, we then analysed the recovery of the functional composition in the restored patch in comparison to the ancient reference grassland by using two different approaches:

1) A direct comparison of mean functional trait attributes between restored and ancient reference grassland.

2) By detecting and analysing plant functional groups.

For the first approach, we looked at differences in the trait attribute expression of ecological meaningful traits between both grassland categories. In the second approach, we applied RLQ analyses (Dolédec et al., 1996) to identify plant functional groups. This method allows to correlate vegetation, functional traits and environment conditions, which all may have an important influence on the individual restoration success. A variation of the RLQ analysis, which was shown to be suitable for investigating changes in the functional trait composition as a function of changes in abiotic conditions are iterative RLQ analyses (Bernhardt-Römermann et al., 2008; Drobnik et al., 2011; Römermann et al., 2009). Hereby, the best trait set explaining changes along an environmental gradient is detected by comparing all possible trait combinations. With this final best trait set we then can detect functional changes during the observation period by conducting a final RLQ for each year and extracting the plant functional groups.

2. Material and methods

2.1. Data

2.1.1. Vegetation data (L-table)

Vegetation data originated from a long-term monitoring carried out in the nature reserve 'Haarberg-Wasserberg', federal state of Baden-Wuerttemberg, in the Southwest of Germany (48°37'35.8"N, 9°44'07.8"E). The area, located in the Swabian Alb, is

characterised by a mean annual temperature of 7 °C, a mean annual precipitation of 1000 mm and is situated at an altitude of 1000 m. The nature reserve is known for the comparable high proportion of calcareous grasslands (*Festuca-Brometea* Br.-Bl. et Tx. 43), which have been managed by extensive sheep grazing since at last the early 19th century (Kiefer, 1998). In the 1950s and 60s, parts of the 109.6 ha large area were afforested with spruce (*Picea abies*) or pine (*Pinus sylvestris* L.). In the course of a project investigating the restoration potential of former species-rich calcareous grasslands, which were afforested or had become overgrown due to secondary succession following management abandonment, part of a 35-year-old spruce afforestation was logged in the winter of 1992/93 (Amler et al., 1999; Kiefer, 1998). Vegetation surveys of the afforestation in the year before the clearing did not reveal any herbaceous species in the understorey (Kiefer, 1998). The restored grassland had a patch size of approximately 0.2 ha and was directly adjacent to a traditionally grazed, species-rich ancient calcareous grassland (=reference grassland). The soil type was a typical Rendzina soil and both sites were located on a southwest exposed slope. Rotational sheep grazing (once to twice a year, mainly in late summer) was reintroduced directly after the clearance and served as mobile connecting vector between the reference and restored grassland. The same grazing regime was thereby applied to the ancient grassland. Ten permanently marked observation plots (size 2×2m) were installed along a transect with evenly spaced plots in each grassland category (restored and reference), and vegetation was monitored since 1993 using the percentage scale according to Schmidt (1974). More detailed information on the experimental design can be found in Kiefer (1998). Vegetation relevées for both grassland categories are available for 1993, 1994, 1995, 2001, 2008, 2013 and 2018, thus covering a period of 25 years. The long-term vegetation data were used to create the L-table with sites as rows and species abundances in percentages as columns. Species that only occurred with one or two individuals during no more than one observation year were excluded. In total, 171 of the 191 detected species were used for the analyses (compare Table A.4).

2.1.2. Environmental data (R-table)

Ellenberg indicator values have been shown to accurately represent the local abiotic habitat conditions (Bartelheimer and Poschlod, 2016; Diekmann, 2003). Therefore, we used mean weighted Ellenberg indicator values for light, moisture, nutrients and soil reaction as environmental parameters (Ellenberg et al., 2001). In addition, the management type (restored or reference grassland) was included. The R-table was created with sites as rows and mean indicator values and respective management category in columns.

Table 1

Data included into the iterative RLQ analyses. The R-table included environmental parameters, here represented by Ellenberg Indicator Values (EIV) and the respective management, the L-table included the vegetation relevées and the Q-table the functional traits with the respective attributes structured according to the challenges of dispersal, establishment and persistence. Data for the Ellenberg Indicator Values were extracted from Ellenberg et al. (2001) while trait data was extracted from BIOPOP [a] (Poschlod et al., 2003), LEDA [b] (Kleyer et al., 2008) and CLO-PLA [c] (Klimešová et al., 2017). Missing values for seed mass and seed number per ramet were supplemented with self-collected data [d] and growth form was classified based on own observations [e]. Attributes of traits that are relevant for several challenges were only described once [f].

Table	Parameter/ Trait	Scale/ Attributes
R	Weighted EIV Light	metric
	Weighted EIV Nutrients	metric
	Weighted EIV Moisture	metric
	Weighted EIV Soil Reaction	metric
	Category of grassland	reference, restoration
L	Ten vegetation relevées per management; plot size 2×2m; recorded in 1993, 1994, 1995, 2001, 2008, 2013 or 2018	according to Schmidt (1974)
Q	*Dispersal-related traits*	
	Dispersal mode – anemochory[b]	no, yes
	Dispersal mode – endozoochory[b]	no, yes
	Dispersal mode – epizoochory[b]	no, yes
	Dispersal mode – hemerochory[b]	no, yes
	Seed bank[b]	transient, persistent
	Seed mass[b, d]	< 0.5 mg, $0.5–2$ mg, > 2 mg
	Establishment-related traits	
	SLA[b]	< 20 mm^2/mg, $20–25$ mm^2/mg, > 25 mm^2/mg
	Seedling emergence[a]	spring, autumn, all year
	Seed mass[f]	
	Persistence-frelated traits	
	Growth form[e]	forb, graminoid, legume, woody
	Seedling emergence[a]	
	Start of flowering[b]	May and earlier, after May
	Seed bank[f]	
	Leaf distribution[b]	basal rosette, no rosette
	Lateral spread[c]	< 0.01 m/year, $0.01–0.25$ m/year, > 0.25 m/year
	Canopy height[b]	< 0.3 m, $0.3–0.6$ m, > 0.6 m
	First flowering[a]	< 1 year, $1–5$ years, > 5 years
	SLA[f]	
	Lifespan[b]	short (annuals & biennials), long (perennials)

2.1.3. Functional traits (Q-table)

In total, 15 functional plant traits and their respective attributes (Table 1) were extracted from BIOPOP (Poschlod et al., 2003), the LEDA traitbase (Kleyer et al., 2008) and CLO-PLA (Klimešová et al., 2017) while missing values for seed mass and seed number per ramet were supplemented by self-collected data. When extracting plant functional traits, the mean of all available values was taken for
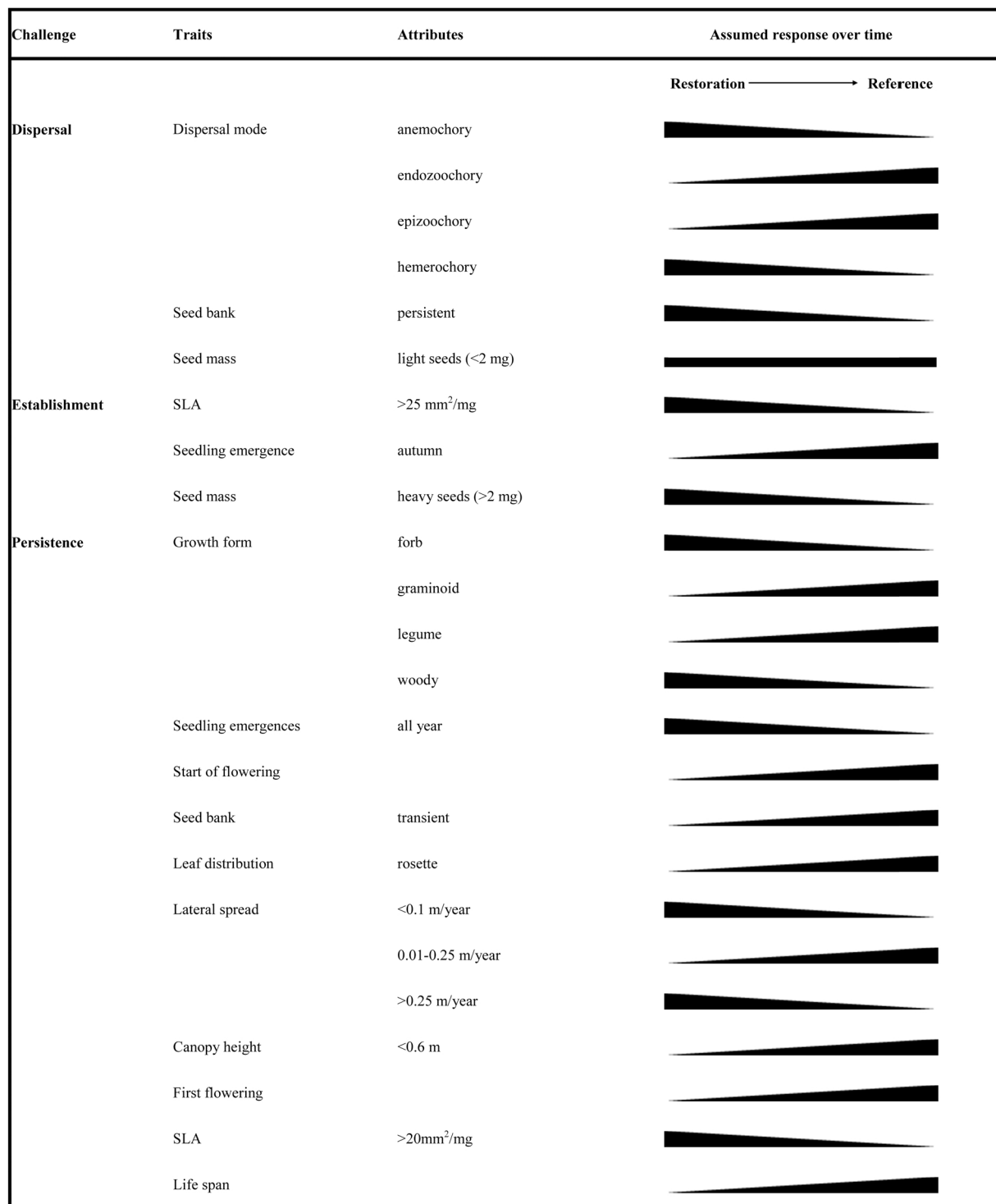
Challenge	Traits	Attributes	Assumed response over time
			Restoration ⟶ Reference
Dispersal	Dispersal mode	anemochory	
		endozoochory	
		epizoochory	
		hemerochory	
	Seed bank	persistent	
	Seed mass	light seeds (<2 mg)	
Establishment	SLA	>25 mm^2/mg	
	Seedling emergence	autumn	
	Seed mass	heavy seeds (>2 mg)	
Persistence	Growth form	forb	
		graminoid	
		legume	
		woody	
	Seedling emergences	all year	
	Start of flowering		
	Seed bank	transient	
	Leaf distribution	rosette	
	Lateral spread	<0.1 m/year	
		0.01-0.25 m/year	
		>0.25 m/year	
	Canopy height	<0.6 m	
	First flowering		
	SLA	>20mm^2/mg	
	Life span		

Fig. 1. Assumed development of plant functional traits in restored grasslands compared to reference grasslands over time (in accordance to Weiher et al., 1999).

metric traits if several data entries were available. For categorical traits, the most frequently mentioned or the highest attribute was taken (e.g. if for seedling emergence 'spring' and 'all year' were given then 'all year' was used). For the traits canopy height, leaf distribution, seed mass and specific leaf area (SLA) classifications were applied as proposed by Kahmen and Poschlod (2004, 2008) and species were assigned to the appropriate category (see Table 1) while the growth form was classified in accordance with Díaz et al. (2007) into forb, graminoid, legume and woody species.

In accordance to Weiher et al. (1999), we differentiated traits according to their relevance for plant species to cope with the challenges of dispersal, establishment and persistence (Fig. 1, Table 1). It should be noted that individual trait attributes are in some cases important for different challenges and can therefore be involved in different processes.

A summary on the relevance of the individual plant traits on these challenges can be found in the Appendix (S. 1).

2.2. Statistical analyses

The proportion of species, which expressed a certain trait attribute, were calculated for the restored and the ancient reference grassland for the different observation years. Using Wilcoxon signed-rank tests significant differences between grassland categories were detected and significant changes in trait expression were then plotted.

In this first approach the different traits and their respective attributes hold an unidentified significance for explaining differences in species composition while, additionally environmental conditions were not taken into account. A method which combines all three information (functional traits, environmental conditions, species abundances) is the RLQ analysis as proposed by Dolédec et al. (1996). Hereby, the environmental data (R-table) is linked to the functional trait data (Q-table) via the vegetation data (L-table). The overall aim of this method is not only to investigate the relationship between traits and species abundances or environmental conditions and species abundances but to find a connection between functional traits and environmental conditions by using species abundances as underlying information. A RLQ analysis can be additionally modified into selecting those traits, which are suggested to be the most relevant for explaining species composition. The method for trait selection, called iterative RLQ analysis, was proposed and described in detail by Bernhardt-Römermann et al. (2008).

For trait selection, these iterative RLQ analyses were carried out separately for each year. The L-table was thereby created by a different set of plant species for the different years, based on the species found during the respective vegetation surveys. Prior to the analysis, the Ellenberg indicator values included in the R-table were standardised by adjusting the values to zero mean and unit deviance. An overview on the dimensions for the R-, L- and Q-table for the respective years is provided in Table 2.

In the first step of the RLQ analysis, the L-table was arcsine-square-root transformed and a correspondence analysis was performed on this table. Then, Hill-Smith ordinations (Hill and Smith, 1976) were carried out on the R-table. Hereby, the row scores of the correspondence analysis on the L-table were used as canonical factor. The same was done for the Q-table. However, here the column scores were used as canonical factor. Next, two separate analyses were performed: one between the constrained ordination on the Q-table and the correspondence analysis on the L-table and one between the constrained ordination on the R-table and the correspondence analysis of the L-table. In the following iterative process, testing all possible combinations of traits, functional traits were extracted that describe the ecosystem response of the plant species along the environmental gradient best (Bernhardt-Römermann et al., 2008). This process was repeated for each year separately and the optimal trait set was identified individually for each of the seven observation years.

A final RLQ analysis was then conducted for each year based on the trait set which was identified in the iterative RLQ analyses. Besides using the altered Q-table, the RLQ analysis was performed as previously described. For detecting functional plant groups, the species scores of the final RLQ analysis per year was subsequently clustered by k-mean clustering. The ideal number of clusters was calculated based on 30 different indices and the number of clusters which was proposed most often was consequently used. Species allocation to clusters and cluster stability were additionally tested by using bootstrapping (Römermann et al., 2009). Once the best clustering for the plant species was calculated, characteristics of the plant functional groups were extracted by summarizing the number of species expressing each attribute. Significant differences between the plant functional groups were tested by using Chi^2-tests for categorical values. As final step, the results of the RLQ analysis per year and the k-mean clustering were plotted based on species scores and cluster allocation and the correlation of the restored plots based on site scores was included (Management Category).

All analyses were conducted using R *v.3.5.2* (R Core Team, 2020) and the packages 'ade4' *v.1.7–13* (Dray and Dufour, 2007), 'exactRangTest' *v0.8–31* (Hothorn and Hornik, 2015), 'fpc' *v.2.2–3* (Hennig, 2019), ggplot2 *v.3.32* (Valero-Mora, 2010) and 'NBClust' *v.3.0* (Charrad et al., 2014).

Table 2
Overview of the dimension of the R-, L- and Q-tables used for the calculation of the iterative RLQ analyses for the respective years.

	1993	1994	1995	2001	2008	2013	2018
R-table (plots x environmental factors)	20 × 5	20 × 5	20 × 5	20 × 5	20 × 5	20 × 5	20 × 5
L-table (species x plots)	20 × 83	20 × 119	20 × 119	20 × 121	20 × 102	20 × 103	20 × 103
Q-table (species x traits)	83 × 15	119 × 15	119 × 15	121 × 15	102 × 15	103 × 15	103 × 15

3. Results

3.1. Differences in trait attributes between grassland categories over the study period

The comparison of functional traits showed clearly that more attributes differed significantly between the reference and restored grassland in the first years of observation than in later years (Table 3). Of the 15 investigated traits, 10 showed significant different trait attribute expressions in 1993. In 1994, 1995, 2001, 2008, 2013 and 2018, the number of significantly different traits amounted to 11, 9, 8, 5, 3 and 3, respectively.

Of the *dispersal*-related traits, hemerochory as well as light seed mass (< 2 mg) showed significant differences between grassland categories during the first two years after restoration, while significant differences for epizoochory were only detected in 2018. Soil seed bank persistence differed at least until 2008.

All traits, correlated with the *establishment* of plant species, showed significant differences during the first year after restoration. Of these, only heavy seeded species differed until 2008, while autumn germinators showed an unclear pattern with additional significant differences in 2001, 2008 and 2018.

Persistence-related traits all showed significant differences for at least the first three years (1993, 1994, 1995) after restoration, with the exception of seedling emergence throughout the year (only significant different in 1993) and start of flowering and leaf distribution (not significant different in 1993). Growth form was the only trait that still showed significant differences in 2018, while traits reflecting the moderate grazing pressure (start of flowering, seed bank and leaf distribution) different until 2001 or 2008, respectively. Traits, that indicate plant species persistence like SLA and life span, differed until 2008, while canopy height and age of first flowering were only significantly different until 1995 (the latter additionally in 2013). Lateral spread showed significant differences until 2013. A graphical illustration of the development of trait attributes displaying significant differences between reference and restored grassland is given in Fig. 1 A-L (except epizoochory as differences were detected in 2018 for the first time).

Table 3
Significant differences in the mean expression of functional traits attributes between the reference and restored grassland for the seven different observation years. For each grassland category 10 observation plots were available. Results are based on Wilcoxon signed-rank tests. Given are the respective p-values.

Trait	Attribute	1993	1994	1995	2001	2008	2013	2018
Dispersal-related								
Dispersal mode	anemochory	0.447	0.725	0.105	0.956	0.839	0.218	0.383
	endozoochory	0.617	0.929	0.783	0.868	0.541	0.868	0.840
	epizoochory	0.671	0.912	0.225	0.955	0.271	0.669	**0.019***
	hemerochory	**0.022***	**0.003****	0.105	0.435	0.669	0.516	0.739
Seed bank	persistent	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001****	**0.004****	0.280	0.566
Seed mass	< 0.5 mg	**0.006****	**0.024***	0.671	0.128	0.342	0.184	0.684
	$0.5 - 2$ mg	**<0.001*****	**0.004****	0.47	0.118	0.565	0.517	0.239
Establishment-related								
SLA	> 25 mm^2/mg	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****	**0.018***	0.566	0.725
Seedling Emergence	spring	**0.037***	0.740	0.225	0.782	0.578	0.726	0.425
	autumn	**0.001*****	0.897	0.467	**>0.001****	**0.045***	0.210	**0.040***
Seed mass	> 2 mg	**<0.014****	0.516	1.000	0.839	1.000	0.382	0.184
Persistence-related								
Growth form	forb	**<0.001*****	**0.002****	**<0.010****	**0.005****	**0.403****	0.403	**0.016***
	graminoid	**<0.001****	**<0.001*****	**<0.001*****	**<0.001*****	**0.002****	0.755	**0.020***
	legume	**0.030***	0.148	0.426	0.093	0.171	0.565	0.697
	woody	0.059	0.529	0.078	0.21	1.000	0.448	0.780
Seedling Emergence	all year	**0.005****	0.670	0.218	0.182	1.000	0.469	0.837
Start of Flowering		0.896	**0.011***	**0.020***	**0.045***	0.403	0.853	0.343
Seed bank	transient	**<0.001*****	**<0.001*****	**<0.001****	**<0.001****	**0.004****	0.280	0.566
Leaf distribution		0.779	**<0.001*****	**0.002****	**0.020***	0.271	0.645	0.470
Lateral spread	< 0.01 m/year	0.698	0.325	0.109	**0.002****	**<0.050***	0.591	0.224
	0.01–0.25 m/year	**0.028***	**0.037***	0.403	**0.024***	0.403	0.424	0.289
	> 0.25 m/year	0.810	0.079	**<0.001*****	**0.011***	**<0.001*****	**0.004****	0.343
Canopy Height	< 0.3 m	**0.001*****	**0.007****	**>0.001****	0.644	0.643	0.796	0.753
	0.3–0.6 m	**<0.001*****	0.248	0.566	0.628	0.956	0.986	0.631
	> 0.6 m	**0.009****	**<0.001*****	**<0.001*****	0.353	0.955	0.725	0.645
First Flowering	< 1 year	**0.005****	**<0.001*****	**0.004****	0.143	0.867	0.271	0.753
	1–5 years	**0.035***	**0.002****	**0.005****	0.342	0.305	0.063	0.239
	> 5 years	**0.002****	**>0.001****	0.159	0.342	0.240	**0.034***	0.210
SLA	< 20 mm^2/mg	**0.006****	**0.020****	**<0.001*****	**<0.001*****	**0.043***	0.927	0.869
	20–25 mm^2/mg	**<0.001*****	**0.043***	0.305	0.085	0.136	0.363	0.898
Life span		**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****	0.184	**0.045***	0.065

Significant differences are illustrated in bold with
* $p < 0.5$,
** $p < 0.01$,
*** $p < 0.001$

3.2. RLQ- and cluster analyses

3.2.1. Optimal trait sets identified by iterative RLQ analyses

The traits that were identified as the optimal set of traits for explaining species composition were identified in the iterative RLQ analyses for each date separately (Table 4). The identified traits were then used to calculate the finals RLQ for each year of observation.

Hemerochory and seed bank persistence were the only two dispersal-related traits that were identified for the optimal traits for several dates (1993–2008 and 1993–2013, respectively). Contrarily, anemochory (1993), endozoochory (2018), epizoochory (1993) and seed mass (1994) were traits that entered the final RLQ analysis only during one date.

For establishment-related traits, again seed mass was only identified for one date (1994) while SLA and seedling emergence entered the final RLQ analysis for five and four dates, respectively (Table 4).

Concerning the persistence of plant species, most frequently identified traits were canopy height (not in 2008), age of first flowering (not in 1993) and seed bank persistence (not in 2018) while plant life span (not 2001, 2013) and SLA (not 1993, 2013) were found for five dates and seedling emergence (not 1994, 1995, 2013) and growth form (not 1993, 1995, 2018) were found for four dates. Both, lateral spread and leaf distribution entered the final RLQ analyses in 2008 and 2013 while start of flowering was not identified for any date.

3.2.2. Final RLQ analyses

An overview on the results of the final RLQ analyses, which were calculated separately for each year based on the optimal final trait set (Table 4), is given in Table 5 (and Appendix Table A.1 for the correlations of the environmental parameters). Over the course of the study, the total inertia explained by the final RLQs declined. In 1993, the total inertia, which represents the variability of the data set, amounted to 1.717 while in 2018, the total variability decline to 0.128.

3.2.3. Cluster identification and characterisation

Three clusters of plant functional groups were detected by k-mean clustering in the years 1993, 1994, 1995, 2001 and 2008, whereas only two remained in 2013 and 2018 (Appendix Table A.2, Fig. 3 A-G).

For the first five years of observation (Fig. 3 A-E), Cluster 1 and Cluster 3 were separated from each other along the first axis which explained between 94.1% and 81.6% of the projected inertia, respectively (Table 5). Cluster 1 was thereby placed in the opposite direction of the restored grassland while Cluster 3 showed a strong correlation with the restored grassland. In addition, Cluster 2 was placed between Cluster 1 and Cluster 3 along the first axis and was separated from the other two clusters by the second axis (explaining between 4.9% and 13.6%).

For 2013 and 2018 (Fig. 3 F-G), the two Clusters were split up along the first axis (54.3% and 65.3% of projected inertia, respectively) while the second axis explained differences within the clusters (37.3% and 22.4%, respectively; Table 4). There was no correlation between the restored grassland and the two clusters.

Significant differences between clusters based on the traits that were used for the final RLQ calculations and thus, cluster identification (Table 4), were calculated based on Chi²-tests. Thereby, we found no significant differences between identified clusters for

Table 4

Overview on traits that were identified by the iterative RLQ-analyses, which were conducted for each year separately, as optimal trait set. Based on the identified traits the final RLQ analysis was calculated for each year. Grey shaded traits were relevant for two challenges and therefore appear twice in the list. Number of traits indicates how many traits were used for the calculation of the final RLQ analysis.

Trait	1993	1994	1995	2001	2008	2013	2018
Number of traits	7	8	6	7	9	6	6
Dispersal-related traits							
Dispersal mode – anemochory	final RLQ	-	-	-	-	-	-
Dispersal mode – endozoochory	-	-	-	-	-	-	final RLQ
Dispersal mode – epizoochory	final RLQ	-	-	-	-	-	-
Dispersal mode – hemerochory	final RLQ	final RLQ	final RLQ	final RLQ	final RLQ	-	-
Seed bank	final RLQ	final RLQ	final RLQ	final RLQ	final RLQ	final RLQ	-
Seed mass	-	final RLQ	-	-	-	-	-
Establishment-related traits							
SLA	-	final RLQ	final RLQ	final RLQ	final RLQ	-	final RLQ
Seedling emergence	final RLQ	-	-	final RLQ	final RLQ	-	final RLQ
Seed mass	-	final RLQ	-	-	-	-	-
Persistence related traits							
Growth form	-	final RLQ	-	final RLQ	final RLQ	final RLQ	-
Seedling emergence	final RLQ	-	-	final RLQ	final RLQ	-	final RLQ
Start of flowering	-	-	-	-	-	-	-
Seed bank	final RLQ	final RLQ	final RLQ	final RLQ	final RLQ	final RLQ	-
Leaf distribution	-	-	-	-	final RLQ	final RLQ	-
Lateral spread	-	-	-	-	final RLQ	final RLQ	-
Canopy height	final RLQ	final RLQ	final RLQ	final RLQ	-	final RLQ	final RLQ
First flowering	-	final RLQ	final RLQ	final RLQ	final RLQ	final RLQ	final RLQ
SLA	-	final RLQ	final RLQ	final RLQ	final RLQ	-	final RLQ
Lifespan	final RLQ	final RLQ	final RLQ	-	final RLQ	-	final RLQ

Table 5

Overview of the results of the final RLQ analyses for the different observation years. Given are the number of traits as identified by the iterative RLQ, the total inertia of the final RLQ and the projected inertia for the first and second axis.

Results of final RLQ	1993	1994	1995	2001	2008	2013	2018
Total inertia	1.717	1.558	0.771	0.638	0.297	0.120	0.128
Projected inertia (%) – Axis 1	88.5	93.8	94.1	87.6	81.6	54.3	65.3
Projected inertia (%) – Axis 2	8.8	5	4.9	10.1	13.6	37.3	22.4

hemerochory in 1993, for lateral spread and seed bank in 2013 and for endozoochory and SLA in 2018. All other traits showed significant differences between clusters (Appendix Table A.2).

Species allocations to the respective clusters is given in the Appendix (Appendix Table A.3). Based on significantly different trait attributes and associated plants species, the three clusters are characterised in the following. Since the functional traits that best describe species composition varied between dates, general patterns were used to define the clusters.

3.2.3.1. Cluster 1 – 'Grassland cluster'. Persistence-related trait attributes that characterised Cluster 1 include the occurrence of small (<0.6 m), mostly perennial species which flowered early in their life cycle (<5 years) and had small SLA values (<25 mm^2/mg). Moreover, the cluster contained the highest proportion of rosette and graminoid species and was dominated by species with transient seeds and forbs. Concerning dispersal, hemerochorously dispersed species were underrepresented while with regard to establishment-related traits autumn germinators occurred most frequently in Cluster 1. Species belonging to Cluster 1 amounted to 40, 60, 38, 41, 63, 88 and 78 species in 1993, 1994, 1995, 2001, 2008, 2013 and 2018, respectively.

Species, which were assigned to Cluster 1 in all seven years were *Briza media* L.*, Campanula rotundifolia* L.*, Carex flacca* Schreb.*, Cirsium acaulon* (L.) Scop.*, Festuca ovina* L.*, Gentiana verna* L.*, Helianthemum nummularium* (L.) Mill.*, Medicago falcata* L.*, Plantago media* L.*, Polygala amarella* Crantz*, Primula veris* L.*, Prunella grandiflora* (L.) Scholler (not recorded in 2008)*, Sanguisorba minor* Scop. *and Scabiosa columbaria* L..

Based on the strong negative correlation of Cluster 1 with the restoration plots in the RLQ analyses (Fig. 2 A-G), this Cluster was defined as 'Grassland cluster'.

3.2.3.2. Cluster 2 – 'Tall species cluster'. Cluster 2 was characterised by tall (>0.6 m), perennial species, which flowered late in their life cycle (>1 year) and produced transient seeds. Further trait attributes that were related to persistence was the high proportion of woody species and the dominance of species with small SLA values. Concerning establishment, this cluster was dominated by spring germinators while for dispersal-related traits hemerochorously dispersed species only had low frequencies in Cluster 2 (except for 1995 and 2001). Species belonging to Cluster 2 amounted to 23, 14, 50, 40, 10, 15 and 25 species in 1993, 1994, 1995, 2001, 2008, 2013 and 2018, respectively.

Some species, which occurred exclusively in Cluster 2 were *Acer campestre* L.*, Carpinus betulus* L. (since 2001)*, Crataegus monogyna* Jacq.*, Fagus sylvatica* L.*, Fraxinus excelsior* L.*, Juniperus communis* L.*, Lonicera xylosteum* L. (since 1995)*, Prunus spinosa* L.*, Quercus robur* L. (since 2001) and *Sorbus aria* (L.) Crantz (since 1994).

The highest species number for Cluster 2 was found in 1995 and 2001. Cluster analysis put only in these two years some more competitive species into this cluster, which were found in previous years for Cluster 1 (e.g. *Achillea millefolium* L.*, Dactylis glomerata* L.*, Knautia arvense* (L.) Coult.*, Pimpinella saxifraga* L.) or Cluster 3 (*Cirsium arvense* (L.) Scop.*, Daucus carota* L.*)*. This Cluster was defined as the 'Tall species cluster'.

3.2.3.3. Cluster 3 – 'Early-succession species cluster'. Regarding persistence-related traits, Cluster 3 was characterized by small (<0.6 m) species, which flowered early in their life cycle and produced persistent seeds. Furthermore, forbs and legumes dominated this cluster while species were indifferent in terms of life span. Trait attributes reflecting the establishment success were the high frequency of species with high SLA values that germinating throughout the year. Regarding dispersal, Cluster 3 generally contained many hemerochorously dispersed species (except 2001).

Species belonging to Cluster 3 amounted to 20, 45, 31, 40 and 29 species in 1993, 1994, 1995, 2001 and 2008, respectively.

Species, which only occurred in Cluster 3 included for example *Alopecurus myosuroides* Huds. (1994/95)*, Capsella bursa-pastoris* (L.) Medik. *(1993–95), Galeopsis ladanum* L.*/ G. tetrahit* L. (1994/95)*, Hieracium murorum* L. (1994/95)*, Lactuca serriola* L. (1994–2001)*, Myosotis arvensis* (L.) Hill (1993–2001)*, Poa annua* L. (1993/94)*, Sonchus asper* (L.) Hill *(1993–95), Stellaria media* (L.) Vill. (1993–95) *and Veronica arvensis* L. (2001–08). In addition, some species were assigned to Cluster 3 until 2008 and were then reassigned to Cluster 1 since 2013 (e.g. *Cerastium holosteoides* Fr.*, Linum catharticum* L.*, Medicago lupulina* L.*, Trifolium repens* L. or *Veronica chaemedrys* L.).

Due to the strong correlation of Cluster 3 with the restored grassland (Fig. 2 A-G), this cluster was defined as 'Early-succession species cluster'.

4. Discussion

4.1. Development of plant functional traits in the restored grassland in comparison to the reference grassland

To estimate restoration success based on the functional composition, traits related to dispersal, establishment and persistence
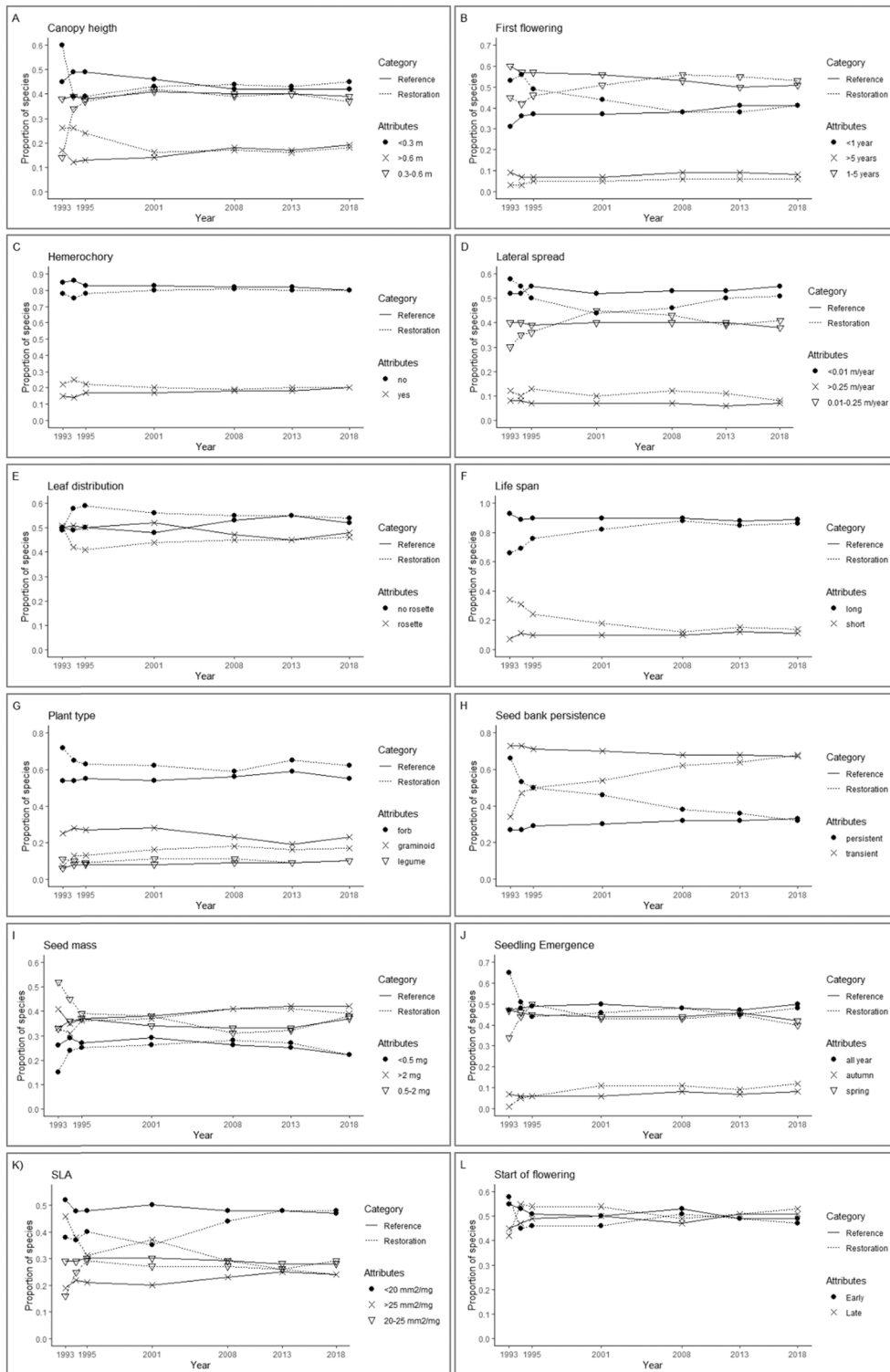
Fig. 2. A-L: Development of trait attributes over the observation period. Included are all trait attributes (except epizoochory) that showed significant differences between reference and restoration plots (compare Table 2).

(Weiher et al., 1999) were compared between restored and reference grassland (Laughlin, 2014). To do so we assumed, based on their ecological meaning, the temporal development of the individual traits on the restored grassland (Fig. 1 & *2.1.3 Functional traits (Q-table)*). The actual development is discussed in the following.
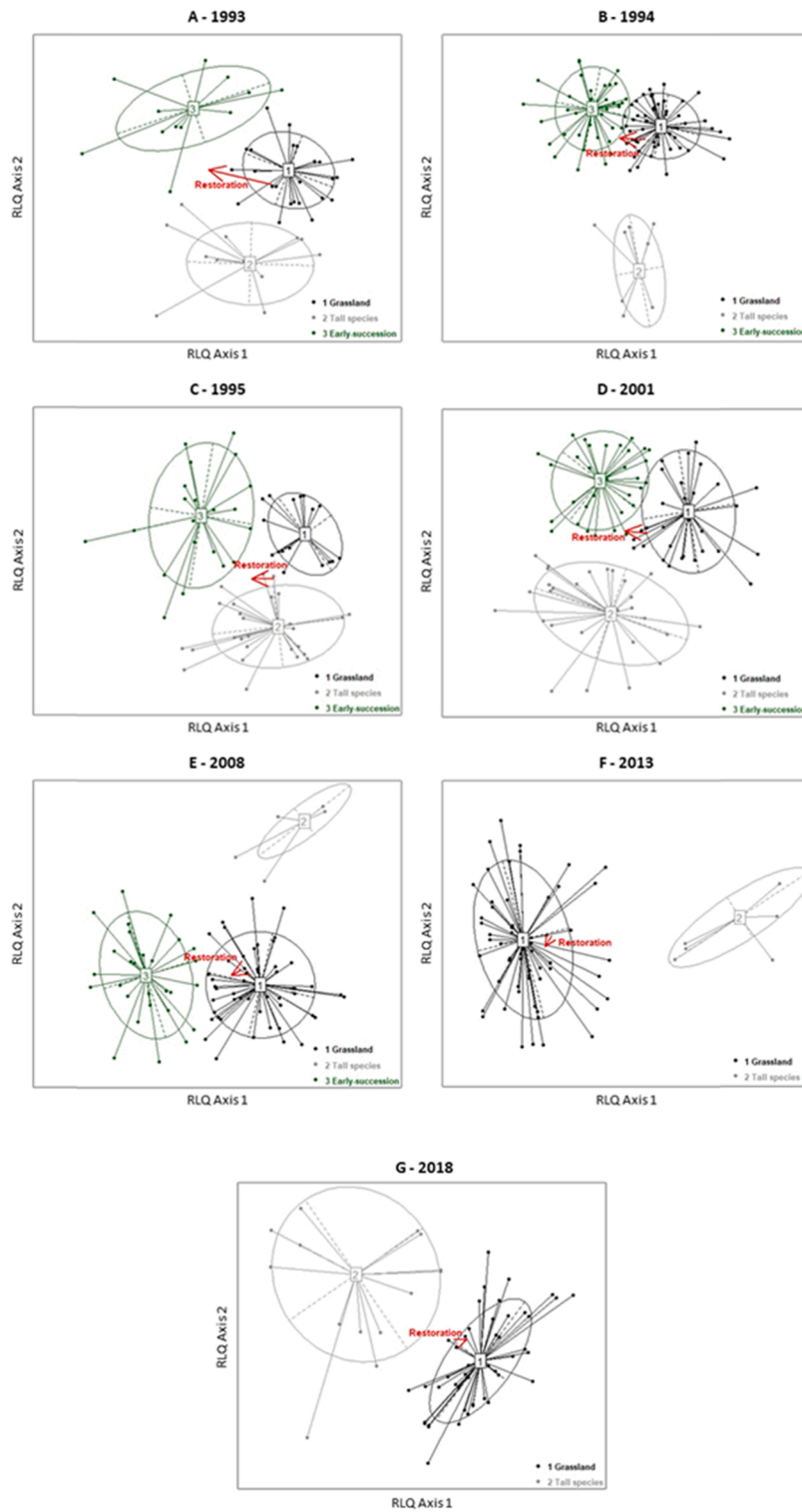
Fig. 3. A–G: Graphical output of the iterative RLQ-analyses for the seven observation years (1993–2018). Illustrated are species scores for the first two axes and cluster division according to the k-mean clustering. The dimension of the R-, L- and Q-tables for the respective years is given in Table 2. Derived from the R-table, the direction of the restored grassland is shown (red arrow). Further information on number of traits (Q-table) included into the final RLQ analyses and percentages of variance explained by the axes is given in Table 4 and Table 5, respectively.

4.1.1. Dispersal related traits

To test the importance of dispersal for the restoration success of a typical calcareous grassland vegetation, we compared traits that are important for dispersal in space and time. We proposed that the dispersal modes anemochory, endozoochory and epizoochory favoured the likelihood of seed dispersal in space while a persistent seed bank, the dispersal mode hemerochory and a low seed mass were attributes correlated with the dispersal of species in time (Bekker et al., 1998).

We thereby assumed that immediately after restoration, anemochorously dispersed species would dominate due to their high spatial dispersal potential, which allows them to arrive at the restored grassland very fast (Bakker et al., 1996b; Von Blanckenhagen and Poschlod, 2005). In contrast, for epi- and endozoochorously dispersed species we assumed a slower arrival rate (Pärtel et al., 1998; Poschlod et al., 1998). However, we found no significant differences between restored and reference grasslands for all three dispersal modes because there were already similar proportions of species during the first year after restoration. We speculate this happened due to the close vicinity of the donor grassland, which in combination with the small size of the restored grassland, enabled the fast dispersal of plant species with wind and grazing animals (Helsen et al., 2013). The rapid arrival of these species (at least zoochorously dispersed ones) is nevertheless unexpected based on previous observations (Piqueray et al., 2015; Von Blanckenhagen and Poschlod, 2005), thus the dispersal in space should perhaps be examined using further characteristics. However, further traits for dispersal in space (e.g. realised dispersal distances) are very difficult to generate and often not available for many species (Cornelissen et al., 2003).

For three other trait attributes (hemerochorously dispersed species, small seed mass, persistent seeds), however, we found higher incidences in the restored grassland during the first years of observation. A correlation of low seed weight with seed persistence has been reported from previous studies (Bekker et al., 1998; Thompson et al., 1977) while an initial high proportion of species with persistent seeds was also found for other clear-cut restoration studies (Poschlod et al., 1998). However, the proportion of typical calcareous grassland species in the long-term persistent seed bank was reported to be comparable low (Bakker et al., 1996a; Von Blanckenhagen and Poschlod, 2005) and accordingly, we rather detected many arable weed species (e.g. *Capsella bursa-pastoris (L.) Medik., Myosotis arvensis (L.) Hill*). The occurrence of these species, characterised with a long-term persistent seed bank, were not unexpected when considering that in earlier times the transition from grazed calcareous grassland and arable field was more common (Poschlod and WallisDeVries, 2002). Thus, we speculate that these species were most likely relicts of former arable farming and persisted as seeds in the soil until they were disturbed by the restoration measure, leading to the reactivation of these seeds (Aksoy et al., 1998; Davies and Waite, 1998; Karlík and Poschlod, 2014; Oberdorfer, 2001). Therefore, this finding reflected the land use history of grasslands, which can be revealed based on species that survived in the soil seed bank (Karlík and Poschlod, 2014).

Summed up, we detected no differences in traits related to dispersal 'in space' (wind and animal-mediated dispersal, (Bakker et al., 1996b)), but found strong evidence, that, at least during the first two years after the clearance, species composition of the restored grassland was influences by the occurrence of mostly non-target species that were dispersed 'in time' (persistent, light seeds that were transported by men, (Bakker et al., 1996b)).

4.1.2. Establishment related traits

We compared traits that have been shown as predictive of plant species establishment (heavy seed mass, seedling emergence season in autumn, high SLA values) for estimating the importance of establishment for the restoration success of calcareous grassland vegetation.

Thereby, high seed mass is supposed to be correlated with nutrient supply for the seedling and thus heavy seeds are assumed to establish more easily (Cornelissen et al., 2003). In our study, however, heavy seeds were underrepresented compared to the reference during the first year after restoration while in later years no differences between grassland categories were found. This is supported by the earlier finding that species with low seed mass usually predominate in grazed calcareous grasslands (Kahmen et al., 2002) and thus, in this habitat type species with heavy seeds are generally of lesser importance.

Additionally, previous studies indicated that the occurrence of grazing pressure in late summer promotes the availability of gaps in the vegetation for species establishment increasing the frequency of autumn germinators (Kahmen et al., 2002; Piqueray et al., 2015). Recurring differences in the proportion of species germinating in autumn were detected throughout the study period. Thereby, a higher proportion of species germinating in autumn were found for the restored grassland since the third year after restoration rather indicating that germination conditions for typical calcareous grassland species were more favourable in the restored grassland than in the reference grassland.

High SLA values are assumed to be positively correlated with the growth rate of the seedling (Cornelissen et al., 2003) and accordingly we found a much higher proportion of species with high SLA values in the restored grassland for at least sixteen years after the initial restoration. However, high SLA values are generally correlated with the overall growth rate of a plant species and hence, are not only important for the seedling establishment itself but also for the overall competitiveness of a plant species (Cornelissen et al., 2003) which makes it difficult to identify the importance of this trait attribute for the establishment. As heavy seeds showed nearly no significant differences and the pattern for autumn germination was inconsistent, we propose that high SLA values in our study are rather an indicator for the general species competitiveness than establishment alone.

Summed up, no final conclusion on the changes in establishment related traits can be given. However, as seed mass recovered quickly and autumn germinators showed higher incidences in the restored grassland since the second year after restoration, species establishment was probably not a limiting factor for species recovery on the restored grassland.

4.1.3. Persistence related traits

Most of the traits, which were investigated for estimating the restoration success, were relevant for explaining plant species persistence in calcareous grasslands in response to moderate grazing disturbance, nutrient poverty and concurrence by more

competitive species (canopy height, first flowering, lateral spread, leaf distribution, life span, growth form, seed bank, SLA, start of flowering and seedling emergence).

Numerous studies have already shown that the occurrence of small plant species with basal rosettes, the ability to spread laterally, the high proportion of species producing transient seeds and the occurrence of autumn germinators are typical adaptations to small scale disturbances caused by moderate grazing pressure (Díaz et al., 2007; Kahmen et al., 2002; Piqueray et al., 2015; Poschlod et al., 1998). Accordingly, differences within restored and reference grasslands were detected for three of the four trait attributes (small, rosette species and the ability for lateral spread) until 2001, while the proportion of autumn germinating species was still higher in the restored grassland in 2018.

Trait attributes associated with the nutrient poverty of calcareous grassland habitats were a belated first flowering age, a prolonged life span, low SLA values, a high proportion of legumes and in general, a higher proportion of forbs than of graminoids (Díaz et al., 2007; Dupré and Diekmann, 2001; Kahmen et al., 2002; Piqueray et al., 2015; Wesuls et al., 2012). In accordance, the proportion of early flowering species decreased while the proportion of perennial species and of species with low SLA values increased, both reaching reference grassland proportions within the third, ninth and sixteenth year, respectively. Non-compliant was the proportions of legumes, which was significantly higher in the restored grassland during the first observation year while the proportion of forbs and graminoids both still showed significant differences between restored and reference grasslands after 25 years. However, the first finding was probably attributed to the occurrence of persistent seeds in the seed bank of the restored grassland (e.g. *Genista sagittalis* L.) while for the latter finding a possible explanation was provided by Diacon-Bolli et al. (2013) who showed that graminoids were dispersed better than forbs in ungrazed calcareous grasslands hinting that the dispersal of some forbs is still ongoing in our study.

Trait attributes that were correlated with the competitiveness of plant species were lateral spread, high canopy height, early first flowering, seedling emergences throughout the year, high SLA values and early start of flowering (Cornelissen et al., 2003). In 2013, there was only one plant trait attribute, associated with competitive behaviour, that had a higher incidence in the restored grassland, namely high lateral spread (>0.25 m/year), while all other attributes converged more quickly.

For persistence related traits (or contrary traits correlated with the competitiveness of plant species), we general detected longer recovery rates in the restored grassland than for traits related to dispersal while establishment and persistence related traits could not be clearly separated from each other (high SLA, autumn germinators). However, we detected no trait attributes that indicated significant functional differences between restored and reference grassland after a period of 25 years since restoration.

4.2. Plant functional groups

For analysing the extracted functional groups, we re-encountered the concept of the CSR-strategy (Grime, 1974). The three identified plant functional groups ('Grassland', 'Tall species, 'Early-succession species') largely resembled the classification of plant species according to this strategy in which competitive (C), stress tolerant (S) and ruderal (R) species are distinguished (Grime, 1977, 1974; Hodgson et al., 1999).

Thereby, Grime (1988) stated that short-lived, fast growing and rapidly reproducing species (= ruderals) are best suited to colonise highly disturbed habitats. The description matched the characteristics of the 'Early-succession species cluster' (e.g. high SLA values, persistent seeds, short-lived species). The high proportion of hemerochorously dispersed species in this plant functional group was linked to the frequent occurrence of weeds, which is also in line with the concept of ruderal strategists (Grime, 1988).

According to the CSR-classification, competitive species are characterised by tall and long-lived plant species that reproduce comparatively late in their life cycle and put considerably more effort into enlarging their surface than into reproduction, which allows species to persist in nutrient-rich and relatively undisturbed habitats (Grime, 1988), which matched the plant functional group of 'Tall species' (e.g. transient seeds, late reproduction). The high occurrence of tree and shrub species is thereby also consistent with the concept of the competitive strategy (Grime, 1988).

Stress-tolerators are small and slowly growing plant species characterised by attributes promoting species resilience towards environmental stress factors in moderately undisturbed habitats (Grime, 1988). Trait attributes of the 'Grassland Cluster' complied with these characteristics (e.g. small growth height, small SLA values, many rosette species).

Hence, in compliance with the CSR-strategy, stress-tolerant species made up the 'Grassland cluster', while the 'Tall species cluster' consisted of competitive and the 'Early-succession species cluster' of ruderal species. Calcareous grasslands, which were in the focus of this study, are characterised by the occurrence of high stress due to the nutrient-poor and dry habitat conditions, while the extensive grazing management caused moderate disturbances of the aboveground biomass (Poschlod and WallisDeVries, 2002). Therefore, it can be expected that stress-tolerant species will cope best with these environmental conditions due to their functional adaptations and will therefore be the dominant in calcareous grassland habitats (Grime, 1988; Moog et al., 2005). Indeed, the development of the plant functional groups in this study was in accordance with this assumption.

Generally, many ruderal species appeared during the first years after restoration, showing suitable adaptations to the massive disturbance caused by the implementation of the clearance measure. However, ruderal species could not establish themselves permanently due to the lack of severe disturbance events providing gaps in the vegetation for establishment and thus gradually disappeared (Hodgson et al., 1999; Moog et al., 2005). After a period of sixteen years, the functional group of ruderals could no longer be detected. Three years after the restoration, competitive species became increasingly dominant, especially in the period between 1995 and 2001. The restored grassland probably had a higher nutrient availability than the reference grassland, which promoted the growth of competitive species (Pywell et al., 2003). However, due to the extensive sheep grazing, competitive species were also reduced as nutrients were constantly depleted. As of the year 2013, approximately 20 years after clearance was applied as restoration measure, the most dominant plant functional group contained stress-tolerant species while a small group of competitive, mostly woody species,

additionally persisted. It can thus be concluded that the functional composition of the restored grassland was in equilibrium with the reference grassland.

However, it must be kept in mind that the characterisation of the plant functional groups was based on the dominant traits found to be significantly different between identified clusters. Although traits correspond to the CSR-strategy classifications, it may be possible that species showed intermediate strategies, e.g. species that were characterised by typical traits of ruderal and stress-tolerant species or of competitive and stress-tolerant species or even all three strategists (Hodgson et al., 1999; Moog et al., 2005). This was for example found for *Fragaria vesca* L. or *Phleum pratensis* L., which both have an affiliation towards all three strategies (CSR-strategists, Hodgson et al., 1999) and hence, were not consistently put into the same plant functional group in the different observation years. However, we mainly recorded species that were assigned constantly to the same group and had a high affiliation towards the respective strategy (e.g. *Briza media* L. or *Carex flacca* Schreb. – S-strategists; *Fraxinus excelsior* L. – C-strategists; *Capsella bursa-pastoris* (L.) Medik. and *Stellaria media* (L.) Vill. – R-strategists, Hodgson et al., 1999).

4.3. Implications given by the functional trait approaches

After approximately 25 years, we only found few trait attributes that still showed significant differences between reference and restored grassland while plant functional groups showed no longer a correlation with either grassland category. Therefore, the two functional trait approaches we used in this study both supported that the functional composition of a calcareous grassland, which was restored on a spruce clear-cut and managed by subsequent sheep grazing, was successfully re-established within the observation period.

Overall, the functional trait composition of the restored grassland showed a clear development towards the reference grassland, with differences in traits related to persistence and competitiveness recovering less quickly than those related to dispersal and establishment. That the functional composition of restored grasslands developed towards surrounding grasslands was also observed in a chronosequence study, which was conducted on grasslands restored by clearance and subsequent grazing by sheep (Piqueray et al., 2015). However, in the study of Piqueray et al. (2015), the maximum age of the restored grasslands covered a period of 15 years and the authors concluded that the restoration process was still ongoing in terms of functional trait recovery. Our results were in line with their conclusion, however, that after a period of more than 25 years, significantly differing traits could rather be attributed to floristic differences (e.g. proportion of graminoids and forbs).

The recovery of the functional composition was moreover supported by the development of plant functional groups over the study period. Here, the importance of functional differences was shown to decreased over the course of the study as the total differences explained by the axes of the ordination plots constantly declined (Table 4). In addition, the plant functional group characterised by trait attributes that were associated with rurality could no longer be detected after more than 20 years of observation. The two remaining groups, stress tolerators and competitors, showed no differences in trait attribute composition between restored and reference grassland indicating that the functional composition of both grassland categories was in equilibrium. Hence, the combination of both functional approaches showed a clear convergence of the two grassland categories and thus indicated a successful functional restoration.

5. Conclusion

Using two different functional trait approaches, we could demonstrate that in terms of functional composition, a former grassland which was restored by clearance of a spruce afforestation and subsequently managed by the traditional management of extensive rotational sheep grazing, could be successfully restored over a period of 25 years. Overall, the present study supports the assumption that functional traits in general, and plant functional groups in particular, can be very good predictors of recovery success.

In our study, restored and reference grassland were directly adjacent to each other, explaining the comparable fast recovery of the trait composition. It was shown that with increasing spatial isolation the restoration success of both floristic and functional composition is slowed down (Helsen et al., 2013). Therefore, dispersal limitations, as indicated by the low response of dispersal related trait attributes, were probably of minor importance for the vegetation recovery in this study, on the one hand due to the small size of the restored grassland, on the other hand also due to the close vicinity of the donor grassland (Helsen et al., 2013). Over the study period, the nutrient content of the soil likely had an more severe influence (Bullock et al., 2001), as traits correlated with the competitive character of significantly differed for more than 15 years while during the same time competitive species, which are promoted by high nutrient availability (Grime, 1988), were more abundant. In the course of the study, differences related to competitiveness and hence, higher nutrient content, gradually decreased. The overall functional recovery was thus much faster than it was recorded for other studies that investigated restoration success on former semi-natural grasslands characterised by a higher soil nutrient content which included in particular restored ex-arable fields (>50 and >35 years, respectively; Fagan et al., 2008; Helm et al., 2019). This study thus provides clear evidence that the functional recovery of nutrient-poor calcareous grasslands can be significantly faster on clear-cut patches that have been exposed to lower nutrient inputs than, for example, fertilised arable land or improved grassland.

To the best of our knowledge, this study is an exceptional example for the investigation of the functional recovery of calcareous grassland, restored by clearance and sheep grazing, where vegetation data was collected on permanent plots continuously and therefore, is available for an extended period (more than 25 years). The results of this study thus supported once more the importance of long-term observations, preferably using permanent plots, as changes may develop over long time (Bullock et al., 2001) and restrictions of chronosequence approaches can be overcome (Helsen et al., 2013).

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Patricia Krickl reports financial support was provided by Germany Federal Ministry of Education and Research.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02509.

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