

Effects of long- and short-term management on the functional structure of meadows through species turnover and intraspecific trait variability

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Abstract The functional structures of communities respond to environmental changes by both species replacement (turnover) and within-species variation (intraspecific trait variability; ITV). Evidence is lacking on the relative importance of these two components, particularly in response to both short- and long-term environmental disturbance. We hypothesized that such short- and long-term perturbations would induce changes in community functional structure primarily via ITV and turnover, respectively. To test this we applied an experimental design across long-term mown and abandoned meadows, with each plot containing a further level of short-term management treatments: mowing, grazing and abandonment. Within each plot, species composition and trait values [height, shoot biomass, and specific leaf area (SLA)] were recorded on up to five individuals per species. Positive covariations between the contribution of species turnover and ITV occurred for height

and shoot biomass in response to both short- and long-term management, indicating that species turnover and intraspecific adjustments selected for similar trait values. Positive covariations also occurred for SLA, but only in response to long-term management. The contributions of turnover and ITV changed depending on both the trait and management trajectory. As expected, communities responded to short-term disturbances mostly through changes in intraspecific trait variability, particularly for height and biomass. Interestingly, for SLA they responded to long-term disturbances by both species turnover and intraspecific adjustments. These findings highlight the importance of both ITV and species turnover in adjusting grassland functional trait response to environmental perturbation, and show that the response is trait specific and affected by disturbance regime history.

Keywords Abandoned meadows · Mesic grassland · Plant height · Specific leaf area · Shoot biomass

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Introduction

Plant functional traits are often studied to assess the response of plant communities to environmental changes

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(Ackerly and Cornwell 2007; Garnier et al. 2007), and the consequences of such changes on ecosystem functions via alterations in community trait composition (Lavorel and Garnier 2002; Reich et al. 2003; de Bello et al. 2010; Valencia et al. 2015). There is a general consensus that species assemblages are predominantly shaped by a hierarchical system of ecological forces: external environmental filters select a pool of adapted species within regions and locations, then internal filters determine local assemblages via the suitability of species' traits (Grime 1973; Keddy 1992; Violle et al. 2012). Community trait response to environmental changes is often described by various measures of trait composition. Using community trait mean values, either weighted by each species' abundance, or simply unweighted, is a common way to assess the role of ecological drivers on the functional structure of plant communities (Garnier et al. 2004; Gross et al. 2008; Violle et al. 2007).

Comparing weighted (CWM) and non-weighted community trait means (CM) is particularly useful for understanding the effects of dominant (with CWM) and subdominant species (with CM) (Cingolani et al. 2007; Pakeman et al. 2008) in response to environmental changes. Most of the studies using CWM and CM have, until now, focused mainly on the variability occurring between species (Kraft et al. 2008), i.e. by using one trait value for each species for all community samples where the species occurs. These studies ignore the potential impact of intraspecific trait variability (ITV) on variation of both CWM and CM across gradients (Jung et al. 2010; Gross et al. 2013; Carmona et al. 2014). However, ITV can represent a non-negligible contribution to the overall functional trait response to environmental variation, being at least as important as species turnover (Albert et al. 2010; Messier et al. 2010; Jung et al. 2014), with significant effects on community assembly (Fridley et al. 2007; Jung et al. 2010; Bolnick et al. 2011; Le Bagousse-Pinguet et al. 2014;). Neglecting ITV when assessing changes to community trait means produces findings which reflect only functional changes attributed to species turnover (i.e. changes in either species composition and/or their abundance). Alternatively, by considering the trait values for a given species across multiple environmental conditions, changes to community trait means reflect both species turnover and ITV effects. Thus, analyses of changes in functional composition should decompose total variability into its relative components attributable to both species turnover and ITV (Lepš et al. 2011).

Few studies have decomposed the relative effect of turnover vs. ITV in response to environmental changes. It is reasonable to expect that major environmental changes acting for long periods should cause functional replacement by species turnover, whereas moderate changes acting on shorter time scales should influence ITV (Auger and Shipley 2013; Jung et al. 2014). To the best of our

knowledge, such expectations have never been empirically tested. Some studies assessing the effect of changes in management on functional traits have reported a large level of community resilience in the first years after the change of treatment, with large trait variability and slow competitive exclusion or colonization rates in grassland communities (de Bello et al. 2011; Galvánek and Lepš 2012; Lepš 2014; Lepš et al. 2011). Although there is generally some functional turnover in response to short-term changes, it usually reflects shifts in species relative abundance, rather than changes in the presence of species (Jung et al. 2014). This suggests that changes in functional composition due to short-term fluctuations or during initial stages of long-term fluctuations should operate mainly through ITV (Carmona et al. 2014; Jung et al. 2014), which can further serve as a buffer against changes in plant composition and protect resident species from extinction (Lepik et al. 2005). Testing the relative roles of species turnover and ITV in functional trait variability due to long- and short-term changes requires disentangling their relative contribution. The method proposed by Lepš et al. (2011) allows such decomposition of species turnover vs. ITV effects. Furthermore, this approach enables us to identify whether species turnover and ITV select for similar dominant trait values via an analysis of their covariation. Most studies reported a positive covariation between species turnover and ITV for changes in functional traits (Auger and Shipley 2013; Lepš et al. 2011; Siefert et al. 2014), although a few studies recorded a negative covariation for some traits (Kichenin et al. 2013; Pérez-Ramos et al. 2012). A positive covariation between the effects of species turnover and ITV suggests that the factors selecting for dominant species with certain trait values may also affect trait plasticity, reinforcing trait selection in the same direction (Lepš et al. 2011).

In this study, we disentangled the relative contributions of species turnover and ITV in the functional trait response of a grassland community to both short- and long-term changes in traditional management, namely, changes through abandonment, mowing, and grazing, reflecting recent changes in land use. Abandonment of traditional management practices, such as mowing and grazing, has progressively changed plant species composition in more than 70 % of grassland communities in Europe over the past 50 years (Güsewell et al. 1998; Ellenberg and Leuschner 2010). Temperate grassland communities host some of the greatest plant diversity in the world (Wilson et al. 2012) and provide several important ecosystem services (de Bello et al. 2010). Effects of management changes on species composition operate mainly through the intensity of biomass loss, and heterogeneity of the disturbance (e.g. Moog et al. 2002). Mowing and grazing may affect species composition differently; whereas grazing results in a more patchy vegetation structure, effects of mowing on species

and trait composition are more uniform (Catorci et al. 2011; Garnier et al. 2007; Moog et al. 2002; Stammel et al. 2003). On the other hand, both mowing and grazing may have similar effects on functional traits, acting as a general disturbance that promotes smaller species with traits associated with greater relative growth rate and more acquisitive resource use (Díaz et al. 2001; Garnier et al. 2004). It is also unclear if short- and long-term changes in traditional management affect community trait structure in the same way (Díaz et al. 2007), illustrated by the inconsistency within the literature on the effect of land use changes on functional traits. Based on our current understanding, we expect:

1. Shifts in functional composition caused by long-term management to result mainly from species turnover, with short-term management resulting in changes from ITV.
2. Positive covariation between the contribution of species turnover and ITV to changes in functional traits, suggesting similar, consistent effects of selection on both inter- and intraspecific levels in response to both short- and long-term management.
3. Generally, a similar effect of mowing and grazing on functional traits, as both treatments lead to biomass removal.
4. But differences in the effects of short- and long-term management regimes on particular functional traits.

Finally, comparing these patterns for abundant and less abundant species by using CWM and CM (see above), we assess if turnover and ITV are operating in the dominant or the subordinate component of the community.

Materials and methods

Study site

The study site is a species-rich mesic meadow in Tri Bubny, Czech Republic (49°56′04″N, 15°51′05″E), at 287 m a.s.l. The mean annual temperature is 8–9 °C and mean annual precipitation is 700–800 mm. Phytosociologically, the vegetation belongs to the dry mesic meadows *Ranunculo bulbosi-Arrhenatheretum elatioris* Ellmauer in Mucina et al. 1993 (Hájková et al. 2007). The dominant species are *Bromus erectus* Huds., *Festuca rupicola* Heuffel, *Poa pratensis* L., *Arrhenatherum elatius* (L.) J. Presl et C. Presl, *Trisetum flavescens* (L.) P. Beauv., *Viola hirta* L., *Securigera varia* (L.) Lassen and *Carex flacca* Schreber. Until the mid 1980s, traditional meadow management here consisted of both regular mowing for hay twice a year, and occasional grazing at the end of the hay-growing season,

throughout the entire site. Since the mid 1980s some scattered parts of the site with insufficient access were progressively abandoned.

Experimental design and sampling

The meadows within the site were categorized as one of two historical (i.e. long-term) management regimes: mown or abandoned (since the mid 1980s, see above). The experiment was set up in ten blocks (6 × 9 m). The blocks were situated in different long-term treatments available within the site—five blocks on the mown part of the site, five on the abandoned part. Each block was then divided into three 3 × 6-m plots; one of three short-term management regimes was implemented in each—mowing, grazing and abandonment. In each plot, one half was used for vegetation records, and the second used for measuring functional traits so as to avoid disturbing and trampling vegetation while the survey was carried out. In the first half of each plot (3 × 3 m), species composition and percentage cover were visually estimated. In the second half of the plot (3 × 3 m) five 20 × 20-cm subplots were randomly selected. The trait data [height, biomass, and specific leaf area (SLA)] were collected in these subplots. In each subplot, one plant individual (or one shoot in the case of clonal plants) per species found was used for trait measurement. The individual closest to the centre point of the subplot was selected, and subsequent trait measurement followed standardized protocols (Cornelissen et al. 2003). The number of individuals sampled reflected species presence in the subplots (in a few cases resulting in only one individual per species sampled within a plot) with often up to five individuals per species and plot measured. Additional trait data were collected for other abundant species that did not occur in the target subplots, but were common in a given plot (for these species we collected up to five individuals when available in subplots devoted to trait sampling, fewer when not available with a minimum of three). In total, height, biomass, and SLA of 61 non-woody plant species were measured. We found very few woody species in the plots of the experiment. All of them were found in the form of seedlings and saplings, and were sufficiently scarce so as to not to be considered in trait sampling and data analyses.

Data analysis

Community trait means were calculated as CWM and CM (see “Introduction” and below) for all traits on a per plot basis. Species relative cover was used as a weighting factor for CWM in accordance with Garnier et al. (2004), whereas all species had the same weight for CM. Species turnover vs. ITV effects on the functional structure of the communities were disentangled by the method proposed by

Lepš et al. (2011), which is based on a repeated measures ANOVA analysis. For both community trait mean indices (CWM and CM), this method requires the calculation of two types of measure for each plot, the so-called fixed and specific community trait mean. We explain how the approach works with the example of CWM, but the same approach can be used also for CM. Specific CWM values were calculated using the species trait values recorded in each specific plot (e.g. average of all individuals of a species found in a plot). Differences across plots in specific CWM can indicate both the effect of species turnover and the effect of ITV. Fixed CWM values were calculated using the mean trait value across all plots of all blocks. Differences in fixed CWM across plots therefore indicate changes in species turnover only. The difference between specific and fixed CWM for a given plot is then caused only by ITV. The distinction between CWM and CM is that, in the case of CWM, both changes in species identities and their relative abundances can cause functional turnover, whereas for CM it can only be caused by species identities. The approach by Lepš et al. (2011) to decompose species turnover, ITV and their covariation is based on a decomposition of the sum of squares in a repeated measures ANOVA, with the repeated measures factor being the type of CWM (or CM) (i.e. fixed or specific). The approach therefore tests for the relative effect of species turnover and ITV in the whole data set, and for each considered environmental predictor. The specific R function proposed by Lepš et al. (2011) was used for this purpose, now available in the package *cati* (<https://cran.r-project.org/web/packages/cati/index.html>). The differences in effects of mowing and grazing on CWM and CM of examined functional traits were analysed by ANOVAs, where plots with short-term abandonment were removed from the analyses. All statistical analyses were performed in R 2.15.2 (R Development Core Team 2014).

Results

Observed variability in functional traits reflected both species turnover and ITV. However, the relative contribution of species turnover and ITV differed among studied traits and management regimes. Species turnover and ITV contributed almost equally to the variability in height (on average 35 and 39 % of the total variability, respectively). Variability in biomass reflected mainly ITV (41 %), whereas the contribution of species turnover was minor (15 %). On the other hand, species turnover made a major contribution to the total variability in SLA (58 %) with ITV accounting for only 27 % of total SLA variability (Fig. 1).

The relative contribution of species turnover and ITV to the variability of the studied functional traits differed when

considering long- or short-term management (Table 1; Fig. 1). The relative contribution of species turnover to the variability in these traits was pronounced when considering the effects of long-term management (2–25 % of variability in individual traits), whereas short-term management had a greater effect on ITV for height and biomass (11–23 % of variability). Though less strong compared with height and biomass, short-term management affected the CWM of SLA, but not the CM. This change in functional composition came about via species turnover and not via ITV (Table 1; Fig. 1). There was a positive covariation (illustrated by horizontal lines above the bars in Fig. 1) between species turnover and ITV effects for height and biomass, suggesting a unidirectional change in plant traits due to changes in community composition and within-species trait variability. In contrast, we observed only minor negative covariation in the case of SLA when considering short-term management effects (Fig. 1).

Long- and short-term management and their interactions significantly affected CWM and CM of these particular functional traits in our grassland community (Table 1; Figs. 1, 2). CWMs and CMs of height and biomass were always positively correlated ($r > 0.54$, $p < 0.03$). Long-term abandoned plots had generally greater height (on average 24.7 vs. 21.4 cm), biomass (0.26 vs. 0.15 g) and SLA (21.7 vs. 17.9 m²/kg) than plots that underwent long-term management. Effects of short-term mowing and grazing did not differ for any of the examined traits (Table 1, Online resource 1). Short-term abandonment generally led to increased biomass and height (Table 1; Fig. 2). While long-term abandonment increased SLA, short-term abandonment tended to result in a decrease in SLA (Fig. 2). Approximately half of the variation in the CWM and CM for height, biomass and SLA was explained by applied long- and short-term management (ML and MS respectively in Fig. 1). In the case of height and biomass, short-term management explained a higher proportion of trait variability than long-term management for both CWM and CM (Fig. 1) Regarding SLA, long-term management explained a greater portion of CWM and CM variability. Short-term management explained only a small amount of the trait variability for SLA, mainly because of negative covariation between species turnover and ITV. The interaction of short- and long-term treatments was significant, particularly for species turnover effects based on CM, and therefore attributable to changes in species identities (Table 1).

The use of CWM vs. CM notably modulated the outcome of the analysis (Table 1; Figs. 1, 2). Using CM generally increased the effect of both long- and short-term management for all three traits, and produced an increase in the effect of ITV for height and biomass (Fig. 1). In the case of SLA, where short-term management did not have

Fig. 1 Decomposition of changes in (1) log (height) (a), biomass (c) and specific leaf area (SLA) (e) using the community weighted trait mean (CWM) based on cover and (2) log (height) (b), biomass (d) and SLA (f) using the community non-weighted trait mean (CM) based on presence/absence. *Black columns* represent the effect of species turnover, whereas *grey columns* indicate the effect of intraspecific trait variability (ITV). *Black bars* denote total variation (i.e. variation in specific averages). The *space* between the *top* of the column and the *bar* corresponds to the effect of covariation; if the *bar is above* the column, the covariation is positive, if the *bar crosses* the column, the covariation is negative. Significance values are indicated by *asterisk* above each column. The positioning of an *asterisk within the -/-* graphic represents significance of the turnover/intraspecific variability/total, respectively. Full results of statistical analyses are presented in Table 1. *ML* Management (long term), *MS* management (short term), *Res.* residuals

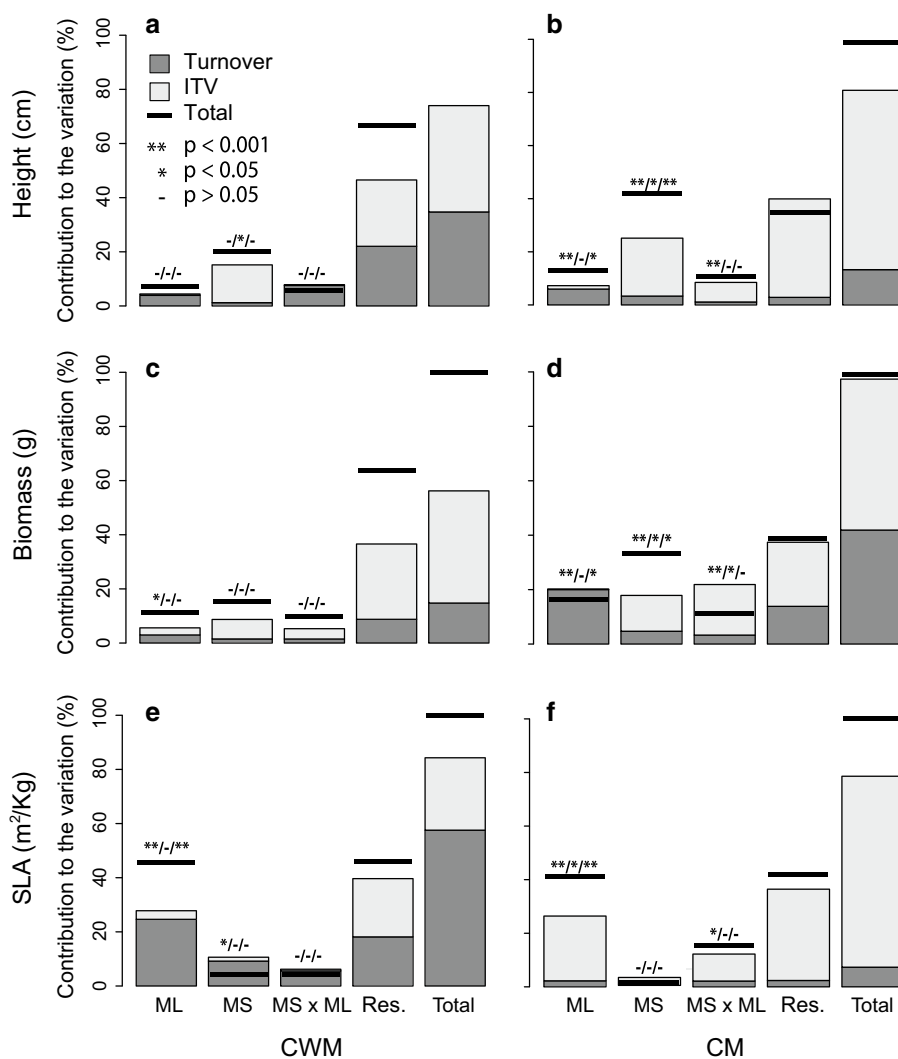


Table 1 *p* Values for each trait indicating significant effects of treatment on communities when analysed by repeated measures ANOVA decomposing species turnover, intraspecific trait variability (ITV) and their covariation using the community weighted trait mean (CWM) based on cover (left value) and the community non-weighted trait mean (CM) based on presence/absence (right value)

Trait	Management	Turnover		Intraspecific variability		Total	
		CWM	CM	CWM	CM	CWM	CM
Height	Long term	0.091	<0.001	0.544	0.441	0.178	0.019
	Short term	0.618	<0.001	0.017	0.015	0.093	<0.001
	Long term × short term	0.070	<0.001	0.901	0.196	0.472	0.092
Biomass	Long term	0.023	<0.001	0.209	0.711	0.092	0.013
	Short term	0.237	<0.001	0.126	0.018	0.144	0.004
	Long term × short term	0.242	<0.001	0.316	0.005	0.273	0.099
SLA	Long term	<0.001	<0.001	0.120	0.002	<0.001	<0.001
	Short term	0.025	0.157	0.559	0.472	0.441	0.737
	Long term × short term	0.089	<0.001	0.778	0.193	0.461	0.118

Significant results are in *italic*
 SLA Specific leaf area

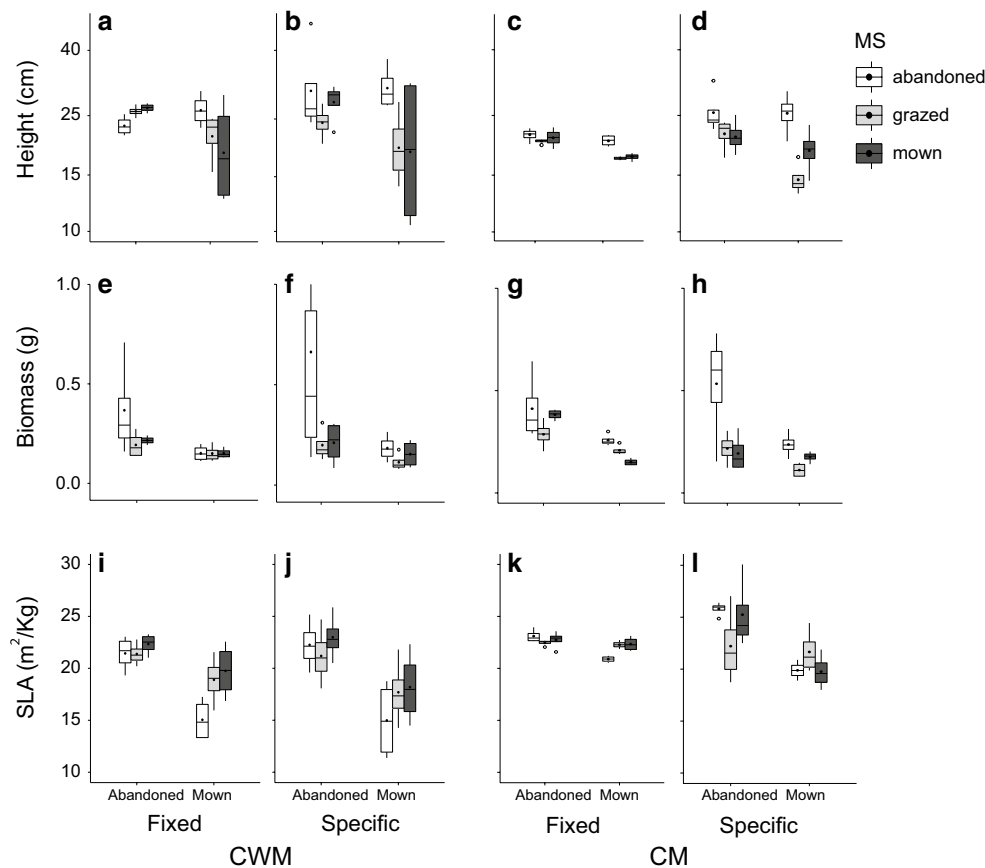


Fig. 2 Interaction plots for (1) fixed and specific CWMs of log (height) (**a**, **b**), biomass (**e**, **f**) and SLA (**i**, **j**) using CWM based on cover and (2) fixed and specific CMs of log (height) (**c**, **d**), biomass (**g**, **h**) and SLA (**k**, **l**) using CM based on presence/absence in each treatment type. For graphical purposes biomass plots were scaled down to 1.0, resulting in the whisker of the abandoned:abandoned

interaction for specific values being cut prematurely (actual upper extent = 1.6). The *boxes* show the first to third quartiles with the medians as *horizontal lines* and means as *full dots*; the *whiskers* show the range. Full results of statistical analyses are presented in Table 1. Note log scale used on y-axis in **a–d**. For *abbreviations*, see Fig. 1

a considerable effect, long-term changes influenced both species turnover and ITV when considering CM, but only turnover when using CWM (Fig. 1).

Discussion

The main aim of this study was to assess the effect of species turnover and ITV on community trait response to short- and long-term management changes. The relative contributions of species turnover and ITV to changes in functional traits of meadow communities resulting from short- and long-term management were not consistent across traits. Long-term management generally led to changes in trait composition due to species turnover, although SLA also varied through ITV, particularly for subdominant species (i.e. CM in Fig. 1). Short-term management changes caused community functional changes through ITV, as expected, but only for height and biomass,

which responded more strongly to short-term management changes compared to SLA. On the other hand, our findings confirmed that ITV and species turnover generally cause a unidirectional functional change in communities (positive covariation), i.e. both response strategies react to disturbance regime changes in the same way. Similarly, while we generally confirm that mowing and grazing provided rather similar effects on the functional composition of vegetation, the results also show opposite effects of short- and long-term management changes on SLA. As such, our study shows far-reaching effects of land-use changes, and the interplay of long- and short-term disturbance changes in both species turnover and ITV as grassland assemblages respond to management changes.

Effect of turnover, ITV and their covariation

Species turnover greatly contributed to trait variability resulting from long-term changes (hypothesis i). Species turnover

has been shown to play an important role in trait variation across communities distributed along steep spatial and temporal gradients, causing competitive exclusion (Ackerly and Cornwell 2007; Kichenin et al. 2013; Lepš 2014). Similarly, our results suggest that long-term changes are likely to induce functional changes by species turnover, although ITV can reinforce these effects (positive covariation). ITV played a dominant role in shoot biomass and height variability when considering short-term management. For these traits, which are commonly associated with ecosystem processes linked to productivity (de Bello et al. 2010), the response to short-term environmental changes was stronger than that of longer term environmental changes, highlighting a rapid adjustment of community structure to short-term changes. This is in agreement with the findings of several recent studies suggesting a prominent role of ITV in determining the functional trait structure among plant communities, possibly providing a flexible response to rapid environmental changes (Albert et al. 2010; Messier et al. 2010; Jung et al. 2014). In fact, high ITV may significantly contribute to the resilience of grassland communities to short-term changes in management such as mowing, leading to relatively slow turnover of species (Lepš 2014). However, we found only an effect of ITV on long-term disturbance changes for less dominant species (CM) for SLA. This is in agreement with findings suggesting organ-level traits, such as SLA, are less prone to ITV than whole plant traits, such as total height (Marks 2007; Seifert et al. 2015). Whereas whole plant traits tend to be best explained by environmental factors, showing higher ITV between sites, organ-level traits tend to be rather conservative (Marks 2007). Responses in community SLA to environmental changes are thus likely to result from species turnover.

The significant positive covariation of species turnover and ITV (hypothesis 2), suggests a community response where environmental pressures not only select for species with certain traits, but also favour a similar plastic response of individuals within species through ITV, thus resulting in a reinforcement of trait selection, as opposed to a compensatory effect. In other words, in sites that are dominated by species which have, for example, high values for height, plant individuals also exhibit values which are larger than average for respective species measured at other sites (Lepš et al. 2011; Seifert et al. 2014). The covariation between species turnover and ITV may indicate that the expression of these traits has similar functional roles, exhibiting comparable responses to environmental changes between and within species (Fajardo and Piper 2011). Either way, whether environmental influences select for a particular set of trait values through species turnover or ITV, the resulting community can, and most likely will, be a product of complex positive and negative covariation and evolutionary trade-offs (Lepš et al. 2011).

Management changes

Concerning particular effects of management changes (hypotheses 3 and 4), long-term abandonment led to communities dominated by tall species with high biomass and high SLA. Secondary succession generally results in replacement of fast-growing species with taller acquisitive species with lower SLA (Garnier et al. 2004; Kahmen and Poschlod 2004). This is due to high SLA allowing for efficient resource capture, but at the cost of being short lived and susceptible to herbivores, with low SLA achieving better resource retention and higher persistence (Coley 1988; Poorter and Van der Werf 1998). We confirmed that height and biomass can increase with succession, which is not surprising given the typical correlation of these two traits, both with a key role to play in resource acquisition and competitive ability (Grime 1973). However, we observed a decrease in SLA with abandonment only in the case of short-term management change on previously mown plots. This shows that succession in previously mown plots was rather rapid after the change of management, resulting in decreasing SLA, caused by changes in species composition, even over a short timescale. On the other hand, short-term abandonment, mowing and grazing of previously abandoned plots did not result in increased SLA, which is at odds with findings of previous studies (MacGillivray et al. 1995; Zhao et al. 2009). This contrasting effect of long- and short-term abandonment on SLA warrants future examination, and could partially go to explaining the generally low consistency in trait response to land-use changes across sites (Díaz et al. 2007). Long-term management can decrease fertility and select for more stress-tolerant species (Wilson et al. 1999), thus leading to communities in mown and grazed conditions with lower SLA values [associated with stress-tolerant species and lower fertility sites (Grime 2001)]. The differences in the effects of applied management on SLA in previously mown and abandoned plots also show that species response is highly dependent on previous management.

Previous studies also reported mowing and grazing selecting for different species composition, as grazing results in more heterogeneous and patchy vegetation, whereas these patterns are absent under mowing (Catorci et al. 2011; Stammel et al. 2003). On the other hand, mowing and grazing had rather similar effects on functional traits in our case. This suggests that the effects of management on functional traits may operate mainly through intensity of biomass loss or biomass recovery rate, which is similar for both these treatments, rather than treatment heterogeneity, which is higher for grazing (Garnier et al. 2007; Moog et al. 2002). Similar effects of mowing and grazing on functional traits indicate that different management may maintain communities with rather similar functional

trait composition, even though species compositions may be different. We conclude that increased competition due to abandonment may result in more rapid changes in community functional traits than minor changes caused by differential disturbance after switching between mowing and grazing.

Species abundance effect

In our study we also show that the relative contribution of ITV and species turnover differed among analyses based on species cover (CWM), and analyses based on species presence-absence (CM). These differences suggest that dominant and subordinate species may respond differently to management, although some patterns may remain the same for both groups of species (Kumordzi et al. 2015). When increasing the weight of subordinate species using CM instead of CWM, ITV made a larger contribution. This was especially pronounced for variation in SLA caused by long-term management. These differences show that for SLA, long-term management could have a major effect on one or several dominant species, resulting in the observed species turnover when analysed using species cover. The higher relative contribution of ITV when increasing the weight of less dominant species by using CM then suggests that long-term management also affected less dominant species, but instead of modifying their abundance, these species expressed changes in their SLA, perhaps adjusting to changes in the dominant species. Since SLA is related to plant assimilation rate and growth trade-offs (Shipley 2002), SLA ITV may help less abundant species to persist in suboptimal abiotic and biotic conditions (Givnish 1988) and serve as a buffer against, or enhance, changes in plant composition.

Conclusion

As many natural landscapes become increasingly artificially altered, understanding the implications of this change on functional traits is critical, as functional traits have direct implications for the functioning of ecosystems (de Bello et al. 2010; Valencia et al. 2015) and the regulation of biodiversity (Violle et al. 2012; Le Bagousse-Pinguet et al. 2014). Here we have seen how temporal scale and management affect the partitioning of functional trait responses into their components (species turnover and ITV), and how these components often exhibit unidirectional change in association with one another. Furthermore, we have demonstrated how short- and long-term management effects are interdependent, each influencing the effect the other has on community trait composition. This results in the situation where the response of plant species to short-term changes is highly dependent on the previous long-term management (Lepš 2014). Our findings suggest that management practices

should be informed by previous management at respective sites. The same management approaches may not be appropriate for grasslands which differ historically in management, even if their species composition may be largely similar, given we have seen how the same species may respond differently to applied management in such cases. In turn, informed management can greatly contribute to a better protection not only of individual species but also of grasslands on the whole, as understanding the factors driving functional trait variability can greatly improve our understanding of the effects underlying ecosystem processes.

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Author contribution statement Y. L. B. P., F. B., L. G., Z. H., Š. J., J. K. and J. L. designed the experimental and analytical approach; Z. H. and Š. J. obtained the data; L. G. and M. V. analysed the data; C. R. and M. V. wrote most of the first draft of the manuscript; C. R. made the language corrections; all coauthors contributed to the discussion of data analysis and results and contributed to the final writing.

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