

Weather fluctuations drive short-term dynamics and long-term stability in plant communities: A 25-year study in a Central European dry grassland

Felícia M. Fischer¹  | Kryštof Chytrý¹  | Jakub Těšitel¹  | Jiří Danihelka^{1,2}  | Milan Chytrý¹ 

¹Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

²The Czech Academy of Sciences, Institute of Botany, Průhonice, Czech Republic

Correspondence

Felícia M. Fischer, Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic.

Email: ffischer@mail.muni.cz

Funding information

FMF received support from the Operational Programme Research, Development and Education – Project Postdoc@MUNI of Masaryk University (No. CZ.02.2.69/0.0/0.0/16_027/0008360). JT, JD and MC were supported by the Czech Science Foundation (19-28491X). In addition, JD was also supported by long-term research development project No. RVO 67985939 of the Czech Academy of Sciences.

Co-ordinating Editor: David Ward

This article is a part of the Special Feature Permanent plots in vegetation science, edited by Francesco de Bello, Enrique Valencia, David Ward and Lauren Hallett.

Abstract

Question: Infrequent events of extreme drought or extreme temperatures may considerably affect the structure and functioning of vegetation. Here we investigate how fluctuations in precipitation and temperature shape year-to-year dynamics and plant species composition in a dry grassland community, and how this variation affects plants with different life histories.

Location: Dry grassland (*Festucion valesiaca*) in the Pavlov Hills, SE Czech Republic.

Methods: Long-term trends in vegetation change in the grassland studied were assessed by the ordination of plot records from vegetation surveys performed between 1930 and 2019. In addition, year-to-year changes in vegetation were studied in seven permanent plots of 16 m² surveyed annually from 1993 to 2018. Variation in species composition and abundances was related to temperature and precipitation in the preceding two springs, summers, autumns and winters using ordinations and mixed-effect linear models.

Results: There were no remarkable directional changes in the grassland community over the period 1930–2019. However, during the last 25 years, the community exhibited pronounced year-to-year fluctuations, which depended on weather conditions in the previous two years. Species with different life histories (e.g. perennials vs. annuals) and different ecology (e.g. ruderal vs. dry-grassland species) responded differently to specific weather patterns. Perennials were sustained by wet summers, annuals benefitted from wet springs and autumns and moderately warm and wet winters, and covers of ruderals of mixed life histories increased after dry summers.

Conclusions: Plant species composition in a Central European dry grassland shows remarkable year-to-year dynamics in response to weather patterns over the previous two years. These community changes are non-directional and contribute to the stability of this grassland, which has not changed considerably over the past 90 years.

Felícia M. Fischer and Kryštof Chytrý have contributed equally.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. *Journal of Vegetation Science* published by John Wiley & Sons Ltd on behalf of International Association for Vegetation Science

However, increasing frequency of drought events because of ongoing climate change can result in a directional change with an expansion of ruderal species.

KEYWORDS

climate change, Czech Republic, drought, permanent plots, plant community, repeated vegetation survey, vegetation dynamics, weather patterns

1 | INTRODUCTION

Climate change is currently considered as one of the major threats to biodiversity, as it might increase the ongoing rate of species extinctions (IPBES, 2019). In addition to extinctions, species distributions are expected to shift following the predicted changes in temperature and precipitation across the globe (e.g. Porfirio *et al.*, 2014). For these reasons, ecologists anticipate directional changes in the composition and structure of plant communities. Climate change is also expected to increase weather fluctuations within single years and between consecutive years (IPCC, 2012; IPBES, 2019). Extreme climatic events and increasing seasonal fluctuations are already being reported around the globe (Spinoni *et al.*, 2018; IPBES, 2019). For this reason, it is necessary to describe and understand fine-scale changes in vegetation following such oscillatory weather patterns.

In dynamic ecosystems such as temperate grasslands, fluctuations in the environment shape community composition (Adler *et al.*, 2006); therefore, such ecosystems are also affected by ongoing climate change (Woodward and Lomas, 2004; Erdős *et al.*, 2018). The composition of communities and change in richness varies from place to place depending on the environment but also on fluctuations in weather conditions, combined with intrinsic population and community dynamics over time (Herben *et al.*, 1993; van der Maarel and Sykes, 1993; Adler *et al.*, 2006). Such dynamics can be best understood by means of detailed long-term observations in permanent plots (e.g. Dunnett *et al.*, 1998; Watkinson and Ormerod, 2001); however, relevant high-quality datasets are rare. Such studies are nevertheless very important because the way in which the communities deal with extreme weather events in the present will define their resistance or resilience to future climate change.

Variations in environmental conditions and resource availability are the key mechanisms that maintain biodiversity by supporting local-scale co-occurrence (Chesson and Warner, 1981; Descamps-Julien and Gonzalez, 2005; Tredennick *et al.*, 2017). Weather fluctuations prevent competitive exclusion between species that co-occur at a site, and at the same time allow species with different strategies and from different climatic domains to co-exist at the edge of their ecological niches (Adler *et al.*, 2006). Differences in response to extremes of climate between species with different ecological strategies can therefore lead to a non-equilibrium coexistence owing to stochastic fluctuations between years (Wilson, 2011). In such cases, when the weather conditions are favourable for a certain type of species strategies, other species may decline and be restricted to small patches partly because of a direct reaction to the environment

and partly because of competition. Once the weather shifts towards a state that is favourable to other types of strategies, species with these strategies spread again, buffering their losses (storage effect; Chesson and Warner, 1981; Adler *et al.*, 2006). This is specifically true for dry grasslands on shallow rocky soils with low water retention which are characterized by considerable species shifts according to weather fluctuations, yet are stable in the longer term (Dostálek and Frantík, 2011; Hroudová and Prach, 1986; Matesanz *et al.*, 2009). Such types of vegetation consist of plants with different life strategies (annuals, biennials and other short-lived species, and perennials) and various adaptations to different climatic conditions such as sclerophylly, succulence, deep-rooting, or ephemeral life-history (Chytrý, 2007).

Here, we used a unique dataset of plant species composition and abundance from dry grassland permanent plots that were surveyed annually for a period of 25 years, complemented with a dataset of non-permanent plots from the same area sampled since 1930. We ask (a) whether there are long-term directional changes in the dry grassland plant community, (b) what is the extent of inter-annual fluctuations in species composition and relative abundance, (c) whether the year-to-year community dynamics depend on weather conditions of the current and previous years, and (d), if so, whether species with contrasting life-histories show specific responses to different weather patterns.

2 | METHODS

The study was conducted on Děvín Hill in the northern part of the Pavlov Hills, southern Moravia, south-eastern Czech Republic. The Pavlov Hills are situated in the Pannonian phytogeographical province (Fekete *et al.*, 2016), which is a part of the Euro-Siberian forest-steppe region (Chytrý *et al.*, 2017; Erdős *et al.*, 2018). The climate of the area is subcontinental with annual temperature means of 8–9.5°C, January (coldest month) means of –1 to –2°C, and July (warmest month) means of 19–20°C. The total annual precipitation is 500–550 mm, of which 300–325 mm falls in the growing season (Tolasz *et al.*, 2007). The temporal variation in precipitation is considerable (CV = 52.4% between seasons of each year for the past 29 years), and long periods of drought are common (Appendix S1). The area is well-known for its high species richness and high diversity of habitats within a relatively small area (Danihelka *et al.*, 2015). Owing to the limestone bedrock, the Pavlov Hills host a significant number of Sub-Mediterranean plant species, which co-occur here

with continental steppe species. South-facing slopes and crests are covered by dry grasslands of *Festucion valesiaca* (on shallow soils) and *Bromo pannonicus*-*Festucion pallentis* (on rock outcrops; Unar, 2004; Chytrý, 2007; Danihelka *et al.*, 2015). Plant taxon concepts and names used in this study follow Danihelka *et al.* (2012) and those of vegetation units follow Chytrý (2007).

Děvín Hill (549 m a.s.l.), the highest in this area, was historically subjected to several vegetation surveys focused on dry grasslands, most notably by Klika (1931), Šmarda (1975), Toman (1976) and Unar (2004). We used plot records from these studies and plots recorded by other researchers in the same area to assess long-term trends in dry grassland plant species composition. These plots (total 96), recorded in ~1930–2019 (called 'historical dataset' hereafter), were extracted from the Czech National Phytosociological Database (Chytrý and Rafajová, 2003) and supplemented by unpublished data sampled by K. Chytrý. A full list of plots including their unique number, author(s), recording date/year and a reference to the published source (if available) is provided in Appendix S2.

To explore year-to-year grassland dynamics, we used another dataset from the same area, called 'permanent-plot dataset'. Seven permanent plots of 4 × 4 m², marked by metal rods, were established in 1993 in the summit area of Děvín at an altitude of ~500–520 m a.s.l. (48°52'04.0"N, 16°38'46.0"E). These plots were placed in a relatively homogeneous area of dry grassland of the alliance *Festucion valesiaca* and intentionally located in places representative of the dry grassland vegetation in a broader area of the Děvín Hill's crest, on the same slope with an inclination of ~20° and SE aspect, with a maximum between-plot distance of 87 m. The general aspect of the vegetation in the area is shown in Figure 1. The bedrock is Jurassic limestone, with Rendzina soil of an average depth of 15 cm, and rock outcrops covering ~10% of the area. Surveys were performed every spring, in May or June, from 1993 until 2018 (except for 1995) by the same surveyor (J. Danihelka, sometimes with additional observers; Danihelka, 2019). All vascular plant species rooted within each plot were recorded and their cover visually estimated using the modified



FIGURE 1 Dry grassland near the summit of Děvín Hill, south-east Czech Republic: the locality of the seven permanent plots sampled annually from 1993 to 2018 (photo by K. Chytrý, May 2019) [Colour figure can be viewed at wileyonlinelibrary.com]

nine-degree Braun-Blanquet scale (Westhoff and van der Maarel, 1978). Species were assigned to life-history categories based on the life-span following Jäger (2011) and our field experience from the study site: annual (summer annual and winter annual), short-lived (biennial and short-lived monocarpic perennial) and perennial. The borders between these categories were not always sharp, with some plants belonging to two categories at the same time. Here, the assignment to one of the three categories is based on the longest life-span of the species (see Appendix S3). The ephemeral seedlings of the trees *Acer pseudoplatanus* and *Fraxinus excelsior*, occasionally found in the plots located close to the forest, and a few records of juvenile individuals of *Carex* species were excluded from the analyses as their inconsistent determination would create noise that might negatively affect the analysis.

Monthly weather data were obtained from the climate stations Dolní Věstonice (from 1993 to 2018, 172 m a.s.l., distance 2.2 km from the study site) and Mikulov (from 1990 to 1992, 268 m a.s.l., distance 6.3 km) for precipitation, and Děvín Hill (from 2006 to 2018, 530 m a.s.l., distance 0.2 km) and Lednice (from 1990 to 2007, 177 m a.s.l., distance 14.2 km) for temperature. The temperature measured in the Lednice station was adjusted to be comparable with the measurements from the Děvín station. To do so, we compared the daily values of temperature of the two climate stations and calculated the differences between them within the two-year overlap in their measuring period. This comparison indicated temperature at the Děvín Hill station to be 0.5°C lower than in Lednice. Therefore, this value was subtracted from the Lednice station data. The total precipitation and mean temperature were calculated for 3-month periods (hereafter referred to as 'seasons') of each year as follows: spring included March, April and May; summer included June, July and August; autumn included September, October and November; and winter included December, January and February. For testing the effect of the environment on community composition, we used information on the previous eight seasons before sampling (i.e. the current and previous year) as illustrated in Figure 2.

2.1 | Statistical analysis

Temporal changes in species composition in both the historical and permanent-plot dataset were analysed using multivariate ordination techniques. The ordination of the historical dataset was calculated based on the square-rooted Euclidean distances between individual vegetation plots based on presence/absence species data. We used presence/absence data in order to minimize possible sampling bias between different surveyors. All the other ordinations were based on the square-rooted Bray-Curtis dissimilarity in species composition and abundances. The Braun-Blanquet cover-abundance values were transformed to mid percentage covers of individual grades and square-root transformed for the purpose of calculating the Bray-Curtis index. We ran principal coordinate analyses (PCoA) on both the historical and permanent-plot datasets to explore general

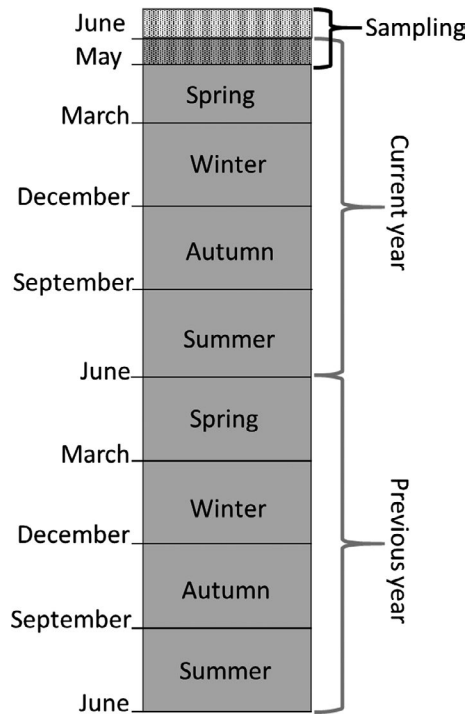


FIGURE 2 A scheme illustrating how temperature and precipitation were averaged within 3-month periods (seasons) and linked to the community data. Permanent plots were sampled annually in May or June and linked to weather in the eight previous seasons, here divided into the 'current year' (up to 1 year before sampling) and the 'previous year' (up to 2 years before sampling)

patterns of vegetation change in dry grasslands of Děvín Hill over the last 90 years, and to characterize changes in species composition in the *Festucion valesiacae* dry grassland on the Děvín Hill summit over the past 25 years, respectively. In addition, for the permanent-plot dataset only, we conducted variation partitioning based on partial distance-based redundancy analysis (db-RDA) to decompose the variability in community composition into components corresponding to plot identity (plots were used as covariates in the analysis), time and the stochastic part. The temporal component was further decomposed into directional and non-directional parts, which was based on a comparison of two db-RDAs in which year of sampling was used as a quantitative or categorical predictor, respectively. Third, we related the temporal variability in community composition to weather dynamics using a partial db-RDA with community composition as a response, the plot identity as a covariate and the mean temperature and precipitation sums for eight 3-month seasons before vegetation sampling as predictors. This partial db-RDA was also used to partition the temporal variation in community composition into that accounted for by weather in the recent four seasons (current spring and previous winter, autumn and summer; hereafter 'current year'), the previous four seasons ('previous year') before sampling and that unexplained by the weather variables.

Effects of all predictors or unique variation components were tested using Monte-Carlo permutation tests with 9,999 permutations. Permutations were conducted within blocks defined by the

plot identity. The db-RDA testing the effect of weather also used a time-series permutation scheme (with mirroring enabled; Šmilauer and Lepš, 2014).

To assess the distribution of species with different life-histories over the study period, their absolute covers were estimated. The mid-percentage cover values of the original Braun-Blanquet codes of all species in the dataset were averaged over all the permanent plots for each year. Further, they were summed for all species and separately for species belonging to each of the three life-history categories (annual, short-lived, perennial) using the algorithm described by Fischer (2015), which assumes random overlap of covers of different species. All the analyses were performed in the R environment (R Core Team, 2019) using tidyverse (Wickham, 2019) and vegan (Oksanen *et al.*, 2019) packages.

3 | RESULTS

The ordination of vegetation plots of the historical dataset (Figure 3) revealed considerable long-term stability of different types of dry grasslands on Děvín Hill between 1930 and 2019. Some sets of plots sampled by the same author formed distinct clusters (e.g. those recorded by J. Unar in the 1980s). Even so, considering the whole dataset, this indirect (i.e. not considering any constraining variables) ordination did not identify any clear directional trend in changes of species composition from the older to the newer plots.

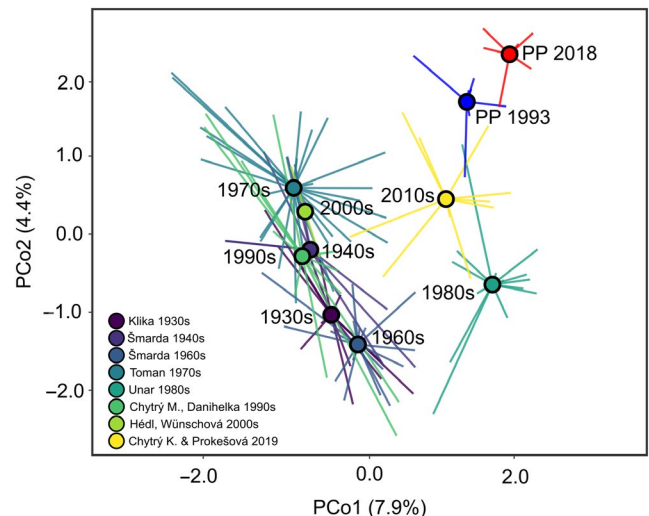


FIGURE 3 Ordination (principal coordinate analysis) of the dataset of historical vegetation plots sampled in the dry grasslands on Děvín Hill. Records from the permanent plots (PP) of the first (1993) and the last (2018) year of sampling are marked in blue and red, respectively. Their outlying position in the ordination space mainly results from their higher species richness, which can be partly caused by higher alpha diversity of the permanent-plot site, sampling in the optimum phenological period for most species including the annuals, and more intensive sampling and long-time experience involved in permanent-plot sampling compared with non-permanent vegetation-survey plots [Colour figure can be viewed at wileyonlinelibrary.com]

In the permanent-plot dataset, we found 120 species during the 25 years of the repeated survey, of which 36 were annuals, 21 short-lived and 63 perennials. The mean number of species per plot was 43 (minimum 24, maximum 57). The complete dataset is provided in Appendix S4 and in the Figshare repository (Danihelka, 2019).

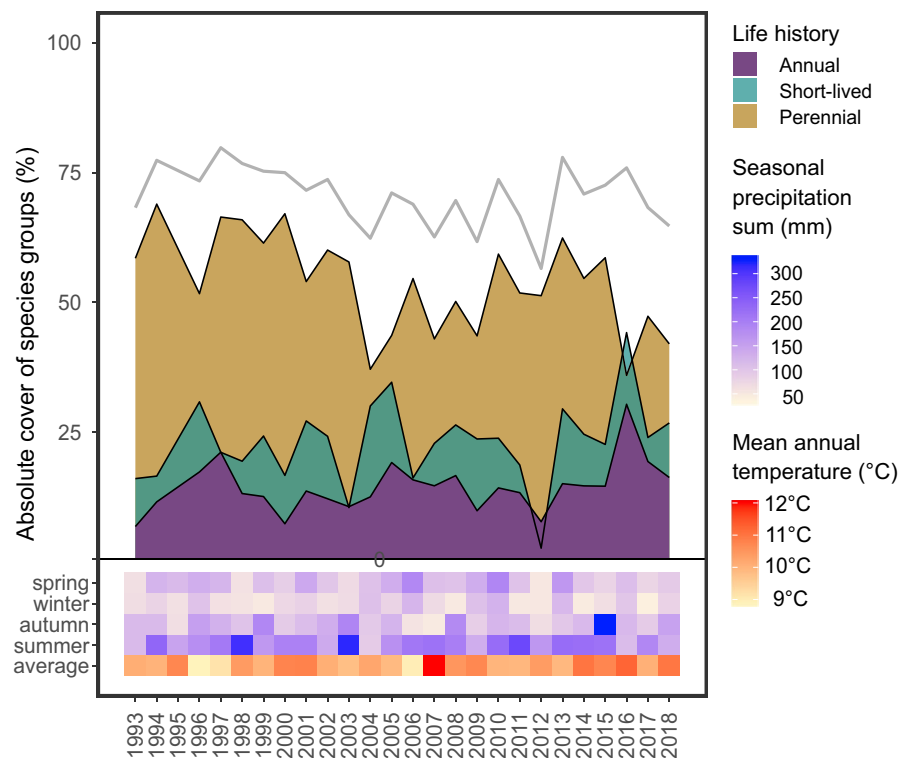
Climatic conditions showed a significant variation over the study period. The annual precipitation varied from 330 mm (in 2003) to 755 mm (in 2014), and the years 2003, 2008, 2011, 2015 and 2018 were extremely dry with precipitation below 400 mm. Dry periods occurred unpredictably in different parts of the growing season, from spring to autumn. The mean annual temperature varied from 8.5°C (in 1996) to 11.7°C (in 2018) (Figure 4 and Appendix S1, Figure S1.1). Drought notably coincided with high temperatures in 2015 and 2018. It was noted that the total abundances of individual species groups (annuals, short-lived and perennials) changed in response to weather patterns (Figure 4).

Principal coordinate analysis of the permanent-plot dataset (Figure 5) revealed that the main differences in species composition were related to the plot identity (principal coordinates 1 and 3), which was confirmed by variation partitioning (Figure 6). Temporal trajectories describing changes in community composition within individual plots showed a stochastic pattern. However, a directional trend seemed to be present in the last 2–5 years, which is visible on the second principal coordinate, where the recent points of the time-series are located at more positive (higher) positions than the previous records from the same plots (Figure 5a). This directional change is associated with an increase in annuals (e.g. *Alyssum alyssoides*, *Arabis auriculata*, *Cerastium semidecandrum* and *Microthlaspi perfoliatum*), which are among the species with the highest values

on the second axis (Appendix S5.1). In contrast, perennial grasses (e.g. *Elymus hispidus*, *Festuca valesiaca*, *Phleum phleoides* and *Poa angustifolia*) have the lowest values on the second axis. Variation partitioning showed that effects of time accounted for 26.3% of the total variation in species composition, but this consisted mostly of the non-directional effect of time (Figure 6).

Variation partitioning relating the temporal changes in community composition to weather predictors identified significant effects of both the current-year and previous-year weather, each explaining approximately one-third of the temporal variation in plant community composition (Figure 6). The effects of weather in the current and previous year were largely independent. Permutation tests of all climatic variables identified their significant marginal and partial effects on community composition at $p < 0.05$ (9,999 permutations; partial effects were defined as a unique contribution to explanatory power after accounting for the effects of all the other predictors). The ordination plot of a db-RDA model containing all the weather predictors (Figure 7) showed strong effects of these predictors on community composition, which was closely associated with species life-history. The first constrained axis gradient corresponded to contrasting weather conditions in summer. The left part of the axis is associated with relatively cold and wet summers, which supported abundance of non-ruderal perennial species typical of dry grasslands, e.g. the grasses *Festuca csikhegyensis*, *F. valesiaca*, *Koeleria macrantha* and *Phleum phleoides*, dicot hemicryptophytes *Achillea pannonica*, *Asperula cynanchica* and *Scabiosa ochroleuca*, and chamaephytes *Jovibarba globifera*, *Teucrium montanum* and *Thymus praecox*. The upper right part of the graph represents wet autumn and spring and mild, relatively warm and wet (oceanic) winter. Such conditions supported annual and short-lived species of dry grasslands such as *Acinos*

FIGURE 4 Time series of the total percentage species cover in permanent plots of plants with different life-histories, compared with weather during the study period. Precipitation in each column refers to the spring in which the survey was done and the previous three quarterly seasons; for example, the column 2010 refers to the precipitation of spring 2010, winter 2009/2010, autumn 2009 and summer 2009. Temperature refers to the mean of the previous three seasons. Total herb-layer cover is represented by the grey line. No sampling was made in 1995 [Colour figure can be viewed at wileyonlinelibrary.com]



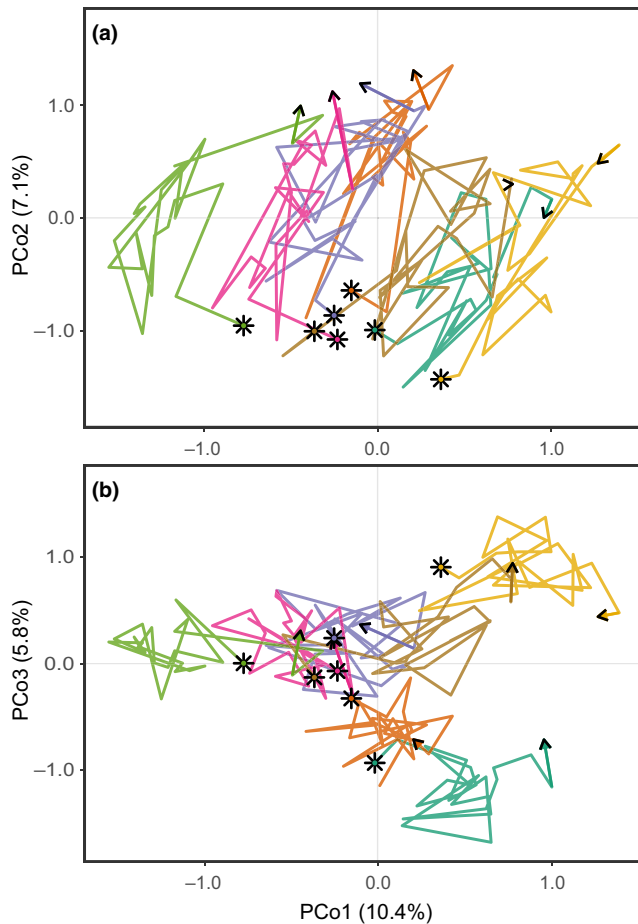


FIGURE 5 Ordination (principal coordinate analysis) of repeated surveys of seven permanent plots on Děvín Hill over 25 years. (a) First and second axis, (b) first and third axis. Each plot is indicated by a unique colour with the lines connecting the consecutive years. The asterisks and arrowheads represent the start (1993) and end (2018) years of the repeated survey, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

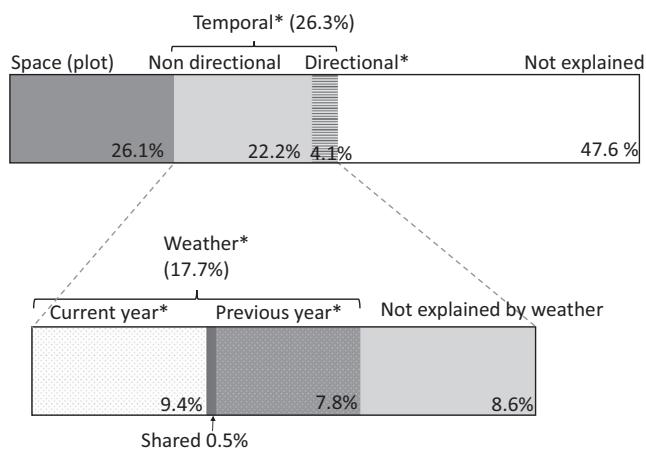


FIGURE 6 Partitioning of the total variation in plant community composition to the components explained by space (plot identity) and time. Temporal variation is further partitioned into directional vs. non-directional components and into fractions explained by the current-year and previous-year weather. Significance tests ($p < 0.001$) for testable components of variability are indicated by asterisks.

arvensis, *Cerastium semidecandrum*, *Medicago minima*, *Saxifraga tridactylites*, *Trifolium arvense* and *Trifolium campestre*. The lower right side of the graph represents dry and hot summers and autumns. Such weather conditions supported a heterogeneous group of species comprising annuals, short-lived species and perennials, most of them with a ruderal tendency, such as *Artemisia absinthium*, *Bromus tectorum*, *Camelina microcarpa*, *Capsella bursa-pastoris*, *Galium aparine* and *Veronica sublobata*. Complete list of species and scores can be found in Appendix S5.2.

4 | DISCUSSION

4.1 | No directional changes in community composition

Our results show that species composition and relative abundances of species in the dry grassland studied have been stable in the longer term. In different sampling campaigns since 1930, plots were placed independently and not exactly in the same locations. Therefore, the apparent clustering in the ordination diagram (Figure 3) can be a result of authors' particular aims, selective sampling of certain grassland types, spatially restricted sampling or sampling in different periods of the year, and probably also recording bias depending on authors' experience. Effects of inter-annual climatic variation on the clustering are also possible. Nevertheless, there was no general directional pattern of species shift in a clear direction over the last 90 years. A similar lack of trend was observed in repeated survey studies in steppe grasslands near Prague, approximately 210–220 km away (Hroudová and Prach, 1986; Dostálek and Frantík, 2011).

The permanent-plot dataset revealed high year-to-year dynamics over the past 25 years with considerably fluctuating trajectories of species composition, which were synchronized among the plots (Figures 5–7). However, consistent with the data from historical surveys, there seems to be no general trend of directional change, perhaps with the exception of the changes observed in the most recent years (2015–2018; Figures 5 and 6), which may be either a start of a directional trend or just another, albeit large, fluctuation. The observed year-to-year changes in species composition occurred in response to seasonal fluctuations in precipitation and temperature (Figures 6 and 7). The effect of climatic variables explained roughly two-thirds of the temporal variation in community composition, which clearly indicated that weather was the dominant driver of local vegetation dynamics. Remarkably, we identified significant partial effects of all the variables describing quarterly precipitation and temperature in the two years before the sampling. This highlights the importance of weather conditions not only in the main growing season but in all periods of the year.

4.2 | Contrasting responses of species groups to weather patterns

There appear to be three main plant groups with specific responses to contrasting weather patterns in the dry grassland studied (Figure 7):

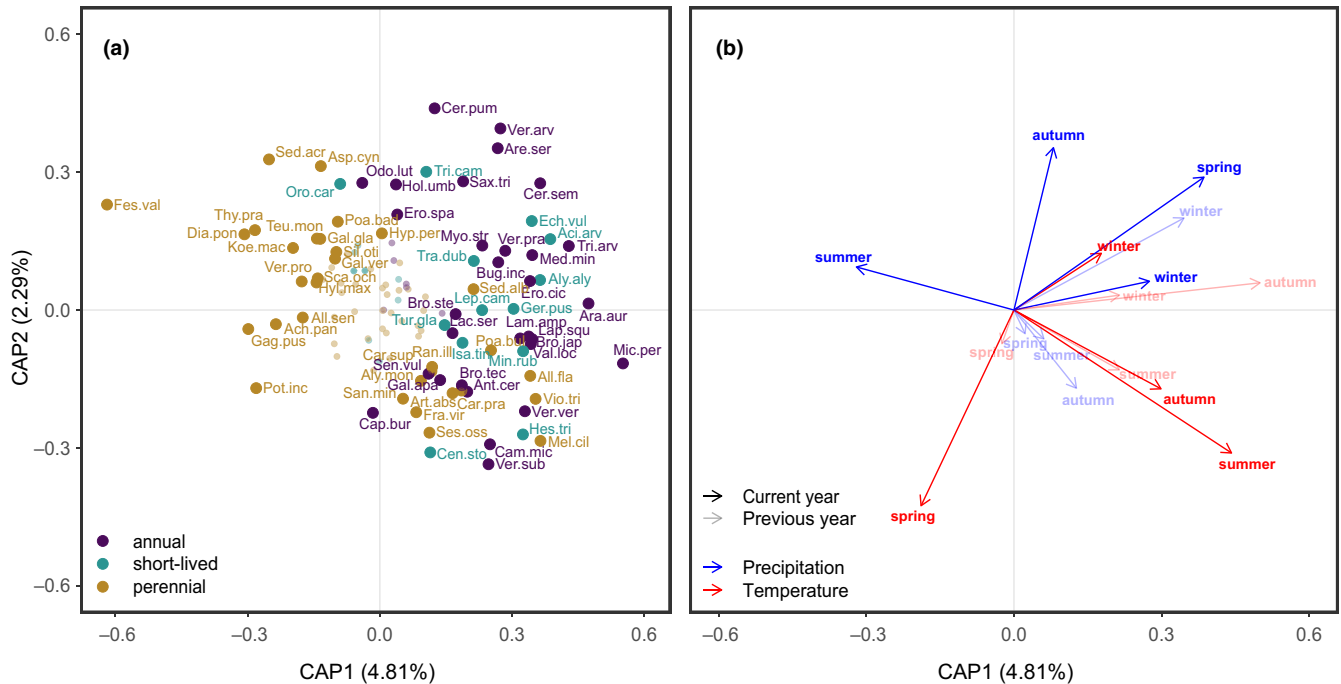


FIGURE 7 Ordination plots of partial distance-based redundancy analysis (db-RDA), showing the effect of precipitation and temperature on the dynamics of grassland community composition on Děvín Hill. Plot identities were used as covariates in the model. Effects of precipitation and temperature are indicated by blue and red, respectively. Dark and light colours represent the current-year seasons and previous-year seasons, respectively (compare Figure 2). Results of Monte-Carlo permutation test for all constrained axes: $p = 0.001$ (under 9,999 permutations). Species with higher scores on the first two axes are represented by the codes: Ach.pan = *Achillea pannonica*, Aci.arv = *Acinos arvensis*, All.fla = *Allium flavum*, All.sen = *Allium senescens* subsp. *montanum*, Aly.aly = *Alyssum alyssoides*, Aly.mon = *Alyssum montanum*, Ant.cer = *Anthriscus cerefolium*, Ara.aur = *Arabis auriculata*, Are.ser = *Arenaria serpyllifolia*, Art.abs = *Artemisia absinthium*, Asp.cyn = *Asperula cynanchica*, Bro.jap = *Bromus japonicus*, Bro.ste = *Bromus sterilis*, Bro.tec = *Bromus tectorum*, Bug.inc = *Buglossoides incrassata* subsp. *splitgerberi*, Cam.mic = *Camelina microcarpa*, Cap.bur = *Capsella bursa-pastoris*, Car.pra = *Carex praecox*, Car.sup = *Carex supina*, Cen.sto = *Centaurea stoebe*, Cer.pum = *Cerastium pumilum*, Cer.sem = *Cerastium semidecandrum*, Dia.pon = *Dianthus pontederiae*, Ech.vul = *Echium vulgare*, Ero.cic = *Erodium cicutarium*, Ero.spa = *Erophila spathulata*, Fes.val = *Festuca valesiaca*, Fra.vir = *Fragaria viridis*, Gag.pus = *Gagea pusilla*, Gal.apa = *Galium aparine*, Gal.gla = *Galium glaucum*, Gal.ver = *Galium verum*, Ger.pus = *Geranium pusillum*, Hes.tri = *Hesperis tristis*, Hol.umb = *Holosteum umbellatum*, Hyl.max = *Hylotelephium maximum*, Hyp.per = *Hypericum perforatum*, Isa.tin = *Isatis tinctoria* subsp. *tinctoria*, Koe.mac = *Koeleria macrantha*, Lac.ser = *Lactuca serriola*, Lam.amp = *Lamium amplexicaule*, Lap.squ = *Lappula squarrosa*, Lep.cam = *Lepidium campestre*, Med.min = *Medicago minima*, Mel.cil = *Melica ciliata*, Mic.per = *Microthlaspi perfoliatum*, Min.rub = *Minuartia rubra*, Myo.str = *Myosotis stricta*, Odo.lut = *Odontites luteus*, Oro.car = *Orobanche caryophyllacea*, Poa.bad = *Poa badensis*, Poa.bul = *Poa bulbosa*, Pot.inc = *Potentilla incana*, Ran.ill = *Ranunculus illyricus*, San.min = *Sanguisorba minor*, Sax.tri = *Saxifraga tridactylites*, Sca.och = *Scabiosa ochroleuca*, Sed.acr = *Sedum acre*, Sed.alb = *Sedum album*, Sen.vul = *Senecio vulgaris*, Ses.oss = *Seseli osseum*, Sil.oti = *Silene otites*, Teu.mon = *Teucrium montanum*, Thy.pra = *Thymus praecox*, Tra.dub = *Tragopogon dubius*, Tri.arv = *Trifolium arvense*, Tri.cam = *Trifolium campestre*, Tur.gla = *Turritis glabra*, Val.loc = *Valerianella locusta*, Ver.arv = *Veronica arvensis*, Ver.pra = *Veronica praecox*, Ver.pro = *Veronica prostrata*, Ver.sub = *Veronica sublobata*, Ver.ver = *Veronica verna*, Vio.tri = *Viola tricolor* subsp. *saxatilis* [Colour figure can be viewed at wileyonlinelibrary.com]

(a) polycarpic perennials, which increase after wet and relatively cold summers; (b) ruderal species of different life forms, which increase after dry and hot summers; and (c) small and competitively weak annuals, which increase after moderately warm winters and wet autumns, winters and springs. Because the winter and summer weather is not correlated, these groups can combine in multiple ways. For example, dry and hot summer followed by wet and warm winter creates the best conditions for small annuals: their germination and growth are supported by benign winter weather, and they can exploit the empty space left after the perennials that declined in the previous summer.

1. Polycarpic perennials are dominants of the dry grassland community studied (left right part of the db-RDA diagram in Figure 7a,

Appendix S5.2). They include narrow-leaved tussock grasses (e.g. *Festuca csikhegyensis*, *F. valesiaca*, *Koeleria macrantha* and *Melica ciliata*), non-graminoid hemicryptophytes (e.g. *Galium glaucum* and *Scabiosa ochroleuca*) and chamaephytes (e.g. *Teucrium chamaedrys*, *T. montanum* and *Thymus praecox*). They grow slowly in early spring, reaching the highest aboveground biomass in late spring and summer. They minimize water losses by having narrow leaves or leaves with a thick cuticle wax layer (e.g. *Festuca* spp., *Teucrium chamaedrys* or *Thymus praecox*). Still, many of these species seem to occur near the dry edge of their moisture niche in the dry grassland studied. Prolonged summer droughts increase their mortality and decrease grassland cover, especially if this is repeated in consecutive years and combined

with high summer temperatures, which increase evaporation. Increased mortality after drought, with subsequent regeneration, was described for the related and ecologically similar tussock grass *Festuca vaginata* in a sandy steppe in central Hungary (Kröel-Dulay and Garadnai, 2008). Conversely, after wet and relatively cool summers, polycarpic perennials tend to increase their cover and dominance in the community.

2. Species with ruderal tendency comprise a mixture of various growth forms, including perennials (especially monocarpic), short-lived species (e.g. biennials) and annuals (bottom-right part of the db-RDA diagram in Figure 7a, Appendix S5.2). Some of these species are considered as archaeophytes in the study area (e.g. *Bromus tectorum*, *Buglossoides incassata* subsp. *splitgerberi*, *Geranium pusillum* or *Lappula squarrosa*; Pyšek *et al.*, 2012). After summer drought events, the grassland opens because of mortality of polycarpic perennials of group (1), allowing an increase in the cover of monocarpic, short-lived and fast-growing annual species. Some of these can temporarily become dominant in the community (e.g. *Camelina microcarpa*, *Geranium pusillum*, *Echium vulgare*, *Lepidium campestre* and *Medicago minima*). Grassland ruderalization after a drought event was also reported in the Bibury experiment in England (Dunnett *et al.*, 1998); however, that study focused on a mesic *Arrhenatherum* grassland. Our results suggest that the effect of summer drought is even more pronounced in a subcontinental dry grassland.
3. Small, competitively weak annuals are a natural component of the dry grassland studied (Geißelbrecht-Taferner *et al.*, 1997; Dúbravková *et al.*, 2010; Willner *et al.*, 2017). This group of species, clustered in the right part of the partial db-RDA ordination diagram (Figure 7a, Appendix S5.2), includes *Arabis auriculata*, *Arenaria serpyllifolia*, *Cerastium pumilum*, *Erophila spathulata* and *Holosteum umbellatum*. They are winter or spring annuals, germinating in autumn and/or late winter. They produce low biomass and usually senesce before the end of May. Our analysis shows that they increase in cover after moderately warm winters and after wet autumns, winters and/or springs, which is a crucial period for their germination and growth. This is consistent with the results from dry grasslands in central Germany, in which this group was shown to be supported by wet spring (Matesanz *et al.*, 2009). Summer weather does not affect them directly because they survive summer as dormant seeds (Hájková and Krekule, 1972). However, dry and hot summers in the previous years can encourage them by reducing the biomass of polycarpic perennials, thus leaving more open space for the germination of annuals. Our analysis suggests that these species are not supported by a warm spring of the current year, which has to be interpreted with caution as a possible artefact: a warm spring may have accelerated their development, such that by the time of sampling some of them may have already partly or entirely disappeared from the community. The same is true for *Gagea pusilla*, a perennial early-flowering bulbous geophyte, which is probably found in all seven plots but recorded only exceptionally when sampling was done relatively early in a year with wet and cold spring.

4.3 | Delayed response to weather and shifts in dominance among species groups

We have shown that plant species dynamics in a dry grassland community responds to precipitation and temperature in different previous seasons. Effects on the community composition can be noted not only for the weather of the current year (0–3 seasons before surveys) but also for the weather of the previous year (4–7 seasons before surveys; Figures 6 and 7). Such a lag in response is probably the result of perennial species causing a cascade effect in the whole community. For example, when perennials are negatively affected by summer drought, their recovery is delayed because of their slow growth rates, while annual and short-lived species, often with ruderal strategy, take advantage of the open niche to increase their abundance (Figures 4 and 7). However, these more dynamic species also depend on specific weather patterns, and they can take this advantage only if weather is favourable for their development. In particular, wet weather in autumn and spring supports annual species, but because of their short life cycle, this effect is most visible in the current year.

Furthermore, shifts in the dominance of species with different life-history strategies are most remarkable after periods of extreme weather. For example, after the dry growing seasons of 2003 and 2015, there was a considerable decrease in the perennial plant cover in the subsequent year. This offered the advantage of more space for short-lived plants and annuals (either those with or without a ruderal tendency). This advantage was taken from the subsequent relatively wet winter and spring, especially in 2016, when winter was warmer than in 2004. In contrast, short-lived species (especially those with ruderal tendency) and to some extent also non-ruderal annuals decreased significantly in 2003 and 2012 owing to a dry winter followed by a dry spring.

4.4 | Short-term community dynamics as a key to long-term community stability

Our study has revealed oscillatory trajectories of species shifts through time (Figure 5) that are related to year-to-year weather fluctuations (Figures 6 and 7). Weather fluctuations combined with different response strategies of individual species groups, and the interactions among them, are key to understanding the long-term stability of species composition (Adler *et al.*, 2006; Tredennick *et al.*, 2017). Stabilizing effects of climatic fluctuations were demonstrated to be the mechanism maintaining diversity in several terrestrial ecosystems (e.g. Chesson, 2000; Adler *et al.*, 2006; Ives and Carpenter, 2007; Doležal *et al.*, 2019). Moderate weather fluctuations, as in the case of our study (where the total cover was always maintained above 50%, Figure 4), enhance species co-existence by means of two main mechanisms: relative non-linearity of competition and the storage effect (Chesson, 2008; Wilson, 2011). Relative non-linearity occurs when species differ in the shape of their response to a resource; if the availability of such resource fluctuates, none of the

species is able to attain permanent competitive superiority and exclude the others from the community (Chesson, 2008). In contrast, the storage effect is based on a fluctuating environmental condition (not a resource) to which species differ in their optima. Conditions favourable for one species lead to an increase in its abundance, which, after time, becomes limited by intraspecific competition. When conditions change to the state favourable for another species, its abundance is low at the beginning but may strongly increase until reaching limitation by intraspecific competition. This makes intraspecific competition more limiting than interspecific and triggers an increase-when-rare population dynamics, which has a strong stabilizing effect on the coexistence of species and community diversity (Chesson, 2008; Wilson, 2011).

Both of these mechanisms seem to be present in the system studied here. Soil water and space, more specifically free patches suitable for seedling establishment, represent the principal resources, while temperature is the key environmental condition. All of these variables display notable fluctuations between and within seasons. The effect of water availability in summer on the dynamics of the ratio between perennial and annual (or short-lived) species (Figure 7) appears to be a case of relative non-linearity of competition because summer water availability determines the abundance of perennials and consequently space availability for annuals. In contrast, the dynamics described by the second db-RDA axis (Figure 7) seems to be a case of storage effect as it is mainly correlated with temperature (cold vs warm spring and autumn). It is also remarkable that the water availability in summer affects the ratio between steppe perennials and (semi)ruderal annuals (i.e. species growing usually in different habitats), which occur at the study site because of its fluctuating intermediate character. Conversely, the species positioned on the opposite sides of the gradient associated with spring temperature and humidity (second db-RDA axis) usually co-occur within the same habitat, as expected for coexistence maintained by the storage effect.

4.5 | Implications for future predictions

Despite the overall trend of increasing temperature over the past 28 years (Appendix S1, Figure S1.2), there is a general lack of directional changes in the plant communities studied (Figure 3). There appears to be a directional trend in species composition towards the dominance of annual or short-lived species only over the last four years (Figure 5a, axis 2), which were all rather dry. However, it is currently not possible to assess whether these changes indicate a new directional trend or only a large cyclic fluctuation. Although the grassland studied was relatively stable in terms of community composition over the past almost 90 years, there is a risk that with the future drought events (IPCC, 2012; IPBES, 2019), especially if they are repeated at short intervals, drought-tolerant ruderal (both annual and perennial) species may increase at the expense of the non-ruderal steppe species. It should also be noted that the grassland type studied is typical of the driest conditions in the area (shallow

limestone soil and sun-facing slope), containing plant species specifically adapted to such conditions, yet it is significantly affected by drought events.

In the present study, we observed the effects of extreme years (e.g. droughts of 2003 and 2015) but we cannot predict how the community dynamics would behave in the case of several years of continuous drought. In terms of species composition, such a trend could possibly lead to a ruderalization of dry grasslands. However, in terms of community processes, it is impossible to foresee whether the intrinsic community stabilizing effects (i.e. the storage effect) will continue to ensure the continuity of the community. Previous studies have shown a cascade effect arising from species-specific responses to adversities and their interactions can lead to chaotic and unpredictable dynamics (Huisman and Welssing, 1999; Károlyi *et al.*, 2000).

Another point to highlight, in relation to future predictions of grassland community dynamics, is that climatic conditions throughout the year are important and cannot be simplified to just one or two parameters (such as mean annual temperature or annual precipitation) as is usually done (e.g. Dunnett *et al.*, 1998).

5 | CONCLUSIONS

Our study revealed non-directional trends in the community dynamics over the past 25 years in a Central European dry grassland. These trends can explain the long-term dynamic stability over the past 90 years by means of the interactions between four main aspects of the system: (a) unpredictable year-to-year fluctuations in precipitation and temperature; (b) different types of response to weather fluctuations by species with different strategies (here represented by life-histories); (c) interactions among groups of species; and (d) the dependence of the current species composition on the weather patterns of not only the current year but also of the previous at least two years. Given the complexity of the community dynamics and the lack of directional changes found in the present study, it is difficult to predict accurately the effect of climate change on the grassland vegetation of the study area. Nevertheless, our analysis suggests that summer droughts increase the abundance of ruderal species, so an increase in the frequency of such events (as predicted for the region; Spinoni *et al.*, 2018) may lead to a ruderalization of dry grasslands.

ACKNOWLEDGEMENTS

We thank Hana Galušková and Helena Prokešová for their help in field sampling and data digitizing, and Tomáš Litschmann for the climatic data from the Děvín climate station.

AUTHOR CONTRIBUTIONS

FMF, JT and KC, with contributions of MC and JD, conceived the study; JD established the permanent plots and performed all sampling and plant identifications in these plots, sometimes with the help of KC and MC, and classified species into life-history categories;

JT and KC performed the data analyses; all the authors discussed and interpreted the results and wrote the manuscript.

DATA AVAILABILITY STATEMENT

The data from the permanent plots used in this study are provided in Appendix S4 and stored in the Figshare repository (Danihelka, 2019; <https://doi.org/10.6084/m9.figshare.9971039.v1>).

ORCID

Felícia M. Fischer  <https://orcid.org/0000-0002-2319-3648>

Kryštof Chytrý  <https://orcid.org/0000-0003-4113-6564>

Jakub Těšitel  <https://orcid.org/0000-0003-3793-3704>

Jiří Danihelka  <https://orcid.org/0000-0002-2640-7867>

Milan Chytrý  <https://orcid.org/0000-0002-8122-3075>

REFERENCES

- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. and Levine, J.M. (2006) Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences of the United States of America*, 103(34), 12793–12798. <https://doi.org/10.1073/pnas.0600599103>
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.34>
- Chesson, P. (2008) Quantifying and testing species coexistence mechanisms. In: Valladares, F., Camacho, A., Elosegui, A., Estrada, M., Gracia, C., Senar, J.C. and Gili, J.M. (Eds.) *Unity in Diversity: Reflections on Ecology after the Legacy of Ramon Margalef*. Bilbao, Spain: Fundación BBVA, pp. 119–164.
- Chesson, P.L. and Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist*, 117(6), 923–943. <https://doi.org/10.1086/283778>
- Chytrý, M. (Ed.) (2007) *Vegetation of the Czech Republic 1. Grassland and Heathland Vegetation (in Czech)*. Praha, Czech Republic: Academia.
- Chytrý, M. and Rafajová, M. (2003) Czech National phytosociological database: basic statistics of the available vegetation-plot data. *Preslia*, 75(1), 1–15.
- Chytrý, M., Danihelka, J., Kaplan, Z., Pyšek, P. (Eds.) (2017) *Flora and Vegetation of the Czech Republic*. Cham, Switzerland: Springer. <https://doi.org/10.1007/978-3-319-63181-3>
- Danihelka, J. (2019) Permanent plots in dry grasslands on Děvín Hill, southern Moravia, Czech Republic. <https://doi.org/10.6084/m9.figshare.9971039.v1> [Accessed 11 October 2019].
- Danihelka, J., Chrtěk, J. Jr and Kaplan, Z. (2012) Checklist of vascular plants of the Czech Republic. *Preslia*, 84(3), 647–811.
- Danihelka, J., Grulich, V. and Chytrý, M. (2015) Pavlov Hills. In: Chytrý, M., Danihelka, J. and Michalčová, D. (Eds.) *Botanical Excursions in Moravia. Field Guide for the 58th IAVS Symposium*. Brno, Czech Republic: Masaryk University.
- Descamps-Julien, B. and Gonzalez, A. (2005) Stable coexistence in a fluctuating environment: an experimental demonstration. *Ecology*, 86(10), 2815–2824. <https://doi.org/10.1890/04-1700>
- Doležal, J., Lanta, V., Mudrák, O. and Lepš, J. (2019) Seasonality promotes grassland diversity: interactions with mowing, fertilization and removal of dominant species. *Journal of Ecology*, 107(1), 203–215. <https://doi.org/10.1111/1365-2745.13007>
- Dostálek, J. and Frantík, T. (2011). Response of dry grassland vegetation to fluctuations in weather conditions: a 9-year case study in Prague (Czech Republic). *Biologia*, 66(5):837–847.
- Dúbravková, D., Chytrý, M., Willner, W., Illyés, E., Janišová, M. and Kállayné Szerényi, J. (2010) Dry grasslands in the Western Carpathians and the northern Pannonian Basin: a numerical classification. *Preslia*, 82(2), 165–221.
- Dunnett, N.P., Willis, A.J., Hunt, R. and Grime, J.P. (1998) A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *Journal of Ecology*, 86(4), 610–623. <https://doi.org/10.1046/j.1365-2745.1998.00297.x>
- Erdős, L., Ambarli, D., Anenkhonov, O.A., Bători, Z., Cserhalmi, D., Kiss, M. et al. (2018) The edge of two worlds: A new review and synthesis on Eurasian forest-steppes. *Applied Vegetation Science*, 21(3), 345–362. <https://doi.org/10.1111/avsc.12382>
- Fekete, G., Király, G. and Molnár, Z. (2016) Delineation of the Pannonian vegetation region. *Community Ecology*, 17(1), 114–124. <https://doi.org/10.1556/168.2016.17.1.14>
- Fischer, H.S. (2015) On the combination of species cover values from different vegetation layers. *Applied Vegetation Science*, 18(1), 169–170. <https://doi.org/10.1111/avsc.12130>
- Geiβelbrecht-Taferner, L., Geiβelbrecht, J. and Mucina, L. (1997) Fine-scale spatial population patterns and mobility of winter-annual herbs in a dry grassland. *Journal of Vegetation Science*, 8(2), 209–216. <https://doi.org/10.2307/3237349>
- Hájková, L. and Krekule, J. (1972) The developmental pattern in a group of therophytes I. Seed dormancy. *Flora*, 120, 111–120. [https://doi.org/10.1016/S0367-2530\(17\)32053-4](https://doi.org/10.1016/S0367-2530(17)32053-4)
- Herben, T., Krahulec, F., Hadincová, V. and Skálová, H. (1993) Small-scale variability as a mechanism for large-scale stability in mountain grasslands. *Journal of Vegetation Science*, 4(2), 163–170. <https://doi.org/10.2307/3236101>
- Hroudová, Z. and Prach, K. (1986) Vegetational changes on permanent plots in a steppe community. *Preslia*, 58, 55–62.
- Huisman, J. and Welsing, F.J. (1999) Biodiversity of plankton by species oscillations and chaos. *Nature*, 402(6760), 407–410. <https://doi.org/10.1038/46540>
- IPBES (2019) *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn, Germany: IPBES Secretariat.
- IPCC (2012) *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of working groups I and II of the Intergovernmental Panel on Climate Change*, 1st edition. Cambridge, UK, and New York, NY: Cambridge University Press.
- Ives, A.R. and Carpenter, S.R. (2007) Stability and diversity of ecosystems. *Science*, 317(5834), 58–62. <https://doi.org/10.1126/science.1133258>
- Jäger, E.J. (Ed.) (2011) *Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband*, 20th edition. Heidelberg, Germany: Spektrum Akademischer Verlag.
- Károlyi, G., Péntek, Á., Scheuring, I., Tél, T. and Toroczkai, Z. (2000) Chaotic flow: The physics of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 97(25), 13661–13665. <https://doi.org/10.1073/pnas.240242797>
- Klika, J. (1931) Studien über die xerotherme Vegetation Mitteleuropas. I. Die Pollauer Berge im südlichen Mähren. *Beihefte zum Botanischen Centralblatt, Abteilung B. Abt. II*, 47, 343–398.
- Kröel-Dulay, G. and Garadnai, J. (2008) The role of disturbances in sand grassland dynamics. In: Kovács-Láng, E., Molnár, E., Kröel-Dulay, G. and Barabás, S. (Eds.) *KISKUN LTER: Long-term ecological research in the Kiskunság, Hungary*. Vác-rátót, Hungary: Institute of Ecology and Botany, Hungarian Academy of Sciences, pp. 41–44.
- Matesanz, S., Brooker, R.W., Valladares, F., and Klotz, S. (2009). Temporal dynamics of marginal steppic vegetation over a 26-year period of substantial environmental change. *Journal of Vegetation Science*, 20(2), 299–310.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D. et al. (2019) *vegan: Community Ecology Package*. Ver. 2.5-6. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Porfirio, L.L., Harris, R.M.B., Lefroy, E.C. and Hugh, S. (2014) Improving the use of species distribution models in conservation planning

- and management under climate change. *PLoS ONE*, 9(11), e113749. <https://doi.org/10.1371/journal.pone.0113749>
- Pyšek, P., Danihelka, J., Sádlo, J., Chrtek, J. Jr, Chytrý, M., Jarošík, V. et al. (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. *Preslia*, 84(2), 155–255.
- R Core Team. (2019) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Šmarda, J. (1975) Plant communities of the rocky steppe in the Pavlov Hills in Moravia (Czechoslovakia) (in Czech). *Československá Ochrana Přírody*, 14(1), 5–58.
- Šmilauer, P. and Lepš, J. (2014) *Multivariate Analysis of Ecological Data Using Canoco 5*. Cambridge: Cambridge University Press.
- Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. and Dosio, A. (2018) Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, 38(4), 1718–1736. <https://doi.org/10.1002/joc.5291>
- Tolasz, R., Míková, T., Valeriánová, A. and Voženílek, V. (Eds.) (2007) *Climate atlas of Czechia (in Czech)*. Praha and Olomouc, Czech Republic: Český hydrometeorologický ústav and Univerzita Palackého v Olomouci.
- Toman, M. (1976) Phytosociological data on the communities of the class Festuco-Brometea in the Pavlov Hills (southern Moravia) (in Czech). *Zborník Pedagogickej Fakulty v Prešove Univerzity P. J. Šafárika v Košiciach, Prírodné Vedy*, 14, 127–134.
- Tredennick, A.T., Adler, P.B. and Adler, F.R. (2017) The relationship between species richness and ecosystem variability is shaped by the mechanism of coexistence. *Ecology Letters*, 20(8), 958–968. <https://doi.org/10.1111/ele.12793>
- Unar, J. (2004) Xerothermic vegetation of the Pavlov Hills (in Czech). *Sborník Přírodovědného Klubu v Uherském Hradišti, Supplementum*, 11, 1–140.
- van der Maarel, E. and Sykes, M.T. (1993). Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science*, 4(2), 179–188.
- Watkinson, A.R. and Ormerod, S.J. (2001) Grasslands, grazing and biodiversity: Editors' introduction. *Journal of Applied Ecology*, 38(2), 233–237. <https://doi.org/10.1046/j.1365-2664.2001.00621.x>
- Westhoff, V. and van der Maarel, E. (1978) The Braun-Blanquet approach. In: Whittaker, R.H. (Ed.) *Classification of Plant Communities*. Dordrecht, the Netherlands: W. Junk, pp. 287–399.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R. et al. (2019) Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686. <https://doi.org/10.21105/joss.01686>
- Willner, W., Kuzemko, A., Dengler, J., Chytrý, M., Bauer, N., Becker, T. et al. (2017) A higher-level classification of the Pannonian and western Pontic steppe grasslands (Central and Eastern Europe). *Applied Vegetation Science*, 20(1), 143–158. <https://doi.org/10.1111/avsc.12265>
- Wilson, J.B. (2011) The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science*, 22(1), 184–195. <https://doi.org/10.1111/j.1654-1103.2010.01226.x>
- Woodward, F.I. and Lomas, M.R. (2004) Vegetation dynamics – simulating responses to climatic change. *Biological Reviews*, 79(3), 643–670. <https://doi.org/10.1017/S1464793103006419>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Figure S1.1. Yearly and monthly variation in temperature and precipitation in the study area during the permanent-plot surveys (1993–2018). Figure S1.2. Variation in average temperature in the study area between 1990 and 2018

Appendix S2. A detailed list of surveys compiled for the historical dataset.

Appendix S3. A list of species found in the permanent plots over the 25 years of surveys, with life-history categories.

Appendix S4. Full species lists with cover values recorded in the permanent-plot surveys (1993–2018).

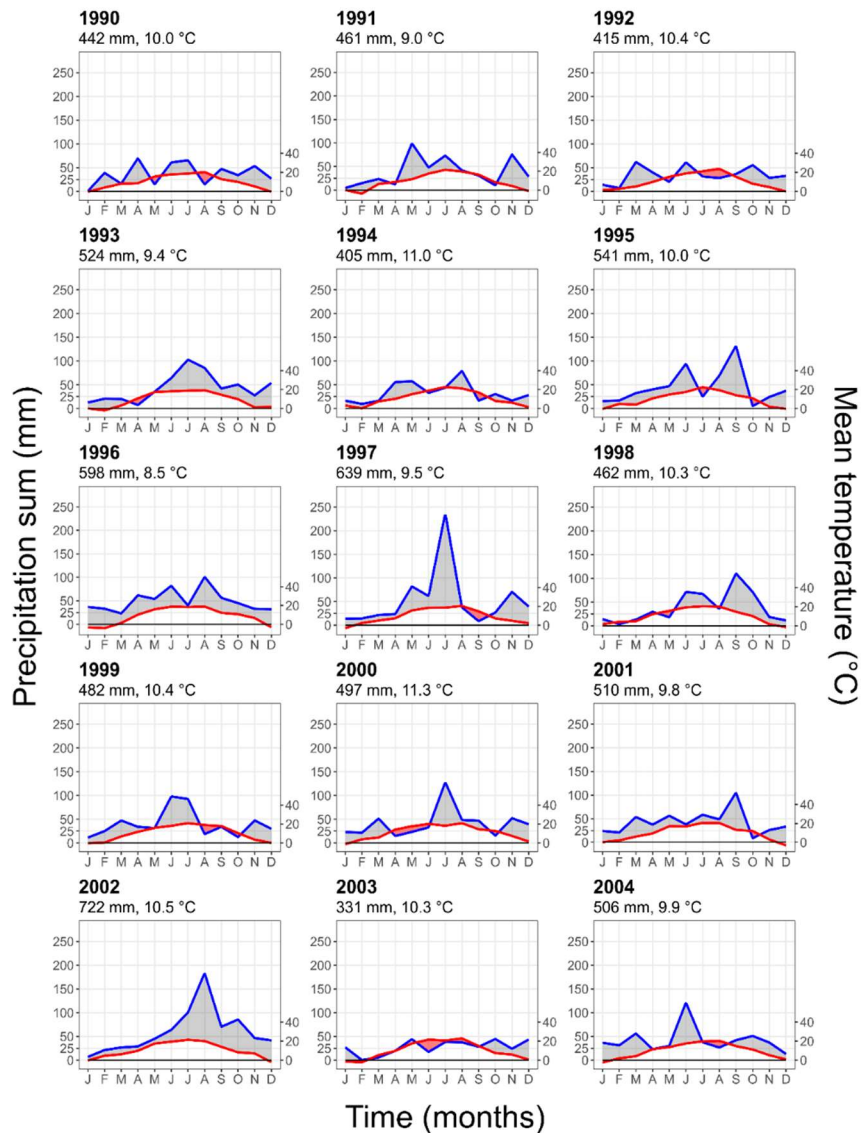
Appendix S5. Site and species scores of PCoA (S5.1) and db-RDA (S5.2) ordinations.

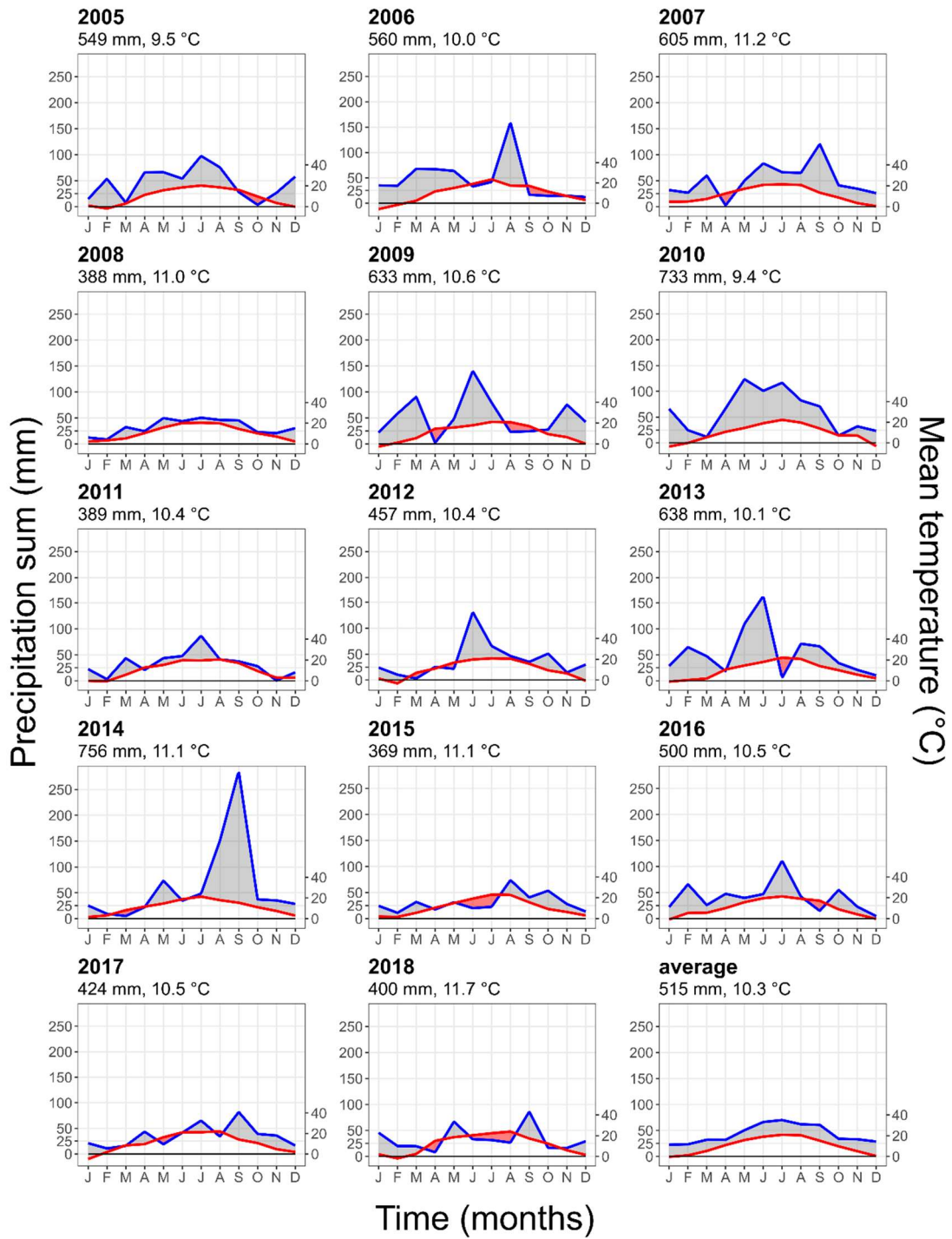
How to cite this article: Fischer FM, Chytrý K, Těšitel J, Danihelka J, Chytrý M. Weather fluctuations drive short-term dynamics and long-term stability in plant communities: A 25-year study in a Central European dry grassland. *J Veg Sci*. 2020;31:711–721. <https://doi.org/10.1111/jvs.12895>

Supporting information to the paper

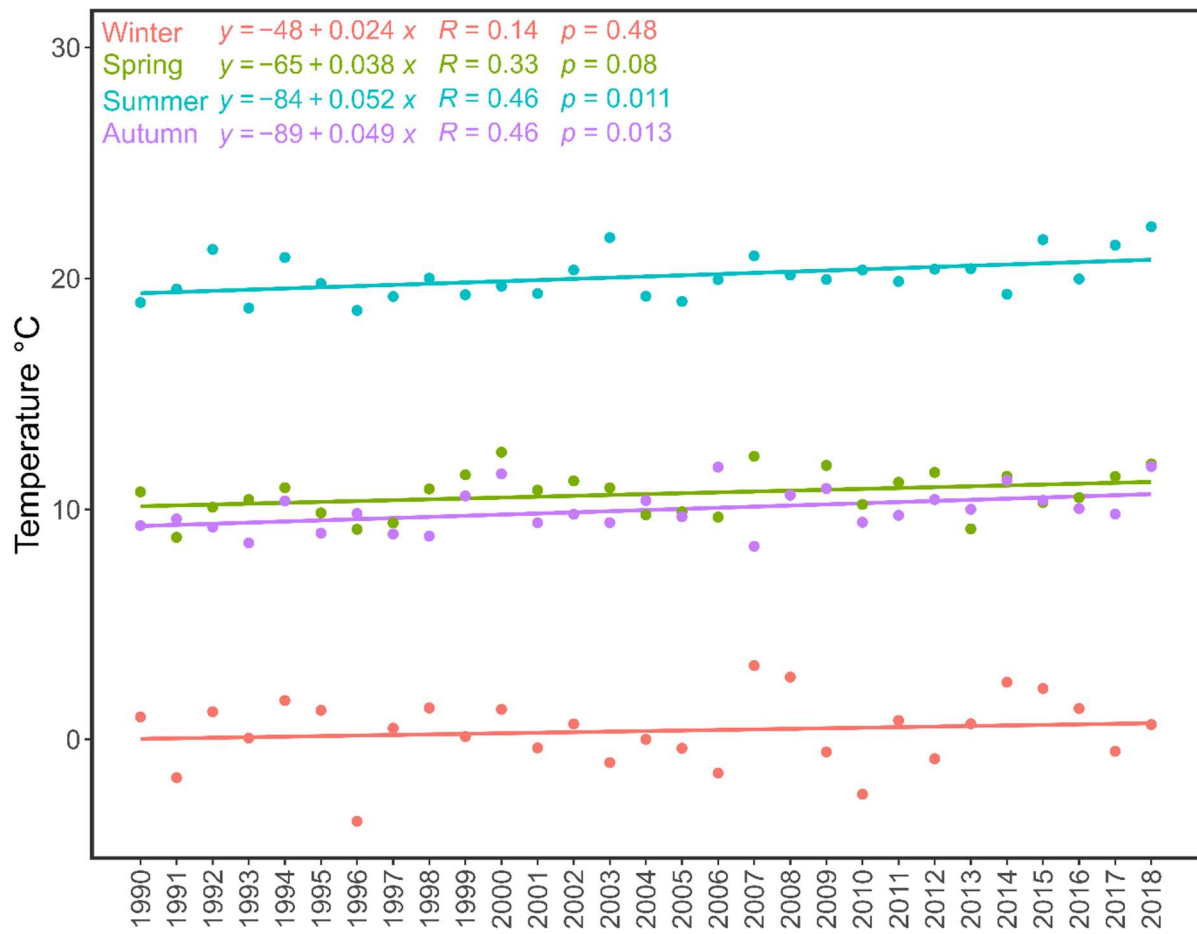
Fischer, F.M. Weather fluctuations drive short-term dynamics and long-term stability in plant communities: a 25-year study in a Central European dry grassland. *Journal of Vegetation Science*.

Appendix S1.1: Monthly weather data from 1990–2018 for Děvín Hill in the northern part of the Pavlov Hills, southern Moravia, Czech Republic (48°52'00"N, 16°38'40"E). Red lines indicate temperature and blue lines indicate precipitation. The average temperature and precipitation of each year are indicated below the year in the graph title. Data were obtained from the climate stations Dolní Věstonice (from 1993 to 2018, 172 m a.s.l., distance 2.2 km from the study site) and Mikulov (from 1990 to 1992, 268 m a.s.l., distance 6.3 km) for precipitation, and Děvín (from 2006 to 2018, 530 m a.s.l., distance 0.2 km) and Lednice (from 1990 to 2007, 177 m a.s.l., distance 14.2 km) for temperature. The temperature measured in the Lednice station was corrected to be comparable with the measurements from the Děvín station (0.5 °C was subtracted from calculated means based on the comparison of values of the two-year overlap). Coefficient of variation (CV) between seasons throughout the whole period (1990-2018) was 69.8% for temperature and 52.66% for precipitation.





Appendix S1.2: Variation in mean temperature in the study area between 1990 and 2018. Values per season were calculated as shown in Fig. 2.



Supporting information to the paper

Fischer, F.M. Weather fluctuations drive short-term dynamics and long-term stability in plant communities: a 25-year study in a Central European dry grassland. *Journal of Vegetation Science*.

Appendix S2. List of plots (relevés) included in the historical dataset. The references are given below the table. For relevés 1–85 their number in the Czech National Phytosociological Database (CNPD; Chytrý & Rafajová 2003) is given as their unique identifier. Plots 86–96 have no CNPD number yet.

Number	CNPD number	Author	Date/year	Reference (if available)
1	400825	M. Chytrý	1996-08-06	
2	400826	M. Chytrý	1996-08-06	
3	401854	M. Chytrý	1992-05-01	
4	403932	M. Chytrý	1992-05-01	
5	410935	J. Šmarda	1965-07-10	Šmarda 1975
6	410936	J. Šmarda	1965-04-02	Šmarda 1975
7	410939	J. Šmarda	1947-04-25	Šmarda 1975
8	410948	J. Šmarda	1965-04-02	Šmarda 1975
9	410949	J. Šmarda	1965-04-04	Šmarda 1975
10	410950	J. Šmarda	1965-04-04	Šmarda 1975
11	410954	J. Šmarda	1947-04-25	Šmarda 1975
12	410955	J. Šmarda	1947-04-25	Šmarda 1975
13	410956	J. Šmarda	1947-04-25	Šmarda 1975
14	410957	J. Šmarda	1961-06-23	Šmarda 1975
15	410960	J. Šmarda	1947-04-25	Šmarda 1975
16	410961	J. Šmarda	1947-04-25	Šmarda 1975
17	410962	J. Šmarda	1961-06-23	Šmarda 1975
18	410963	J. Šmarda	1946-04-25	Šmarda 1975
19	410964	J. Šmarda	1965-04-02	Šmarda 1975
20	410965	J. Šmarda	1965-04-02	Šmarda 1975
21	410966	J. Šmarda	1961-06-18	Šmarda 1975
22	410967	J. Šmarda	1961-06-18	Šmarda 1975
23	410968	J. Šmarda	1965-04-04	Šmarda 1975
24	410969	J. Šmarda	1961-08-01	Šmarda 1975
25	410976	J. Šmarda	1961-06-01	Šmarda 1975
26	410977	J. Šmarda	1961-06-01	Šmarda 1975
27	410978	J. Šmarda	1947-04-25	Šmarda 1975
28	410979	J. Šmarda	1961-06-18	Šmarda 1975
29	438140	J. Unar	1984-06	
30	438141	J. Unar	1984-06-06	
31	438142	J. Unar	1984-06-06	
32	438143	J. Unar	1984-06-06	
33	438144	J. Unar	1984-06-06	
34	438145	J. Unar	1984-06-06	
35	438146	J. Unar	1984-06-06	
36	438147	J. Unar	1984-06-14	
37	438148	J. Unar	1984-06-14	
38	438149	J. Unar	1986-08-18	
39	438150	J. Unar	1986-07-18	

Number	CNPD number	Author	Date/year	Reference (if available)
40	438151	J. Unar	1986-07-18	
41	438152	J. Unar	1986-09-25	
42	438153	J. Unar	1986-09-25	
43	439033	A. Wünschová	2001-05-14	Wünschová 2003
44	453508	M. Toman	1970-08	Toman 1975
45	453509	M. Toman	1970-08	Toman 1975
46	453510	M. Toman	1970-08	Toman 1975
47	453521	M. Toman	1970-08	Toman 1975
48	453522	M. Toman	1970-08	Toman 1975
49	453524	M. Toman	1970-08	Toman 1975
50	453525	M. Toman	1970-08	Toman 1975
51	453531	M. Toman	1970-08	Toman 1975
52	453532	M. Toman	1970-08	Toman 1975
53	453533	M. Toman	1970-08	Toman 1975
54	453534	M. Toman	1970-08	Toman 1975
55	453541	M. Toman	1970-08	Toman 1975
56	453542	M. Toman	1970-08	Toman 1975
57	453543	M. Toman	1970-08	Toman 1975
58	453544	M. Toman	1970-08	Toman 1975
59	453545	M. Toman	1970-08	Toman 1975
60	453562	M. Toman	1970-08	Toman 1975
61	453563	M. Toman	1970-08	Toman 1975
62	453564	M. Toman	1970-08	Toman 1975
63	453565	M. Toman	1970-08	Toman 1975
64	453566	M. Toman	1970-08	Toman 1975
65	453572	M. Toman	1970-08	Toman 1975
66	453573	M. Toman	1970-08	Toman 1975
67	453574	M. Toman	1970-08	Toman 1975
68	453575	M. Toman	1970-08	Toman 1975
69	453576	M. Toman	1970-08	Toman 1975
70	453583	M. Toman	1970-08	Toman 1975
71	453587	M. Toman	1970-08	Toman 1975
72	453588	J. Klika	1930	Klika 1931
73	453591	J. Klika	1930	Klika 1931
74	453593	J. Klika	1930	Klika 1931
75	453599	J. Klika	1930	Klika 1931
76	453600	J. Klika	1930	Klika 1931
77	453601	J. Klika	1930	Klika 1931
78	453602	J. Klika	1930	Klika 1931
79	453603	J. Klika	1930	Klika 1931
80	453606	J. Klika	1930	Klika 1931
81	453638	J. Klika	1930	Klika 1931
82	453639	J. Klika	1930	Klika 1931
83	453641	J. Klika	1930	Klika 1931
84	453645	J. Klika	1930	Klika 1931
85	462719	R. Hédl	2002-08-01	
86	-	K. Chytrý	2018-08-30	Chytrý K. 2019

Number	CNPD number	Author	Date/year	Reference (if available)
87	-	K. Chytrý	2018-08-30	Chytrý K. 2019
88	-	K. Chytrý	2018-08-30	Chytrý K. 2019
89	-	K. Chytrý & H. Prokešová	2019-04-08	
90	-	K. Chytrý & H. Prokešová	2019-04-08	
91	-	K. Chytrý & H. Prokešová	2019-04-08	
92	-	K. Chytrý & H. Prokešová	2019-04-19	
93	-	K. Chytrý & H. Prokešová	2019-04-19	
94	-	K. Chytrý & H. Prokešová	2019-04-19	
95	-	K. Chytrý & H. Prokešová	2019-04-19	
96	-	K. Chytrý & H. Prokešová	2019-04-19	

References

- Chytrý, K. 2019. Struktura expoziční lesostepi ve střední Evropě. Structure of exposure-related forest-steppe in Central Europe. Bachelor thesis, Department of Botany and Zoology, Masaryk University, Czech Republic, https://is.muni.cz/auth/th/tq01u/Chytry-2019_Thesis_with-Appendix-1-3.pdf.
- Klika, J. 1931. Studien über die xerotherme Vegetation Mitteleuropas. I. Die Pollauer Berge im südlichen Mähren. Beihefte zum Botanischen Centralblatt, Abteilung II, 47: 343–398.
- Šmarda, J. 1975. Rostlinná společenstva skalnaté lesostepi Pavlovských kopců na Moravě (ČSSR). Československá ochrana přírody 14: 5–58.
- Wünschová, A. 2003. Biologie, ekologie a rozšíření *Laser trilobum* (L.) Borkh., *Scrophularia vernalis* L. a *Iris humilis* Georgi subsp. *arenaria* (Waldst. et. Kit.) Á. et D. Löve na Moravě [Biology, ecology and distribution of *Laser trilobum*, *Scrophularia vernalis* and *Iris humilis* subsp. *arenaria* in Moravia]. Master theses, Institute of Botany, Masaryk University, Czech Republic, <https://is.muni.cz/auth/th/hw76p/text.pdf>.

Supporting information to the paper

Fischer, F.M. Weather fluctuations drive short-term dynamics and long-term stability in plant communities: a 25-year study in a Central European dry grassland. *Journal of Vegetation Science*.

Appendix S3. A list of species found in the permanent plots along the 25 years of surveys, and life forms/strategies. Codes are informed for the species according to Figure 7.

Taxon	life history	codes
<i>Achillea pannonica</i>	perennial	Ach.pan
<i>Acinos arvensis</i>	short-lived	Aci.arv
<i>Allium flavum</i>	perennial	All.fla
<i>Allium senescens</i> subsp. <i>montanum</i>	perennial	All.sen
<i>Alyssum alyssoides</i>	short-lived	Aly.aly
<i>Alyssum montanum</i>	perennial	Aly.mon
<i>Anthriscus cerefolium</i>	annual	Ant.cer
<i>Arabis auriculata</i>	annual	Ara.aur
<i>Arabis sagittata</i>	perennial	
<i>Arenaria serpyllifolia</i>	annual	Are.ser
<i>Arrhenatherum elatius</i>	perennial	
<i>Artemisia absinthium</i>	perennial	Art.abs
<i>Artemisia campestris</i>	perennial	
<i>Asperula cynanchica</i>	perennial	Asp.cyn
<i>Aurinia saxatilis</i>	perennial	
<i>Bromus japonicus</i>	annual	Bro.jap
<i>Bromus sterilis</i>	annual	Bro.ste
<i>Bromus tectorum</i>	annual	Bro.tec
<i>Buglossoides incrassata</i> subsp. <i>splitgerberi</i>	annual	Bug.inc
<i>Camelina microcarpa</i>	annual	Cam.mic
<i>Capsella bursa-pastoris</i>	annual	Cap.bur
<i>Carex praecox</i>	perennial	Car.pra
<i>Carex supina</i>	perennial	Car.sup
<i>Centaurea stoebe</i>	short-lived	Cen.sto
<i>Centaurea triumfetti</i>	perennial	
<i>Cerastium pumilum</i>	annual	Cer.pum
<i>Cerastium semidecandrum</i>	annual	Cer.sem
<i>Chaerophyllum temulum</i>	short-lived	
<i>Chenopodium album</i>	annual	
<i>Chenopodium hybridum</i>	annual	
<i>Convolvulus arvensis</i>	perennial	
<i>Conyza canadensis</i>	annual	
<i>Dianthus lumnitzeri</i>	perennial	
<i>Dianthus pontederiae</i>	perennial	Dia.pon
<i>Echium vulgare</i>	short-lived	Ech.vul
<i>Elymus hispidus</i>	perennial	
<i>Erodium cicutarium</i>	annual	Ero.cic
<i>Erophila spathulata</i>	annual	Ero.spa
<i>Eryngium campestre</i>	perennial	
<i>Erysimum durum</i>	short-lived	

Taxon	life history	codes
<i>Erysimum odoratum</i>	short-lived	
<i>Euphorbia cyparissias</i>	perennial	
<i>Festuca csikhegyensis</i>	perennial	
<i>Festuca rupicola</i>	perennial	
<i>Festuca valesiaca</i>	perennial	Fes.val
<i>Fragaria viridis</i>	perennial	Fra.vir
<i>Gagea pusilla</i>	perennial	Gag.pus
<i>Galium album</i> subsp. <i>album</i>	perennial	
<i>Galium aparine</i>	annual	Gal.apa
<i>Galium glaucum</i>	perennial	Gal.gla
<i>Galium spurium</i>	annual	
<i>Galium verum</i>	perennial	Gal.ver
<i>Geranium pusillum</i>	short-lived	Ger.pus
<i>Hesperis tristis</i>	short-lived	Hes.tri
<i>Holosteum umbellatum</i>	annual	Hol.umb
<i>Hylotelephium maximum</i>	perennial	Hyl.max
<i>Hypericum perforatum</i>	perennial	Hyp.per
<i>Inula oculus-christi</i>	perennial	
<i>Iris pumila</i>	perennial	
<i>Isatis tinctoria</i> subsp. <i>tinctoria</i>	short-lived	Isa.tin
<i>Jovibarba globifera</i>	perennial	
<i>Koeleria macrantha</i>	perennial	Koe.mac
<i>Lactuca serriola</i>	annual	Lac.ser
<i>Lamium amplexicaule</i>	annual	Lam.amp
<i>Lappula squarrosa</i>	annual	Lap.squ
<i>Lepidium campestre</i>	short-lived	Lep.cam
<i>Lotus borbasii</i>	perennial	
<i>Medicago falcata</i>	perennial	
<i>Medicago minima</i>	annual	Med.min
<i>Medicago prostrata</i>	perennial	
<i>Melica ciliata</i>	perennial	Mel.cil
<i>Microthlaspi perfoliatum</i>	annual	Mic.per
<i>Minuartia rubra</i>	short-lived	Min.rub
<i>Minuartia setacea</i>	perennial	
<i>Myosotis arvensis</i>	annual	
<i>Myosotis ramosissima</i>	annual	
<i>Myosotis stricta</i>	annual	Myo.str
<i>Odontites luteus</i>	annual	Odo.lut
<i>Ornithogalum kochii</i>	perennial	
<i>Orobanche alba</i>	short-lived	
<i>Orobanche caryophyllacea</i>	short-lived	Oro.car
<i>Phleum phleoides</i>	perennial	
<i>Pilosella cymosa</i>	perennial	
<i>Plantago media</i>	perennial	
<i>Poa angustifolia</i>	perennial	
<i>Poa badensis</i>	perennial	Poa.bad
<i>Poa bulbosa</i>	perennial	Poa.bul

Taxon	life history	codes
<i>Potentilla incana</i>	perennial	Pot.inc
<i>Ranunculus illyricus</i>	perennial	Ran.ill
<i>Reseda lutea</i>	short-lived	
<i>Reseda luteola</i>	short-lived	
<i>Sanguisorba minor</i>	perennial	San.min
<i>Saxifraga tridactylites</i>	annual	Sax.tri
<i>Scabiosa ochroleuca</i>	perennial	Sca.och
<i>Securigera varia</i>	perennial	
<i>Sedum acre</i>	perennial	Sed.acr
<i>Sedum album</i>	perennial	Sed.alb
<i>Senecio jacobaea</i>	short-lived	
<i>Senecio vulgaris</i>	annual	Sen.vul
<i>Seseli osseum</i>	perennial	Ses.oss
<i>Silene otites</i>	perennial	Sil.oti
<i>Taraxacum</i> sect. <i>Erythrosperma</i>	perennial	
<i>Teucrium chamaedrys</i>	perennial	
<i>Teucrium montanum</i>	perennial	Teu.mon
<i>Thymus praecox</i>	perennial	Thy.pra
<i>Tragopogon dubius</i>	short-lived	Tra.dub
<i>Trifolium arvense</i>	annual	Tri.arv
<i>Trifolium campestre</i>	short-lived	Tri.cam
<i>Turritis glabra</i>	short-lived	Tur.gla
<i>Valerianella locusta</i>	annual	Val.loc
<i>Verbascum chaixii</i> subsp. <i>austriacum</i>	perennial	
<i>Verbascum lychnitis</i>	short-lived	
<i>Veronica arvensis</i>	annual	Ver.arv
<i>Veronica praecox</i>	annual	Ver.pra
<i>Veronica prostrata</i>	perennial	Ver.pro
<i>Veronica sublobata</i>	annual	Ver.sub
<i>Veronica verna</i>	annual	Ver.ver
<i>Veronica vindobonensis</i>	perennial	
<i>Vincetoxicum hirundinaria</i>	perennial	
<i>Viola tricolor</i> subsp. <i>saxatilis</i>	perennial	Vio.tri

Table with columns representing years from 2007 to 2018 and rows representing various numerical data points. The table contains a dense grid of numbers and symbols (such as asterisks and 'z') arranged in a structured, repeating pattern across the years.

Supporting information to the paper

Fischer, F.M. Weather fluctuations drive short-term dynamics and long-term stability in plant communities: a 25-year study in a Central European dry grassland. *Journal of Vegetation Science*.

Appendix S5.1. Species scores in the PCoA model (Fig. 5).

Taxon	PCo1	PCo2	PCo3
<i>Achillea pannonica</i>	0.101056	-0.20992	0.110956
<i>Acinos arvensis</i>	0.026145	0.299444	-0.02246
<i>Allium flavum</i>	-0.20999	0.385856	-0.0925
<i>Allium senescens</i> subsp. <i>montanum</i>	-0.05041	-0.00922	0.014346
<i>Alyssum alyssoides</i>	0.114603	0.440348	-0.35044
<i>Alyssum montanum</i>	-0.22656	0.014878	0.60502
<i>Anthriscus cerefolium</i>	0.097509	0.0015	-0.1257
<i>Arabis auriculata</i>	0.192066	0.310824	-0.07998
<i>Arabis sagittata</i>	0.003148	0.014084	-0.0102
<i>Arenaria serpyllifolia</i>	0.03538	0.127444	0.047356
<i>Arrhenatherum elatius</i>	0.631134	-0.15583	-0.01002
<i>Artemisia absinthium</i>	0.03736	0.152301	-0.52449
<i>Artemisia campestris</i>	0.213082	-0.16241	-0.03171
<i>Asperula cynanchica</i>	-0.45631	0.092046	-0.42321
<i>Aurinia saxatilis</i>	0.011023	-0.00342	0.013396
<i>Bromus japonicus</i>	0.322093	0.336002	0.116682
<i>Bromus sterilis</i>	0.083899	0.006915	0.062352
<i>Bromus tectorum</i>	0.037319	0.054252	-0.0523
<i>Buglossoides incrassata</i> subsp. <i>splitgerberi</i>	0.230152	0.245002	0.048798
<i>Camelina microcarpa</i>	-0.01943	0.0972	-0.01946
<i>Capsella bursa pastoris</i>	-0.00162	0.002432	-0.00338
<i>Carex praecox</i>	0.159758	-0.05243	-0.27695
<i>Carex supina</i>	0.006572	0.03978	-0.03186
<i>Centaurea stoebe</i>	0.038931	0.109003	-0.02177
<i>Centaurea triumfetti</i>	0.092786	-0.17074	-0.42906
<i>Cerastium pumilum</i>	0.069854	-0.10021	0.128738
<i>Cerastium semidecandrum</i>	0.011589	0.317153	0.135411
<i>Chaerophyllum temulum</i>	0.00222	0.009936	-0.00831
<i>Chenopodium album</i>	-0.00462	0.011033	-0.01185
<i>Chenopodium hybridum</i>	0.003039	0.004033	-0.00046
<i>Convolvulus arvensis</i>	0.504921	-0.00854	-0.07963
<i>Conyza canadensis</i>	-0.00476	0.00656	0.001438
<i>Dianthus lumnitzeri</i>	-0.09598	-0.03325	0.052232
<i>Dianthus pontederiae</i>	-0.31182	-0.03852	0.229766
<i>Echium vulgare</i>	-0.00369	0.11341	0.012591
<i>Elymus hispidus</i>	0.178257	-0.15023	-0.41192
<i>Erodium cicutarium</i>	0.273371	0.27155	0.248677
<i>Erophila spathulata</i>	-0.57712	0.148534	0.120086
<i>Eryngium campestre</i>	0.459613	-0.11968	-0.22682
<i>Erysimum durum</i>	0.06403	-0.01336	0.053036
<i>Erysimum odoratum</i>	-0.00793	0.058069	-0.04421

Taxon	PCo1	PCo2	PCo3
<i>Euphorbia cyparissias</i>	-0.20135	-0.16619	0.08583
<i>Festuca csikhegyensis</i>	-0.43243	0.026959	0.102685
<i>Festuca rupicola</i>	0.105823	-0.23095	0.418577
<i>Festuca valesiaca</i>	-0.46663	-1.62853	0.27314
<i>Fragaria viridis</i>	-0.01207	0.020913	0.003635
<i>Gagea pusilla</i>	0.107414	-0.08144	0.097147
<i>Galium album</i> subsp. <i>album</i>	-0.01236	0.004822	0.004809
<i>Galium aparine</i>	0.05425	0.047242	-0.14744
<i>Galium glaucum</i>	-0.22182	-0.05465	0.121465
<i>Galium spurium</i>	0.002673	0.016369	-0.01123
<i>Galium verum</i>	0.138044	0.035132	0.381162
<i>Geranium pusillum</i>	0.63346	-0.09528	0.083485
<i>Hesperis tristis</i>	0.17951	0.16662	-0.14694
<i>Holosteum umbellatum</i>	0.179035	0.029567	0.339217
<i>Hylotelephium maximum</i>	0.081753	-0.13617	-0.26578
<i>Hypericum perforatum</i>	0.06933	0.137304	-0.15113
<i>Inula oculus christi</i>	0.513673	-0.16835	0.570826
<i>Iris pumila</i>	0.310623	-0.07105	0.315281
<i>Isatis tinctoria</i> subsp. <i>tinctoria</i>	0.057219	0.006004	-0.03487
<i>Jovibarba globifera</i>	-0.62201	0.022373	0.100659
<i>Koeleria macrantha</i>	-0.32251	-0.14857	-0.31067
<i>Lactuca serriola</i>	0.033281	0.054065	-0.06694
<i>Lamium amplexicaule</i>	0.30538	0.218807	-0.19207
<i>Lappula squarrosa</i>	-0.0981	0.160951	-0.00046
<i>Lepidium campestre</i>	0.369412	0.089915	0.334471
<i>Lotus borbasii</i>	0.02052	0.180245	-0.211
<i>Medicago falcata</i>	0.055257	0.056002	0.139357
<i>Medicago minima</i>	0.029013	0.531901	0.199597
<i>Medicago prostrata</i>	-0.06142	0.085459	0.084206
<i>Melica ciliata</i>	0.088555	0.211822	0.194402
<i>Microthlaspi perfoliatum</i>	0.351844	0.426928	0.263598
<i>Minuartia rubra</i>	-0.44154	0.321637	0.201754
<i>Minuartia setacea</i>	0.001409	0.01277	-0.00849
<i>Myosotis arvensis</i>	0.04609	-0.01366	0.023488
<i>Myosotis ramosissima</i>	0.019327	0.066791	0.024297
<i>Myosotis stricta</i>	0.135858	0.097657	0.000811
<i>Odontites luteus</i>	-0.13005	0.001155	0.026054
<i>Ornithogalum kochii</i>	0.127422	-0.01578	0.128967
<i>Orobanche alba</i>	-0.05561	-0.01195	-0.00396
<i>Orobanche caryophyllacea</i>	0.016996	-0.0287	0.087559
<i>Phleum phleoides</i>	0.001552	-0.2593	-0.05026
<i>Pilosella cymosa</i>	-0.00026	-0.01356	-0.0153
<i>Plantago media</i>	-0.0452	-0.0125	0.014861
<i>Poa angustifolia</i>	0.230513	-0.20966	-0.49644
<i>Poa badensis</i>	-0.53422	0.107257	0.020107
<i>Poa bulbosa</i>	-0.20375	0.336639	-0.15693
<i>Potentilla incana</i>	-0.49539	-0.02195	-0.08765

Taxon	PCo1	PCo2	PCo3
<i>Ranunculus illyricus</i>	0.469282	-0.09826	0.023397
<i>Reseda lutea</i>	0.00271	-0.01338	0.022825
<i>Reseda luteola</i>	-0.00147	-0.00031	0.001152
<i>Sanguisorba minor</i>	-0.00555	0.00637	-0.00126
<i>Saxifraga tridactylites</i>	-0.36289	0.269997	-0.12458
<i>Scabiosa ochroleuca</i>	-0.32732	0.031419	0.168579
<i>Securigera varia</i>	-0.01518	0.100886	0.36915
<i>Sedum acre</i>	-0.05917	-0.35861	0.051093
<i>Sedum album</i>	0.08774	0.213523	0.178179
<i>Senecio jacobaea</i>	0.00112	0.010877	-0.01391
<i>Senecio vulgaris</i>	-0.00502	0.009575	0.003567
<i>Seseli osseum</i>	-0.37557	0.048682	0.006038
<i>Silene otites</i>	-0.61038	0.037646	0.142398
<i>Taraxacum</i> sect. <i>Erythrosperma</i>	-0.09745	-0.03674	-0.30177
<i>Teucrium chamaedrys</i>	1.023026	0.135103	-0.47975
<i>Teucrium montanum</i>	-0.21416	-0.05415	0.03227
<i>Thymus praecox</i>	0.007494	-0.14695	-0.03195
<i>Tragopogon dubius</i>	-0.01866	0.091985	0.126759
<i>Trifolium arvense</i>	0.483804	0.126835	-0.02985
<i>Trifolium campestre</i>	0.446327	-0.14841	-0.08099
<i>Turritis glabra</i>	0.276305	0.008325	0.251804
<i>Valerianella locusta</i>	0.475789	-0.00873	0.136197
<i>Verbascum chaixii</i> subsp. <i>austriacum</i>	-0.01322	0.001486	0.001382
<i>Verbascum lychnitis</i>	-0.00353	0.055211	-0.06239
<i>Veronica arvensis</i>	0.258235	0.10674	-0.0023
<i>Veronica praecox</i>	-0.11154	0.257277	-0.06581
<i>Veronica prostrata</i>	-0.06952	-0.04277	-0.05531
<i>Veronica sublobata</i>	0.171768	0.183088	-0.30227
<i>Veronica verna</i>	-0.091	0.194344	0.043994
<i>Veronica vindobonensis</i>	0.089613	-0.04214	-0.10966
<i>Vincetoxicum hirundinaria</i>	-0.15728	-0.14976	-0.31992
<i>Viola tricolor</i> subsp. <i>saxatilis</i>	0.108306	0.060457	-0.08801

Appendix S5.2. Species scores in the db-RDA model (Fig. 7).

Taxon	CAP1	CAP2
<i>Achillea pannonica</i>	-0.17099	0.065274
<i>Acinos arvensis</i>	0.295261	0.130582
<i>Allium flavum</i>	0.171086	-0.09843
<i>Allium senescens</i> subsp. <i>montanum</i>	-0.06509	-0.00465
<i>Alyssum alyssoides</i>	0.300274	0.165354
<i>Alyssum montanum</i>	0.084067	-0.07082
<i>Anthriscus cerefolium</i>	0.079087	-0.09585
<i>Arabis auriculata</i>	0.248725	0.018044
<i>Arabis sagittata</i>	0.007391	0.012274

Taxon	CAP1	CAP2
<i>Arenaria serpyllifolia</i>	0.188078	0.204213
<i>Arrhenatherum elatius</i>	0.066594	-0.16528
<i>Artemisia absinthium</i>	0.082524	-0.08042
<i>Artemisia campestris</i>	-0.04004	-0.05997
<i>Asperula cynanchica</i>	-0.10423	0.170414
<i>Aurinia saxatilis</i>	-0.00112	0.005866
<i>Bromus japonicus</i>	0.244769	-0.00086
<i>Bromus sterilis</i>	0.040694	-0.01963
<i>Bromus tectorum</i>	0.031172	-0.06058
<i>Buglossoides incrassata</i> subsp. <i>splitgerberi</i>	0.320007	0.041997
<i>Camelina microcarpa</i>	0.086462	-0.08812
<i>Capsella bursa pastoris</i>	0.003545	-0.01317
<i>Carex praecox</i>	0.080233	-0.0785
<i>Carex supina</i>	0.034348	-0.01981
<i>Centaurea stoebe</i>	0.045125	-0.11256
<i>Centaurea triumfetti</i>	-0.01393	0.033857
<i>Cerastium pumilum</i>	0.024319	0.279762
<i>Cerastium semidecandrum</i>	0.259952	0.224699
<i>Chaerophyllum temulum</i>	0.004757	0.008325
<i>Chenopodium album</i>	0.004882	0.001334
<i>Chenopodium hybridum</i>	0.005029	0.003196
<i>Convolvulus arvensis</i>	0.06392	0.007841
<i>Conyza canadensis</i>	0.005029	0.003196
<i>Dianthus lumnitzeri</i>	-0.01265	0.005949
<i>Dianthus pontederiae</i>	-0.13374	0.118204
<i>Echium vulgare</i>	0.368578	0.389007
<i>Elymus hispidus</i>	0.006258	-0.00057
<i>Erodium cicutarium</i>	0.284299	0.070611
<i>Erophila spathulata</i>	0.010647	0.118437
<i>Eryngium campestre</i>	-0.04922	0.022497
<i>Erysimum durum</i>	-0.00902	0.01672
<i>Erysimum odoratum</i>	-0.08382	0.1594
<i>Euphorbia cyparissias</i>	0.107872	-0.0027
<i>Festuca csikhegyensis</i>	-0.00443	0.028066
<i>Festuca rupicola</i>	-0.09924	-0.07002
<i>Festuca valesiaca</i>	-0.97073	0.433189
<i>Fragaria viridis</i>	0.015647	-0.04009
<i>Gagea pusilla</i>	-0.229	-0.03384
<i>Galium album</i> subsp. <i>album</i>	0.010851	-0.00455
<i>Galium aparine</i>	0.048341	-0.02605
<i>Galium glaucum</i>	-0.06815	0.112901
<i>Galium spurium</i>	-0.00519	0.019593
<i>Galium verum</i>	-0.08347	0.097465
<i>Geranium pusillum</i>	0.26735	-0.00948
<i>Hesperis tristis</i>	0.161798	-0.11623
<i>Holosteum umbellatum</i>	-0.01592	0.176917
<i>Hylotelephium maximum</i>	-0.05174	0.021309

Taxon	CAP1	CAP2
<i>Hypericum perforatum</i>	-0.01756	0.165545
<i>Inula oculus christi</i>	-0.04609	0.043491
<i>Iris pumila</i>	0.003496	-0.03565
<i>Isatis tinctoria</i> subsp. <i>tinctoria</i>	0.035912	-0.03312
<i>Jovibarba globifera</i>	-0.06422	0.067367
<i>Koeleria macrantha</i>	-0.21867	0.15939
<i>Lactuca serriola</i>	0.051186	0.004131
<i>Lamium amplexicaule</i>	0.154141	-0.05358
<i>Lappula squarrosa</i>	0.214887	-0.0461
<i>Lepidium campestre</i>	0.260658	-0.08317
<i>Lotus borbasii</i>	0.03923	0.000993
<i>Medicago falcata</i>	0.049058	0.008007
<i>Medicago minima</i>	0.809019	0.277826
<i>Medicago prostrata</i>	0.007794	0.009136
<i>Melica ciliata</i>	0.178988	-0.14772
<i>Microthlaspi perfoliatum</i>	0.363905	-0.06371
<i>Minuartia rubra</i>	0.21451	-0.05945
<i>Minuartia setacea</i>	0.001093	0.011756
<i>Myosotis arvensis</i>	0.011081	0.038499
<i>Myosotis ramosissima</i>	0.032229	0.019331
<i>Myosotis stricta</i>	0.067662	0.092405
<i>Odontites luteus</i>	-0.00792	0.148137
<i>Ornithogalum kochii</i>	-0.01192	0.031154
<i>Orobanche alba</i>	-0.01062	0.036068
<i>Orobanche caryophyllacea</i>	-0.03408	0.098013
<i>Phleum phleoides</i>	-0.02408	-0.06321
<i>Pilosella cymosa</i>	-0.01082	0.00133
<i>Plantago media</i>	-0.01846	0.008205
<i>Poa angustifolia</i>	-0.0117	-0.0265
<i>Poa badensis</i>	-0.08697	0.169034
<i>Poa bulbosa</i>	0.15594	-0.07098
<i>Potentilla incana</i>	-0.21613	-0.14008
<i>Ranunculus illyricus</i>	0.028619	-0.04027
<i>Reseda lutea</i>	0.00098	0.004791
<i>Reseda luteola</i>	-0.00258	0.008318
<i>Sanguisorba minor</i>	0.003545	-0.01317
<i>Saxifraga tridactylites</i>	0.080313	0.256302
<i>Scabiosa ochroleuca</i>	-0.09623	0.047543
<i>Securigera varia</i>	0.074214	-0.02837
<i>Sedum acre</i>	-0.26866	0.455825
<i>Sedum album</i>	0.156321	0.105822
<i>Senecio jacobaea</i>	-0.00029	-0.00372
<i>Senecio vulgaris</i>	0.00605	-0.01018
<i>Seseli osseum</i>	0.112522	-0.16161
<i>Silene otites</i>	-0.0831	0.085336
<i>Taraxacum</i> sect. <i>Erythrosperma</i>	-0.19451	-0.05977
<i>Teucrium chamaedrys</i>	-0.10133	0.23958

Taxon	CAP1	CAP2
<i>Teucrium montanum</i>	-0.06862	0.041871
<i>Thymus praecox</i>	-0.12099	0.101669
<i>Tragopogon dubius</i>	0.093499	0.036489
<i>Trifolium arvense</i>	0.361535	0.091804
<i>Trifolium campestre</i>	0.174674	0.303937
<i>Turritis glabra</i>	0.042118	-0.02606
<i>Valerianella locusta</i>	0.183464	-0.06094
<i>Verbascum chaixii</i> subsp. <i>austriacum</i>	-0.00596	0.01128
<i>Verbascum lychnitis</i>	-0.08906	-0.02788
<i>Veronica arvensis</i>	0.182468	0.309346
<i>Veronica praecox</i>	0.13125	0.096591
<i>Veronica prostrata</i>	-0.22107	0.06802
<i>Veronica sublobata</i>	0.114529	-0.22367
<i>Veronica verna</i>	0.231694	-0.12715
<i>Veronica vindobonensis</i>	0.017524	-0.03456
<i>Vincetoxicum hirundinaria</i>	-0.03453	0.073193
<i>Viola tricolor</i> subsp. <i>saxatilis</i>	0.15658	-0.06876