

## RESEARCH ARTICLE

# Seasonal beta-diversity of dry grassland vegetation: Divergent peaks of above-ground biomass and species richness

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## Abstract

**Question:** Temperate grasslands are known for their high plant diversity and distinct seasonality. However, their intra-annual community dynamics are still largely overlooked by ecologists. Therefore, we explored the seasonal alpha- and beta-diversity patterns of vascular plants and their relationships to above-ground biomass in a rocky steppe (*Festucion valesiacae*).

**Location:** Pavlov Hills, SE Czech Republic.

**Methods:** For one year, we monitored the plant community of the rocky steppe at monthly intervals in 42 permanent plots of 0.25 m<sup>2</sup>. We examined seasonal changes in above-ground biomass (estimated from the cover and height of living plant parts) and seasonal beta-diversity, which we partitioned into turnover and nestedness components and their quantitative counterparts: balanced changes and abundance gradients.

**Results:** We identified a pronounced seasonal pattern of above-ground biomass, species richness and composition. Total above-ground biomass was highest in June (summer), with a peak representing only 60% of total annual production (sum of individual species' maxima). However, the observed peak in species richness occurred in March (early spring), with 80% of the total species number recorded throughout the year. Accordingly, nestedness and abundance gradient patterns differed in the spring months, while seasonal turnover and balanced changes in abundance were generally congruent. Annual, short-lived, and perennial species exhibited different seasonal patterns of species richness and biomass production, although a sharp increase in biomass and a peak in species richness in spring were universal across the community.

**Conclusions:** Seasonal climatic constraints on plant growth are key determinants of primary production dynamics. Plants adapt to these constraints by adjusting their life cycles in different ways. In dry grasslands, the complexity of plant responses to climatic seasonality can result in seasonal beta-diversity patterns with divergent peaks in biomass and species richness.

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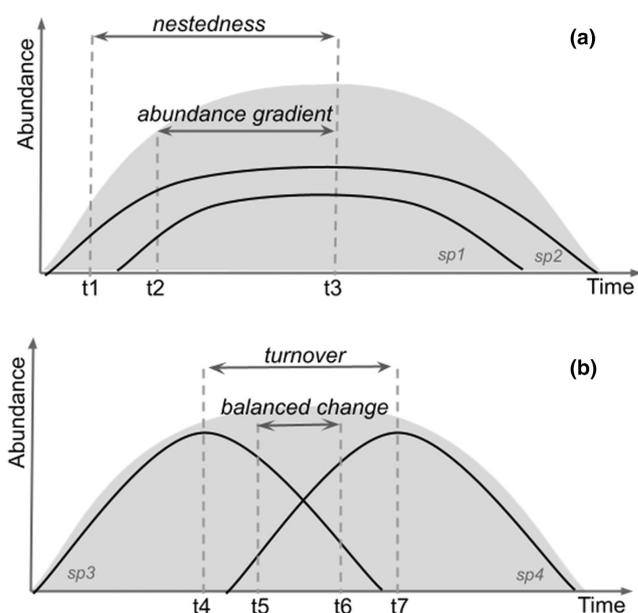
## KEYWORDS

beta-diversity, biomass, dry grassland, permanent plots, plant community, primary production, seasonal dynamics, species richness, vascular plants

## 1 | INTRODUCTION

Temperate grasslands are globally recognized for their high species diversity (Wilson et al., 2012; Squires et al., 2019; Sabatini et al., 2022). Their universal ecosystem feature is climatic seasonality. Annual cycles of temperature, water availability, and photoperiod create favorable periods for plant growth that alternate with unfavorable periods. Plants respond to these seasonal changes in abiotic conditions by adjusting their life-cycle timing (phenology), which is considered critical for community patterns and processes, including species interactions, coexistence, and biodiversity (Grubb, 1977; Moulin et al., 2021). Primary production also varies with seasonal changes (Sala, 2001), which can affect other ecosystem components, such as herbivores and pollinators. There is ample empirical evidence of seasonal patterns of ecosystem processes in temperate grasslands thanks to the monitoring of bulk community metrics, assessed either at short range (e.g., phenocams; Brown et al., 2016) or remotely (e.g., NDVI; Potter & Alexander, 2020). Unfortunately, these data are of limited value for community-level patterns and processes, such as diversity or ecological interactions, because they lack species resolution.

In community ecology, it is a standard practice to use species-level resolution for studying mechanisms of interspecific interactions (Wolf et al., 2017) and species coexistence (Adler et al., 2006). This approach has significant implications for understanding the effects of climate change on biodiversity (Forrest & Miller-Rushing, 2010). However, most such studies rely on a single snapshot of community composition, in temperate grasslands usually performed during its peak phenology in spring or early summer (Dengler et al., 2008). Sampling during peak phenology stems mostly from pragmatic reasons; flowering plants are easier to identify, which has a positive effect on the quality of the data. It reflects the assumption that seasonal variation in biomass and species richness is congruent, hence sampling during peak biomass production captures the highest species richness of the community. However, several previous studies have shown a relatively high seasonal beta-diversity in some kinds of temperate grasslands, associated with the changing abundance or presence of some species during the growing season (Thórhallsdóttir, 1990; Kohler et al., 2004; Vymazalová et al., 2012). They also showed that species interactions are highly seasonal (Thórhallsdóttir, 1990). Rocky grasslands in particular are characterized by distinct spring and summer phases (Vymazalová et al., 2012). Most often, the issue of high seasonal beta-diversity in the community is treated with a compromise on sampling time in order to capture both spring and summer phases and, therefore, to maximize the species richness. Implications of this methodological approach are still unclear, and available information on the intra-annual dynamics of grassland plant communities is sparse. The studies mentioned above considered only the growing



**FIGURE 1** Conceptual illustration of seasonal beta-diversity and the associated abundance-based dissimilarity framework. The graphs show two contrasting cases of abundance distribution of two species (black lines) over time during a single season. In both cases, total abundance (biomass; in gray) shows the same unimodal trend. In (a), sp1 occurs over a period that is a subset of the growth period of sp2, resulting in community nestedness (t1–t3). The dynamics of species abundance show an abundance gradient (t2–t3) because the abundances of the two species increase synchronously, and thus both contribute to an increase in total abundance. In (b), two species (sp3 and sp4) replace each other over time. This results in a balanced change in abundance (between time points t5 and t6) and, in the extreme case, in turnover when the replacement between the species is complete (t4–t7)

season, while those examining community dynamics throughout the whole year are even rarer and refer to grasslands outside the temperate zone (e.g., Singh & Yadava, 1974).

Here, we use the modern beta-diversity framework (Baselga & Orme, 2012; Baselga, 2013) to assess seasonal fluctuations in community composition and link patterns of community and ecosystem processes. This framework allows the quantification of seasonal beta-diversity and its partitioning into turnover and nestedness components. While the original concept of beta-diversity components considers presence/absence data only (Baselga, 2010), the abundance-based community composition data may be partitioned into balanced changes in abundance and abundance gradients, which correspond to turnover and nestedness, respectively (Figure 1; Baselga, 2013).

The current prevailing methodology in vegetation ecology consists of a single sampling per year (Dengler et al., 2008). It relies on the

assumption that the seasonal peak of species richness coincides with the peak of above-ground biomass. Consequently, vegetation data collected at the time of peak biomass are considered representative of the overall community composition. These assumptions would be valid if seasonal community dynamics followed an abundance gradient (i.e., a directional change in total abundance across all species) and exhibited a nested pattern in species composition (Figure 1a; Baselga, 2013). In other words, the record of peak community biomass would contain nearly all species from the local community species pool, while species composition at other times of the year would be only a subset of this peak biomass record. Such a pattern would indicate strong climatic control of the growing season, with the entire species pool of the local community responding in the same way. Alternatively, intra-annual community dynamics may include balanced changes in species abundances (i.e., abundance increases for some species and decreases for others, while total abundance remains the same) and, eventually, turnover in species composition, that is, the presence of different species in the living above-ground biomass in different periods of the year (Figure 1b; Baselga, 2013). Such complexity may act as a mechanism for species coexistence in the context of temporal niche partitioning within the year (Wilson, 2011; Doležal et al., 2019; Moulin et al., 2021). This difference in strategy may influence the phenology of species and lead to reduced competition with other species, which is thought to be most intense in periods most favorable for plant growth (Wilson, 2011; Doležal et al., 2019), that is, when the community produces the peak above-ground biomass.

This article aims to contribute to the understanding of the seasonal dynamics of plant communities by systematic monthly monitoring of permanent plots in dry grassland throughout the year. We focused on community dynamics and above-ground primary production as the most important processes in the vegetation. We tested two basic hypotheses underlying the methodological assumption of standard vegetation sampling: (1) community and ecosystem patterns are congruent, that is, there is a strong correlation between observed species richness and living above-ground biomass; and (2) seasonal beta-diversity follows the pattern of nestedness/abundance gradient rather than the pattern of turnover/balanced changes in abundance (Figure 1). This pattern might be expected where species with different life histories coexist. Because previous studies in the region have identified plant life forms as a correlate with growing season timing (Vymazalová et al., 2012) and as a predictor of plant response to climate dynamics (Fischer et al., 2020), we also tested these hypotheses for individual life-history types of plants that occur in the dry grassland under study.

## 2 | METHODS

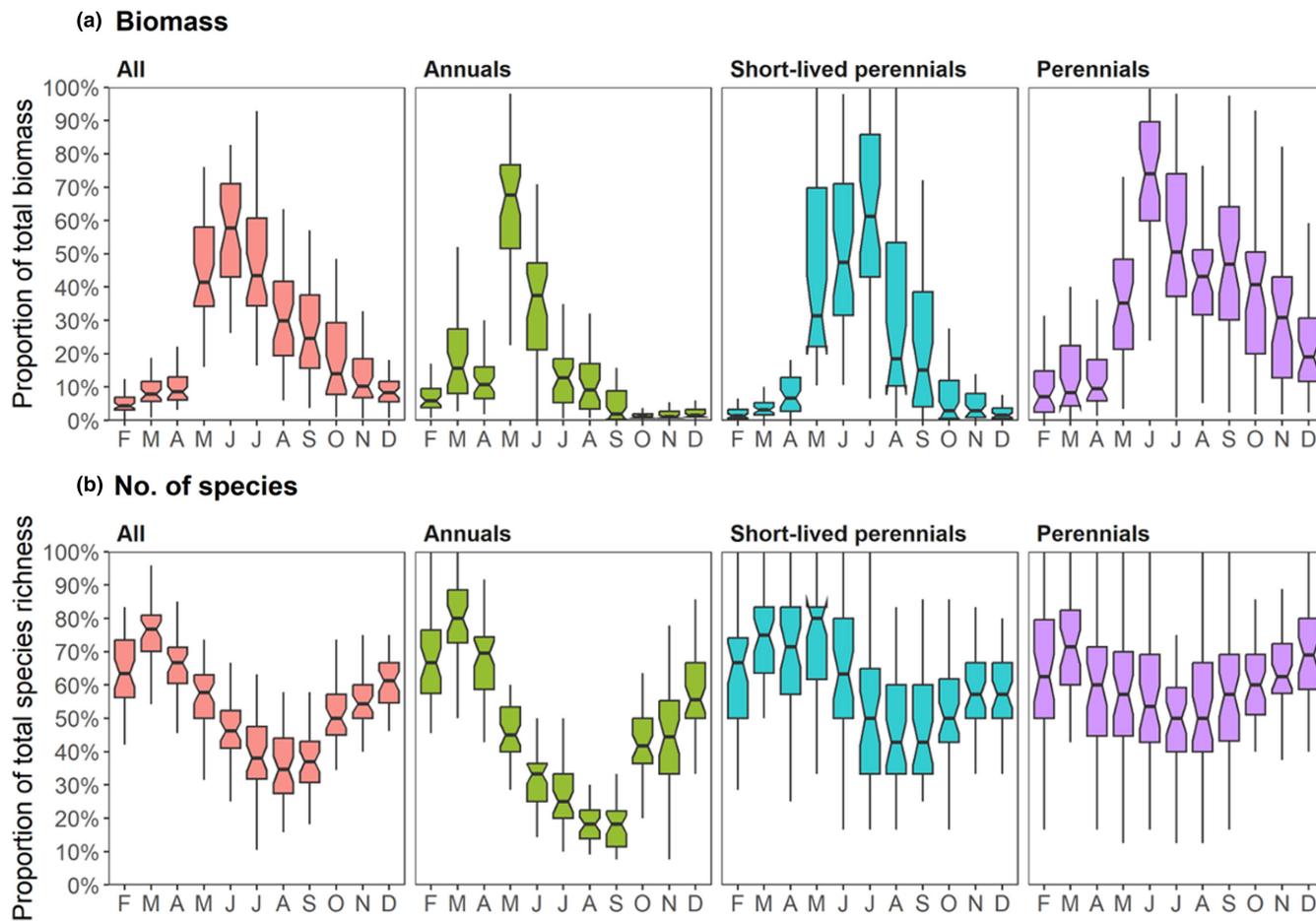
### 2.1 | Field sampling

The study was conducted in the Pavlov Hills in the southeastern Czech Republic (48.868° N, 16.646° E; Danihelka et al., 2015). The climate in this area is temperate subcontinental and seasonal, with

significant differences between summer and winter (Figure 2). The mean annual temperature and the temperature of the coldest month (January) range between 8 and 9.5°C and from -1 to -2°C, respectively. Total annual precipitation ranges between 500 and 550 mm, of which 300–325 mm fall from April to September (Tolasz et al., 2007). Although there are no arid periods on average in the long term, a large temporal variation in precipitation leads to frequent dry spells in different parts of the year (for details, see Appendix S1 and Fischer et al., 2020: their Appendix S1). We sampled a rocky limestone steppe in the summit area of the Děvín Hill (550 m a.s.l.) at an elevation of approximately 500–520 m a.s.l., in a relatively homogeneous area of dry grassland of the alliance *Festucion valesiacae* (Chytrý, 2007). This vegetation is dominated by tussocky grasses (mainly *Festuca valesiaca*, *Koeleria macrantha*, and *Phleum phleoides*) and perennial forbs (e.g., *Galium glaucum* and *Potentilla incana*), including succulents (*Sedum acre* and *Sedum album*) and dwarf semi-shrubs (e.g., *Teucrium chamaedrys*). Annual species are also common (e.g., *Arenaria serpyllifolia*, *Cerastium pumilum* and *Medicago minima*). Biogeographically, central European plant species occur here together with species of sub-Mediterranean dry grasslands and continental steppes (Chytrý, Prokešová, et al., 2022).

We used seven monitoring plots (4 m<sup>2</sup> × 4 m<sup>2</sup> quadrats, hereafter “blocks”) established in 1993 (see Fischer et al., 2020 for details). These blocks were located on a SE-facing slope with an inclination of approximately 20° and a maximum distance between them of up to 100 m. Within each block, we laid out six (42 plots in total) non-contiguous plots of 0.5 m<sup>2</sup> × 0.5 m<sup>2</sup>. These plots were surveyed 11 times, approximately once per month, between February 2019 and January 2020 (19–20 Feb, 25–26 Mar, 29–30 Apr, 28 May, 26 Jun, 31 Jul, 24 Aug, 25 Sep, 6 Nov, 4 Dec and 1 Feb).

During the surveys, each plant species rooted in the plot was recorded, its maximum vegetative height was measured, and its cover was estimated using the modified nine-degree Braun-Blanquet scale (Westhoff & van der Maarel, 1978). Only living (green) plant parts were considered in the height and cover measurements. For analysis, we converted the Braun-Blanquet scale degrees into cover area estimates (in cm<sup>2</sup>) by multiplying the mid-percentage value for each scale degree by plot area. Further, we multiplied the estimated cover area by the maximum vegetative plant height of each species observed in the given plot at the time of sampling. The resulting values are treated as biomass hereafter. This non-destructive method has been shown to provide a relatively reliable estimate of standing live biomass in similar dry grasslands in the same area (*biomass estimate-raw*, Axmanová et al., 2012). We used this method because destructive sampling (biomass clipping and weighing) could not be combined with the repeated sampling of permanent plots. Plant taxon concepts and names follow Danihelka et al. (2012). The full species list is available in Danihelka (2019). To understand the dynamics of species with different life histories, we also classified them as annual, short-lived perennial (mostly biennial or monocarpic perennial), and perennial species following Fischer et al. (2020).



**FIGURE 2** Above-ground biomass and species richness throughout the year. Monthly values from February (F) to December (D) are expressed as proportions of annual totals measured in 42 permanent plots in dry grassland. For biomass, 100% equals the sum of the maximum biomass values of each species found. For species richness, 100% represents the total number of species recorded in a given plot throughout the sampling period. Proportions were calculated separately for annual ( $n = 23$ ), short-lived ( $n = 12$ ) and perennial species ( $n = 39$ ). Boxplots express the median, lower and upper quartiles. Comparisons with biomass and species richness trends in the two subsequent years of the study can be found in Appendix S2

## 2.2 | Data analysis

Total species richness was determined as the total number of species recorded in a given plot during the entire sampling period (i.e., one year). Total biomass production in the plot was estimated as the sum of the maximum biomass of all species found in the given plot throughout the sampling period. After 2019, we continued sampling at bimonthly intervals, but we did not analyse data from subsequent sampling events in this article. We only used the data to demonstrate the representativeness of the trends observed in 2019 (Appendix S2).

To examine variation in species composition among samples from different parts of the year independently of plot identity, we used partial principal coordinate analysis (partial PCoA, i.e., an ordination analysis that includes conditioning predictor terms but no constraining predictors; see Šmilauer & Lepš, 2014) with plot identity as the conditional term. We created two sets of between-sample dissimilarity matrices, one based on species abundances (square root-transformed values of biomass) and the other based on presence/absence data. In each set, we calculated

overall dissimilarity based on the Bray–Curtis and Sørensen indices for abundance-based and presence/absence-based analyses, respectively (Oksanen et al., 2019). Then, we partitioned the dissimilarity in community composition into components according to Baselga (2013; see also Figure 1). The first component is the balanced changes in abundance (for species abundance data) and turnover (for presence/absence data), which measure the degree to which the abundance or presence of one species is replaced by the same amount of abundance or presence of other species. The second component is the abundance gradient (for species abundance data) and nestedness (for presence/absence data), which measure the degree of change at which the total abundance or the total number of species increases or decreases. We obtained six dissimilarity matrices (total dissimilarity and its two components, for both abundance and presence/absence data). Each of these matrices was used to compute a partial PCoA with plot identity as the conditional term. The partial PCoAs were based on square-rooted dissimilarities and computed using the “capscale” function from the *vegan* package (Oksanen et al., 2019).

We performed all analyses in R 4.0.5 (R Core Team, 2021) using the *tidyverse* package (Wickham et al., 2019), which we also used for drawing the ordination diagrams. Seasonal beta-diversity was partitioned using the *betapart* package (Baselga & Orme, 2012), and partial PCoAs were computed using the *vegan* package (Oksanen et al., 2019). The full R code for the analyses is available in Appendix S3.

## 3 | RESULTS

### 3.1 | Biomass, richness, and life histories

We recorded a total of 72 vascular plant species in the 42 plots during the 11 repeated surveys in 2019 (all data are available in Appendix S4). The community showed remarkable variation in both biomass and species richness throughout the year, and the maxima of biomass and richness were not synchronized (Figure 2). A peak in above-ground biomass occurred in June (late spring to early summer in the Northern Hemisphere), whereas the highest species richness was recorded in March (early spring), with an average of 17.3 species per plot. A similar asynchrony was observed for minima: lowest biomass values were recorded during the cold period between October and February (autumn to winter), whereas the lowest species richness occurred in August–September (average 8.3 species). The same trends in variation in biomass and species richness were observed in the two subsequent years (Appendix S2).

Biomass and species richness of the different life-history types followed the same overall wave pattern, but some differences were found. The peaks in biomass production occurred in May, July and June for annuals, short-lived perennials, and perennials, respectively. Biomass minima occurred in cold months of the year in all groups, but there were some differences. In annuals, the minimum biomass occurred in October and then biomass increased until March when we recorded a secondary peak preceding a moderate decline in April. In short-lived perennials, the minimum biomass extended from December to February. The biomass minimum of perennials occurred in early spring (Feb–Apr) and was less pronounced than in the other two types. The maximum species richness was recorded in early spring in all life-history types, whereas the minima were located in late summer. The pattern in richness was highly pronounced in annuals, less so in short-lived perennials, and almost homogeneous in perennials.

### 3.2 | Community composition and beta-diversity

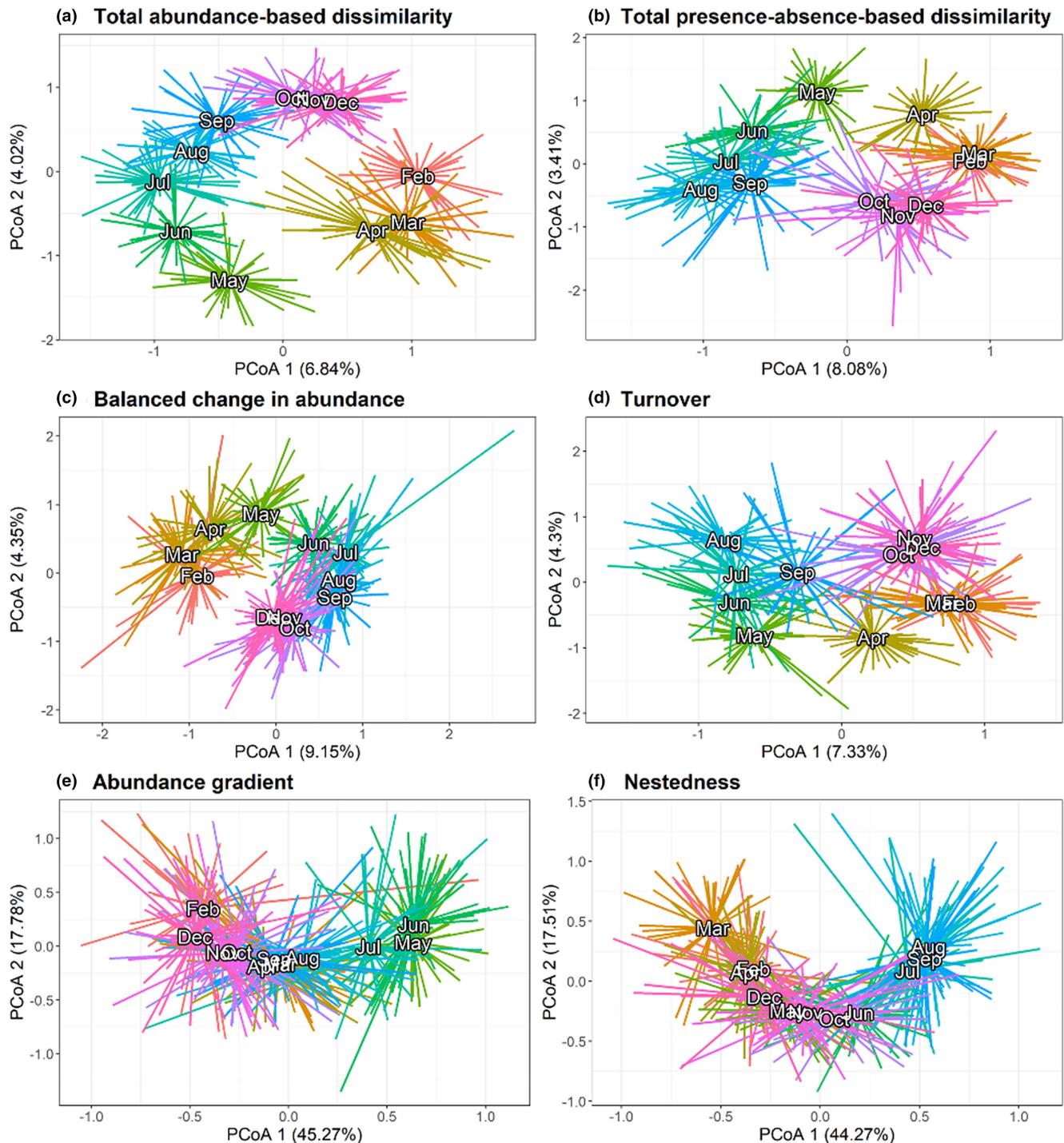
The highest values of beta-diversity (dissimilarity in community composition) within plots between two months were 0.685 (Bray–Curtis; Feb–Jun) and 0.464 (Sørensen; Mar–Sep) on average. Partial PCoA based on the total dissimilarity measure revealed circular patterns approximating the order of months in the year when computed for both abundance-based and presence/absence data

(Figure 3a,b). Both analyses also indicate certain clustering of late autumn (Oct–Dec) and early spring (Feb–Apr) data, while the variability is more continuous during the main growth season (May–Sep). Correspondingly, the most pronounced differences between consecutive months occurred between April and May (spring) and September and October (autumn). A similar pattern emerged from the analysis of balanced changes in abundance (Figure 3c). However, the analysis of turnover identified a slightly different structure. Two distinct groups of samples are separated on the first axis gradient corresponding to warm (May–Aug) and cold (Oct–Feb) seasons with April and September located between the two (Figure 3d). In contrast, the analysis of the abundance gradient revealed an interpretable pattern only along the first axis. The positions of the months correspond to the pattern in biomass production (Figure 2a) here, with high biomass in the late spring/early summer months (May–Jul) on the right and the other months forming a gradient from the left (Dec, Feb) to the central part of the first axis (Figure 3e). A similar trend was observed in the nestedness analysis but the temporal trend was shifted with respect to the abundance gradient. The early spring months (Feb–Apr) occupied the left side of the main gradient while the late summer months formed a distinct cluster on its right side (Figure 3f), corresponding generally to the dynamics of species richness (Figure 2b). Species scores on the ordination axes can be found in Appendix S5.

## 4 | DISCUSSION

We found that both biomass and species richness exhibited a wave-like distribution throughout the year with a single peak and single minima. However, these were not congruent as we initially hypothesized. The observed biomass minimum in winter and the maximum in late spring are consistent with expectations for a temperate grassland (Sala, 2001), although the timing seems to be relatively early. A similar early peak of biomass was previously reported from managed grasslands, where it was caused by mowing (Doležal et al., 2019). In fact, most temperate grasslands in Europe are managed and therefore exhibit such early biomass peaks. By contrast, in continental temperate grasslands, biomass is accumulated throughout the summer (Piao et al., 2005; Zuo et al., 2013). In our study system, the gradual increase of biomass is interrupted by harsh summer conditions that severely limit plant growth (Fischer et al., 2020; Appendix S1), as in Mediterranean ecosystems (Chollet et al., 2014). At our site, the summer drought is primarily caused by the dry and relatively warm macroclimate but its effect is amplified by the presence of shallow rocky soil which enhances heat accumulation and evaporation (Chytrý, Willner, et al., 2022).

In contrast to biomass, the timing of the species richness minimum in mid-summer, which is the peak growing season, and of the maximum in early spring, even before the onset of the growing season, are rather surprising. We assume that the key to understanding the temporal distribution of species richness is the co-occurrence of multiple groups of species with different life histories associated



**FIGURE 3** Partial principal coordinate analysis (PCoA) of biomass-weighted species composition (abundance, left column) and presence/absence data (right column). Each color represents a different survey month, and lines connect each plot to the monthly centroid (average). In all models, plot identity was used as a covariate, accounting for 48% of the variation ( $df = 41$ ). The different graphs represent (a, b) total dissimilarity, (c, d) balanced changes in abundance or turnover, and (e, f) unidirectional abundance gradient or nestedness

with contrasting strategies for exploiting periods suitable for growth and survival under harsh conditions. Shallow-rooting annual plants that survive dry periods only as seeds (Hájková & Krekule, 1972) are concentrated mainly in spring and in part in autumn and winter if not too cold (Geißelbrecht-Taferner et al., 1997). In contrast, short- and long-lived perennials mostly sustain dry summer conditions but survive winter only in dormant states. The highest overlap between these two groups occurs in spring when annual plants have their

optima and perennial plants gradually leave dormancy. However, this alone does not sufficiently explain why we observed the peak of species richness as early as in March. In fact, there is a strong additional contribution of seedlings of perennial species that occur throughout winter, if not too cold, and especially early spring before adult plants leave dormancy. In March, they coincide with the first germinating annual species and the few perennial species that stay active throughout winter. The resultant species richness peak

in March is hence ephemeral and likely dependent on temporarily suitable conditions that occur between the too cold winter and too hot-and-dry summer.

In line with the dynamics of biomass and species richness and in contrast to what we initially hypothesized, the relative contribution of an abundance gradient and balanced changes in abundance as well as presence/absence-based turnover and nestedness varied over time. The turnover prevailed in the initial part of the growing season between March and May and then during its terminal part between September and October. In principle, it separated the summer and spring phases of the studied grassland. The former is characteristic of perennial and especially short-lived perennial species that have their optima in summer, while the latter hosts mainly winter annuals and a number of seedlings, together with a few species that live throughout the year. The pattern of the balanced change in abundance was similar, albeit slightly delayed. The abundance gradient and nestedness occurred between the beginning of the growing season and mid-summer when it coincided with the minimum species richness. Together with the peaks in biomass and species richness, this defines a remarkable period of co-occurrence in early spring when all life-history types are growing intensively. Apart from this period, species of different life-history types show temporal vicariance, creating opportunities for temporal niche separation (Doležal et al., 2019) and mechanisms of species coexistence based on a fluctuating environment (Wilson, 2011; Moulin et al., 2021).

Regarding the methodology of vegetation ecology, the complex community and productivity dynamics found in this study raise the question of whether it is sufficient to sample community composition only once a year, at or around the time of peak biomass. Even in our grassland with pronounced seasonal beta-diversity, a single sampling can yield data suitable for vegetation classification or mapping. Such sampling should be conducted in May to capture most of the maximum species richness present earlier in the spring while biomass is already near its peak. The representativeness of the May samples is supported by their location in the middle of the first PCoA axes of beta-diversity (Figure 3). Nevertheless, such a single survey may only capture 60% of the total annual species richness, mainly due to the earlier dieback of annuals. Therefore, we recommend including already dead but still identifiable annuals that can still be found in May. Nevertheless, it is important to note that May sampling does not record the maximum cover of dominant perennial species, which, when combined with recording senescent annuals, results in a higher estimate of evenness than is typical for most of the year. In contrast, if the study is aimed at understanding species' coexistence and community assembly rather than vegetation classification, more than one sampling per year is necessary.

## 5 | CONCLUSIONS AND IMPLICATIONS FOR FUTURE STUDIES

Our data set describing the seasonal beta-diversity recorded by repeated surveys at monthly intervals throughout the year is the first to demonstrate that primary biomass production occurs year-round

in a temperate dry grassland community. We related biomass production to community composition patterns using the beta-diversity framework (Baselga, 2013), which we propose as a standard for similar studies in the future. In particular, decomposing beta-diversity into its components provides information on the nature of seasonal community dynamics, which is critical for assessing ecosystem processes. For example, in communities with high turnover or high balanced changes in abundance, vegetation composed of species that differ in their traits may trigger multifaceted patterns in ecosystem processes such as productivity, multitrophic interactions, or decomposition. Trait values can also vary intraspecifically with the season (Römermann et al., 2016), but this variation is usually much smaller than the differences between species (Albert et al., 2010). Therefore, variability in ecosystem processes should also be smaller and simpler in seasonally nested communities than in communities with large seasonal turnover (Doležal et al., 2019). The pattern and magnitude of these effects likely vary over time and among different grassland communities, which calls for an extension of our single-site study to other grassland types and over a longer time period. Such explicit consideration of the seasonal dynamics of community composition and ecosystem processes in future studies over broader scales could not only improve our ecological knowledge but also contribute to conservation management planning and ecological restoration.

### AUTHOR CONTRIBUTIONS

Felícia M. Fischer, Jakub Těšitel and Kryštof Chytrý, with contributions from Milan Chytrý, conceived the study; Felícia M. Fischer, Jakub Těšitel and Kryštof Chytrý established the permanent plots and, with Helena Chytrá, performed all sampling and plant identifications in these plots; Jakub Těšitel and Kryštof Chytrý performed the data analyses; all authors discussed the results and wrote the manuscript.

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### DATA AVAILABILITY STATEMENT

All data and scripts used for this study are provided in the Supporting Information.

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## SUPPORTING INFORMATION

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

**Appendix S1.** Climate diagrams displaying local climatic conditions at Děvín Hill, Czech Republic (550 m a.s.l.).

**Appendix S2.** Seasonal patterns of species richness and biomass production in 2019 (the year of the study) and the two subsequent years.

**Appendix S3.** R scripts for the analyses and graphs presented in the article.

**Appendix S4.** Data on species' covers, height and biomass in the monthly surveys. Also species' life histories.

**Appendix S5.** Species scores on the ordination axes presented in Figure 3.

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