

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Review

Biodiversity of Palaearctic grasslands: a synthesis

Jürgen Dengler^{a,b,*}, Monika Janišová^c, Péter Török^{d,e}, Camilla Wellstein^f^a Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany^b Synthesis Centre (sDiv), German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany^c Institute of Botany, Slovak Academy of Sciences, Ľumbierska 1, 974 11 Banská Bystrica, Slovakia^d Department of Ecology, University of Debrecen, PO Box 71, 4010 Debrecen, Hungary^e MTA-DE Biodiversity and Ecosystem Services Research Group, Egyetem sqr. 1, 4032 Debrecen, Hungary^f Faculty of Science and Technology, Universitätsplatz 5, 39100 Bozen-Bolzano, Italy

ARTICLE INFO

Article history:

Received 3 December 2013

Received in revised form 6 December 2013

Accepted 10 December 2013

Available online 13 January 2014

Keywords:

Conservation

Disturbance

Land use

Semi-natural

Species richness

Steppe

ABSTRACT

This article introduces a Special Issue on biodiversity of Palaearctic grasslands and provides a synthesis of the current knowledge on this topic. Four major categories of grasslands can be distinguished in the Palaearctic biogeographic realm: (a) zonal steppes (in areas too dry for forests), (b) arctic-alpine grasslands (in areas too cold for forests), (c) azonal and extrazonal grasslands (where hydrology, soil conditions, relief or natural disturbances within the forest biomes prevent tree growth locally) and (d) secondary grasslands (which replace natural forests in consequence of human land use). We summarize the present knowledge about species richness patterns (mainly of vascular plants) along abiotic and land use gradients. Further, we highlight the usefulness of diversity measures not based on species richness, namely functional diversity, phylogenetic diversity and within-species diversity. The strong differences observed for diversity patterns according to analyzed biodiversity parameter, spatial scale or taxonomic group call for comparative studies and caution when generalizing results. A particular challenge are the extreme plot-scale species richness values found in grasslands of a few European regions. We propose a conceptual model that explains the findings by an interplay of various factors acting at different levels: (i) The largest species pool is expected for habitats under conditions that prevailed over the last few million years, with a slight shift towards intermediate positions, i.e. for the Palaearctic in open, semi-dry, base-rich situations. (ii) The landscape-level species pool is increased by continuity of a grassland patch in space and time and heterogeneity of the surrounding landscape. (iii) The coexistence of regionally available species at a plot scale is due to reduced competitive exclusion according to Intermediate Disturbance Hypothesis, mowing once a year without fertilization being particularly effective. Ecosystem functions and services of Palaearctic grasslands are often positively connected to their biodiversity. At the same time, these communities and their biota are nowadays highly endangered. The semi-natural (High Nature Value) grasslands of Europe are mainly threatened by agricultural intensification or abandonment on low-productive sites in remote areas, while the natural steppes of the Palaearctic have largely been destroyed by conversion into arable land. Finally, we present some promising conservation and management approaches and call for a strong and comprehensive *Convention on Grassland Conservation*.

© 2013 Elsevier B.V. All rights reserved.

Contents

1. Introduction.....	2
2. What are Palaearctic grasslands?.....	2
2.1. Steppes.....	2
2.2. Arctic-alpine grasslands.....	3
2.3. Azonal and extrazonal grasslands.....	3

* Corresponding author at: Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany. Tel.: +49 921 55 2360; fax: +49 921 55 2315.

E-mail addresses: juergen.dengler@uni-bayreuth.de (J. Dengler), monika.janisova@savba.sk (M. Janišová), molinia@gmail.com (P. Török), camilla.wellstein@unibz.it (C. Wellstein).

2.4.	Secondary grasslands	3
2.5.	Origin of Palaearctic grasslands	3
2.6.	Development and present status of secondary grasslands	3
3.	Diversity patterns along abiotic gradients	3
4.	Anthropogenic influences on diversity	4
5.	Beyond counting species: what other ways of measuring diversity can tell us	5
6.	How general are the patterns?	5
7.	Puzzling diversity of Palaearctic grasslands	6
7.1.	Background	6
7.2.	Conceptual model	6
8.	Ecosystem functions and services of grasslands as related to biodiversity	8
9.	Threats and management of grassland diversity	9
10.	Conclusions and outlook	10
	Acknowledgements	10
	References	10

1. Introduction

Palaearctic grasslands are known for their high biodiversity in many taxa. For example, at small spatial scales vascular plant diversity of certain European grasslands even exceeds tropical rainforests (Wilson et al., 2012), which are normally considered the most diverse ecosystems on earth. A high proportion of the flora and fauna of Europe are grassland specialists, including many endemics (e.g. Hobohm and Bruchmann, 2009; WallisDeVries and van Swaay, 2009). Yet Eurasian grasslands do not show up on the global map of vascular plant diversity (Barthlott et al., 2005) because this map considers biodiversity patterns at 10,000-km² resolution only. Moreover, among the 35 global biodiversity hotspots defined by Mittermeier et al. (2011) only two of the seven Palaearctic ones (Irano-Anatolian, Mountains of Central Asia) have a large share of grasslands. The underrepresentation of Palaearctic grasslands among the biodiversity hotspots is probably largely due to the fact that Mittermeier et al. (2011) focused on natural habitats, while grasslands in most parts of Europe are semi-natural, meaning that they have emerged through centuries or millennia of low-intensity human land use from forests as potential natural vegetation (Bohn et al., 2004; Ellenberg and Leuschner, 2010; Pott, 1995). Therefore, major explanations brought forward for high biodiversity in other ecosystems like naturalness, lack of disturbance or huge area seem not to be the main drivers of European grassland diversity, while agricultural management obviously plays an important role. Moreover, there are huge differences in diversity between grasslands types, and even ecologically similar grassland types may differ significantly in their diversity between regions.

We hereby introduce the Special Issue on “Biodiversity of Palaearctic grasslands: processes, patterns and conservation”, initiated at the 8th European Dry Grassland Meeting, 13–17 June 2011, in Uman', Ukraine. The European Dry Grassland Meetings are the annual scientific conferences of the *European Dry Grassland Group* (EDGG), an international network of nearly 1000 researchers and conservationists dealing with all aspects of natural steppes and semi-natural, steppe-like grasslands in the Palaearctic (see Habel et al., 2013; Vrahnakis et al., 2013; or www.edgg.org). A second Special Issue on biodiversity of European grassland ecosystems (including more zoological and mycological contributions) has recently been published in *Biodiversity and Conservation* (Habel et al., 2013), and a Virtual Special Feature on large-scale typology of European grasslands has been started in *Applied Vegetation Science* (Dengler et al., 2013).

The 14 research articles of this Special Issue originate from more than a dozen countries, ranging from Germany and Switzerland in the West to China in the East and from Italy and Turkey in the South to Sweden in the North. While the majority of papers deals with vascular plants, two address (also) other plant groups (Turtureanu

et al., 2014; Zulka et al., 2014) and two animals (birds: Ambarlı and Bilgin, 2014; multiple invertebrate groups: Zulka et al., 2014). The articles in this Special Issue are arranged in five groups: (i) multi-taxon studies (Turtureanu et al., 2014; Zulka et al., 2014); (ii) species richness patterns along various gradients (Ambarlı and Bilgin, 2014; Janišová et al., 2014; Reitalu et al., 2014; Wanner et al., 2014); (iii) diversity of seed banks related to aboveground vegetation (Valkó et al., 2014b; Zeiter et al., 2013); (iv) functional diversity (Carboni et al., 2014; Niu et al., 2014; Wellstein et al., 2014) and (v) conservation, management and restoration of grassland diversity (Babai and Molnár, 2014; Prach et al., 2014; Rédei et al., 2014).

The present introduction is intended as a synthesis on grassland diversity to give an overview of Palaearctic grasslands (Section 2) and summarize the state-of-the-art on their biodiversity patterns (Sections 3–6). Section 7 is then devoted to the eminent “world record” grasslands and develops a refined conceptual framework to explain their outstanding position. The following two sections shed light on the interplay of biodiversity and ecosystem functioning of grasslands as well as their endangerment and conservation, before the final résumé highlights research frontiers and points out ways forward.

2. What are Palaearctic grasslands?

While there are many definitions of “grassland” (Gibson, 2009), that of Janišová et al. (2011) is adopted here in a slightly modified version as *herbaceous vegetation types that are mostly dominated by grasses (Poaceae) or other graminoids (Cyperaceae, Juncaceae) and have a relatively dense vegetation cover (usually > 25%), thus excluding plant communities mostly composed of shrubs (shrublands), dwarf shrubs (heathlands), bryophytes and lichens as well as those with very scattered vegetation (e.g. deserts, semi-deserts, screes)*. Grasslands of the Palaearctic biogeographic realm (i.e. Europe, North Asia and Africa north of the Sahara: Olson et al., 2001) can be grouped into four major types (Sections 2.1–2.4) according to their origin and ecology (adapted from Hejman et al., 2013; Janišová et al., 2011; Vrahnakis et al., 2013).

2.1. Steppes

These are zonal grasslands (i.e. large-scale natural vegetation = climax) in regions that are too dry to support the growth of forests, but sufficiently humid to allow for a closed vegetation. Steppes are the natural vegetation of the moister part (>100 mm annual precipitation) of the Dry midlatitudes ecozone (≈zonobiome VII in Breckle, 2002) and form a huge, continuous area from South Ukraine in the West to North China in the East (Jacobs et al., 1999; Lapola et al., 2008; Schultz, 2002; Werger and van Staalduinen, 2012). The information on the original spatial extent

of this biggest steppe biome of the world largely varies, depending on the definition used, but the actual size might be in the range between 8 million km² (based on figures and maps in Schultz, 2002) and over 13 million km² (Wesche and Treiber, 2012). Additionally, grass and shrub steppes (with winter rain) occur as a relatively narrow transition zone between the Dry tropics and subtropics ecozone (\approx zonobiome III) and the Subtropics with winter rain ecozone (\approx zonobiome IV) from Morocco in the West to Iran in the East, covering some 1–2 million km² (Schultz, 2002). In the transition to the adjacent forest ecozones/zonobiomes (Boreal zone/VIII; Temperate midlatitudes/VI; Subtropics with winter rain/IV), so-called “forest steppes” occur, landscape-scale macro-mosaics of forests and steppes, where relief position and soils determine which formation occurs where (Bohn et al., 2004; Breckle, 2002).

2.2. Arctic-alpine grasslands

These are zonal grasslands at high altitudes or latitudes that are too cold to support the growth of forests. Only a fraction of arctic-alpine environments are covered by grasslands, while others are occupied by heathlands, moss and lichen communities, open communities on instable ground or cold deserts (Ellenberg and Leuschner, 2010).

2.3. Azonal and extrazonal grasslands

These are natural grasslands occurring locally at small scale within the forest biomes on soils that are too wet, too dry, too saline, too shallow, too instable or otherwise too extreme to allow tree growth (Ellenberg and Leuschner, 2010; Janišová et al., 2011; Klötzli et al., 2010). Furthermore, grasslands might occur as temporary successional stages following natural disturbance events in forests (wild fire, wind throw, avalanches, flooding in consequence of beaver dams, intensive browsing by wild herbivores) (e.g. Hejman et al., 2013).

2.4. Secondary grasslands

These are anthropogenic grasslands at sites whose natural vegetation is forest. *Semi-natural grasslands* are an essential part of the cultural landscape of Europe and resulted from centuries or millennia of low-intensity land use since the beginning of the Neolithic period (Ellenberg and Leuschner, 2010; Hejman et al., 2013; Poschod et al., 2009; Pott, 1995). Such grasslands are mainly used for grazing by livestock (pastures) or hay-making (meadows), but might also be a successional stage of abandoned arable fields. Nowadays, such semi-natural grasslands (also termed High Nature Value grasslands: Veen et al., 2009) are more and more transformed into *improved (intensive) grasslands* by artificial fertilization, increased cutting frequency (meadows) or stocking rate (pastures) and frequent re-sowing with a limited set of agronomically valuable species (Dierschke and Briemle, 2002; Hejman et al., 2013; Stevens et al., 2010).

2.5. Origin of Palaearctic grasslands

The origin of the grass family (Poaceae) dates back to the Cretaceous period (89–83 million years ago), but the diversification and the development of grass-dominated ecosystems happened much later (Gibson, 2009). The expansion of grasslands and their associated grazers started about 34 million years ago in South America, probably in response to increased aridity (Gibson, 2009; Jacobs et al., 1999). In the Palaearctic, grasslands similar to present-day steppes are much younger, perhaps only 5 million years old (Jacobs et al., 1999; Pärtel et al., 2005). At least since the Pleistocene (the last 2.4 million years), natural grasslands have continuously existed

in Europe, covering most of the continent during the glaciations (extensive steppe-tundra over permafrost, xerothermic grasslands further south) and retreating to small areas during the interglacials, when forests expanded (Lang, 1994; Pärtel et al., 2005).

2.6. Development and present status of secondary grasslands

During the present interglacial, the Holocene, semi-natural grasslands (see Section 2.4) have emerged from forests through pastoralism and arable farming by Neolithic settlers, which occurred in Central Europe about 7500–6800 years ago, but less than 5000 years ago in the Baltic region and Scandinavia (Hejman et al., 2013; Pärtel et al., 2005). However, some types of semi-natural grasslands are of much younger origin, resulting from specific land-use practices. For example, the phytosociological alliance *Arrhenatherion elatioris* of mesic, nutrient-rich hay meadows, nowadays widespread throughout temperate Europe, seems to have developed only after the Middle Ages (Hejman et al., 2013; Poschod et al., 2009).

In 2010, 634,090 km² of the area of the 28 member states of the European Union plus Iceland, Norway, Switzerland and Montenegro were covered by agriculturally used grasslands (semi-natural and intensive, probably also including a minor fraction of natural grasslands; category “permanent grassland” in Eurostat, 2013). This corresponds to 13.1% of the total surface or 35.3% of the utilized agricultural area. Permanent grasslands constitute a particularly high fraction of the territory in Ireland (57.8%) and the United Kingdom (44.6%) and an above-average fraction in the Benelux, Portugal, Spain and Greece as well as Austria and Romania (all in the range 16.4–26.3%), while the relative grassland cover is particularly low in the Nordic and Baltic countries (except Iceland) with 0.1–10.2% (own calculations based on Eurostat, 2013).

3. Diversity patterns along abiotic gradients

One of the most frequently studied topics is the relationship between grassland diversity and habitat productivity (Grime, 2001; Kelemen et al., 2013; Mittelbach et al., 2001; Pierce, 2014; Tilman et al., 1997). In temperate grasslands including the Eurasian steppes and secondary semi-dry grasslands, local species richness increases with productivity up to about 200–300 g/m² of above-ground biomass (Ma et al., 2010; Zobel and Liira, 1997) and decreases from 400 to 500 g/m² onwards (Crawley et al., 2005; Hejman et al., 2010; Kelemen et al., 2013; Zobel and Liira, 1997). In communities with lower production limited by water availability, this relationship seems to follow a simple positive trend (Bai et al., 2007; Lavrenko et al., 1993). In highly productive secondary grasslands, biomass removal by appropriate management is necessary to maintain high local species richness (Köhler et al., 2005; Ruprecht et al., 2010).

Productivity is controlled by several factors (water and nutrient availability being the most crucial ones) which, each in their own way, also affect grassland diversity. In spite of the supporting effect of increasing nutrient availability on biomass production and the above-mentioned positive productivity–diversity relationship, negative effects of excess nutrients (especially phosphorus, nitrogen and potassium) have been reported from various types of grassland vegetation (Austheim, 2002; Hejman et al., 2010; Janssens et al., 1998; Merunková and Chytrý, 2012). Not only total amounts of individual nutrients are important determinants of grassland diversity, but also the balance in their availability. The N/P ratio, for example, is sometimes considered even more important than the phosphorus concentration alone (Güsewell, 2004; Wassen et al., 2005).

Nutrient availability is significantly moderated by the non-resource factors, such as soil pH, temperature and salinity.

In grasslands of temperate and boreal Eurasia, the species richness–pH relationship is usually unimodal when a sufficiently broad pH range is studied, with a peak at about pH 6–7 (Chytrý et al., 2007; Merunková and Chytrý, 2012; Schuster and Diekmann, 2003). However, at pH values lower than 6, the species richness–pH relationship in grasslands is nearly always positive (Crawley et al., 2005).

Soil moisture is known to affect nutrient availability in various habitat types (Loiseau et al., 2005; Rodríguez-Iturbe et al., 1999). Water limitation reduces productivity as it reduces the ability of dominants to develop sufficient growth, even under nutrient-rich conditions. According to available information, overall plant diversity typically declines with decreasing water availability (Pausas and Austin, 2001). The topographically structured soil moisture is often considered the main controller of local plant diversity patterns in grasslands (Moeslund et al., 2013). However, patterns of water availability often co-vary with other ecological or geographical gradients, making it difficult to separate the influences of different factors (see also Valkó et al., 2014b). Conversely to the patterns in the established vegetation, diversity and density of the seed bank is often very high in drought-stressed grasslands, where regeneration from seeds is a strategy that allows bridging unfavorable environmental conditions (Bossuyt and Honnay, 2008). In contrast to that general finding, Valkó et al. (2014b) reported that a combination of high levels of drought with salinity also affects the soil seed bank negatively. In such cases grassland diversity is likely driven by spatial dispersal and re-establishment or clonal growth and not by the locally persistent seed bank.

Given that altitudinal and latitudinal richness gradients generally belong to the most studied macroecological patterns, it is astonishing how little is known with respect to Palaearctic grasslands. Austrheim (2002) in his study of semi-natural grasslands in Norway found for vascular plants that total richness per altitudinal zone decreases with altitude, while small plots (0.25 m²) showed a mid-elevational peak below the timberline. By contrast, richness of non-vascular plants at all spatial scales increased with altitude. In Switzerland, the richness of vascular plants in all types of grasslands increased from the colline (approx. 28 species on 10 m²) to the subalpine and alpine belts (approx. 42 species on 10 m²), while on the same plots bryophytes showed a strong continuous increase from 3 species (colline) to 19 (alpine), and snails a monotonous decrease (Koordinationsstelle Biodiversitäts-Monitoring Schweiz, 2009). Surprisingly, the plot-scale richness peaks never coincide with the peaks of the total flora or fauna per belt, which in all three groups are in the montane belts (Koordinationsstelle Biodiversitäts-Monitoring Schweiz, 2009). These discrepancies indicate that different mechanisms are relevant for species richness at small and large grain sizes. A high species pool does not necessarily translate into a high small-scale species density and biodiversity patterns at different scales might even be reversed. Due to a lacking standardized monitoring across the Palaearctic grasslands, latitudinal and longitudinal patterns are even less clear than altitudinal ones, but generally the effects of regional drivers (see Section 7) seem to exceed those of potential large-scale patterns. At least there is some preliminary indication that plot-scale plant species richness of grasslands might on average be higher in the hemiboreal compared to the temperate zone (Dengler et al., 2006), which would coincide with the Swiss altitudinal patterns.

4. Anthropogenic influences on diversity

Grime (1973) was the first who suggested that plant species richness of herbaceous communities should peak at intermediate intensities of management (i.e. grazing, mowing, burning or trampling) and demonstrated this for a trampling

gradient in a European grassland. Later this idea became part of the Intermediate Disturbance Hypothesis (IDH), which assumes that such unimodal relationships between diversity and intensity, frequency or extent of various types of disturbances are widespread across ecosystems (Connell, 1978). While there are many slightly differing explanations for this empirical pattern, the basic assumption is that at a very low level of disturbance competitive exclusion reduces the number of co-occurring species, while in case of too frequent/intense disturbances only few species have the necessary adaptations (e.g. short life cycle) to survive (Connell, 1978; Grime, 1973). Subsequently, researchers developed concepts and published empirical proofs how disturbance (i.e. mainly grazing in the case of grasslands) interacts with other major drivers of diversity, thus refining the IDH (reviewed by Hanke et al., 2014). The most important interacting factor might be productivity, which is assumed to shift the hump of the diversity–disturbance gradient so that disturbance basically decreases richness at very low-productive sites and increases it at highly productive sites, while the “classical” hump is clearly visible only at intermediate productivity levels (Dynamic Equilibrium Model, DEM: Huston, 1979; see also Bakker et al., 2006; Kondoh, 2001; Milchunas et al., 1988). Olf and Ritchie (1998) suggested that increasing environmental stress might modify the response of communities to disturbance in a similar way as decreasing productivity does, and could demonstrate this in a European salt marsh where grazing decreased richness at the most saline sites and increased it at the least saline sites. Finally, grassland ecosystems with an evolutionary long history of grazing are supposed to show a weaker response to disturbances by large herbivores than evolutionary naïve systems (Milchunas et al., 1988), but it is generally hard to quantify “evolutionary history”.

Studies that compared several different levels of grazing intensity in Palaearctic grasslands usually found that small-scale species densities peak somewhere between heavy grazing and abandonment, i.e. at light to moderate grazing (e.g. Cheng et al., 2011; Dupré and Diekmann, 2001; Proulx and Mazumder, 1998; Škornik et al., 2010). In a study of five sites along a rainfall gradient in Spain with three grazing intensities per site, de Bello et al. (2007) could demonstrate that plant species diversity patterns follow the predictions of the DEM very closely, both for α -diversity at different scales and for β -diversity. Wanner et al. (2014) also found support for the IDH for 1-m² plant species richness in the upper North Sea salt marshes, while grazing intensity did not affect species density in the lower marshes, contrasting to Olf and Ritchie (1998) who reported a decrease in richness through grazing. Turtureanu et al. (2014) did not find a significant effect of grazing vs. abandonment in Transylvanian dry grasslands, but this might partly be because they did not differentiate grazing intensities.

The differences between grazing and mowing are another relevant, albeit less frequently addressed aspect. Low-intensity grazing is often considered a good management technique (and even better than mowing) because it is expected to create small-scale heterogeneity through varying grazing, trampling and defecation patterns of the livestock, which should allow more species to co-exist than under the homogenizing regime of mowing (Redecker et al., 2002; Voß, 2001). By contrast, Turtureanu et al. (2014) found that plant species richness was far higher in mown than in grazed dry grasslands (+25.8 species = 51% at 10 m²) of otherwise similar conditions, and this difference existed across all spatial scales tested (1 cm² to 100 m²). Similarly, Stammel et al. (2003) found significantly higher plant richness in mown vs. grazed fen grasslands (+ 7.3 species = 17% at 25 m²) and Hansson and Fogelfors (2000) a strong increase after 15 years of grazing in a hemiboreal grassland, while richness remained unchanged under grazing. Fischer and Wipf (2002), on the other hand, found no effect of changing the traditional mowing regime to grazing on plot-scale richness of subalpine meadows. While Löbel et al. (2006) did not

detect a direct effect of mowing vs. grazing in dry grasslands of the Baltic Island of Öland, they found that microrelief increased richness of vascular plants and bryophytes, and that this was at least partly caused by grazing livestock. Since some of the dry grasslands of Öland are intermittently wet, here and in the example of wet grasslands (Voß, 2001), the trampling might cause more plant-relevant niche differentiation than it does on well-drained soils. Actually, in both examples hummock-hollow structures of up to 30 cm height difference occurred, leading to microhabitats with very different moisture conditions. Why, contrastingly, in other cases, low-intensity mowing (once a year or less) favours so many more species than grazing, is an open question (see Section 7.2, point 5). However, with higher cutting frequency, richness dropped dramatically, while higher grazing intensity had little effect on plant diversity in mesic, mostly nutrient-rich lowland grasslands (Socher et al., 2012). The latter study also found substantial differences between three regions in Germany, calling for caution when generalizing results.

Long-term atmospheric nitrogen deposition may be the major source of excess nitrogen at grassland sites, which has been identified as a reason for decreasing species richness in grasslands (Bai et al., 2010; Bobbink et al., 2010; Dupré et al., 2010; Stevens et al., 2004). Jandt et al. (2011) demonstrated with a huge vegetation-plot database of semi-dry basiphilous grasslands in Germany that many species had consistent trends over a 75-year period (1927–2003). Species with positive temporal trends had higher Ellenberg indicator values for moisture and nutrients compared to those with negative trends, which the authors interpret as consequence of nitrogen deposition and land-use changes. Simultaneously, grasses and species with competitive strategy generally became more frequent.

5. Beyond counting species: what other ways of measuring diversity can tell us

Functional diversity captures the functional dimension of biodiversity and has been emphasized as an important facet of biodiversity. Trait-based approaches characterize organisms in terms of multiple biological attributes, which describe the organisms' functional response to the abiotic and biotic environment (Wellstein et al., 2011). At the ecosystem level, functional diversity is defined as “the value and range and relative abundance of functional traits present in a community” (Tilman, 2001). Several methods have been proposed to estimate functional diversity, referring to its different components (cf. Schleuter et al., 2010). The trait-based approach helps to shed new light on the processes that assemble plant communities. Recent developments in the study of such assembly rules are trait-based and focus on revealing the background of species coexistence and the strategy of species dealing with novel environmental challenges (e.g. Bernard-Verdier et al., 2012; Carboni et al., 2014; Wellstein et al., 2014). Previous trait-based studies on grasslands sometimes found random patterns of multiple traits (see Götzenberger et al., 2012). In a detailed analysis of community assembly along a soil-depth gradient in a Mediterranean grasslands, Bernard-Verdier et al. (2012) detected significant changes of community-weighted mean trait values in relation to this gradient for most tested traits. Further, vegetative traits diverged on shallow soils, indicating coexistence of distinct water- and nutrient-use strategies in these habitats, whereas they converged with increasing resource availability. Wellstein et al. (2014) highlight the importance of excluding strong biotic filters from the modelling when aiming at understanding the coexistence of subordinate species, which represent most of the grasslands plant diversity. Both, Carboni et al. (2014) and Wellstein et al. (2014) emphasize the relevance of fine spatial scales for

mechanisms of species coexistence and demonstrate that assembly rules are strongly context-dependent.

To evaluate temporal dynamics (i.e. resistance and/or resilience) of grasslands, phylogenetic diversity can be also used. Phylogenetic diversity expressed as the diversity of different evolutionary lineages (Faith, 1992) reflects the evolutionary history of the respective community and provides an insight how persistent it might be in the long run in the face of environmental changes, such as anthropogenic climate change. Reitalu et al. (2014) found that the small-scale species richness was negatively correlated with phylogenetic diversity. While species richness was found to be highest at intermediate stress and disturbance levels in accordance with the IDH *sensu* Grime (2001; compare Section 4), phylogenetic diversity was highest in the most stressed habitats, covered only by a thin layer of soil. This was because the high levels of stress prevented the development of a closed vegetation cover and continuously provided open gaps for colonization.

Ecological differences do not only exist between species but also within. This intraspecific variation has attracted recent attention in plant community ecology (e.g. Albert et al., 2011; Wellstein et al., 2013). In grassland plants, this variation can be driven by environmental factors (Wellstein et al., 2013), but also management regimes can affect the selection pressure in grassland plants differently (Pluess, 2013). Intraspecific variation comprises both phenotypic and genetic variation. While phenotypic plasticity gives a plant the ability to adjust its functional performance in response to varying environmental conditions throughout its lifespan, inheritable differences in gene function (i.e. epigenetic changes) and the genotype are the base of long-term adaptation and evolution (for an overview see Wellstein et al., 2013, and references therein).

It is becoming apparent that plant intraspecific diversity can influence the species diversity and structure of whole ecosystems with their plant and animal communities (Fridley and Grime, 2010; Jones et al., 2011; Peter-Schmid et al., 2008). For example, genetically diverse plant patches had 18% more arthropod species and a greater abundance of omnivorous and predacious arthropods compared with monocultures (Johnson et al., 2006). Thus, the genotype of a plant can determine the composition and structure of the multi-trophic arthropod community. Consequently, a reduction in genetic diversity at the producer level can affect the wider food web and associated ecosystem services (Bukovinszky et al., 2008; Jones et al., 2011).

6. How general are the patterns?

Biodiversity is a multi-faceted phenomenon (Gaston and Spicer, 2004; Jürgens et al., 2012). This far, however, analyses focused on one or a few aspects only, i.e. complexity levels (genes, taxa, ecosystems), dimensions (composition, structure, function, evolution), components (richness, evenness) or hierarchy levels (alpha, beta, gamma), and did so for a single taxonomic group at one spatial scale.

The studies in this Special Issue that cover more than one biodiversity aspect usually found strong differences. Janišová et al. (2014) report that alpha diversity on the one hand and beta and gamma diversity on the other hand mostly showed opposing trends. A negative relationship between plot-scale species richness and phylogenetic diversity is reported by Reitalu et al. (2014). Niu et al. (2014) found in a Tibetan steppe that fertilization decreased species diversity but increased functional diversity.

Regarding spatial scale (grain size), theory predicts that different drivers should prevail at different spatial scales (Shmida and Wilson, 1985), and recent meta-analyses confirmed this view (Field et al., 2009; Siefert et al., 2012). Certain drivers might even change the direction in which they affect biodiversity with spatial scale.

Tamme et al. (2010), for example, could show that spatial heterogeneity decreased richness at smallest scales, while it had positive effects at larger scales. For Mediterranean grasslands, Giladi et al. (2011) demonstrated how relevance of drivers of vascular plant diversity shift across four grain sizes from 0.06 to 225 m², with plant density being most important at smallest scales and patch area as well as habitat heterogeneity at larger scales. Similarly, Turtureanu et al. (2014) found in temperate grasslands scale dependency of drivers of diversity that was largely consistent with the theoretical predictions and previous meta-analyses. None of the considered predictors was relevant across all seven orders of magnitude in grain size (0.0001–100 m²), most rather for two to four subsequent grain sizes. At least the ranking of different management variants with regard to plant species richness was scale-invariant, i.e. the species–area curves of the management types were more or less parallel over five or seven orders of magnitude in Wanner et al. (2014) and Turtureanu et al. (2014), respectively. By contrast, Dupré and Diekmann (2001) have shown that the positive effect of grazing vs. abandonment on plant diversity at small scales diminishes with increasing grain size, and the species–area curves intersect at about 100–1000 m².

Only two papers in this Special Issue studied more than one taxonomic group. When comparing the three major groups of primary producers in terrestrial habitats—vascular plants, bryophytes and lichens—Turtureanu et al. (2014), like similar studies by Löbel et al. (2006) or Jeschke et al. (2008), found pronounced differences in the relevance of environmental factors related to differences in life histories. In their unique study, Zulka et al. (2014) even compared two taxonomic groups of plants with eleven of invertebrates and found many idiosyncrasies. Generally plot-scale richness of grassland specialists among plants was most strongly affected by gravel content of the soil (+) and aboveground biomass (–), while for invertebrates in general, most important were landscape factors (– distance to next bigger grassland patch, + fraction of dry grasslands in the surroundings) and historical patch area (+).

Taken together, the presented findings urge for utmost caution when generalizing results across biodiversity aspects, scales and taxa. It is evident that a representative picture can only be gained by studying multiple aspects, spatial scales and taxonomic groups. As it is generally not feasible to include all of these in one single study, a well-informed selection is required. Exemplary multi-taxon studies (e.g. Zulka et al., 2014), multi-scale studies (e.g. de Bello et al., 2007; Turtureanu et al., 2014) and multi-aspect studies (e.g. Hanke et al., 2014) can guide the choice of parameters with maximum complementarity or least redundancy.

7. Puzzling diversity of Palaearctic grasslands

7.1. Background

Wilson et al. (2012) showed that nearly all global records (across all biomes) of vascular species densities at grain sizes below 100 m² are from Palaearctic grasslands (the two from Transylvania are included in the analysis of Turtureanu et al., 2014), and nobody beat these values so far. The fact that 98 vascular plant species can co-exist on 10 m² of a Transylvanian meadow, challenges ecological theory as it questions the principle of competitive exclusion (see den Boer, 1986). Can we reasonably assume that all these species have different niches or how else do they manage to survive? All the European richness records (except those for 1 cm² and less) come from semi-dry basiphilous grasslands, a vegetation type that generally is among those with the highest plot-scale richness in Central Europe (e.g. Hobohm, 1998) and beyond. However, although this vegetation type is, because of its diversity and conservation relevance, generally well-studied across Europe,

the maximum richness values originate from only a few spatially very restricted regions: Western Estonia, Southern Öland (Sweden), the White Carpathians (Czech Republic) and the Transylvanian Plateau (Romania) (for references, see Wilson et al., 2012), plus a region in the Ukrainian Carpathians that was newly found after that publication (Roleček et al., 2014). The striking point is that in these very regions, the semi-dry basiphilous grasslands are much richer than in other parts of Europe, also on average. For example, Dengler et al. (2012) reported a mean of 66 vascular plant species on 10 m² for Transylvania, whereas the stands of the same phytosociological alliance (*Cirsio-Brachypodium*) in Northeast Germany reach only 30 species on the same area (Dengler, 2005). Strong differences can even occur across much shorter distances: Merunková et al. (2012) found that the mean vascular plant species richness at 1 m² and 100 m² in the White Carpathians was about 25–30% higher than in similar grasslands of southern Moravia and the Inner Western Carpathians (20–200 km away).

What makes the dry grasslands of these few narrow regions so extraordinary at regional to global scale? Roleček et al. (2014) demonstrated that the grasslands of the White Carpathians, the Ukrainian Carpathians, the Transylvanian Plateau and Western Estonia despite their geographic distance are similar in many respects (and most of the points are also true for the alvar sites on Öland, see Reitalu et al., 2014): (i) the species composition is very similar; (ii) the soils are base-rich (but the pH is lower than in other *Festuco-Brometea* communities; Dengler et al., 2012; Merunková et al., 2012); (iii) the climate and site conditions are slightly cooler and moister than usual for stands of the class *Festuco-Brometea*; (iv) the sites are managed by mowing once a year without fertilization; (v) the grassland patches are large and typically interspersed with forests, scrubs or fens; (vi) there are indications of a long continuity as open grasslands (many centuries to millennia; e.g. Hájková et al., 2011). Merunková et al. (2012) conclude that the extreme richness of the White Carpathian grasslands cannot be explained by a single factor, but that it is the unique combination of factors that increases the plot-scale richness, which is in line with the idea of the multiple direct and indirect controls of species densities in herbaceous communities by Grace (1999).

7.2. Conceptual model

Founded on the facts and arguments provided by Zobel (1992), Merunková et al. (2012), Roleček et al. (2014) and Michalcová et al. (2014), we suggest five preconditions for extraordinarily high species richness at plot scale (Fig. 1):

- (1) *Large evolutionary species pool*: A striking aspect of the maximum richness community types is that they all grow in open, dry, and base-rich habitats, while such site conditions are rare to very rare in the natural vegetation of their regions. Located in the nemoral biome (i.e. the humid part of the midlatitudes), without human interference, the respective countries would be covered to 90% or more by forest (Bohn et al., 2004). Moreover, the soils are predominantly acidic (Pärtel, 2002) and the surplus of rain should lead to a predominance of mesic to wet site conditions. On the other hand, the site conditions of the semi-dry basiphilous grasslands are similar to the peaks (Korneck et al., 1998) or the medians (Ewald, 2003) of the frequency distributions of the overall vascular flora of Central Europe along these major ecological gradients according to the Ellenberg Indicator Values (EIVs; Ellenberg et al., 1991). For the whole flora, the medians are 7 for the EIV of light (L), between 4 and 5 for the EIV of moisture (F), and between 6 and 7 for the EIV of soil reaction (R), while the mean EIVs of the extremely species-rich grasslands in four sites are 6.7–7.0 for light, 3.6–4.6 for moisture, and 6.7–7.4 for soil reaction (Roleček et al., 2014). Pärtel

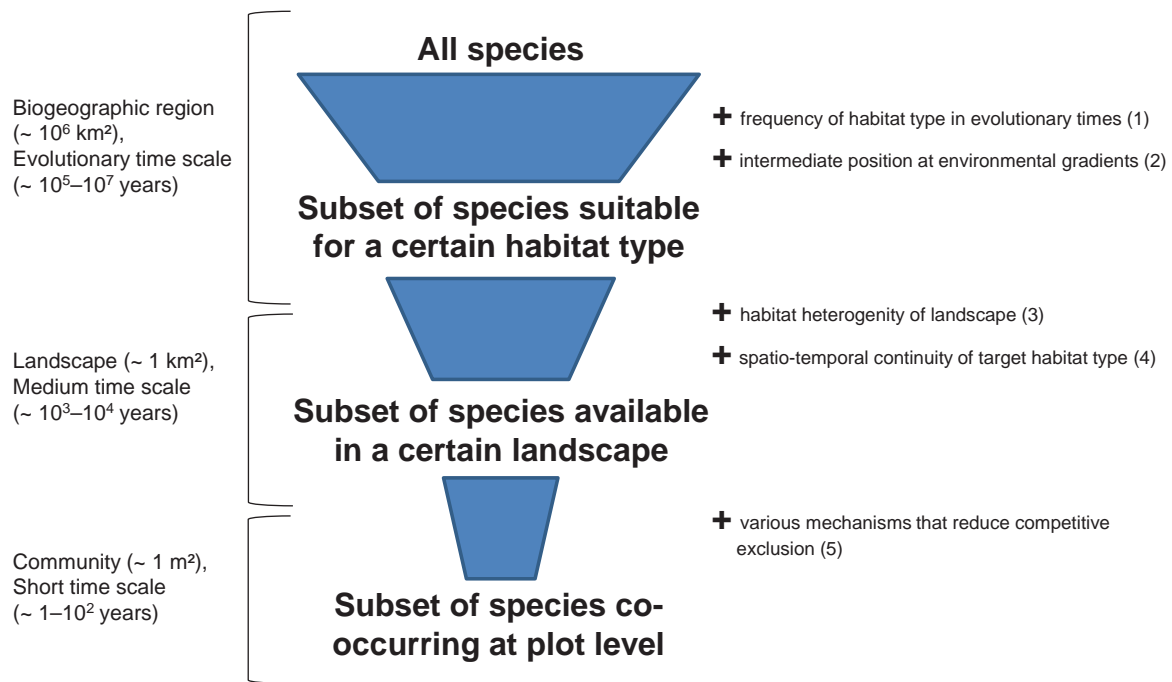


Fig. 1. Various processes at different spatio-temporal scales determine which fraction of the flora from a biogeographic region actually occurs at plot-scale. The five main factors that increase the fraction of species remaining from one level to the next (see text for details) are listed in the right column. The upper two scales and their processes are usually addressed in biodiversity models, whereas the lowest scale (i.e. mechanisms reducing competitive exclusion) is poorly known despite its probably crucial role.

(2002) and Ewald (2003) explained this discrepancy between soil pH distribution and pH preference distribution of the flora by the evolutionary history in Europe (and the whole of the Palaearctic), which was strongly affected by the expansion and retraction of the glaciers during the Pleistocene. Each glaciation forced the species to retract from boreal and temperate regions southwards, for example to the Mediterranean Basin, where limestone and other base-rich bedrocks prevail. Since the duration of the glaciations was generally much longer than that of the interglacials (Lang, 1994; Pärtel et al., 2005), the evolutionary history of the present Palaearctic flora is dominated by the environmental conditions of the first. Based on the fact that species' average life spans, depending on taxonomic group, are in the range of 0.5–13 million years (Lawton and May, 1995), a significant proportion of the present-day Palaearctic flora should have evolved during the Pleistocene and thus mainly under the environmental conditions of the glaciations. In those times the conditions throughout Europe and the Palaearctic, also in the steppe-tundra over permafrost closer to the glaciers, were much drier and soils more base-rich than in the interglacials, such as the present Holocene, and forests were restricted to small pockets (Lang, 1994; Pärtel et al., 2005). With this in mind, it appears that Pärtel's (2002) and Ewald's (2003) theory on pH preferences of the temperate and boreal European flora can be extended to its light and moisture preferences so that the frequency of habitat preferences in the present flora largely corresponds to the frequency of such environmental conditions during the last few million years in the biogeographic region and its (southern) surroundings.

- (2) *Intermediate position along environmental gradients:* While the direction of deviations from "intermediate" conditions are the same for the Pleistocene environment and the extremely species-rich grassland stands, the average conditions during the glaciations were probably even lighter, drier and more basic. Two major reasons could favour higher species richness towards intermediate conditions of certain environmental gradients: (i) If species have a certain amplitude of

tolerable conditions (physiological or fundamental niche) and the mid-points of these amplitudes are placed randomly, inevitably more niches overlap in the middle of the environmental range, an equivalent to the mid-domain effect postulated for geographic domains (Colwell and Lees, 2000). (ii) In addition, both extremes of environmental gradients usually require specific adaptations of species to survive, which seemingly have not often evolved because of the associated metabolic costs. For example, extremely low pH (<4.5 in KCl) results in concentrations of soluble exchangeable aluminium ions, which are toxic for most plants (Tyler, 2003), while at very high pH (>7.5), the availability of the micronutrients manganese and iron becomes increasingly problematic for plants (Tyler and Olsson, 2001).

- (3) *Landscape heterogeneity/mass effect:* So far all available data indicate that maximum richness values in Palaearctic grasslands are restricted to semi-natural types and do not occur in natural steppes (Wilson et al., 2012). This is supported by the standardized EDGG expedition data on mean species richness (including bryophytes and lichens, which in all cases play only a very minor role) of 10 m² of base-rich dry grasslands (all types combined), which are (maxima in parentheses) 53 (101) in Transylvania (forest biome; Dengler et al., 2012), 41 (67) in Central Podolia (Ukraine, forest-steppe ecotone; A. Kuzemko et al., unpubl.) and 49 (75) in Khakassia (South Siberia, steppe biome, Janišová et al., 2013). What could explain the counter-intuitive finding that grasslands are richer at plot scale when they are secondary? One reason could be that semi-natural dry grasslands are, unlike natural steppes, typically embedded in a mosaic of other habitat types with quite different species pools (see Michalčová et al., 2014). Actually, all records of extremely rich semi-dry grasslands come from sites with pronounced habitat heterogeneity at the landscape scale. Not only in the hemiboreal wooded meadows (Kull and Zobel, 1991), but also in the meadows of the White Carpathians and the other sites, there are always individual shrubs and groups of trees nearby. Moreover, the sites exhibit local-scale heterogeneity

of soil moisture, resulting from slope movements (sliding) in the case of the White Carpathians and the Transylvanian Plateau (Roleček et al., 2014) and from small elevational variation in the case of hemiboreal wooded meadows and alvars. In consequence, the semi-dry grasslands have sources of species-rich forest, forest-edge, mesic meadow and fen communities nearby, and through the mass effect (Zonneveld, 1994) these sources can increase the grassland species density. This theory is supported by Janišová et al. (2014), who could demonstrate that plot-scale richness of grasslands is much higher when there are more and more diverse natural and semi-natural habitats in the surroundings.

- (4) *Continuity of habitat patches in space and time*: Several authors have demonstrated that historical habitat size during the past decades, centuries and millennia is highly influential on present-day plot-scale richness (Bruun et al., 2001; Helm et al., 2006; Pärtel et al., 2007). While it is not easy to quantify the local development of grassland area over the whole Holocene, there are indications that most of the sites that are extremely rich nowadays had a continuity of grasslands throughout the Holocene because human settlement took place very early and re-opened the advancing forests before they could close (e.g. Hájková et al., 2011). The continuous existence of extensive grassland lead to an accumulation of suitable species that migrated through the region in consequence of changing climate (Roleček et al., 2014, e.g. highlight that the extremely rich grasslands often contain some species with very disjunct distribution) and, at the same time reduced the risk of local extinction (see Michalcová et al., 2014). In some cases, extensive long-lasting grassland landscapes even gave rise to speciation during the Holocene, as for example in the case of the alvars of Öland and Gotland (Jonsell and Karlsson, 2004).
- (5) *Reduction of competitive exclusion*: While (1) and (2) provided reasons why the temperate European flora contains particularly many species that could survive under the site conditions of the extremely rich grasslands, and (3) and (4) suggest mechanisms how a huge amount of suitable species reached a particular grassland site, none of these factors per se can explain why so many species co-occur on small scale, say, 0.1 or 10 m². At this grain size, species directly interact and thus competitive exclusion (den Boer, 1986) should happen. Here, obviously the management regime plays a role. It appears that practically all extreme-richness sites are mown once a year and not fertilized. This management of biomass and litter removal suppresses dominants and supports low-growing, poorly competitive species or, more generally speaking, reduces the asymmetry in competition for light (see Roleček et al., 2014). Highest species densities at a management level between abandonment and frequent cuts is precisely what the IDH predicts (see Grime, 1973; and Section 4). While a recent simulation study has shown that under simplistic assumptions disturbances cannot ensure species co-existence in the long run (Fox, 2013), it is sufficient to add a bit more realistic complexity to the model to get indeed a maximum of small-scale species co-existence for intermediate levels of both disturbance and productivity (Kondoh, 2001; Svensson et al., 2012). For plot-scale richness, mowing generally seems to be more favourable than grazing (see Section 4), and this is probably due to the “equalizing” effects of this management. All species experience a similar biomass reduction, while under grazing regimes some species are always preferably eaten and others avoided (Dierschke and Briemle, 2002). It might even be that mowing promotes species coexistence via negative frequency dependence (Fox, 2013), since tall, dominant species loose proportionally more of their superficial biomass through a cut than small, low-grown ones. Another mechanism that might reduce competition in

extremely species-rich grasslands, was put forward by Dengler and Boch (2008). Following the observation that plot-scale richness of xerothermic herbaceous communities often increases with altitude and latitude (see Section 3), they suggest that the shorter vegetation period at higher elevation might reduce the annual duration of competition in communities mostly composed of hemicryptophytes. Finally, there are some recent ideas that generally question the relevance of competition between species. (i) Mayfield and Levine (2010) argue that, contrary to common assumption, competition under certain circumstances even favours the co-existence of species with similar traits, or assuming some niche conservatism, phylogenetically closely related species. (ii) Trait variability within single grassland species might be as large as or even larger than between different species (Albert et al., 2010). (iii) Seed-addition experiments in species rich grasslands usually do not find support for any saturation in community composition – as should be expected in case of competitive exclusion – but in some cases the invasibility even increases with richness (e.g. Zeiter and Stampfli, 2012).

In contrast to points (1)–(5), two other factors sometimes suggested to increase plot-scale richness have little support in the case of the world record grasslands: (a) All stands of the extremely species-rich grasslands appear visually particularly homogenous (own observations, J.D.), making plot-scale abiotic heterogeneity an unlikely driver of high richness. (b) A recent study by Michalcová et al. (2014) could at least for the White Carpathians also dismiss a positive effect of the regional species pool (based on grid cells of 8 km² size).

8. Ecosystem functions and services of grasslands as related to biodiversity

Ecosystem functions are the habitat, biological or system properties or processes of ecosystems, *ecosystem services* are the benefits humans obtain from these functions (Costanza et al., 1997). Grasslands provide all kinds of ecosystem services, namely supporting, provisioning, regulating and cultural services (World Resources Institute, 2005) which are based on multiple ecosystem functions. For example, the production function (biomass production) serves the provisioning services.

Importantly, the role of biodiversity has been proven fundamental in ensuring the performance of ecosystem functioning (e.g. Balvanera et al., 2006; Hector and Bagchi, 2007). Functional diversity is likely to be one of the major factors affecting ecosystem functioning (Hooper et al., 2005). Plant species can exert different influences on ecosystem functions through their traits (effect traits: Lavorel and Garnier, 2002), and hence trait changes may result in ecosystem effects (e.g. Cornelissen et al., 2003). Changes in species abundance as well as in species composition can cause shifts in ecosystem functions (Suding et al., 2008) and related ecosystem services. While ecosystem functioning at a given time is chiefly determined by trait values of the dominant contributors to plant biomass (biomass-ratio hypothesis: Grime, 1998), intraspecific trait variability should be considered when studying responses in ecosystem functioning over longer time scales (Albert et al., 2011). This is because intraspecific variability influences species turnover and might be strongly influenced by the variance of the trait value distribution (see Albert et al., 2011, and references therein). Generally, biomass production of European grasslands shows a log-linear relationship to species richness and a linear one to functional richness (Hector et al., 1999). More diverse grasslands generally use resources more completely, take up more nitrogen and occupy more of the available space (Spehn et al., 2005).

Climate change in Europe is generally increasing mean temperatures, but most severely in Mediterranean Europe, while temperature variability increases also nearly everywhere, but strongest in Central Europe (Schär et al., 2004). Further, it is widely acknowledged that the frequency and severity of droughts has already increased and likely will further increase during the next decades (IPCC, 2012). So far it is not particularly well understood how these processes will affect the functions of grasslands. In an experimental setting, Beierkuhnlein et al. (2011) found that warming had no or very limited effects on the biomass production of typical grassland grass species, while severe drought negatively impacted the performance of most provenances of most species. With regard to climatic extremes (in this case: drought), Jentsch et al. (2011) showed that ecosystem regulating functions, such as water and nutrient cycling, gas exchange and compositional dynamics are initiated, while primary production surprisingly remained unchanged. Community composition, complementary responses in species interactions, which are most likely based on their functional differences, contribute to buffering primary production of grassland communities without changing community composition (Jentsch et al., 2011; Wang et al., 2007). Kreyling et al. (2011) found that the extreme drought of the year 2003 naturally reduced the biomass yield of the very year, but had no lasting effects in subsequent years. Species richness was not negatively affected either in the drought years or afterwards. However, the drought event initiated stochasticity in successional trajectories. Overall, available experimental studies suggest that at least temperate European grasslands are remarkably stable (i.e. resistant and/or resilient) towards present levels of climate change. This coincides with a simulation study from the Netherlands that predicts for 2050 increased drought stress of grasslands in consequence of elevated temperatures, but suggests that overall the biomass yield from will even benefit (Kroes and Supit, 2011). Studies on the effects of climatic changes on the invasibility of grasslands are scarce, and currently there is no clear picture of these effects. However, grasslands generally seem to be quite resistant against vascular plant invasions as they are among the habitat types least invaded by neophytes (average cover values for different grassland types only 0.1–1.7%; Chytrý et al., 2005).

9. Threats and management of grassland diversity

Grasslands of Europe account for a high fraction of the continent's biodiversity in many taxonomic groups despite only a small fraction of Europe would be covered naturally by grasslands (Bohn et al., 2004), and the fraction of threatened species is particularly high in this habitat type. For example, among 22 formations in Germany, dry grasslands host the highest number of vascular plants (16.3% of the flora), even more than mesophilous forests (14.7%) with their far larger area, while also wet (6.8%), mesic (6.2%) as well as acidic grasslands and heathlands (6.2%) are quite rich (Korneck et al., 1998). Considering the number and fraction of threatened species, various grassland formations are on top, just after oligotrophic wetlands (Korneck et al., 1998). In the case of butterflies even 63% of their European fauna are associated with dry grasslands and steppes alone, and these species show a more negative population trend than generalists and specialists of other habitat types (WallisDeVries and van Swaay, 2009). Finally, among the European bird species, 152 (29%) are associated with grasslands, and 59% of these have an unfavorable conservation status, the situation being worst for birds of steppic habitats (Nagy, 2009).

During the last century, Palaearctic grasslands experienced a dramatic loss in area. In Central, North and West Europe semi-natural grasslands were made to intensive grasslands using synthetic fertilizers and pesticides, drainage of wet grasslands,

increased cutting frequency and lowered cutting height in meadows, higher stocking rates on pastures as well as frequent re-sowing with artificial seed mixtures. This happened mainly on productive sites. For example, Stevens et al. (2010) report that 90% of the former semi-natural grasslands have been lost in Wales. In more marginal and less productive sites, the utilization of semi-natural grasslands was largely given up and they either developed into shrublands or forests through natural succession (e.g. 59–94% of the alvar grasslands in Estonia: Helm et al., 2006; significant parts of the Bulgarian mountain grasslands: Vassilev et al., 2011) or were afforested, often with non-native species (e.g. in Romania: Ruprecht et al., 2009). Grassland loss through transformation into arable land, quarries or settlements and infrastructure also occurred, but is generally of lower importance than the twin threats of intensification and abandonment (Valkó et al., 2012). In the natural steppes of Eastern Europe and Central Asia, the situation was different, but in some cases even more dramatic. In the former Soviet Union and China (but luckily not in Mongolia), the state aimed at transforming the “unproductive” steppes into productive arable land, leading to an extensive destruction of steppes, partly even in nature reserves (Werger and van Staalduinen, 2012). Most severely affected was Ukraine, where only 3% of the former steppes are left (Korotchenko and Peregrym, 2012), but serious losses also occurred in Russia and Kazakhstan (Hölzel et al., 2002; Kamp et al., 2011). By contrast, the damage to the Dahurian steppes (i.e. Mongolia and surrounding regions in Russia and China) was less severe. Here, 72% of the natural steppes were still extant by the turn of the century (White et al., 2000). Ambarlı and Bilgin (2014) report that also the Anatolian (partly natural, partly semi-natural) steppes experienced substantial losses in the 20th century.

At the landscape scale, the continuous grasslands became fragmented, and their area and connectivity decreased. Reduced landscape-scale heterogeneity of surrounding habitats negatively influences the spillover of grassland species and decreases the chance of dispersal between the remaining grassland patches (Zulka et al., 2014). Moreover, with decreasing patch size the influence of surrounding agricultural and urban habitats (i.e. pollution, immigration of invasive species) increases (Römermann et al., 2005). Landscape configuration i.e. the type of adjacent habitats is also crucial in maintaining local species richness (Janišová et al., 2014). Rédei et al. (2014) found that for most of the sand steppe specialists the mosaic landscape is easily permeable because these species can persist in small forests and disperse through them, which enables them to bridge gaps between grasslands patches. Other authors suggest that the effect of surrounding landscape is strongly dependent on the affected grassland type. Janiřová et al. (2014) point out that in the same landscape, the grassland species pool along a soil moisture gradient is differently affected by the adjacent habitat patches. Generally, grassland diversity exhibits relatively long lag times to management changes so that present-day patterns often better reflect past than present management (Helm et al., 2006; Reitalu et al., 2014).

Agri-environmental schemes (AEs) as part of the current agricultural policy subsidize nature-friendly management of grasslands in the European Union, but for obtaining such subsidies, it is often only required to implement the corresponding management in a relatively small area of the managed grasslands including also grassy margins (Kleijn et al., 2004). The beneficial effect on species richness is questionable in landscapes with only few natural habitats, and in some cases – especially in extensively used landscapes with a relatively high proportion of natural habitats – even negative effects were found (Batáry et al., 2011; Kleijn et al., 2006). It is also important to decrease landscape-scale fragmentation by creating buffer zones around grassland fragments to mitigate the negative influences and corridors between them to restore migration routes and meta-population dynamics (Critchley et al., 2003).

Prach et al. (2014) suggested that restoration using regional seed mixtures could be a promising option and Babai and Molnár (2014) that effective conservation of species richness is feasible by combining traditional grassland management with extensive mosaic management at the scale of the entire landscape. There is a general lack of tested landscape-scale conservation strategies that also consider alternative grassland management techniques, such as rotational mosaic mowing (Buri et al., 2013), prescribed burning (Valkó et al., 2014a) or extensive semi-open pasture landscapes (Redecker et al., 2002).

10. Conclusions and outlook

Reflecting both the topics of the articles and our own expertise, this synthesis is biased towards semi-natural grasslands in temperate Europe (at the expense of semi-natural grasslands in the Mediterranean Basin and natural steppes of Eastern Europe, Central Asia, the Irano-Anatolian region and North Africa) and towards vascular plants (at the expense of bryophytes, lichens, fungi, animals and microbes). There is certainly more knowledge on some prominent animal groups, such as birds, butterflies and grasshoppers, but the majority of the animal kingdom is not usually covered in grassland studies (Zulka et al., 2014, being a rare exception). Studies on grassland fungal diversity (apart from the numerous mycorrhiza studies, which so far usually do not provide the link to fungal species) are largely nonexistent (but see Öster, 2008). While there are many publications on steppe biodiversity in Russian, Ukrainian, Chinese and Turkish language in regional or national journals, only rarely such information is published in English and thus available to the international scientific audience – the recent steppe book by Werger and van Staalduinen (2012) with chapters from all the mentioned regions written by regional experts being a laudable exception. Therefore, we call to put more research efforts on the less documented regions and understudied taxa.

This Special Issue supports the notion that biodiversity has many different facets, which often behave differently. Since these different facets, such as species richness vs. functional diversity, alpha diversity vs. beta diversity, evenness vs. richness or diversity at 0.01 m², 100 m² and 1 km² all carry valuable complementary information, we recommend employing sampling and monitoring schemes that serve several of them. The implementation of standardized sampling schemes with standardized plot sizes across larger gradients seems to be a promising tool in this context (e.g. the EDGG Expeditions; see Turtureanu et al., 2014).

This synthesis also made clear that even for a well-studied group in a well-studied region like vascular plants in semi-natural grasslands of temperate Europe, we are still far from full comprehension of how the various drivers interact in producing the biodiversity patterns we see. These open questions have been exemplified by the “world record holders” among the European grasslands, and an attempt has been made to explain how such an extraordinary “packing” of species could emerge. We explain maximum richness by the interplay of various factors at different levels. These ideas require thorough testing, which could not only solve the riddle but also contribute to the general understanding of the processes underlying biodiversity patterns. One approach to the solution of the riddle is the sampling of new high-quality, multi-scale and multi-taxon diversity data along major environmental gradients across the whole Palaearctic – as EDGG attempts it with its research expeditions (see Turtureanu et al., 2014). Another approach will be the emerging pan-European vegetation-plot database *European Vegetation Archive* (EVA), which will unite hundreds of thousands of plots from all over Europe (see Dengler et al., 2011; Schaminée et al., 2009). This database will, through its sheer size and despite the undoubted biases in such databases (e.g. Chytrý, 2001; Chytrý et al.,

2014) in connection with GIS layers of multiple environmental drivers (e.g. climate, land use, soil) for the first time allow modelling plot-scale richness across a larger spatial extent. In addition, the particularly challenging last point of the conceptual framework (cf. point 5 of Section 7.2) requires innovative, well-thought experimentation and simulation.

Finally, it should be stressed that for securing grassland biodiversity in the Palaearctic realm international support for national NGOs is necessary, for example by policy tools of international organizations like the *Smolenice Grassland Declaration* (http://www.edgg.org/edgg_meeting.html) or the *Steppe Appeal* (http://www.edgg.org/publ/bulletin/Bulletin_EDGG.12.pdf) of EDGG. The *Smolenice Grassland Declaration* (signed by 362 scientists from 41 countries) highlights that, while there are international frameworks and well-developed national strategies for forests and aquatic ecosystems, a coherent vision and an integrated policy approach for grasslands is still missing. The major goal of the *Steppe Appeal* was to promote the protection, restoration and sustainable development of Ukrainian steppes. To convince decision makers on both national and international levels to subsidize grassland conservation and restoration actions, a strong and comprehensive *Convention on Grassland Conservation* and a well-developed grassland biodiversity strategy are necessary.

Acknowledgements

The is a joint effort by the authors, Sections 1, 2, 4, 6, 7 and 10 being mainly drafted by J.D., Section 3 by M.J., Section 9 by P.T. and Sections 5 and 8 by C.W., while all authors revised the final manuscript. We are grateful to Anna Kuzemko and the National Dendrological Park “Sofievka”, National Academy of Science of Ukraine, for organizing and hosting the 8th European Dry Grassland Meeting in Uman; to Jürg Fuhrer and Jean-Paul Aeschlimann from Agriculture, Ecosystems and Environment who made this Special Issue possible and supported its development; to the authors for their exciting contributions and to the reviewers who spent much time in guiding the revisions. J.D. received funding from the project SIGNAL (European gradients of resilience in the face of climate extremes), funded by the ERA-Net BiodivERsA, with the national funders Belgian Science Policy Office, Bulgarian Science Fund, Ministère de l'Écologie, du Développement durable et de l'Énergie de la République Française and German Federal Ministry of Education and Research, part of the 2011–2012 BiodivERsA call for research proposals (BMBF: 01LC1201A). P.T. was supported by the OTKA PD 100 192 and by TÁMOP-4.2.4.A/2-11-1-2012-0001 proposals during the manuscript preparation. Aiko Huckauf kindly polished the English of this synthesis.

References

- Albert, C.H., Grassein, F., Schurr, F., Vieilledent, G., Violle, C., 2011. When and how should intraspecific variability be considered in trait-based plant ecology. *Perspect. Plant Ecol. Evol. Syst.* 13, 217–225.
- Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P., Lavorel, S., 2010. Intraspecific functional variability: extent, structure and sources of variation. *J. Ecol.* 98, 604–613.
- Ambarlı, D., Bilgin, C.C., 2014. Effects of landscape, land use and vegetation on bird community composition and diversity in Inner Anatolian steppes. *Agric. Ecosyst. Environ.* 182, 37–46.
- Austrheim, G., 2002. Plant diversity patterns in semi-natural grasslands along an elevational gradient in southern Norway. *Plant Ecol.* 161, 193–205.
- Babai, D., Molnár, Z., 2014. Small-scale traditional management of highly species-rich grasslands in the Carpathians. *Agric. Ecosyst. Environ.* 182, 123–130.
- Bai, Y., Wu, J., Pan, Q., Huang, J., Wang, Q., Li, F., Buyantuyev, A., Han, X., 2007. Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. *J. Appl. Ecol.* 44, 1023–1034.
- Bai, Y., Wu, J., Clark, C.M., Naeem, S., Pan, Q., Huang, J., Zhang, L., Han, X., 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from Inner Mongolia grasslands. *Global Change Biol.* 16, 358–372.

- Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G., Knops, J.M.H., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecol. Lett.* 9, 780–788.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Barthlott, W., Mutke, J., Rafiqpoor, D., Kier, G., Kreft, H., 2005. Global centers of vascular plant diversity. *Nova Acta Leopoldina N. F.* 92, 61–83.
- Batáry, P., Báldi, A., Kleijn, D., Tschamtker, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. Lond. B* 278, 1894–1902.
- Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E., Kreyling, J., 2011. Ecotypes of European grass species respond differently to warming and extreme drought. *J. Ecol.* 99, 703–713.
- Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., Garnier, E., 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *J. Ecol.* 100, 1422–1433.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., de Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* 20, 30–59.
- Bohn, U., Gollub, G., Hettwer, C., Neuhausová, Z., Raus, T., Schlüter, H., Weber, H., Hennekens, S. (Eds.), 2004. Map of the Natural Vegetation of Europe. Scale 1:2 500 000. Interactive CD-ROM: Explanatory Text, Legend, Maps. Bundesamt für Naturschutz, Bonn.
- Bossuyt, B., Honnay, O., 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *J. Veg. Sci.* 19, 875–884.
- Breckle, S.-W., 2002. *Walter's vegetation of the Earth*. In: *The Ecological Systems of the Geo-biosphere*, 4th ed. Springer, Berlin.
- Bruun, H.H., Fritzboeger, B., Rindell, P.O., Hansen, U.L., 2001. Plant species richness in grasslands: the relative importance of contemporary environment and land-use history since the Iron Age. *Ecography* 24, 569–578.
- Bukovinsky, T., van Veen, F.J.F., Jongema, Y., Dicke, M., 2008. Direct and indirect effects of resource quality on food web structure. *Science* 319, 804–807.
- Buri, P., Arlettaz, R., Humbert, J.-Y., 2013. Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: evidence drawn from field-scale experimentation. *Agric. Ecosyst. Environ.* 181, 22–30.
- Carboni, M., de Bello, F., Janeček, Š., Doležal, J., Horník, J., Lepš, J., Reitalu, T., Klimešová, J., 2014. Changes in trait divergence and convergence along a productivity gradient in wet meadows. *Agric. Ecosyst. Environ.*, <http://dx.doi.org/10.1016/j.agee.2013.12.014>.
- Cheng, Y., Tsubo, M., Ito, T.Y., Nishihara, E., Shinoda, M., 2011. Impact of rainfall variability and grazing pressure on plant diversity in Mongolian grasslands. *J. Arid Environ.* 75, 471–476.
- Chytrý, M., 2001. Phytosociological data give biased estimates of species richness. *J. Veg. Sci.* 12, 439–444.
- Chytrý, M., Pyšek, P., Tichý, L., Knollová, I., Danihelka, J., 2005. Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia* 77, 339–354.
- Chytrý, M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kočí, M., Kubešová, S., Lustyk, P., Otyápková, Z., Popov, D., Roleček, J., Rezníčková, M., Šmarda, P., Valachovič, M., 2007. Plant species richness in continental southern Siberia: effects of pH and climate in the context of the species pool hypothesis. *Global Ecol. Biogeogr.* 16, 668–678.
- Chytrý, M., Tichý, L., Hennekens, S.M., Schaminée, J.H.J., 2014. Assessing vegetation change using vegetation-plot databases: a risky business. *Appl. Veg. Sci.*, <http://dx.doi.org/10.1111/avsc.12050>.
- Colwell, R.K., Lees, D.C., 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.* 15, 70–76.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Naeem, S., Limburg, K., Paruelo, J., O'Neill, R.V., Raskin, R., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Crawley, M.J., Johnston, A.E., Silvertown, J., Dodd, M., de Mazancourt, C., Heard, M.S., Henman, D.F., Edwards, G.R., 2005. Determinants of species richness in the Park Grass Experiment. *Am. Nat.* 165, 179–192.
- Critchley, C.N.R., Burke, M.J.W., Stevens, D.P., 2003. Conservation of lowland semi-natural grasslands in the UK: a review of botanical monitoring results from agri-environment schemes. *Biol. Conserv.* 115, 263–268.
- de Bello, F., Lepš, J., Sebastià, M.-T., 2007. Grazing effects on the species-area relationship: variation along a climatic gradient in NE Spain. *J. Veg. Sci.* 18, 25–34.
- den Boer, P.J., 1986. The present status of the competitive exclusion principle. *Trends Ecol. Evol.* 1, 25–28.
- Dengler, J., 2005. Zwischen Estland und Portugal – Gemeinsamkeiten und Unterschiede der Phytodiversitätsmuster europäischer Trockenrasen. *Tuexenia* 25, 387–405.
- Dengler, J., Boch, S., 2008. *Forest-edge communities (Trifolio-Geranietea sanguinei)* on the island of Saaremaa (Estonia): phytosociology and biodiversity patterns. *Mitt. Arbeitsgem. Geobot. Schleswig-Holstein Hamb.* 65, 257–286.
- Dengler, J., Löbel, S., Boch, S., 2006. Dry grassland communities of shallow, skeletal soils (*Sedo-Scleranthenea*) in northern Europe. *Tuexenia* 26, 159–190.
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Lopez-Gonzalez, G., Finckh, M., Mucina, L., Rodwell, J.S., Schaminée, J.H.J., Spencer, N., 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *J. Veg. Sci.* 22, 582–597.
- Dengler, J., Becker, T., Ruprecht, E., Szabó, A., Becker, U., Beldean, M., Bita-Nicolae, C., Dolnik, C., Goia, I., Peyrat, J., Sutcliffe, L.M.E., Turtureanu, P.D., Uğurlu, E., 2012. *Festuco-Brometalia* communities of the Transylvanian Plateau (Romania) – a preliminary overview on syntaxonomy, ecology, and biodiversity. *Tuexenia* 32, 319–359.
- Dengler, J., Bergmeier, E., Willner, W., Chytrý, M., 2013. Towards a consistent classification of European grasslands. *Appl. Veg. Sci.* 16, 518–520.
- Dierschke, H., Brieme, G., 2002. *Kulturgasland – Wiesen, Weiden und verwandte Staudenfluren*. Ulmer, Stuttgart.
- Dupré, C., Diekmann, M., 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. *Ecography* 24, 275–286.
- Dupré, C., Stevens, C.J., Ranke, T., Bleeker, A., Peppeler-Lisbach, C., Gowing, D.J.G., Dise, N.B., Dorland, E., Bobbink, R., Diekmann, M., 2010. Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. *Global Change Biol.* 16, 344–357.
- Ellenberg, H., Leuschner, C., 2010. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*, 6th ed. Ulmer, Stuttgart.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. Scripta Geobot. 18, 1–248.
- Eurostat, 2013. Agri-environmental indicator – cropping patterns. http://epp.eurostat.ec.europa.eu/statistics_explained/index.php/Agri-environmental_indicator_-_cropping_patterns (accessed 24.11.13).
- Ewald, J., 2003. The calcareous riddle: why are there so many calciphilous species in the Central European flora? *Folia Geobot.* 38, 357–366.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.
- Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Turner, J.R.G., 2009. Spatial species-richness gradients across scales: a meta-analysis. *J. Biogeogr.* 36, 132–147.
- Fischer, M., Wipf, S., 2002. Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biol. Conserv.* 104, 1–11.
- Fox, J.W., 2013. The intermediate disturbance hypothesis should be abandoned. *Trends Ecol. Evol.* 28, 86–92.
- Fridley, J.D., Grime, J.P., 2010. Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology* 91, 2272–2283.
- Gaston, K.J., Spicer, J.I., 2004. *Biodiversity: An Introduction*, 2nd ed. Blackwell, Oxford.
- Gibson, D.J., 2009. *Grasses and Grassland Ecology*. Oxford University Press, Oxford.
- Giladi, I., Ziv, Y., May, F., Jeltsch, F., 2011. Scale-dependent determinants of plant species richness in a semi-arid fragmented agro-ecosystem. *J. Veg. Sci.* 22, 983–996.
- Götzenberger, L., de Bello, F., Bräthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., Zobel, M., 2012. Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biol. Rev.* 87, 111–127.
- Grace, J.B., 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspect. Plant Ecol. Evol. Syst.* 2, 1–28.
- Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910.
- Grime, J.P., 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Wiley, New York.
- Güsewell, S., 2004. N:P ratios in terrestrial plants: variation and functional significance. *New Phytol.* 164, 243–266.
- Habel, J.C., Dengler, J., Janišová, M., Török, P., Wellstein, C., Wieszik, M., 2013. European grassland ecosystems: threatened hotspots of biodiversity. *Biodivers. Conserv.* 22, 2131–2138.
- Hájková, P., Roleček, J., Hájek, M., Horsák, M., Fajmon, K., Polák, M., Jamrichová, E., 2011. Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts (Czech Republic and Slovakia). *Preslia* 83, 185–204.
- Hanke, W., Böhner, J., Dreber, N., Jürgens, N., Schmiedel, U., Wesuls, D., Dengler, J., 2014. The impact of livestock grazing on plant diversity in drylands: an analysis across biomes and scales in southern Africa. *Ecol. Appl.* (in press).
- Hansson, M., Fogelfors, H., 2000. Management of a semi-natural grassland: results from a 15-year-old experiment in southern Sweden. *J. Veg. Sci.* 11, 31–38.
- Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multi-functionality. *Nature* 448, 188–190.
- Hejman, M., Češková, M., Schellberg, J., Pätzold, S., 2010. The Rengen Grassland Experiment: effect of soil chemical properties on biomass production, plant species composition and species richness. *Folia Geobot.* 45, 125–142.

- Hejcman, M., Hejcmanová, P., Pavlů, V., Beneš, J., 2013. Origin and history of grasslands in Central Europe – a review. *Grass Forage Sci.* 68, 345–363.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högborg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127.
- Helm, A., Hanski, I., Pärtel, M., 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecol. Lett.* 9, 72–77.
- Hobohm, C., 1998. Pflanzensoziologie und die Erforschung der Artenvielfalt – Überarbeitete und erweiterte Fassung der an der Universität Lüneburg eingereichten und angenommenen Habilitationsschrift. *Arch. Naturwiss. Diss.* 5, 1–231.
- Hobohm, C., Bruchmann, I., 2009. Endemische Gefäßpflanzen und ihre Habitate in Europa – Plädoyer für den Schutz der Grasland-Ökosysteme. *Ber. Reinhold-Tüxen-Ges.* 21, 142–161.
- Hölzel, N., Haub, C., Ingelfinger, M.P., Otte, A., Pilipenko, V.N., 2002. The return of the steppe: large-scale restoration of degraded land in southern Russia during the post-Soviet era. *J. Nat. Conserv.* 10, 75–85.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81–101.
- IPCC, 2012. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. In: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. Cambridge University Press, New York.
- Jacobs, B.F., Kingston, J.D., Jacobs, L.L., 1999. The origin of grass-dominated ecosystems. *Ann. Miss. Bot. Gard.* 86, 590–643.
- Jandt, U., von Wehrden, H., Bruehlheide, H., 2011. Exploring large vegetation databases to detect temporal trends in species occurrences. *J. Veg. Sci.* 22, 957–972.
- Janišová, M., Barthá, S., Kiehl, K., Dengler, J., 2011. Advances in the conservation of dry grasslands – introduction to contributions from the 7th European Dry Grassland Meeting. *Plant Biosyst.* 145, 507–513.
- Janišová, M., Becker, T., Becker, U., Demina, O., Dembic, I., Ermakov, N., Filibeck, G., Frank, D., Guarino, R., Jaunatre, R., Kozub, L., Polyakova, M., Suzuki, K., Dengler, J., 2013. Steppes of Southern Siberia – experiences from the 6th EDGG Research Expedition to Khakassia, Russia (22 July–1 August 2013). *Bull. Eur. Dry Grassl. Group* 19/20, 31–48.
- Janišová, M., Michalcová, D., Bacaro, G., Ghisla, A., 2014. Landscape effects on diversity of semi-natural grasslands. *Agric. Ecosyst. Environ.* 182, 47–58.
- Janssens, F., Peeters, A., Tallowin, J.R.B., Bakker, J.P., Bekker, R.M., Fillat, F., Oomes, M.J.M., 1998. Relationship between soil chemical factors and grassland diversity. *Plant Soil* 202, 69–78.
- Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., Hein, R., Lara, M., Mirzaee, H., Nadler, S.E., Nagy, L., Otieno, D., Pritsch, K., Rascher, U., Schädler, M., Schlöter, M., Singh, B.K., Stadler, J., Walter, J., Wellstein, C., Wöllecke, J., Beierkuhnlein, C., 2011. Climate extremes initiate ecosystem regulating functions while maintaining productivity. *J. Ecol.* 99, 689–702.
- Jeschke, M., Kiehl, K., Pfadenhauer, J., Gigon, A., 2008. Langfristige Auswirkungen ehemaliger Bewirtschaftungsvarianten auf die Diversität von Blütenpflanzen. Moosen und Flechten eines Kalkmagerrasens. *Bot. Helv.* 118, 95–109.
- Johnson, M.T., Lajeunesse, M.J., Agrawal, A.A., 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.* 9, 24–34.
- Jones, T.S., Allan, E., Härrä, S.A., Krauss, J., Müller, C.B., van Veen, F.J.F., 2011. Effects of genetic diversity of grass on insect species diversity at higher trophic levels are not due to cascading diversity effects. *Oikos* 120, 1031–1036.
- Jonsell, B., Karlsson, T., 2004. Endemic vascular plants in Norden. In: Jonsell, B. (Ed.), *Flora Nordica – General Volume*. Royal Swedish Academy of Sciences, Stockholm, pp. 139–159.
- Jürgens, N., Schmiedel, U., Haarmeyer, D.H., Dengler, J., Finckh, M., Goetze, D., Gröngöft, A., Hahn, K., Koulbaly, A., Luther-Mosebach, J., Muche, G., Oldeland, J., Petersen, A., Porembski, S., Rutherford, M.C., Schmidt, M., Sinsin, B., Strohbach, B.J., Thiombiano, A., Wittig, R., Zizka, G., 2012. The BIOTA Biodiversity Observatories in Africa – a standardized framework for large-scale environmental monitoring. *Environ. Monit. Assess.* 184, 655–678.
- Kamp, J., Urazaliev, R., Donald, P.F., Hölzel, N., 2011. Post-Soviet agricultural change predicts future declines after recent recovery in Eurasian steppe bird populations. *Biol. Conserv.* 144, 2607–2614.
- Kelemen, A., Török, P., Valkó, O., Migléc, T., Tóthmérész, B., 2013. Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. *J. Veg. Sci.* 24, 1195–1203.
- Kleijn, D., Berendse, F., Smit, R., Gillissen, N., Smit, J., Brak, B., Groeneveld, R., 2004. Ecological effectiveness of agri-environmental schemes in different agricultural landscapes in the Netherlands. *Conserv. Biol.* 18, 775–786.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tschamtké, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* 9, 243–254.
- Klötzli, F., Dietl, W., Marti, K., Schubiger-Bossard, C., Walther, G.-R., 2010. Vegetation Europas. Das Offenland im vegetationskundlich-ökologischen Überblick unter besonderer Berücksichtigung der Schweiz. Ott, Bern.
- Köhler, B., Gigon, A., Edwards, P.J., Krüsi, B., Langenauer, R., Lüscher, A., Ryser, P., 2005. Changes in the species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements. *Perspect. Plant Ecol. Evol. Syst.* 7, 51–67.
- Kondoh, M., 2001. Unifying the relationships of species richness to productivity and disturbance. *Proc. R. Soc. Lond. B* 268, 269–271.
- Koordinationsstelle Biodiversitäts-Monitoring Schweiz, 2009. Zustand der Biodiversität in der Schweiz – Ergebnisse des Biodiversitätsmonitorings Schweiz (BDM) im Überblick. Stand: Mai 2009. Umwelt-Zustand 09/11, pp. 1–112.
- Korneck, D., Schnittler, M., Klingenstein, F., Ludwig, G., Takla, M., Bohn, U., May, R., 1998. Warum verarmt unsere Flora? – Auswertung der Roten Liste der Farn- und Blütenpflanzen Deutschlands. *Schriftenr. Vegetationskd.* 29, 299–444.
- Korotchenko, I., Peregrin, M., 2012. Ukrainian steppes in the past at present and in the future. In: Werger, M.J.A., van Staalduinen, M.A. (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Springer, Dordrecht, pp. 173–196.
- Kreyling, J., Jentsch, A., Beierkuhnlein, C., 2011. Stochastic trajectories of succession initiated by extreme climatic events. *Ecol. Lett.* 14, 758–764.
- Kroes, J.G., Supit, I., 2011. Impact analysis of drought, water excess and salinity on grass production in The Netherlands using historical and future climate data. *Agric. Ecosyst. Environ.* 144, 370–381.
- Kull, K., Zobel, M., 1991. High species richness in an Estonian wooded meadow. *J. Veg. Sci.* 2, 711–714.
- Lang, G., 1994. Quartäre Vegetationsgeschichte Europas. Fischer, Jena.
- Lapola, D.M., Oyama, M.D., Nobre, C.A., Sampaio, G., 2008. A new world natural vegetation map for global change studies. *An. Acad. Bras. Cienc.* 80, 397–408.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
- Lavrenko, E.M., Karamysheva, Z.V., Borisova, I.V., Popova, T.A., Guricheva, N.P., Nikulina, R.I., 1993. Steppes of the former Soviet Union and Mongolia. In: Coupland, R.T. (Ed.), *Natural Grasslands: Eastern Hemisphere and Résumé*. Elsevier, Amsterdam, pp. 3–55.
- Lawton, J.H., May, R.M. (Eds.), 1995. *Extinction Rates*. Oxford University Press, Oxford.
- Löbel, S., Dengler, J., Hobohm, C., 2006. Species richness of vascular plants, bryophytes and lichens in dry grasslands: the effects of environment, landscape structure and competition. *Folia Geobot.* 41, 377–393.
- Loiseau, P., Louault, F., Le Roux, X., Bardy, M., 2005. Does extensification of rich grasslands alter the C and N cycles, directly or via species composition? *Basic Appl. Ecol.* 6, 275–287.
- Ma, W., He, J.-S., Yang, Y., Wang, X., Liang, C., Anwar, M., Zeng, H., Jang, J., Schmid, B., 2010. Environmental factors covary with plant diversity–productivity relationships among Chinese grassland sites. *Global Ecol. Biogeogr.* 19, 233–243.
- Mayfield, M.M., Levine, J.M., 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* 13, 1085–1093.
- Merunková, K., Chytrý, M., 2012. Environmental control of species richness and composition in upland grasslands of the southern Czech Republic. *Plant Ecol.* 213, 591–602.
- Merunková, K., Preislerová, Z., Chytrý, M., 2012. White Carpathian grasslands: can local ecological factors explain their extraordinary species richness? *Preslia* 84, 311–325.
- Michalcová, D., Chytrý, M., Pechanec, V., Hájek, O., Jongepier, J.W., Danihelka, J., Grulich, V., Šumberová, K., Preislerová, Z., Ghisla, A., Bacaro, G., Zelený, D., 2014. High plant diversity of grasslands in a landscape context: a comparison of contrasting regions in Central Europe. *Folia Geobot.*, <http://dx.doi.org/10.1007/s12224-013-9173-1> (in press).
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* 132, 87–106.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? *Ecology* 82, 2381–2396.
- Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: the critical role of hotspots. In: Zachos, F.E., Habel, J.C. (Eds.), *Biodiversity Hotspots – Distribution and Protection of Conservation Priority Areas*. Springer, Berlin, pp. 3–22.
- Moeslund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., Ejrnæs, R., Odgaard, M.V., Svenning, J.-C., 2013. Topographically controlled soil moisture drives plant diversity patterns within grasslands. *Biodivers. Conserv.* 22, 2151–2166.
- Nagy, S., 2009. Grasslands as bird habitat. In: Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J. (Eds.), *Grasslands in Europe of High Nature Value*. KNNV Publishing, Zeist, pp. 35–41.
- Niu, K., Choler, P., de Bello, F., Mirotnick, N., Du, G., Sun, S., 2014. Fertilization decreases species diversity but increases functional diversity: a three-year experiment in a Tibetan alpine meadow. *Agric. Ecosyst. Environ.* 182, 106–112.
- Olff, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* 13, 261–265.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51, 933–938.
- Öster, M., 2008. Low congruence between the diversity of Waxcap (*Hygrocybe* spp.) fungi and vascular plants in semi-natural grasslands. *Basic Appl. Ecol.* 9, 514–522.

- Pärtel, M., 2002. Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* 83, 2361–2366.
- Pärtel, M., Bruun, H.H., Sammul, M., 2005. Biodiversity in temperate European grasslands: origin and conservation. *Grassl. Sci. Eur.* 10, 1–14.
- Pärtel, M., Helm, A., Reitalu, T., Liira, J., Zobel, M., 2007. Grassland diversity related to Late Iron Age human population density. *J. Ecol.* 95, 574–582.
- Pausas, J.G., Austin, M.P., 2001. Patterns of plant species richness in relation to different environments: an appraisal. *J. Veg. Sci.* 12, 153–166.
- Peter-Schmid, M.K.I., Boller, B., Kolliker, R., 2008. Habitat and management affect genetic structure of *Festuca pratensis* but not *Lolium multiflorum* ecotype populations. *Plant Breed.* 127, 510–517.
- Pierce, S., 2014. Implications for biodiversity conservation of the lack of consensus regarding the humped-back model of species richness and biomass production. *Funct. Ecol.*, <http://dx.doi.org/10.1111/1365-2435.12147> (in press).
- Pluess, A.R., 2013. Meta-analysis reveals microevolution in grassland plant species under contrasting management. *Biodivers. Conserv.* 22, 2375–2400.
- Poschold, P., Baumann, A., Karlik, P., 2009. Origin and development of grasslands in Central Europe. In: Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J. (Eds.), *Grasslands in Europe of High Nature Value*. KNNV Publishing, Zeist, pp. 15–26.
- Pott, R., 1995. The origin of grassland plant species and grassland communities in Central Europe. *Fitosociologia* 29, 7–32.
- Prach, K., Jongepierová, I., Řehouňková, K., Fajmon, K., 2014. Restoration of grasslands on ex-arable land using regional and commercial seed mixtures and spontaneous succession: successional trajectories and changes in species richness. *Agric. Ecosyst. Environ.* 182, 131–136.
- Proulx, M., Mazumder, A., 1998. Reversal of grazing impact on plant species richness on nutrient poor vs. nutrient rich ecosystem. *Ecology* 79, 2581–2592.
- Redecker, B., Finck, P., Härdtle, W., Rieckens, U., Schröder, E. (Eds.), 2002. *Pasture Landscapes and Nature Conservation*. Springer, Berlin.
- Rédei, T., Szitár, K., Czúcz, B., Barabás, S., Lellei-Kovács, E., Pándi, I., Somay, L., Csecserits, A., 2014. Weak evidence of long-term extinction debt in Pannonian dry sand grasslands. *Agric. Ecosyst. Environ.* 182, 137–143.
- Reitalu, T., Helm, A., Pärtel, M., Bengtsson, K., Gerhold, P., Rosén, E., Takkis, K., Znamenskiy, S., Prentice, H.C., 2014. Determinants of fine-scale plant diversity in dry calcareous grasslands within the Baltic Sea region. *Agric. Ecosyst. Environ.* 182, 59–68.
- Rodriguez-Iturbe, I., D'Odorico, P., Porporato, A., Ridolfi, L., 1999. On the spatial and temporal links between vegetation, climate, and soil moisture. *Water Resource Res.* 35, 3709–3722.
- Roleček, J., Čornej, I.L., Tokarjuk, A.I., 2014. Understanding the extreme species richness of semi-dry grasslands in east-central Europe: a comparative approach. *Preslia* (in press).
- Römermann, C., Dutoit, C., Poschold, P., Buisson, E., 2005. Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. *Biol. Conserv.* 121, 21–33.
- Ruprecht, E., Szabó, A., Enyedi, M.Z., Dengler, J., 2009. Steppe-like grasslands in Transylvania (Romania): characterisation and influence of management on species diversity and composition. *Tuexenia* 29, 353–368.
- Ruprecht, E., Enyedi, M.Z., Eckstein, R.L., Donath, T.W., 2010. Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation. *Biol. Conserv.* 143, 449–456.
- Schaminée, J.H.J., Hennekens, S.M., Chytrý, M., Rodwell, J.S., 2009. Vegetation-plot data and databases in Europe: an overview. *Preslia* 81, 173–185.
- Schär, C., Vidale, P.L., Lützi, D., Frei, C., Häberli, C., Liniger, M.A., Appenzeller, C., 2004. The role of increasing temperature variability in European summer heatwaves. *Nature* 427, 332–336.
- Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. *Ecol. Monogr.* 80, 469–484.
- Schultz, J., 2002. The Ecozones of the World. In: *The Ecological Division of the Geosphere*, 2nd ed. Springer, Berlin.
- Schuster, B., Diekmann, M., 2003. Changes in species density along the soil pH gradient – evidence from German plant communities. *Folia Geobot.* 38, 367–379.
- Shmida, A., Wilson, M.V., 1985. Biological determinants of species diversity. *J. Biogeogr.* 12, 1–20.
- Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yépiz, J.C., Carter, B.E., Glennon, K.L., Heberling, J.M., Jo, I.S., Pontes, A., Sauer, A., Willis, A., Fridley, J.D., 2012. Scale dependence of vegetation–environment relationships: a meta-analysis of multivariate data. *J. Veg. Sci.* 23, 942–951.
- Škornik, S., Vidrih, M., Kaligarič, M., 2010. The effect of grazing pressure on species richness, composition and productivity in North Adriatic Karst pastures. *Plant Biosyst.* 144, 355–364.
- Socher, S.A., Prati, D., Boch, S., Müller, J., Klaus, V.H., Hölzel, N., Fischer, M., 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J. Ecol.* 100, 1391–1399.
- Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimatrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Höglberg, P., Huss-Danell, K., Jump, P., A., Koricheva, J., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G.O., Otway, S.J., Palmpong, C., Pereira, J.S., Pfisterer, A.B., Prinz, A., Read, D.J., Schulze, E.-D., Siamantziouras, A.-S.D., Terry, A.C., Troubis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol. Monogr.* 75, 37–63.
- Stammel, B., Kiehl, K., Pfadenhauer, J., 2003. Alternative managements on fens: response of vegetation to grazing and mowing. *Appl. Veg. Sci.* 6, 245–254.
- Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J.G., 2004. Impacts of nitrogen deposition on the species richness of grasslands. *Science* 303, 1876–1879.
- Stevens, D.P., Smith, S.L.N., Blackstock, T.H., Bosanquet, S.D.S., Stevens, J.P., 2010. *Grasslands of Wales – A Survey of Lowland Species-Rich Grasslands 1987–2004*. University of Wales Press, Cardiff.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biol.* 14, 1125–1140.
- Svensson, J.R., Lindegarth, M., Jonsson, P.R., Pavia, H., 2012. Disturbance-diversity models: what do they really predict and how are they tested? *Proc. R. Soc. Lond. B* 279, 2163–2170.
- Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., Pärtel, M., 2010. Environmental heterogeneity, species diversity and co-existence at different spatial scales. *J. Veg. Sci.* 21, 796–801.
- Tilman, D., 2001. Functional diversity. In: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*. Academic Press, San Diego, CA, pp. 109–120.
- Tilman, D., Lehman, C.L., Thomson, K.T., 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. U.S.A.* 94, 1857–1861.
- Turtureanu, P.D., Palpurina, S., Becker, T., Dolnik, C., Ruprecht, E., Sutcliffe, L.M.E., Szabó, A., Dengler, J., 2014. Scale- and taxon-dependent biodiversity patterns of dry grassland vegetation in Transylvania. *Agric. Ecosyst. Environ.* 182, 15–24.
- Tyler, G., 2003. Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behaviour – contribution to a debate. *Folia Geobot.* 38, 419–428.
- Tyler, G., Olsson, T., 2001. Plant uptake of major and minor mineral elements as influenced by soil acidity and liming. *Plant Soil* 230, 307–321.
- Valkó, O., Török, P., Matus, G., Tóthmérész, B., 2012. Is regular mowing the most appropriate and cost-effective management maintaining diversity and biomass of target forbs in mountain hay meadows? *Flora* 207, 303–309.
- Valkó, O., Török, P., Deák, B., Tóthmérész, B., 2014a. Prospects and limitations of prescribed burning as a management tool in European grasslands. *Basic Appl. Ecol.*, <http://dx.doi.org/10.1016/j.baec.2013.11.002>.
- Valkó, O., Tóthmérész, B., Kelemen, A., Simon, E., Migléc, T., Lukács, B.A., Török, P., 2014b. Environmental factors driving seed bank diversity in alkali grasslands. *Agric. Ecosyst. Environ.* 182, 80–87.
- Vassilev, K., Pedashenko, H., Nikolov, S.C., Apostolova, I., Dengler, J., 2011. Effect of land abandonment on the vegetation of upland semi-natural grasslands in the Western Balkan Mts., Bulgaria. *Plant Biosyst.* 145, 654–665.
- Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J. (Eds.), 2009. *Grasslands in Europe of High Nature Value*. KNNV Publishing, Zeist.
- Voß, K., 2001. Die Bedeutung extensiv beweideten Feucht- und Überschwemmungsgründlandes in Schleswig-Holstein für den Naturschutz. *Mitt. Arbeitsgem. Geobot. Schleswig-Holstein Hamb.* 61, 1–185.
- Vrahnakis, M.S., Janišová, M., Rüsiņa, S., Török, P., Venn, S., Dengler, J., 2013. The European Dry Grassland Group (EDGG): stewarding Europe's most diverse habitat type. In: Baumbach, H., Pfützenreuter, S. (Eds.), *Steppenlebensräume Europas – Gefährdung, Erhaltungsmaßnahmen und Schutz*. Thüringer Ministerium für Landwirtschaft, Forsten, Umwelt und Naturschutz, Erfurt, pp. 417–434.
- WallisDeVries, M.F., van Swaay, C.A.M., 2009. Grasslands as habitats for butterflies in Europe. In: Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J. (Eds.), *Grasslands in Europe of High Nature Value*. KNNV Publishing, Zeist, pp. 27–34.
- Wang, Y., Yu, S., Wang, J., 2007. Biomass-dependent susceptibility to drought in experimental grassland communities. *Ecol. Lett.* 10, 401–410.
- Wanner, A., Suchrow, S., Kiehl, K., Meyer, W., Pohlmann, N., Stock, M., Jensen, K., 2014. Scale matters: impact of management on plant species richness and vegetation type diversity in Wadden Sea salt marshes. *Agric. Ecosyst. Environ.* 182, 69–79.
- Wassen, M.J., Olde Venterink, H., Lapshina, E.D., Tanneberger, F., 2005. Endangered plants persist under phosphorus limitation. *Nature* 437, 547–550.
- Wellstein, C., Schröder, B., Reineking, B., Zimmermann, N.E., 2011. Understanding species and community response to environmental change – a functional trait perspective. *Agric. Ecosyst. Environ.* 145, 1–4.
- Wellstein, C., Chelli, S., Campetella, G., Bartha, S., Galiè, M., Spada, F., Canullo, R., 2013. Intraspecific phenotypic variability of plant functional traits in contrasting mountain grasslands habitats. *Biodivers. Conserv.* 22, 2353–2374.
- Wellstein, C., Campetella, G., Spada, F., Chelli, S., Mucina, L., Canullo, R., Bartha, S., 2014. Context-dependent assembly rules and the role of dominating grasses in semi-natural abandoned sub-Mediterranean grasslands. *Agric. Ecosyst. Environ.* 182, 113–122.
- Werger, M.J.A., van Staalduinen, M.A. (Eds.), 2012. *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Springer, Dordrecht.
- Wesche, K., Treiber, J., 2012. Abiotic and biotic determinants of steppe productivity and performance – a view from Central Asia. In: Werger, M.J.A., van Staalduinen, M.A. (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Springer, Dordrecht, pp. 3–43.
- White, R.P., Murray, S., Rohweder, M., 2000. *Pilot Analysis of Global Ecosystems: Grassland Ecosystems*. World Resources Institute, Washington, DC.
- Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. *J. Veg. Sci.* 23, 796–802.
- World Resources Institute (Ed.), 2005. *Ecosystem and Human Well-being: Biodiversity Synthesis – A Report of the Millennium Ecosystem Assessment*. World Resources Institute, Washington, DC.
- Zeiter, M., Stampfli, A., 2012. Positive diversity–invasibility relationship in species-rich semi-natural grasslands at the neighbourhood scale. *Ann. Bot. (Lond.)* 10, 1385–1393.

- Zeiter, M., Preuschkas, J., Stampfli, A., 2013. [Seed availability in hay meadows: land-use intensification promotes seed rain but not the persistent seed bank.](#) *Agric. Ecosyst. Environ.* 171, 55–62.
- Zobel, K., Liira, J., 1997. [A scale-independent approach to the richness vs biomass relationship in ground-layer plant communities.](#) *Oikos* 80, 325–332.
- Zobel, M., 1992. Plant species coexistence – the role of historical, evolutionary and ecological factors. *Oikos* 65, 314–320.
- Zonneveld, I.S., 1994. [Vicinity and mass effect.](#) *J. Veg. Sci.* 5, 441–444.
- Zulka, K.P., Abensperg-Traun, M., Milasowszky, N., Bieringer, G., Gereben-Krenn, B.-A., Holzinger, W., Hölzler, G., Rabitsch, W., Reischütz, A., Querner, P., Sauberer, N., Schmitzberger, I., Willner, W., Wrabka, T., Zechmeister, H., 2014. [Species richness in dry grassland patches in eastern Austria: a multi-taxon study on the role of local, landscape and habitat quality variables.](#) *Agric. Ecosyst. Environ.* 182, 25–36.