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Coexistence of plant species in fragmented landscape

Ph.D. Thesis

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Annotation

Semi-natural grasslands are hotspots of biodiversity in the present-day landscape. The thesis focuses on various effects and processes affecting plant species coexistence at two different scales. At the local scale, the effects of management and fertilization were assessed in relation to abiotic gradients and species functional traits. At the landscape scale, the patch spatial configuration, land use and plant functional traits may influence species distribution. The diversity pattern in fragmented landscape is also modified according to availability of suitable patches and landscape heterogeneity.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

Májeková, M., Janeček, Š., Mudrák, O., Horník, J., **Janečková, P.**, Bartoš, M., Fajmon, K., Jiráská, Š., Götzenberger, L., Šmilauer, P., Lepš, J. & de Bello, F. (2016). Consistent functional response of meadow species and communities to land-use changes across productivity and soil moisture gradients. Applied vegetation science, 19(2), 196-205. (IF= 2.331)

PJ participated in data collection in the field and manuscript preparation.

Janečková, P., Janeček, Š., Klimešová, J., Götzenberger, L., Horník, J., Lepš, J., & de Bello, F. (2017). The plant functional traits that explain species occurrence across fragmented grasslands differ according to patch management, isolation, and wetness. Landscape Ecology, 32(4), 791-805. (IF=3.833)

PJ was responsible for making the GIS layer from field data, statistical analyses and writing the manuscript.

Janečková, P., Janeček, Š., Horník, J., Klimešová, J. Effects of grassland fragmentation and management on community-specific taxonomic, functional and phylogenetic diversity. (manuscript)

PJ was responsible for making the GIS layer from field data, statistical analyses and writing the manuscript.

Contents

Chapter I

General Introduction

Grasslands in present-day landscape

In present, predominantly agricultural landscape of Central Europe, remaining semi-natural grasslands are considered to be the most species richest habitats and biodiversity hotspots in landscape matrix (Kull & Zobel 1991; Poschlod & Wallis De Vries 2002; Wilson et al. 2012, Chytrý et al. 2015). These grassland habitats were are maintained by human activities, mostly by low-intensity grazing or mowing since the Neolithic period (Hejcman et al. 2013) and they continue to be dependent on this traditional management (Křenová & Lepš 1996, Dengler et al. 2014). However, during the last century, such extensive management activities became less common and remaining grassland fragments are endangered by many processes that cause the species loss and decrease of the biodiversity.

At the local scale, the most important processes are fertilization, cessation of regular management and changes in water regime. Increased agricultural intensification is linked especially to increased fertilization that changes the competition in plant communities. These excessive nutrients support mostly high, dominant species with rapid growth and consequently lead to local extinction of less competitive species and loss of biodiversity. Similar consequences for former extensively managed grasslands has the management cessation. When both factors, eutrophication and abandonment co-occur the negative changes in species composition and structure of semi-natural grasslands are even faster (Janeček et al. 2013).

At the landscape level, it is especially fragmentation and related loss of the total grassland area, decreasing patch area and loss of their connectivity. New barriers between neighboring patches and the establishment of large blocks of monocultures that are more suitable for agricultural technics, impair dispersal of species and the landscape is losing the habitat connectivity and heterogeneity important for maintaining plant population metacommunities.

Another factor influencing grassland diversity is the change of hydrological conditions at the site (Prach 2008). For example, in Czechia around one-tenth of the landscape (Prach 2015) and in Hungary even 74% of wetlands were drained for agriculture (Green 1978). Worldwide more than 50% of the wetland area was lost since 1900 (Davidson 2014). The soil moisture is linked not only to the water supply of community but may influence the species composition, biomass production, decomposition (Galvánek & Lepš 20+) or nutrient accessibility (Araya et al. 2013).

Fragmentation

The fragmentation is seen as one of the biggest threat for biodiversity at the landscape scale. It is generally accepted that the remaining habitat fragments in the landscape matrix can be seen as true islands based on the Theory of Island Biogeography (MacArthur & Wilson 1967, Haila 2002). According to this theory, both, size of islands corresponding to remaining habitat patches and their isolation can contribute to different colonization and extinction rates along the fragmentation gradient (Brown & Lomolino 2000). In the process of fragmentation originally large and continuous habitats are divided into smaller habitat patches and fragments become more isolated. Newly created barriers then obstruct plant propagule to spread as well as lower the probability of recolonization suitable patches (Dupré & Ehrlén 2002, Soons 2003, Ozinga et al. 2009). In consequence, plant populations shrink and become disconnected. This has a strong impact on species survival at the regional level (Jacquenym et al. 2002, 2003).

The effects of fragmentation for plant species can be divided into ecological and genetic consequences and are often studied separately (Leimu et al. 2010). Ecological consequences are represented by the higher probability of extinction because of small population size or due to changed environmental conditions in isolated patch or due to increasing edge effect with decreasing patch area. Fragmentation also disrupts relationship among organisms like decreased pollinator movement among the fragments and less attractiveness of smaller population (Xiao et al. 2016, Becker et al. 2011, Potts et al. 2010) or loss of seed disperser (Auffret & Cousins 2013). Genetic consequences for plant populations represent reduced genetic variation and mutation accumulation that result in increased threats of inbreeding depression and consequently reduced fitness in smaller populations (Young et al. 1996, Leimu et al. 2006). The low genetic diversity also increases sensitivity to stochastic events and prohibit adaptability to changing environment.

Spatial effects of fragmentation on species diversity are reduced area, increased isolation and increased edge effect (Aavik et al. 2013, Fahrig 2003, Brudwig et al. 2015, Gieselman et.al. 2013, Niemandt & Greve 2016). However, most of these spatial effects are acting at the same time and to disentangle the individual impact of each is difficult (Fahrig 2003, Smith et al. 2009, Haddad et al. 2015). We can use more than 40 spatial measures when evaluating landscape fragmentation and landscape heterogeneity (McGarigal et al. 2012, Wang et al. 2014). And most of these metrics are strongly correlated to habitat amount metrics (Wang et al. 2014). That's why Fahrig (2013) replaced both main effects of fragmentation, the patch area and patch isolation, with a single predictor, the habitat amount. However, empirically it was shown that Island biogeography theory was even better than this habitat amount hypothesis in predicting plant specialist presence or species richness in grassland fragments (Haddad et al. 2017, Lindgren & Cousins 2017). At the patch level acts another spatial effect often linked to fragmentation - the edge effect, which describes the different abiotic and biotic conditions for species surviving along the patch edges compared to patch core area (Hansen et al 1992, Laurance et al. 2007). This effect, however, could be different for specialist and generalist species (Harrison 1997).

Still, the loss of total habitat area and decreased size of individual patches are the most commonly reported reasons for species richness decline, as describe the well-known relationship between area and number of species (Arrhenius 1921, Gleason 1922, Horník et al. 2012). On the other hand, the fragmentation per se, dividing larger areas into smaller pieces, has been recognized by many studies to have a neutral or even positive effect on biodiversity (reviewed by Fahrig 2003, 2017) often as a consequence of increased landscape heterogeneity and therefore the detrimental effect of fragmentation per se is recently considered to be a „zombie" idea that has been refuted many times but still survives (Fahrig et al. 2019).

Functional traits

The effect of landscape fragmentation may be evaluated by means of functional traits. Functional traits are defined as species indigenous characteristics that influence the species performance and are directly or indirectly linked to fitness (Cornelissen et al. 2003, Violle et al. 2007) and underlie important functions of the ecosystem (Violle et al. 2007, Diaz et al. 2013, Lavorel & Garnier 2002). This duality is reflected in the description of response and effect traits. Response traits are those associated with species response to environmental conditions (e.g. growth form) and effect traits are those related to ecosystem functions (e.g. flammability) (Suding et al. 2008, Violle et al. 2007, Diaz et al. 2013). However, the same trait could be seen as both the response and effect trait. Traits mediate plant species coexistence at different scales and are a better tool than species identity itself for generalization how diversity changes along environmental gradients. However, it assumes that traits in consideration are those with the strongest impact on species performance and ecosystem functioning (Walker et al. 1999). Two decades ago Westoby (1998) proposed a scheme based on three important functional traits (plant height, seed mass and specific leaf area) and linked to fundamental plant life processes (persistence, dispersal and establishment). Later, more other traits have been revealed to be of importance and most of them were systematically gathered in large databases such as LEDA (Kleyer et al. 2008), BiolFlor (Klotz et al. 2002), D^3 (Hintze et al. 2013), Clo-Pla (Klimešová et al. 2017). Because the interaction of functional traits with abiotic conditions and spatial configuration of the habitat patches has a predictive power for species diversity (Mayfield et al. 2010), many studies used the functional traits to explain the species occurrence along environmental gradients (Moraes et al. 2016), in relation to land-use (Garnier et al. 2007, Velbert et al. 2017), spatial configuration of landscape (Miller et al. 2018) or evaluation of community assembly rules (Batalha et al. 2015, Chalmandrier et al. 2017).

The species in the regional species pool, the set of species present in the surrounding landscape, are filtered to suitable habitat patches according to their dispersal and competitive ability. For example, isolated communities can support species with good dispersal ability, e. g. light seeds (Westoby et al. 1996, Helsen et al. 2013), high releasing height (Soons et al. 2004) and low terminal velocity (Jongejans & Telenius 2001). In patches where competition is the main factor shaping the community, filtering prefer species that are high, have a good vegetative propagation ability to persist on the spot or/and a long lifespan (Lindborg 2007, Lindborg & Eriksson 2004, Bossuyt & Honnay 2006). Moreover, results of forest herbaceous species indicate that common and rare species may be threatened differently by fragmentation depending on their specific life history characteristics (Kolb & Diekmann 2005) but no such difference was found regarding species of calcareous grasslands (Römermann et al. 2008).

Management and productivity

Most seminatural European grasslands are very competitive communities that depend on appropriate management activities to maintain high species richness. The Intermediate Disturbance Hypothesis assumes the highest species diversity under intermediate frequencies or intensities of disturbances by reducing species density (Grime 1973, Petraitis et al. 1989). Such medium intensity disturbance can be seen the regular management usually applied to grasslands, typically mowing or extensive grazing, that determines the small scale diversity (Cousins at al. 2009, Pykälä et al. 2005). The main mechanism underlying the loss of species after the abandonment and fertilization was recognized the competition for light (Hautier et al. 2009, Rajaniemi 2003). In case of appropriate management, removing relatively more biomass of taller and larger species causes a shift in aboveground competition and enables the coexistence of strong competitors as well as subordinate species with lower competitive ability. At the same time, the small scale disturbances caused by grazing animals or mowing tools increase the environmental heterogeneity and make gaps in vegetation suitable for successful seedling establishment (Špačková & Lepš 2004, Vítová & Lepš 2011). The removal of the biomass enhances nutrient export and favors species adapted to nutrient-poor conditions which would be otherwise outcompeted by tall and fast-growing species (Lepš 1999). Therefore, the management cessation represents a threat to the species richness as secondary succession, encroaching of shrubs again increases the competition for light and lead to the exclusion of smaller and short-living species. And following litter accumulation inhibits seedling recruitment (Galvánek & Lepš 2008) and select species with heavy seeds that are more likely to establish below the thick litter layer (Křenová & Lepš 1996) especially in wet conditions when the productivity is high (Loydii et al. 2013).

The next factor influencing the biodiversity in grassland communities is the productivity level. The hump-shaped pattern of the relationship between species richness and productivity was first described by Grime (1973) with increasing richness at low to intermediate level of productivity and decreasing at higher levels. This general relationship was supported by many studies, but failed in others (Grace et al. 2007, Gillman & Wright 2006, reviewed by Mittlebach et al. 2001, Rajaniemi 2003), which suppose may indicate a scale-dependent relationship (Gillman & Wright 2006). Across biomes the diversity generally increases with productivity while at the local scales the pattern is less consistent (Grace et al. 2007, Gillman & Wright 2006, Adler et al. 2011) suggesting that other factors such the disturbance, heterogeneity or regional history may influence the diversity pattern more strongly than the productivity level (Fukami & Morin 2003, Zobel & Pärtel 2008, Ma et al. 2010, Adler et al. 2011). In grassland communities, Wilson & Tilman (1993) described the shift from belowground to aboveground competition along the productivity gradient. The aboveground competition probably underlies the often reported decrease in diversity after fertilization (Galvánek & Lepš 2008, Liira et al. 2012, Humbert et al. 2018, Kotas et al. 2017, Stevens et al. 2010), however, available species pool and distribution of functional trait of dominant species modify the speed of the species decrease (Gross & Mittlebach 2017). Clonal and tall species are the winners, especially when the productivity and moisture levels are high (Klimešová et al. 2008, Janeček et al. 2013). By decreasing the species number eutrophication weakens the stabilizing effect of diversity in grasslands with large consequences for ecosystem services (Hautier et al. 2014).

Diversity measures

Explaining the mechanisms underlying species coexistence is fundamental for understanding the maintenance of biodiversity at a local scale and the effects of biodiversity on ecosystem functioning. It is generally assumed that more diverse communities support the temporal stability in ecosystems than less diverse ones (Allan et al. 2011).

The biodiversity is evaluated by means of various measures, however, the choice of diversity metrics affect the interpretation of diversity. If the assessment of diversity across scales is needed, we use the concept of alfa, beta, gamma diversities (Whittaker 1960, 1972), where alfa is the within community component, beta component refers to between-communities diversity and gama is the landscape level diversity. However, in this case usually the simplest and most cost-efficient measure, the species richness is used. Other diversity indices describe not only the richness part linked to presence data but include often the evenness, the measure that considers the individual species abundance and shows how evenly the species in the community are distributed. Both richness and evenness are then incorporated into Shannon (Shannon & Weaver 1949; Strong 2016) and Simpson indices (Simpson 1949).

Recently it was recognized that not only taxonomic diversity but also diversity based on functional traits and phylogeny should be considered (Nipperess et al. 2010, Funk & Wolf 2016, Barber et al. 2017, Winter et al. 2013). As taxonomical measures treat all the species in the same manner, phylogenetic consider the history and the evolutionary relatedness among species in detail and functional diversity links the main functions of the community and species with their functional traits.

When only presence data are used, they reflect the species turnover, new coming and extinct species, so their sensitivity to changing environment is blurred by the phenomenon of extinction debt (Helm et al. 2006; Kuussaari et al. 2009; Krauss et al. 2010, Lampinen et al. 2018). When abundance-weighted measures are considered they reflect also changes in species populations and can also provide deep insight into assembly rules of communities. However, the redundancy in functional traits or phylogenetic lineage prevents the immediate loss of functions when species richness decreased (Walker et al. 1999).

Because most of the diversity measures are correlated, researches debate the possibility of using one part of the diversity as a surrogate for another facet. However, the results are ambiguous. For example, Verdú et al. (2012) recommended phylogenetic diversity as a cost-efficient proxy of functionality to monitor restoration and Flynn et al. (2011) found that phylogeny explains more than species richness or functional diversity in variation of grassland productivity. On the other hand, Venail et al. (2015) claim that phylogenetic diversity is not better than species richness in predictions of grassland functioning and Lososová et al. (2016) suggest that the phylogeny is a weak proxy for functional diversity of urban plant communities. Some studies support using of more complementary diversity measures. For example, Almeida et al. (2018) advocate that species richness should be used as a complementary measure together with functional diversity for ecosystem managing. These contrasting results indicate that the relationships among various diversity metrics may be community specific as found for instance by Morelli et al. (2018) across common landscape environments - farmland, grassland, and forest.

Individual biodiversity measures can be also differently affected by various processes such as environmental filtering under different habitat conditions or/and by changed competition because of the disturbance and management. Giehl (2015) revealed that the flooding influences more the taxonomy, while different soil conditions have a higher impact on functional and phylogenetic diversity. An experiment in the alpine hay meadow shows highest diversities at moderate irrigation and fertilization level (Lessard-Therrien et al. 2017). Other studies detect the impact of different management practices on diversity, reflecting rather in functional and phylogenetic measures than in species richness solely (Rader et al. 2014, Mauchamp 2014).

Model landscape and methods

During the 20th century, the landscape of the Czech Republic underwent large changes in management. During the communist time (1948-1989) small strips of fields were unified into large fields more intensively managed and fertilized. The percentage of forest area slightly increased. A large amount of extensively managed grasslands was abandoned or even afforested which led to condition deterioration, fragmentation, and loss of species diversity. All these changes decrease the heterogeneity of the landscape and connectivity of grassland patches (Fig. 1). The lower heterogeneity in the matrix means also lower heterogeneity in management timing. Since the 1990s the land came back to the hands of private owners and the agriculture were transformed. Many former fields were conversed back to the grasslands, sometimes by means of spontaneous succession, but mostly by sowing species-poor commercial mixtures with high productive species. Some attempts were also made to use for grassland restoration regional species-rich mixtures (Jongepierová et al. 2007). However, many grassland patches of high value became highly fragmented within the landscape and do not support the good metapopulation dynamics of grassland species (Hemrová & Münzbergová 2015).

All studies included in this thesis were carried out in the landscape of central Bohemia, in an area of 385 km2 (26,5 km x 15 km). The region includes a large portion of Železné hory Protected Landscape Area and partly Žďárské vrchy Protected Landscape Area. The elevation ranges from 268 to 668 m a.s.l. and the mean annual precipitation from 550 to 850 mm. The landscape consists of a matrix of arable land, forests, urban areas, intensive used meadows and fragments of semi-natural grasslands. Their percentage in our selected region is higher (3.43%) than in the whole Czech Republic (1.89%) (calculated from GIS data provided by AOPK). These patches of grasslands vary considerably in productivity, moisture, soil reaction and often suffer from fertilization and/or management abandonment. Seventy years ago the landscape was a fine matrix of small fields, forest patches urban area and extensively used grasslands (Fig. 1A) compared to current conditions (Fig. 1B). However, many of these meadows were afforested, plowed into fields, abandoned or the management shift from extensive to intensive by adding artificial fertilizers or sowing species poor seed mixtures to increase productivity. There were identified 1307 distinct grassland patches in this area and their community composition was surveyed and the relative species abundance using Braun-Blanquet scale for the whole patch was estimated (Chapter III-IV). The patches were categorized according to their abiotic conditions and species composition to distinct grassland types. Their spatial characteristics as patch area and connectivity were calculated from GIS layer created on the field-work basis.

Wet meadows were the most common type of semi-natural grassland in our model landscape. They are often hot spots of local biodiversity and provide important ecological services such as water retention. At the same time, they are sensitive to ongoing land-use changes such as management intensification or management cessation. To study the changes in community composition in response to management and fertilization at the local scale, an experiment with baseline data on 17 wet meadows was carried out within the model landscape (Chapter II). On each site, one permanent plot containing eight blocks with four treatment combinations was established. The combinations of treatments were: mown+fertilized, mown+unfertilized, unmown+fertilized, unmown+unfertilized. The phytosociological releveés documenting the community composition were sampled first before the experimental treatments were applied and then every two years (2009, 2011, 2013) in the same phenological phase.

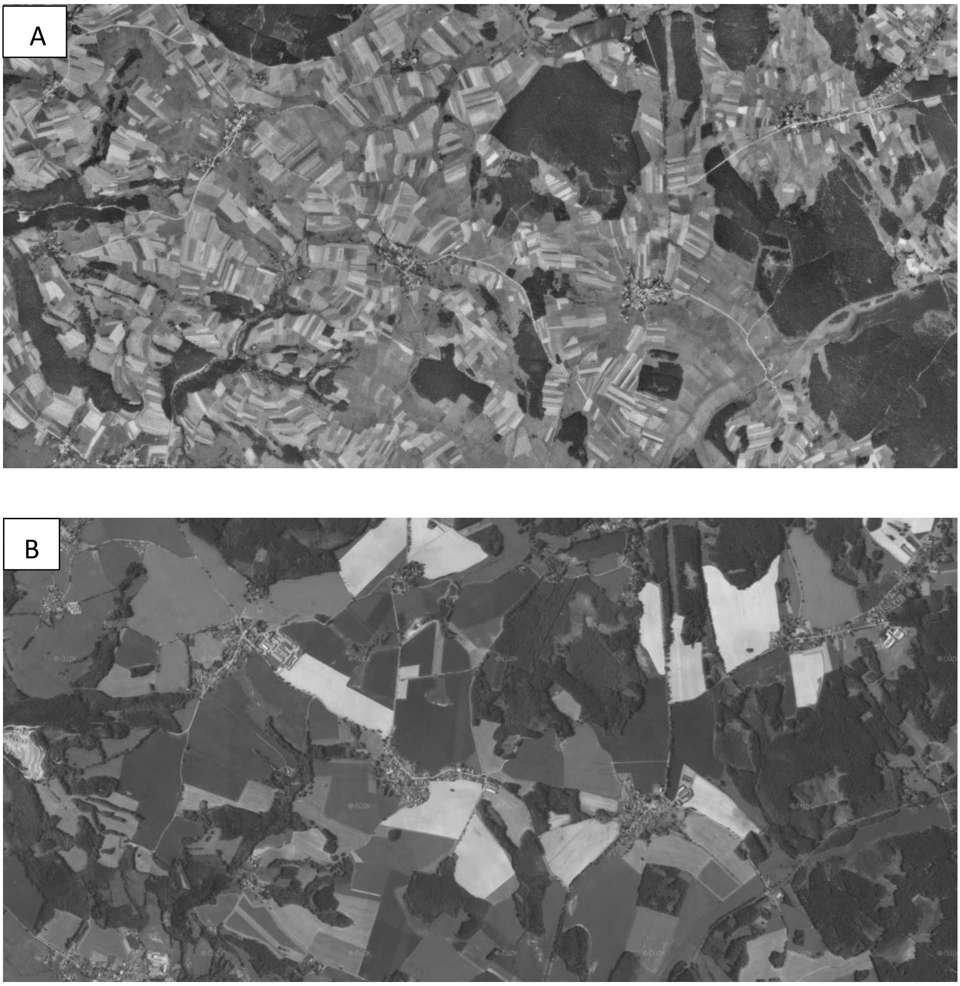

Fig 1. Orthophoto maps of the same piece of landscape fragment (A) in 1953 and (B) in 2015 showing as fine scale mosaic of the landscape changed lo large scale one due to agricultural intensification.

Objectives of the study

The main aims of the study were to explore which factors drive the plant species coexistence at the local scale and how is the species survival at the landscape scale influenced by factors acting at both, the landscape and patch level. I asked these questions:

(i) if functional traits can predict the community changes caused by fertilization and/or abandonment under various productivity and moisture conditions.

(ii) what is the effect of patch characteristics and indigenous plant traits on species occurrence in the present-day landscape.

(iii) how the diversity patterns based on the taxonomy, functional traits and phylogeny are influenced by landscape structure (size and connectivity of grassland patches) and management activities, whether these patterns change in different grassland communities.

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Chapter II

Consistent functional response of meadow species and communities to land-use changes across productivity and soil moisture gradients

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Consistent functional response of meadow species and communities to land-use changes across productivity and soil moisture gradients

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Abstract

Questions: Wet meadows have traditionally been managed at low intensity, promoting the co-existence of a variety of plant species. The remaining fragments of these meadows are now being degraded by either mowing abandonment or by agricultural intensification, such as increased fertilization. We tested the theoretical expectation that certain functional traits can explain vegetation changes along gradients of productivity and soil moisture in response to these land-use changes.

Location: Železné hory Mts., Czech Republic, Central Europe

Methods: We set up a long-term experiment where we applied a full factorial design of fertilization and abandonment to 17 traditionally mown wet meadows covering a broad range of productivity and soil moisture conditions found within the region. Plant functional traits that cover different aspects of plant ecological strategies – plant height, specific leaf area (SLA), leaf dry matter content (LDMC), seed mass and clonality – were used to explain both species and whole community response to land-use change. We employed linear mixed effect models to test for the consistency of functional changes across different productivity and soil moisture conditions.

Results: We found that the functional response of species and whole communities to land-use change was consistent across meadows differing substantially in their productivity and soil moisture. Specifically, irrespective of the local conditions, both fertilization and abandonment selected for tall species within communities, highlighting the effect of increased competition for light. Traits related to a more exploitative strategy in species (higher SLA, more prominent clonal growth and smaller seeds) were consistently favoured with increased fertilization.

Conclusions: We show that within a given region with a common land-use his- tory, certain functional traits consistently explain and can help to predict changes in plant communities caused by land-use change, irrespective of different productivity and soil moisture conditions. Our results demonstrate a simple way to use functional traits in applied nature conservation. We hope this will encourage practitioners to use functional traits to complement existing knowledge on composition and productivity of considered habitats to enhance the planning of management practices. We encourage practitioners to build regional trait databases to actively use trait information for the purpose of habitat management.

Keywords

Competition; Exploitative strategy; Fertilization; Functional traits; Mowing abandonment; Plant height; Specific leaf area; Vegetation changes

Introduction

Wet meadows have traditionally been managed by low-intensity mowing that promotes the co-existence of a wide variety of plant species (Lepš 1999; Wilson et al. 2012). However, today the last fragments of these meadows are among the communities most threatened by land-use change, while at the same time representing hotspots of biodiversity (Isselstein et al. 2005; Lepš 2014). Over the last decades, management of wet meadows has shifted towards either intensification of their productivity via increased fertilization or towards their abandonment by cessation of traditional mowing (Klimešová et al. 2010). These changes alter resource availability as well as disturbance regimes in plant communities, and thus may trigger considerable changes in species composition and a general decrease in biodiversity. An open challenge remains to find suitable indicators and tools to predict the response of plant communities to land-use changes and to generalize results beyond specific locations and taxa. It has been advocated that simple plant functional traits are useful to predict which types of species are going to be favoured, or not, by changes in land-use management (Díaz et al. 1999; Lavorel & Garnier 2002; McIntyre & Lavorel 2007).

It is necessary to understand if and in which cases the predictive power of functional traits can be generalized. While traits have been used to develop indicator systems (de Bello & Mudrák 2013), very few studies have shown that simple traits predict species response to given land-use changes consistently in different regions (Díaz et al. 2001; Garnier et al. 2007). Most studied plant traits have reflected adaptations to both changes in land-use management and to specific site conditions (Díaz et al. 1999, 2007; Vesk & Westoby 2001). The predictive power of traits differs between sites with markedly different climatic conditions or land-use history (Díaz et al. 1999; de Bello et al. 2005; Pakeman et al. 2009). Productivity and soil moisture were also shown to play an important role in defining how well traits predict the effects of land-use change (Kleyer 1999; Osem et al. 2004; Pakeman 2004; Pakeman et al. 2009). The inconsistent response may be attributed to the fact that the pool of functional traits available in a given site changes across different habitats, causing the effect of land-use changes to be contingent upon the ecological strategies available to species (de Bello et al. 2005). For example, if grazing favours annuals in drier areas, but there are few annuals present in temperate habitats, then life cycle as a trait cannot be used as a general predictor.

Nutrient addition and cessation of disturbance (i.e. grazing or mowing) can filter out species with specific functional strategies (Lind et al. 2013; Lepš 2014). As these two filters can select for the same functional strategies in species, predictions may also be contingent upon their specific combinations. Most studies have focused on management by grazing (Díaz et al. 1999; Vesk & Westoby 2001; Pakeman 2004; de Bello et al. 2005), and relatively few studies have assessed the effect of mowing on plant traits (e.g. Louault et al. 2005; Römermann et al. 2009). While grazing is extremely variable because of different types of grazers, grazing intensity and grazing selectivity, mowing is easier to control and standardize, and could therefore provide more consistent predictions. Mowing has a stronger effect on taller species, as these lose higher proportions of above-ground biomass compared to short species (Klimešová et al. 2010), and the effect should be more pronounced in more productive and wetter conditions, where vegetation is naturally taller (see schematic summary in Fig.1a).

We have considered a set of functional traits that relate to different dimensions of plant ecological strategies and can be easily measured for many different species (Cornelissen et al. 2003; Laughlin 2014): plant height, specific leaf area (SLA), leaf dry matter content (LDMC), seed mass and capacity for clonal growth (hereafter referred to as 'clonality'). Regular disturbance, such as mowing, directly influences the light availability in plant communities, and plant height is linked to competition for light (Keddy & Shipley 1989). Therefore, we expected plant height to be affected by mowing abandonment. Fertilization enhances the nutrient availability for plants, and therefore can cause a shift of plant communities' functional composition along the resource acquisition trade-off. SLA and LDMC are the traits most involved in the trade-off between rapid nutrient uptake and nutrient conservation (e.g. Wright et al. 2004). Both leaf traits are also regarded as predictors of soil fertility (Hodgson et al. 2011 and references within), thus, we expected them to be related to increased fertilization management. By altering light and/or nutrient availability, both the spatial structure and the biotic interactions change as well. Thus, traits related to the competition in plant communities might prove to be important for predicting species responses to land-use changes.

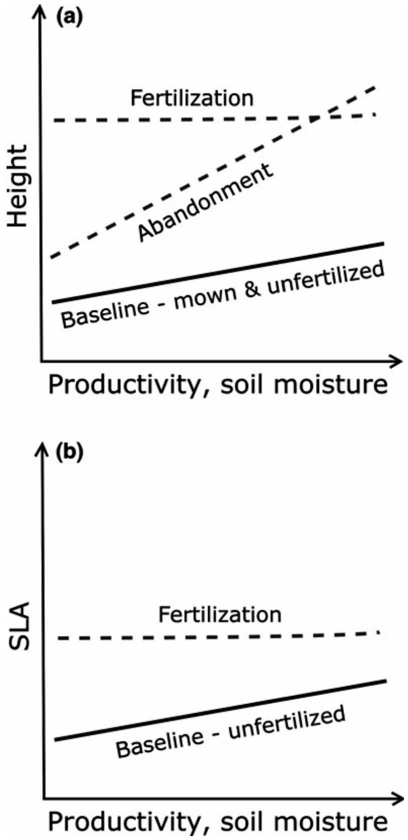

Fig. 1. A conceptual figure depicting our hypotheses that (1) the effect of fertilization on the functional response of plant height is more pronounced in the less productive and/or drier conditions and the effect of abandonment on the functional response of plant height is more pronounced in the more productive and/or wetter conditions, whereas (2) the effect of fertilization on the functional response of SLA is more pronounced in the less productive and/or drier conditions.

Besides plant height, seed mass is linked to the competition–colonization trade-off in plant communities (Westoby 1998). Clonality represents the ability of species to spread vegetatively (Klimešová et al. 2011) and has been related to the space acquisition strategy (Weiher et al. 1999).

We aimed to provide an insight into the effects of land-use management and environmental differences between sites on functional responses of species and communities. We set up a long-term experiment where we applied fertilization and abandonment to a variety of traditionally mown wet meadows over gradients of productivity and soil moisture. We expected (1) abandonment to alter light conditions in favour of competitively stronger, i.e. taller, species (Keddy & Shipley 1989). We expected (2) fertilization to enhance the nutrient availability for plants and therefore to cause a shift of plant communities' functional composition along the resource acquisition trade-off axis towards more exploitative plant strategies, e.g. expressed by less tough leaves (Wright et al. 2004), and towards competitively stronger strategies, e.g. expressed by taller species (Keddy & Shipley 1989). We also tested the hypothesis (3) that different levels of productivity and soil moisture will modify the predictive power of individual traits. We expected plant height to better explain community changes caused by abandonment in more productive and wetter communities, where tall species already dominate, and a lower effect of fertilization on plant height in the same conditions (Fig. 1a). We also expected that traits related to a more exploitative strategy would better explain the changes in the communities caused by fertilization in less productive and drier conditions, where fertilization should have larger potential for changes in the community (Fig. 1b).

Methods

Study site

The study area is located in the Železné hory Mts. (east Bohemia, Czech Republic) at an elevation of 340–620 m a.s.l. Wet meadows persist in this region as small patches in a landscape consisting mainly of arable land, forests, cultural meadows and urban areas (see Klimešová et al. 2011 for a map of the area). Seventeen meadows were selected that (1) represented a semi-natural, traditionally mown type of wet meadow, and (2) differed in species composition, productivity and soil moisture, as visually summarized in an RDA diagram in Appendix S1.These meadows belong to four alliances along a gradient of decreasing wetness, commonly referred to in Central Europe as the alliances *Sphagno warnstorfiani-Tomenthypnion, Caricion fuscae, Calthion* and *Molinion*. Characteristic species are represented mainly by graminoids *Agrostis* spp., *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Molinia caerulea*, different species of *Carex* and numerous forbs such as *Filipendula ulmaria*, *Lathyrus pratensis* and *Lysimachia vulgaris* (see also Electronic Appendix 2 in Klimešová et al. (2011) for the full list of species recorded on the sites in 2007 and 2009).

Productivity was measured as the standing dried biomass, clipped from two 1 x 1 m plots on each meadow at the beginning of the experiment in July 2007. It varied substantially across the assessed meadows from 255 to 680 g·m^{-2} (see Appendix S1 for the detailed values for each site). Soil moisture was assessed as the average groundwater depth and ranged from 4 to 64 cm (see Appendix S1 for the detailed values for each site). The measurements were repeated at monthly intervals from Apr to Nov during the years 2008–2010 and the mean values were used for analyses. For more details on the study system see also Klimešová et al. (2011), Horník et al. (2012) and Janeček et al. (2013).

Experimental design

In early spring 2007 two replicate blocks were selected on each of the 17 sites of wet meadows. Within each block four 2 x 2 m plots were established, and in Jul 2007 species cover was recorded to provide baseline data. In a fully factorial design, mowing abandonment (hereafter referred to as 'abandonment') and fertilization treatments were assigned to each block: mown and unfertilized, mown and fertilized, abandoned and fertilized, and abandoned and not fertilized. The mown and unfertilized treatment combination served in subsequent years as a control, as these conditions were traditionally applied and have resulted in the current species composition of these meadows. Fertilizer was applied at 20 g·m^{-2} of granular mineral NPK (10% N, 10% P_2O_2, and 10% K_2O)at the end of Jul 2007, and at 50 gm^{-2} in the second half of Apr in subsequent years. Similar doses of fertilizer are applied in high-intensity managed grasslands within the area. A buffer zone between the plots was established (0.5 m wide). Species cover was then recorded again after 2, 4 and 6 yr (2009, 2011 and 2013, respectively).

Plant functional traits

We used five traits: plant height, specific leaf area (SLA), leaf dry matter content (LDMC), seed mass and clonality. These traits were selected from a broader list of traits available (see Appendix S2) because they: (1) relate to key plant functions (Cornelissen et al. 2003), (2) represent different dimensions of plant variability (Laughlin 2014), (3) are widely used and therefore easier to compare with other studies, and (4) are not strongly correlated (except for leaf traits; see correlation matrix of the full set of traits and PCA of the selected set of traits in Appendix S2). SLA is measured as area of a fresh leaf divided by its dry mass (m^2·kg^{-1}); LDMC is measured as the ratio of leaf dry mass to its fresh mass (g·kg^{-1}; Cornelissen et al. 2003). Although SLA and LDMC were correlated ($r = -0.52$) we used them both, as they are known to contain different biological information (Cornelissen et al. 2003). Trait values for plant height, SLA, LDMC and seed mass were taken from the LEDA database (Kleyer et al. 2008) and seed mass values were log-transformed. Clonality was considered as a categorical predictor distinguishing species that are capable of clonal spread and reproduction (hereafter 'clonal species') and species that are not (hereafter 'non-clonal species'; following CLO-PLA database [Klimešová & de Bello 2009]). Clonal index was also considered as an option to account for species capacity for clonal growth; however, as it yielded results concordant with clonality, the latter was chosen for simplicity in modelling.

Species-level analyses

Prior to the analyses, we quantified the response of each species to treatments over time. To do this, we averaged percentage species cover from the two replicate plots, i.e. with the same treatment, within each of the 17 sites of the wet meadows and year in order to account for site heterogeneity. We calculated the differences in species cover between the plots with a specific treatment combination (abandonment, fertilization, combined abandonment and fertilization) and the control plots within each site and year. Such differences indicated changes in species composition not caused by temporal variability but by management regimes. Subsequently, for each species and site separately, we correlated these differences with time (2007, 2009, 2011, 2013) using Spearman's rank correlation. The correlations then represented the response of a species to the specific treatment combination over time. The correlation coefficient values closer to -1 characterized a constant decrease of species abundance over time in a particular treatment combination compared to the control, whereas values closer to 1 represented constant increase. Values closer to zero represented no net change after 6 yr of the experiment.

We then tested (1) the explanatory power of traits on species response to the applied treatments over time, and (2) the consistency of this relationship along the gradients of productivity and soil moisture. To do so, we employed linear mixed effect models (LMM) with species response to particular treatment (Spearman's correlation coefficients) as the response variables. Species traits, abiotic gradients (productivity or soil moisture in separate models) and the two-way interactions between them were used as fixed factors; site was used as a random factor. For clearer interpretation within the models, we divided the productivity gradient into three categories as less productive, intermediate and productive sites. The thresholds of productivity values were selected as 330 and 480 g·m^{-2}. Similarly, we created three categories within the gradient of soil moisture as wet, intermediate and drier sites with the thresholds of groundwater depth being 15 and 27 cm beneath the surface. The threshold selection reflects the main habitat types within the considered range of productivity and soil moisture conditions in our study system (Appendix S1). This was based on local knowledge of the type of meadows within the region and finally chosen to provide us with as balanced categories as possible. The terms used to describe the individual categories should then be considered within the context of our study system.

All LMM were conducted using the STATISTICA software v 12 (StatSoft, Tulsa, IK, US). We also used linear mixed effect models within the package *lme4* using R software (R Foundation for Statistical Computing, Vienna, AT), which gave very similar results, and therefore are not shown here. We also assessed whether species traits and species response to treatments exhibited a phylogenetic signal using an age-calibrated phylogeny of species (Durka & Michalski 2012) by calculating Pagel's lambda (Pagel 1999; for more details see Appendix S3).

Community-level analyses

At the community level we focused on the changes in the community-weighted mean (CWM) of traits as a function of treatments over time and whether these changes were consistent along the gradients of productivity and soil moisture. CWM of a given trait represents the average of a trait value in a community weighted by species abundances. We computed CWMs for traits for each plot (i.e. 17 sites x 4 plots x 4 yr) using *FD* package in R. We then used LMM, where in each model the CWM of a particular trait was used as the response variable. Fertilization, abandonment, time and abiotic gradient (productivity or soil moisture) were used as categorical predictors. All main terms and two-way interactions were kept in the analyses. From three-way interactions, we were interested in the interaction between treatments, time and abiotic gradients (e.g. changes caused by management over time), therefore the other combinations were omitted to simplify the models. Four-way interactions between treatments, time and abiotic conditions were included to test for the consistency of the community response to treatments over time along productivity and soil moisture gradients. Site was used as a random factor. Interactions of site (random factor) with both time and the interactions between treatment, time and abiotic gradient were included to serve as the error mean square.

Results

Species level

The response of individual species to the applied treatments (fertilization, abandonment of mowing, or combination of both) over time (i.e. Spearman's correlation coefficient of vegetation changes in time with respect to the baseline conditions of mown and unfertilized meadows; see Methods) was significantly related to species height, SLA and clonality (Table 1). Specifically, species with higher SLA, taller species and clonal species increased their abundance with fertilization (Table 1). Taller species increased their abundance with abandonment, and both taller species and species with higher SLA increased their abundance when the abandonment was combined with fertilization (Table 1). Interactions of the selected traits with abiotic gradients (productivity and soil moisture) were not significant for any of the models assessed (Table 1, Fig. 2). This shows that the explanatory power of a particular trait for a particular treatment did not change across different productivity levels and soil moisture conditions. Species response to the treatments was neither phylogenetically conserved when tested in individual sites, nor when averaged over all sites. The strength of the phylogenetic signal of the individual traits within the assembly of species of each site varied slightly with the different community structure over assessed sites (for more detailed information see Appendix S3).

Community level

The CWM of SLA increased with fertilization, and CWM of height increased with abandonment, but not with fertilization as observed at the species level (Table 2). In addition to patterns observed at the species level, CWM of seed mass decreased with fertilization and CWM of clonality was not related to any of the treatments (Table 2). None of the interactions between treatments, abiotic gradients and time were significant (Table 2, Fig. 2), which suggests a consistent functional response of CWMs to the treatments along the abiotic gradients over time.

Table 1. Results of LMM at the species level, where we predicted the species response to treatments (Spearman's correlation coefficient) using species functional traits, abiotic gradients and their interactions. In all of the models, all main terms and two-way interactions were included, but only traits that were selected as significant predictors of species response to treatments are shown in the table together with their insignificant interactions with abiotic gradients, which represent the consistent species response to the treatments along the abiotic gradients of soil moisture and productivity. Treatments: fertilization (F), mowing abandonment (A) or both treatments combined (FA). Abiotic gradients: productivity (P) and soil moisture (SM).

Model	Predictor	*df*	Slope	*F*	*P*
F, P	SLA	1, 753	0.01	23.1	<0.001
	Height	1, 753	0.40	10.8	0.001
	SLA x P	2, 753		0.3	n.s.
	Height x P	2, 753		0.1	n.s.
A, P	Height	1, 724	0.32	15.2	<0.001
	Height x P	2, 724		0.7	n.s.
FA, P	Height	1, 726	0.42	27.7	<0.001
	SLA	1, 726	0.01	8.7	0.003
	Height x P	2, 726		2.9	n.s.
	SLA x P	2, 726		0.8	n.s.
F, SM	SLA	1, 753	0.01	20.5	<0.001
	Clonal	1, 753	0.23	6.9	0.009
	Height	1, 753	0.25	4.9	0.03
	SLA x SM	2, 753		2.5	n.s.
	Clonal x SM	2, 753		0.5	n.s.
	Height x SM	2, 753		4.8	0.009
A, SM	Height	1, 724	0.13	13.9	<0.001
	Height x SM	2, 724		1.5	n.s.
FA, SM	Height	1, 726	0.39	27.6	<0.001
	SLA	1, 726	0.01	7.3	0.007
	Height x SM	2, 726		1.0	n.s.
	SLA x SM	2, 726		0.0	n.s.

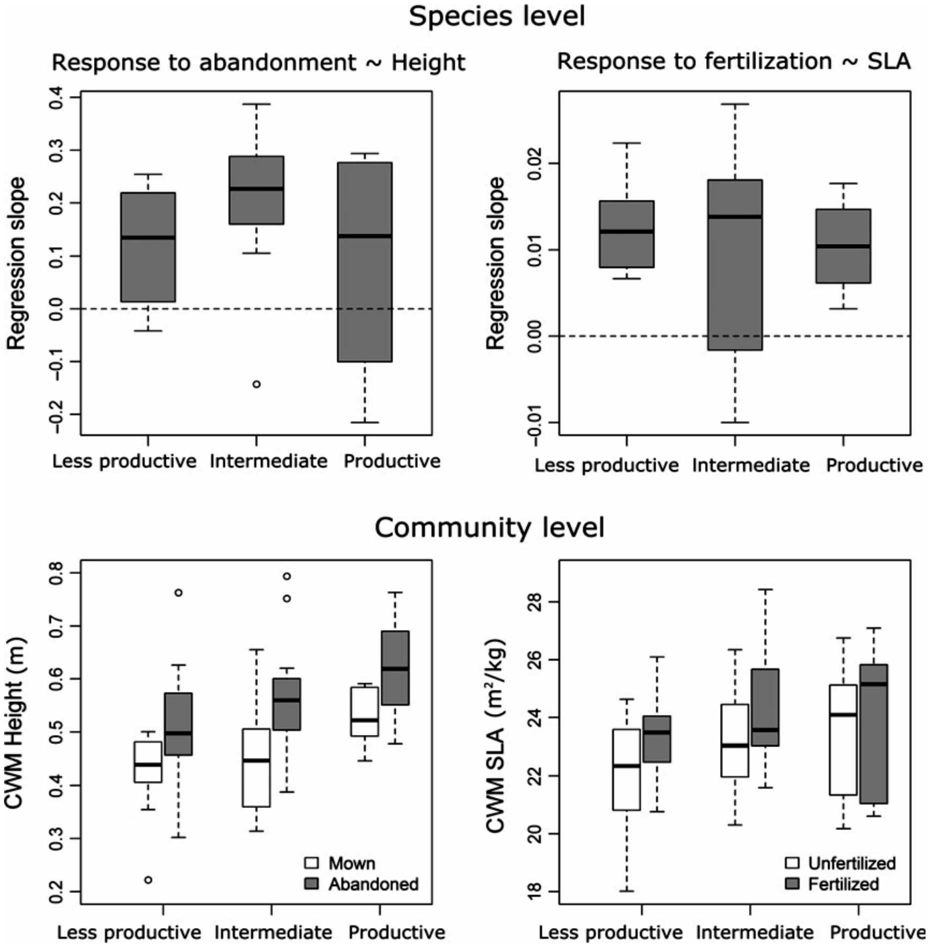

Fig. 2. Boxplots showing the functional responses of species (top panels) and of whole communities (bottom panels) to fertilization (right panels) and to mowing abandonment (left panels) across the productivity gradient. At the species level, the consistency of the functional response is illustrated by comparing the similarity of the regression slopes of LMM (Table 1) between the species response to treatments (Spearman's correlation coefficient) and traits in the three productivity levels. At the community level, the consistency of the functional response is illustrated by comparing the response of the traits CWM (community-weighted mean) to treatments in the three different productivity levels.

Discussion

Consistency of functional response to land-use changes. Our results show that the functional responses of species and whole communities to land-use changes were consistent across meadows differing substantially in their productivity and soil moisture within a region. Congruent results across species- and community-level analyses enhance the robustness of these findings. Interestingly, our results challenge the conclusions reached by several studies that investigated the consistency of functional response to different land-use changes (Kleyer 1999; Osem et al. 2004; Pakeman 2004), as well as our own hypotheses (Fig. 1). We expected the functional response of species and communities to fertilization and mowing abandonment to be contingent upon site productivity and soil moisture. Specifically, we expected a larger potential for change after fertilization in the drier and/or less productive conditions (due to the higher relative change in nutrients) and after abandonment in more productive and/or wetter conditions (larger changes in species composition expected; Fig. 1). However, we found that the functional response to both treatments was consistent along both abiotic gradients – the taller, faster growing and clonal species with smaller seeds were favoured by increased fertilization and abandonment irrespective of the particular baseline site conditions. This did not confirm our initial hypotheses (Fig. 1) and, based on the results presented, we can conclude that within a given region the functional response of both species and communities to fertilization and abandonment is consistent across different site conditions.

Several rationales could explain the consistency of functional response to land-use changes found in our experiment. First, our experimental design was built to encompass different communities within one climatic region in order to minimize the effects of comparing pools of species with different adaptations to major climatic conditions. Therefore, the consistent response we observed was based mostly on differences in the productivity and soil moisture conditions, whereas the inconsistent response observed previously was based mainly on differences in climatic conditions, which can cause bigger changes in the functional pools and thus also in the functional response (Díaz et al. 1999, 2007; de Bello et al. 2005; but see Garnier et al. 2007). Second, the inconsistency of trait responses found previously within one climatic region might be an artefact of aspects of experimental design such as using too small a sample size and too short a time scale, studying only two meadows over 3 yr (Lanta et al. 2011), and other differences in the experimental design applied to individual sites (the intensity and frequency of management or the use of different type of grazers; Pakeman 2004; de Bello et al. 2005; but see Garnier et al. 2007). Our study aimed to eliminate these confounding effects by considering a much larger temporal and spatial range of samples (17 meadows over 7 yr) as well as by applying identical treatments that simulated the land-use changes to each of the sites considered.

Functional response to fertilization and mowing abandonment

Both fertilization and abandonment of mowing caused the selection of species with similar traits within the communities (Table 1). Specifically, species with higher SLA values, a trait related to leaf economics spectrum (Wright et al. 2004), responded with increased abundance to the increase in nutrient availability induced by fertilization. This trend was apparent at both species and community level. A similar trend was observed by Díaz et al. (2004) and Garnier et al. (2007) at the community level where the cessation of fertilization led to a shift in dominance from exploitative species (high SLA) to species with more conservative nutrient economics (low SLA). Additionally, with increased nutrient availability, clonal species and species with smaller seeds were favoured at the species and community level, respectively. All three traits point to a more exploitative strategy of species adapted to conditions with no or little nutrient limitations, and thus to their more rapid uptake and investment in growth (Wright et al. 2004; Moles et al. 2005; Dickson et al. 2014). The response of plant height at the species level to both fertilization and abandonment highlights the joined effect of these two treatments, i.e. taller species responded to

Table 2. Results of LMM at the community level, where we predicted community-weighted mean (CWM) of traits by treatments, time, abiotic gradients and their interactions. In all the models, all main terms, all two-way interactions, three-way interactions between treatments, time and abiotic gradients, and four-way interactions between treatments, time and abiotic conditions were included. This table presents only significant models; therefore models with LDMC and clonality are not shown. From all the main terms and interactions, we focus here on presentation of the effect of fertilization and abandonment on community response to these treatments and on the insignificant interactions of treatments with time and abiotic gradients, which represent the consistent functional response of traits' CWM to the treatments along the abiotic gradients. Treatments: fertilization (F), mowing abandonment (A). Abiotic gradients: productivity (P) and soil moisture (SM).

Model	Predictor	*df*	*F*	*P*
P, Height		1, 56	4.3	0.04
		1, 56	42.6	<0.001
	F x P x Time	6, 56	1.0	n.s.
	A x P x Time	6, 56	0.1	n.s.
P, SLA		1, 56	14.0	<0.001
		1, 56	11.1	0.002
	F x P x Time	6, 56	0.7	n.s.
	A x P x Time	6, 56	1.1	n.s.
P, Seed mass		1, 56	5.3	0.03
	A	1, 56	5.6	0.02
	F x P x Time	6, 56	1.8	n.s.
	A x P x Time	6, 56	0.2	n.s.
SM, Height	F	1, 56	5.0	0.03
	A	1, 56	46.0	<0.001
	F x SM x Time	6, 56	0.5	n.s.
	A x SM Time	6, 56	0.2	n.s.
SM, SLA	F	1, 56	17.3	<0.001
	A	1, 56	12.9	0.001
	F x SM x Time	6, 56	1.7	n.s.
	A x SM x Time	6, 56	0.8	n.s.
SM, Seed mass	F	1, 56	4.3	0.04
	A	1, 56	4.6	0.04
	F x SM x Time	6, 56	0.4	n.s.
	A x SM x Time	6, 56	0.7	n.s.

both increased nutrients and changes in light availability. When both treatments were applied together, the explanatory power of plant height as a predictor increased, suggesting increased competitive strength of taller species. These findings support the hypothesis that nutrient addition and cessation of disturbance favour species with similar functional strategies (Lind et al. 2013; Lepš 2014). These results might be of particular interest in the scenario of meadow abandonment with the increase in atmospheric nutrient deposition, which should reinforce each other in the increase of above-ground competition between plants.

Implications for nature conservation and management

We posit that for applied nature conservation, our results show that simple plant functional traits can be used to explain species and communities´ responses caused by land-use changes within a given regional species pool. We suggest that using traits can help to complement the knowledge of local practitioners regarding composition, productivity and abiotic conditions of the considered habitats, and enable the development of management schemes that are based on the combination of all this information. For example, the trait plant height is already widely used as an indicator of grassland status (de Bello et al. 2010). Data on functional traits on most of European species are freely available in databases (e.g. LEDA, BiolFlor), meaning that one does not have to spend time collecting such data, and we show that using such data is feasible, making it a cost-effective and useful potential tool for practitioners. Nevertheless, it would be very beneficial if practitioners would build regional databases where they can combine existing data with a few easily measurable traits (as plant height, leaf traits, seed mass, clonality) and complement this information with more specific functional traits that could be relevant for the specific vegetation and habitats available within a region.

Conclusions

Consistent indicator systems to predict changes in meadow vegetation are increasing in importance for habitat management (de Bello et al.

2010; de Bello & Mudrák 2013). Existing theories about functional traits posit that predictions derived from given traits cannot be easily generalized beyond locations. Our results challenge this view and suggest that earlier inconsistencies across studies might have derived from considering contrasting climatic regions or different management changes. On the contrary, predictions within a given region, even covering a set of different productive and moisture conditions, were found to be consistent, suggesting that consistent indicator systems could be established within given landscapes, such as protected areas or national parks.

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Supporting Information

Appendix S1. Differences among sites at the baseline time of the experiment.

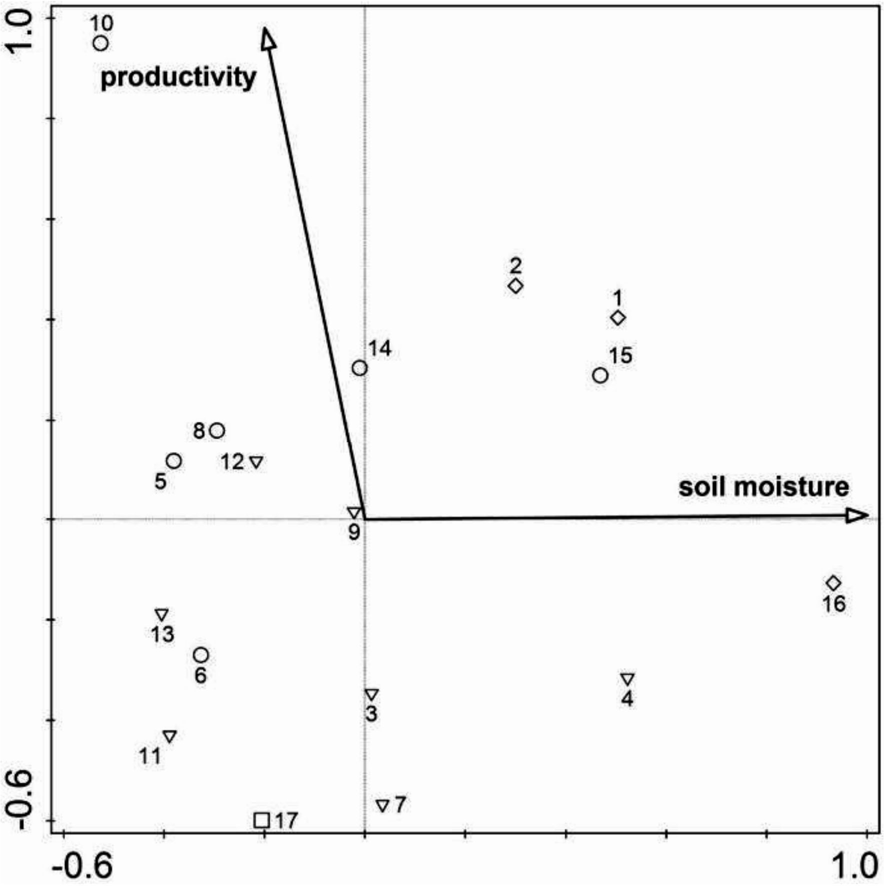

Fig. S1. Differences among sites at the baseline time of the experiment. Redundancy analysis (RDA) summarizing the differences in sites species composition at the baseline of the experiment in July 2007 explained by two dominant environmental gradients, productivity and soil moisture. Axis 1 and Axis 2 explain 11% and 7.7% of the total variation respectively (pseudo-F = 1.5, *P* = 0.004; test on all axes). Diamond, *Molinion*; down triangle, *Caricion fuscae*; circle, *Calthion*; square, *Sphagno warnstorfiani-Tomenthypnion*.

Table S1. Detailed information on the productivity (measured as dried standing biomass from one square meter), soil moisture (measured as an averaged groundwater depth), and alliance (according to Moravec 1995) for each of the 17 sites.

Locality	Biomass (g.m^{-1})	GD (cm)	Alliance
1	483.44	46	*Molinion*
2	510.75	38	*Molinion*
3	314.14	26	*Caricion fuscae*
4	295.00	47	*Caricion fuscae*
5	455.42	10	*Calthion*
6	352.00	12	*Calthion*
7	255.47	27	*Caricion fuscae*
8	467.39	14	*Calthion*
9	410.04	25	*Caricion fuscae*
10	680.34	4	*Calthion*
11	313.85	10	*Caricion fuscae*
12	446.56	17	*Caricion fuscae*
13	377.57	9	*Caricion fuscae*
14	484.73	25	*Calthion*
15	455.50	45	*Calthion*
16	322.28	64	*Molinion*
17	260.13	17	*Sphagno warnstorfiani-Tomenthypnion*

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Appendix S2. Detailed information on traits.

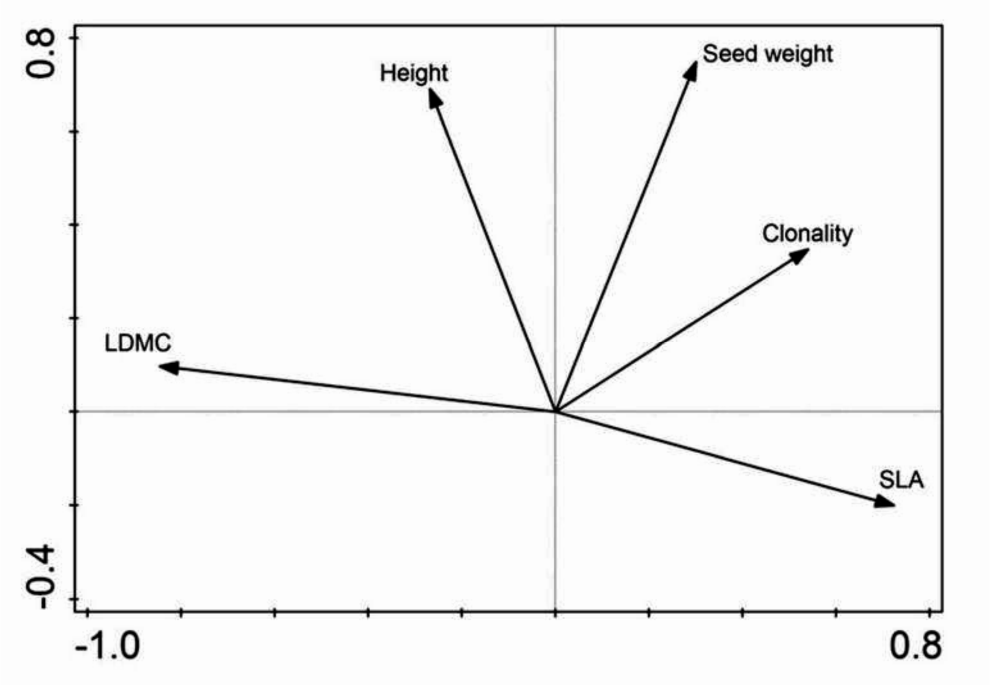

Fig. S2. Species traits relationships visualized with the principal components analysis (PCA). Axis 1 and Axis 2 explain 34% and 24% of the data variability respectively.

Appendix S3: Phylogenetic analyses

In analyses that use species as units of observation, these observations, e.g. trait values, are not necessarily independent, because closely related species share common ancestors and thus are likely to be more similar than unrelated species. We tested whether traits and response exhibited a signal of phylogenetic relatedness as described in the following section.

Methods

We used an age-calibrated phylogeny of species (Durka & Michalski 2012) and calculated Pagel's lambda (Pagel 1999) using the package *phytools* (Revell 2012) in R software (R Core Team 2014). Pagel's lambda is a measure of how well trait values of species are explained by their phylogeny, assuming a Brownian motion model of evolutionary change. It ranges between 0 and 1, where 0 indicates that trait values are completely independent of the phylogeny and a lambda of 1 indicates that trait values are a result of trait evolution under the Brownian motion model. Lambda values between 0 and 1 indicate varying degree of phylogenetic signal. If the strength of the signal is significant it can be assessed by comparing the lambda value to a distribution of lambdas generated by randomizing the trait values along the tips of the phylogeny. We calculated lambda and its significance for the specific assembly of species within each of the 17 sites as well as for the whole dataset. In the latter case, species response to a treatment was averaged over sites.

Results

Species response to the treatments was neither phylogenetically conserved when tested in individual sites (Table S3), nor when the response of individual species to either fertilization or abandonment was averaged over all sites (response to fertilization: lambda = 0.05, $P = 0.58$; response to abandonment: lambda = 0.58, $P = 0.37$; response to abandonment and fertilization, lambda < 0.001, $P = 1$). The strength of the phylogenetic signal of the individual traits within the assembly of species of each site varied slightly with the different community structure over assessed sites (Table S3). When testing over the whole species pool, height was not conserved (lambda = 0.27, $P = 0.71$) whereas SLA was (lambda = 0.67, $P < 0.001$). As we didn't detect any phylogenetical signal in the species response to individual treatments, we refrained from conducting phylogenetic regressions.

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Table S3. Phylogenetic signal assessed as Pagel's lambda for each of the sites separately. Phylogenetic signal was calculated for the response variable used for the linear models on the population level, i.e. species response to treatments (Spearman's rank correlations), as well as for the species traits selected in the linear models as significant predictors of species response to a treatment (refer also to Table 1 in the main text). Values of lambda together with their values of significance are given for each site and variable. Response to fertilization ('F'), mowing abandonment ('A'), or both treatments combined ('FA').

		Traits				Response to treatments		
	Site	Height	SLA	Seed mass	Clonality	F	A	FA
lambda	1	0.72	0.59	0.69	0.26	<0.001	<0.001	<0.001
P		0.03	0.001	0.11	0.06	1	1	1
lambda	2	0.07	0.36	0.72	<0.001	0.17	0.06	<0.001
P		0.66	0.06	0.04	1	0.51	0.63	1
lambda	3	<0.001	0.40	<0.001	0.31	<0.001	<0.001	<0.001
P		1	0.002	1	0.09	1	1	1
lambda	4	<0.001	0.18	0.93	1	0.16	<0.001	<0.001
P		1	0.35	0.007	<0.001	0.50	1	1
lambda	5	0.25	0.57	0.65	0.30	0.10	<0.001	<0.001
P		0.38	0.01	0.07	0.15	0.80	1	1
lambda	6	<0.001	0.54	0.80	<0.001	<0.001	0.27	<0.001
P		1	<0.001	<0.001	1	1	0.09	1
lambda	7	0.51	0.23	0.91	0.15	0.19	0.34	0.13
P		0.45	0.17	<0.001	0.13	0.21	0.23	0.59
lambda	8	0.11	0.53	0.86	0.27	<0.001	<0.001	<0.001
P		0.45	0.002	0.002	0.21	1	1	1
lambda	9	0.71	0.29	0.85	0.06	<0.001	<0.001	<0.001
P		0.03	0.02	<0.001	0.63	1	1	0.35
lambda	10	<0.001	0.66	0.85	0.23	<0.001	<0.001	<0.001
P		1	<0.001	0.02	0.30	1	1	1
lambda	11	<0.001	0.29	0.50	<0.001	<0.001	<0.001	<0.001
P		1	0.05	0.07	1	1	1	1
lambda	12	<0.001	0.30	0.56	0.07	<0.001	<0.001	<0.001
P		1	0.13	0.47	0.74	1	1	1
lambda	13	<0.001	0.33	0.84	0.20	0.25	<0.001	<0.001
P		1	0.01	0.002	0.48	0.05	1	1
lambda	14	<0.001	0.36	0.75	0.23	<0.001	<0.001	<0.001
P		1	0.002	0.001	0.09	1	1	0.86
lambda	15	<0.001	0.16	0.17	0.41	<0.001	<0.001	<0.001
P		1	0.34	0.29	0.20	1	1	1
lambda	16	<0.001	<0.001	<0.001	0.56	<0.001	<0.001	<0.001
P		1	1	1	0.02	1	1	1
lambda	17	<0.001	0.45	0.78	1	<0.001	<0.001	0.43
P		1	0.01	0.30	<0.001	1	1	0.36

Chapter IV

The plant functional traits that explain species occurrence across fragmented grasslands differ according to patch management, isolation, and wetness

Landscape Ecology, 32(4), 791-805

The plant functional traits that explain species occurrence across fragmented grasslands differ according to patch management, isolation, and wetness

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Abstract

Context Landscape fragmentation significantly affects species distributions by decreasing the number and connectivity of suitable patches. While researchers have hypothesized that species functional traits could help in predicting species distribution in a landscape, predictions should depend on the type of patches available and on the ability of species to disperse and grow there.

Objectives To explore whether different traits can explain the frequency of grassland species (number of occupied patches) and/or their occupancy (ratio of occupied to suitable patches) across a variety of patch types within a fragmented landscape.

Methods We sampled species distributions over 1300 grassland patches in a fragmented landscape of 385 km^2 in the Czech Republic. Relationships between functional traits and species frequency and occupancy were tested across all patches in the landscape, as well as within patches that shared similar management, wetness, and isolation.

Results Although some traits predicting species frequency also predicted occupancy, others were markedly different, with competition- and dispersal-related traits becoming more important for occupancy. Which traits were important differed for frequency and occupancy and also differed depending on patch management, wetness, and isolation.

Conclusions Plant traits can provide insight into plant distribution in fragmented landscapes and can reveal specific abiotic, biotic, and dispersal processes affecting species occurrence in a patch type. However, the importance of individual traits depends on the type of suitable patches available within the landscape.

Keywords Functional traits · Habitat suitability · Isolation · Management · Potential occurrence · Wetness

Introduction

Several studies have shown that the distribution and abundance of plant species in a landscape are governed by a set of processes largely mediated by plant functional traits (Maurer et al. 2003; Soons and Ozinga 2005; Herben et al. 2012). Functional traits, i.e., characteristics directly or indirectly linked to species fitness (Cornelissen et al. 2003; Violle et al. 2007), could therefore help predict which species from a regional species pool are likely to become more, or less, abundant in the region (Cornwell and Ackerly 2010). For such analyses, however, researchers should precisely distinguish habitat types, because plants specialized in those types of patches that are more common in a landscape will also be regionally more abundant than plants specialized in infrequent habitat types (Jacquemyn et al. 2003). When habitat features are not taken into account, plant traits can be misinterpreted as determining species abundance in a region (Ozinga et al. 2005a, b; Riibak et al. 2014). To remove the effect of habitat availability, researchers can focus on only one habitat type and define the species pool accordingly.

A habitat-specific species pool is generally defined as all species of the region typical for ecological conditions of a focus habitat type (de Bello et al. 2016). Observed diversity at a site obviously represents only a subset of the species that are able to exist under the local abiotic conditions. Species are absent because of dispersal limitation or a variety of abiotic and biotic effects. Defining habitat-species pools allows researchers to focus on that part of biodiversity that is absent but that could be present at a site given its prevailing ecological conditions. This absent part of diversity is sometimes called "dark diversity" (Pärtel et al. 2011). Assessing habitat-specific species pools is necessary for understanding species distribution, enables comparison of functions of present and absent parts of the species pool, and may reveal mechanisms behind local extinction and colonization (Lewis et al. 2016).

When focusing on a particular habitat type, researchers should further consider the main characteristics of a landscape mosaic, including the frequency, size, and connectivity of suitable patches. These attributes are known to affect plant distribution via meta-community dynamics (Koyanagi et al. 2012; Michalcová et al. 2013) because plant species can disperse among patches and compensate for local extinction via immigration. For example, small and isolated patches host fewer species than larger and connected ones and have species with different traits. The isolated patches may be more easily reached by anemochorous plants with low seed mass (Westoby et al. 1996), low terminal velocity (Jongejans and Telenius 2001), and high releasing height (Soons et al. 2004a). Plants with large and heavy seeds, in contrast, have difficulty colonizing isolated patches (Helsen et al. 2013), and their populations may become locally extinct unless they have a good vegetative propagation ability or a long lifespan (Lindborg and Eriksson 2004; Bossuyt and Honnay 2006).

Furthermore, although a habitat type is defined according to environmental conditions, each habitat type has biotic and small-scale abiotic filters that influence its plant distribution. Even if the species diaspores are able to reach the suitable patch, the species can be filtered out because of traits related to establishment or persistence capability that reduce the species competitiveness. For example, wet meadows in one landscape may differ in intensity of management or water availability, and the resulting gradients affect interspecific competition and therefore the establishment and persistence of plants in the community (Janeček et al. 2013). The increase in competition for light under wetter conditions can cause taller, perennial clonal plants, with less conservative resource-use strategies (often associated with a high specific leaf area and/or low leaf dry matter content) to become abundant (Janeček et al. 2013). Similarly, abandoned patches that are not regularly managed (i.e., that are not mown or grazed) are often overgrown by taller species with greater competitive abilities and vegetative spread (Klimešová et al. 2011). In more intensively managed patches, however, traits such as investment in fast growth, shoot architecture, and sexual rather than clonal reproduction may become more important in determining which species will establish

(McIntyre et al. 1995; Klimešová et al. 2011).

In the previous paragraphs, we have highlighted the importance of the following three factors that govern plant abundance in a landscape and that may provide insight into the mechanism of plant distribution: (1) the frequency of a habitat type in a landscape; (2) the properties of the mosaic of suitable patches, including their size and connectivity; and (3) biotic and abiotic gradients in the habitat types. We also pointed out that plant traits of those species that are missing in particular suitable patches in comparison with the traits of resident species may provide further insight into the causes of biodiversity impoverishment. A research approach that simultaneously considers these points should help disentangle the causes of contemporary plant distribution in landscapes affected by land use changes resulting from the abandonment of traditional management and habitat fragmentation.

Using this approach in the current study, we determined the degree to which management, abandonment, and habitat fragmentation have affected species distribution in grasslands in a hilly landscape of central Europe. We performed the study on 1307 semi-natural grassland patches within a 385 km^2 area; the patches differed in abiotic conditions, isolation, and management. We considered the actual species occurrence (''frequency'') and the ratio of occupied to suitable patches (''occupancy'') in combination with information on the species traits with the goal of identifying which traits cause species filtering within the landscape. Considering observed vs. potential distributions of species, we ask whether species traits associated with frequency and occupancy in the landscape depend on patch types.

Methods

Study area and vegetation mapping

This study was carried out in the central part of the Czech Republic, including a large portion of the Železné hory Protected Landscape Area. We chose an area of 14 × 27.5 km (centre: 49°48´N, 15°48´E) within this landscape (Fig. 1). The altitude ranges from 268 to 668 m a.s.l., and the mean annual precipitation varies from 550 to 850 mm. The landscape is a mosaic of forest, arable fields, and semi-natural grasslands. Sixty years ago, extensively used grasslands were abundant and forests were infrequent in this region. This pattern changed in the 1970s, when many grassland patches were abandoned or afforested, causing fragmentation, or when grassland patches shifted from extensive to intensive management, including the application of additional fertilizer to increase production.

Within the study area, all semi-natural grassland patches were identified via remote sensing and were subsequently subjected to field observations. We identified 1307 patches of grassland communities, excluding highly degraded grasslands (i.e., abandoned stands that had a high degree of eutrophication or that were overgrown by shrubs and trees) and intensive agricultural grasslands (i.e., species-poor grasslands sown with conventional seed mixtures to improve production). Species composition was recorded, and the cover of individual species was estimated using the Braun-Blanquet scale (see Mueller-Dombois and Ellenberg 1974) at the patch scale. To sample all patches, the field work was carried out over five consecutive years (2008–2012) at the peak of the growing season following a random selection of patches within the landscape to minimize potential variability among years. The regularly mown patches were sampled before mowing. For example, Arrhenatherion communities were sampled earlier (late May, June) than wetter habitats that attained their vegetation peak a bit later (the end of August). For each patch, we recorded land use (mowing or grazing vs. no management). Although both management types occurred, mown patches prevailed over grazed ones. The spatial characteristics of the patches (patch area and edge-to-edge distance from other patches) were determined with ArcGIS software (ESRI 2011).

Extent of species presence and potential occurrence

For each grassland species, we computed frequency, which was defined as the number of grassland patches in which the species occurred.

To estimate species occupancy (i.e., the realized occurrence of a species in relation to the suitability of patches in the landscape for this species), we used the following approach. First, we estimated the likelihood that a species could occur in each of the 1307 patches (potential occurrence). For this, we used a co-occurrence approach based on the Beals smoothing index (Beals 1984, ‘’Beals index’’ hereafter), which was described and validated by Ewald (2002)

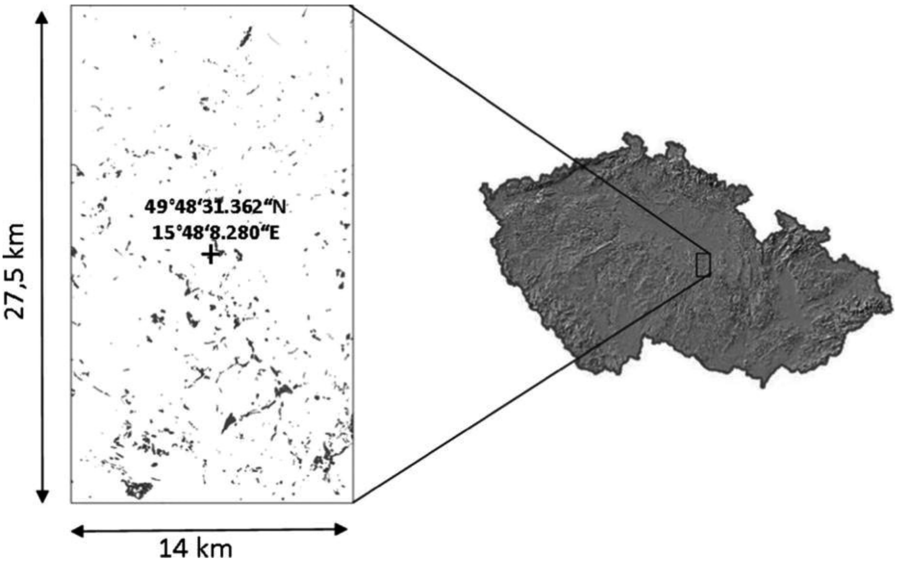

Fig. 1 Distribution of 1307 grassland patches (*grey areas*) in the study region, which was a 385-km^2 area in the central Czech Republic

and Hemrová and Münzbergová (2012) and was also applied by Riibak et al. (2014). The values of the Beals indices determine the probability that the species will occur in a particular community (patch). This probability is calculated from the joint occurrence of the target species and other species in the communities across the landscape. The probability increases when the community in the site contains many species frequently co-occurring with the target species at the landscape scale (Münzbergová and Herben 2004). We expected the Beals index to be generally unsuitable for rare species, because we did not have enough replicates of rare species to accurately estimate co-occurrence patterns. For this reason, we removed species occurring in fewer than 21 patches (i.e., 'rare' species, n = 323 of 551 species found) from further analyses. To determine whether this procedure excluded species sharing some specific trait values, we tested whether the values of rare species differed from those of more common species (Welch two-sample *t* test, see Results and Online Appendix 1). The 'common' species (n = 228), i.e., those occurring in <20 patches, were used in further analyses. Beals probabilities were then used to calculate the ''occupancy index'' for each of these grassland species as follows:

$$\text{Occupancy index} = \frac{\text{Sum of Beals probabilities across all patches}}{\text{Number of occupied patches for a species}}$$

The occupancy index reflects the observed occurrence of a species in relation to the expected occurrence. The higher the index, the more times a species occurs in all suitable patches. Values <1 indicate a "deficit" in species occurrence, whereas values >1 indicate that species also occur in communities where they are not expected to occur. Frequency and occupancy values are given in Online Appendix 2 for all species considered. It should be noted that we use occupancy here in a different sense than is frequently used in animal ecology, where it is mostly related to the modelling of metapopulation dynamics (e.g., Hanski 1994).

Plant traits

Plant functional traits were selected to determine whether similar functional characteristics explain the frequency and habitat occupancy of species and if so, if this consistency is maintained across different patch types (see Table 1, for trait's description and the source of the data, see Online Appendix 2 for trait values). We selected traits reflecting persistence, dispersal ability, and regeneration, all of which are related to survival of species at a particular site. These traits represent the major axes of species strategy differentiation (Cornelissen et al. 2003) and are only weakly correlated. Pearson correlations among selected traits were checked (Online Appendix 3), and correlations were visualized using principal component analysis (Fig. 2) in the Canoco program (Šmilauer and Lepš 2014). Plant height was considered as the most important trait related to competition for light, with tall species having an advantage over shorter ones, whereas shorter, smaller species were expected to be better adapted to stressful environmental conditions (climate and/or nutrients). We considered the clonal index (Johansson et al. 2011) to be another important trait determining the ability of a species to persist and occupy space in a horizontal dimension. The clonal index was calculated as the sum of ordinal values of multiplication rate and lateral spread from the CLO-PLA database

Table 1. Plant traits considered; description and sources.

Trait	Range of values in dataset	Data transformation	Source	References, notice
Apomictic or sexual reproduction	0-1(1 for apomictic)	None	BiolFlor database	Klotz et al. (2002)
Average height of plant [cm]	0.05-2.5	log	LEDA traitbase	Kleyer et al. (2008)
Average seed mass [mg]	0.005-49	log	LEDA traitbase,	Kleyer et al. (2008)
Average specific leaf area [SLA, mm^2mg^{-1}]	3.65-75.27	None	LEDA traitbase	Kleyer et al. (2008) We measured SLA for 6 species missing in database
Start of flowering [month]	1-8	None	BiolFlor database	Klotz *et al.* (2002)
Clonal index	0-7 (0 for non-clonal species)	None	CLOPLA database as source for lateral spread and multiplication rate values used for computing	Values calculated according Johansson et al. (2011); Klimešová and de Bello (2009*)*
Duration of flowering [month]	1-11	log	BiolFlor database	Klotz *et al.* (2002)
Life span [annual/biennial/perennial]	0-1 (0 for annual)	None	BiolFlor database	Klotz *et al.* (2002)
Rosette status	0-1 (0 for erosulate)	None	CLOPLA database	Klimešová and de Bello (2009*)*
Seed releasing height [m]	0.1-4	None	LEDA traitbase	Kleyer et al. (2008) Used to compute dispersal distances
Terminal velocity (the maximum rate of fall in still air)[ms^{-1}]	0.07-4.9	None	LEDA traitbase	Kleyer et al. (2008) Used to compute dispersal distances
Maximum dispersal distance [m]	0.14-2735	log		Calculation based on seed releasing height and terminal velocity

(Klimešová and de Bello 2009). Species with extensive clonal growth (lateral spread and/or multiplication rate) are likely to be good competitors for space and are likely to survive longer at a locality once established than non-clonal species (Johansson et al. 2011). We hypothesized that increased isolation of suitable patches will affect species with apomictic seeds less than species with sexual seeds, because apomictic species do not depend on pollinators. As isolation increases, lack of pollinators represents another factor that may limit the dispersal of plants with sexually developed seeds. The SLA (the ratio of leaf area to dry biomass) reflects a species relative growth rate and nutrient acquisition, leaf lifespan, and investment in leaf defence. A higher SLA is usually associated with a fast growth rate and more productive sites (Poorter and De Jong 1999; Cornelissen et al. 2003).

The response of a species to management can also be related to shoot architecture (rosette vs. erosulate shoots), plant lifespan (annual vs. perennial species), starting time of flowering, and reproductive mode (clonal growth vs. generative reproduction, seed dispersal distance; McIntyre et al. 1995). Dispersal distances for seeds were calculated based on predictive models by Tamme et al. (2014). These models, which predict maximal dispersal distances based on a model species and their trait values (in this case, seed releasing height and terminal velocity), were compared to trait values of our species set. Seed mass is another trait related to plant dispersal and regeneration ability. Although heavier seeds may be dispersed over shorter distances than lighter seeds, heavier seeds may enhance seedling establishment, especially when light or nutrients are in short supply (Leishman et al. 2000). Description of all used traits and their database sources are listed in Table 1. For some species, a particular trait value was not available; this was true for 31 of 228 species (highlighted values in Online Appendix 2). Rather than omitting these species from the analyses, we substituted the missing value with the average of this trait across all species.

Data analysis

We linked species frequency and occupancy to multiple functional traits, using stepwise linear regressions. This was performed using the default configuration of the 'step' function in R (R Development Core Team 2014), which provides a

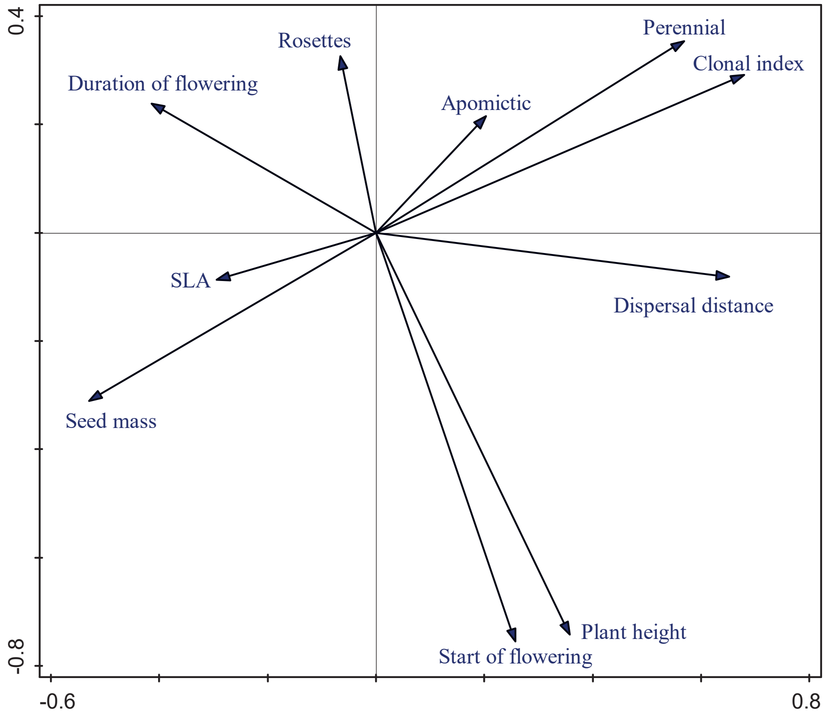

Fig. 2 Ordination of plant species according to their functional traits. Angles between trait arrows indicate their correlations. Principal component analysis (PCA, traits centered and standardized) was used. The 1st and 2nd ordination axis explained 19.87 and 16.53%, respectively, of the variability. For a correlation matrix among traits, see Online Appendix 3

combination of both forward and backward selections. Data type and processing are visually described in Fig. 3 to clarify the data analysis approach described in the text. In our statistical models, which relate either species frequency or occupancy to species traits, each data point in the analysis is a species. First, we computed frequency and occupancy of a species across all patches in a region. Then, to test for the effect of environmental characteristics of the patches, we calculated species frequency and occupancy within different patch types (abandoned vs. managed patches, isolated vs. less isolated patches, and wetter vs. drier patches). Finally, species frequency and occupancy, either across all patches or within a particular patch type, were related to species trait values. This may cause a slightly different number of species in analyses of different patch types, because not all species occurred in all patch types.

Similar models were used to test the effect of species frequency in the landscape on species occupancy (Online Appendix 5). To classify patches into different 'types', we considered three main environmental variables in the landscape: management, isolation, and wetness.

As noted earlier, patches were divided into types according to management, isolation, and wetness. Patches were considered managed if any indications of mowing or grazing were evident. Patches were also divided into two categories according to isolation. We computed the isolation index (McGarigal et al. 2002):

$$\sum_{s=1}^{n} \frac{A_{ijs} * sim_{ij}}{h_{ijs}^{2}}$$

where A_{ijs} is the area of each neighbouring patch j located within a 1-km broad buffer zone around the centroid of the considered patch; sim_{ij} is the similarity between target (i) and each neighbouring patch, calculated as 1 minus Bray–Curtis dissimilarities; and h_{ijs} is the edge-to-edge distance between the target and each neighbouring patch (which reflects the minimum distance that a species must overcome to reach the next suitable patch). Bray–Curtis dissimilarities are based on the species composition of patches and describe more precisely the natural continuum of patches than artificially made categories of subjectively defined vegetation types. Because the same species is usually able to grow in more than one vegetation type, the similarity of patches provides a measure of composition shift between each pair of patches. To avoid any edge effect on the isolation index resulting from a lack of complete data for patches located near the landscape border, we did not include patches found within the 1-km edge of the studied landscape. To run models described below and in Fig. 3, it was necessary to split patches into more isolated vs. less isolated ones. Based on the distribution of isolation index values, we considered patches to be isolated when the isolation index was <50 and non-isolated when the isolation was >800; the 221 patches (17% of all patches) with intermediate values were excluded to minimize subjective decisions.

To determine how explanatory variables (management, isolation, and wetness) were related to the composition of plant communities, we ordinated

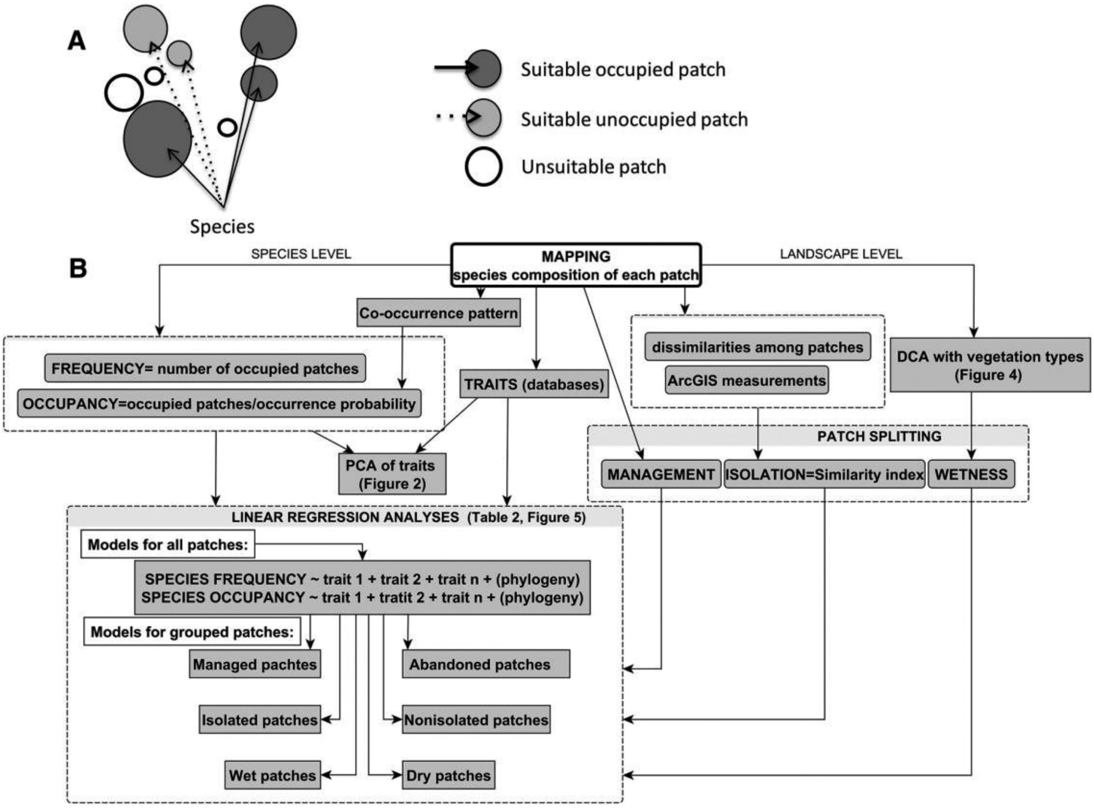

Fig. 3 Schematic illustration of the approach and data analyses used in this study. The *upper part* shows a simplified landscape with patches of different size and distance from each other. A particular species will occupy some of these patches, but often not all, and often not even all suitable ones. Frequency is defined as the number of occupied patches. Occupancy is defined as the proportion of all suitable patches occupied by a species. Here, the suitability of a patch is defined by Beals' smoothing using species co-occurrence data. The scheme in the *lower part* shows how the data were processed from field mapping through the calculating of indices and the decision of patch splitting into the final linear models. First, we analysed the relationship between frequency/occupancy and species traits using frequency and occupancy computed in all patches ('all patches'). Then we focused on species frequency and occupancy only within particular patch types. We repeated tests relating species frequency and occupancy to traits, recalculating frequency and occupancy in a abandoned and managed patches, separately; b isolated and less isolated patches, separately; and c wetter and drier patches, separately

plant communities of individual patches and calculated relationships with canonical axes. Community weighted means of Ellenberg moisture values for individual patches were calculated with Canoco software (Šmilauer and Lepš 2014) and then used as a supplementary variable in Detrended correspondence analysis (Fig. 4).

Several linear models were then run to test the relationship between species frequency and occupancy with species traits. As noted earlier, we repeated the test relating species distribution and traits for all patches together (n = 1307), and then these patches were grouped several times as follows: a/abandoned (n = 554) and managed (n = 714) patches, separately; b/isolated (n = 487) and less isolated (n = 599) patches, separately; and c/wetter (n = 929) and drier (n = 378) patches, separately. In individual analyses, some patches were excluded if information about their management or isolation was lacking. For each of these groups of patches, species frequency and occupancy were calculated based on the number of patches in the respective group. Because rare species were excluded earlier during data cleaning, most species remaining in the data set occurred in most, if not all, patch types, leading to similar species numbers for all of the models. Observed differences in results between patches of contrasting patch type pairs would then result from the fact that certain species prefer one of these types, leading to higher frequencies/occupancies of these species in patches of that type.

The modelling approach was then adopted using either species traits alone or using species traits plus phylogenetic information on the species. The latter was done to account for possible non-independence of trait values among closely related species (de Bello et al. 2015). Phylogenetic information for all considered species was extracted from the Daphne phylogenetic tree (Durka and Michalski 2012), which contains the most comprehensive and up-to-date phylogenetic information for Central European flora. The phylogenetic information was included in linear models using phylogenetic eigenvector regressions (Diniz-Filho et al. 2012). This approach enabled us to combine and compare the analyses with and without phylogenetic information. All statistical analyses were carried out using R software (R Development Core Team 2014).

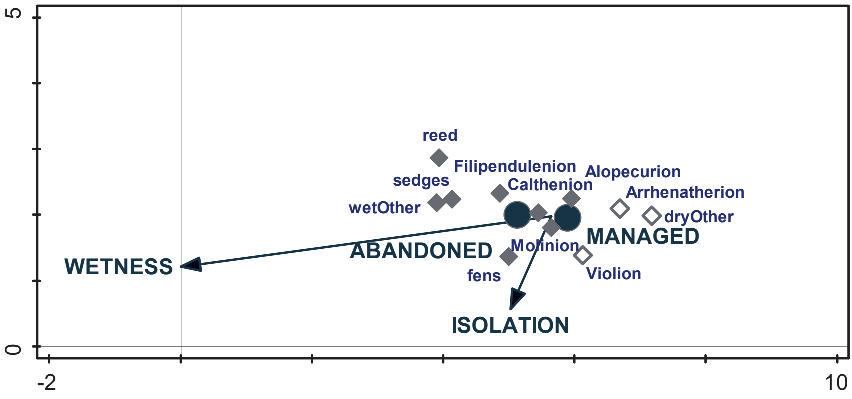

Fig. 4 Detrended correspondence analysis (DCA) with supplementary variables showing 11 categories of habitat types according to Natura 2000 standards, where each point represents the centroid of a vegetation type. Wet habitats (reed beds, tall sedges, Filipendulenion, Calthenion, fens, Molinion, Alopecurion, and wetOther) are marked *grey*, and dry habitats (Nardion, Arrhenatherion, and dryOther) are marked white. The dryOther group includes broadleaved dry grasslands, mesic herbaceous fringes, and acidophilous grasslands on shallow soils. The wetOther group includes eutrophic and mesotrophic vegetation of muddy substrata, annual hygrophilous herbs, perennial amphibious herbs, and fringes of montane streams. The 1st and 2nd ordination axis explained 7.69 and 3.31% of the variability, respectively

Results

The factor that was most tightly correlated with the main differences in community compositions was moisture (Fig. 4). The correlation coefficient between moisture and the 1st DCA ordination axis was −0.8535. Management was also related to the 1st canonical axis (the correlation coefficient was 0.4309), whereas isolation was correlated with the 2nd ordination axis (the correlation coefficient was −0.2540)

We used a set of models that predicted either species frequency or occupancy by species functional traits (Table 2, visualized in Fig. 5). Life span and SLA were the best predictors for the present species distribution (frequency) when considering all grassland patches. This pattern slightly changed within different patch types, according to management, isolation, and wetness. Perennial species and those with a high SLA, however, were more frequent regardless of patch subgrouping, except in abandoned patches (Table

2; Fig. 5). We generally obtained similar results with models that included phylogenetic information, although the importance of a few plant traits changed.

If we consider species occupancy, i.e., species distribution in relation to patch suitability, the significant traits at the regional scale were different from those predicted by the frequency models (Table 2; Fig. 5). The most distinctive trait was dispersal distance, but seed mass and plant height also contributed significantly to model predictions. Because seed mass and dispersal distance were negatively correlated (Online Appendix 3), the results indicate different reproductive strategies to occupy suit- able patches. As before, the patterns changed when we focused on only certain patch types with respect to their management, isolation, or wetness. We found a significant but weak negative correlation between species frequencies in the region and their occupancy indices ($n = 228$, $r = -0.14$, $R^2 = 0.02$; $p = 0.036$; Online Appendix 4). This relationship is caused mainly by relatively rare species, which are not typical grassland species but which sometimes occur in these communities (e.g., *Alisma plantago-aquatica* and *Eleocharis palustris*). Most importantly, comparing results from present and potential species distributions revealed some key differences. Lifespan was important exclusively for models based on species frequency, whereas dispersal distance was significant in occupancy models but not in frequency models. Moreover, the percentage of variance explained was generally lower (sometimes 50% lower) for models predicting species frequency than for those predicting occupancy.

Interestingly, we detected clear sets of opposite traits predicting species occurrence in pairs of contrasting patch types, and this was especially true for occupancy. For example, small, non-clonal plants with rosette shoots, higher SLA, short dispersal distance, lighter seeds, and long flowering times increased with species occupancy in managed patches but decreased in abandoned patches. This set of traits were characteristic of species that were under-represented in abandoned patches, whereas the opposite set of traits (taller, clonal species etc.) were characteristic of species that were under-represented in managed patches. Similarly, wetness of patches differentiated species with different clonality and plant heights (Table 2). Frequency models for opposite types of patches followed the patterns of the general model, but models for occupancy indices included more marked differences in traits when considering distinct patch types. Wetness mostly influenced plant height and clonality, while management seemed to filter species according to SLA, plant height, clonality, shoot architecture, flowering longevity, seed mass, and dispersal distance. Finally, when comparing grasslands in terms of isolation, we found that species with longer dispersal distance had a higher occupancy than species with shorter dispersal distances in both isolated and less isolated patches, although the species in these two kinds of patches differed in length of flowering, seed mass, and rosette status.

Because we excluded rare species from the analyses (i.e., those with frequencies >21 in the entire regional dataset; see Methods), we also tested whether rare species were functionally different from those included in the analyses. Rare species did not differ from frequent species in height, seed mass, start of flowering, or apomixis. However, rare species were less clonal and had a higher SLA, a shorter lifespan, a shorter dispersal distance, and a slightly longer flowering period Online Appendix 1). Because frequency in the landscape can substantially influence a species occurrence in a target patch, we also tested the effect of species commonness on occupancy, i.e., we included species frequency as a predictor of species occupancy together with traits (for results, see Online Appendix 5). As before, the general model for the entire region hid the effects of landscape heterogeneity, whereas habitat types at opposite ends of the stress gradient (management or moisture) contained species with different traits.

Discussion

General patterns

This study shows that while plant traits can help predict species occurrence in a region (Herben et al. 2012), the predictive power of individual traits depended on patch wetness, isolation, and management regime across fragmented grasslands. To uncover dispersal, abiotic, and biotic filtering processes at the landscape scale, researchers should measure species occurrence not only in the terms of total occurrence but also in relation to the availability of suitable patches. Ozinga et al.

Table 2 Relationships between frequency/occupancy and plant functional traits as determined by stepwise regressions using a combination of forward and backward selection without (before the slash) and with phylogenetic corrections (after the slash

Trait	All patches		Management				Isolation			
			Managed ($n^p = 714$; $n^s = 228$)		Abandoned ($n^p = 554$; $n^s = 227$)		Isolated ($n^p = 487$; $n^s = 228$)		Non-isolated ($n^p = 599$; $n^s = 228$)	
	Frequency	Occupancy	Frequency	Occupancy	Frequency	Occupancy	Frequency	Occupancy	Frequency	Occupancy
Plant height		(?)*/(?)*		(–)./(–).	(?)./(?).	(?)**/(?)**	(?)/			
Clonal index				(–)./(–).	(?)**/(?)**	(?)./(?).				
Perennial	(?)**/(?)*		(?)*/(?)*				(?)**/(?)*		(?)*/(?)*	
SLA	(?)*/(?)*		(?)*/(?)**	(?)**/(?)**	/(?)	(–)*/(–)*	(?)*/(?)**		(?)./(?)*	
Rosettes			(?)*/(?)	(?)*/(?)*		(–)**/(–)**	(?)/	(–)*/(–)*	(?)/	
Start of flowering										
Duration of flowering			(?)/(?).	(?)**/(?)**		(–)*/(–)*	(?)./(?)	(?)/(?)		(–)**/(–).
Seed mass		(?)./(?)**		(–)./(–).		(?)*/(?)**		(?)**/(?)**		
Apomictic	(?)/(?)		(?)*/(?)*				(?)*/(?).			(–)/
Dispersal distance		(?)***/(?)***		(–)***/ (–)***		(?)***/(?)***		(?)***/(?)***		(?)/(?)*
Adj. R^2	0.04/0.06	0.11/0.19	0.06/0.07	0.21/0.21	0.05/0.06	0.26/0.30	0.06/0.06	0.07/0.07	0.04/0.05	0.05/0.12

Table 2 continued

Trait	Wetness			
	Wet (n^p = 929; n^s = 221)		Dry (n^p = 378; n^s = 207)	
	Frequency	Occupancy	Frequency	Occupancy
Plant height		(?)***/(?)**		(–)*/(–)*
Clonal index	(?)*/	(?)***/(?)***	(–)*/(–)	(–)***/(–)***
Perennial	(?)/(?)*		(?)**/(?)*	
SLA	(?)./(?)*		(?)./(?)*	
Rosettes			(?)/(?)*	
Start of flowering				
Duration of flowering		(–)*/	(?)**/(?)*	(?)**/(?)*
Seed mass		/(?)		
Apomictic			(?)**/(?)*	
Dispersal distance		/(+)*		
Adj.R^2		0.17/0.20	0.19/0.10	0.13/0.17

The number of species (n^s) and patches (n^p) considered in analysis are indicated under each patch type; (?) or (–) indicate a positive or negative direction of the relationship, respectively, and a blank space indicates that the variable was excluded from the model. The absence of these symbols indicates that a trait was not statistically significant but that its inclusion significantly improved the model

***, **, *, and. indicate p \ 0.001, \ 0.01, \ 0.05, and \ 0.1, respectively

(2005a) and Riibak et al. (2014) previously assessed the role of plant traits oncommunity composition by comparing the traits of observed and expected species. Here, we extended this approach to the landscape level using an occupancy index. Based on the proportion of suitable patches occupied, we could determine which types of species are most often excluded from suitable patches.

Researchers have hypothesized that the frequency of a species is highly dependent on the patch type that dominates in the region (Jacquemyn et al. 2003). When only the observed presence of a species is considered, the role of dispersal and biotic processes on species selection can therefore be 'masked' by the effects of prevailing abiotic conditions. It follows that predictions of species distributions using functional traits may mostly depend on the prevailing patch types in a region. This problem may be avoided by the use of an occupancy index, which in the present study enabled us to detect sets of traits that predict the potential distributions of species in different habitat types (Fig. 5). In our study region, for example, general models indicated that perennials and species with a higher SLA are among the most frequent. Only when we used occupancy results were we able to confirmed our expectations that species with traits associated with long dispersal have a higher occupancy. In calculating the dispersal distance, we considered two traits, i.e., releasing height and terminal velocity, which are closely related to autochory and wind-dispersed diaspores (Tamme et al. 2014). Other dispersal modes, such zoochory (for which we did not have enough information available), can be associated with long dispersal distances and high seed mass (Thomson et al. 2011). This might explain the observed effects of greater seed mass together with the dispersal distance on occupancy. Furthermore, heavier seeds may favour establishment and seedling competition (Leishman et al. 2000), thus indicating that different reproductive strategies are required to occupy suitable patches that differ in fundamental properties.

As expected, we found that different traits predicted which species occurred in managed vs. unmanaged conditions. Particularly when occupancy was used, the sets of traits detected depended on management type. Species with high SLA, small stature, and rosette arrangement of leaves had higher occupancy rates in managed patches, while species with traits related to competition (tall, erosulate) had higher occupancy rates in abandoned patches. We also found that competitive traits were more important in moist, productive grasslands than in drier, less productive grasslands. In summary, dispersal and biotic processes in

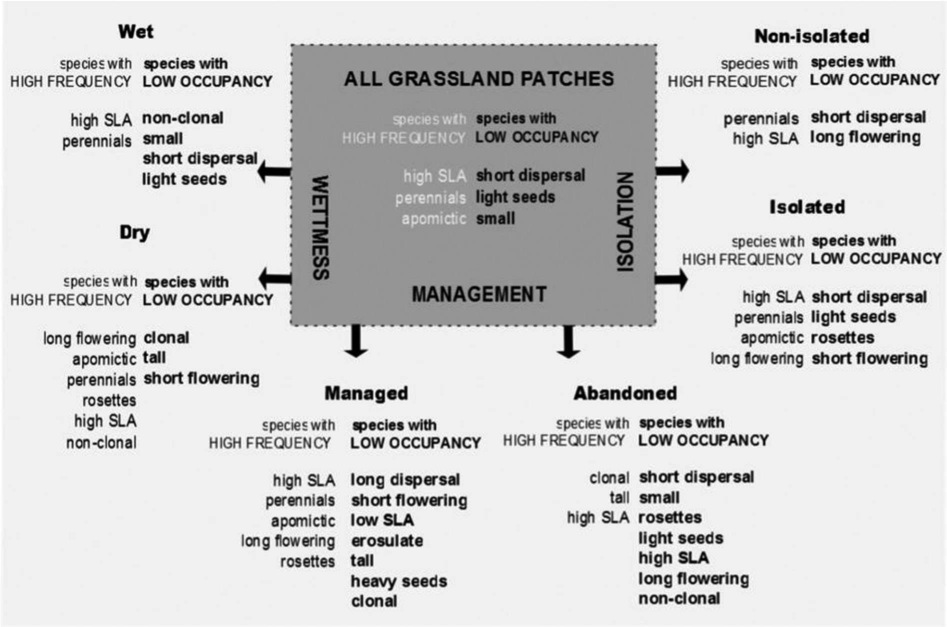

Fig. 5 A graphic depiction of the results from Table 2, showing the pattern of functional traits occurring with high frequency across all grassland patches and in a particular patch type, together with traits of species with low occupancy. Trait sets differ according to patch isolation, management, and wetness. Traits are ordered by their significance level in models with phylogenetic corrections

species selection were found to be more important in the models based on occupancy than in the models based on frequency. In addition, results based on occupancy revealed clearer patterns of trait differentiation between habitats. These findings highlight the value of considering the potential distribution of a species when assessing the importance of species traits.

We generally found a low predictive power of traits for species frequency and occupancy (low adjusted R^2 values). This is usually due to unmeasured trait trade- offs between species (Kleyer et al. 2012) and possibly to the use of trait data extracted from databases that do not account for intraspecific trait variability of local populations. We also suspect that the low percentage of explained variability was caused by the unmeasured effects of other factors such as stochastic processes or mass effects. However, we were mainly interested in comparisons of trait importance across patch types and in predicting frequency vs. occupancy.

In our models, the consideration of phylogenetic relatedness slightly modified the results but not the general patterns detected. Including phylogeny improved some models, probably because phylogeny accounted for some trait information unavailable for our species but reflected in their phylogeny (Cadotte et al. 2012). In other cases, the predictive power of traits decreased when phylogeny was considered, indicating that traits are most likely phylogenetically conserved. As a result, including phylogeny in the models as a covariate results in some redundancy of information, which reduces the significance attributed to traits (de Bello et al. 2015).

Effect of different patch types

Dispersal limitation effects have been reported in the literature Ozinga et al. (2005b). Because long-distance dispersal often relies on repeated stochastic events that could rapidly decrease with increasing landscape fragmentation (Soons et al. 2004b), we expected a higher importance of dispersal traits under more fragmented conditions. In our study, dispersal distance was more often positively correlated with species occupancy than with frequency (considering isolated and even non-isolated, wet and abandoned grasslands, but not dry and managed patches; Table 2), indicating that most species are in fact dispersal limited with respect to the patches that could be occupied. On the other hand, frequency models for isolated patches did not indicate any importance of dispersal limitation in the region, showing again that the dispersal patterns can be masked by the use of observed rather than potential distributions of species.

When managed and abandoned patches were considered separately, many traits in occupancy models acted in opposite ways. More competitive traits such as height, high clonality, erosulate status, low SLA, and short flowering period were correlated with occupancy in abandoned patches. It is widely accepted and has been repeatedly confirmed that rosette species are favoured by mowing and grazing—two main management regimes—because of the smaller loss of biomass, while erect competitor species are disadvantaged by mowing and grazing (e.g., Klimešová et al. 2008). In contrast to managed sites, litter accumulation on abandoned sites disadvantages species with lighter seeds (that therefore have little storage for seedlings), which are outcompeted by heavy-seeded species (Table 2; Fig. 5). This trait, however, was not confirmed as a predictor by the frequency model.

We anticipated that different processes affect grasslands along a moisture gradient. On wet sites, perennials and species with a higher SLA were more frequent, suggesting that these environments support competitive species that invest more in growth and persistence than in seed production and other competition-avoiding strategies in time (early growth) and space (long-distance dispersal). From the potential distribution point of view, wet sites more often host tall and clonal species, i.e., competitive species, but also those with long dispersal and heavier seeds, reflecting the general model. Clonal species are thought to be more abundant under wet, cold, and shaded conditions (Klimeš et al. 1997). In accordance with these findings, our results showed that clonal species occurred more often in abandoned and wet patches. In contrast, dry sites hosted smaller, non-clonal species with longer flowering periods; these species are weaker competitors but can tolerate the less productive environments that prevail in dry grasslands. As we have shown, wetness was clearly related to the main gradient of species composition variability. Nevertheless, other abiotic factors can play important role especially in other landscapes and/or vegetation types and should be explored in future studies.

Conclusions

In this study, we explored different ways of assessing which traits affect species success in a landscape, a research topic that has interested ecologists because of its relevance to understanding the effect of ongoing changes in land use and climate. We show that combining analyses of the frequency and potential species distribution in the region can help disentangle the role of abiotic, biotic, and dispersal filters. Results based only on species frequency, in contrast, are largely influenced by the type of patches available in a landscape, causing an underestimation of the biotic and dispersal factors that limit distribution. The pattern of species distribution in a fragmented landscape is shaped by how plant traits are filtered in different patch types. The importance of competition-related traits is reduced in managed patches, which promotes ruderal species. At more productive wet sites, the importance of competition-related traits increases. Isolation of patches increases the importance of long-distance dispersal, a crucial trait influencing occupancy in fragmented landscapes.

Acknowledgements

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Supporting Information

Appendix 1. Trait differences between common (n=228) and rare (n=323) species in t he region using Welch two-sample *t*-tests.

Trait	Rare species have	p-level
Apomixis		not significant
Log (height of plant)		not significant
Log (seed weight)		not significant
Log (specific leaf area)	Higher SLA	<0.001
Start of flowering		not significant
Clonal index	Lower clonal index	<0.001
Log (duration of flowering)		not significant
Perennial	More annuals	<0.001
Rosettes		not significant
Log (dispersal distance)	Shorter dispersal distance	<0.002

Appendix 2. Species included in the analyses (n=228) and their traits. Species average heights, seed weights, duration of flowering, and dispersal distances were used as logarithmic values in the analyses. Highlighted are average values for the trait instead of non-available values. Also indicated are naturalized or invasive species and species belonging to archeophytes or neophytes (Sádlo et al 2007).

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Species	Family	Naturalized/invasive	Archeophyte/ neophyte	Clonalindex	SLA [g/cm2]	Height [m]	Seed mass[mg]	Rosettes [0=nonrosettes,	Perennial [0=annual, 1=perennial]	Apomictic [0=nonapomictic,	Start of flowering [month]	Duration of flowering [month]	Maximum Dispersal distance [m]	Frequency [number out of 1307 patches in the landscape]	Occupancy index
Achillea.millefolium.agg.	Poaceae			5	18.94	0.4	0.26	0.42	1	0	6	5	3.77	491	0.855
Achillea.ptarmica	Poaceae			5	16.3	0.78	0.25	0	1	0	7	3	2.44	119	0.731
Aegopodium.podagraria	Asteraceae			3	28.8	0.56	2.2	0.5	1	0	6	2	1.38	214	0.819
Agrimonia.eupatoria	Asteraceae			3	18.45	0.33	15	0.3	1	0	6	4	3.21	21	0.927
Agrostis.canina	Apiaceae			5	27.29	0.3	0.06	0.5	1	0	6	3	200.80	311	0.792
Agrostis.capillaris	Rosaceae			4	34.43	0.25	0.07	0.17	1	0	6	2	74.16	314	0.844
Agrostis.stolonifera	Poaceae			5	31.33	0.3	0.07	0.38	1	0	6	2	55.42	145	0.770
Ajuga.reptans	Lamiaceae			5	34.7	0.16	1.4	0.38	1	0	5	4	0.56	272	0.782
Alchemilla.sp.	Rosaceae			5	18.65	0.37	0.46	0	1	1	6	3	7.12	564	0.837
Alisma.plantago.aquatica	Alismataceae			3	29.73	0.33	0.5	1	1	0	7	2	38.75	31	1.234
Alopecurus.pratensis	Poaceae			3	25.04	0.45	0.8	0.5	1	0	5	2	17.41	690	0.832
Anemone.nemorosa	Ranunculaceae			4	27.4	0.14	3	0	1	0	3	3	3.64	246	0.777
Angelica.sylvestris	Apiaceae			0	26.93	0.78	2.74	0.5	0	0	7	3	7.22	479	0.798
Anthoxanthum.odoratum	Poaceae			0	29.77	0.17	0.53	0.5	1	0	5	2	15.34	522	0.800
Anthriscus.sylvestris	Apiaceae			3	31.19	0.73	4.16	0.5	1	0	5	4	1.39	143	0.735
Arrhenatherum.elatius	Poaceae	inv	ar	5	28.25	1.28	2.8	0.4	1	0	6	5	17.99	379	0.897
Astragalus.glycyphyllos	Fabaceae			0	25.71	0.58	4.8	0	1	0	6	2	1.29	21	0.815
Avenella.flexuosa	Poaceae			5	17.5	0.08	0.56	0.5	1	0	6	3	25.43	88	0.908
Avenula.pubescens	Poaceae			4	20.74	0.6	2.14	0.5	1	0	5	2	15.97	120	0.750

Bellis.perennis	Asteraceae	5	27.08	0.06	0.13	1	1	0	1	11	1.35	102	0.863
Betonica.officinalis	Lamiaceae	2	19.72	0.31	11.4	0.08	1	0	7	2	2.30	49	0.773
Bistorta.major	Polygonaceae	2	24.65	0.38	4.81	0	1	0	5	3	0.53	590	0.833
Brachypodium.pinnatum	Poaceae	4	22.75	0.8	2.8	0	1	0	6	2	20.89	30	0.940
Briza.media	Poaceae	4	21.57	0.17	0.4	0.5	1	0	5	2	14.07	284	0.767
Bromus.erectus	Poaceae	3	17.03	0.5	1.921	0.5	1	0	5	6	12.16	37	0.908
Bromus.hordeaceus	Poaceae	0	27.35	0.3	1.48	0.13	0	0	5	4	14.26	24	0.851
Calamagrostis.canescens	Poaceae	5	19.53	1	0.06	0	1	0	7	2	133.14	189	0.967
Calamagrostis.epigejos	Poaceae	4	13.05	1	0.064	0.5	1	0	7	2	38.75	273	0.838
Calamagrostis.villosa	Poaceae	4	24.93	0.35	0.064	0	1	0	7	2	378.56	22	0.921
Calluna.vulgaris	Ericaceae	0	11.73	0.83	0.03	0	1	0	8	3	12.41	61	0.838
Caltha.palustris	Ranunculaceae	3	27.59	0.26	1.1	0.5	1	0	4	3	3.15	399	0.803
Campanula.patula	Campanulaceae	0	34.89	0.28	0.02	0.5	0	0	5	3	2.91	279	0.825
Campanula.rapunculoides	Campanulaceae	0	53.34	0.38	0.13	0.5	1	0	6	4	1.82	27	0.750
Campanula.rotundifolia.agg.	Campanulaceae	3	24.09	0.19	0.06	0.5	1	0	6	5	1.79	142	0.874
Cardamine.amara	Ranunculaceae	4	20.35	0.25	0.6	0	1	0	4	3	0.71	63	1.047
Cardamine.pratensis.agg.	Brassicaceae	4	20.35	0.25	0.6	0.5	1	0	4	3	0.88	301	0.757
Carex.acuta	Cyperaceae	5	13.78	0.9	1.25	0.5	1	0	5	2	3.27	212	1.011
Carex.acutiformis	Cyperaceae	4	16	0.75	1.09	0.5	1	0	6	2	7.21	49	0.874
Carex.brizoides	Cyperaceae	5	24.83	0.5	0.28	0.5	1	0	5	2	4.19	49	0.849
Carex.canescens	Cyperaceae	5	25.65	0.33	0.3	0.75	1	0	5	2	2.35	185	0.822
Carex.caryophyllea	Cyperaceae	4	20.52	0.09	1.13	1	1	0	4	2	2.00	24	0.733
Carex.echinata	Cyperaceae	4	14.98	0.25	0.86	0.88	1	0	5	2	1.95	170	0.762
Carex.elongata	Cyperaceae	4	40.16	0.5	0.61	1	1	0	5	2	2.59	39	0.972
Carex.flacca	Cyperaceae	5	15.21	0.28	0.87	0.6	1	0	5	3	2.36	31	0.657
Carex.flava.agg.	Cyperaceae	4	21.98	0.5	1.05	0.5	1	0	5	5	38.75	100	0.707
Carex.hartmanii	Cyperaceae	4	17.79	0.5	0.714	0.5	1	0	5	2	2.01	150	0.716
Carex.hirta	Cyperaceae	5	18.34	0.45	2.74	0.6	1	0	5	2	1.48	200	0.785
Carex.nigra	Cyperaceae	4	17.79	0.11	0.78	0.93	1	0	5	2	4.56	508	0.818
Carex.ovalis	Cyperaceae	3	23.62	0.24	0.58	0.67	1	0	6	2	3.43	288	0.754
Carex.pallescens	Cyperaceae	4	30.18	0.33	0.96	0.67	1	0	5	3	2.38	394	0.746
Carex.panicea	Cyperaceae	5	20.57	0.15	2.32	0.8	1	0	5	2	1.33	410	0.767
Carex.paniculata	Cyperaceae	4	15.98	0.53	0.75	1	1	0	5	2	3.41	23	0.801

Carex.pilulifera	Cyperaceae			4	19.43	0.1	1.1	0.75	1	0	5	2	1.07	189	0.787
Carex.rostrata	Cyperaceae			4	15.62	0.5	1.2	0.5	1	0	6	1	2.19	214	0.930
Carex.vesicaria	Cyperaceae			5	16.55	0.55	0.496	0.63	1	0	6	1	1.86	367	0.901
Carlina.acaulis	Asteraceae			0	10.96	0.31	4.05	0.67	1	0	7	3	10.79	87	0.889
Centaurea.jacea	Asteraceae			3	16.41	0.85	1.06	0	1	0	6	6	0.90	187	0.821
Centaurea.scabiosa	Asteraceae			0	19.2	0.83	6.5	0.5	1	0	7	2	1.15	26	0.809
Cerastium.arvense	Caryophyllaceae			4	21.44	0.11	0.21	0.17	1	0	4	4	0.70	36	0.823
Cerastium.holosteoides	Caryophyllaceae			0	21.44	0.11	0.21	0	1	0	5	4	1.32	452	0.806
Chaerophyllum.aromaticum	Apiaceae			3	24.09	0.6	15.27	0.5	1	0	7	2	38.75	82	0.825
Chaerophyllum.hirsutum	Apiaceae			5	27.91	0.58	15.27	0.5	1	0	5	2	2.13	92	0.858
Cirsium.arvense	Asteraceae	inv	ar	6	15.4	0.86	1.3	0	1	0	7	3	59.74	234	0.818
Cirsium.canum	Asteraceae			3	24.09	0.45	3.63	0.5	1	0	7	2	0.46	39	0.785
Cirsium.heterophyllum	Asteraceae			5	26.4	0.55	3.63	0.5	1	0	7	2	97.96	60	0.762
Cirsium.oleraceum	Asteraceae			4	30.08	0.8	3.63	0.5	1	0	6	4	0.50	371	0.846
Cirsium.palustre	Asteraceae			3	18.1	0.85	1.67	0.5	0	0	7	3	46.02	659	0.850
Cirsium.rivulare	Asteraceae			4	24.09	0.35	3.63	0.5	1	0	5	2	0.51	66	0.650
Convolvulus.arvensis	Convolvulaceae	nat	ar	5	28.39	0.26	14.5	0.22	0	0	6	4	1.18	39	0.872
Crepis.biennis	Asteraceae			0	31.23	0.58	1.23	0.5	0	0	5	4	12.88	86	0.811
Crepis.mollis.subsp.hieracioides	Asteraceae			3	24.09	0.23	0.85	0.5	1	0	6	3	12.77	85	0.686
Crepis.paludosa	Asteraceae			3	37	0.45	0.57	0.25	1	0	6	3	7.82	192	0.782
Cynosurus.cristatus	Poaceae			3	23.92	0.55	0.5	0.5	1	0	6	2	14.60	54	0.803
Dactylis.glomerata	Poaceae			4	21.8	0.75	0.9	0.5	1	0	5	3	20.68	556	0.870
Dactylorhiza.majalis	Orchidaceae			3	22.91	0.5	0.005	0.67	1	0	5	2	38.75	124	0.712
Danthonia.decumbens	Poaceae			4	16.94	0.1	1.6	0.5	1	0	6	2	11.28	85	0.758
Daucus.carota	Apiaceae			0	19.62	0.39	1	0.5	0	0	6	4	3.63	40	0.939
Deschampsia.cespitosa	Poaceae			4	14.72	0.43	0.24	0.5	1	0	6	2	26.50	697	0.849
Dianthus.deltoides	Caryophyllaceae			5	16.05	0.22	0.2	0	1	0	6	4	1.06	28	0.932
Eleocharis.palustris.agg.	Cyperaceae			5	10.31	0.53	0.76	0	1	0	5	4	1.20	35	1.108
Elytrigia.repens	Poaceae			6	23.62	0.75	2.1	0	1	0	6	3	20.07	55	0.782
Epilobium.angustifolium	Onagradaceae			5	22.61	0.5	0.26	0	1	0	7	2	2734.79	22	0.805
Epilobium.palustre	Onagradaceae			5	33.61	0.28	0.04	0	1	0	7	3	341.72	129	0.791
Epilobium.sp.	Onagradaceae			5	36.1	0.18	0.27	0	0.5	0	5	3	271.02	103	0.861
Equisetum.arvense	Equisetaceae			6	10.35	0.33	0.005	0	1	0	3	2	38.75	168	0.769

Equisetum.fluviatile	Equisetaceae	6	9.45	1	0.005	0	1	0	5	2	38.75	196	0.904
Equisetum.palustre	Equisetaceae	6	8.62	0.3	0.005	0	1	0	6	4	38.75	244	0.795
Equisetum.sylvaticum	Equisetaceae	6	24.58	0.33	0.005	0	1	0	4	2	38.75	220	0.823
Eriophorum.angustifolium	Cyperaceae	4	10.46	0.2	0.45	0.61	1	0	4	2	31.90	163	0.834
Euphorbia.cyparissias	Euphorbiaceae	3	22.57	0.18	1.91	0	1	0	4	2	2.30	53	0.917
Festuca.filiformis	Poaceae	4	14.8	0.23	0.36	0.5	1	0	5	3	22.55	95	0.804
Festuca.gigantea	Poaceae	3	28.73	0.98	3.12	0.4	1	0	7	2	10.47	28	0.842
Festuca.ovina	Poaceae	4	14.8	0.15	0.94	0.83	1	0	5	4	11.76	137	0.889
Festuca.pratensis.agg.	Poaceae	4	25.07	0.55	2.2	0.5	1	0	6	2	14.61	262	0.759
Festuca.rubra.agg.	Poaceae	5	19.36	0.48	1.1	0.5	1	0	6	2	13.01	803	0.854
Festuca.rupicola	Poaceae	4	24.09	0.33	0.58	0.75	1	0	5	3	43.09	23	1.292
Ficaria.verna	Ranunculaceae	3	24.09	0.15	2.64	0.46	1	0	3	2	1.13	37	0.883
Filipendula.ulmaria	Rosaceae	4	24.3	0.79	0.8	0.17	1	0	6	3	11.49	593	0.881
Fragaria.vesca	Rosaceae	5	23.17	0.11	0.3	0.5	1	0	5	2	38.75	52	0.827
Galeopsis.sp.	Lamiaceae	0	33.83	0.35	3.88	0	0	0	7	3	1.37	116	0.826
Galium.aparine	Rubiaceae	0	34.68	0.71	8.9	0	0	0	6	5	1.84	154	0.896
Galium.boreale	Rubiaceae	5	21.78	0.4	0.64	0	1	0	6	2	2.03	55	0.756
Galium.mollugo.agg.	Rubiaceae	4	26.88	0.5	0.71	0	1	0	5	3	2.06	403	0.870
Galium.palustre.agg.	Rubiaceae	4	34.14	0.44	0.91	0	1	0	5	5	1.40	463	0.844
Galium.pumilum	Rubiaceae	0	38.67	0.28	0.5	0	1	0	7	3	38.75	44	0.797
Galium.uliginosum	Rubiaceae	0	33.02	0.27	0.35	0	1	0	6	4	1.88	414	0.782
Galium.verum.agg.	Rubiaceae	4	20.79	0.38	0.58	0	1	0	6	4	1.78	94	0.856
Geranium.pratense	Geraniaceae	3	21.18	0.41	9	0.5	1	0	6	3	0.35	72	0.928
Geum.rivale	Rosaceae	3	20.62	0.32	1.01	0.5	1	0	4	4	12.03	110	0.687
Geum.urbanum	Rosaceae	2	38.46	0.37	1.9	0.05	1	0	5	6	6.22	63	0.830
Glechoma.hederacea	Lamiaceae	6	34.72	0.27	0.69	0	1	0	4	3	38.75	107	0.794
Glyceria.sp.	Poaceae	4	35.53	0.5	1.2	0	1	0	5	4	38.75	187	0.879
Heracleum.sphondylium	Apiaceae	0	22.17	1.23	7.5	0.5	1	0	6	4	5.81	252	0.864
Hieracium.pilosella.agg.	Asteraceae	5	18.63	0.06	0.2	0.81	1	1	5	6	14.78	86	1.027
Holcus.lanatus	Poaceae	4	34.04	0.33	0.3	0.39	1	0	6	3	39.90	688	0.836
Holcus.mollis	Poaceae	5	40.27	0.28	0.3	0.3	1	0	6	3	31.35	356	0.822
Hypericum.maculatum.agg.	Hypericaceae	5	24.98	0.4	0.03	0	1	0	7	2	3.16	575	0.831
Hypericum.perforatum	Hypericaceae	4	26.06	0.36	0.2	0	1	1	7	2	2.92	94	0.976

Hypochaeris.radicata	Asteraceae			2	22.22	0.07	0.8	1	1	0	6	4	38.75	128	0.907
Impatiens.noli.tangere	Balsaminaceae			0	45.38	0.42	4.98	0	0	0	7	2	1.35	76	1.025
Impatiens.parviflora	Balsaminaceae	inv	neo	0	14.55	0.46	8	0	0	0	6	4	0.61	42	1.012
Iris.pseudacorus	Iridaceae			4	16.05	0.75	49	0.5	1	0	5	2	1.24	31	1.303
Juncus.articulatus	Juncaceae			5	19.38	0.3	0.02	0.36	1	0	7	3	2.13	118	0.764
Juncus.conglomeratus	Juncaceae			5	4.9	0.72	0.02	0	1	0	5	3	5.01	249	0.755
Juncus.effusus	Juncaceae			5	10.94	0.9	0.02	0	1	0	6	3	3.11	562	0.884
Juncus.filiformis	Juncaceae			4	9.83	0.3	0.02	0.08	1	0	6	3	1.55	256	0.801
Knautia.arvensis.agg.	Dipsacaceae			0	19.71	0.43	4.24	0.5	1	0	7	2	1.24	258	0.833
Laserpitium.prutenicum	Apiaceae			0	12.81	0.36	2.546	0.5	0	0	7	2	38.75	24	0.713
Lathyrus.pratensis	Fabaceae			5	25.42	0.57	12	0	1	0	6	3	0.93	469	0.792
Leontodon.autumnalis	Asteraceae			3	25.91	0.07	0.7	1	1	0	7	3	6.90	122	1.077
Leontodon.hispidus	Asteraceae			3	25.8	0.24	1.1	1	1	0	6	5	5.46	251	0.870
Leucanthemum.vulgare.agg.	Asteraceae			4	19.27	0.36	0.41	0.5	1	0	6	5	1.06	396	0.840
Linaria.vulgaris	Scrophulariaceae	nat	ar	4	19.98	0.42	0.16	0	1	0	6	5	21.52	33	0.903
Linum.catharticum	Linaceae			0	30.16	0.12	0.15	0	0	0	6	2	2.00	22	0.803
Lolium.perenne	Poaceae			4	25.67	0.13	2	0.5	1	0	5	6	12.10	49	0.922
Lotus.corniculatus.agg.	Fabaceae			0	23.65	0.43	1.16	0	1	0	6	3	38.75	241	0.878
Lotus.uliginosus	Fabaceae			0	31.6	0.35	1	0	1	0	6	2	0.32	105	0.778
Luzula.campestris.agg.	Juncaceae			4	22.97	0.27	0.6	0.5	1	0	3	2	0.56	468	0.816
Lychnis.flos.cuculi	Lamiaceae			0	24.22	0.41	0.19	0.44	1	0	5	3	38.75	581	0.806
Lycopus.europaeus	Lamiaceae			5	63.35	0.57	0.3	0	1	0	7	3	5.07	163	0.992
Lysimachia.nummularia	Primulaceae			5	29.94	0.45	0.179	0	1	0	5	3	0.40	300	0.824
Lysimachia.vulgaris	Primulaceae			5	26.32	0.9	0.14	0	1	0	6	3	0.92	583	0.917
Lythrum.salicaria	Lythraceae			0	27.11	0.71	0.68	0	1	0	7	3	5.77	273	0.953
Medicago.lupulina	Fabaceae			0	27.24	0.25	1.6	0.17	0.3	0	5	6	1.28	38	0.985
Mentha.sp.	Lamiaceae			5	41.83	0.25	0.2	0	1	0	6	5	2.36	186	0.776
Molinia.caerulea.agg.	Poaceae			2	19.64	0.79	0.7	1	1	0	7	3	26.78	122	0.778
Myosotis.palustris.agg.	Boraginaceae			5	43.06	0.28	0.31	0	1	0	5	5	1.41	495	0.803
Nardus.stricta	Poaceae			4	10.39	0.12	0.4	0.5	1	1	5	2	12.49	265	0.815
Pedicularis.sylvatica	Orobanchaceae			0	11.55	0.12	1.07	0.5	0.3	0	6	3	0.14	39	0.760
Persicaria.amphibia	Polygonaceae			6	18.38	0.5	0.666	0	1	0	6	4	38.75	69	0.844
Peucedanum.palustre	Apiaceae			0	18.56	0.86	2.51	0.5	0.3	0	7	2	38.75	153	0.940

Phalaris.arundinacea	Poaceae	5	24.42	1.45	0.7	0	1	0	6	2	30.11	294	0.916
Phleum.pratense.agg.	Poaceae	3	25.08	0.37	0.4	0.5	1	0	6	3	38.75	207	0.785
Phragmites.australis	Poaceae	5	16.3	2.5	0.11	0	1	0	7	3	38.75	84	1.011
Pimpinella.major	Apiaceae	0	23.58	0.66	2.2	0.5	1	0	6	4	1.89	51	0.865
Pimpinella.saxifraga	Apiaceae	0	15.8	0.41	1.26	0.5	1	0	7	3	2.36	196	0.914
Plantago.lanceolata	Plantaginaceae	0	18.52	0.16	1.3	0.75	1	0	5	6	3.89	531	0.884
Plantago.major.agg.	Plantaginaceae	2	22.45	0.37	0.2	0.6	1	0	6	5	3.17	88	0.756
Plantago.media	Plantaginaceae	0	19.26	0.17	0.32	0.78	1	0	5	5	4.53	43	0.825
Poa.angustifolia	Poaceae	4	21.19	0.3	0.17	0.5	1	1	5	2	31.38	22	0.772
Poa.palustris	Poaceae	4	29.28	0.82	0.184	0.17	1	1	6	2	44.91	157	0.734
Poa.pratensis.agg.	Poaceae	5	21.19	0.3	0.3	0.5	1	1	5	2	22.63	395	0.823
Poa.trivialis	Poaceae	4	30.98	0.65	0.2	0.5	1	0	6	2	38.75	380	0.838
Polygala.vulgaris.agg.	Polygalaceae	0	18.4	0.05	1.8	0	1	0	5	4	1.59	47	0.763
Potentilla.anserina	Rosaceae	6	23.07	0.13	0.9	0.47	1	0	5	4	5.12	61	0.735
Potentilla.erecta	Rosaceae	2	25.68	0.17	0.4	0.08	1	0	5	4	19.43	454	0.812
Potentilla.palustris	Rosaceae	4	19.02	0.35	0.43	0	1	0	6	2	7.08	159	0.881
Prunella.vulgaris	Lamiaceae	5	29.55	0.12	1.2	0	1	0	6	4	1.10	276	0.817
Ranunculus.acris	Ranunculaceae	3	23.07	0.26	1.5	0.55	1	0	5	5	5.85	702	0.842
Ranunculus.auricomus.agg.	Ranunculaceae	3	31.93	0.18	2.36	0.5	1	0	4	2	38.75	386	0.755
Ranunculus.bulbosus	Ranunculaceae	3	18.14	0.18	2.566	0.5	1	0	5	3	2.54	21	0.833
Ranunculus.flammula	Ranunculaceae	4	16.99	0.22	0.47	0.3	1	0	5	5	3.98	217	0.803
Ranunculus.repens	Ranunculaceae	6	24.45	0.24	2.5	0.45	1	0	5	4	4.33	538	0.835
Rhinanthus.minor	Orobanchaceae	0	19.8	0.38	2.51	0	0	0	5	5	1.56	50	0.714
Rubus.idaeus	Rosaceae	4	24.7	1.2	1.4	0	1	0	5	2	5.69	59	0.763
Rubus.sp.	Rosaceae	4	15.63	0.48	2.23	0	1	1	5	3	38.75	115	0.874
Rumex.acetosa	Polygonaceae	3	29.34	0.51	0.8	0.5	1	0	5	3	1.86	690	0.840
Rumex.acetosella	Polygonaceae	5	24.09	0.15	0.7	0.5	1	0	5	3	0.58	33	0.851
Rumex.aquaticus	Polygonaceae	4	24.32	1	2.11	0.5	1	0	7	2	0.41	50	0.988
Rumex.crispus	Polygonaceae	0	24.1	0.64	1.5	0.5	1	0	6	3	1.59	92	0.764
Rumex.obtusifolius	Polygonaceae	0	29.71	0.51	1.5	0.5	1	0	7	2	0.99	269	0.810
Sanguisorba.minor	Rosaceae	0	20.5	0.21	7.3	0.38	1	0	5	4	2.21	30	0.791
Sanguisorba.officinalis	Rosaceae	2	22.01	0.48	2.1	0.13	1	0	6	4	5.28	717	0.846
Scirpus.sylvaticus	Cyperaceae	6	22.39	0.78	0.13	0.5	1	0	5	3	6.06	575	0.864

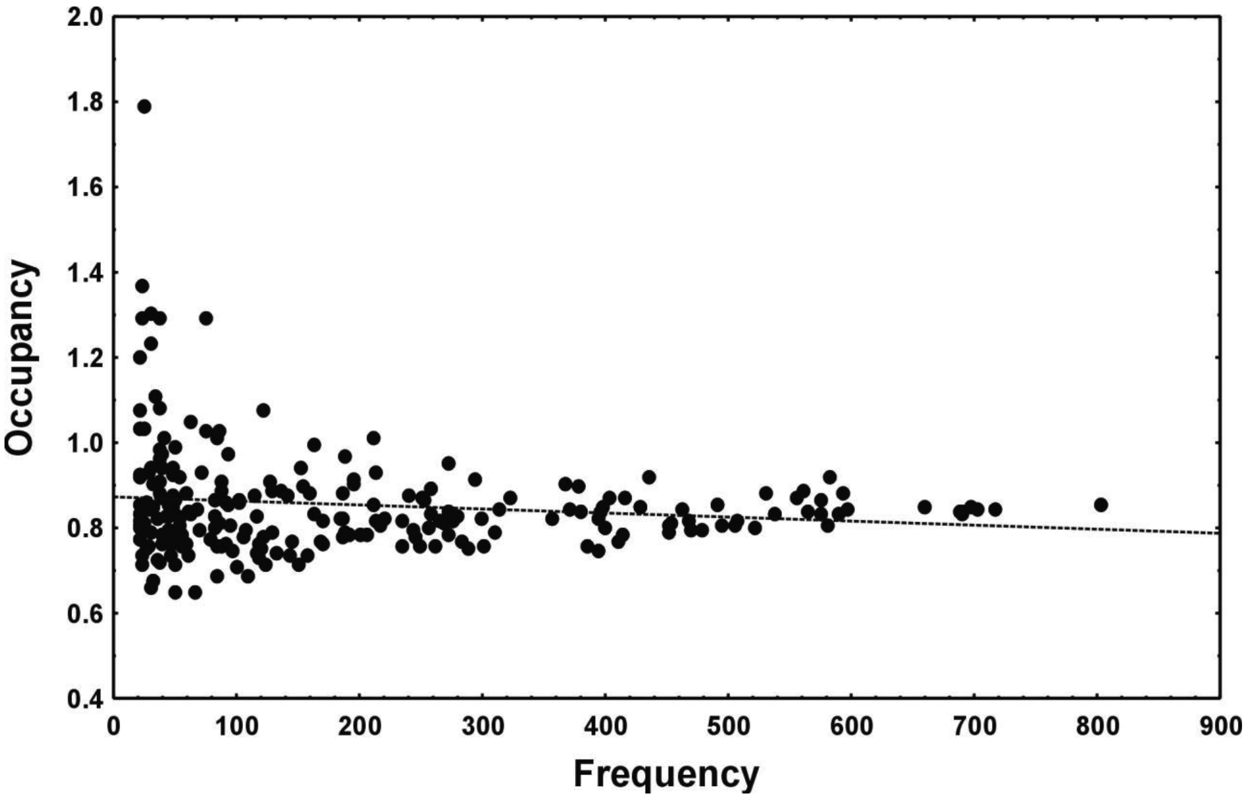
Scorzonera.humilis	Asteraceae			0	19.13	0.25	4.07	0.5	1	0	5	2	38.75	36	0.725
Scrophularia.nodosa	Scrophulariaceae			4	26	0.58	0.11	0	1	0	6	4	38.75	53	0.824
Scutellaria.galericulata	Lamiaceae			6	39.51	0.24	0.75	0	1	0	6	4	0.64	259	0.891
Securigera.varia	Fabaceae			4	30.31	0.44	3.3	0	1	0	6	3	1.00	49	0.943
Selinum.carvifolia	Apiaceae			3	18.79	0.48	1.49	0.5	1	0	7	2	3.13	116	0.741
Senecio.ovatus	Asteraceae			5	32.83	0.9	1.17	0	1	0	7	3	20.41	129	0.885
Solanum.dulcamara	Solanaceae			5	34.64	0.87	44	0	1	0	6	3	38.75	23	1.369
Sparganium.erectum	Typhaceae			5	19.49	0.38	16.67	0.5	1	0	6	3	38.75	37	1.292
Stachys.sylvatica	Lamiaceae			5	41.8	0.49	1.4	0	1	0	6	4	3.07	45	0.853
Stellaria.alsine	Caryophyllaceae			5	34.9	0.19	0.09	0	1	0	5	3	38.75	60	0.880
Stellaria.graminea	Caryophyllaceae			4	28.95	0.31	0.27	0	1	0	5	3	0.90	506	0.805
Stellaria.nemorum	Caryophyllaceae			5	46.38	0.33	0.26	0	1	0	5	5	1.12	21	1.033
Succisa.pratensis	Dipsacaceae			2	17.94	0.34	1.3	0.21	1	0	7	3	1.24	235	0.758
Symphytum.officinale	Boraginaceae			0	25.02	0.57	11.13	0.5	1	0	5	3	1.17	83	0.798
Tanacetum.vulgare	Asteraceae	nat	ar	5	20.61	0.83	0.2	0	1	0	7	3	6.44	79	0.771
Taraxacum.sp.	Asteraceae			0	29.08	0.2	0.7	0.67	1	0	4	2	14.23	416	0.872
Tephroseris.crispa	Asteraceae			3	24.09	0.45	0.523	0.5	1	0	5	2	38.75	97	0.748
Thymus.pulegioides	Lamiaceae			0	24.68	0.18	0.15	0	1	0	6	5	1.91	82	0.864
Tragopogon.orientalis	Asteraceae			0	30.81	0.4	5.07	0.5	0	0	5	3	13.10	22	1.201
Trifolium.dubium	Fabaceae			0	25.96	0.23	0.4	0	0	0	5	5	1.29	70	0.796
Trifolium.hybridum	Fabaceae			0	24.9	0.35	0.7	0	1	0	5	5	0.54	50	0.648
Trifolium.medium	Fabaceae			0	20.61	0.4	1.8	0	1	0	6	3	0.32	27	0.859
Trifolium.pratense	Fabaceae			0	23.37	0.28	1.5	0.08	1	0	6	4	1.15	428	0.850
Trifolium.repens	Fabaceae			6	31.44	0.35	0.6	0	1	0	5	5	1.29	398	0.849
Trisetum.flavescens	Poaceae			4	20.73	0.55	0.4	0.4	1	0	5	2	62.01	323	0.868
Trollius.altissimus	Ranunculaceae			3	22.59	0.28	1	0.5	1	0	5	2	3.87	32	0.678
Typha.angustifolia	Typhaceae			6	6.58	1.5	0.16	0	1	0	7	2	783.12	26	1.789
Typha.latifolia	Typhaceae			6	11.59	1.5	0.1	0	1	0	7	2	1150.65	75	1.290
Urtica.dioica	Urticaceae			6	28.48	0.88	0.1	0	1	0	7	4	38.75	436	0.918
Vaccinium.myrtillus	Ericaceae			4	20.72	0.31	0.3	0	1	0	4	5	38.75	37	0.965
Vaccinium.vitis.idaea	Ericaceae			3	7.66	0.13	0.3	0	1	0	5	4	38.75	25	1.030
Valeriana.dioica	Valerianaceae			4	30.3	0.18	0.55	0.25	1	0	5	2	3.11	132	0.739
Veronica.arvensis	Plantaginaceae	nat	ar	0	25.75	0.11	0.12	0	0	0	3	8	3.50	28	0.756

Veronica.beccabunga	Plantaginaceae			5	24.78	0.33	0.14	0	1	0	5	4	10.33	37	1.080
Veronica.chamaedrys.agg.	Plantaginaceae			4	31.6	0.25	0.21	0	1	0	5	3	4.03	597	0.841
Veronica.officinalis	Plantaginaceae			3	27.61	0.13	0.13	0	1	0	6	3	4.31	170	0.818
Veronica.scutellata	Plantaginaceae			5	28.67	0.17	0.19	0	1	0	6	4	4.81	45	0.825
Veronica.serpyllifolia	Plantaginaceae			4	22.86	0.14	0.05	0	1	0	5	5	5.50	49	0.776
Vicia.angustifolia	Fabaceae	nat	ar	4	22.41	0.38	38.6	0	0	0	5	3	0.83	21	0.853
Vicia.cracca.agg.	Fabaceae			5	25.43	0.88	14.7	0	1	0	6	3	1.10	451	0.787
Vicia.sativa.agg.	Fabaceae			0	22.86	0.55	38.6	0	0	0	5	3	0.14	22	1.078
Vicia.sepium	Fabaceae			4	38.71	0.47	18.7	0	1	0	5	2	0.22	37	0.719
Viola.canina	Violaceae			0	24.37	0.1	1.11	0	1	0	5	2	0.46	47	0.733
Viola.palustris	Violaceae			3	36.63	0.09	0.81	1	1	0	5	2	0.70	211	0.853

Appendix 3. Matrix of Pearson correlation coefficients (r) between species functional traits. The matrix included trait data only for the most frequent species included in the models, i.e., only for species occurring in > 20 patches (n=228). ***, **, *, and n.s. indicate p<0.001, <0.01, <0.05, and non-significant, respectively.

Trait	Clonal index	SLA	Plant height	Seed mass	Rosettes	Perennial	Apomictic	Start of flowering	Duration of flowering
SLA	-0.05 n.s								
Plant height	0.10 n.s.	-0.05 n.s.							
Seed mass	-0.29 ***	0.09 n.s.	0.10 n.s.						
Rosettes	-0.08 n.s.	-0.14 *	-0.23 ***	0.15* n.s.					
Perennial	0.44***	-0.08 n.s.	0 n.s.	-0.20**	0.10 n.s.				
Apomictic	0.10 n.s.	-0.10 n.s.	-0.07 n.s.	-0.05 n.s.	0.01 n.s.	0.07 n.s.			
Start of flowering	-0.10 n.s.	0 n.s.	0.45***	-0.03 n.s.	-0.14 *	0.04 n.s.	-0.03 n.s.		
Duration of flowering	-0.11 n.s.	0.14 *	-0.21 **	-0.05 n.s.	-0.11 n.s.	-0.14 *	-0.01 n.s.	-0.26 ***	
Dispersal distance	0.25 ***	-0.11 n.s.	0.18**	-0.34***	0.01 n.s.	0.11 n.s.	0.09 n.s.	0.18 **	-0.16 *

Appendix 4. The correlation between species frequency and occupancy in the landscape.



Appendix 5. Models for the occupancy index with and without frequency, including all patches and models with phylogenetic corrections considering habitat management, isolation, and wetness. (+) or (-) indicate a positive or negative direction of the relationship, respectively. ***, **, *, and . indicate $p < 0.001$, < 0.01, < 0.05, and < 0.1, respectively; the absence of these symbols indicates that the trait was not significant but that its inclusion significantly improved the model.

Type of patches	All patches		Management				Isolation				Wetness			
			Managed		Abandoned		Isolated		Non-isolated		Wet		Dry	
Explained variable	Occupancy		Occupancy		Occupancy		Occupancy		Occupancy		Occupancy		Occupancy	
Traits	Without frequency	Including frequency	Without frequency	Including frequency	Without frequency	Including frequency	Without frequency	Including frequency	Without frequency	Including frequency	Without frequency	Including frequency	Without frequency	Including frequency
Plant height	(+)*	(+)*	(-).	(-)**	(+)**	(+)**					(+)**	(+)**	(-)*	(-)*
Clonal index			(-).	(-)	(+).	(+)*					(+)***	(+)***	(-)***	(-)***
Perennial				(-)										
SLA			(+)**	(+)**	(-)*	(-).								
Rosettes			(+)*	(+)	(-)**	(-)*	(-)*	(-)*						
Start of flowering														
Duration of flowering			(+)**	(+)**	(-)*	(-).	(+)	(+)	(-).	(-).			(+)*	(+)*
Seed mass	(+)**	(+)**	(-).		(+)**	(+)*	(+)**	(+)**			(+)	(+)		
Apomictic														
Dispersal distance	(+)***	(+)***	(-)***	(-)***	(+)***	(+)***	(+)***	(+)***	(+)*	(+)*	(+)*	(+)*		
Frequency				(+)***		(-)***								
Adj. R^2	0.19	0.19	0.21	0.28	0.30	0.33	0.07	0.07	0.12	0.12	0.20	0.20	0.17	0.17

Chapter IV

Effects of grassland fragmentation and management on community-specific taxonomic, functional and phylogenetic diversity

Manuscript

Effects of grassland fragmentation and management on community-specific taxonomic, functional and phylogenetic diversity

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Abstract

The diversity of semi-natural grasslands in the present-day landscape is endangered by many ongoing processes such as loss of habitat area, loss of connectivity or changes in management. Our evaluation of individual risks is, nevertheless, dependent on the way in which we consider diversity. Using different facets of diversity could help to evaluate the effects of fragmentation not only on species composition but also on phylogenetic relatedness within communities or community functions. In this study we tested the mutual relationships between taxonomic, functional and phylogenetic diversity measures, including either richness only, or both richness and evenness. Further, the influence of patch area, connectivity, presence of traditional management and community type on different measures of diversity was assessed. On the example of Central European grasslands, we found richness-based measures of diversity to be more influenced by patch area and patch connectivity than the other diversity measures including evenness. This, however, does not apply to the taxonomic component of diversity that was also the only one reflecting the management regime. Although our study demonstrates that taxonomic diversity, which is the most often used in

conservation practices, is the most sensitive to landscape fragmentation and management, we should keep in the mind that especially abundance-weighted measures of taxonomical, functional and phylogenetical diversities do not strongly correlate and their relationship is not consistent through the community types. In consequence different diversity facets have different meaning and suitability for nature conservation.

Introduction

Habitat loss and fragmentation are some of the main reasons behind the deterioration of biodiversity in our world. Smaller habitat fragments can host smaller numbers of individuals, smaller populations are prone to extinction, and recolonization of patches is hindered by the scarcity of long-distance dispersal and a lack of vectors (Ozinga et al. 2009, Damschen et al. 2008). The edge effect is becoming more important because it brings in potentially highly competitive species from surrounding communities (Sengl et al. 2016), and small patches are more prone to land use changes (Koper et al. 2010). The effect of fragmentation on biodiversity, as compared to that of habitat loss, has recently become a topic of debate in which it is argued that fragmentation per se may not be as detrimental as habitat loss (Fahrig 2013, 2017, Fahrig et al. 2019). To test this idea it would require landscapes differing in a degree of a habitat fragmentation but not in habitat total area, which is not easy to find. We propose that focusing on other facets of diversity beyond the number of species may help us to better understand the effect of landscape fragmentation on the biota.

Biological diversity as a measure of habitat value can be based not only on taxonomy (species richness) but also on function (i.e. functional diversity) and phylogeny (phylogenetic diversity; Stuart-Smith et al. 2013, Verdú et al. 2012). Functional diversity is measured using the most important plant traits reflecting plant life-history strategies and ecosystem functions (Tilman et al. 1997, Flynn et al. 2011) and reflects the extent of trait values that individuals within communities attain. Functional diversity within a community may be reduced by changed abiotic or biotic conditions and may signalize a deterioration of ecosystem services provided by the community, potentially threatening ecosystem sustainability (Cadotte et al. 2011, Fontaine et al. 2005). The use of functional diversity is, however, based on the assumption that all important plant functions are covered, which is not usually the case, because our knowledge about some plant functions (for example nutrient acquisition, Freschet & Rumet 2018) is still rudimentary. Phylogenetic diversity is considered a surrogate to functional diversity because plant relatedness tacitly encompasses similarity in functional traits (Cadotte et al. 2009, Egorov et al. 2014). Therefore, communities recruiting species from unrelated clades are expected to have greater functional diversity than communities composed from related taxa.

Besides richness itself, diversity may include another characteristic, referred to as evenness. It expresses the degree to which a community is dominated by a single species, functional or taxonomic group (Mulder et al. 2004). Increasing dominance may be one of the first warning signals before a drop in diversity because rare species are easily lost as a result of random processes (Fischer & Stöcklin 2002). However, it does not mean that with rare species we also lose functions, as there is a functional redundancy in communities (Joner et al. 2011). Functional and phylogenetic evenness may, therefore, be the least sensitive measure of landscape degradation.

Although all diversity measures have been applied to various systems, their responses to different biotic and abiotic factors are difficult to generalize. Sometimes functional and phylogenetic richness responded to environmental gradients or land use changes in the same way (Flynn et al. 2011, Verdú et al. 2012), but sometimes each measure of diversity responded uniquely (Rader et al. 2014, Mauchamp 2014, Giehl 2015, Morelli et al. 2018), or their response was discrepant for different communities (Morelli et al. 2018). Abundance-weighted diversity measures (e.g. evenness), moreover, are yet to be studied at the landscape level, as for this level there is a lack of data on plant abundance.

In our study, we attempted to test idea that by using different diversity measures it is possible to reveal how seriously habitat loss and fragmentation affect communities. We hypothesized that, with decreasing patch size and connectivity, species richness, but not necessarily functional and phylogenetic richness, would decrease. We also predicted that functional and phylogenetic evenness would be the least affected by patch degradation (Barber et al. 2017). We specifically aimed at answering the following questions: (1) Are different measures of diversity correlated and do these correlations depend on the type of community? (2) How are different diversity measures influenced by factors of current landscape fragmentation (patch size and connectivity)? and (3) Is this relationship affected by management intensity and community type?

We attempted to answer these questions by comparing 752 patches of grassland communities of four types subjected to different management regimes, all located within a 15×26.5 km landscape quadrat in the central part of Czechia. The patches differed in their size and connectivity, and for each of them we calculated species, functional and phylogenetic diversity either based on presence of species (richness) or on presence and abundance (evenness).

The communities under study represent semi-natural grasslands, which are often seen as hotspots of biodiversity in the European landscape (Poschlod and Wallis De Vries 2002, Wilson et al. 2012, Chytrý et al. 2015). They originated under low-intensity grazing or mowing and once covered a large area in Central Europe; however, during the last century, habitat loss, fragmentation and degradation caused by management intensification, homogenization and abandonment led to a considerable loss of biodiversity at various trophic levels (Gibson 1992, Kruess & Tscharntke 2002).

Methods

Study landscape

The study landscape, 395 km^2 in area, is situated in central Bohemia (center: 49°48′ N, 15°48′ E). The area includes a large part of the Železné hory and Ždárské vrchy Protected Landscape Areas. For more information, see Janečková et al. (2017). Grassland communities in this region underwent dramatic changes over the course of the last century, namely: (1) Small fields were joined into large plots so that they could be managed by heavy machinery, (2) marginal plots were abandoned and afforested, and (3) their management was intensified by fertilization and the introduction of nutrient-demanding, high-productive species. Today, grasslands under extensive use represent only 3.8% of the area of the region under study and cessation of management severely threatens the species diversity of these remnants.

Vegetation mapping

We sampled all grassland patches within the landscape and recorded four community types (according to classification in Chytrý 2007, 2011): (1) dry-mesic tall grassland (classified as the *Arrhenatherion elatioris* alliance), (2) dry short *Nardus* grassland (*Violion caninae* alliance), (3) fens and mires (*Sphagno warnstorfii-Tomentypnion nitensis*, *Caricion canescenti-nigrae* and *Sphagno-Caricion canescentis* alliances) and (4) wet grasslands (*Calthion palustris*, and *Molinion caerulae* alliances), which were the most common habitat type (Table 1). We recorded the species composition and abundance in each grassland at the patch scale (using the Braun–Blanquet system, see Mueller-Dombois and Ellenberg 1974). For more information on individual grassland types, see Table 1.

Table 1. Description of differences between habitat types.

Community type	**Number of patches**	**% of managed patches**	**Mean area [ha]**	**Logarithm of mean connectivity**	**Number of species in the species pool**	**Mean number of species**
Arrhenatherion	182	96%	1.48	1.687	311	37
Violion	45	33%	0.39	2.286	173	38
Wet meadows	461	62%	0.75	2.092	362	43
Fens	64	50%	0.46	2.969	218	38
All patches	752	67%	0.88	2.080	431	41

Fragmentation parameters

To measure fragmentation we assessed the connectivity of each individual patch as the similarity index (McGarigal et al. 2002) within a 1-km buffer zone, defined as follows:

$$\text{Similarity index } \sum_{s=1}^{n} \frac{A_{ijs} * sim_{ij}}{h_{ijs}^2},$$

where A_{ijs} is the patch area of neighboring grasslands, sim_{ij} is the similarity between individual patch pairs calculated as (1 – Bray–Curtis dissimilarity), and h_{ijs} is the edge to edge distance to each neighbor patch. Greater values of this index represent connected patches; low values indicate isolated patches. Patch area was measured using QGIS (QGIS Development Team 2017). Both patch area and connectivity were used as their logarithmic values in subsequent statistical analyses.

Diversity parameters

For each patch we calculated values of different diversity measures – taxonomic, functional and phylogenetic. The group of indices based on presence includes the number of species, functional richness (Mason et al. 2005) and Faith’s index (Faith 1992) as the parameters of taxonomic, functional and phylogenetic richness, respectively. Functional richness is the volume of functional space occupied by a community (Villéger et al. 2008, Mason et al. 2005) and Faith’s index represents the sum of branch lengths connecting all species in a community (Faith 1992). The second group of indices based on abundance describes diversity independent of richness (at least mathematically). For taxonomic diversity it was Simpson’s index (Simpson 1949), for functional diversity Rao’s index (Rao 1982) and for phylogenetic diversity phylogenetic Rao’s index (Hardy & Jost 2008), all three indices reflecting species richness as well as evenness. Both functional and phylogenetic Rao’s index are derived from Simpson’s index of diversity (Rao 1982; as quadratic entropy Pavoine et al. 2005; Hardy & Jost 2008, de Bello et al. 2010). Functional Rao’s index measures the average functional distance whereas phylogenetic Rao’s index measures the average phylogenetic distance between any two individuals randomly selected from the assemblage.

Table 2. Description of functional traits considered in the calculation of functional diversity indices.

Trait	**Description**	**Scale**	**Source**
<u>Competition:</u>			
Life history	0. annuals; 1. biennials + monocarpic; 2. perennial, non-clonal; 3. clonal index = 2,3 4. clonal index = 4,5 5. clonal index = 6,7	ordinal	CLOPLA 3.3 + calculation of the clonal index (Johansson, Cousins & Eriksson 2011; Klimešová et al. 2017)
Plant height		continuous – log transformed	Kleyer et al (2008)
SLA	specific leaf area [mg/g]	continuous	Kleyer et al (2008)
<u>Reproduction:</u>			
Pollination mode	1. insect; 2. selfing	nominal	Kleyer et al (2008)
Flowering length	Length of flowering period [number of months]	ordinal	Kühn et al. (2004)
Flowering start	Start of flowering period 1. January–April 2. May 3. June	ordinal	Kühn et al. (2004)
	4. July–August		
<u>Dispersal:</u>			
Dispersal distance	Maximum dispersal distance based on terminal velocity and release height	continuous – log transformed	Kleyer et al (2008) Values of release height and terminal velocity used to compute dispersal distances
Seed mass	Weight of germinule [mg]	continuous – log transformed	Kleyer et al (2008)

Functional traits for the estimation of functional diversity were selected to include traits relevant to competition, reproduction and dispersal ability (Table 2). Based on the observed taxa, the phylogenetic tree in Newick format was extracted from Zanne et al. (2014). To avoid overweighting of early-diverged clades, we excluded Equisetophyta and Polypodiophyta from the phylogenetic tree. To this tree, we added the species *Polygonatum verticillatum,* with the node dividing it from *P. multiflorum* dated to 4.08 million years BP, so the final tree included 431 species.

Statistical analyses

We used both groups of diversity metrics in generalized linear models to reveal their pattern in relation to patch characteristics related to landscape structure (patch area and connectivity) and patch conditions (management regime and community type), which can directly influence diversity patterns (Table 3). For both continuous factors (area and connectivity) we used logarithms of their values. In the cases of categorical explanatory factors (community type and management), we also added their interactions to the models. We fitted the generalized linear models using Statistica (Dell Inc. 2015). To describe the relationships among the diversity measures across all community types, we used the standardized major axis approach as implemented in the 'smatr' package in R (R Development Core Team 2014).

Results

Relationship among diversity measures

Presence-based diversity measures were, in most cases, highly correlated across habitats, in contrast to abundance-weighted measures, where correlations were much weaker or even non-significant, depending on the type of community (Fig. 1, Table 4). Although the correlations were mostly positive when significant (with one exception: a negative relationship of functional vs phylogenetic diversity on *Nardus* grasslands), the common slopes usually differed between community types (Table 4). In the cases of presence-based indices, the most obvious was a slower increase of functional richness than species richness in dry meadows compared to wet meadows

Fig. 1 Correlations among diversity indices. Lines indicate significant correlations within community types (dry meadows – blue, wet meadows – green, *Nardus* grasslands – red, fens – yellow)

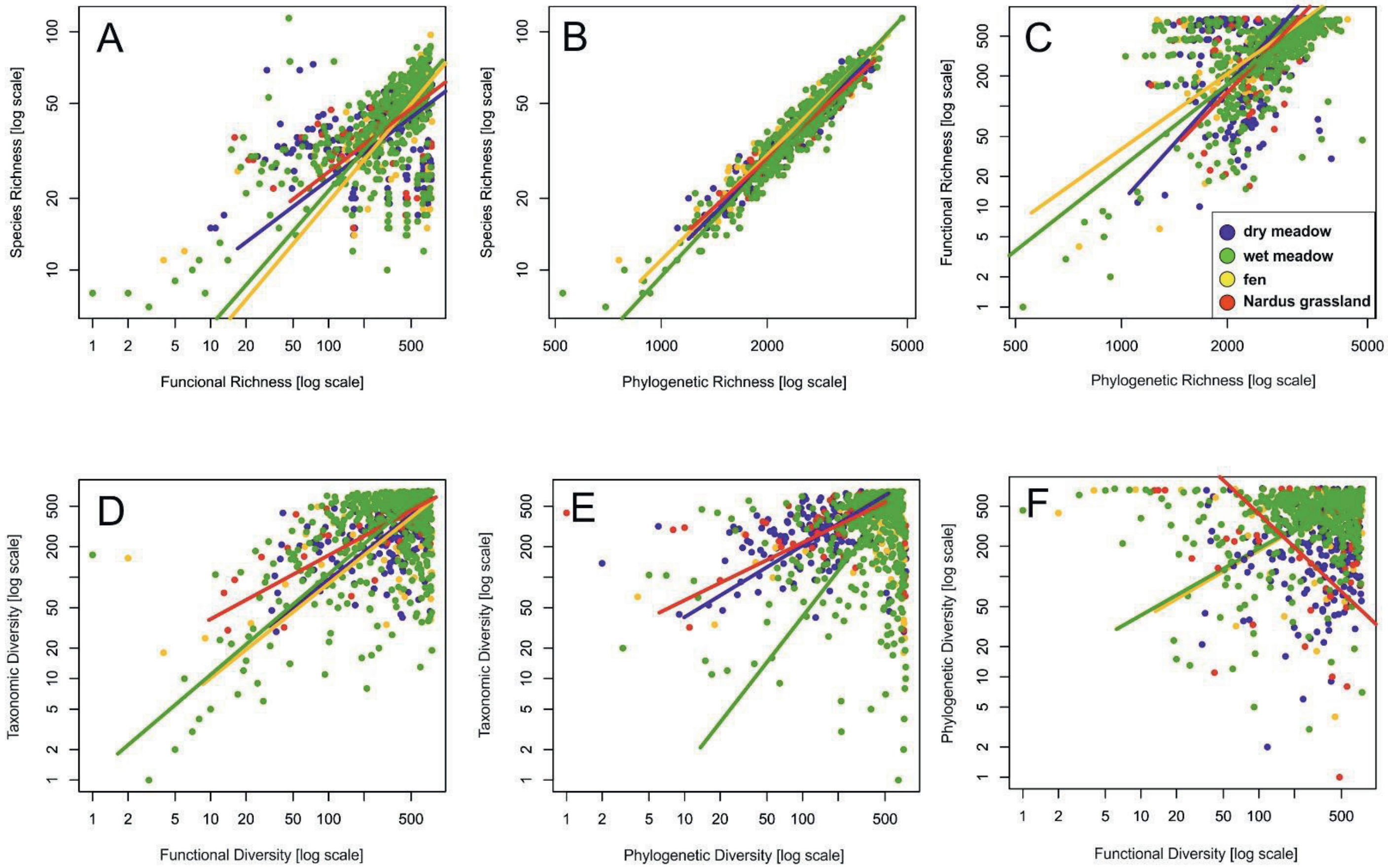


Table 3 Generalized linear models for **(A)** presence-based measures (species richness, functional richness and phylogenetic richness – Faith's index) and **(B)** abundance-weighted diversity measures reflecting both species richness and evenness (taxonomic, functional and phylogenetic diversity) in relation to patch area, connectivity, habitat type and management regime; n=752; arrows the indicate direction (↗ – positive, ↘ – negative) of significant relationships (*** – P < 0.001, ** – P < 0.01, * – P < 0.05).

	(A) Presence-based measures			***(B) Abundance-weighted measures***		
	Species Richness	**Functional Richness**	**Phylogenetic Richness**	**Taxonomic Diversity**	**Functional Diversity**	**Phylogenetic Diversity**
Factor	*F-value*	*F-value*	*F-value*	*F-value*	*F-value*	*F-value*
log area	↗**90.89*** **	↗**42.08*** **	↗**72.96*** **	↗**37.65*** **	0.14	2.78
log connectivity	↗**18.40*** **	↗**9.49** **	↗**14.75*** **	↗ **8.01** **	1.79	0.52
"habitat"	4.64	7.72	6.36	1.31	**11.65** **	**54.53*** **
"management"	↗**4.05* **	0.53	2.40	↗**6.61** **	1.00	0.00
"habitat"*"management"	**9.77* **	7.37	7.33	4.92	2.08	6.85

and fens (Fig. 1A). Dry meadows also differed from wet meadows in the relationship between phylogenetic and functional richness. In dry meadows, compared to wet meadows and fens, functional richness increased quicker than phylogenetic richness (Fig, 1C).

For abundance-weighted indices, significant correlations for all relationship were found only for wet and *Nardus* grasslands (Fig. 1D–F). The most frequently strongly correlated were taxonomic diversity and functional diversity. This correlation was significant for all community types (Fig. 1D). This relationship most obviously differed in the case of *Nardus* grasslands, where taxonomic diversity increased slower with functional diversity compared to meadows of the other types (Fig. 1D). In dry meadows, in contrast to meadows of other types, taxonomic diversity increased more slowly than phylogenetic diversity (Fig. 1D). In fens, taxonomic diversity did not significantly correlate with phylogenetic diversity, and a non-significant relationship was found also between functional and phylogenetic diversity in dry meadows. The only significant negative relationship was shown between functional and phylogenetic diversity in *Nardus* grasslands (Fig. 1F).

Diversity response to patch characteristics

Diversity metrics based on presence reflected their dependence on patch area (Fig. 1). Functional and phylogenetic richness highly correlated with each other as well as with species richness (Fig. 1, Table 4), so adding species with increasing patch area influenced all richness-based measures of diversity (Table 3A, Fig. 2). A similar pattern cropped up also in the relation with patch connectivity (Table 3A). None of the richness metrics differed between the community types. Species richness was the only presence-based metric influenced significantly by the management regime and differences concerning interaction with community type show distinct reactions to management if accounting for individual community types (Table 3A).

Abundance-weighted metrics, which are mathematically independent of species richness, showed significant differences between habitats when considering functional and phylogenetic, but not taxonomic, diversity (Table 3B). Patch area and connectivity correlated significantly only with increasing values of Simpson’s index (i.e. species evenness), and when management was applied, we found greater values of taxonomic, but not of functional and phylogenetic diversity (Table 3B).

Discussion

Using a suit of diversity measures based either on species presence or abundance and representing different facets of taxonomic, functional or phylogenetic diversity, our objective was to reveal the effects of habitat fragmentation on grassland communities in the central part of Czechia. We.

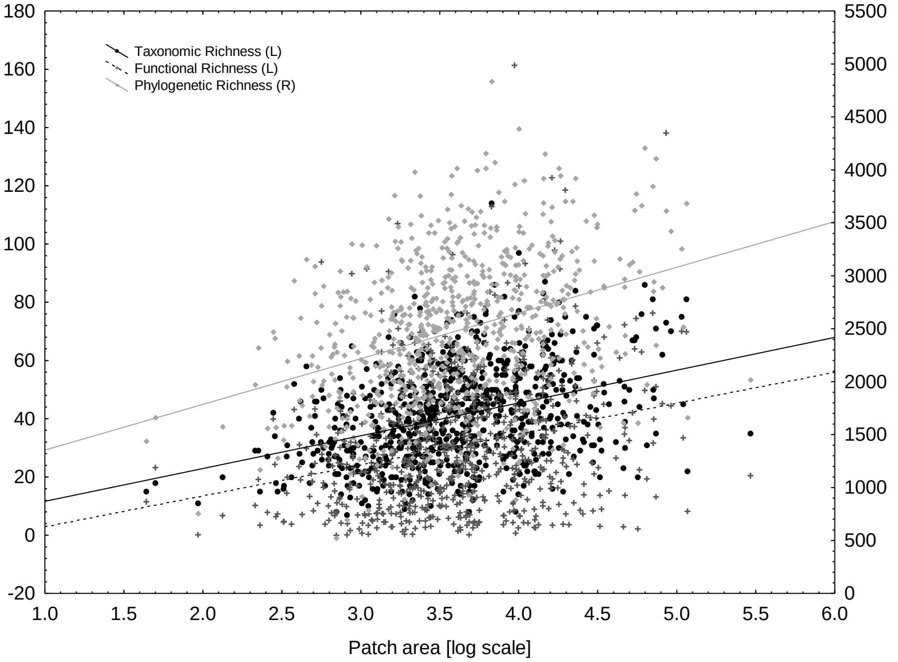


Fig. 2 The relationships between the patch area [log scale] and richness diversity indices (taxonomic, functional and phylogenetic richness)

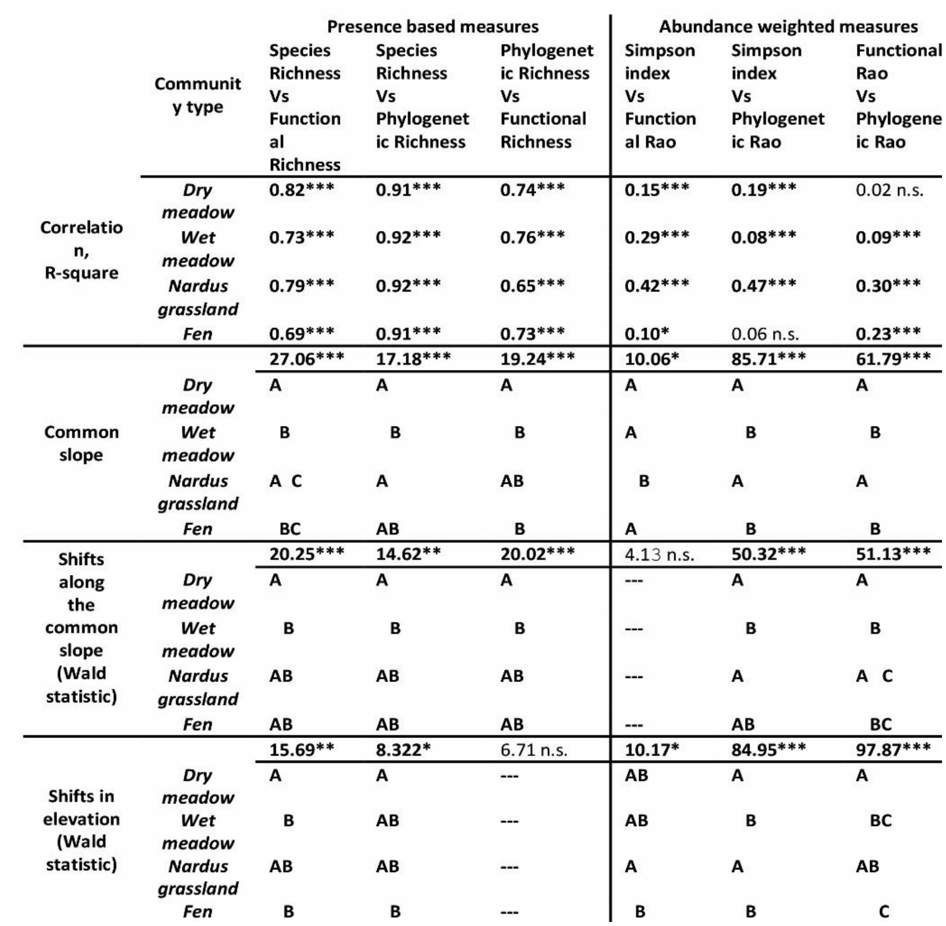
found a positive correlation among all presence-based measures wherein the addition of species directly increases functional and phylogenetic richness Correlations of abundance-weighted measures were, on the other hand, weaker and there were larger differences between community types. In addition, we assessed the relationships between the different diversity measures and landscape properties of grassland patches (i.e. patch size and connectivity), management and community type. Taxonomic diversity was the most sensitive measure, responding to all factors. Functional and phylogenetic diversity were positively correlated with patch size and connectivity but did not respond to community type and management. Functional and phylogenetic evenness (abundance-weighted diversity indices) were affected only by community type, not responding to habitat fragmentation. These results support our idea that different diversity measures differ in their sensitivity to habitat fragmentation, taxonomic diversity being the most sensitive, functional and phylogenetic richness less sensitive, and functional and phylogenetic evenness the least sensitive. This difference can be explained by functional redundancy of grassland species.

Taxonomic versus functional and phylogenetic diversity

Our results do not support the hypothesis that species richness, but not necessarily functional and phylogenetic richness, decreases with decreasing habitat patch size and connectivity in the grassland communities under study. All biodiversity measures based on species presence were similarly sensitive to patch size and connectivity, although species richness was affected by community type and through community type also by management. Communities in small and remote habitat patches are therefore not only poor in species, but these species, moreover, possess a narrower range of trait values and represent limited phylogenetic diversity. These results point out that, in the grassland communities under study, landscape degradation, despite functional redundancy, has consequences not only for species diversity but also for the functioning of the communities and their ecosystem services.

Although the relationship between diversity measures and patch size was significant, it was not narrow. Moreover, especially for patches of intermediate size, species, functional and phylogenetic diversity differed substantially, indicating that other effects of patch quality than those considered in the analysis are important. This is probably due to the fact that environmental conditions in larger patches are more heterogeneous, which allows the survival of a greater number of species with a wider range of functional traits and phylogenetic richness than in smaller, more homogeneous patches. This has been confirmed at the landscape level (Cousins et al. 2007, Öster et al. 2007) but refuted by experiments at smaller scales (Lundholm 2009, Reynolds et al. 2007), which indicates a scale-dependent relationship. At smaller scales,

Table 4. Results of correlations among diversity measures using the standardized major axis approach. **Correlations**: R^2, strength of relationships for individual habitat types. **Common slope**: statistical tests determining whether the slopes for individual habitat types differ from the common slope followed by a post-hoc test if they do. **Shifts along the common slope:** tests determining whether the different habitat types are shifted along the common slope (i.e. along the x-axis) followed by a post-hoc test if they do. **Shifts in elevation**: tests determining whether the individual groups are shifted elevation-wise (i.e. along the y-axis) followed by a post-hoc test if they do. All variables were log-transformed prior to the analysis. Groups with the same letters did not differ significantly in post-hoc tests. Significance levels for correlations: n.s. – P > 0.05; * – 0.05 > P > 0.01; ** – 0.01 > P > 0.001; *** – P < 0.001.



		Presence based measures			Abundance weighted measures		
	Community type	Species Richness Vs Functional Richness	Species Richness Vs Phylogenetic Richness	Phylogenetic Richness Vs Functional Richness	Simpson index Vs Functional Rao	Simpson index Vs Phylogenetic Rao	Functional Rao Vs Phylogeneic Rao
Correlation, R-square	*Dry meadow*	0.82***	0.91***	0.74***	0.15***	0.19***	0.02 n.s.
	Wet meadow	0.73***	0.92***	0.76***	0.29***	0.08***	0.09***
	Nardus grassland	0.79***	0.92***	0.65***	0.42***	0.47***	0.30***
	Fen	0.69***	0.91***	0.73***	0.10*	0.06 n.s.	0.23***
Common slope		27.06***	17.18***	19.24***	10.06*	85.71***	61.79***
	Dry meadow	A	A	A	A	A	A
	Wet meadow	B	B	B	A	B	B
	Nardus grassland	A C	A	AB	B	A	A
	Fen	BC	AB	B	A	B	B
Shifts along the common slope (Wald statistic)		20.25***	14.62**	20.02***	4.13 n.s.	50.32***	51.13***
	Dry meadow	A	A	A	---	A	A
	Wet meadow	B	B	B	---	B	B
	Nardus grassland	AB	AB	AB	---	A	A C
	Fen	AB	AB	AB	---	AB	BC
Shifts in elevation (Wald statistic)		15.69**	8.322*	6.71 n.s.	10.17*	84.95***	97.87***
	Dry meadow	A	A	---	AB	A	A
	Wet meadow	B	AB	---	AB	B	BC
	Nardus grassland	AB	AB	---	A	A	AB
	Fen	B	B	---	B	B	C

the environmental conditions are more similar, so the effects of biotic interactions, such as competition or facilitation, which limit within-community similarity, are more profound (Chalmandrier et al. 2017, MacArthur & Levins 1967, Yang et al. 2014). At the landscape scale, it makes sense to include heterogeneity in patch conditions in analyses to better define differences in diversity between patches.

Another aspect of landscape fragmentation with severe consequences for species richness is decreased habitat connectivity (Damschen et al. 2006, Fischer & Lindenmayer 2007). Isolated patches often suffer from low numbers of propagules and limited pollinator movement among patches (Soons & Heil 2002, Auffret et al. 2017), and due to their poor connectivity, random mortality events cannot be counterbalanced by immigration. Successful establishment is usually the bottleneck in the plant life cycle and it may be hindered not only by the availability of propagules but also by the availability of places suitable for establishment (Piqueray et al. 2013, Vítová & Lepš 2011). Not all plant species are affected by failed regeneration in the same way, as they differ in seed dispersibility and because especially clonal species are more resistant to competitive exclusion. How fast the process of species richness deterioration in a grassland is depends also on its level of productivity (Janeček et al. 2013). In extreme cases, we can speak of extinction debt, a phenomenon in which species for which conditions are no longer sufficiently favorable survives at a site without being able to reproduce effectively. This has been reported especially for long-lived, often clonal plant species (Helm et al. 2006; Kuussaari et al. 2009; Krauss et al. 2010, Lampinen et al. 2018, Otsu et al. 2017). Extinction debt has been found to play a role in some fragmented communities (Johanson et al. 2011) but not in others (Adriaens et al. 2006, Cousins et al. 2007). It probably also affected the diversity measures in our study.

Abundance-weighted diversity measures

We predicted that abundance-weighted indices would be less sensitive to habitat fragmentation than presence-based measures. We have confirmed this idea, as functional and phylogenetic diversity, the measures which include evenness, responded only to community type and not to habitat fragmentation. Although the grassland communities in our landscape quadrat are losing species, ecological functional groups and whole taxonomic groups, they are still balanced with regard to functional traits and phylogenetic composition.

Some studies suggest that traits of the most abundant species could be more relevant to ecosystem functioning than any other diversity measure, including the traits of all species in the community (Mokany et al. 2008, Griffin et al. 2009, Sasaki & Lauenroth 2011); however, the proportion of abundant species is scale-dependent. Species dominant in smaller patches are usually more evenly distributed in larger patches, where they are subdominant. This is probably again linked to the greater heterogeneity of environmental conditions in larger patches. It seems that, in the case of taxonomic diversity, both richness and evenness increased in larger patches whereas neither functional nor phylogenetic diversity changed with patch area. We, therefore, assume that phylogenetic diversity and vegetation functions are similar in small and large patches. A similar relationship between functional diversity and patch area has been described by Karadimou et al. (2015) for plant communities on volcanic islands.

Our results show a similar positive relationship between connectivity and taxonomic diversity, but neither in functional nor in phylogenetic abundance-based diversity measures. This indicates random loss of species rather than loss of certain specific functions or phylogenetic groups. In other words, with decreasing patch connectivity, rare species are lost first; however, rare species possess a similar combination of functional traits as common species. More isolated patches then host fewer species without losing their main ecological functions. This can be both good and bad news at the same time because, when a landscape is losing habitat connectivity, the functions of the ecosystem in isolated patches are preserved, albeit with lower species richness. On the other hand, the resilience of the grasslands to further deterioration decreased and, in such a case, poorly connected patches may be more endangered. However, appropriate management can increase species richness in small and isolated patches and improve the conditions in remnant grassland patches so that they support more species and improve regional connectivity and diversity (Williams et al. 2006).

We encourage the use of taxonomic richness and diversity as suitable measures for assessing the effects of fragmentation at the landscape level because they are the most sensitive measures compared to measures of the phylogenetic and functional components of diversity. Other facets of diversity may, however, bring about a deeper understanding of the consequences of habitat loss and fragmentation. Our results further imply that heterogeneity of large habitat patches and extinction debt are preventing us from gaining a full understanding of ongoing processes by measuring diversity only. At the same time, however, large patches may serve as refuge until habitat quality improves, for example as a result of conservation management.

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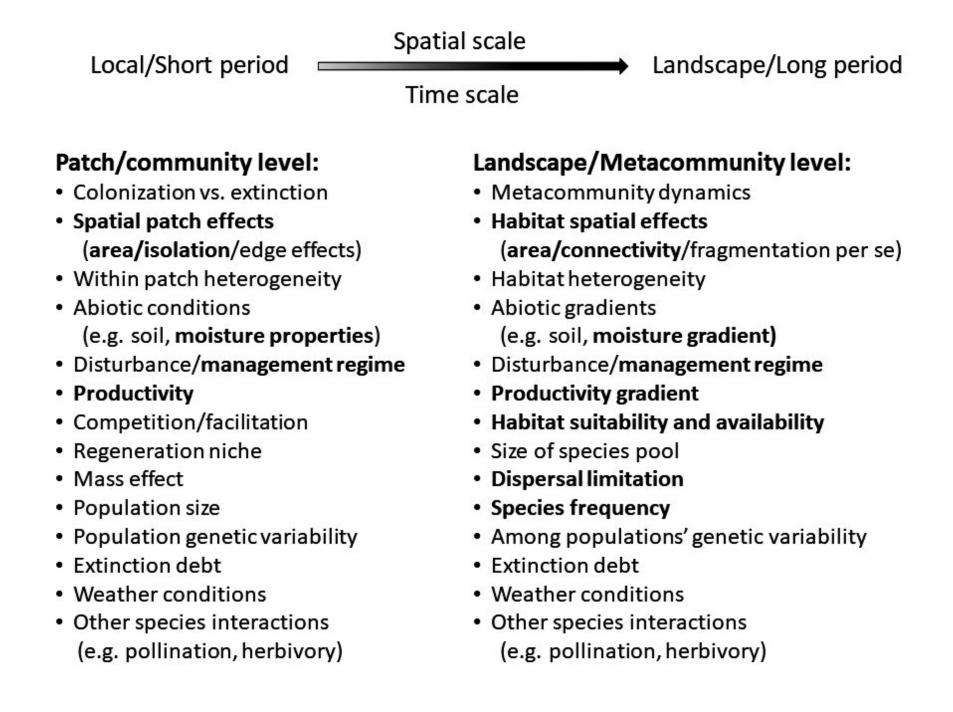
Chapter V

Summary

Summary

Plant species coexistence can be seen as a dynamic system with some stable equilibria operating at different spatial and time scales. The changes in landscape take place simultaneously and along many environmental gradients (moisture, productivity, elevation, land-use intensity), In addition, the most important factors at appropriate scale driving the species coexistence may be different between regions. Processes at small scale affect the pattern at larger scales and vice versa. I listed the most often reported processes and effects that act at different spatial and time scales in Fig. 1. and highlighted those which were considered in this thesis.



Patch/community level:

- Colonization vs. extinction
- **Spatial patch effects**
  (**area/isolation**/edge effects)
- Within patch heterogeneity
- Abiotic conditions
  (e.g. soil, **moisture properties**)
- Disturbance/**management regime**
- **Productivity**
- Competition/facilitation
- Regeneration niche
- Mass effect
- Population size
- Population genetic variability
- Extinction debt
- Weather conditions
- Other species interactions
  (e.g. pollination, herbivory)

Landscape/Metacommunity level:

- Metacommunity dynamics
- **Habitat spatial effects**
  (**area/connectivity**/fragmentation per se)
- Habitat heterogeneity
- Abiotic gradients
  (e.g. soil, **moisture gradient)**
- Disturbance/**management regime**
- **Productivity gradient**
- **Habitat suitability and availability**
- Size of species pool
- **Dispersal limitation**
- **Species frequency**
- Among populations' genetic variability
- Extinction debt
- Weather conditions
- Other species interactions
  (e.g. pollination, herbivory)

Fig. 1 Processes and effects underlying the dynamics in plant species coexistence at different spatial and time scales. Studied factors are given in bold.

In chapter II we focused on small scale plant species coexistence in wet meadow communities and described the changes after the fertilization and abandonment, the two main factors that threaten the species richness and influence the community functioning. The functional response of species and whole communities were consistent across meadows that substantially differed in their moisture and productivity level. Both, the fertilization and abandonment consistently increased the proportion of species with high specific leaf area, lighter seeds and clonal growth, irrespective of grasslands´ moisture and productivity baseline conditions. The main process driving the species coexistence was the competition for light which supports taller and clonal species investing more in rapid nutrient uptake and growth.

The landscape scale factors influencing the species occurrence and plant diversity were evaluated in Chapters III and IV. While functional traits can explain a part of the variability in species distribution, the predictive power of individual traits largely depended on patch characteristics such as habitat connectivity, management regime or moisture level. We found more competitive species occurring rather in wetter, more productive grassland communities than in drier meadow types. Management activities favored species with more ruderal traits, smaller, with leaves in rosettes and high specific leaf area. Because the species occurrence was assessed not only based on simple species frequency in patches across the region but also taking into account species potential distribution and suitability of patches, we confirmed a strong effect of the availability of suitable patches within the landscape (Chapter III). For example, the assumption that increased patch isolation hinders species dispersal was confirmed only when potential distribution was considered. The results show that habitat suitability and their availability in the region may considerably change the species distribution (Chapter III).

In Chapter IV the effect of spatial effects such the patch size and patch connectivity was evaluated in relation to different diversity measures. We evaluated the effect of spatial patch characteristics such as degree of isolation and patch area, as well as the effect of management and community type, that include the whole set of environmental conditions. We compared the sensitivity of presence based diversity measures (richness measures) in contrast to abundance-weighted measures (including evenness). The richness measures were all sensitive to fragmentation related factors, the patch size and connectivity, but only taxonomic component reflects also the management. When considering evenness diversity measures, the pattern was the same for taxonomy but the functional and phylogenetic diversity reflected only the community type and their sensitivity to other factors was low.

Although the impact of patch properties on plant diversity may be blurred by other factors such as extinction debt or patch heterogeneity, taxonomic richness can be used as a cost-effective diversity measure sensitive to contemporary landscape changes. Other diversity components, the functional and phylogenetic measures are less sensitive and inconsistent through the community types.

The presented thesis provides a detailed view on the plant coexistence at two spatial scales, the local and landscape scale. The ongoing changes affecting grasslands in the present landscape often include the habitat loss and land-use changes. In particular, management regime and fertilization are factors crucially affecting different components of plant diversity at local scale, while the species occurrence at landscape scale is influenced by moisture level, land-use and the connectivity of remaining habitat patches. At the same time, the plant functional traits may substantially modify the species’ response to biotic and abiotic conditions at both scales. The thesis emphasized that the conservation efforts should be focused not only on the individual localities but consider also the processes at the landscape level.

Chapter VI

Curriculum vitae

Curriculum vitae

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Talk: Pollination and pollinators of an endangered species *Gentianella praecox* subsp. *bohemica* **Janečková**, **P.,** Janeček, Š, Bartoš, M., Hrázský, Z.

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Talk: Reproductive system of the critically endangered species *Gentianella praecox* subsp. *bohemica* **Janečková**, **P.,** Janeček, Š, Bartoš, M., Hrázský, Z.

Talk by Michael Bartoš: Correlation of floral and life history traits with self-compatibility and autonomous selfing at wet meadows communities. Bartoš, M., Janeček, Š., **Janečková**, **P.**, Padyšáková, E., Tropek, R., Götzenberger, L., Klomberg, Y.

Poster: Reproductive traits affecting pollen limitation of plants in a fragmented landscape. Jersáková, J., Janeček, Š., **Janečková**, **P.**, Padyšáková, E., Tropek, R., Götzenberger, L., Klomberg, Y., Bartoš, M.

25–27. 9. 2017, Czech Society for Ecology, Prague, Czechia

Poster: UV reflection and visitors of African *Hypericum*. Padyšáková E., **Janečková P.**, Tropek R., Janeček Š.

28.8.-1.9.2017, 9th International Symposium of Syrphidae (Curitiba, PR, Brazil)

Talk by Ximo Mengual: Spurred flowers and short-proboscid pollinators: challenging Darwin. Vlašánková, A., Padyšáková, E., Bartoš, M., Mengual, X., **Janečková, P.** & Janeček, Š.

10-24. 7. 2015, 58th Annual Symposium of the International Association for Vegetation Science: Understanding broad-scale vegetation patterns Brno, Czechia

Talk: Drivers of taxonomical and functional diversity within fragmented grasslands **Janečková**, P. Janeček, Š., Horník, J., Rocchini, D., de Bello, F.

06.-13. 5. 2001, Conference on Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations Location: České Budějovice, Czechia

Poster: Key factors affecting shoot growth and flowering performance of *Dactvlorhiza fuchsia*. **Janečková, P.,** & Kindlmann, P.

Publications:

Janečková, P., Janeček, Š., Bartoš, M., & Hrázský, Z. (2019). Reproductive system of the critically endangered taxon *Gentianella praecox* subsp. *bohemica*. *Preslia, 91*, 77-92.

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