



The response of simulated grassland communities to the cessation of grazing



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ABSTRACT

Changes in land-use are supposed to be among the severest prospective threats to plant diversity worldwide. In semi-natural temperate grasslands, the cessation of traditional land use like livestock grazing is considered to be one of the most important drivers of the diversity loss witnessed within the last decades. Despite of the enormous number of studies on successional pathways following grazing abandonment there is no general pattern of how grassland communities are affected in terms of diversity, trait composition and pace of succession. To gain a comprehensive picture is difficult given the heterogeneity of environments and the time and effort needed for long-term investigations. We here use a proven individual- and trait-based grassland community model to analyze short- and long-term consequences of grazing abandonment under different assumptions of resource availability, pre-abandonment grazing intensity and regional isolation of communities.

Grazing abandonment led to a decrease of plant functional type (PFT) diversity in all but two scenarios in the long-term. In short-term we also found an increase or no change in Shannon diversity for several scenarios. With grazing abandonment we overall found an increase in maximum plant mass, clonal integration and longer lateral spread, a decrease in rosette plant types and in stress tolerant plants, as well as an increase in grazing tolerant and a decrease in grazing avoiding plant types. Observed changes were highly dependent on the regional configuration of communities, prevalent resource conditions and land use intensity before abandonment. While long-term changes took around 10–20 years in resource rich conditions, new equilibria established in resource poor conditions only after 30–40 years.

Our results confirm the potential threats caused by recent land-use changes and the assumption that oligotrophic communities are more resistant than mesotrophic communities also for long-term abandonment. Moreover, results revealed that species-rich systems are not per se more resistant than species-poor grasslands.

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1. Introduction

Changes in land-use are considered to be among the severest threats to plant diversity worldwide (Sala et al., 2000). In semi-natural temperate grasslands, the cessation of traditional land use practices is considered to be one of the most important drivers of the diversity loss witnessed within the last decades (Poschlod et al., 2005; Hodgson et al., 2005; Habel et al., 2013). These species-rich habitats have mainly evolved through a long history of human

management by livestock grazing or mowing (Ellenberg, 1996; Cousins and Eriksson, 2002; Drobniak et al., 2011; Habel et al., 2013). Thus, such regular biomass removal is a disturbance inherent to the system (Zobel, 1992; Klimeš et al., 2013) and its lapse may have major impacts on species richness, composition and functioning of these communities (Bakker and Ruyter, 1981; Kahmen and Poschlod, 2004; Castro et al., 2010).

So far, the results of the existing grazing abandonment studies have a few findings in common: communities tend to become dominated by taller plant types (Prach and Pyšek, 1997; Kahmen and Poschlod, 2004; Lavorel et al., 2011; Peco et al., 2012; Janeček et al., 2013) with increasing lateral spread (Kahmen and Poschlod, 2004; Klimešová et al., 2008) and an increase in erect/erosulate growth forms respectively the decrease of rosette plants (Dupré and Diekmann, 2001; Peco et al., 2012). Moreover, an increase

Abbreviations: PFT, plant functional type; ZOI, zone of influence; SR, seed rain; SLA, specific leaf area; CWM, community weighted mean.

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in competitors and a decrease of ruderals (sensu Grime, 1977) is repeatedly observed (Drobnik et al., 2011; Prévosto et al., 2011; Paušič, 2012). However, further consistent findings of how communities change following grazing abandonment are missing. This is especially true for species diversity measures: while several studies found decreases in species diversity with land use abandonment (Pykälä et al., 2005; Enyedi et al., 2008; Castro et al., 2010; Ruprecht, 2012; Janeček et al., 2013) others observed no or only minor effects (Luoto et al., 2003; Kahmen and Poschlod, 2004; Peco et al., 2006, 2012; Öckinger et al., 2006; Marriott et al., 2009; Furusawa et al., 2013) or even an increase in diversity (Cremene et al., 2005). Moreover, the “unpredictability” (e.g. Kahmen and Poschlod, 2004) of community changes also applies to different trait patterns (e.g. seed mass, see Kahmen and Poschlod, 2004) and to the pace of community changes (Ellenberg, 1996). Given the heterogeneity of the studied grassland types and environments this variety of responses is not surprising. Moreover, long-term investigations, needing time and effort are rare (but see e.g. the fallow experiments by Schreiber initiated 1974, e.g. Drobnik et al., 2011; Enyedi et al., 2008).

The importance of prevailing soil abiotic conditions has been repeatedly shown for abandoned grassland systems (Douma et al., 2012; Janeček et al., 2013; Klimeš et al., 2013). It has been found in different studies that communities in unproductive habitats respond less strongly or more slowly in diversity and/or composition than communities of rather productive habitats (Pykälä, 2004; Klimeš et al., 2013; Janeček et al., 2013; but see Peco et al., 2006), i.e. they are more resistant to land use changes. Here, we use resistance in terms of the ease or difficulty of changing the system from the stable state (Folke et al., 2004). Other studies found this relationship being dependent on the history of land use and its intensity (Benjamin et al., 2005; Bernhardt-Römermann et al., 2011) or the species richness prior to abandonment (McNaughton, 1977; Prévosto et al., 2011; Vogel et al., 2012). In addition, the regional process of seed dispersal among local communities influences community responses toward land use changes (Ellenberg, 1996; Leibold et al., 2004).

In this study we use a mechanistic individual- and trait-based community grassland model (IBC-grass) to systematically analyze short- and long-term consequences of grazing abandonment on simulated plant communities in specified environments. The model describes the development of a community of perennial plant functional types (PFTs) and was adapted to an extensive vegetation dataset of semi-natural grasslands in Central Europe (Weiss et al., 2014). It has been shown to be a suitable approach to explore and better understand drivers of real-world community patterns (Körner et al., 2014; Weiss et al., 2014). With our approach we ask: (1) How do PFT richness, PFT Shannon diversity, biomass production and functional trait composition change over a time of up to 100 years following abandonment? (2) Do PFT diversity and trait composition change in the same way and – how fast do these changes occur? and (3) How is the resistance of communities related to productivity and species richness prior to abandonment? We analyze these questions in a simulation experiment with 24 scenarios differing in two levels of resource availability, three intensities of pre-abandonment grazing and four modes of regional isolation of communities (i.e. seed rain).

2. Methods

To analyze the effects of grazing abandonment on plant communities we enhanced the individual-based community model of grassland (IBC-grass) developed by May et al. (2009) and as refined by Weiss et al. (2014). A detailed model description that follows the ODD (overview, design concepts, details) protocol for describing individual-based models (Grimm et al., 2006, 2010) is given

in the Supplement Appendix A. We here give a short overview of the model and describe the new features for our analyses (see also Fig. 1 for a graphical view of the model and scheduling of model processes).

2.1. General purpose

The model describes the development of a community of perennial plant functional types (PFTs). It was originally designed to evaluate the response of plant functional type (PFT) diversity toward grazing under different local environmental conditions and differentiated assumptions about plant–plant competition (May et al., 2009). It was enhanced by the incorporation of clonal plant types and adapted to an extensive vegetation dataset of semi-natural grasslands in Central Europe to reproduce effects of grazing intensity, resource availability and external seed rain on small-scale community patterns observed at different hierarchical levels (Weiss et al., 2014). These adaptations concern the initialization of the model with an empirically found regional species/PFT pool and the application of “realistic” scenarios in terms of below-ground resource availabilities and grazing intensities. (Please see also Supplementary data in Appendix B where we shortly describe details of this adaptation to real grassland data implemented in the model.) New modifications presented here address different modes of regional isolation, respectively seed rain into simulated communities.

2.2. Overview of the IBC-grass model

The model is individual-based and spatially explicit and includes the entities seeds, individual plants and grid cells. Each cell can be occupied by the stemming point of one individual plant only, but an individual can cover more than one grid cell depending on its size. The grid is made up of 173×173 discrete cells, each representing 1 cm^2 , simulating an area of approximately 3 m^2 . This scale is justified by the extent of the vegetation records used to adapt the model to data (Weiss et al., 2014; see also Appendix B on adaptation). The state of a grid cell is defined by two constant resource availabilities, above and below ground.

Plant individuals, i.e. individual ramets in the case of clonal plant types or non-clonal individual plants, are characterized by state variables representing their grid position, the mass of three plant compartments (shoot, root and reproductive mass), the presence of growing spacers in case of clonal plant types, and 12 parameters related to traits defining the plant’s functional type. Plant functional types differ in their attributes of six functional trait syndromes that are based on well-documented trade-offs: (1) growth form (the ratio between leaf mass and total shoot mass), (2) maximum plant mass (positively correlated with individual seed mass and negatively correlated with seed number and dispersal distance), (3) resource response (implemented as maximal resource utilization per time step and ZOI area) integrating the trade-off between competitive ability and stress tolerance), (4) grazing response (tolerance by fast re-growth or avoidance by a low palatability, corresponding to SLA), (5) clonal integration (the potential of sharing resources between ramets via persistent connective tissues) and (6) length of clonal spread (including the trade-off between number and length of spacers between ramets). See also Appendix A and trait result figures in the Supplementary data Appendix D for an overview of trait attributes and their assumed values.

Competitive interactions between plant individuals were described using the “zone-of-influence” (ZOI) approach (Schwinning and Weiner, 1998; Weiner et al., 2001). Plants have a ZOI, i.e. a circular area around their stems’ location, on which the plant acquires resources; if the ZOIs of neighboring plants overlap, they compete for the resources on the overlapping

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