

## Effect of management on species richness of grasslands: sward-scale processes lead to large-scale patterns

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### Abstract

Grasslands are important land-use systems of Central Europe that have undergone a drastic species decline in the past decades due to agricultural improvement or land abandonment. Besides environmental factors and evolutionary grazing histories, it is mainly management practices that influence the species composition and structure of grassland communities. Here, we briefly discuss how the main management mechanisms, fertilization and disturbance operate at the sward-level and determine the vertical and horizontal structure of plant neighbourhoods and whole plant canopies. We elucidate the main selection mechanisms that are responsible for the coexistence of specific species groups with growth forms and life history traits specifically adapted to prevailing growth constraints. We discuss why species persist in grassland communities and what role soil dwelling organisms may play in that. We point out the methodological difficulties related to non-linear processes in projecting sward level dynamics to community level patterns and how changes in management practices may lead to drastic changes in species composition due to transient dynamics in species interactions. We conclude in highlighting which local and global environmental aspects may have to be considered in the development of sustainable management plans.

Keywords: clonal plants, community structure, defoliation, disturbance, spatio-temporal heterogeneity

### Introduction

Semi-natural, temperate grasslands of Europe are man-made ecosystems dating back to the periods when natural forests were deforested at large scale for livestock and forage production (Ellenberg, 1982), although the process of deforestation dates back to the Neolithic. Different climatic, edaphic, and management factors produced meadow and pasture communities with varying species numbers yet usually with distinctive species compositions. These grasslands depend critically on repeated grazing, cutting, or fire, as these disturbance mechanisms halt succession to woodland and favour certain plant strategies or growth forms. Foliage removal confers nutrient loss and depending on the productivity and management of the system nutrients are replenished in form of excreta return (dung and urine) or manure or artificial fertilizer application. Both adverse mechanisms, i.e., defoliation, trampling, treading, soil compaction and compensatory mechanisms i.e., plant growth potential resource supply, shape the structural and botanical composition of managed grasslands both at the patch and at the community scale. However, predicting plant, species, and community responses to grazing and management is difficult. First, there are two confounding sources of variation that potentially affect the spatial pattern and structure of vegetation: 1.) high natural variation in grazing patterns and 2.) high spatio-temporal variation in the abiotic and biotic environment (Adler *et al.*, 2001; Watkinson and Ormerod, 2001). Second, observable small scale changes in tiller dynamics of grasses may be affected by several endogenous and exogenous factors simultaneously, e.g. plant life history traits, growth forms, grazing, seasonal and annual variation in weather conditions, density effects, and plant neighbourhoods. Also, grazing affects vegetation change differently in the course of the year (Bacon, 1990; Bullock *et al.*, 1994).

In the following text, we will highlight the major disturbance and fertilization effects of extensively managed meadow and pasture communities on 1.) plant population dynamics of different species at the community level and on 2.) plant-plant interactions (including resource competition) and plant

neighbourhood dynamics at the patch level. Finally, we will briefly address potential feedback mechanisms between different management practises and individual plants, populations, neighbourhoods, and species assemblages both as important determinants for local and community spatio-temporal species dynamics and as crucial processes promoting species coexistence and maintaining species diversity in grassland communities.

#### Grassland management: a short overview of mechanisms

##### Meadows

Meadow communities consist primarily of perennial and a few biennial and annual grass and dicot species with a variety of different growth forms and life-history attributes. In meadows, the primary source of disturbance is foliage removal by repeated mowing either manually with scythes or with machines. Cutting is an abrupt and short, yet severe disturbance event that removes the complete canopy down to ca. 4 cm stubble height. Depending on the productivity of meadows, cutting frequency ranges between 1 and 2(3) times per year. Cutting rarely kills plants adapted to defoliation or creates open gaps. Fertilizer (manure application) is homogeneously applied once a year (autumn). Hence, management effects generally do not create open microsites to facilitate seedling emergence of resident species or the establishment of diaspores or propagules of species from more remote areas. Thus, meadows maintain a more or less stable species pool. Seedling recruitment of resident species depends on seed and microsite availability which both depend on the cutting and fertilization frequency of the meadows. In nutrient poor grasslands, canopies are usually open and plants can develop flowers and shed seeds before they get cut. In more fertile meadows, fast growing plants are the first ones to close the canopy. In this case, plants seldom produce flowers and set seeds before the first cutting. Thus, on fertile sites, regeneration from seeds is not as common as on less fertile sites. Species responses to seasonal cutting effects are remarkably diverse. Species-specific differences in life-cycles (developmental stage), phenological stage (vegetative or regenerative phase), and growth forms (clonal with indeterminate growth, non-clonal with determinate growth) (Sackville Hamilton and Harper, 1987; Bullock *et al.*, 1994, 2001) explain this diversity. At the beginning of a growing season, when plants are still short in height, light is equally distributed and thus equally accessible to all plants within a stand. In fertile meadows, it is usually the tall tussocks with densely packed tillers (phalanx type, *sensu* Lovett Doust, 1981) of e.g. *Arrhenatherum elatius*, *Alopecurus pratensis* that absorb most of the light and dominate plant stands by early summer just prior to the first cutting. In the first regrowth period, dicots become more abundant when air temperatures rise above those in early spring. Dicots form either rosettes (*Plantago lanceolata*, *Hieracium pilosella*, *Taraxacum officinale*, *Bellis perennis*) erect, axially branched stems (*Anthriscus sylvestris*, *Ranunculus acris*, *Knautia pratensis*, *Chrysanthemum leucanthemum*) or horizontal spacer organs (e.g., stolons *Ranunculus repens*, *Ajuga reptans*). In calcareous, nutrient poor meadows characterized by *Bromus erectus*, *Festuca rubra*, or *Avenochloa pubescens*, the proportion of grasses and dicots is usually balanced. Since cutting frequency is reduced to a single mowing event, hierarchically structured canopies with differently sized individuals and species develop. In open stands, growth forms with widely spaced ramets, (the guerilla type, *sensu* Lovett Doust, 1981) allow plants to explore their neighbourhoods horizontally via stolons or rhizomes and to place daughter ramets (tillers, rosettes) in favourable microsites ("foraging concept", *sensu* Hutchings and de Kroon, 1994). Hence, different edaphic conditions together with periodic removals of the canopy create environmental conditions that are best utilised by species with complementary growth strategies and plant traits promoting these species to coexist. Most meadow species are sensitive to grazing and trampling. Plants with determinate growth differentiate apical meristems into inflorescences and seeds. Those plants usually lack stocks of basal meristems and/or the ability of phenotypic (morphological) plasticity. In this case, investment in sexual reproduction and genetic diversity occurs at the expense of vegetative reproduction and adaptive plasticity.

##### Pastures

Grazing by cattle exerts one prime effect on the plant canopy and that is continuous leaf removal throughout the growing season. Grazing management plans vary in defoliation frequency (continuous versus rotational grazing) and grazing intensity, e.g. low or high stocking rate, which both affect plant

growth, plant interactions, and plant community structure. Soil resource availability in pastures is usually higher than in unfertilised meadows, however the distribution of resources is rather heterogeneous spatially and temporally, as most of the N input comes from urine depositions and most of the P input comes from dung depositions. In contrast to the leaf removal through cutting, leaf removal through grazing has multiple side effects on plants and plant canopies, which are: trampling, treading, soil compaction, scorching by urine, and covering by dung. These disturbance effects often kill plants locally and/or create open gaps. Pasture species rarely set seeds, however they have a high potential to regenerate vegetatively by spreading and branching laterally via rhizomes (*Poa pratensis*, *Agropyron repens*) or stolons (*Trifolium repens*) or by a relatively high potential to produce new tillers (e.g. *Lolium perenne*). Open gaps or dung patches are either colonised by tillers from surrounding plants or by spontaneous seed arrival (mostly of dicots) (Bullock *et al.*, 1994) from remote areas. Local disturbance sites within pastures provide habitats for a potentially larger number of species than equivalent patches unaffected by disturbance. Demographic changes in plant populations of pasture species are very sporadic and local as the development of flowers and seed production are only possible on ungrazed areas, i.e. dung patches, newly colonised gaps, populations of spiny or toxic pasture weeds. The species pool of pasture communities is usually small, yet the horizontal and vertical structure of the canopy is highly variable and diverse. Unlike in meadows, the structure and density of the aboveground canopy is not primarily influenced by soil and light resource availability, but by the palatability and quality of the standing biomass.

All pasture plants are negatively affected by defoliation, yet they vary in their ability to tolerate and to recover from defoliation (Briske, 1996). Prostrate growth forms (e.g. rhizomes, stolons, basal rosettes) are usually more resistant to frequent and intensive defoliation than twining, scrambling or erect growth forms, as in these plants, the apical meristems remain close to or beneath the ground and thereby inaccessible to grazers (Booyesen *et al.*, 1963). Defoliation acts on individual plants, yet this has direct implications for higher levels of biological organisation: defoliation interrupts the intraplant C and N relations when grazed plants re-establish the photosynthesising tissue (Briske and Richards, 1995). A plant's potential to regenerate (i.e., endogenously controlled number of basal axillary buds) and to access and compete for locally distributed resources will determine plant population density, competitive interactions, neighbourhood dynamics and ultimately plant community pattern.

In pastures, non-equilibrium processes, i.e., unpredictable temporal and spatial disturbance patterns, variable resource availability, and gap dynamics, all lead to a fluctuating species pool at the community level. At the level of plant neighbourhoods, where local disturbances become effective, the rates of species turnover and change in community composition and structure is high. This is functionally related to altered competitive interactions and changes in the competitive hierarchies due to new gap colonisers.

#### Basic mechanisms/processes that operate at the sward/ramet level

##### Vertical dimension

Defoliation largely affects the vertical structure of grassland canopies. With increasing defoliation frequency and intensity the size structure of a canopy is reduced to a single-canopy layer and light availability is not that much limiting. Technically, this means that grassland management introduces limits on size that a plant ramet can attain. This limit may be physical (when mowing or grazing comes before a ramet has attained its maximum size) or indirect (since grasslands are dominated by species that are selected for this kind of disturbance and do not invest into their ramets after a certain size has been attained (de Kroon and Kalliola, 1995)). The limit on the maximum plant size has profound effects on the nature of the (aboveground) competition among ramets. While size growth in non-clonal plants such as annuals or most forest trees is usually proportional to the ramet size (bigger plants grow faster; see e.g. Hara, 1988), grassland plants show two important differences to this pattern: (i) the ramets that approach the maximum ramet size tend to slow down their growth, at least when expressed on an absolute scale, and (ii) smaller ramets may be supported by translocation of photosynthates from their mother ramets. Both these processes effectively weaken the size-dependence of the ramet growth; as a result, the ramet increase in size is usually independent of the ramet size. Also competition between ramets is more symmetric (Schwinning and Weiner, 1998) and self-thinning at the plant (i.e., between ramets) or population level is rare in grassland canopies.

As a result, overtopping is not necessarily the best strategy how to attain dominance in a grassland. Therefore, most of the plants present there are clonal and use two other strategies to attain dominance: (i) invest into organs of horizontal spreading (such as rhizomes, stolons and roots) that enable them to capture space in the horizontal dimension. This leads to the prevalence of the horizontal (clonal) growth and to pronounced horizontal spatial structure (see below) with all its dynamical consequences. Clonal growth then also serves as the main mechanism through which a species persists in the community. (ii) invest into storage organs that enable fast vertical growth in early growing season long before the maximum ramet size has been attained. Only in this early stage of plant growth, it is possible to overtop other plants and to attain dominance later; success in this is largely dependent on the amount of resources available in storage organs from the previous vegetation season. Therefore, investment into storage is often a much better means to attain dominance than investment into organs of vertical growth (Suzuki and Hutchings, 1997; Suzuki and Hara, 2001). Both these strategies are a kind of a 'replacement' of the vertical growth investment found in plants whose size is not limited. Whether plant-plant interactions are primarily competitive or facilitative may depend on the abundance (dominant versus subordinate species), and the spatial arrangement of these species and consequently on the frequency of intra and interspecific encounters in the surrounding neighbourhood (Stoll and Prati, 2001).

#### Horizontal dimension

Lateral clonal growth is the dominant form of reproduction in grasslands and contributes significantly to the horizontal spatial structure of grasslands. Plants with short connections between tillers form densely packed tussocks with the phalanx growth form. Plants with long connections (rhizomes, stolons) between tillers or tiller groups form coarsely spaced plants with guerrilla growth form. The survival rate of young tillers is higher than that of seedlings, as young tillers are supplied with resources from parental tillers. Tiller populations of most grass species are controlled by density-dependent mechanisms, however these may only become effective in high productive seasons of the year. These density-dependent mechanisms are often mediated by cues like light quality that either inhibit or enhance tillering in the course of canopy closure (decrease in red:far-red ratio) or after leaf removal through grazing (increase in red:far-red ratio), respectively. Long-lived rhizomatous and stoloniferous plants (genets) may be exposed to a high degree of spatial and temporal abiotic and biotic environmental heterogeneity during their life cycle, which may favour the selection of highly plastic genotypes (Scheiner, 1993). The position of meristems along spacer organs close to or beneath the soil surface and the lateral growth both evolved as an effective mechanism to enhance grazing tolerance and to protect the bud bank from grazers (Briske and Richards, 1995). Primarily external factors, e.g., high soil nutrient concentrations and/or a change in light quality and/or quantity trigger meristem activation and the development of daughter ramets. Hence, lateral growth facilitates initially rapid colonization of favourable sites, and consequently the production of new ramets. Rhizome or stolon connections either remain intact and thereby facilitate reciprocal assimilate and resource exchange between daughter ramets or die off or more frequently are severed through trampling leaving isolated rooting ramets behind. The former growth type maintains large, physiologically integrated plants that intermingle with plants of the same or other species and occupy a relatively large horizontal space. In this case, the overall inter-ramet competition is low, interplant competition high. The latter growth type, however, increases local plant density and thereby intraspecific competition between individuals of the same genet. In pastures, where disturbance events are frequent and unpredictable and nutrient accumulations occur locally, the variability in plant density and consequently in intra and interspecific interaction dynamics may be fairly high. Lastly, species performance is also affected by the immediate biotic environment, as some plants are able to distinguish between individuals of their own and other species (Huber-Sannwald *et al.*, 1998).

#### Guild structure of grassland plants

While stands with predominantly vertical structure are usually strongly determined by competition for light (Twolan-Strutt and Keddy, 1996), predominantly horizontal structure in grassland communities is likely to favour a diversity of mechanisms through which different species may coexist. Guilds are usually defined as groups of species with strong intra-guild interactions and weak interactions with species not belonging to the guild. Guilds can be identified in three possible ways: (i) By searching

for patterns of traits that are assumed to be correlated with species interactions (extrinsic guilds, Wilson and Roxburgh, 2001), (ii) by identifying groups of species that tend to exclude each other spatially (intrinsic guilds, Wilson and Roxburgh, 1994), or by (iii) pairwise competition experiments (Mitchley and Grubb, 1986; Wilson and Roxburgh, 2001). The trait-based guilds are always based on the assumption that the researcher is able to identify the relevant traits; needless to say, this is difficult to demonstrate (Weiher *et al.*, 1998). Recent studies have indicated that grassland communities in some cases have an identifiable structure based on intrinsic guilds; this means that plant species within certain groups tend not to co-occur at a single microsite, while plants from different groups would co-occur freely (Wilson and Roxburgh, 1994; Wilson and Whittaker, 1995; Wilson, 1999). Unfortunately, such statistical studies do not provide any indication of mechanisms that underlie the guild structure. In some cases however, trait-defined guilds have been shown to correlate with intrinsic guilds to some extent (Wilson and Roxburgh, 1994) or with guilds identified by competition experiments (Wilson and Roxburgh, 2001) that already gives rather strong support to functional differentiation among species in grasslands.

#### Interactions with other organisms

A variety of symbiotic and pathogenic soil microorganisms dwell in the rhizosphere of plants. The interaction between these soil microorganisms may critically affect plant growth, plant-plant interactions, and potentially plant community composition and structure (Clay, 1990). Pathogenic soil bacteria, fungi, and nematodes usually greatly reduce plant growth, survival and fecundity of plants, while fungal and bacterial symbionts enhance plant growth and survival and often improve resistance against herbivory and pathogens. Hence, soil pathogens may lead to a reversal in competitive abilities of dominant and subordinate species, which will ultimately reduce competitive exclusion and enhance plant species diversity (Olff *et al.*, 2000).

In contrast, the symbiosis of plants with arbuscular mycorrhizal (AM) and endophytic fungi improves the supply of less accessible soil resources (e.g. P, NH<sub>4</sub><sup>+</sup> and water) and enhances plant defence against plant pathogens and herbivory. Mycorrhizal hyphae form dense networks and transportation systems between plants with different competitive abilities. This symbiosis increases species richness by preventing inferior competitors from being excluded (Grime *et al.*, 1987). In addition, different associations of AM isolates with grassland species affect plant species diversity of grasslands differently (van der Heiden *et al.*, 1998).

The underlying mechanisms associated with plant, population, and community responses to both plant symbionts and plant pathogens may not only be related to switches in competitive hierarchies but also to complex signalling mechanisms within and between plants, which may have important implications for our understanding of plant population dynamics, plant species coexistence, and plant community structure (Ballaré, 1999).

#### Species-pool effects

As shown above, grassland richness is regulated by low-level processes acting on ramet interactions, both in the vertical and in the horizontal dimension, that are made possible by the disturbance introduced by mowing or grazing. One should keep in mind, however, that these processes operate on a set of species that exist in a given landscape and are able to reach the site in question by migration. This set of species is constrained by both evolutionary and migration histories of the particular site (Zobel, 1997) which in turn may reflect the evolutionary history of the community. Although this kind of relationship is difficult to test operationally and is in a sense trivial, it should not be overlooked as a source of variation in species richness per area when different regions or different substrates (such as siliceous vs. limestone) are compared. In such comparisons, the low-level processes at the sward level filter species from the species pool of available species; the availability means that the species is able to reach the site both over long (Zobel, 1992) and short (Poschlod and Bonn, 1998) temporal scales. Species in the persistent seed bank naturally also have to be counted in the pool of available species (Bekker *et al.*, 1998) making the species richness determined by both small-scale (sward-level interactions) and large-scale (species pool available) processes.



### Links between small-scale processes and large-scale patterns: the effects of management

The sward-level processes ultimately determine the patterns of species richness and other large-scale patterns of grasslands. In the following section, we discuss some obvious mechanisms behind well-known large-scale patterns associated with current management change. Perhaps it should be noted here that a direct prediction of what kind of large-scale effect a given change in low-level processes will have is often methodologically difficult. Any grassland system is a highly non-linear system with an important spatial component whose formal representation is rather non-trivial (Dieckmann *et al.*, 2000); even when a formal representation of such a system is made, prediction of its behaviour may not be easily attained by current analytical techniques (see e.g. Hastings, 1996).

#### Change in disturbance regime

A change in the disturbance regime is linked to a change in the grazing and/or cutting management of grasslands and has direct implications on the species diversity of these communities. In species rich meadows, any change in the disturbance regime will influence the vertical size structure of the plant canopy and thereby alter the resource (including niche) availability and thus competitive environment of coexisting species. An increase in cutting frequency will both eliminate all species sensitive to high cutting frequencies and inhibit the sexual reproduction of the remaining species when cutting dates are early. This will impoverish the genetic and species diversity of non-clonal plants, usually forbs, and enhance the vegetative spread of clonal plants, usually grasses. Several mechanisms are responsible for species decline: i) the reduction in seed production, ii) a short-lived seedbank (O'Connor, 1991), iii) a generally low dispersal ability of grassland plants and iv) adverse conditions (including competition, herbivory, predation) for emerging seedlings during establishment. A decrease in cutting frequency will also lead to a decline in species diversity simply because tall, fast-growing species will close the canopy and thereby exclude slower-growing or smaller species from the community (asymmetric competition).

Higher grazing frequency and intensity in pasture communities will lead to a decrease in species diversity, as species highly sensitive to trampling and with limited regeneration potentials (low bud bank) will be eliminated. As with increasing disturbance frequency the number of open gaps increases, it will be mainly plants with high colonizing ability (guerrilla type) that will dominate. In addition, as seed production of resident species is fairly low and consequently, also seedling recruitment and seedling survival, these disturbance conditions favour the invasion and successful expansion of a few unpalatable weed species with high dispersal rates, high annual seed production, and high competitive abilities. A decrease in grazing intensity may mean a decrease in species richness as well. If a regular disturbance ceases to put a limit on maximum plant size, competition may become more asymmetric, leading to a similar array of changes to those related to increased productivity (see below).

Along a grazing gradient, species diversity follows a hump-backed curve with maximum diversity occurring at intermediate grazing levels (Milunchas *et al.*, 1988). Small-scale, i.e. sward level, changes in species richness depend on the intensity and timing of disturbance, its effect on competitive hierarchies, and thus the dynamics of plant neighbourhood composition. On the other hand, community scale diversity is modulated by the evolutionary grazing history of an area and the associated selection pressures. Selection pressures for adaptive characteristics typically shift along grazing gradients. At low grazing sites, it is a few tall-statured species, i.e. the effective light competitors that dominate, while at high grazing sites, it is the prostrate grazing tolerant species that are abundant. Both the evolutionary grazing history and the current dynamic, non-linear feedback between vegetation, and grazers introduce factors of uncertainty that make short-term and long-term predictions on changes in species diversity associated with changes in grazing management highly difficult.

#### Change in productivity

The second major management change is productivity change, usually due to fertilization. When nutrients cease to be limiting, plants will become bigger and there will be an increased competition for light. This has several consequences. First, competition among plant individuals becomes more asymmetric (Keddy *et al.*, 1996) and smaller individuals face stronger per-unit-size competition. In

response to this, plants begin to invest more into structures of vertical growth (such as stems); mean ramet size increases and smaller individuals are likely to be out competed. This leads to a decrease of species diversity, both since some species are not able to grow tall enough to sustain this kind of competition, and since the lower number of big ramets cannot sustain larger number of species (Zobel and Liira, 1997). Second, asymmetric competition and prevailing investment into the vertical growth mean that the role of the horizontal structure becomes less important. The increased investment into the structures of vertical growth means that plants do not possess resources they can invest into horizontal growth and the role of clonality tends to diminish. In particular, most plants of the guerrilla growth form (long stolons or rhizomes) disappear; in these plants, usually the proportional investment into horizontal growth structures is largest. At the same time, the role of guild structure also decreases; in a highly productive environment, the only measure of a plant's success is its vertical growth leaving little opportunity for other kinds of niche differentiation. All these changes essentially mean reduction of a potential for diversity, both at the species-level and growth-form level. As a result, the large-scale richness decreases.

### Conclusion

Grasslands are ecological communities that are extremely sensitive to changes in environmental conditions and respond to such changes rather fast. This is due to balanced effects at the sward level that take place owing to the fact that vertical competition is prevented by mowing or grazing. If levels of mowing or grazing change, vertical competition begins to play a different role and the whole system may change rather fast. For this reason grasslands often serve as good model objects for studies of ecological interactions and, in particular, for the ways how small scale sward level processes project to large-scale patterns. The legendary small-scale richness of grasslands is in most cases linked to the processes taking place under "right" levels of mowing or grazing. They occur often under conditions of low productivity where plant individuals are small; this high species richness, however, primarily reflects prevalence of vertical structure over horizontal competition. It is also due to large pools of available species that have evolved in regions with a long and sustained history or grazing of large ungulates.

Recent interest in preservation of species richness in grassland, together with stress on low output agricultural systems, have led to designs of management strategies that maintain the fine balance of processes and keep the richness high. It has become clear that any feasible maintenance of these habitats has to be based on management strategies that reasonably well mimic management under which these grasslands have developed. However, since the low-input agricultural techniques are often economically not feasible, the design of new management strategies has to be based on thorough understanding of sward-level processes and their effects on species richness.

Furthermore, besides plant species diversity sustainable management plans for grassland communities should also consider ecosystem functioning aspects, as grasslands provide important habitats for mammals, birds, invertebrates, and microorganisms that together form complex food chains and contribute significantly to the plant community dynamics. Hence, altering the canopy structure of grasslands may have multiple 'side' effects on the habitat and food availability for organisms of higher trophic levels; and this may have additional indirect effects on the composition and dynamics of grassland communities. Finally, one has to bear in mind that current management decisions will have to be revised in the future as human-induced environmental changes (e.g., atmospheric N-deposition, elevated CO<sub>2</sub>, temperature change) may have profound effects on the structure and species composition of grasslands.

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