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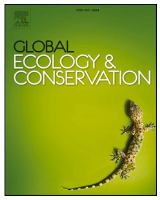

Conservation notes

Vanishing biodiversity: The creeping degradation of central European calcareous grasslands

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ABSTRACT

Calcareous grasslands in Central Europe are among the most species-rich habitats, yet they are undergoing a gradual but pervasive decline in habitat quality despite ongoing conservation efforts. Recent studies indicate that the expansion of Upright Brome (*Bromus erectus*), driven by climate change, atmospheric nitrogen deposition, and prevailing management practices, is leading to structural and floristic homogenisation. This process reduces bare-soil availability while threatening specialist plants and their associated fungi and animals, including pollinators and herbivorous insects. Traditional late-season mowing has proven insufficient to counter these changes, and current conservation strategies often fail to maintain the structural diversity necessary to sustain biodiversity. To halt the gradual degradation of calcareous grasslands, we argue that conservation practices must be fundamentally reconsidered. Adaptive management approaches – including year-round or temporary grazing, early-season mowing, and prescribed burning – should be implemented to restore habitat heterogeneity and support biodiversity. Timely adoption of such measures, accompanied where possible by regular monitoring, is essential to prevent further biodiversity loss in these valuable ecosystems.

1. Introduction

Semi-dry grasslands hold the fine-scale world record for vascular plant species richness and are overall among the most species-rich habitats across Europe (Wilson et al., 2012; Roleček et al., 2019; Fartmann, 2024). For centuries – and likely much longer – traditional land management has created and preserved these grasslands (Bonari et al., 2017; Feurdean et al., 2018; Molnár et al., 2023). Among semi-dry grasslands, calcareous grasslands in particular are hotspots of plant and animal species richness, harbouring many rare and threatened species (van Swaay, 2002; Wilson et al., 2012; Bonari et al., 2017; Fartmann, 2024). Those that are characterised by a long continuity of traditional land use – especially grazing – usually exhibit high structural diversity, including heterogeneous swards with patches of bare soil, gravel, stones, scattered shrubs and, occasionally, rocks. This heterogeneity is key to the high richness of species and flowers within calcareous grasslands (Diacon-Bolli et al., 2012; Janišová et al., 2023; Fartmann, 2024).

Despite their high value for biodiversity conservation, calcareous grasslands are highly threatened (Olmeda et al., 2019). For many decades, they have suffered severe losses due to afforestation, scrub encroachment, and urbanisation (WallisDeVries et al., 2002;

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Howard et al., 2003; Löffler et al., 2020). Today, their remnants often occur as isolated fragments within human-dominated landscapes (Rösch et al., 2013; Poniatowski et al., 2018b). Due to their great importance for biodiversity conservation and the severe threats calcareous grasslands have faced, they were included in the EU Habitats Directive (habitat type 6210; 92/43/EEC). Orchid-rich stands of calcareous grasslands are even considered priority habitats and receive special protection (Olmeda et al., 2019). The primary goal of the directive is to achieve and maintain a favourable conservation status for these grasslands.

However, these EU conservation objectives remain largely unmet. In the atlantic, continental, and Mediterranean biogeographic regions, calcareous grasslands are assessed as unfavourable–bad (Olmeda et al., 2019) and are listed as vulnerable in the EU Red List of terrestrial habitats (Janssen et al., 2016). Over recent decades, the abandonment of traditional management has facilitated widespread shrub encroachment, resulting in the loss of open, thermophilous grassland stands and contributing to this unfavourable status (Poschlod et al., 2005; Henle et al., 2008; Neuenkamp et al., 2016; Poniatowski et al., 2020).

While the adverse effects of severe shrub encroachment are well studied (e.g., Barbaro et al., 2001; Poniatowski et al., 2020), more recent observations indicate that even continuously managed calcareous grasslands are undergoing substantial changes in habitat quality and species composition. Local conservationists have noted a strong increase of the Upright Brome (*Bromus erectus*), a tall perennial tussock grass, in large parts of Central European calcareous grasslands. Initially, these changes were unquantified, and their causes remained poorly understood.

However, comparative studies of historical and current data have provided deeper insights into these developments. A re-survey from the Kaiserstuhl region in south-western Germany revealed that the cover of *B. erectus* in semi-dry calcareous grasslands increased by a factor of 1.6–2.0 between the initial surveys (1978–1981) and the re-survey in 2020 (Fartmann et al., 2025). This expansion has led to structural and floristic homogenisation, transforming previously species-rich stands into monotonous ones dominated by *B. erectus* (Fig. 1). Similar trends have been reported for dry calcareous grasslands in central Germany (Meier et al., 2022), where *B. erectus* increased significantly over 20 years, while plant species richness declined. Furthermore, Poniatowski et al. (2018a) demonstrated that the loss of phytodiversity in semi-dry calcareous grasslands invaded by *B. erectus* was associated with decreases in primary consumers (leafhoppers), likely also affecting higher trophic levels such as predatory arthropods. Understanding the mechanisms

Fig. 1. In the course of global change, many calcareous grasslands are shifting from (a) species- and flower-rich communities to (b) grass-dominated stands. This is leading to increasing structural and floristic homogenisation, particularly in the lowlands and lower elevations of the uplands of Central Europe. Examples are shown from the Kaiserstuhl, a low mountain range in the Upper Rhine Valley, south-western Germany (Photo credits: a – Dominik Poniatowski; b – Thomas Fartmann).

behind this deterioration in habitat quality is therefore essential to explain the ongoing loss of biodiversity in calcareous grasslands.

2. Causes and consequences of the deterioration in habitat quality

Over the past 20–30 years, *B. erectus* has become dominant in many calcareous grasslands in the lowlands and lower elevations of the uplands in Central Europe (e.g., Poniatowski et al., 2018a; Meier et al., 2022; Fartmann et al., 2025; A. Zehm, conservation specialist at the Bavarian State Ministry of the Environment and Consumer Protection, pers. comm.). This suggests that milder winters and summer droughts, which have become more frequent due to climate change, have contributed to the expansion of this grass species (Fartmann et al., 2025). Indeed, *B. erectus* is very drought-tolerant and can develop extensive roots on deep soils to access water during dry periods (Grime et al., 2007; Pérez-Ramos et al., 2013; Madaj et al., 2023). Moreover, as an evergreen species, it can also grow during mild winter days, unlike many other vascular plants in the temperate zone, such as its antagonist, Tor grass (*Brachypodium pinnatum*) (Corcket and Liancourt, 2003; Kahlert et al., 2005; Grime et al., 2007). In addition, the latter is a mesophilic species that is sensitive to water stress during warm and dry springs. Pleurocarpic mosses also benefit from mild winters, often covering patches of bare soil and further reducing habitat heterogeneity (Peppler-Lisbach and Könitz, 2017; van Kleef et al., 2025). Atmospheric nitrogen deposition additionally promotes the growth of both *B. erectus* and competitive mosses (Meier et al., 2022; Fartmann et al., 2025; Peppler-Lisbach and Könitz, 2017; van Kleef et al., 2025).

The consequences of the structural and floristic homogenisation are severe: many specialised plant species require bare soil for germination (Grime et al., 2007; Ödman et al., 2012; Wagner et al., 2016). Reduced plant species richness translates into fewer host plants, pollen, and nectar sources for specialised insects, including butterflies, wild bees, and other pollinators (Fartmann et al., 2021). It may also reduce the availability of suitable host plants and substrates for specialised fungi (Lepinay et al., 2024). The loss of bare soil also negatively affects xero-thermophilic insect species that depend on it for nesting, oviposition, or larval development (Fartmann et al., 2021; Gardein et al., 2022; van Kleef et al., 2025). Furthermore, increasing vegetation height and density alters the microclimate, making the stands moister and cooler, which may adversely affect the occurrence and population dynamics of xero-thermophilic arthropods (WallisDeVries and Van Swaay, 2006; Roth et al., 2021).

3. Implications for conservation

Given the widespread changes in vegetation structure and species composition described above, the implications for conservation management are profound. Although many of the remaining calcareous grasslands are still actively managed, their habitat quality is gradually deteriorating. Grass species, particularly *B. erectus*, have expanded, and competitive mosses are proliferating, further reducing habitat heterogeneity. These developments indicate that these unique grassland ecosystems cannot be maintained under a "business-as-usual" management approach.

Current conservation strategies in Central Europe should therefore be reconsidered, especially in regions experiencing mild winters, summer droughts and/or high atmospheric nitrogen deposition. It has been shown that *B. erectus* benefits from a single cut in late summer or autumn (Moog et al., 2002; Köhler et al., 2005; Lemmer et al., 2021). Accordingly, traditional late-season mowing, commonly applied in many calcareous grasslands, is insufficient to address this issue. Moreover, mowing alone rarely creates bare soil, allowing a dense moss layer to establish between the tussocks of *B. erectus*, which further inhibits the germination of specialist plant species.

In the following, we outline potential measures to counteract these developments and restore habitat quality in calcareous grasslands (see also Fartmann et al., 2025). These strategies aim to increase structural heterogeneity and maintain patches of bare soil, thereby supporting both flora and fauna adapted to these semi-dry grassland ecosystems. All management recommendations should be considered in the context of climate change. As the growing season starts increasingly earlier, management activities can likewise be conducted earlier. Fixed management dates – particularly those established 20–30 years ago – are no longer appropriate under current conditions, especially since shifts in vegetation phenology may not be immediately matched by the behaviour of other species (e.g., bird nesting or insect development), highlighting the importance of locally adapted, flexible management timing supported by regular monitoring.

3.1. *Year-round grazing*

Year-round grazing with genuine grazers, such as horses or cattle, at low stocking rates has well-documented positive effects on vegetation structure and species richness of grassland ecosystems (Kooijman and van der Meulen, 1996; Rosén and Bakker, 2005; Köhler et al., 2016; Søndergaard et al., 2025). The behaviour of the large herbivores helps to suppress *B. erectus* and to establish a balanced ratio of herbs and grasses (cf. Rosenthal et al., 2012; Fartmann et al., 2025). Moreover, it regularly creates patches of bare soil, preventing mosses from becoming dominant. During drought periods, however, stocking density should be carefully monitored and reduced if necessary to prevent overgrazing. Stocking densities should generally be adjusted according to the available winter forage. As a rough guideline, 0.1–0.3 livestock units per hectare are recommended (cf. Köhler et al., 2016).

3.2. *Early-season management: temporary grazing or conservation mowing*

Temporary grazing in winter or early spring, as soon as new growth appears, is recommended because young grass tillers and leaves are highly palatable, also for sheep (Ellenberg and Leuschner, 2010). This helps to reduce the dominance of *B. erectus* and other competitive grasses. On sites with vigorous growth, a second grazing period six to eight weeks later can further enhance floristic diversity. By contrast, grazing should largely be avoided during summer to prevent negative impacts on flora and fauna (Fartmann et al., 2025) and because *B. erectus* is less palatable at this time, as nutrients have already been relocated to the roots (Ellenberg and Leuschner, 2010). Historically, winter and early spring grazing were common in semi-natural grasslands (Kapfer, 2010; Janišová et al., 2023), whereas current conservation protocols often restrict grazing to periods from mid-June to September (e.g., Weiss et al., 2013); a reconsideration of these restrictions by regional conservationists is therefore recommended.

Where grazing – either year-round or temporary – is not feasible, early conservation mowing can serve as an effective alternative to reduce *B. erectus*. Mowing should be carried out in March to April, with a possible repeat after six to eight weeks; winter mowing may also be beneficial, similar to temporary grazing. However, mowing alone generally fails to reduce moss dominance, as it rarely creates bare soil in calcareous grasslands (Vanderpoorten et al., 2004; Ingerpuu and Kupper, 2007).

Given this strong dependence on species phenology and life-history stage, the impacts of comparatively intensive early-season management on flora and fauna remain insufficiently studied and warrant further research. Previous syntheses indicate that early grassland management can have neutral or even positive effects on biodiversity, although outcomes depend strongly on site conditions and management regimes (e.g., Tälle et al., 2016). Nevertheless, recent results from a multi-taxon study by Panassiti et al. (2025) suggest that initially negative effects of early grazing on fauna may diminish over the course of the summer and can even become positive later in the season.

3.3. Prescribed burning

While fire causes immediate damage to flora and fauna, prescribed burning, when conducted on a small scale and in a mosaic pattern, provides important conservation benefits by facilitating the regeneration of vegetation and associated animal communities (Valkó et al., 2016; Kerdoncuff et al., 2023; Hamřík et al., 2025). For example, prescribed burning can effectively reduce or even eliminate *B. erectus* in treated areas (Moog et al., 2002; Grime et al., 2007; Kahlert et al., 2005). Fires also remove accumulated litter and create bare soil, especially when burning is conducted under dry conditions in summer (Vermeire et al., 2020; Brüggeshemke et al., 2025). These processes generate habitat structures that are especially important for less competitive and often highly specialised species, for example by providing suitable conditions for seed germination or oviposition (see above). Despite its ecological benefits, fire management currently requires significant public outreach and is only feasible on a very limited scale in conservation practice (Pais et al., 2025).

In addition to adapting management practices (see above), another key focus should be the restoration of calcareous grasslands subject to widespread shrub encroachment. Following shrub removal, tall ruderal vegetation often establishes within the first growing season, thereby enhancing habitat heterogeneity in the herbaceous layer and providing structural resources for a range of species. This supports not only specialised plant species but also diverse primary consumers (e.g., leafhoppers) and pollinators (e.g., wild bees) (Poniatowski et al., 2020; Helbing et al., 2021; Kettermann et al., 2025). Furthermore, tall and dense vegetation, which creates a cooler and moister microclimate, offers refugia for drought-sensitive species (Stuhldreher and Fartmann, 2018; Poniatowski et al., 2020). Against this background, it is also important to preserve larger structural elements, such as solitary trees, small scattered shrubs, and woody patches, during shrub removal, as these features fulfill key ecological functions, support species already mentioned, and further enhance habitat heterogeneity (Teleki et al., 2020; Fartmann et al., 2022; Lőrincz et al., 2024; Gyalus et al., 2025). Consequently, maintaining high habitat heterogeneity is critical under climate change to conserve the biodiversity of calcareous grasslands (Fartmann, 2024).

4. Prospects

Environmental conditions have strongly altered over the past 20–30 years in calcareous grasslands. Today, climate change, atmospheric nitrogen deposition, and inappropriate habitat management are affecting grassland communities, even in protected areas. A structural and floristic homogenisation of these grasslands is often the result. Such signs of degradation are currently particularly evident in the lowlands and lower elevations of the uplands in Central Europe, where mild winters and summer drought occur more regularly due to climate change.

By contrast, in the highest elevations of the uplands (e.g., Swabian Jura) and in the high mountain ranges (Alps, Carpathians), a deterioration of habitat quality due to climate change is not yet apparent. Vegetation there remains rich in herbs and flowers (cf. Bonari et al., 2017; Pittarello et al., 2020; own observation), although even in subalpine calcareous grasslands, subtle changes in species composition have already been detected (e.g., Zettlemoyer et al., 2024). With ongoing climate change, the observed trend is likely to continue and to expand even upwards along the elevational gradients.

Currently, however, attention should focus on those regions where the habitat quality in calcareous grasslands has already clearly deteriorated. Without a significant reconsideration of current management practices, the formerly species- and flower-rich vegetation will gradually transform into grass- and moss-dominated stands (Fig. 1). Although the habitat type 'calcareous grassland' is likely to persist, it is expected to become increasingly unsuitable for many specialised plant and animal species.

Ethical declaration

The authors confirm that this study was conducted in accordance with Elsevieŕs ethical guidelines. No further ethical concerns are to be declared.

CRediT authorship contribution statement

Dominik Poniatowski: Writing – original draft, Conceptualization. **Thomas Fartmann:** Writing – review & editing, Supervision.

Declaration of Generative AI and AI-assisted technologies in the writing process

We have used AI to enhance English grammar, improve clarity, and ensure conciseness.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Declaration of Competing Interest

The authors are not involved in any potential conflicts of interest.

Data availability

No data was used for the research described in the article.

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