

# Insect decline in Central Europe: causes and solutions

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## TREFWOORDEN

Conservation, grasslands, species assemblages

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Temperate, semi-natural grasslands are among the most species-rich ecosystems on earth. However, due to land-use intensification, abandonment, and afforestation, their extent has greatly decreased, and the remaining grassland patches have become fragmented. Habitat quality, size, and connectivity are considered the main drivers of patch occupancy of grassland insects in our fragmented landscapes. Conservation management to support grassland insects should aim to (i) increase the quality of the remaining patches, (ii) enlarge them, and (iii) improve functional connectivity between them. The disturbance regime in grasslands should maintain or create heterogeneous swards with some patches of bare ground and high plant species richness. When implementing conservation measures, the focus should be on increasing heterogeneity at all spatial scales, because this has a positive impact on biodiversity and buffers extreme weather events such as droughts. The stabilisation of the water level or the restoration of the natural water table is also an invaluable measure for mitigating the negative effects of climate change. Low-intensity land use and, at best, low levels of fertilisation are of vital importance for high habitat quality in temperate, semi-natural grasslands. In most cases, grazing with low stocking rates should be preferred over mowing. Low-intensity grazing systems are highly effective in shaping heterogeneous grasslands with species-rich insect assemblages.

## Introduction

Temperate, semi-natural grasslands are among the most species-rich ecosystems across the globe (Bonari *et al.* 2017, Fartmann 2024, Fartmann *et al.* 2021a). They hold the world record in fine-scale species richness of vascular plants and are hot-spots of insect diversity. For centuries, traditional land use has created and maintained these grasslands, with their outstanding biodiversity across Europe. However, the transition from pre-industrial land use to modern agriculture – especially after World II – has greatly reduced their extent, and the remaining patches are now fragmented.

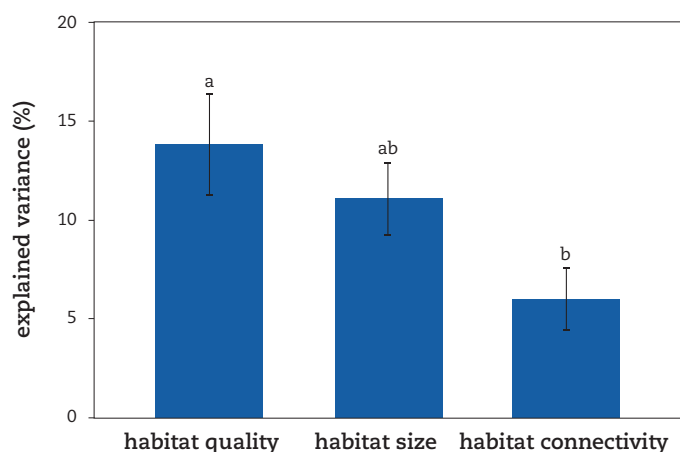
Two contrasting, large-scale processes have been responsible for the habitat loss and fragmentation, namely: (i) land-use intensification on the one hand and (ii) abandonment and afforestation on the other hand (Fartmann 2024). The former includes the conversion of nutrient-poor, semi-natural grasslands to improved grasslands or arable fields. Land-use intensification has mainly occurred on productive soils in the lowlands (Fartmann *et al.* 2021a, Löffler *et al.* 2023). However, during the past decades, grassland management has also been intensified in low-mountain ranges (Fartmann 2024, Fartmann *et al.* 2021a). By contrast, abandonment and afforestation have taken place on marginal land.

Today, the remaining patches of semi-natural grasslands are embedded in a hostile matrix, which is mainly used for intensive agriculture (e.g., arable fields) (Poniatowski *et al.* 2018, Fartmann *et al.* 2021a, b). Additionally, grassland remnants often suffer from habitat deterioration due to: (i) inappropriate management (Fartmann 2024, Poniatowski & Fartmann 2026), (ii) eutrophication because of airborne nitrogen deposition (Vogels *et al.* 2023), and (iii) climate change (Harvey *et al.* 2023).

## Drivers of insect persistence in fragmented grasslands

Habitat quality, size, and connectivity are considered the main drivers of patch occupancy of grassland insects in our fragmented landscapes (Poniatowski *et al.* 2018) (figure 1). However, the relative importance of each of the three parameters varies depending on the population structure of the species, which is related to its mobility and the landscape composition (Fartmann *et al.* 2021a). Insect species with low mobility, e.g., many flightless Orthoptera, often form closed populations (Poniatowski *et al.* 2018, Cardoso *et al.* 2020). They can survive for longer time periods, even in isolated grasslands, if the patches are characterised by a permanently high habitat quality and are large enough to contain a viable population. By contrast, insect species capable of flight, and therefore with higher mobility, such as many butterflies, often build metapopulations (Fartmann 2024, Fartmann *et al.* 2026). Besides habitat quality and habitat size, the connectivity of the patches is also crucial for the long-term survival of such species (Poniatowski *et al.* 2018, Cardoso *et al.* 2020). Metapopulation species vitally depend on a network of well-connected, high-quality grassland patches of sufficient size.

Overall, habitat quality is the most important predictor of patch occupancy of grassland insects. All species depend on habitats that exhibit suitable habitat quality, irrespective of differences in their population structure and the composition of the landscape surrounding the patches. High habitat connectivity is crucial for metapopulation species, particularly in highly fragmented landscapes. For range shifts, however, all insect species need a certain degree of connectivity between the habitat patches.



1. Explanatory power of habitat quality, size and connectivity with respect to the patch occupancy of 13 habitat specialists (butterflies, grasshoppers, leafhoppers) in calcareous grasslands of the Diemel Valley (central Europe), expressed as the mean ( $\pm$  SE) proportion of variance explained exclusively by the respective parameter. Different letters indicate significant differences between the parameters ( $P < 0.05$ ). Source: Poniatowski et al. (2018)

1. Verklaring van habitatkwaliteit, grootte en connectiviteit met betrekking tot de bezetting van leefgebieden door 13 habitatspecialisten (vlinders, sprinkhanen, cicaden) in kalkrijke graslanden van het Diemeldal (Midden-Europa), uitgedrukt als het gemiddelde ( $\pm$  SE) aandeel van de variantie dat uitsluitend door de betreffende parameter wordt verklaard. Verschillende letters geven significante verschillen tussen de parameters aan ( $P < 0,05$ ). Bron: Poniatowski et al. (2018)

## Habitat quality

Habitat quality for grassland insects is mainly determined by (i) habitat heterogeneity (i.e., environmental heterogeneity at the patch level) and (ii) plant species richness, which are often correlated (Fartmann 2024, Fartmann et al. 2026). High habitat heterogeneity fosters species richness of grassland insects in three ways: (i) by being necessary for many taxa that undergo microhabitat shifts during their life cycle (Figure 2), (ii) by generally enhancing species richness through a variety of environmental conditions, and (iii) by functioning as a buffer against extreme weather events. Patches of early-successional stages with bare ground are important, since many species prefer warm microhabitats for breeding and other life functions (Fartmann et al. 2026).



2. Species like the wartbiter *Decticus verrucivorus* use bare soil for oviposition, and the tiny young nymphs also prefer these warm microhabitats. By contrast, the larger older nymphs, and in particular the huge adults, favour taller and more dense vegetation that provides shelter against predators and can also be used as a song post by the adult males. Photo: Thomas Fartmann

2. Soorten zoals de wrattenbijter *Decticus verrucivorus* gebruiken kale grond om hun eieren te leggen, en de kleine jonge nimfen geven ook de voorkeur aan deze warme microhabitats. Daarentegen geven de grotere oudere nimfen, en vooral de enorme volwassen dieren, de voorkeur aan hogere en dichtere begroeiing die beschutting biedt tegen roofdieren en ook kan worden gebruikt als zangpost door de volwassen mannetjes.

Many phytophagous grassland insects, such as bees, butterflies, leafhoppers, or true bugs, exhibit high host-plant specificity (Fartmann et al. 2021a, Helbing et al. 2023). Consequently, their species richness increases with plant diversity, which also benefits predatory insects and parasitoids (Fartmann et al. 2026).

Habitat heterogeneity, including the availability of early-successional stages rich in bare ground, and phytodiversity depend on the (i) disturbance regime and (ii) productivity of the grassland (Fartmann et al. 2026). Low to intermediate intensity and frequency of disturbances result in high habitat heterogeneity and plant-species richness. On more productive soils, both peak at higher disturbance levels than under more nutrient-poor and drier conditions. The same applies to insect species richness of grasslands (e.g., Helbing et al. 2023, Samways et al. 2020).

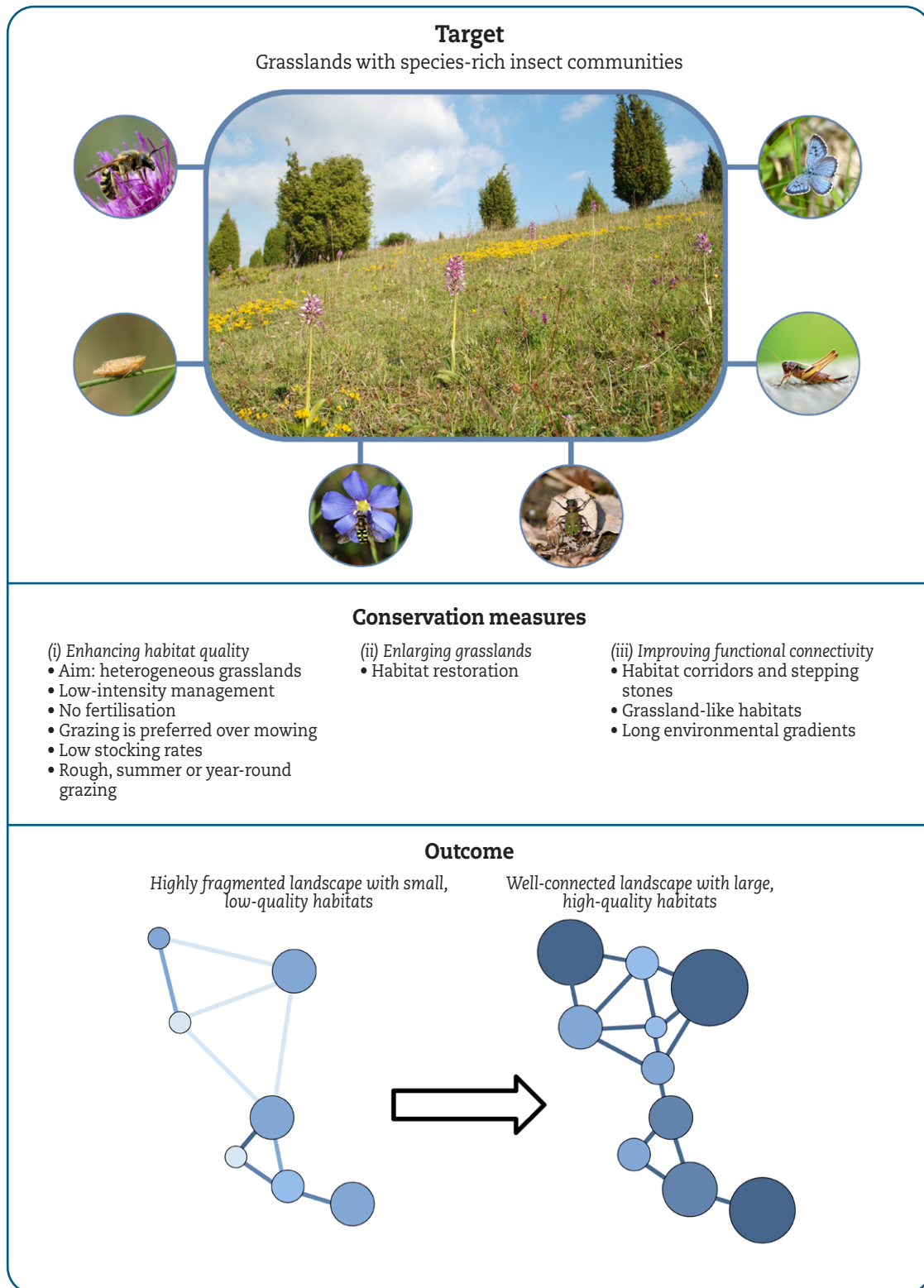
## Habitat size

The size of grassland patches is directly related to three parameters that are of prime importance for species richness of insects: (i) habitat heterogeneity (see above), (ii) edge effects due to the adjacent matrix and (iii) the minimum area requirements of the taxa (Fartmann et al. 2021a). Usually, with increasing patch size, environmental heterogeneity increases, edge effects decrease, and the number of insect species rises (Fartmann 2024). Among the matrix habitats, arable fields may cause particularly strong negative edge effects due to pesticide and nutrient application (Fartmann et al. 2021a). Large areas are required for some butterfly species with metapopulation dynamics. An example is the niobe fritillary *Fabriciana niobe*, which requires at least 100 ha of well-connected grasslands supporting its host plants (violets *Viola*) (Salz & Fartmann 2009).

## Habitat connectivity

Habitat connectivity implies more than simply edge-to-edge distance between grassland patches (Euclidean distance) (Poniatowski et al. 2016). The permeability of the matrix biotopes between the patches is also crucial for successful inter-patch movements (functional connectivity). Overall, low-growing grassland-like biotopes favor dispersal of grassland insects, whereas taller land cover types typically impede it.

By contrast, modern-day arable fields rank among the most hostile environments for grassland specialists among insects (Fartmann et al. 2021a). They largely lack nectar resources and



**3.** The overall target of all conservation measures is to maintain and restore grasslands with species-rich insect communities. To achieve this goal: (i) enhancing habitat quality of the remaining grasslands, (ii) enlarging them, and (iii) improving functional connectivity between the patches are necessary. These measures result in the establishment of a well-connected landscape with large, high-quality habitats. Additional information: Target – a species-rich calcareous grassland with common juniper *Juniperus communis*, military orchid *Orchis militaris*, and horse-shoe vetch *Hippocrepis comosa* as characteristic plant species and large blue *Phengaris arion*, bog bush-cricket *Metrioptera brachyptera*, green tiger beetle *Cicindela campestris*, migrant hoverfly *Eupeodes corollae*, the leafhopper *Adarrus multinotatus* and great banded furrow bee *Halictus scabiosae* as typical insect species is shown. Outcome – the darker the blue, the higher the habitat quality and the functional connectivity of the patches. Source: Fartmann (2024). Photos: F. Helbing (*A. multinotatus*), D. Poniatowski (*E. corolla*), T. Fartmann (all others)

**3.** Het algemene doel van alle natuurbeschermingsmaatregelen is het behouden en herstellen van graslanden met soortenrijke insectenpopulaties. Om dit doel te bereiken is het nodig om: (i) de habitatkwaliteit van de overgebleven graslanden te verbeteren, (ii) deze uit te breiden, en (iii) de functionele connectiviteit tussen de stukken te verbeteren. Deze maatregelen leiden tot een goed verbonden landschap met grote, hoogwaardige habitats. Extra informatie: Doel – een soortenrijk kalkgrasland met gewone jeneverbes *Juniperus communis*, soldatenorchis *Orchis militaris* en paardenhoeftklaver *Hippocrepis comosa* als kenmerkende plantensoorten en tijmblauwtje *Phengaris arion*, heidesabelsprinkhaan *Metrioptera brachyptera*, groene zandloopkever *Cicindela campestris*, terrasjes-kommazweefvlieg *Eupeodes corollae*, de dwergcicade *Adarrus multinotatus* en breedbandgroefbij *Halictus scabiosae* als typische insectensoorten. Resultaat – hoe donkerder het blauw, hoe hoger de habitatkwaliteit en de functionele connectiviteit van de stukken. Bron: Fartmann (2024)

host plants, and any pesticides that may be applied are directly detrimental. As a result, arable fields surrounding grasslands have repeatedly been reported to decrease patch occupancy of mobile insects, which move between patches (Fartmann 2024).

Typically, (i) flightless insects and (ii) habitat specialists depend on high functional connectivity for dispersal between grassland patches. By contrast, (i) species capable of flight and (ii) small insects that are light in weight and might be passively dispersed by wind, such as ballooning spiders, can colonise even more remote and isolated grassland patches (Fartmann 2024, Fartmann et al. 2021a). Habitat generalists are also more successful in colonising grassland patches in fragmented landscapes.

### Climate change meets grassland fragmentation – a lethal cocktail for insects

Global warming is causing changes in (i) phenology, (ii) species interactions, including temporal and spatial mismatches, and (iii) distribution patterns of grassland insects (Fartmann et al. 2026). Both gradual changes and extreme events (e.g., droughts, fires, floods) due to climate change contribute to this, but effects of the latter are much more severe, particularly in fragmented grasslands (e.g., Piessens et al. 2009, Fartmann et al. 2022). Extreme events are highly unpredictable both spatially and temporally, strongly reducing potential selective responses of insects (Harvey et al. 2023). Species at higher trophic levels that occur in small or homogeneous grassland patches are especially susceptible to extreme events. Climate change-mediated extreme events were recently responsible for local population declines and extirpations of grassland insects (e.g., Fartmann et al. 2022, Piessens et al. 2009).

As for the more tangible drivers of species richness in fragmented grasslands (see above), life-history traits of the insect taxa also strongly determine the response to climate change. Overall, particularly among hygrophilous and cold-adapted habitat specialists with low mobility, insects are suffering from global warming in grasslands (Fartmann 2024, Fartmann et al. 2026). However, for example, during recent climate change-mediated drought periods, insect populations or assemblages collapsed even in mesic and dry grasslands (Fartmann 2024, Fartmann et al. 2026). By contrast, many thermophilous and mobile habitat generalists were able to expand their ranges due to climate change (Fartmann et al. 2021a, 2021b, Poniatowski et al. 2020). However, even for these species, the range shifts lag behind the increase in temperature since their dispersal is also constrained by habitat fragmentation (Cardoso et al. 2020, Fartmann et al. 2021a). In general, climate change has led to biotic homogenisation of grassland insects favoring some habitat generalists at the expense of many specialised species (Fartmann 2024, Poniatowski & Fartmann 2026).

### Conserving grassland insects in times of global change

It is assumed that habitat availability and global warming will determine the distribution of insects in temperate, semi-natural grasslands in the future (Fartmann et al. 2021a, b). Accordingly, and based on the aforementioned, conservation management should aim to (i) enhance the habitat quality of the remaining grasslands, (ii) enlarge them, and (iii) improve functional connectivity between patches (Fartmann et al. 2021a, Samways et al. 2020, Stuhldreher & Fartmann 2018) (figure 3). When conducting such measures, focus should be on increasing heterogeneity at all spatial scales due to its buffering effect against extreme weather events, such as drought periods (Fartmann et al. 2021a). For centuries, most landscapes in temperate regions had been

intensively drained by humans. Accordingly, the stabilisation of the water level or the restoration of the natural water table is crucial for mitigating the effects of climate change on insects.

### Enhancing habitat quality of the remaining habitat patches

Low-intensity land use and, at best, low levels of fertilisation are of vital importance for high habitat quality in semi-natural grasslands (Fartmann et al. 2021a, Poniatowski et al. 2018). Overall, habitat management should aim to maintain and create nutrient-poor grasslands with heterogeneous swards that exhibit some bare ground and a high phyto-diversity. In most cases, pastures with low stocking rates should be preferred to meadows.

Suitable low-intensity grazing systems that shape heterogeneous grasslands with species-rich insect assemblages are rough grazing by sheep (and goats in shrub-rich grasslands), summer grazing by cattle and year-round grazing with horses, cattle or indigenous grazers such as red deer *Cervus elaphus* or European bison *Bison bonasus* (Fartmann et al. 2021a, Fartmann et al. 2026). Particularly in regions with increased nitrogen deposition rates (e.g., the Benelux countries or north-western Germany) or mild winters, grazing in winter or early spring is important (Fartmann et al. 2021a). In former times, winter and spring grazing was much more widespread than today. It is the basis for high plant and insect species richness in many grasslands. It secures open swards in spring where light-demanding plants can germinate and provides warm microclimatic conditions for the successful development of many insects. Additionally, it weakens the competitive power of invasive species, such as the Upright brome *Bromus erectus* (Poniatowski & Fartmann 2026). Moreover, grazing animals produce dung, the food source of coprophagous insects. Accordingly, the application of pesticides for parasite control in livestock, such as ivermectin, should be avoided (Samways et al. 2020).

### Enlarging grassland patches

In particular, abandoned grasslands encroached by shrubs and afforested grasslands adjacent to existing grasslands should be restored (Fartmann et al. 2021a). In contrast to grasslands that have been converted to arable fields, they are usually characterised by low nutrient contents comparable to those of the original grassland (Fartmann 2024). Additionally, if cessation of grassland management occurred no more than two to three decades ago, the soils often contain a viable seed bank. Accordingly, after cutting and removing woody plants, grassland vegetation can establish without the need for seed or hay transfer.

### Improving functional connectivity between grassland patches

Habitat corridors and stepping-stones that resemble the habitat structure and plant species composition of the grasslands they should connect, have the highest functional value for the facilitation of inter-patch movements (Poniatowski et al. 2018, Samways et al. 2020). Existing linear structures, such as roadside verges or powerline corridors, play an important role in establishing functional connectivity between grassland patches. To allow insects to adapt to extreme weather events and to track climate warming, it is also essential to include semi-natural grasslands across long environmental gradients (e.g., large differences in aspect, elevation, moisture, or shade) into the large-scale conservation corridors. Within such habitat corridors, conservation management should aim to maintain and restore semi-natural grasslands following the guidelines described above.

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## Samenvatting

### Achteruitgang van insecten in Midden-Europa: oorzaken en oplossingen

Gematigde, semi-natuurlijke graslanden behoren tot de meest soortenrijke ecosystemen op aarde. Door intensivering van het landgebruik, verwaarlozing en bebossing is hun omvang echter sterk afgenomen, en de overgebleven graslanden zijn versnipperd geraakt. De kwaliteit van de habitat, de grootte en de verbindingen worden beschouwd als de belangrijkste factoren voor het voorkomen van graslandinsecten in onze gefragmenteerde landschappen. Beheer voor het behoud van graslandinsecten zou moeten streven naar (i) het verbeteren van de kwaliteit van de overgebleven stukken, (ii) de oppervlakte ervan vergroten en (iii) de functionele verbindingen ertussen verbeteren. Het verstoringsregime in graslanden zou moeten zorgen voor heterogene grasmatten met enkele plekken met kale grond en een hoge plantensoortenrijkdom. Bij het uitvoeren van beschermingsmaatregelen moet de focus liggen op het vergroten van de heterogeniteit op alle ruimtelijke schalen, omdat dit een positief effect heeft op de biodiversiteit en extreme weersomstandigheden zoals droogte kan opvangen. Het stabiliseren van het waterpeil of het herstellen van de natuurlijke grondwaterstand is ook een waardevolle maatregel om de negatieve effecten van klimaatverandering te beperken. Laag-intensief landgebruik en, bij voorkeur, lage niveaus van bemesting zijn enorm belangrijk voor een hoge kwaliteit van habitats in gematigde, halfnatuurlijke graslanden. In de meeste gevallen heeft begrazing met lage vee-dichtheden de voorkeur boven maaien. Laag-intensieve begrazingssystemen zijn zeer effectief in het vormgeven van heterogene graslanden met soortenrijke insectenpopulaties.



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