Effect of mowing on snail communities in wet meadows

Roland Farkas Corresp., [1, 2, 3], **Miklós Bán** [3], **Zoltán Barta** [3]

[1] Bükk National Park Directorate, Eger, Hungary
[2] Juhász-Nagy Pál Doctoral School, University of Debrecen, Debrecen, Hungary
[3] ELKH-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary

Corresponding Author: Roland Farkas
Email address: farkasro@yahoo.com

Wet meadows are renowned for harboring rich biodiversity, rendering them pivotal ecosystems worldwide. These habitats are commonly utilized for grazing or mowing practices aimed at producing forage. Nevertheless, regular mowing can exert a notable influence on these habitats, potentially leading to significant repercussions on various species populations residing therein. In order to scrutinize the ramifications of land management practices, our primary research objective entailed a comparative analysis of snail communities in mowed and unmowed wet meadows situated in the northern region of Hungary. The findings indicate that the act of mowing has engendered a decrease in species abundance, as well as in the number and diversity of species present. Consequently, our results suggest a deleterious impact of routine wet meadow cultivation on the snail fauna. We contend that, in instances where meadows are subjected to regular agricultural management, it is imperative to designate uncultivated patches within those areas where environmental conditions closely resemble the original natural state. By doing so, these patches can serve as potential colonization sites, facilitating the restoration of the meadow's ecological balance.

Effect of mowing on snail communities in wet meadows

Roland Farkas[1,2,3], Miklós Bán[3], Zoltán Barta[3]

[1]Bükk National Park Directorate, Eger, Hungary

[2]Juhász-Nagy Pál Doctoral School, University of Debrecen, Debrecen, Hungary

[3]ELKH-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary

Corresponding Author:
Roland Farkas
Sánc u. 6., Eger, H-3304, Hungary
Email address: farkasr@bnpi.hu

Abstract

Wet meadows ~~are renowned for~~ harbor~~ing~~ rich biodiversity, rendering them pivotal ecosystems worldwide. These habitats are commonly ~~utilized~~ for grazing or mowing practices ~~aimed at~~ produc~~ing~~ forage. Nevertheless, regular mowing can ~~exert a notable~~ influence ~~on~~ these habitats, potentially leading to significant repercussions on various species populations residing therein. In order to scrutinize the ramifications of land management practices, ~~our primary research objective entailed a~~ comparative analysis of snail communities in mowed and unmowed wet meadows ~~situated~~ in ~~the~~ northern ~~region of~~ Hungary. ~~The findings indicate that the act of~~ mowing has ~~engendered a~~ decrease ~~in~~ species abundance, as well as ~~in the number~~ and diversity of species ~~present.~~ Consequently, our results suggest a deleterious impact of routine wet meadow cultivation on the snail fauna. We contend that, in instances where meadows are subjected to regular agricultural management, it is imperative to designate uncultivated patches within those areas where environmental conditions closely resemble the original natural state. By doing so, these patches can serve as potential colonization sites, facilitating the restoration of the meadow's ecological balance.

Introduction

The condition of meadows is subject to the influence of both climatic factors and human activities. Climate change presents various future scenarios, the majority of which project unfavorable outcomes with respect to both habitats and their utilization (Joyce et al., 2016). Human activities encompass a wide range, spanning from sustainable farming practices to the complete transformation of natural habitats. The outcomes arising from these natural and anthropogenic processes can have significant implications, particularly for sensitive areas such as wetlands. Wet meadows, akin to other wetland types, have experienced substantial reduction in area across Europe over the past centuries (Zedler & Kercher, 2005). Presently, most wet meadows are utilized for agricultural purposes, thereby necessitating their survival to a large extent on appropriate management practices. Even undisturbed wet meadows require periodic intervention due to their susceptibility to invasive species (Zedler & Kercher, 2004).

Grazing and mowing represent the predominant methods employed for the cultivation of meadows. However, the outcomes of these regular management practices cannot be universally applied to all habitats (Oelmann et al., 2009). For instance, the response of indicator taxa or abiotic traits to the same management practice can differ across distinct habitats, making it inappropriate to extrapolate findings from dry meadows to wet meadows (Oelmann et al., 2009).

Due to a greater emphasis on studying the effects of various land use practices in dry and semi-dry habitats, such as hay meadows (e.g. Bakker et al., 2002; Moog et al., 2002; Kormann et al., 2015), compared to wet meadows (Pech et al., 2015), it becomes crucial to conduct additional research in water-influenced habitats.

In order to effectively monitor the impacts of management practices, it is valuable to investigate diverse and sensitive species groups that serve as reliable indicators of changes and exhibit rapid responses to different management techniques (Plantureux et al., 2005). The relationship between land use intensity and vegetation is frequently examined (e.g. Bakker et al., 2002; Moog et al., 2002; Zechmeister et al., 2003; Socher et al., 2012). This is crucial because vegetation plays a pivotal role in shaping the overall habitat by influencing its structural characteristics, biomass, and species composition. Additionally, heterotrophic organisms can exert a significant influence on habitats. Invertebrates, for instance, are particularly important members of communities, occupying various niches within the habitat structure, thereby making them well-suited for assessing the effects of management practices from a perspective distinct from studies primarily focused on vegetation (e.g. butterflies: Johst et al., 2006; Konvicka et al., 2008; Dover et al., 2010; dung beetles: Frank et al., 2017; snails: Książkiewicz, 2014; Wehner et al., 2019; orthopterans: Chisté et al., 2016; spiders: Szmatona-Túri et al., 2017).

The litter layer, which exists just above the soil surface, represents a distinct component of wetland habitats. It serves as the site where a majority of deceased plant matter undergoes decomposition by detritivores. Processes occurring within the litter layer are critical for the nutrient cycle of the entire habitat. Gastropods, commonly known as snails, typically play a significant role in these detritivore processes (Newell, 1967). Aside from their own consumption activities, they contribute indirectly to decomposition processes. Snails facilitate the activity of microbial detritivores by shredding materials, and their excretion of feces and production of mucus create favorable conditions for the proliferation of microbial life (Theenhaus & Scheu, 1996). Wetland habitats, including the litter layer and the vegetation layers immediately above it, often harbor diverse snail communities. Due to their limited dispersal capabilities and high water content in their bodies, snails are highly susceptible to changes in environmental conditions. Consequently, they serve as excellent indicators of the prevailing conditions within these habitats (Čejka & Hamerlík, 2010; Pech et al., 2015; Wehner et al., 2019). Studies have indeed demonstrated that snail assemblages in wet meadows are strongly influenced by abiotic factors such as moisture, pH, and calcium content (Martin & Sommer, 2004a; Cernohorsky et al., 2010; Hettenbergerová et al., 2013; Horsák et al., 2014; Wehner et al., 2019). Different land-use practices can directly impact snail assemblages, with changes in abiotic factors resulting from management activities often leading to alterations in species richness and abundance (Wehner et al., 2019).

The hilly counties in northern Hungary exemplify the coexistence of diverse land-use practices within a mosaic structure, which serves as an adaptive response to the varying topographical and environmental factors. Our research focused on sites located in the Putnok Hills and Cserehát Hills, characterized by narrow valleys traversed by small streams. Historically, the hill slopes were subject to extensive cultivation until the end of the previous century. Subsequently, they transitioned into large hay meadows or were left abandoned, leading to the establishment of dry shrub vegetation. The lower portions of the valleys, influenced by a high groundwater level, were predominantly utilized for mowing or grazing, as they were unsuitable for ploughing. Over time, many of these wet meadows in the valley bottoms have also been abandoned, resulting in the encroachment of shrubs, willows, and notably reed in certain areas.

In 2003, Birdlife Hungary initiated a reconstruction program in the region. The program implemented traditional land-use methods in the most ecologically valuable sections of the valley bottoms, prioritizing the preservation of important habitats and vulnerable species. Management activities, specifically regular mowing of abandoned valley bottoms, commenced in seven closely situated valleys.

Concurrent with the restoration efforts, a comprehensive biotic survey was initiated to systematically monitor the impacts of the project. To investigate and assess the effects of mowing, designated managed and control plots were established within both the mowed and unmanaged regions of each valley. As previously mentioned, snail communities hold significant ecological importance within comparable ecosystems and are considered highly responsive to environmental changes, rendering them ideal candidates for assessment purposes. Consequently, we evaluated the effects of the management practices implemented in the valleys by comparing the snail communities inhabiting the managed and control plots.

Materials & Methods

Study area

The study was conducted within the Putnok Hills and Cserehát Hills, ~~located in the~~ northern ~~region of~~ Hungary (**Fig. 1**). ~~These hills predominantly consist of slope and fluvial sediments, contributing to their geological composition.~~ The elevations of the hills surrounding the studied valleys range from 250 to 350 meters above sea level (asl), while the specific areas of the valleys under investigation are situated at approximately 220 to 250 meters asl. The study area falls within the temperate continental climatic zone, characterized by an average annual temperature of 8.5 to 9 °C and an average annual precipitation ranging between 550 to 600 mm (Mezősi, 1998; Dobány, 2010).
~~Of the seven designated study sites, six are located within the Putnok Hills, specifically in the vicinity of Gömörszőlős, Kelemér, and Zádorfalva, with distances ranging from 0.4 to 3.5 km between them. The seventh site is situated in the Cserehát Hills near the village of Abod, approximately 25 km away from the other sites (**Table 1**).~~
Experimental plots, comprising both managed and control conditions, were established within the study sites. The managed plots were ~~specifically located~~ within areas subjected to mowing. In close proximity to each managed plot, with an average distance of 204.8 ± 117.7 meters, a corresponding control plot was established in unmowed areas. All plots were positioned at the valley bottoms, accompanied by small streams. Each pair of control and managed plots shared the same valley floor, ensuring comparability between the two conditions.
The managed and control plots exhibited a complete absence of shrubs or willows throughout the duration of the study. ~~No evidence of their presence was observed.~~ Typically, the valley bottoms ~~were characterized by the~~ dominance of sedge marsh vegetation. Over the decades of abandonment, the sedge species *Carex acutiformis* and reed (*Phragmites australis*) emerged as the predominant plant species, covering the areas in similar proportions. Grasses and forbs were present in all plots; however, their distribution was moderate, and they did not occupy a substantial portion of the surface.
The management procedures were initiated in 2003, whereby both managed and control plots were established within the same patches of vegetation. Initially, there were no discernible differences between the vegetation of the managed and control plots. The managed areas of the sites underwent annual mowing, with the cut plant material systematically removed from the habitats. Consistent methodologies were employed for all managed sites, ensuring uniformity in the management practices.

Sampling ~~of snail communities~~

The ~~experimental~~ design encompassed the placement of five ~~sampling~~ quadrats measuring 25 by 25 cm within each plot. These quadrats were equidistantly positioned along a 50-meter transect.

A total of 15 transects were established, with eight located within managed plots and seven within control plots. At the Buda-völgy site (no. 2), two managed plots were set up due to the presence of two mowed patches on either side of the control plot.

The ~~malacological field study~~ was conducted ~~over the course of two years, specifically~~ in 2007 and 2008, ~~employing consistent methodologies~~. ~~Sampling took place during the months of~~ July and August, subsequent to the completion of the management activities. The transects were ~~precisely~~ positioned in the same locations in both years. In total, 15 samples were collected throughout the two-year investigation.

Sampling procedures involved the complete removal of litter and the top 1 cm layer of soil from each quadrat. These samples were collected and stored in plastic bags. The snail shells (Gastropoda) were manually separated from the litter samples using a delicate nipper and subsequently identified under a stereomicroscope. Identification protocols followed the guidelines of Kerney et al. (1983) and Glöer and Meier-Brook (2003). Only fresh shells, characterized by intact whorls and non-eroded periostracum, were selected for further analysis. All fresh shells were identified at the species level. Slugs were not included in the survey due to the unsuitability of this method for accurate quantitative estimation of their abundance, as noted by Cameron and Pokryszko (2005).

~~For each sampling quadrat, data were recorded based on the identified snails, including (i) the total number of individuals found, (ii) species richness (number of species), and (iii) the Shannon diversity index (Shannon and Weaver, 1949).~~

Statistical analyses

To analyze the impact of management practices on species abundance and presence/absence, we employed a multilevel modeling framework recommended by Jackson et al. (2012). This framework enables us to examine the effects of environmental factors on both the community and individual species (Jackson et al., 2012). In our initial model, the response variable was the number of individuals of each species observed in a sample. Fixed effects included the type of management, year, and their interaction. Random effects encompassed a random intercept within plot ID nested within site ID, a random intercept within species ID, and random slopes for management and years within each species. Considering the apparent over-dispersion in the data, a negative binomial error distribution was employed. The fixed terms provide estimates of the overall (across all species) effects of management and year, while the random slopes estimate the effects of management and year specific to each species. Model fitting was performed using the 'glmmTMB' function from the 'glmmTMB' package (Brooks et al., 2017).

In our second model, the presence/absence of species in a sample was considered as the response variable. The fixed and random effects structure mirrored that of the first model. However, a zero-inflated binomial error distribution was utilized for this analysis. Again, the 'glmmTMB' function was used to fit this model.

Furthermore, we investigated the impact of management on biodiversity by calculating the Shannon-Weaver diversity index for each sample, which served as the response variable in our third model. The fixed terms in this model remained consistent with the previous ones. Additionally, we included plot ID within area ID as a random effect. Since species identity was not relevant in this case, no species-related random terms were included in the model. Model fitting was conducted using the 'glmmTMB' function.

Following the fitting of the full models, we conducted tests to examine the effects of random terms by comparing models with and without a specific random effect using likelihood-ratio tests performed with the 'anova' function. Non-significant random terms related to species were eliminated from the model, while we retained the plot and area random effects regardless of their significance to maintain the integrity of the experimental design. Subsequently, we assessed the significance of fixed terms by sequentially removing non-significant terms ($p > 0.05$) from the model using the 'drop1' function in R. The least significant term, identified by the highest p-value, was initially eliminated. The elimination process ceased when only significant interactions, their main effects, or significant main effects remained in the model. However, we retained non-significant fixed terms if they were involved in a random slope term as well. Post hoc comparisons between levels of explanatory variables were conducted using the 'emmeans' package (Lenth et al., 2020). Marginal means ± standard error (SE) are reported in the text. All species collected were included in the statistical analyses.

All statistical analyses were carried out in the R interactive statistical environment (version 4.0.3, R Core Team, 2020).

Results

~~Throughout the survey~~, ~~a total of~~ 11,629 specimens belonging to 34 snail species ~~were collected~~ (**Table S1**).

All random terms exhibited significant effects on species abundance, indicating considerable variation among areas ($\chi^2_1 = 146.43$, $p < 0.001$) and species ($\chi^2_1 = 883.92$, $p < 0.001$). Additionally, random slopes accounted for a significant portion of abundance variation (management: $\chi^2_1 = 22.73$, $p < 0.001$; year: $\chi^2_1 = 10.27$, $p = 0.001$), indicating that different species reacted differently to management practices and the passage of time. However, a general effect of the year was not observed ($\chi^2_1 = 0.27$, $p = 0.604$), suggesting that changes in species abundance over time offset each other. Nonetheless, management exerted a significant overall ~~(fixed)~~ effect (control: 0.32 ± 0.15, managed: 0.20 ± 0.10, $t_{5091} = 2.149$, $p = 0.032$), indicating that, despite variable responses, species abundances generally decreased in response to mowing (**Fig. 2a**).

Similar to species abundance, the presence/absence of species exhibited substantial variability both among areas ($\chi^2_1 = 40.25$, $p < 0.001$) and species ($\chi^2_1 = 594.24$, $p < 0.001$). Furthermore, there was significant variation in species-specific responses to management practices ($\chi^2_1 = 8.88$, $p = 0.003$), while the influence of the year was negligible ($\chi^2_1 = 0.00$, $p = 1.000$). Following model simplification, only the effect of management remained significant, indicating that the presence of species was less likely in managed areas (control: 0.193 ± 0.073, managed: 0.126 ± 0.052, t_{5093} = 2.287, p = 0.022; **Fig. 2b**).

The analysis of Shannon diversity revealed that the variation among plots and areas was not statistically significant (χ^2_2 = 2.00, p = 0.367). However, among the fixed terms, the effect of management was found to be significant, indicating that snail communities exhibited lower diversity in managed areas (control: 0.785 ± 0.021, managed: 0.709 ± 0.020, t_{145} = 2.80, p = 0.006; **Fig. 2c**).

Discussion

Regular mowing exerted a detrimental impact on all the assessed characteristics of the snail communities under investigation. These findings align with previous studies that have reported similar outcomes. For instance, Pech et al. (2015) observed decreased snail abundance and species richness on mowed plots within wet meadows. Chisté et al. (2016) also documented comparable results for orthopterans. The intensive mowing of wet meadows has been shown to diminish slug abundance (Everwand et al., 2013). Similar negative effects on abundance have been observed in other taxa as well, such as spiders (Cattin et al., 2003) and dung beetles (Frank et al., 2017). Our study indicates that some of the adverse effects associated with regular mowing can be detected within a relatively short period (4-5 years in our case) following the initiation of cultivation. It should be noted that longer-term treatments in the examined area may impact additional community attributes.

Abiotic characteristics of the habitat, such as moisture levels and litter thickness, are believed to influence snail communities (Martin & Sommer 2004b; Dvořáková & Horsák, 2012; Pech et al.,, 2015). Therefore, it is plausible that management practices modify snail communities by altering these habitat traits. For instance, studies have demonstrated that vegetation mowing leads to increased direct radiation, temperature, and decreased soil moisture (Lepš 1999; Zechmeister et al., 2003). However, in certain cases, when the abiotic traits of the habitat remain in good original condition, they may mitigate the severe effects of mowing and still provide favorable and tolerable conditions for snails. In our study, focusing solely on the impact of mowing proved sufficient to detect changes in snail communities. This suggests that the effect of management was decisive and exerted a stronger influence than the potential impact of abiotic habitat traits.

Regular management practices have the potential to reduce the abundance of vulnerable and specialist species, even when their numbers are already below critical levels (Książkiewicz, 2014; Kormann et al., 2015). While meadow management offers economic benefits, it is crucial to prioritize the preservation of ecological values (Joyce et al., 2016; Felipe-Lucia et al., 2020). This is particularly important in the context of wet meadows characterized by their high ecological value, as well as in habitats housing vulnerable taxa.

Given the diverse requirements of different invertebrate taxa, finding suitable management methods is a challenging task. Therefore, it is crucial to consider a patchy composition of management at both the landscape and managed unit levels (Pech et al., 2015). In the context of our study, this entails leaving unmowed patches within wet meadows to ensure the survival of diverse snail communities. These areas are expected to undergo ecological succession over the long term. Our study focused on abandoned areas where shrub growth had not yet commenced and was not observed until the end of the project. Consequently, the response of the studied snail community to slow succession could not be assessed within the relatively short duration of the study. In the case of prolonged abandonment, the untreated areas may experience the establishment of shrubs and forests, leading to the transformation of the snail community. To preserve the snail community of a meadow, it is essential to vary the locations of mowed and unmowed patches in both space and time, avoiding fixed patterns.

To address the challenges posed by management practices, alternative approaches can be explored. The specific implementation details of management, such as timing, equipment used, and the handling of mowed biomass, can have varying effects on plant and invertebrate communities (e.g., Humbert et al., 2010, Humbert et al., 2012), particularly when considering the specific traits of the habitats involved. Conducting further studies on the interaction between management practices and local habitat traits is crucial for gaining a comprehensive understanding of the underlying mechanisms operating in managed wet meadows. This research would contribute to identifying appropriate strategies for the sustainable management and cultivation of wet meadow ecosystems.

Conclusions

Wet meadows represent fragile ecosystems, and alterations in snail communities serve as reliable indicators of their ecological status. In this study, we conducted experimental investigations to assess the impact of mowing on snail communities within wet meadows. Through rigorous statistical analyses, we confirmed that mowing exerted negative effects, leading to reductions in species abundance, species presence, and Shannon diversity. These findings emphasize the importance of considering these detrimental effects when formulating management strategies for wet meadows. We recommend maintaining unmown patches in wet meadows.

Acknowledgements

The authors would like to express their sincere gratitude to Barna Páll-Gergely for providing valuable feedback on the manuscript, and to Bernadett Virókné Fodor for their assistance with linguistic corrections. Special thanks are extended to György Dudás for his insightful suggesstions regarding the interpretation of the results.

References

Bakker JP, Elzinga JA, Vries, Y (2002) Effects of long-term cutting in a grassland system: Perspectives for restoration of plant communities on nutrient-poor soils. Appl Veg Sci 5: 107–120. https://doi.org/10.1111/j.1654-109X.2002.tb00540.x

Brooks M, Kristensen K, van Benthem K, Magnusson A, Berg CW, Nielsen A, Skaug H, Mächler M, Bolker B (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J 9:378–400. https://doi.org/10.32614/RJ-2017-066

Cameron R, Pokryszko BM (2005) Estimating the species richness and composition of land mollusc communities: Problems, consequences and practical advice. J Conchol 38:529–248.

Cattin MF, Blandenier G, Banašek-Richter C, Bersier LF (2003) The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. Biol Conserv 113:179–188. https://doi.org/10.1016/S0006-3207(02)00297-5

Čejka T, Hamerlík L (2010) Land snails as indicators of soil humidity in Danubian woodland (SW Slovakia). Pol J Ecol 57:741-747.

Cernohorsky N, Horsák M, Cameron R (2010) Land snail species richness and abundance at small scales: The effects of distinguishing between live individuals and empty shells. J Conchol 40:233–241.

Chisté MN, Mody K, Gossner MM, Simons NK, Köhler G, Weisser WW, Blüthgen N (2016) Losers, winners, and opportunists: How grassland land-use intensity affects orthopteran communities. Ecosphere 7, e01545. https://doi.org/10.1002/ecs2.1545

Dobány Z (2010) A Cserehát történeti földrajza (18–20. század). ANP Füzetek VIII. Aggteleki Nemzeti Park Igazgatóság, Jósvafő, Hungary.

Dover J, Rescia A, Fungariño S, Fairburn J, Carey P, Lunt P, Dennis R, Dover C (2010) Can hay harvesting detrimentally affect adult butterfly abundance? J Insect Conserv 14:413–418. https://doi.org/10.1007/s10841-010-9267-5

Dvořáková J, Horsák M (2012) Variation of Snail Assemblages in Hay Meadows: Disentangling the Predictive Power of Abiotic Environment and Vegetation. Malacologia 55:151–162. https://doi.org/10.4002/040.055.0110

Everwand G, Scherber C, Tscharntke T (2013). Slug responses to grassland cutting and fertilizer application under plant functional group removal. Acta Oecol 48:62–68. https://doi.org/10.1016/j.actao.2013.01.015

Felipe-Lucia M, Soliveres S, Penone C, Fischer M, Ammer C, Boch S, Boeddinghaus R, Bonkowski M, Buscot F, Fiore-Donno AM, Frank K, Goldmann K, Gossner M, Hölzel N, Jochum M, Kandeler E, Klaus V, Kleinebecker T, Leimer S, Allan E (2020) Land-use intensity alters networks between biodiversity, ecosystem functions, and services. Proc Natl Acad Sci 117:28140–28149. https://doi.org/10.1073/pnas.2016210117

Frank K, Hülsmann M, Assmann T, Schmitt T, Blüthgen N (2017) Land use affects dung beetle communities and their ecosystem service in forests and grasslands. Agric Ecosyst Environ 243:114–122. https://doi.org/10.1016/j.agee.2017.04.010

Glöer P, Meier-Brook C (2003) Süsswassermollusken: Ein Bestimmungsschlüssel für die Bundesrepublik Deutschland. Deutscher Jugendbund für Naturbeobachtung, Göttingen

Hettenbergerová E, Horsák M, Chandran R, Hájek M, Zelený D, Dvořáková J (2013) Patterns of Land Snail Assemblages along a Fine-Scale Moisture Gradient. Malacologia 56:31–42. https://doi.org/10.4002/040.056.0227

Horsák M, Zelený D, Hájek M () Land snail richness and abundance along a sharp ecological gradient at two sampling scales: Disentangling relationships. J Molluscan Stud 80:256–264. https://doi.org/10.1093/mollus/eyu027

Humbert JY, Ghazoul J, Sauter G, Walter T (2010) Impact of different meadow mowing techniques on field invertebrates. J Appl Entomol 134:592–599. https://doi.org/10.1111/j.1439-0418.2009.01503.x

Humbert JY, Pellet J, Buri P, Arlettaz R (2012) Does delaying the first mowing date benefit biodiversity in meadowland? Environ Evid 1, 9. https://doi.org/10.1186/2047-2382-1-9

Jackson M, Turner M, Pearson S, Ives A, (2012) Seeing the forest and the trees: multilevel models reveal both species and community patterns. Ecosphere 3, art 79. https://doi.org/10.1890/ES12-00116.1

Johst K, Drechsler M, Thomas J, Settele J (2006) Influence of mowing on the persistence of two large blue butterfly species. J Appl Ecol 43:333–342. https://doi.org/10.1111/j.1365-2664.2006.01125.x

Joyce CB, Simpson M, Casanova M (2016) Future wet grasslands: ecological implications of climate change. Ecosyst Health Sustain 2, e01240. https://doi.org/10.1002/ehs2.1240

Kerney MP, Cameron RAD, Jungbluth JH (1983) Die Landschnecken Nord- und Mitteleuropas: ein Bestimmungsbuch für Biologen und Naturfreunde. Paul Parey, Hamburg und Berlin

Konvicka M, Benes J, Cizek O, Kopecek F, Konvička O, Vitaz L (2008) How too much care kills species: Grassland reserves, agri-environmental schemes and extinction of Colias myrmidone (Lepidoptera: Pieridae) from its former stronghold. J Insect Conserv 12:519–525. https://doi.org/10.1007/s10841-007-9092-7

Kormann U, Rösch V, Batáry P, Tscharntke T, Orci K, Samu F, Scherber C (2015) Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. Divers Distrib 21. https://doi.org/10.1111/ddi.12324

Książkiewicz Z (2014) Impact of land use on populations of Vertigo moulinsiana (Dupuy, 1849) and Vertigo angustior (Jeffreys, 1830) (Gastropoda: Pulmonata: Vertiginidae): Ilanka River Valley (W. Poland). Folia Malacol 22:277–282. https://doi.org/10.12657/folmal.022.019

Lenth R, Buerkner P, Herve M, Love J, Miguez F, Riebl H, Singmann H (2020) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.2-1. https://CRAN.R-project.org/package=emmeans

Lepš J (1999). Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. J Veg Sci 10:219–230. https://doi.org/10.2307/3237143

Martin K, Sommer M (2004a) Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. J Biogeog 31:531–545. https://doi.org/10.1046/j.1365-2699.2003.01005.x

Martin K, Sommer M (2004b) Effects of soil properties and land management on the structure of grassland snail assemblages in SW Germany. Pedobiologia 48:193–203. https://doi.org/10.1016/j.pedobi.2003.12.004

Mezősi G (1998) A Borsodi-dombság tájföldrajzi jellemzése. Földrajzi Értesítő 47:395-408.

Moog D, Poschlod P, Kahmen S, Schreiber KF (2002) Comparison of species composition between different grassland management treatments after 25 years. Appl Veg Sci 5:99–106. https://doi.org/10.1111/j.1654-109X.2002.tb00539.x

Newell PF (1967) Mollusca. In Burgess A, Raw F. (ed) Soil Biology. Academic Press, London, pp. 413-444.

Oelmann Y, Brol, G, Hölzel N, Kleinebecker T, Vogel A, Schwartze P (2009) Nutrient impoverishment and limitation of productivity after 20 years of conservation management in wet grasslands of north-western Germany. Biol Conserv 142:2941–2948. https://doi.org/10.1016/j.biocon.2009.07.021

Pech P, Dolanský J, Hrdlička R, Leps J (2015) Differential response of communities of plants, snails, ants and spiders to long-term mowing in a small-scale experiment. Community Ecol 16:115–124. https://doi.org/10.1556/168.2015.16.1.13

Plantureux S, Peeters A, McCracken D (2005) Biodiversity in intensive grasslands: Effect of management, improvement and challenges. Agron Res 3:153–164.

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Shannon C, Weaver W (1949) The Mathematical Theory of Communication. Urbana, IL: University of Illinois Press.

Socher S, Prati D, Boch S, Müller J, Klaus V, Hölzel N, Fischer M (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. J Ecol 100:1391–1399. https://doi.org/10.1111/j.1365-2745.2012.02020.x

Szmatona-Túri T, Vona-Túri D, Magos G, Urbán L (2017) The effect of grassland management on diversity and composition of ground-dwelling spider assemblages in the Mátra Landscape Protection Area of Hungary. Biologia 72. https://doi.org/10.1515/biolog-2017-0075

Theenhaus A, Scheu S (1996) The influence of slug (*Arion rufus*) mucus and cast material addition on microbial biomass, respiration, and nutrient cycling in beech leaf litter. Biol Fertil Soils 23:80–85. https://doi.org/10.1007/BF00335822

Wehner K, Renker C, Brückner A, Simons NK, Weisser WW, Blüthgen N (2019) Land-use in Europe affects land snail assemblages directly and indirectly by modulating abiotic and biotic drivers. Ecosphere 10:1–20. https://doi.org/10.1002/ecs2.2726

Zechmeister H, Schmitzberger I, Steurer B, Peterseil J, Wrbka T (2003) The influence of land-use practices and economics on plant species richness in meadows. Biol Conserv 114:165–177. https://doi.org/10.1016/S0006-3207(03)00020-X

Zedler JB, Kercher S (2004). Causes and Consequences of Invasive Plants in Wetlands: Opportunities, Opportunists, and Outcomes. Crit Rev Plant Sci 23:431–452. https://doi.org/10.1080/07352680490514673

Zedler JB, Kercher S (2005) WETLAND RESOURCES: Status, Trends, Ecosystem Services, and Restorability. Annu Rev Environ Resour 30:39–74. https://doi.org/10.1146/annurev.energy.30.050504.144248

Table 1(on next page)

The central geocoordinates (WGS84) of the study sites

Table 1 The central geocoordinates (WGS84) of the study sites

	Site	X coordinate	Y coordinate	Location
1	Alsó-rét	20.43000429	48.36829780	Putnok Hills
2	Buda-völgy	20.44406537	48.36418337	Putnok Hills
3	Dobos-völgy	20.45862631	48.36365842	Putnok Hills
4	Latrány-völgy	20.47224009	48.40253237	Putnok Hills
5	Pozsok-völgy	20.43727243	48.38070310	Putnok Hills
6	Rácsa-völgy	20.44926240	48.36222388	Putnok Hills
7	Abod	20.80986361	48.40052216	Cserehát Hills

Figure 1

Overview of the study area

Study sites are identified by numbers of Table 1

Fig. 1 Overview of the study area. Study sites are identified by numbers of Table 1

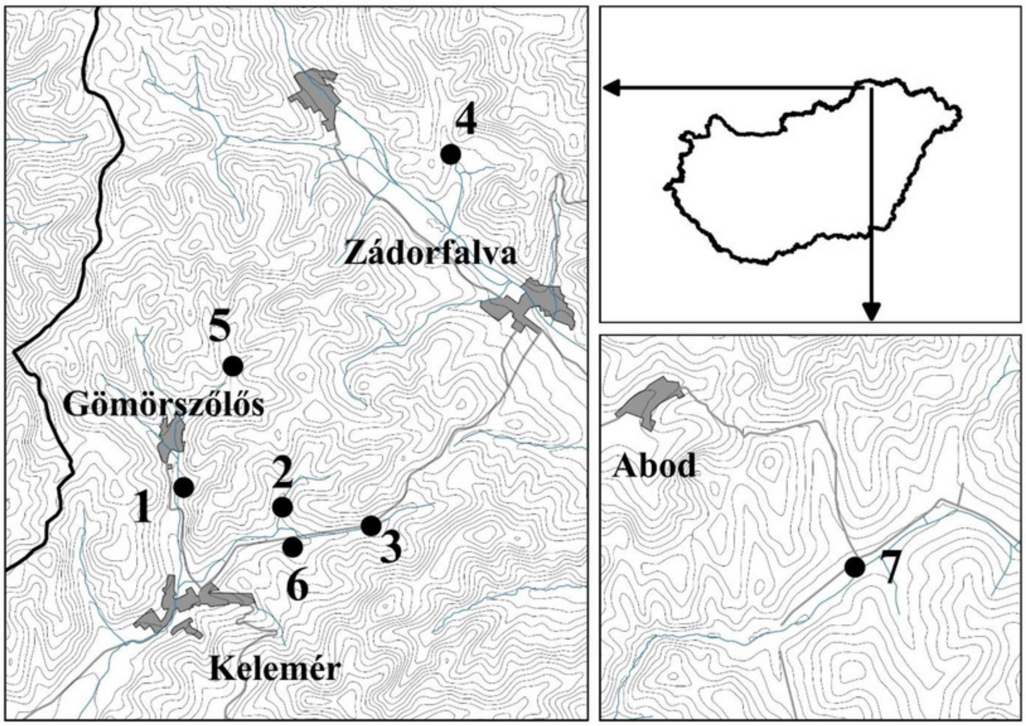

Figure 2

The effect of treatment on the traits of snail communities (only significant effects shown)

a) the effect of treatment on the species abundance, b) the effect of treatment on the number of species and c) the effect of treatment on Shannon diversity. Columns show the marginal means of the given variables estimated by fitting mixed-effect models (see main text for details). Error bars show standard errors.

Fig. 2 The effect of treatment on the traits of snail communities (only significant effects shown): a) the effect of treatment on the species abundance, b) the effect of treatment on the number of species and c) the effect of treatment on Shannon diversity. Columns show the marginal means of the given variables estimated by fitting mixed-effect models (see main text for details). Error bars show standard errors.