GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 68 (2023) 13–22

Basic and Applied Ecology

www.elsevier.com/locate/baae

RESEARCH PAPER

Reconciling the control of the native invasive *Jacobaea aquatica* and ecosystem multifunctionality in wet grasslands

Marie-Therese Krieger[a,1,*], Leonardo H. Teixeira[a,1,*], Kerstin Grant[b], Johannes Kollmann[a,c], Harald Albrecht[a]

[a]*Technical University of Munich, TUM School of Life Sciences, Chair of Restoration Ecology, Emil-Ramann-Str. 6, 85354 Freising, Germany*
[b]*Agricultural Centre for Cattle Production, Grassland Management, Dairy Farming, Fisheries and Wildlife Baden-Wuerttemberg (LAZBW), Aulendorf, Germany*
[c]*Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway*

Received 24 March 2022; accepted 10 February 2023
Available online 24 February 2023

Abstract

Grasslands are managed to provide multiple goods and services. During recent decades, abandonment of marginal grasslands and intensification of the most productive sites resulted in biodiversity losses and reduced ecosystem services (ESs). Moreover, invasion by unwanted plants impaired ESs, as seen in *Jacobaea aquatica*, a poisonous native invader in pre-alpine grasslands of Central Europe. Invasion by this plant compromises fodder quality and endangers animal health, resulting in abandonment of grassland use. We tested different management regimes to reduce *J. aquatica* in wet grasslands of Southern Germany and assessed how its regulation affects grassland multifunctionality. We monitored indicators associated with productivity and conservation, such as the abundance of *J. aquatica*, forage quality, yield, abundance of specialists, and pollinator-relevant plants. Intensive management favoured multifunctionality by promoting productivity and biodiversity, yet also increasing the abundance of *J. aquatica*. Reduced management regulates *J. aquatica* cover close to an acceptable threshold while also reducing ESs. Thus, we conclude that moderate management strikes a balance between the control of the poisonous plant and the supply of grassland multifunctionality.

Keywords: Conservation grassland; Functioning thresholds; Management intensity; Marsh ragwort; Trade-off; Weed control

Introduction

The capacity to perform manifold functions and to deliver several goods and services is expected from virtually every ecosystem in the world (Felipe-Lucia et al., 2018; Lefcheck et al., 2015). In grasslands, the maintenance of ecosystem multifunctionality is particularly prominent, because human societies strongly depend on these functions (Bengtsson et al., 2019). Managed grasslands provide various goods and services that constitute important aspects of human well-being (Kemp et al., 2013), such as food (animal products and grains), raw materials (livestock fodder and bedding) and protection against environmental hazards (Gabryszuk, Barszczewski, & Wróbel, 2021). Contrasting to their high importance to human societies, many grasslands are substantially degraded (Bardgett et al., 2021; Duprè et al., 2010).

*Corresponding authors.
E-mail addresses: marie-therese.krieger@tum.de (M.-T. Krieger), leonardo.teixeira@tum.de (L.H. Teixeira).
[1] These authors contributed equally

https://doi.org/10.1016/j.baae.2023.02.001

Ecosystem functions and the resulting services are not always positively correlated (Byrnes et al., 2014a). In fact, they can exhibit marked synergies, e.g. between soil retention and carbon sequestration, or trade-offs, e.g. forage provisioning impairing soil retention (Kong et al., 2018). While such synergies and trade-offs are frequently discussed in grassland management (Bengtsson et al., 2019), actual farming practice often jeopardises ecosystem multifunctionality (Isselstein, Jeangros, & Pavlu, 2005) by focussing either on production-related services or biodiversity conservation (Raudsepp-Hearne, Peterson, & Bennett, 2010). For example, while high intensity management promotes fodder production (Wittwer et al., 2021), it has negative effects on regulatory or cultural services (Raudsepp-Hearne et al., 2010), leading to trade-offs between high biomass production, soil nutrient retention, groundwater protection and carbon sequestration (Austrheim et al., 2016; Kim, Jobbágy, & Jackson, 2016). Conversely, abandonment reduces forage quality, nutrient cycling, and recreation (Johansen, Taugourdeau, Hovstad, & Wehn, 2019). Another example is the conflict between the promotion of rare species and the suppression of invasive plants in conservation grasslands. While regular management is needed to maintain plant diversity (Joyce, 2014), invaders can profit from the associated disturbance and resource fluctuations (Shen et al., 2011).

Invasive species frequently cause losses of ecosystem services (ESs) (Charles & Dukes, 2008). An example is the poisonous *Jacobaea aquatica* (marsh ragwort). While the abundance of this wetland specialist declined in Northern Germany (Diekmann et al., 2019), a strong increase is reported in pre-alpine wet grasslands of Southern Germany, Austria and Switzerland (Suter & Lüscher, 2011). Invasion by *J. aquatica* directly reduces the economic value of the affected grasslands, since contaminated fodder cannot be used (Chizzola, Bassler-Binder, Karrer, & Kriechbaum, 2018). Consequently, overabundance of *J. aquatica* may lead to grassland abandonment, further compromising supply of ESs. Previous research assessed effects of invasive species on multifunctionality (Gallardo et al., 2019), while it is still unclear how suppression management affects ESs. However, management decisions should consider synergies and trade-offs among multiple ESs to minimize potential negative effects (Manning et al., 2018).

Thus, we investigated how management designed to reduce the abundance of *J. aquatica* affects ecosystem multifunctionality of wet grasslands. Based on the community assembly framework suggested by Funk, Cleland, Suding, and Zavaleta (2008), we established treatments with different mowing intensities at 13 wet grasslands with high conservation value in Southern Germany. Our aim was to control the poisonous species and to find management options that allow further agricultural use by optimizing ecosystem multifunctionality. We monitored abundance of *J. aquatica*, forage quality and yield as well as biodiversity, and used these measures to assess ESs and multifunctionality of the grasslands.

We hypothesized that: (i) due to trade-offs between provisioning and regulating services linked to grassland management, measured indicators related to provisioning ESs of wet grasslands will benefit from more intensive management, whereas indicators related to regulating ESs will be favoured by reduced management. We expected: (ii) a positive relationship between management intensity and multifunctionality driven by production-oriented indicators; (iii) that intermediate management can control *J. aquatica,* while allowing for high multifunctionality, since *Jacobaea* is suppressed by very low management, whereas provisioning ESs benefit from intermediate to high management; and (iv) that the relationship between management and multifunctionality will become weaker when higher levels of service supply are expected, because of trade-offs among different ES indicators.

Materials and methods

Study species

Jacobaea aquatica (marsh ragwort) is native to wet grasslands in Central Europe. The biennial to short-lived perennial Asteraceae usually germinates in autumn or spring, and after the development of a rosette, it produces shoots with several yellow flower heads from late June to August. When cut, plants quickly regenerate flowering shoots. The wind-dispersed seeds rapidly germinate under favourable conditions but otherwise establish persistent seed banks (Suter & Lüscher, 2012). All parts of the plant contain toxic pyrrolizidine alkaloids, which are highly poisonous to livestock. Thus, the given level of tolerated abundance is 0.1−0.2 plants m^{-2} (Gehring et al., 2019).

The early-successional, light-demanding species is favoured by grassland disturbance, rewetting after drainage and moderate nitrogen fertilization (Suter & Lüscher, 2008). Moreover, changes in species abundances at local communities can lead to rapid increase of *J. aquatica* (Bassler, Karrer, & Kriechbaum, 2016; Suter & Lüscher, 2008). Due to its effective dispersal and the resulting establishment of dominant stands (Suter & Lüscher, 2011), the species poses increasing problems to farmers who manage grasslands in the pre-alpine regions.

Study design and measurements

Thirteen wet grasslands invaded by *J. aquatica* were chosen in pre-alpine Germany. All sites were extensively managed based on agri-environmental schemes and cover a wide range of site conditions. They were classified according to their estimated productivity and preceding use (see Appendix A: Table S1; cf. Krieger et al., 2022). In cooperation with local experts, experimental treatments were developed to suppress the unwanted species (Krieger et al., 2022, 2022). As the very low intensities should create high competition for light and prevent gaps in the sward, the consistent attribute of these treatments was cessation of mowing. Low productive sites were characterized by delay of the first cut and a mowing frequency adapted to flowering; regionally common management was the reference (Table 1; see Appendix A: Table S2). At each of the six very low productive sites five treatments were established and at each of the seven low productive sites eight treatments were implemented, resulting in a total of 86 study plots. During the first phase of the experiment control measures were consistently implemented, then management was re-adjusted to ordinary usage and suppression effects were evaluated.

Treatment plots were 3.7 m × 6.0 m in size and arranged in one row. At the time of the first cut of the reference treatment in June 2018−2021, cover of aboveground vascular vegetation, litter, bare soil and mosses were estimated for each plot. In order to detect subtle changes in species composition (Peratoner & Pötsch, 2015), we additionally recorded the number and identity of occurring species and their relative percentage of total cover. Before mowing, biomass of 1 m^2 per plot was manually cut at a height of 8 cm and weighted before and after drying at 100 °C for 24 h, to obtain the amount of dry matter and to calculate yield (kg m^{-2}). To determine forage quality, fodder values and legume cover were estimated. Vegetation surveys and literature were combined to calculate weighted fodder and Ellenberg indicator values (EIVs) for moisture, and to determine the number and cover of pollinator-relevant species (Dierschke & Briemle, 2002; Landolt et al., 2010; Leuschner & Ellenberg, 2017). Cover of legumes and number of specialist species of wet grasslands were determined as well. These variables were adopted as indicators of selected ESs (see Appendix A: Table S3; Garland et al., 2021). To obtain a gradient of management intensity, treatments were categorized by summing the number of mowing events conducted in 2018, 2019 and 2020 (Table 1, see Appendix A: Table S2 for details). Considering the influence on plant development (i.e. earlier mowing is more detrimental), each event was additionally weighted according to the time of implementation from mid-June (6) to mid-October (1). The calculated intensities cover a wide range from 0 (fallow 3 yr.) to 36 (3-times cut). Compared to the management intensity practice in grasslands of the Allgäu region, where several cuts per year are common (≥5 cuts) even at organic sites (cut May, June, July, Aug and Sept; intensity index >77; Diepolder & Raschbacher, 2010), our sites are at the lower range of grassland productivity.

Data processing and statistical analysis

Prior to assessing effects of management intensity, we tested pairs of variables for potential collinearity. This was performed with a Kendall matrix checking for strong correlations (>|0.7|) that could limit interpretations on multifunctionality (Dormann et al., 2013). We observed a negative correlation (−0.71) between cover of vegetation and mosses and litter cover. Still, both variables were kept given their importance for different ESs (see Appendix A: Fig. S1). To prevent correlated variables of disproportionately affecting multifunctionality, we applied a hierarchical clustering (using the Elbow method) to identify and down-weight subsets of related variables (Manning et al., 2018). Four clusters were determined, and variables within

Table 1. Mowing treatments implemented at the two productivity levels within wet grasslands in S Germany. Provided are management focus and intensities calculated for each treatment.

	Treatment type	Main management focus	Management intensity index
Very-low productive sites	Fallow (3 yr.)	Cessation of mowing for more than one year	0
	Fallow (1 yr.), late seasonal cut	Cessation of mowing for one year, followed by a yearly cut at the end of vegetation period	4
	Fallow (1 yr.), early seasonal cut	Cessation of mowing for one year	10
	Late cut August	Delayed first cut and low fertilization with solid manure	11
	Reference treatment	Regionally specific mowing regime with cuts in July and September	21
Low productive sites	Late cut October (3 yr.)	Off-season cut for three years	3
	Fallow (2 yr.)*	Cessation of mowing for two full years	7
	Fallow (1 yr.)*	Cessation of mowing for two consecutive vegetation periods with resumption of mowing in September 2019	9
	Late cut October (2 yr.)	Off-season cut for two years	9
	Late cut August	Delay of first cut to mid-season; skip of second cut	13
	Cut June with shift	Skip of second cut followed by a time-shift in the regionally specific mowing	19
	Cut June	Skip of second cut	21
	Reference treatment	Regionally specific mowing regime with cuts in June and August	27
	Three-times cut	One additional cut during flowering season of *J. aquatica*	36

*Plots had to be split by sites as treatments could only be implemented on part of the sites (fallow 2 yr., n = 4; fallow 1 yr., n = 3).

each cluster were equally weighted summing up to one (see Appendix A: Fig. S2). Afterwards, we fitted linear mixed-effects models testing management effects (expressed by the intensity index calculated) on *J. aquatica* cover and on 11 other ES indicators (see Appendix A: Table S3). All indicators and the intensity index were log-transformed. The (log [x + 1]) transformation was applied for counting variables when zeroes were observed (Ives, 2015). Indicator responses to management were individually assessed with an lmer using the R package lme4 (Bates, Mächler, Bolker, & Walker, 2015). We used the management intensity index as fixed predictor and, to account for potential spatio-temporal autocorrelation, time (monitoring years), field sites and plots (nested within sites) were set as random factors.

To assess grassland multifunctionality, we applied the averaging and the thresholds approach (Byrnes et al., 2014a) with the R package multifunc. Even though, *J. aquatica* cover can be related to multiple aspects of ESs and disservices, we excluded it from the multifunctionality analysis to avoid overestimating the synergy between *J. aquatica* cover and management treatments. The averaging approach combines the different indicators in a single index via the calculation of the average value of standardized indicators, ranging from zero to one (Maestre et al., 2012). The thresholds approach reveals the number of indicators exceeding functioning thresholds of a pre-defined maximum and allows the simultaneous evaluation of different levels of service supply (Byrnes et al., 2014a; Zavaleta, Pasari, Hulvey, & Tilman, 2010). All indicators were standardized using the z-transformation method and cover of bare soil was inverted, so that lower values indicated higher service supply (Byrnes et al., 2014b; Maestre et al., 2012). We assessed management effects with mixed-effects models and random structure as above.

Afterwards, we analysed the performance of multiple ESs considering thresholds from low (20−40%) to intermediate-high levels of service supply (60−80%) observed at a plot compared to an optimum level of service supply. We defined the optimum as the mean of the 34 (10%) top-functioning plots for each ES indicator monitored (Zavaleta et al., 2010). This calculation did not exclude values observed at reference sites. Finally, we tested the number of ESs above a given threshold in response to management intensity using linear mixed-effects models (Byrnes et al., 2014b). Again, monitoring time, field sites and plots were random factors. We performed all statistical analyses using R Statistical Computing version 4.1.1 (R Core Team, 2021).

Results

Management effects on Jacobaea aquatica *and indicators of grassland ecosystem services*

Cover of *J. aquatica* increased with increasing management intensity (Fig. 1L). This shows that under the usual management (control: red line), high abundances of *J. aquatica* occur, while reduced intensity diminished the cover to ≤50% (see Appendix A: Fig. S3). The other indicators showed contrasting responses to increased management, and seven indicators were significantly affected (Fig. 1, Table 2). Increased management reduced EIV soil moisture and litter cover (Fig. 1B, D), whereas cover of vegetation and mosses, yield of grassland sites, and the cover of legumes increased (Fig. 1C, E, G). Number and cover of pollinator-relevant species were also positively affected by management intensity (Fig. 1J, K). The remaining variables were not significantly affected by management.

Impacts of Jacobaea aquatica *control on grassland multifunctionality*

As well as some of the individual indicators also the averaged multifunctionality showed a positive response to management (Fig. 2; χ^2 = 12.6, df = 1, p < 0.001). Averaged multifunctionality values for different management intensities ranged from 0.5 to 0.8 with highest levels occurring at intensively managed grasslands, i.e. management intensity of the regionally specific mowing regimes or higher. However, these treatments also led to higher abundances of *J. aquatica* (Fig. 1L).

Reduced grassland multifunctionality at high thresholds

Complementing the results using the averaging approach, the single threshold approach revealed that multiple ES indicators could not simultaneously reach high levels of service supply (threshold ≥60%) along the management gradient (Fig. 3). While the average value of multiple properties generally increased with management, no such effect appeared when assessing the number of indicators performing at or above functioning thresholds of 60 and 80% (χ^2 = 2.3, df = 1, p = 0.1, and χ^2 = 0.4, df = 1, p = 0.5, respectively). Thus, intensively managed wet grasslands fail to supply high levels of multiple ESs. Nevertheless, positive effects of increased management on multiple indicator performance occurred, when thresholds were set at intermediate to low thresholds of service supply (40 or 20%: χ^2 = 3.9, df = 1, p = 0.05; χ^2 = 25.8, df = 1, p < 0.001).

Simultaneous performance of all indicators across different management intensity is presented in Appendix A, Fig. S5. Again, higher levels of *J. aquatica* cover under more intense management (intensity index >20) indicate insufficient control in frequently mown grasslands. However, indicators of high productivity (i.e. legumes cover and yield) reached higher levels of service supply under increased management. The remaining indicators showed minor variation in service supply among management categories. Intermediate management intensity provided only

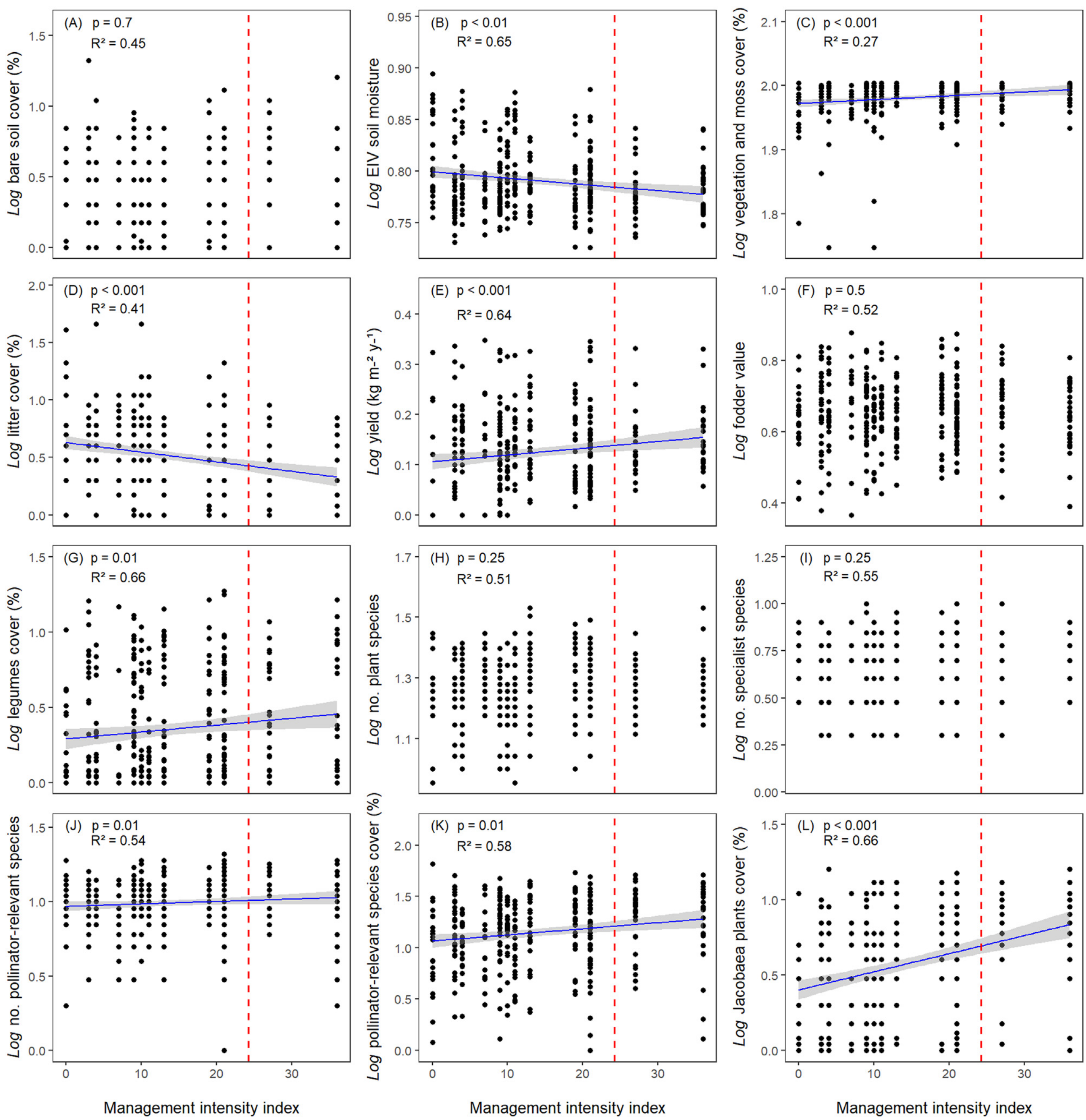

Fig. 1. Effects of management intensity on *Jacobaea aquatica* cover and the individual ecosystem service indicators monitored in wet grasslands in S Germany. Note that increased values in the cover of bare soil (Fig. 1A) and *J. aquatica* cover (Fig. 1L) represent a reduction in grassland service supply. Red dashed lines show the mean management intensity in reference plots representing the regional standard. The regression lines (blue) indicate the overall trend with 95% confidence interval depicted in gray.

average results in *J. aquatica* suppression as well as in providing multiple ESs. Nevertheless, as most indicators showed a combination of high levels of service supply with reduced *Jacobaea* cover at intensity indices of 11−20, such intermediate intensities produced the most promising results to reconcile *J. aquatica* suppression and grassland multifunctionality (see Appendix A: Fig. S5).

Discussion

Management effects on Jacobaea aquatica *cover and individual ecosystem service indicators*

Number and cover of pollinator-relevant species increased with management intensity. These results are consistent with

Table 2. Effects of management intensity on *Jacobaea aquatica* cover and individual ecosystem service indicators in wet grasslands. Results of the linear mixed-effects models fit by REML on the significance of management intensity as the predictor of service supply; statistically significant effects are shown in bold ($p < 0.05$, n = 344).

	Management intensity index				
Ecosystem service indicator	**Estimate ± SE**	**Chisq**	**df**	**p-value**	**Marginal R^2**
Bare soil cover (%)	−0.01 ± 0.03	0.2	1	0.7	0.0003
EIV soil moisture	−0.01 ± 0.003	8.2	1	**<0.01**	0.01
Vegetation and moss cover (%)	0.02 ± 0.004	14.3	1	**≤0.001**	0.04
Litter cover (%)	−0.2 ± 0.04	25. 1	1	**≤0.001**	0.05
Yield (kg m^{-2} yr.$^{-1}$)	0.05 ± 0.008	40.0	1	**≤0.001**	0.05
Fodder value	0.008 ± 0.01	0.5	1	0.5	0.001
Legumes cover (%)	0.08 ± 0.03	6.6	1	**0.01**	0.008
No. plant species	0.02 ± 0.02	1.3	1	0.25	0.004
No. specialist species	0.03 ± 0.03	1.3	1	0.25	0.07
No. pollinator-relevant species	0.06 ± 0.02	6.7	1	**0.01**	0.02
Pollinator-relevant species cover (%)	0.09 ± 0.04	6.3	1	**0.01**	0.01
Jacobaea aquatica cover (%)	0.02 ± 0.02	37.4	1	**≤0.001**	0.006

Ford, Garbutt, Jones, and Jones (2012), who report higher numbers of flowering forbs ('pollinator-relevant species') in regularly managed coastal grasslands. However, cover of *J. aquatica* was also higher at higher management intensities, indicating insufficient suppression.

Furthermore, legume cover and grassland yield increased with increased management intensity. Both indicators are related to provisioning ESs, as they report on the amount and quality of harvested biomass (Elsäßer, 2004). Moreover, legumes increase productivity through positive effects on nitrogen cycling (Mulder, Jumpponen, Högberg, & Huss-Danell, 2002).

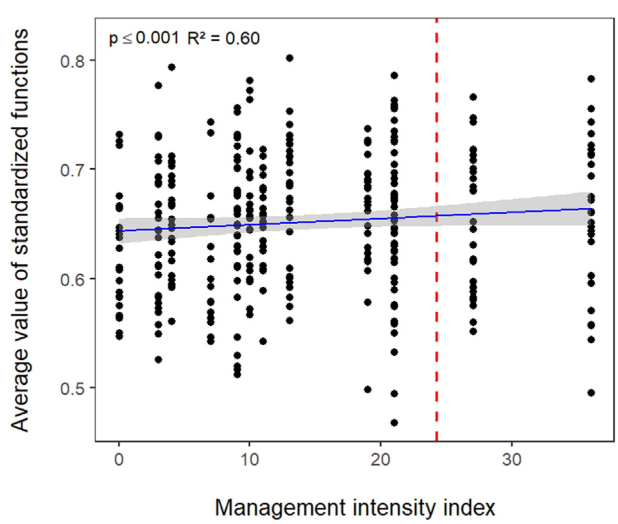

Fig. 2. Effects of management intensity on averaged service supply of eleven standardized ecosystem service indicators in wet grasslands. Management intensity significantly increased averaged multifunctionality ($p < 0.001$). Red dashed line represents the mean management intensity in reference plots. The regression line (blue) indicates the overall trend with 95% confidence interval depicted in gray. While the conditional R^2 is depicted in the figure, marginal R^2 value is 0.02.

Contrarily, litter and EIV soil moisture were higher at lower management intensities. This means that the corresponding regulating ESs had higher supply under less intense management. EIV soil moisture reflects water regulation aspects of grassland sites (Rose, Coners, & Leuschner, 2012), whereas litter contributes to nutrient cycling and promotes micro-climatic amelioration (Loydi, Donath, Otte, & Eckstein, 2015). High litter cover often hinders seedling germination and can suppress establishment of weeds, but can also delay spring growth, and impact flowering (Facelli & Picket, 1991; Tälle et al., 2018).

These results support the hypothesis that indicators related to provisioning ESs increase with higher management, while trade-offs occurred among indicators of regulating ESs. The management gradient also showed a positive relation to cultural ESs, because ceased management frequently impacts grasslands aesthetics such as flower numbers or species richness (Johansen et al., 2019). The analysis of the individual indicators already presents the difficulties for farmers who often rely on production-oriented use of meadows, even if they are managed under conservation aspects. While the regular management (control treatments) would benefit their needs, the forage material of invaded sites harvested during the flowering period of *J. aquatica* (July, August) often exceeds critical doses of toxicity and must not be fed (Chizzola et al., 2018), thus calling for the control of the poisonous plant species.

Ecosystem multifunctionality of wet grasslands

We observed increased multifunctionality with higher management intensity. Although contradicting other studies reporting on the negative effects of intensification on

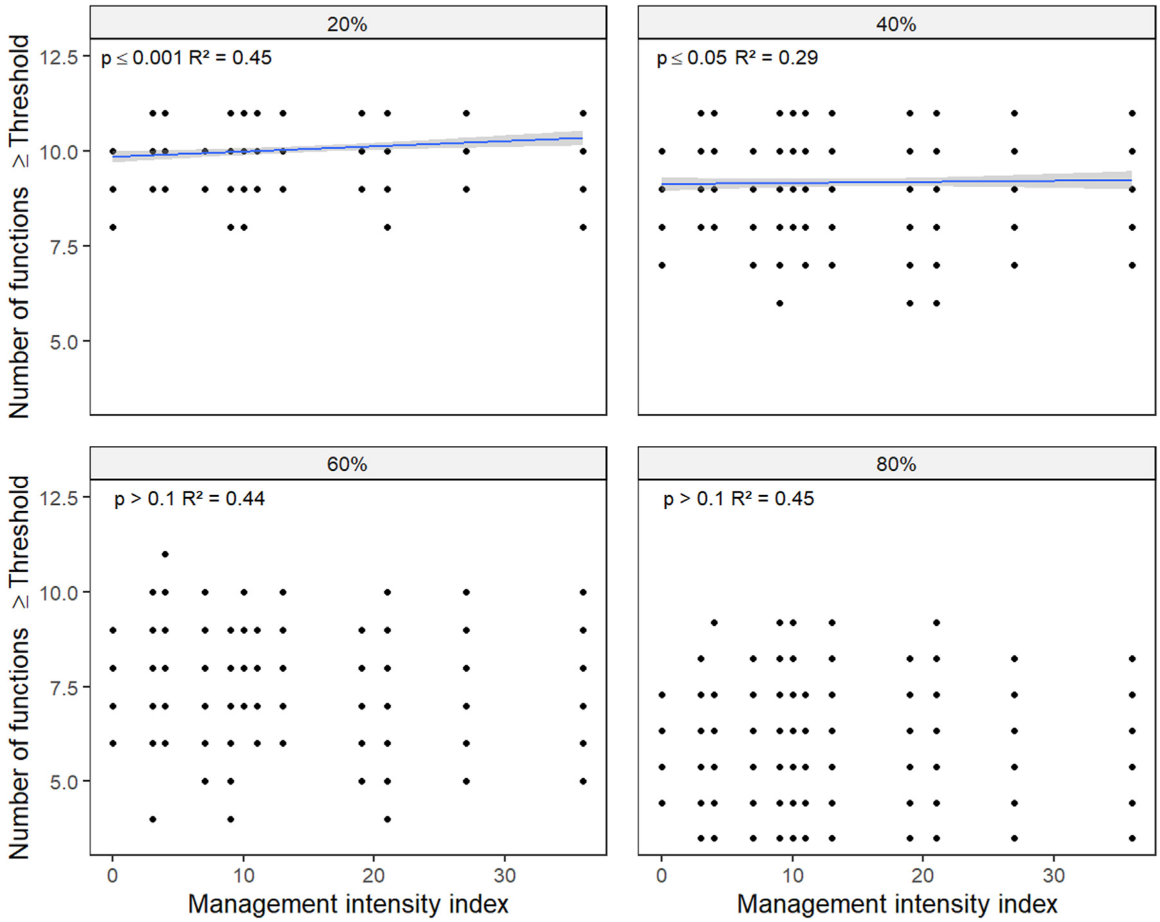

Fig. 3. Effects of management on the number of indicators exceeding a pre-defined threshold (20, 40, 60 and 80%) of optimum service supply in wet grasslands. Increased management positively affected grassland multifunctionality, but only at low to intermediate levels (i.e. 20 and 40% thresholds). While conditional R^2 values are depicted in the figure, marginal R^2 values are 0.08 (20%), 0.01 (40%), 0.005 (60%), and 0.001 (80% threshold). The full range of thresholds is shown in Appendix A, Fig. S4.

multifunctionality (Allan et al., 2015; Schils et al., 2022), our study only refers to relatively low levels of management intensity (0 − 36 from 0 − 77 index points attainable under practical conditions). Such findings underline the importance of management to sustain these ecosystems (Valkó et al., 2018), and the threats of abandonment to multifunctionality (Ford et al., 2012). Especially, low-intensity grassland management can sustain provisioning as well as cultural and regulating services at moderate levels (Neyret et al., 2021), including biodiversity conservation (Babai & Molnár, 2014).

Reconciling the control of Jacobaea aquatica *and grassland multifunctionality*

Positive effects of management intensity were detected when the averaging approach of multifunctionality was applied. However, when using the single threshold approach, management intensity was only important at intermediate to low levels of multifunctionality. This supports the hypothesis of a weaker relationship between management intensity and multifunctionality when high levels of service supply are required. These differences suggest that assessments of multifunctionality should consider patterns obtained by different approaches when pertinent (Byrnes et al., 2014b; Meyer et al., 2018). While the averaging multifunctionality approach might strongly depend on indicators responding more sensitively to the applied treatments, i.e. number of pollinator-relevant species and legume cover (see Appendix A: Fig. S6), responses of the threshold approach might be influenced by outliers with highest service supply (Byrnes et al., 2014b; Meyer et al., 2018). Nevertheless, both approaches indicate losses of ESs under management strategies aiming to suppress *J. aquatica,* i.e. lower management intensity.

Individual assessment of the levels of ES supply revealed only small changes between management categories in most indicators. Highest differences were found for *J. aquatica*, indicating that it had a much stronger response than all other investigated indicators (see Appendix A: Fig. S5). However, similar to previous results, we observed highest levels of 'species number' and 'number of specialist species' under intermediate management (Humbert, Pellet, Buri, & Arlettaz, 2012), while abandonment as well as intensification may lead to the loss of specialists (Zechmeister, Schmitzberger, Steurer, Peterseil, & Wrbka, 2003). The literature suggests that greater species richness benefits multifunctionality (Allan et al., 2015; Zavaleta et al., 2010), and that specialist species play an important role in ecosystem functioning (Clavel, Julliard, & Devictor, 2011). Moreover, in our results, provisioning ESs (indicated by yield and legume cover) were best provided at intermediate to high management (intensity index >11), while lower cover of *J. aquatica* (reduction to less than 50%; see Appendix A: Fig. S3) was only achieved under lower intensities (0 − 10).

To sum up, intermediate management (intensity index 11−20) supported simultaneously delivery of multiple services (i.e. all indicators >25% of service supply), while a reduction in cover of *J. aquatica* was already achieved. This confirms the third hypothesis that intermediate management can already reduce *J. aquatica* cover, while still allowing multifunctionality.

Conclusions

In our study, higher grassland management intensity positively affected multifunctionality at intermediate threshold levels via promotion of higher productivity and positive effects on biodiversity. Nevertheless, control of this species must accept lower levels of ES multifunctionality since effective regulation of *J. aquatica* (reduction in cover ≥50%) is only achieved at reduced management intensity. To minimize the reduction in multifunctionality, we recommend that intermediate management (i.e. delayed cutting) is the most effective way to control *J. aquatica* abundance and to simultaneously maintain high grassland ecosystem service multifunctionality.

Author contributions

HA, JK, KG and MTK designed the research; MTK with help of KG collected the field data; LHT analysed the data and all authors discussed the results; MTK and LHT wrote the manuscript, supported by all co-authors.

Data Availability

All data included in this manuscript are deposited at MediaTUM.

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.

Acknowledgements

This work was funded by LfU and LUBW (5103184). We thank our project partners and Barteline Martina Baaij, Julia Ditton, Franz Härtl, Franziska Hirt, Kathrin Möhrle and Anne-Katharina Rückel for assistance in the field. Special thanks go to Andreas Stauss, Holger Bayer, Alexander Martin and the team from LAZBW for managing the sites. We are grateful to the farmers providing their fields for the experimental treatments. Earlier versions of this paper benefitted from helpful comments by the editor and the reviewers.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2023.02.001.

References

Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N., et al. (2015). Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecology Letters*, *18*, 834–843. doi:10.1111/ele.12469.

Austrheim, G., Speed, J. D. M., Evju, M., Hester, A., Holand, Ø., Loe, L. E., et al. (2016). Synergies and trade-offs between ecosystem services in an alpine ecosystem grazed by sheep − An experimental approach. *Basic and Applied Ecology*, *17*, 596–608. doi:10.1016/j.baae.2016.06.003.

Babai, D., & Molnár, Z. (2014). Small-scale traditional management of highly species-rich grasslands in the Carpathians. *Agriculture, Ecosystems and Environment*, *182*, 123–130. doi:10.1016/j.agee.2013.08.018.

Bardgett, R. D., Bullock, J. M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., et al. (2021). Combatting global grassland degradation. *Nature Reviews Earth & Environment*, *2*, 720–735. doi:10.1038/s43017-021-00207-2.

Bassler, G., Karrer, G., & Kriechbaum, M. (2016). The impact of different cutting regimes on population density of *Jacobaea aquatica* (Hill) G. Gaertn., B. Mey. & Scherb. and grassland vegetation. *Agriculture, Ecosystems & Environment*, *226*, 18–24. doi:10.1016/j.agee.2016.04.018.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*. doi:10.18637/jss.v067.i01.

Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., et al. (2019). Grasslands-more important for ecosystem services than you might think. *Ecosphere (Washington, D.C)*, *10*. doi:10.1002/ecs2.2582.

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., et al. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, *5*, 111–124. doi:10.1111/2041-210X.12143.

Byrnes, J. E. K., Lefcheck, J. S., Gamfeldt, L., Griffin, J. N., Isbell, F., & Hector, A. (2014). Multifunctionality does not imply that all functions are positively correlated. *Proceedings of the National Academy of Sciences*, *111*, 5490. doi:10.1073/pnas.1419515112.

Charles, H., & Dukes, J. S. (2008). Impacts of invasive species on ecosystem services. In NentwigW. (Ed.), *Biological invasions* (pp. 217−237). BerlinHeidelberg: Springer. doi:10.1007/978-3-540-36920-2_13.

Chizzola, R., Bassler-Binder, G., Karrer, G., & Kriechbaum, M. (2018). Pyrrolizidine alkaloid production of *Jacobaea aquatica* and contamination of forage in meadows of Northern Austria. *Grass and Forage Science*, 1–10. doi:10.1111/gfs.12391.

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, *9*, 222–228. doi:10.1890/080216.

Diekmann, M., Andres, C., Becker, T., Bennie, J., Blüml, V., Bullock, J. M., et al. (2019). Patterns of long-term vegetation change vary between different types of semi-natural grasslands in Western and Central Europe. *Journal of Vegetation Science*, *30*(2), 187–202. doi:10.1111/jvs.12727.

Diepolder, M., & Raschbacher, S. (2010). *Leistungsfähiges grünland und verzicht auf mineralische düngung*. (pp. 13−19).

Dierschke, H., & Briemle, G. (2002). *Kulturgrasland*. Verlag Eugen Ulmer.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. doi:10.1111/j.1600-0587.2012.07348.x.

Duprè, C., Stevens, C. J., Ranke, T., Bleeker, A., Peppler-Lisbach, C., Gowing, D. J. G., et al. (2010). Changes in species richness and composition in European acidic grasslands over the past 70 years: The contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology*, *16* (1), 344–357. doi:10.1111/j.1365-2486.2009.01982.x.

Elsäßer, M. (2004). Optimum management intensity of legume- and grass-based grassland swards. In LüscherA. , JeangrosB. , KesslerW. , HugueninO. , LobsigerM. , MillarN. , SuterD. (Eds.), *Land use systems in grassland dominated regions. Proceedings of the 20th General Meeting of the European Grassland Federation* (pp. 510−512). LuzernSwitzerland: Vdf Hochschulverlag AG an der ETH Zurich.

Facelli, J. M., & Picket, S. T. A. (1991). Plant litter: Its dynamics and effects on plant community structure. *The Botanical Review*, *57*, 1–32.

Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., et al. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, *9*, 4839. doi:10.1038/s41467-018-07082-4.

Ford, H., Garbutt, A., Jones, D. L., & Jones, L. (2012). Impacts of grazing abandonment on ecosystem service provision: Coastal grassland as a model system. *Agriculture, Ecosystems & Environment*, *162*, 108–115. doi:10.1016/j.agee.2012.09.003.

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology and Evolution*, *23*(12), 695–703. doi:10.1016/j.tree.2008.07.013.

Gabryszuk, M., Barszczewski, J., & Wróbel, B. (2021). Characteristics of grasslands and their use in Poland. *Journal of Water and Land Development*, *51*, 243–249. doi:10.24425/jwld.2021.139035.

Gallardo, B., Bacher, S., Bradley, B., Comín, F. A., Gallien, L., Jeschke, J. M., et al. (2019). InvasiBES: Understanding and managing the impacts of Invasive alien species on Biodiversity and Ecosystem Services. *NeoBiota*, *50*, 109–122. doi:10.3897/neobiota.50.35466.

Garland, G., Banerjee, S., Edlinger, A., Miranda Oliveira, E., Herzog, C., Wittwer, R., et al. (2021). A closer look at the functions behind ecosystem multifunctionality: A review. *Journal of Ecology*, *109*, 600–613. doi:10.1111/1365-2745.13511.

Gehring, K., Gottschalk, C., Höck, R., Kotzi, J., Kuhn, G., Ostertag, J., et al. (2019). *Wasser-Kreuzkraut: Erkennen - regulieren - vermeiden*. .

Humbert, J., Pellet, J., Buri, P., & Arlettaz, R. (2012). Does delaying the first mowing date benefit biodiversity in meadowland? *Environmental Evidence*, *1*(9). doi:10.1186/2047-2382-1-9.

Isselstein, J., Jeangros, B., & Pavlu, V. (2005). Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe : A review. *Agronomy Research*, *3*, 139–151.

Ives (2015). For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution*, *6*, 828–835. doi:10.1111/2041-210X.12386.

Johansen, L., Taugourdeau, S., Hovstad, K. A., & Wehn, S. (2019). Ceased grazing management changes the ecosystem services of semi-natural grasslands. *Ecosystems and People*, *15*, 192–203. doi:10.1080/26395916.2019.1644534.

Joyce, C. B. (2014). Ecological consequences and restoration potential of abandoned wet grasslands. *Ecological Engineering*, *66*, 91–102. doi:10.1016/j.ecoleng.2013.05.008.

Kemp, D. R., Guodong, H., Xiangyang, H., Michalk, D. L., Fujiang, H., Jianping, W., et al. (2013). Innovative grassland management systems for environmental and livelihood benefits. *Proceedings of the National Academy of Sciences*, *110*, 8369–8374. doi:10.1073/pnas.1208063110.

Kim, J. H., Jobbágy, E. G., & Jackson, R. B. (2016). Trade-offs in water and carbon ecosystem services with land-use changes in grasslands. *Ecological Applications*, *26*, 1633–1644. doi:10.1890/15-0863.1.

Kong, L., Zheng, H., Xiao, Y., Ouyang, Z., Li, C., Zhang, J., et al. (2018). Mapping ecosystem service bundles to detect distinct types of multifunctionality within the diverse landscape of the Yangtze River Basin, China. *Sustainability*, *10* (3), 857. doi:10.3390/su10030857.

Krieger, M.-. T., Ditton, J., Albrecht, H., Baaij, B. M., Kollmann, J., & Teixeira, L. H. (2022). Controlling the abundance of a native invasive plant does not affect species richness or functional diversity of wet grasslands. *Applied Vegetation Science*, (3), 25. doi:10.1111/avsc.12676.

Krieger, M.-. T., Ditton, J., Albrecht, H., Linderl, L., Kollmann, J., & Teixeira, L. H. (2022). Effects of shading and site conditions on vegetative and generative growth of a native grassland invader. *Ecological Engineering*, *178*. doi:10.1016/j.ecoleng.2022.106592.

Landolt, E., Bäumler, B., Ehrhardt, A., Hegg, O., Klötzli, F., Lämmler, W., et al. (2010). *Flora indicativa: Ökologische zeigerwerte und biologische kennzeichen zur flora der schweiz und der alpen* (2nd ed.). Haupt.

Lefcheck, J. S., Byrnes, J. E. K., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., et al. (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications*, *6*, 6936. doi:10.1038/ncomms7936.

Leuschner, C., & Ellenberg, H. (2017). *Ecology of central European non-forest vegetation: Coastal to alpine, natural to man-made habitats: Vegetation ecology of central Europe: II*Springer.

Loydi, A., Donath, T. W., Otte, A., & Eckstein, R. L. (2015). Negative and positive interactions among plants: Effects of competitors and litter on seedling emergence and growth of forest and grassland species. *Plant Biology*, *17*, 667–675. doi:10.1111/plb.12287.

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., et al. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science (New York, N.Y.)*, *335*, 214–218. doi:10.1126/science.1215442.

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., et al. (2018). Redefining ecosystem multifunctionality. *Nature Ecology & Evolution*, *2*, 427–436. doi:10.1038/s41559-017-0461-7.

Meyer, S. T., Ptacnik, R., Hillebrand, H., Bessler, H., Buchmann, N., Ebeling, A., et al. (2018). Biodiversity−multifunctionality relationships depend on identity and number of measured functions. *Nature Ecology & Evolution*, *2*, 44–49. doi:10.1038/s41559-017-0391-4.

Mulder, C., Jumpponen, A., Högberg, P., & Huss-Danell, K. (2002). How plant diversity and legumes affect nitrogen dynamics in experimental grassland communities. *Oecologia*, *133*, 412–421. doi:10.1007/s00442-002-1043-0.

Neyret, M., Fischer, M., Allan, E., Hölzel, N., Klaus, V. H., Kleinebecker, T., et al. (2021). Assessing the impact of grassland management on landscape multifunctionality. *Ecosystem Services*, *52*, 101366. doi:10.1016/j.ecoser.2021.101366.

Peratoner, G., & Pötsch, E.M. (2015). *Erhebungsmethoden des Pflanzenbestandes im Grünland. 20. Alpenländisches Expertenforum*, 15−22.

R Core Team. (2021). R: A language and environment for statistical computing *(4.1.1). R foundation for statistical computing*. . https://www.r-project.org/.

Raudsepp-Hearne, C., Peterson, G. D., & Bennett, E. M. (2010). Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences*, *107*, 5242–5247. doi:10.1073/pnas.0907284107.

Rose, L., Coners, H., & Leuschner, C. (2012). Effects of fertilization and cutting frequency on the water balance of a temperate grassland. *Ecohydrology*, 64–72. doi:10.1002/eco.

Schils, R. L. M., Bufe, C., Rhymer, C. M., Francksen, R. M., Klaus, V. H., Abdalla, M., et al. (2022). Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality. *Agriculture, Ecosystems & Environment*, *330*, 107891. doi:10.1016/j.agee.2022.107891.

Shen, X. Y., Peng, S. L., Chen, B. M., Pang, J. X., Chen, L. Y., Xu, H. M., et al. (2011). Do higher resource capture ability and utilization efficiency facilitate the successful invasion of native plants? *Biological Invasions*, *13*(4), 869–881. doi:10.1007/s10530-010-9875-8.

Suter, M., & Lüscher, A. (2008). Occurrence of *Senecio aquaticus* in relation to grassland management. *Applied Vegetation Science*, *11*, 317–324. doi:10.3170/2007-7-18438.

Suter, M., & Lüscher, A. (2011). Measures for the control of *Senecio aquaticus* in managed grassland. *Weed Research*, *51*, 601–611. doi:10.1111/j.1365-3180.2011.00875.x.

Suter, M., & Lüscher, A. (2012). Rapid and high seed germination and large soil seed bank of *Senecio aquaticus* in managed grassland. *The Scientific World Journal*. doi:10.1100/2012/723808 2012.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., & Milberg, P. (2018). Similar effects of different mowing frequencies on the conservation value of semi-natural grasslands in Europe. *Biodiversity and Conservation*, *27*, 2451–2475. doi:10.1007/s10531-018-1562-6.

Valkó, O., Venn, S., Zmihorski, M., Biurrun, I., Labadessa, R., & Loos, J. (2018). The challenge of abandonment for the sustainable management of Palaearctic natural and semi-natural grasslands. *Hacquetia*, *17*, 5–16. doi:10.1515/hacq-2017-0018.

Wittwer, R. A., Bender, S. F., Hartman, K., Hydbom, S., Lima, R. A. A., Loaiza, V., et al. (2021). Organic and conservation agriculture promote ecosystem multifunctionality. *Science Advances*, *7*, 1–13. doi:10.1126/sciadv.abg6995.

Zavaleta, E. S., Pasari, J. R., Hulvey, K. B., & Tilman, G. D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences*, *107*, 1443–1446. doi:10.1073/pnas.0906829107.

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