

Shifts in ground-dwelling predator communities in response to changes in management intensity in Alpine meadows

Julia Plunger^{1*}, Elia Guariento¹, Michael Steinwandter¹, Filippo Colla¹, Alexander Rief³ and Julia Seeber^{1,2}

¹ Institute for Alpine Environment, Eurac Research, Viale Druso 1, 39100 Bozen/Bolzano, Italy

² Department of Ecology, University of Innsbruck, Technikerstrasse 25, 6020 Innsbruck, Austria

³ Freelance arachnologist, Rudolfstrasse 18, 6060 Hall in Tirol, Austria

* Corresponding author, e-mail: Julia.Plunger@eurac.edu

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Abstract

Land-use changes, especially agricultural intensification has increased in the last decades leading to a decrease in biodiversity. In Europe, grasslands have been influenced by humans for centuries and millennia and management intensity has increased since the 20th century. In this small-case study, we investigate how management intensity affects ground-dwelling predators in montane hay meadows in South Tyrol, an Alpine region in Northern Italy, using the pitfall trap method.

As expected, species composition differed significantly when comparing the predator communities of extensive and intensive meadows, with the former supporting a higher predator species richness, and the latter showing higher proportions of frequent and euryoecious species. Regarding their activity densities and Shannon diversity, we did not find clear differences. Investigating selected ecological species traits, we found differences for moisture requirements and ecological tolerance between the two management types, with xerophilous species being more abundant in the extensive meadows, and stenoecious species more abundant in intensive meadows.

In this study, we found management intensity of montane grasslands to have a limited influence on the biodiversity patterns of ground-dwelling predators. However, individual predator groups showed clear reactions to the intensity of management (i.e., decrease or increase in activity density, species richness and Shannon diversity). We conclude that a intensive management of grasslands in combination with local habitat specifics does not lead to a homogenisation of the predatory arthropod community like it was found in other studies. Our study contributes to a better understanding of scarcely investigated predator communities and their diversity in differently managed Alpine grasslands.

Keywords Soil | Arachnida | Coleoptera | Formicidae | species diversity

1. Introduction

Intensification of agriculture has increased in the last decades, leading to negative effects on environment and nature. Several studies have found a decline in biodiversity in various habitats (Robinson & Sutherland 2002), and agricultural intensification is considered one of the main drivers for the global biodiversity loss (e.g. Matson

et al. 1997, Billeter et al. 2008, Maxwell et al. 2016). Although the negative impact of intensive agriculture on biodiversity is generally well known (Tsiafouli et al. 2015, le Provost et al. 2020), the individual mechanisms leading to biodiversity loss are often not yet fully explicable (Littlewood et al. 2012), since different land-use practices can have different effects on biodiversity. In Europe, almost all grasslands have been modified by

humans over centuries or millennia and are increasingly used more intensively. Negative impacts of grassland management intensification have been observed for plants (e.g., Niedrist et al. 2009, Humbert et al. 2016), for herbivorous and carnivorous invertebrates (e.g., Bell et al. 2001, di Giulio et al. 2001, Nickel & Hildebrandt 2003, Andrey et al. 2016) as well as for pollinating insects (Power et al. 2012).

Optimal agricultural management systems that can, for example, support and preserve all soil-dwelling arthropods, are not yet known, as each taxonomic group reacts differently to different management techniques. Several observations and experimental studies have shown that the diversity of plants and invertebrates decreases with an increase in mowing frequency (e.g., Vickery et al. 2001, Marini et al. 2008, Woodcock et al. 2009, Tälle et al. 2016), with increasing fertilization intensity (e.g., Haddad et al. 2009, van den Berg et al. 2011), or with increasing grazing intensity (Ryder et al. 2005, Sjödin et al. 2008). While the effects of land use on plants are often direct (e.g., mowing removes phytomass and hinders the seed production of late flowering plants), the impacts on higher trophic levels such as predatory invertebrates, may be either direct or indirect via the changes in plant and prey communities (Simons et al. 2014).

Ground-dwelling invertebrate predators are important elements in grassland ecosystems, playing essential roles in pest control, soil structure development, and as food sources for various vertebrates (Holland 2002, Cole et al. 2006, Gobbi et al. 2015). One of their most important functions is the top-down control of herbivorous arthropods (Hunter & Price 1992), and thus a decline in predatory species could have a negative impact on primary production (Attwood et al. 2008). Predators react more sensitively to land-use changes than polyphagous or omnivorous species (Dennis et al. 1998, 2001, Toft & Bilde 2002, Pfiffner & Luka 2003, Purtauf et al. 2005, Gobbi & Fontaneto 2008), and are thus a suitable group to assess management changes. Indeed, due to their diversity and abundance (e.g., 82% of the Austrian fauna), arachnids and insects have a high potential to be used as bioindicators and therefore to investigate the effects of anthropogenic interventions (Komposch 2022). However, studies addressing predatory arthropods often report variable and inconsistent effects of management intensification. While negative effects by grassland management intensification such as mowing and cattle grazing have been shown for the species richness of Arachnida and Staphylinidae (Hilpold et al. 2018, Kormann et al. 2015), abundances reacted both positively (Grandchamp et al. 2005) or negatively (Dittrich & Helden 2012) for predatory arthropods.

Besides assessing species richness and abundance, trait-based approaches may contribute to a better understanding of the mechanisms on how management intensification affects biodiversity and thus potentially ecosystem functions (Verberk et al. 2013, Fournier et al. 2015, Birkhofer et al. 2017). Trait approaches have often been used to assess land-use change and intensity on landscape scale (Schweiger et al. 2005), whereas the local effects of land-use change on traits of multiple ground-dwelling predator groups in agroecosystems have not yet been sufficiently studied (but see Wood et al. 2015).

The present small-scale case study will contribute to fill existing knowledge gaps on soil biodiversity in mountain and Alpine regions (Guerra et al. 2020). Here, we aimed at assessing how communities of ground-dwelling predators are affected by management intensity in montane hay meadows in the Central European Alps. Specifically, we evaluated the impact of key management practices, namely the number of cuttings per year and the amount of applied fertilizers, on species composition, frequency, and selected species traits. The following questions were investigated: (1) How does grassland management intensity influence abundance, richness, diversity, and community composition of ground-dwelling arthropod predators? (2) Do these patterns differ for single predator groups? (3) Does management intensity alter ecological species traits such as habitat specificity, moisture requirements and species rarity?

2. Material and methods

2.1 Study site

The study was carried out in the Province of South Tyrol, the northernmost part of Italy, located in the Central European Alps (Fig. 1). Grasslands, especially meadows and pastures, represent a large part of the study area, which has a strong agricultural tradition. Another important mainstay of the South Tyrolean agriculture is husbandry. It is practiced almost throughout the entire Province and is the most important source of income for mountain farmers. Of the total agricultural area in South Tyrol, 30.5% is used as meadows (Lafis 2020, Tappeiner et al. 2020) but only a minor part of the agricultural area is extensively managed (2.4%). The study sites were located in the municipality of Barbian/Barbiano in the Eisack Valley at an elevation between 1100 and 1240 m above sea level (GPS coordinates: 46.41106° N, 11.51205° E).

We selected six montane hay meadows: three were subjected to extensive and three to intensive agricultural practices. Extensively used hay meadows (EH) were not

fertilized and mowed only once a year; these meadows were not grazed by livestock. In contrast, intensively used hay meadows (IH) were mowed up to five times a year, fertilized regularly and irrigated if needed. These meadows were grazed in autumn by cattle for up to three weeks; all three meadows belonged to the same farmer and were therefore subjected to the same treatment. We define this sites as intensive meadows, however, in a European context they might be better described as semi-intensive managed meadows.

2.2 Study design

We installed four pitfall traps per hay meadow for a period of four weeks in both autumn 2018 and spring 2019. The active sampling period in autumn spanned from 15th September to 13th October 2018 (29 days); in spring from 3rd April to 5th May 2019 (31 days). We sampled two seasons to account for different life cycles of the ground-dwelling invertebrates: e.g., Carabidae can be classified either as autumn breeders, which reproduce in autumn and hibernate as larvae in the soil, or as spring breeders, which reproduce in spring (Larsson 1939). As traps we used yogurt cups (volume of 500 ml) with an opening diameter of 9.5 cm and a height of 11.5 cm. The pitfall traps were

filled with 200 ml of a saturated saline solution (360 g salt on 1000 ml of water) as collection fluid, resulting in 48 pitfall traps in total (i.e., 2 treatments \times 3 plots \times 2 seasons \times 4 pitfall traps). A transparent polycarbonate roof protected the traps against rain and debris.

2.3 Identification of ground-dwelling predators

After the collection of the traps, all invertebrates were rinsed with water and stored in 75 % ethanol. We identified them under a stereo microscope (SMZ-171, Motic, Hong Kong, China) – where possible – to family level and predatory groups at least to genus level. A full list of the recorded ground-dwelling macro-invertebrates can be found in the supplementary data (Tab. S1). The predatory groups Araneae and Opiliones (both Arachnida), Carabidae and Staphylinidae (both Coleoptera), and Formicidae (Hymenoptera) were identified to species level using corresponding identification keys (Nentwig et al. 2022, Martens 1978, Müller-Motzfeld 2004, Assing & Schülke 2011, Seifert 2018, respectively), following the taxonomic information of the Fauna Europaea Database (de Jong et al. 2014), the World Spider Catalogue (2022), and Martens (1978).

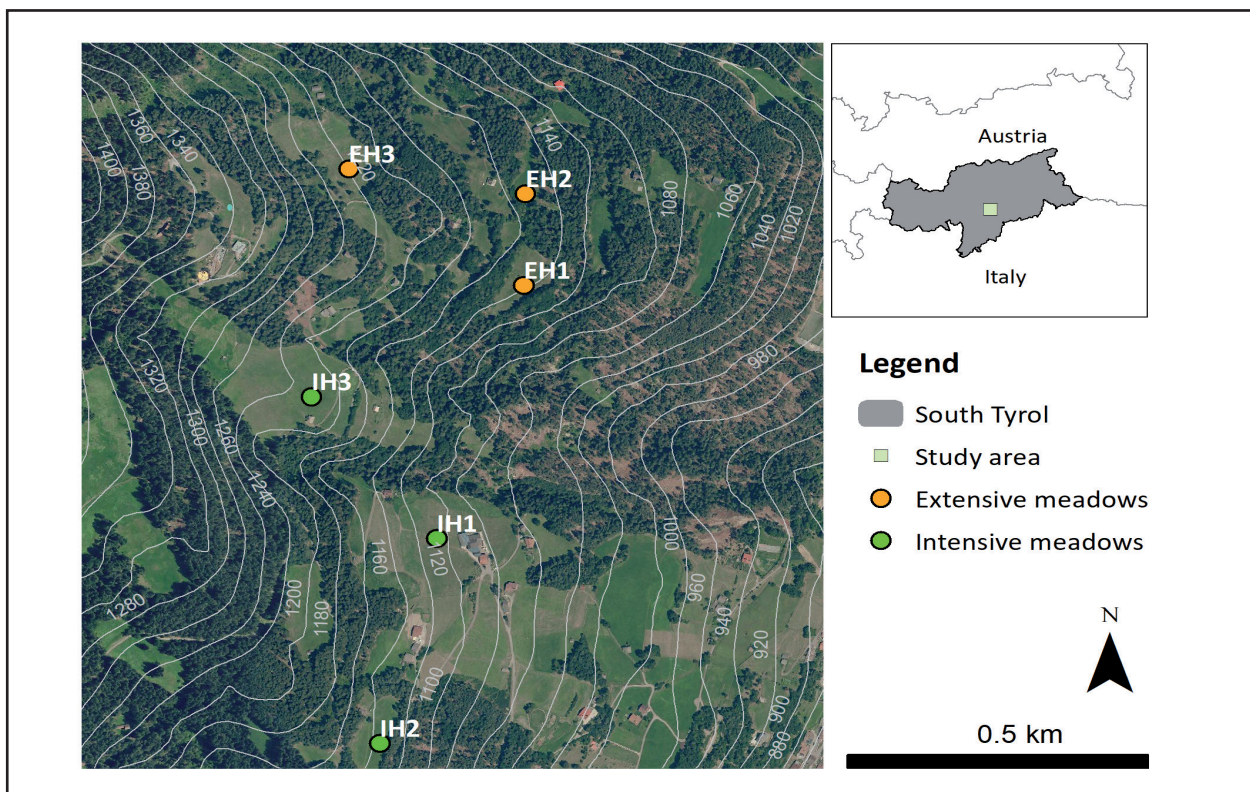


Figure 1. Maps of the distribution of the six selected hay meadows (EH = extensively used hay meadows; IH = intensively used hay meadows) located in Barbian/Barbiano in the Autonomous Province South Tyrol, Italy.

2.4 Ecological species traits and Red List statuses

We assigned three ecological traits to each species: moisture requirement, species rarity, and ecological tolerance (i.e., habitat specificity) (see Tab. S1 for full list); the information was taken from ecological literature (Koch 1989, Hilpold et al. 2018, Kahlen 2018, Seifert 2018, Pekár et al. 2021, Nentwig et al. 2022). Moisture requirements were categorized as *xerophilous*, *mesophilous*, *hygrophilous*, and *euryhygric*. Xerophilous species are adapted to dry habitats, hygrophilous on wet habitats, while euryhygric species have no preference for moisture requirements. For ecological tolerance (i.e., habitat specificity), we used the three categories *stenoecious*, *mesoecious*, and *euryoecious*. A stenoeccious species is a species with a low ecological tolerance and therefore it can be considered as specialist species, while mesoecious have a moderate and euryoecious a high tolerance. For rarity we used three categories (*rare*, *scattered*, and *frequent*): a species was defined as rare if the area of distribution in the Province of South Tyrol (Italy) was small (see also Hilpold et al. 2018). For Arachnida we used the local plant and animal distribution portal FloraFaunaSüdtirol (2022, url: <https://www.florafaua.it>, Nature Museum South Tyrol, Bozen/Bolzano, Italy). For Carabidae, Staphylinidae, and Formicidae we relied on literature (Koch 1989, Hilpold et al. 2018, Kahlen 2018, Seifert 2018, Pekár et al. 2021) and the judgements of the authors.

Additionally, the Red List status of each predator species for South Tyrol – where available – is given (Gapp 1994 for Araneae; Kahlen 2018 for Coleoptera, Table S1). Due to missing or outdated data for South Tyrol, additional Red List statuses from Austria (Opiliones) and Germany (Araneae, Blick et al. 2016, and Formicidae, Seifert 2018) were added.

2.5 Statistical analyses

All computations and graphs were generated with the statistical programming software R (R version 4.2.2, R Core Team 2022). All abundance data were analysed on the level of single pitfall traps. Abundance was standardized to the days of exposure resulting in an activity density dimension of individuals per sampling day (ind./day). All following analyses included the predatory species only. Species richness represented the observed species per pitfall trap and the species diversity was represented by the exponential Shannon-Wiener index (calculated in the package VEGAN v. 2.6-4; Oksanen et al. 2022).

We tested the effect of management on activity density (ind./day), species richness, and diversity using a linear mixed model (LMM, function *lmer* in the package LME4 v. 1.1-31; Bates et al. 2015). Season and the field ID were modelled as random factors (to account for temporal and spatial autocorrelation). To test for trait differences between management types, a χ^2 test was applied with each individual predator trait score as data entry.

Variation in community composition between management type was tested with a PERMANOVA (using Bray-Curtis dissimilarities and 999 permutations; function *adonis* in VEGAN) and graphically plotted with a non-metric multidimensional scaling (NMDS; function *metaMDS* in the package VEGAN based on Bray-Curtis dissimilarities). To improve ordination stability, a dummy species with the lowest abundance for each trap was added for the Carabidae, Staphylinidae, and Formicidae communities (Clarke et al. 2006). Accumulation curves based on individual abundances were computed to compare the supported diversity between management categories and sampling completeness (iNEXT package v. 3.0.0; Chao et al. 2014). All graphics were produced using the package GGPLOT2 (v. 3.4.0, Wickham 2016).

3. Results

3.1 Predator abundance and diversity

In total we captured 1868 ground-dwelling predatory arthropod specimens (i.e., Arachnida, Carabidae, Staphylinidae, and Formicidae), belonging to 113 species: 776 individuals in the extensively and 1092 individuals in the intensively managed hay meadows. In detail, we identified 55 species from 14 different Araneae families and 4 species from three Opiliones families in both seasons. For Coleoptera, we identified 18 different Carabidae and 20 Staphylinidae species; furthermore, 16 Formicidae species were found in the pitfall traps (Tab. S1).

While management type did not influence neither activity density, species richness nor diversity of the ground-dwelling predators on community level (Fig. 2), on group level Carabidae and Staphylinidae displayed a significant management effect (Fig. S1). Carabidae showed a higher species richness (LMM: $\text{Chi}^2 = 4.39$, $p = 0.037$) and diversity (LMM: $\text{Chi}^2 = 5.77$, $p = 0.016$) in the extensively used hay meadows, while Staphylinidae contrarily had a higher species richness (LMM: $\text{Chi}^2 = 5.01$, $p = 0.024$) and diversity (LMM: $\text{Chi}^2 = 4.62$, $p = 0.032$) in the intensive hay meadows, mainly driven by the species found in spring (Fig. S1).

Accumulation curves based on species richness (Hill number $q = 0$, Fig. 3) resulted to be not yet fully saturated for both management types, indicating a not fully covered sampling for the predatory arthropod community. This pattern was mostly driven by the species-rich Arachnida (Tab. S1). Species richness (Hill number $q = 0$) does not differ between management types, however, when considering the accumulation curves based on species diversity that downweights rare species (Hill number $q = 1$, Fig. 3), we see a clear differentiation of the two management types, with a higher diversity supported by the extensively managed hay meadows. The same pattern was observed for Arachnida and Formicidae, while Carabidae and Staphylinidae displayed a non-significant differentiation between management types (Fig. S2).

3.2 Community composition

We found significant differences in predator species composition between management types and seasons (see PERMANOVA results in Tab. 1). In an unconstrained ordination of the predator community, season is mainly described by the first axis, while the two management types are well separated by the second axis (Fig. 4).

On group level the pattern was similar: the community composition of Arachnida, Carabidae, and Staphylinidae showed a significant differentiation by management type and season (Fig. S3), with the only exception that for Staphylinidae the management effect appears to be more important than season (see also Tab. 1). Formicidae show the most indistinct pattern in the unconstrained

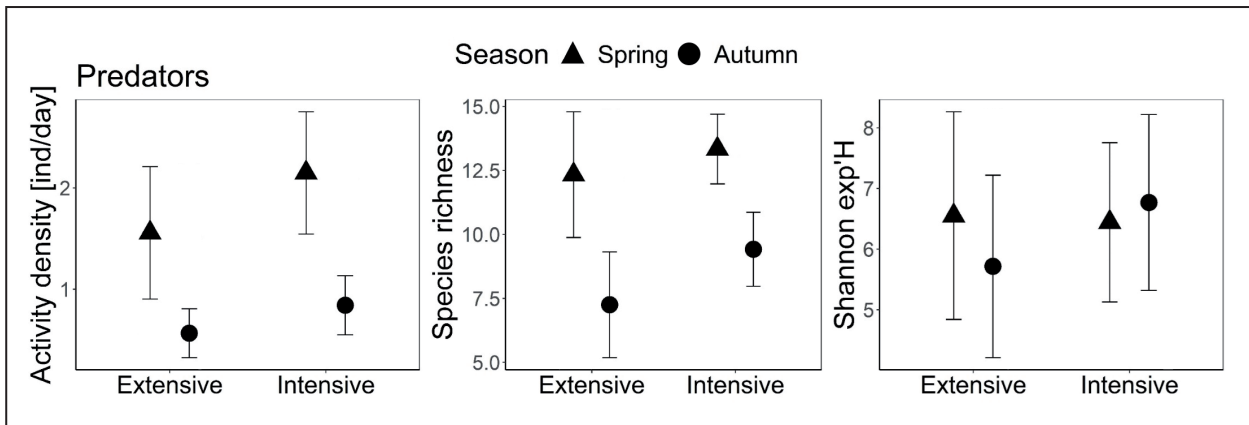


Figure 2. The mean (and 95% confidence interval) activity density (individuals per sampling day), species richness, and exponential Shannon diversity of ground-dwelling predatory arthropods from montane extensively and intensively used hay meadows and two sampling seasons (spring and autumn) in South Tyrol, Italy. No significant effect of management was detected for any biodiversity index.

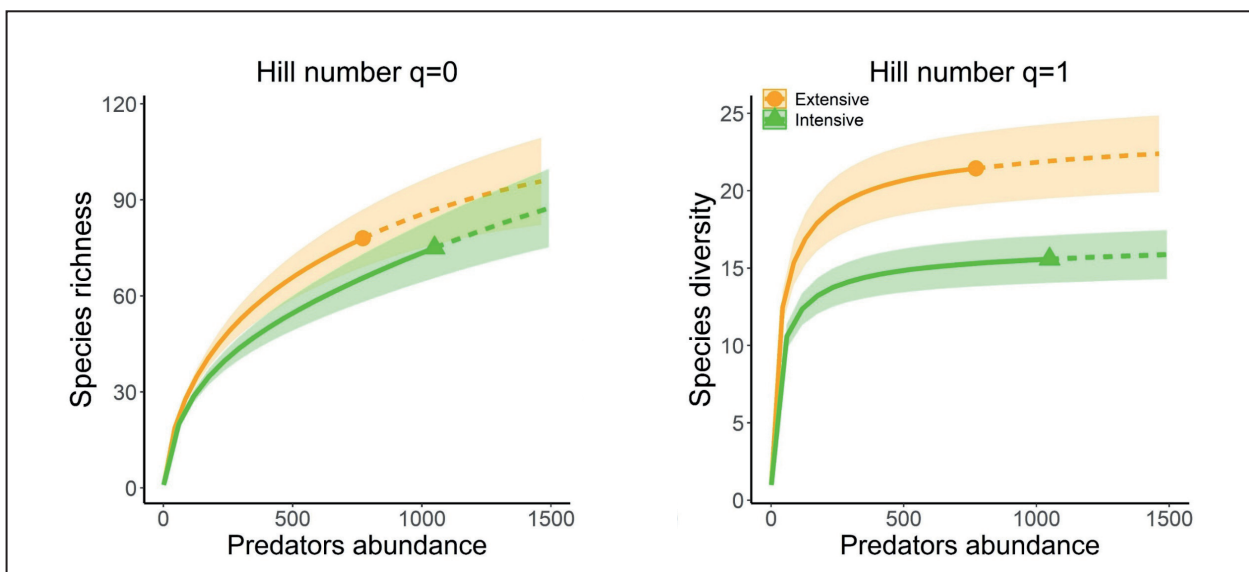


Figure 3. Abundance based accumulation curves for predatory arthropods based on Hill numbers N0 and N1 confronting extensively and intensively used montane hay meadows in South Tyrol, Italy.

ordination, with no clear differentiation by management type or season (Fig. S3).

3.3 Ecological species traits and Red List statuses

By investigating the effects of intensive agriculture on predator species traits, we found that xerophilous species were more often found in extensively managed

hay meadows, whereas mesophilous species more in intensively managed hay meadows (Fig. 5). A similar situation was found for hygrophilous predators, mainly due to one extensively managed meadow having especially moist soil conditions (i.e., EH3).

Regarding the rarity we did not find clear differences for rare and scattered species, but frequent species were found to be more abundant in the intensively managed hay meadows. The results of the ecological tolerance showed that euryoecious and stenoecious species were

Table 1. PERMANOVA results table for the different ground-dwelling predator groups (Arachnida, Carabidae, Staphylinidae, and Formicidae) from montane hay meadows in South Tyrol, Italy. The analysed factors were treatment (i.e., extensive and intensive management) and season (i.e., spring and autumn) using Bray-Curtis distances and 999 permutations; df – degrees of freedom; F – F value by permutation; p – p value. Significance levels: * <0.05; ** <0.01; *** <0.001.

Management type				
	df	residuals	F	p
All predators	1	44	6.742	0.001 ***
Arachnida	1	44	8.659	0.001 ***
Carabidae	1	36	4.178	0.001 **
Staphylinidae	1	34	4.867	0.001 ***
Formicidae	1	37	2.642	0.007 **
Season				
	df	residuals	F	p
All predators	1	44	11.050	0.001 ***
Arachnida	1	44	12.241	0.001 ***
Carabidae	1	36	7.066	0.001 ***
Staphylinidae	1	32	3.148	0.002 **
Formicidae	1	39	1.157	0.013 *

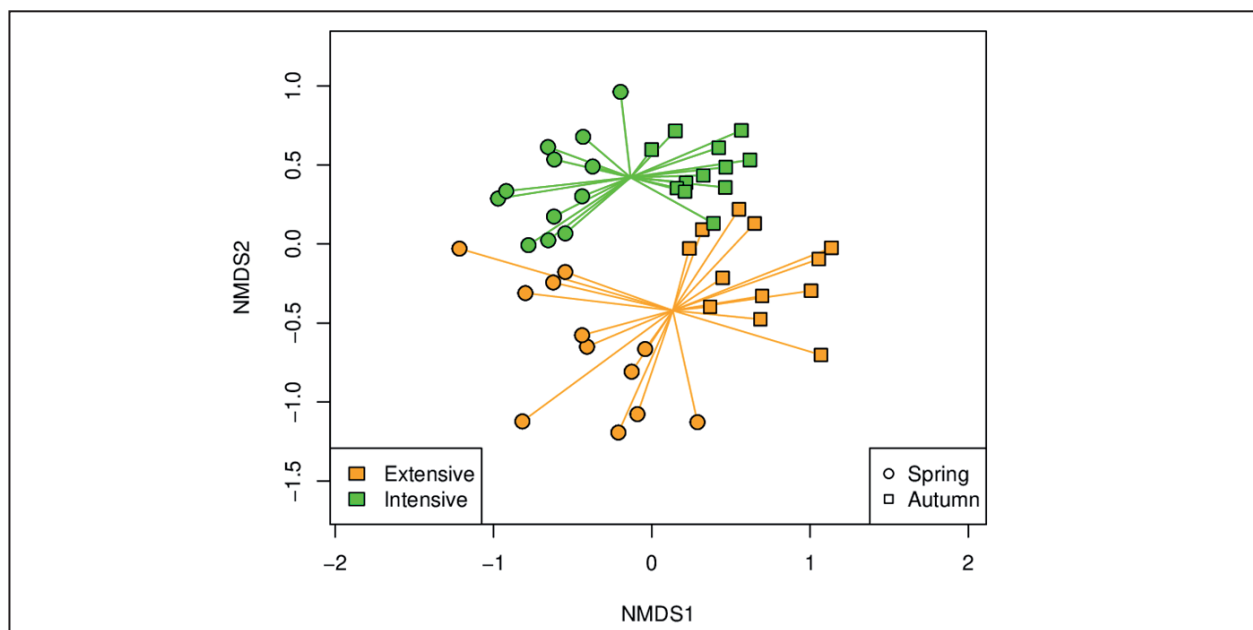


Figure 4. Non-metric multidimensional scaling (NMDS) of the full species community of predatory invertebrates, including the two treatments (intensive and extensive) and the two seasons (spring and autumn). Each spot represents one pitfall trap. Spider web centres represent the weighted centroids of each management type.

more abundant in the intensively used hay meadows, whereas mesoecious species had a significantly higher abundance in the extensively used hay meadows (Fig. 5).

For Red List statuses, we could find most species being categorized as least concern (LC, 74.3%), followed by near threatened (NT, 9.7%), vulnerable (VU, 3.5%) and endangered species (EN, 1.8%) (see Tab. S1). A significant higher occurrence of the categories LC, NT, and VU could be found in the intensively managed hay meadows, while the category EN was equally found in the two management types (Fig. S4).

4. Discussion

Knowledge on mountain soil and ground-dwelling invertebrates (among other soil organism groups) was reported to be still too scarce (Guerra et al. 2020), even though increasingly available (e.g., Gilgado et al. 2022, Mathieu et al. 2022, Seeber et al. 2022) and found to be of top priority for soil nature conservation (Guerra et al. 2022). In this small-scale case study, we contribute to filling these gaps as we quantified the impact of intensive grassland management on ground-dwelling predatory arthropod communities in a Central European mountain area of South Tyrol, Italy. Further, by including traits we follow recommendations to overcome present frontiers in soil ecology (Eisenhauer et al. 2022). We were able to observe changes in the community composition with management intensification and that extensive management potentially supports higher species diversity. Contrary to our expectations, we did not observe significant overall changes in abundance and species richness with increasing management intensity.

4.1 Predator diversity and community patterns

A high arthropod species richness is often reported from extensively used grasslands (e.g., Attwood et al. 2008; Pfiffer & Luka 2003, Guariento et al. 2020), so the small differences in terms of total predator richness (see left graph in Fig. 3) between the two management intensities were contrary to our expectations. Our hay meadow sites were embedded in a complex landscape made of differently managed grasslands and forest patches (see Fig. 1). Therefore, an edge effect and immigration of mobile ground-dwelling predators into the sites might have further limited the direct management effect. Kormann et al. (2015) reported that a high habitat connectivity supported the predator biodiversity (among other taxa) in embedded grasslands in Central Germany, which applies also to our study site and might lead to a relatively high diversity for the intensively managed hay meadows. Thus, in order to be able to detect effects, not only a greater sample size (including the seasonal component) must be taken into account, but also local characteristics specific to the study area. Finally, when downweighing the random occurrences in our study, we found that overall, the extensively managed hay meadows support a significantly higher predator diversity (Fig. 3, Hill number $q = 1$).

Concerning single predatory groups, we found different responses to grassland management intensification. For example, Staphylinidae displayed significantly higher species richness and diversity in the intensive meadows in spring (Fig. S1). This could be explained by the fact that fertilization boosts phytomass production (Lessard-Therrien et al. 2017) and therefore more food resources for herbivores are available, which may then lead to a positive bottom-up effect for higher trophic levels (Hunter & Price 1992). On the

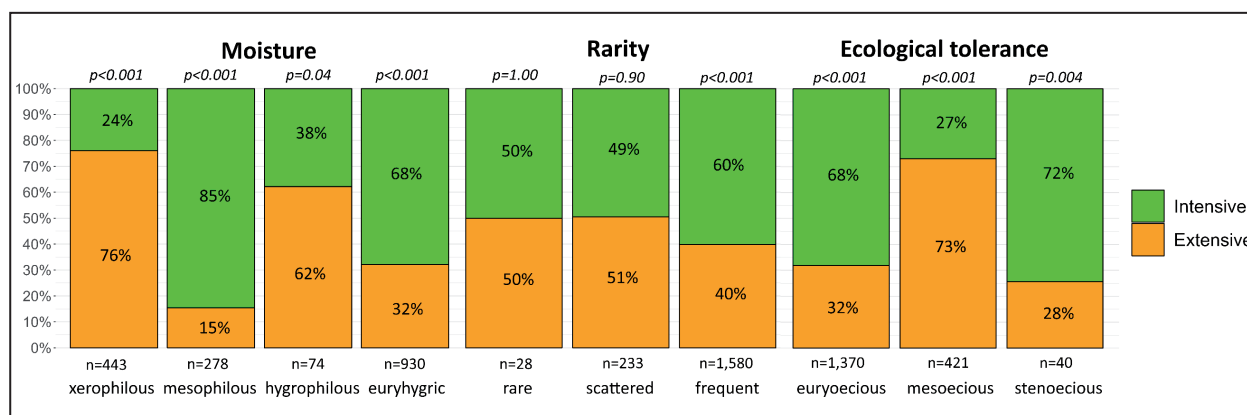


Figure 5. Proportions and χ^2 -test results for the ecological species traits moisture, rarity and ecological tolerance of ground-dwelling predatory arthropods (Arachnida, Carabidae, Staphylinidae, Formicidae) from extensively and intensively managed hay meadows in South Tyrol, Italy.

other hand, Carabidae showed higher species richness and diversity in the extensively used hay meadows. The lower species richness in the intensively used hay meadows might be related to the dynamics of prey density. For example, Andrey et al. (2016) showed that in montane and subalpine grasslands the abundance of Auchenorrhyncha (a typical prey for Carabidae; Thiele 1977) decreases along an intensity gradient, resulting in less prey and less favourable feeding conditions for Carabidae. For Arachnida and Formicidae, the patterns were variable, implying that management intensity was not a major factor driving for these predator groups.

For the full predatory community, the shift in community composition observed was in line with our expectations. The extensively used hay meadows harboured a higher total number of species than our intensively used meadows (82 vs. 69 out of 133 species: Tab. S1). The latter had more similar species compositions for the three investigated plots, therefore it is likely that predator species in intensively used hay meadows are better adapted to withstand land-use disturbances such as high mowing and fertilization frequencies. This result is in line with other studies, where management intensification caused changes in species composition (Samu et al. 1999, Holzinger et al. 2012, Birkenhofer et al. 2015, Meyer et al. 2019). Generally, mowing and fertilizing lead to a decline in plant species richness (Kleijn et al. 2009, Socher et al. 2012), resulting in a loss of specialized herbivores and an increase in generalist species (Huston & Gilbert 1996, Gámez-Virués et al. 2015, Simons et al. 2016, Hilpold et al. 2018).

Our results indicate that the management intensity does not significantly change overall diversity and abundance of ground-dwelling predators. For the individual arthropod groups, however, we see an effect of the intensive management specific to the montane region. A comparable outcome of a decline of specialist species was reported by Gossner et al. (2016) for Central Europe, where even small changes in management intensity negatively affected arthropod groups.

4.2 Ecological species traits and Red List statuses

Regarding the traits of the predator species, we found significant differences for the moisture requirements. Xerophilous species were found more often in the extensively used hay meadows (Fig. 5), which is in line with our expectations and the literature (e.g., Kotze et al. 2011). The intensively managed hay meadows are regularly irrigated and therefore represent an unsuitable habitat for dryland species. Interestingly,

also hygrophilous species (mainly Coleoptera) were significantly more present in extensively managed hay meadows, which can be partly explained by the presence of springs close to the meadows.

Regarding rarity, we found frequent species (i.e., common for the region of South Tyrol) to be more abundant in intensively used hay meadows, while no differences were found for rare species (e.g., rare Araneae species occur in both meadow types, see Tab. S1). This picture applies also for the proportion of Red List statuses of the predator species, where endangered species represent a smaller part in the IH than in EH meadows (Fig. S4). Also in South Tyrol, Hilpold et al. (2018) found a clear decline of rare and specialist species (among them the same ground-dwelling predator groups) after land-use intensification, leading to the presence of more frequent species. In our study, rare species were found equally in both meadow types (Fig. 5), with many of them having an euryoecious ecological tolerance (Tab. S1). Taking a closer look, rare and stenoecious species (e.g., Thomisidae and Staphylinidae species) were expected to be more abundant in the extensively used meadows but were present also in the intensively used hay meadows, such as the Staphylinidae *Xantholinus audrasi* (Coiffait, 1956) which represents a new record for South Tyrol (see Colla et al. 2021).

For Formicidae, the species *Lasius niger* (Linnaeus, 1758) was found exclusively in the intensively used hay meadows; the species is adapted to urban and rural environments, and it is less sensitive to intensive management practices, like fertilization, frequent mowing or mechanic stress on the topsoil (Seifert 2018). The ant species *Formica pratensis* (Retzius, 1783), also recorded in the intensive meadows only, is a further example of individuals coming into the site from the meadow margins, since this species does not withstand intensive meadow management.

5. Conclusion

In this study, we report a clear shift in the community composition of ground-dwelling predators in montane grasslands with different management intensity. Overall biodiversity indices were not able to detect this effect on site level, however, the single predator groups showed clear responses. As our montane meadows were embedded in forest ecosystems, highly mobile predators may migrate between different habitats, blurring the management effect on biodiversity. However, we found a clear separation of the two hay meadow types on predator community level, with the extensively managed hay

meadows supporting a higher predator species richness and the intensively managed hay meadows harbouring higher proportions of common species.

Future studies should better elucidate the seasonal changes that affect the community and diversity of ground-dwelling predator and measure the ecosystem functions of these arthropod groups which could change depending on management intensity and season.

6. Acknowledgement

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7. Supplementary Data

Additional tables and figures and the abundance raw data can be found in the supplementary data of this article. The raw data are available at the open science repository ZENODO (doi: 10.5281/zenodo.7358867).

8. References

- Andrey, A., J. Y. Humbert & R. Arlettaz (2016): Functional response of leaf-and planthoppers to modern fertilisation and irrigation of hay meadows. – *Basic and Applied Ecology* **17**(7): 627–637 [https://doi.org/10.1016/j.baae.2016.07.002].
- Assing, V. & M. Schülke (2012): Die Käfer Mitteleuropas, Bd. 4: Staphylinidae (exklusive Aleocharinae, Pselaphinae und Scydmaeninae). – Spektrum Akademischer Verlag, Heidelberg: 560 pp.
- Attwood, S. J., M. Maron, A. P. N. House & C. Zammit (2008): Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? – *Global Ecology and Biogeography* **17**(5): 585–599 [https://doi.org/10.1111/j.1466-8238.2008.00399.x].
- Bates, D., M. Mächler, B. Bolker, & S. Walker (2015): Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**(1): 1–48 [https://doi.org/10.18637/jss.v067.i01].
- Bell, James R., C. P. Wheeler & W. R. Cullen (2001): The implications of grassland and heathland management for the conservation of spider communities: A review. – *Journal of Zoology* **255**(3): 377–387 [https://doi.org/10.1017/S0952836901001479].
- Billeter, R., J. Liira, D. Bailey, R. Bugter, P. Arens, I. Augenstein, S. Aviron, J. Baudry, R. Bukacek, F. Burel & et al. (2008): Indicators for biodiversity in agricultural landscapes: A Pan-European Study. – *Journal of Applied Ecology* **45**(1): 141–50 [https://doi.org/10.1111/j.1365-2664.2007.01393.x].
- Birkhofer, K., M. M. Gossner, T. Diekötter, C. Drees, O. Ferlian, M. Maraun, S. Scheu, W. W. Weisser, V. Wolters, S. Wurst & et al. (2017): Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. – *Journal of Animal Ecology* **86**(3): 511–20 [https://doi.org/10.1111/1365-2656.12641].
- Birkhofer, K., T. Diekötter, C. Meub, K. Stötzel & V. Wolters (2015): Optimizing arthropod predator conservation in permanent grasslands by considering diversity components beyond species richness. – *Agriculture, Ecosystems & Environment* **211**: 65–72. [https://doi.org/10.1016/j.agee.2015.05.014].
- Blick, T., O.-D. Finch, K. H. Harms, J. Kiechle, K.-H. Kielhorn, M. Kreuels, A. Malten, D. Martin, C. Muster, D. Nährig, et al. (2016): Rote Liste und Gesamtartenliste der Spinnen (Arachnida: Araneae) Deutschlands. – In: Gruttke, H.; Balzer, S.; Binot-Hafke, M.; Haupt, H.; Hofbauer, N.; Ludwig, G.; Matzke-Hajek, G. & Ries, M. (eds): Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 4: Wirbellose Tiere (Teil 2). – Münster (Landwirtschaftsverlag). – *Naturschutz und Biologische Vielfalt* **70** (4): 383–510.
- Chao A, N. J. Gotelli, T. C. Hsieh, E.L. Sander, K. H., R. K. Colwell & A. M. Ellison (2014) Rarefaction and extrapolation with Hill numbers, a framework for sampling and estimation in species diversity studies – *Ecological Monographs* **84** (1):45–67 [https://doi.org/10.1890/13-0133.1].
- Clarke, K. R., P. J. Somerfield & M. G. Chapman (2006): On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. – *Journal of Experimental Marine Biology and Ecology* **330**(1): 55–80 [https://doi.org/10.1016/j.jembe.2005.12.017].
- Cole, L. J., M. L. Pollock, D. Robertson, J. P. Holland & D. I. McCracken (2006): Carabid (Coleoptera) Assemblages in the Scottish Uplands: The influence of sheep grazing on ecological structure. – *Entomologica Fennica* **17**(3): 229–240 [https://doi.org/10.33338/ef.84335].
- Colla, F., A. Zanetti, E. Guariento, J. Plunger, J. & J. Seeber (2021): *Xantholinus audrasi* (Coiffait, 1956) (Coleoptera: Staphylinidae), new record for South Tyrol. – *Gredleriana*: 165–167. [https://doi.org/10.5281/zenodo.5141216].
- De Jong, Y. M., M. Verbeek, V. Michelsen, P. de Place Bjørn, W. Los, F. Steeman, N. Bailly, C. Basire, P. Chylarecki, E. Stloukal & et al. (2014): Fauna Europaea - all European animal species on the web. – *Biodiversity Data Journal* **2**: e4034 [https://doi.org/10.3897/BDJ.2.e4034].
- Dennis, P., M. R. Young & I. J. Gordon (1998): Distribution and abundance of small insects and arachnids in relation to

- structural heterogeneity of grazed, indigenous grasslands. – *Ecological Entomology* **23**(3): 253–264 [https://doi.org/10.1046/j.1365-2311.1998.00135.x].
- Dennis, P., M. R. Young & C. Bentley (2001): The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus Stricta* grassland in upland Scotland. – *Agriculture, Ecosystems & Environment* **86**(1): 39–57 [https://doi.org/10.1016/S0167-8809(00)00263-2].
- Di Giulio, M., P. J. Edwards & E. Meister (2001): Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. – *Journal of Applied Ecology* **38**(2): 310–19.
- Dittrich, A. D. K. & A. J. Helden (2012): Experimental Sward Islets: The effect of dung and fertilisation on Hemiptera and Araneae. – *Insect Conservation and Diversity* **5**(1): 46–56 [https://doi.org/10.1111/j.1752-4598.2011.00133.x].
- Eisenhauer, N., S. F. Bender, I. Calderón-Sanou, F. T. de Vries, J. J. Lembrechts, W. Thuiller, D. H. Wall, R. Zeiss, M. Bahram, R. Beugnon et al. (2022): Frontiers in Soil Ecology—Insights from the World Biodiversity Forum 2022. – *Journal of Sustainable Agriculture and Environment*: 1–17 [https://doi.org/10.1002/sae2.12031].
- FloraFaunaSüdtirol (2022): FloraFaunaSüdtirol – Das Portal zur Verbreitung von Tier- und Pflanzenarten in Südtirol. – Naturmuseum Südtirol, Bozen, Italien [http://www.florafaua.it].
- Fournier, B., F. Gillet, R. C. le Bayon, E. A. D. Mitchell & M. Moretti (2015): Functional responses of multitaxa communities to disturbance and stress gradients in a restored floodplain. – *Journal of Applied Ecology* **52**(5): 1364–1373 [https://doi.org/10.1111/1365-2664.12493].
- Gámez-Virués, S., D. J. Perović, M. M. Gossner, C. Börschig, N. Blüthgen, H. De Jong, N.K. Simons, A.M. Klein, J. Krauss, G. Maier et al. (2015): Landscape simplification filters species traits and drives biotic homogenization. – *Nature Communications* **6**(1): 1–8 [https://doi.org/10.1038/ncomms9568].
- Gapp, J. (1994): Rote Liste gefährdeter Tierarten Südtirols. Abteilung für Landschafts- und Naturschutz Autonome Provinz Bozen/Südtirol, Bozen: 420 pp.
- Gilgado, J. D., H. P. Rusterholz, B. Braschler, S. Zimmermann, Y. Chittaro & B. Baur (2022): Six groups of ground-dwelling arthropods show different diversity responses along elevational gradients in the Swiss Alps. – *PLOS One* **17**(7): e0271831 [https://doi.org/10.1371/journal.pone.0271831].
- Gobbi, M. & D. Fontaneto (2008): Biodiversity of Ground Beetles (Coleoptera: Carabidae) in different habitats of the Italian Po lowland. – *Agriculture, Ecosystems and Environment* **127** (3–4): 273–276 [https://doi.org/10.1016/j.agee.2008.04.011].
- Gobbi, M., D. Fontaneto, N. Bragalanti, L. Pedrotti & V. Lencioni. (2015): Carabid Beetle (Coleoptera: Carabidae) richness and functional traits in relation to differently managed grasslands in the Alps. – *Annales de La Societe Entomologique de France* **51**(1): 52–59 [https://doi.org/10.1080/00379271.2015.1060008].
- Gossner, M. M., T. M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, S. D. Prati, K. Birkhofer, S.C. Renner, J. Sikorski, T. Wubet (2016): Land-use intensification causes multitrophic homogenization of grassland communities. – *Nature* **540**(7632): 266–269 [https://doi.org/10.1038/nature20575].
- Grandchamp, A. C., A. Bergamini, S. Stofer, J. Niemelä, P. Duelli & C. Scheidegger. (2005): The influence of grassland management on ground beetles (Carabidae, Coleoptera) in Swiss montane meadows. – *Agriculture, Ecosystems and Environment* **110**(3–4): 307–317 [https://doi.org/10.1016/j.agee.2005.04.018].
- Guariento, E., F. Colla, M. Steinwandter, J. Plunger, U. Tappeiner & J. Seeber (2020): Management intensification of hay meadows and fruit orchards alters soil macro-invertebrate communities differently. – *Agronomy* **10**(6): 767 [https://doi.org/10.3390/agronomy10060767].
- Guerra, C. A., A. Heintz-Buschart, J. Sikorski, A. Chatzinotas, N. Guerrero-Ramírez, S. Cesarz, L. Beaumelle, M.C. Rillig, F.T. Fernando, M. Delgado-Baquerizo et al. (2020): Blind spots in global soil biodiversity and ecosystem function research. – *Nature Communications* **11**(1): 1–13 [https://doi.org/10.1038/s41467-020-17688-2].
- Guerra, C. A., M. Berdugo, D. J. Eldridge, N. Eisenhauer, B. K. Singh, H. Cui, S. Abades, F. D. Alfaro, A. R. Bamigboye & F. Bastida (2022): Global hotspots for soil nature conservation. – *Nature* **610**(7933): 693–698 [https://doi.org/10.1038/s41586-022-05292-x].
- Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops & D. Tilman (2009): Plant species loss decreases arthropod diversity and shifts trophic structure. – *Ecology Letters* **12**(10): 1029–1039 [https://doi.org/https://doi.org/10.1111/j.1461-0248.2009.01356.x].
- Hilpold, A., J. Seeber, V. Fontana, G. Niedrist, A. Rief, M. Steinwandter, E. Tasser & U. Tappeiner. (2018): Decline of rare and specialist species across multiple taxonomic groups after grassland intensification and abandonment. – *Biodiversity and Conservation* **27**(14): 3729–3744 [https://doi.org/10.1007/s10531-018-1623-x].
- Holzinger W., T. Friess, T., C. Komposch & W. Paill (2012): Tierökologische Bewertung von WF-Rotflächen ein und vier Jahre nach Einstieg in die WF-Maßnahme. – *Ländlicher Raum - Online-Fachzeitschrift des Bundesministeriums für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft* **2012** (02): 1–15.
- Holland, J. M. (2002): *The Agroecology of Carabid Beetles*. Intercept Limited, Andover: 356 pp.
- Humbert, J. Y., J. M. Dwyer, A. Andrey & R. Arlettaz (2016): Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: A systematic review. – *Global Change Biology* **22**(1): 110–120 [https://doi.org/10.1111/gcb.12986].

- Hunter, M. D. & P. W. Price (1992): Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. – *Ecology* **73**: 724–732 [https://doi.org/10.2307/1940152].
- Huston, M. & L. Gilbert (1996): Consumer Diversity and Secondary Production. In: Orians, G. H., R. Dirzo & J. H. Cushman (eds): *Biodiversity and Ecosystem Processes in Tropical Forests*. – *Ecological Studies*, vol 122. Springer, Berlin, Heidelberg: 33–47 [https://doi.org/10.1007/978-3-642-79755-2_3].
- Kahlen, M. (2018): *Die Käfer von Südtirol: Ein Kompendium*. Naturmuseum Südtirol, Bozen: 602 pp.
- Kleijn, D., F. Kohler, A. Baldi, P. Batáry, E. D. Concepción, Y. Clough, M. Díaz, D. Gabriel, A. Holzschuh, E. Knop & et al. (2009): On the relationship between farmland biodiversity and land-use intensity in Europe. – *Proceedings of the Royal Society B: Biological Sciences* **276**(1658): 903–909 [https://doi.org/10.1098/rspb.2008.1509].
- Koch, K. (1989): *Die Käfer Mitteleuropas: Ökologie*. – Goecke & Evers, Krefeld. Band. 1: 440 pp.
- Komposch, C. (2009): Rote Liste der Weberknechte (Opiliones) Österreichs. In: Zulka, K. P. (eds.): *Rote Liste gefährdeter Tiere Österreichs. Checklisten, Gefährdungsanalysen, Handlungsbedarf. Teil 3: Flusskrebse, Köcherfliegen, Skorpione, Weberknechte, Zikaden. Grüne Reihe des Lebensministeriums (Gesamtherausgeberin Ruth Wallner)* – Wien, Böhlau. Band **14/3**: 397–483.
- Komposch, C. (2022): Spinnentiere und Insekten – Artendiversität, Lebensräume und Bedeutung. In: Wiegele, E., M. Jungmeier & M. Schneider (eds): *Handbuch Naturschutzfachkraft. Praktischer Naturschutz für Baustellen, Betriebsgelände und Infrastrukturen*. – Fraunhofer IRB Verlag, Stuttgart: 487–514.
- Kormann, U., V. Rösch, P. Batáry, T. Tscharrntke, K. M. Orci, F. Samu, & C. Scherber (2015): Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. *Diversity and Distributions* **21**: 1204–1217 [https://onlinelibrary.wiley.com/doi/10.1111/ddi.12324].
- Kotze, D. J., P. Brandmayr, A. Casale, E. Dauffy-Richard, W. Dekoninck, M. J. Koivula, G. L. Lövei, D. Mossakowski, J. Noordijk, W. Paarmann et al. (2011): Forty years of carabid beetle research in Europe—from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. – *ZooKeys* **100**: 55–148 [https://doi.org/10.3897/zookeys.100.1523].
- LAFIS (2020): Amt für Landwirtschaftliche Informationssysteme. – Retrieved from url: http://www.provinz.bz.it/de/kontakt.asp?orga_orgaid=948.
- Larsson, S. G. (1939). Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden, *Entomologische Meddelelser* **20**: 277–560.
- Le Provost, G., I. Badenhausser, Y. le Bagousse-Pinguet, Y. Clough, L. Henckel, C. Violle, V. Bretagnolle, M. Roncoroni, P. Manning & N. Gross (2020): Land-use history impacts functional diversity across multiple trophic groups. – *Proceedings of the National Academy of Sciences of the United States of America* **117**(3): 1573–1579 [https://doi.org/10.1073/PNAS.1910023117].
- Lessard-Therrien, M., J. Y. Humbert & R. Arlettaz (2017): Experiment-based recommendations for biodiversity-friendly management of mountain hay meadows. – *Applied Vegetation Science* **20**(3): 352–362 [https://doi.org/10.1111/avsc.12309].
- Littlewood, N. A., A. J. A. Stewart & B. A. Woodcock (2012): Science into practice - how can fundamental science contribute to better management of grasslands for invertebrates? – *Conservation and Diversity* **5**: 1–8 [https://doi.org/10.1111/j.1752-4598.2011.00174.x].
- Marini, L., P. Fontana, M. Scotton & S. Klimek (2008): Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. – *Journal of Applied Ecology* **45**(1): 361–370 [https://doi.org/https://doi.org/10.1111/j.1365-2664.2007.01402.x].
- Martens, J. (1978): Spinnentiere, Arachnida: Weberknechte, Opiliones. In: Senglaub, F., H. J. Hannemann & H. Schumann (eds.): *Die Tierwelt Deutschland 64*. – VEB Gustav Fischer Verlag, Jena: 464 pp.
- Matson, P. A, W. J. Parton, A. G. Power & M. J. Swift (1997): Agricultural intensification and ecosystem properties. – *Science* **277**(5325): 504–509 [https://doi.org/10.1126/science.277.5325.504].
- Mathieu, J., A. C. Antunes, S. Barot, A. E. Bonato Asato, M. L. C. Bartz, G. G. Brown, I. Calderon-Sanou, T. Decaëns, S. J. Fonte, P. Ganault, et al. (2022): sOilFauna - a global synthesis effort on the drivers of soil macrofauna communities and functioning: Workshop Report. – *Soil Organisms* **94**(2): 111–126 [https://doi.org/10.25674/so94iss2id282].
- Maxwell, S. L., R. Fuller, T. M. Brooks & J. E. Watson (2016): Biodiversity: The ravages of guns, nets, and bulldozers. – *Nature* **536**: 143–145 [https://doi.org/10.1038/536143a].
- Meyer, S. T., L. Heuss, H. Feldhaar, W. W. Weisser & M. M. Gossner (2019): Land-use components, abundance of predatory arthropods, and vegetation height affect predation rates in grasslands. – *Agriculture, Ecosystems & Environment* **270**: 84–92. [https://doi.org/10.1016/j.agee.2018.10.015].
- Müller-Motzfeld, G. (2004): *Käfer Mitteleuropas, Bd. 2: Adephega I: Carabidae*. – Spektrum Akademischer Verlag, Heidelberg: 521 pp.
- Nentwig W., T. Blick, D. Gloor, A. Hänggi & C. Kropf (2022): *Spiders of Europe*. Version 11.2022. Online at url: <https://www.araneae.nmbe.ch> [https://doi.org/10.24436/1].
- Nickel, H. & J. P. Hildebrandt (2003): Auchenorrhyncha communities as indicators of disturbance in grasslands (Insecta, Hemiptera)—a case study from the Elbe flood plains (Northern Germany). – *Agriculture, Ecosystems & Environment* **98**: 183–199 [https://doi.org/10.1016/S0167-8809(03)00080-X].

- Niedrist, G., E. Tasser, C. Lüth, J. Dalla Via & U. Tappeiner (2009): Plant diversity declines with recent land use changes in European Alps. – *Plant Ecology* **202** (2): 195–210 [https://doi.org/10.1007/s11258-008-9487-x].
- Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs & et. al (2022): *Vegan: Community ecology package*. R package version 2.6-4 [Retrieved from url: https://CRAN.R-project.org/package=vegan].
- Pekár, S., J. O. Wolff, L. Černecká, K. Birkhofer, S. Mammola, E. C. Lowe, C. S. Fukushima, M. E. Herberstein, A. Kucura, B. A. Buzzatto, et al. (2021): The World Spider Trait database: a centralized global open repository for curated data on spider traits. – *Database* Vol. 2021 (2021): baab064 [https://doi.org/10.1093/database/baab064].
- Pfiffner, L. & H. Luka (2003): Effects of low-input farming systems on carabids and epigeal spiders—a paired farm approach. – *Basic and Applied Ecology* **4**(2): 117–127 [https://doi.org/10.1078/1439-1791-00121].
- Power, E. F., D. L. Kelly & J. C. Stout (2012): Organic farming and landscape structure: effects on insect-pollinated plant diversity in intensively managed grasslands. *PLOS ONE* **7**(5): e38073 [https://doi.org/10.1371/journal.pone.0038073].
- Purtauf, T., J. Dauber & V. Wolters (2005): The response of carabids to landscape simplification differs between trophic groups. – *Oecologia* **142**(3): 458–464.
- R Core Team (2022): *R: A language and environment for statistical computing*. – R Foundation for Statistical Computing, Vienna, Austria. url: https://www.R-project.org/.
- Robinson, R. A. & W. J. Sutherland (2002): Post-war changes in arable farming and biodiversity in Great Britain. – *Journal of Applied Ecology* **39**(1): 157–176 [https://doi.org/10.1046/j.1365-2664.2002.00695.x].
- Ryder, C., J. M. R. Mc Donnell & M. Gormally (2005): Conservation implications of grazing practices on the plant and dipteran communities of a Turlough in Co. Mayo, Ireland. – *Biodiversity & Conservation* **14**(1): 187–204 [https://doi.org/10.1007/s10531-005-5045-1].
- Samu, F., K. D. Sunderland & C. Szinetar (1999): Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: a review. – *Journal of Arachnology* **27**: 325–332.
- Schweiger, O., J. P. Maelfait, W. van Wingerden, F. Hendrickx, R. Billeter, M. Speelmans, I. Augenstein, B. Aukema, S. Aviron, D. Bailey, et al. (2005): Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. – *Journal of Applied Ecology* **42**(6): 1129–1139 [https://doi.org/10.1111/j.1365-2664.2005.01085.x].
- Seeber, J., M. Steinwandter, E. Tasser, E. Guariento, T. Peham, J. Rüdiger, B.C. Schlick-Steiner, F. M. Steiner, U. Tappeiner & E. Meyer (2022): Distribution of soil macrofauna across different habitats in the Eastern European Alps. – *Scientific Data* **9**: 632 [https://doi.org/10.1038/s41597-022-01717-4].
- Seifert, B. (2018): *The Ants of Central and North Europe*. – lutra Verlags- und Vertriebsgesellschaft, Tauer: 408 pp.
- Simons, N. K., M. M. Gossner, T. M. Lewinsohn, S. Boch, M. Lange, J. Müller, E. Pašalić, S.A. Socher, M. Türke, M. Fischer & et al. (2014): Resource-mediated indirect effects of grassland management on arthropod diversity. – *PLOS ONE* **9**(9): e107033 [https://doi.org/10.1371/journal.pone.0107033].
- Simons, N. K., W. W. Weisser & M. M. Gossner (2016): Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. – *Ecology* **97**(3): 754–764.
- Sjödin, N. E., J. Bengtsson & B. Ekbom (2008): The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. – *Journal of Applied Ecology* **45**(3): 763–772.
- Socher, S.A., D. Prati, S. Boch, J. Müller, V.H. Klaus, N. Hölzel & M. Fischer (2012): Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. – *Journal of Ecology* **100**(6): 1391–1399 [https://doi.org/10.1111/j.1365-2745.2012.02020.x].
- Tälle, M., B. Deák, P. Poschlod, O. Valkó, L. Westerberg & P. Milberg (2016): Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. – *Agriculture, Ecosystems & Environment* **222**(4): 200–212 [https://doi.org/10.1016/J.AGEE.2016.02.008].
- Tappeiner, U., T. Marsoner & G. Niedrist (2020): *Landwirtschaftsreport zur Nachhaltigkeit Südtirol*. Eurac Research, Bozen: 141 pp.
- Thiele, H. U. (1977). *Carabid Beetles in Their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour*. Springer-Verlag, Berlin, Heidelberg: 369 pp.
- Toft, S. & T. Bilde (2002): *Carabid Diets and Food Value*. In: Holland, J. M (eds): *The Agroecology of Carabid Beetles*. Intercept Limited, Andover: 81–110.
- Tsiafouli, M. A., E. Thébault, S. P. Sgardelis, P. C. de Ruiter, W. H. van der Putten, K. Birkhofer, L. Hemerik, F. T. de Vries, R. D. Bardgett, M. V. Brady & et al. (2015): Intensive agriculture reduces soil biodiversity across Europe. – *Global Change Biology* **21**(2): 973–985 [https://doi.org/https://doi.org/10.1111/gcb.12752].
- Van den Berg, L. J. L., P. Vergeer, T. C. G. Rich, S. M. Smart, D. Guest & M. R. Ashmore (2011): Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. – *Global Change Biology* **17**(5): 1871–1883 [https://doi.org/https://doi.org/10.1111/j.1365-2486.2010.02345.x].
- Verberk, W. C. E. P., C. G. E. van Noordwijk & A. G. Hildrew (2013): Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. – *Freshwater Science* **32**(2): 531–547 [https://doi.org/10.1899/12-092.1].
- Vickery, J., J. R. Tallwin, R. Feber, E. Asteraki, P. W. Atkinson, R. J. Fuller & V. K. Brown (2001): The management of

- lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. – *Journal of Applied Ecology* **38**(3): 647–664 [<https://doi.org/10.1046/j.1365-2664.2001.00626.x>].
- Wickham, H. (2016): Package ggplot2: elegant graphics for data analysis. – Springer-Verlag, New York: 276 pp.
- Wood, S. A., D. S. Karp, F. De Clerck, C. Kremen, S. Naeem & C. A. Palm (2015): Functional traits in agriculture: agrobiodiversity and ecosystem services. – *Trends in Ecology and Evolution* **30**(9): 531–539 [<https://doi.org/10.1016/j.tree.2015.06.013>].
- Woodcock, B. A., S. G. Potts, T. Tscheulin, E. Pilgrim, A. J. Ramsey, J. Harrison-Cripps, V. K. Brown & J. R. Tallwin (2009): Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. – *Journal of Applied Ecology* **46**(4): 920–929 [<https://doi.org/https://doi.org/10.1111/j.1365-2664.2009.01675.x>].
- World Spider Catalog (2022): World Spider Catalog. Version 23.5. – Natural History Museum Bern. Online at url: <http://wsc.nmbe.ch> [<https://doi.org/10.24436/2>].

