Abrupt boundaries between mountain meadows and forests separate ground-dwelling invertebrate communities: a case study from South Tyrol, Italy

Helene Blasbichler[1], Julia Plunger[1], Julia Seeber[1,2] and Michael Steinwandter[1,*]

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

[2] Universität Innsbruck, Department of Ecology, Technikerstrasse 25, 6020 Innsbruck, Austria

* Corresponding author: michael.steinwandter@eurac.edu

Abstract

In mountain regions, available agricultural land is often limited by the rugged topography and therefore an efficient and small-scale land use is needed to ensure food and fodder security. In the European Alps, mountain meadows at mid-elevations were created in medieval times by clearing and are therefore often still embedded in forest areas. The transition between these two habitats is mostly smooth due to the presence of a shrub strip, but sometimes sharp, as it is the case in our study. It is not well known whether such abrupt shrub-free habitat shifts affect the exchange of ground-dwelling macro-invertebrates between habitats and whether this may affect local biodiversity.

We set up nine straight transects with five pitfall traps each, running from montane open extensive meadows through the sharp ecotone lines to mixed forest plots in South Tyrol, Northern Italy. Invertebrate activity densities, distribution, and biodiversity patterns were assessed.

We found well separated invertebrate communities for the meadows and forests, with the ecotone communities being similar to those of the forests and not forming a distinct intermediate cluster. Araneae were significantly more abundant in the meadows and decreased towards the meadow edges and forests. In contrast, Diplopoda and Isopoda were significantly more abundant in the ecotone and forest plots. The meadow plots and partly the edge plots were inhabited by threatened Red List species.

In heterogeneous mountain regions such as South Tyrol, where agricultural land is scarce and therefore must be used efficiently, sharp shifts between habitat types result in distinct invertebrate communities impeding species exchange. Maintaining the extensive management of grasslands and the establishment of buffering shrub strips are therefore desirable measures to support the local soil invertebrate biodiversity, as species may not be able to spill over the abrupt ecotone borders and seek shelter during management activities.

1. Introduction

Mountains are considered to be biodiversity hotspots and comprise 12.3 % of Earth's total terrestrial area (Körner et al. 2017). Since millennia, sustainable and small-scaled agricultural practices, which also support a high biodiversity, result in a wide range of ecosystems services (e.g. Hopkins 2011, Babai & Molnár 2014), not only for the mountain population (i.e. about 20 % of world's population) but also for people in the adjacent lowlands (Payne et al. 2020). The montane grasslands in the European Alps developed as a result of human activity, such as clearing by local farmers in medieval times (Bätzing 2015). This was necessary because

suitable agricultural areas in mountain regions are generally limited and natural grassland developed mainly above the natural tree line after the retreat of the glaciers following the last ice age, and this alpine grassland is of limited use (Leuschner & Ellenberg 2017a).

South Tyrol, Italy's northernmost province, lies within the Central and Southern European Alps and is therefore characterised by a rugged topography. Consequently, the area used for agricultural purposes is limited and relatively small, representing only 24 % of South Tyrol's total area (i.e. 178,109 out of a total of 739,997 ha, Autonomous Province of Bolzano – South Tyrol 2023); for comparison, Italy's agricultural area is 52 % of its total area (CREA – Centro di ricerca Politiche e Bioeconomia 2021). Most grasslands in South Tyrol are located at mid- and high elevations and provide essential ecosystem services for mountain farmers such as fodder for their livestock (mainly cattle and sheep; Tappeiner et al. 2020). Extensively used meadows, which have been managed traditionally for centuries (i.e. mowing late only once a year, little or no irrigation, no fertilisation or grazing), now account for only 2.23 % of South Tyrol's total agricultural area (versus 48.36 % for intensively managed agricultural areas: crop fields, hay meadows, apple orchards, and vineyards). In fact, the dominant element of the South Tyrolean landscape is the forest, which covers 51 % of the total area. Coniferous species predominate (mainly afforested European spruce *Picea abies* (L.) H.Karst. (61 %) and European Larch *Larix decidua* Mill. (19 %) (Tappeiner et al. 2020, Autonomous Province of Bolzano – South Tyrol 2023), which have increasingly replaced naturally occurring deciduous trees to obtain higher timber yields. Thus, the last remaining extensively managed mid-elevation meadows are often embedded in areas of semi-natural and managed forests.

Such extensively used mountain grasslands, even if created by human activities, were found to be of high conservational value and are – compared to intensively managed meadows – considered to support a high biodiversity, as has been shown for example for plants and grasshoppers (Kampmann et al. 2008) and for ground-dwelling (Hilpold et al. 2018) and soil invertebrates (Guariento et al. 2020). A high diversity of ground-dwelling taxa – often dominated by Araneae, Coleoptera, and Myriapoda – is important for ecosystem functioning and is commonly used as an ecological indicator in temperate grassland systems (Solascasas et al. 2022). Araneae, Staphylinidae, and many species of Carabidae are predators and were found to regulate invertebrate populations, while granivorous Carabidae can act as weed controllers; all surface invertebrates are themselves an important resource for larger predators such as birds and small mammals (Vickery et al. 2001, Gobbi et al.

2015). These invertebrates tend to have preferences for either grassland or forest. For example, sunlight exposure, woody plant cover, ground vegetation cover, and mosses – which vary greatly between grassland and forest habitats – are important drivers of carabid beetle assemblages (Mullen et al. 2008, Bergmann et al. 2012). Vegetation type has been shown to play an important role in shaping spider communities (Argañaraz et al. 2020, Nardi & Marini 2021). Forest–grassland ecotones (also known as field margins), which typically include a shrub layer, can therefore be a particularly species-rich and beneficial buffer zone for invertebrates (Marshall & Moonen 2002, Leuschner & Ellenberg 2017b), as they provide habitat and shelter for both forest and grassland invertebrate communities, in addition to their own ecological niches. This transition zone can also act as an important spill-over zone for arthropods, which may, for example, use the shrub strips and forest stands as a shelter after the mowing of grasslands (Tölgyesi et al. 2018). However, due to the scarcity of space in mountainous areas, farmers are forced to use land as efficiently as possible. This often results in sharp, shrub-free boundaries in the forest–grassland ecotone, dispensing with field margins and with tall trees starting right at the edge of the meadow. This can change species assemblages significantly and abruptly, impeding a spill-over and further reducing the local biodiversity as less ecological niches are present (i.e. due to no shrub layer).

In this study, we established transects from extensively managed grasslands to mixed forests to assess ground-dwelling macro-invertebrate communities. We hypothesise that (i) taxa show different distribution and biodiversity patterns in the grasslands and forests, (ii) the activity densities along these short transects differ for individual taxa and regarding the taxonomic levels used, and (iii) abrupt forest–grassland ecotone like in our case without shrub strips impede a specifically high ground-dwelling invertebrate diversity. We used pitfall traps set at regular intervals along the transects to assess changes in the ground-dwelling communities along the transects.

2. Material & 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. This area is characterised by species-rich mixed forests (e.g. oak, larch, spruce, beech, birch, chestnut) and some scattered and embedded managed grasslands and settlements (Fig. 1). Our study site was

located near the locality of 'Dreikirchen/Tre Chiese' in the municipality of Barbian/Barbiano in the Eisack Valley at an elevation between 1150 and 1210 m a.s.l. (46.61410° N, 11.51277° E).

2.2. Study design

We selected three extensively used mountain meadows (EH) surrounded by mixed forest (e.g. European spruce *Picea abies* (L.) H. Karst., European beech *Fagus sylvatica* L., Downy oak *Quercus pubescens* Willd., Silver birch *Betula pendula* Roth); see Fig. 1. All three meadows – hereafter referred to as sites – were owned by the same farmer and extensively managed for the last 30 years: they were neither fertilised nor grazed by livestock, but mown once a year (see also Plunger et al. 2022), following the requirements to obtain regional subsidies (so-called 'Landscape Conservation Premiums'). The meadows have a relatively small size between 0.4 and 0.7 ha (EH2 and EH3, respectively, Fig. 1). They are dominated by the grasses *Brachypodium rupestre* (Host)

Roem. & Schult. and *Bromopsis erecta* (Huds.) Fourr., EH3 also by *Molinia caerulea* (all Poaceae). All three grasses are typical elements of montane grasslands in South Tyrol, the former are found commonly at the steep slopes of Eisack Valley and the latter two in the montane slopes and plains (see www.florafauna.it for distribution patterns within South Tyrol). Some shrub and tree seedlings were recorded in the meadows as remnants of the semi-natural forests. These extensively managed meadows were species-rich with on average 32 plant species (and in total 59 species) compared to adjacent intensively managed hay meadows (i.e. on average 12 and in total 17 species, see Plunger et al. 2022).

The semi-natural mixed forest areas were managed according to the local forestry regulations (i.e. maintaining a balanced stand structure and creation conditions for the natural regeneration of the stands). The edges of each meadow had sharp and narrow boundaries to the forest, with tall trees of 10–15 m and no or only few scattered shrubs established at the edges (Fig. 1, and A1 in Appendix A). Three linear and parallel transects were established at each site, traversing the three habitat types
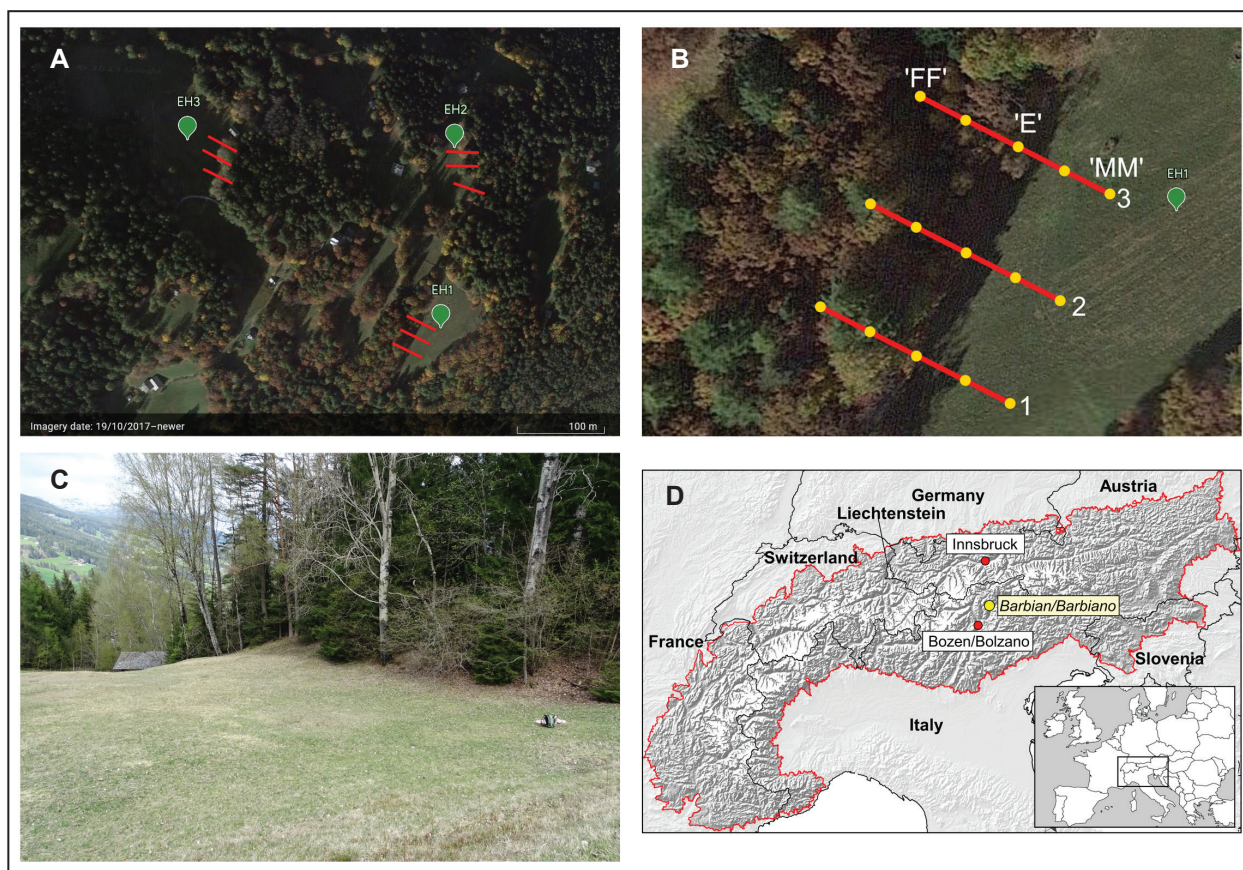

Figure 1. Overview map of the study area of Barbian/Barbiano, South Tyrol (Italy), showing the three extensively managed meadows and the linear transects towards the forests. (**A**) Overview of the three meadows that are embedded in montane mixed forests. (**B**) Detailed view of a site showing the sampling design ('MM' – meadow, 'E' – ecotone, 'FF' – forest). (**C**) Photo of the plot EH3 (Photo credit: Michael Steinwandter). (**D**) Position of the study site of Barbian/Barbiano within the European Alps (red border). Aerial photographs by Google Earth.

(meadows, ecotones, and forests) spanning a distance of 40 m, with transects separated by at least 10 m. To assess the activity densities of the ground-dwelling fauna, five pitfall traps were placed along each transect, with traps separated by 10 m (referred to as plots). Two pitfall traps were installed inside the meadows (code-named 'MM' and 'M', the former being more distant from the boundaries), one exactly on the narrow ecotone line between the abrupt shift from meadows and forests ('E'), and two in the forests ('F' and 'FF', the latter being more distant from the boundaries).

The active sampling period took place in spring and lasted from 3rd April to 5th May 2019 (i.e. 31 days). We are aware that the abundance and community composition of ground-dwelling arthropods changes with the seasons due to the different phenologies of species, and that a sampling date is only a small snapshot in time. However, it has been shown that predatory arthropods in particular, which make up a large proportion of the ground-dwelling invertebrate community, are most abundant in spring (Cheng et al. 2021, Plunger et al. 2022).

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 (Fig. A1). The pitfall traps were filled with a mixed solution of 60 % propylene glycol, 30 % water, and 10 % of 96 % ethanol. A transparent polycarbonate roof protected the traps from rain and debris. In total we installed 45 single pitfall traps (3 sites × 3 transects × 5 pitfall traps). Traps were emptied every 10–11 days to better preserve the sampled animals, but the abundance data were summed for each individual pitfall trap.

2.3 Identification of ground-dwelling macro-invertebrates

After the pitfall traps collection, all invertebrates were rinsed with tap water and preserved in 75 % ethanol. We identified the specimens under a stereomicroscope (SMZ-171, Motic, Hong Kong, China) – where possible – to family level using the identification keys of Klausnitzer (2011, 2019) for most invertebrates, and Hauser & Voigtländer (2019) for Diplopoda. Araneae and Formicidae were identified to species level using the identification keys of Nentwig et al. (2023) and Seifert (2018), respectively. Taxa such as Diptera (adults and larvae) and Lumbricidae were documented but not included in the analyses as they were not target groups of the pitfall trap method; see Tab. B1 for a full list of the documented taxa. The Red List status for Araneae and Formicidae species – where available – was assessed according to Gapp (1994, Red List South Tyrol) and Seifert (2018, Red List Germany), respectively.

2.4 Statistical analyses

For all analyses, the activity densities from the three sampling dates of each individual pitfall trap were summed up, resulting in a single value for 31 days of exposure for each of the 45 pitfall traps. Activity densities were processed as absolute values for the calculation of accumulation curves and biodiversity indices, and were standardised for the ordination plots. For Formicidae, numbers of an abundant species (i.e. workers of *Lasius fuliginosus* (Latreille, 1798)) were capped at 200 individuals (i.e. the highest total number) to avoid statistical over-predictions (Gotelli et al. 2010). Analyses were performed at three taxonomic levels: (i) at the highest resolution available, (ii) at the family level, and (iii) at the species level for Araneae and Formicidae. All calculations, unless otherwise stated, were performed in the open-source statistical programming environment R (version 4.3.2, R Core Team 2023) in RStudio (version 2023.09.1+494, RStudio Team 2023).

Abundance-based accumulation curves were generated by summing up each pitfall trap data at plot level (i.e. each 9 pitfall traps per habitat plot 'MM', 'M', etc.) and sorting them from highest to lowest values using the R package ɪNEXT (version 3.0.0., Chao et al. 2014). To assess patterns of invertebrate diversity along the transects, we calculated accumulation curves by using four widely used diversity indices for the total communities at the highest taxonomic resolution (i.e. species and family level where possible), and for Araneae at species level. These diversity indices were: sampling coverage to test whether sampling was sufficient to assess the invertebrate community, taxa and species richness (Hill number q = 0) to analyse the number of different taxa found at each plot, and Shannon (q = 1) as well as Simpson alpha diversity (q = 2) that take into account also the abundances and frequencies of the taxa (Roswell et al. 2021). The same procedure was performed for the faunal communities at family level (Fig. A4), but this was not possible for Formicidae due to their aggregated occurrences.

All figures (i.e. accumulation curves and boxplots with jitter) were generated using the R package ɢɢPLOT2 (version 3.4.4, Wickham 2016); for the boxplots we pooled Diplopoda and Isopoda due to their ecological and functional similarity. Biodiversity indices (i.e. taxa and species richness, Shannon and Simpson alpha diversity) were calculated using the R package ᴠEGAN (v. 2.6-4, Oksanen et al. 2022). Due to the nested sampling design (three transects per site), we tested whether linear mixed effects models with *site* as a random effect (i.e. LME) were necessary by calculating the intraclass correlation coefficient (ICC, function *ICC1.lme* from the R package PSYCHOMETRIC v. 2.4, Fletcher 2023). These analyses

showed no dependencies between sites (all ICCs < 0.1), so negative binomial generalised linear models with Tukey's HSD post-hoc tests were used to analyse differences in activity densities between the five habitats. These models were selected due to overdispersed count data, and we ran residual diagnostics for all models using the R package DHARMa (v. 0.4.6, Hartig and Lohse 2022). Differences in biodiversity indices between plots were analysed with one-way ANOVAs and Tukey's HSD post-hoc tests.

In addition, ordination analyses with standardised activity density data (ind./day) were done in the multivariate data exploration software CANOCO 5 (version 5.15, ter Braak & Šmilauer 2018). Due to a gradient length of 3.2 SD units, a unimodal method with an unconstrained Detrended Correspondence Analysis (DCA) was chosen, where data were log-transformed and rare taxa were downweighed. PERMANOVAs (permutational multivariate analysis of variance) were calculated on the ordination plots in the R package VEGAN to detect significant differences between the habitat plots. Again, DCA plots were calculated for the fauna at family level and for Araneae species (Fig. A2), but this was not possible for Formicidae species. Further, indicator taxa were identified by using the method after Dufrêne & Legendre (1997) in the statistic software PAST (version 4.14, Hammer et al. 2001).

3. Results

3.1 Community composition

We captured 5,134 specimens of ground-dwelling macro-invertebrates from 157 taxa during the 1-month sampling period (3,986 excluding Formicidae). The highest number of individuals was found in the ecotone 'E' (1,576), but most of these were ants (754). The second highest number of captured animals (1,141 specimen, 40 of them being Formicidae) was recorded for the meadow plots 'MM', while we found a gradual decrease from the ecotones towards the forest plots 'FF' (631, 71 being Formicidae). The most abundant invertebrate group was Araneae (40.11 %), followed by Formicidae (22.36 %) and Coleoptera (21.50 %). Within the Araneae, 16 families and 70 species (plus 19 at genus level) were identified, the most abundant being Lycosidae (33.71 %), Tetragnathidae (23.65 %, only 1 species), and Linyphiidae (16.95 %), the latter being the most diverse family with 34 species. We identified 22 families of Coleoptera, the most abundant being Carabidae (37.77 %), Staphylinidae (35.24 %), and Latridiidae (9.33 %). For Formicidae, 17 species (and two taxa at genus level) were identified. See the mean activity

densities in Tab. 1 (at family level) and a full table in the Supplementary Data (Tab. B1).

3.2 Community patterns along the gradient

The unconstrained DCA plot (Fig. 2) showed well-separated ground-dwelling macro-invertebrate communities for the meadows and forests along the axis 1 at the highest taxonomic resolution (PERMANOVA, $F = 4.217$, $p = 0.001$). Specifically, we found two significantly different groups comprising of the meadows ('MM' and 'M') and the other three habitat plots ('E', 'F', and 'FF'); in addition 'E' and 'FF' were significantly different. Important and frequent taxa (i.e. present in more than five pitfall traps) driving the separation in the ordination were *Xysticus bifasciatus* C. L. Koch, 1837 (Thomisidae), *Alopecosa cuneata* (Lycosidae), and *Pachygnatha degeeri* Sundevall, 1830 (Tetragnathidae) for the meadows (axis 1 loadings of 1.12, 0.78, and 0.67, respectively), and *Amaurobius fenestralis* (Ström, 1768) (Amaurobiidae), and *Centromerus silvicola* (Kulczyński, 1887) and *Mecopisthes silus* (O. Pickard-Cambridge, 1873) (both Linyphiidae) for the forests (axis 1 loadings
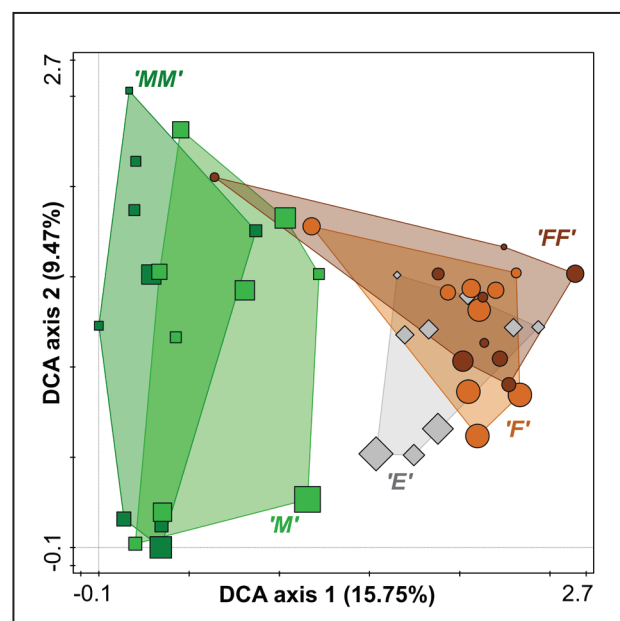
Figure 2. Unconstrained Detrended Canonical Analyses (DCA) of log-transformed abundances of ground-dwelling macro-invertebrates from montane meadows and mixed forests in South Tyrol, Italy. Data for the highest available taxonomic resolution was used (i.e. Araneae and Formicidae at species level, all other on family level, where possible). Each data point represents a pitfall trap along a linear transect starting from extensively managed hay meadows ('MM' and 'M', squares) across an abrupt ecotone ('E', diamonds) towards mixed forest stands ('F' and 'FF', circles). The size of the data points represents the number of taxa from min. 15 to max. 41.

of 3.98, 3.86, and 3.43, respectively). The analysis also showed that the ecotone communities clustered with the forest communities and were well separated from the meadows. The two meadow plots ('MM' and 'M') showed a higher variability resulting in much larger species areas compared to the other three habitat plots. Plots of the total fauna at family level and the Araneae at species level showed similar patterns (Fig. A2).

When looking at the dominant and indicator taxa, we found different patterns along our short but sharp transects (Tab. 1, Fig. 3). On average, Araneae were significantly more abundant in the meadows ('MM') mainly due to significantly higher numbers of Tetragnathidae, Lycosidae, and Thomisidae, and decreased significantly

already within the meadow edges ('M'); the activity densities decreased further towards the forests (AIC = 384.30, 2x loglik = -372.30). The indicator species analysis confirmed this pattern, as these spider families had the highest indicator values for 'MM' and 'M'. Hemiptera abundances (i.e. Heteroptera, Sternorrhyncha, and Auchenorrhyncha) were also significantly higher in the meadows, mainly due to Auchenorrhyncha, which was also confirmed by the indicator species analysis (see Tab. 1 and 2).

In contrast, Diplopoda and Isopoda (i.e. Oniscidea) increased significantly towards the ecotone ('E') and forest edge 'F' (AIC = 182.27, 2x loglik = -170.27), and then decreased slightly in the forests ('FF'), showing the
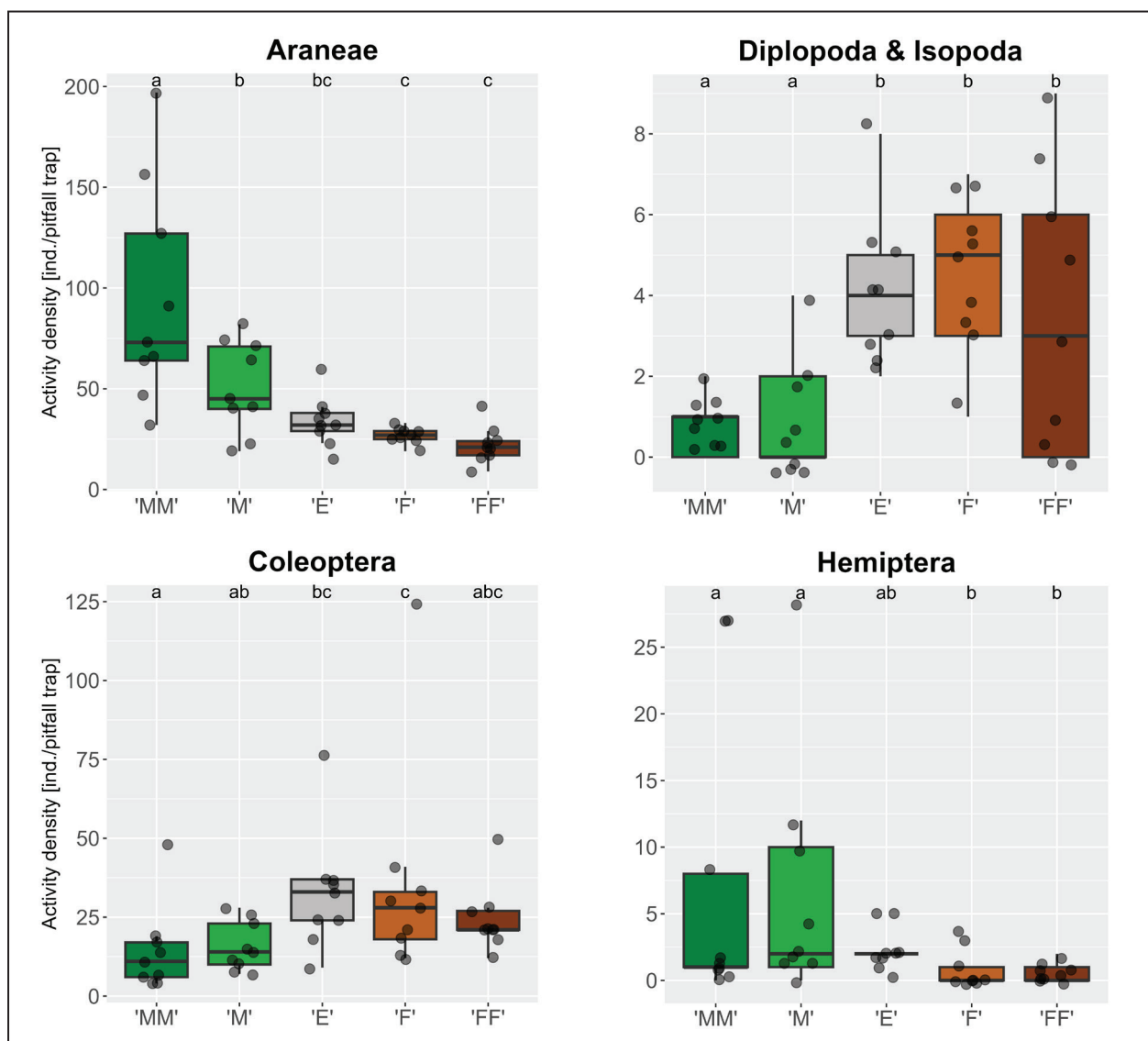
Figure 3. Boxplots with jitter of ground-dwelling macro-invertebrate activity densities from montane meadows and mixed forests in South Tyrol, Italy. Each data point represents a pitfall trap along a linear transect starting from extensively managed hay meadows ('MM' and 'M') across an abrupt ecotone ('E') towards mixed forest stands ('F' and 'FF'). Significant differences between the habitat plots (i.e. on the X-axes) according to GLM and Tukey's HSD post-hoc tests are indicated with different letters at top of each plot.

highest variability in these plots. The most abundant Diplopoda and Isopoda taxa in the forests were Polyxenidae (not significant, Tab. 2), while Julidae were significantly more abundant in and representative for the ecotone area ('E') (Tab. 1). Coleoptera families showed few significant differences regarding their abundances, but put together they had higher mean activity densities in the ecotones ('E') and forest edges ('F') due to high abundances of Carabidae, Staphylinidae, and Latridiidae, while the lowest activity was found in the meadows ('MM'). This was confirmed by the indicator species analysis with Coleoptera families being under the top five taxa for the ecotones and forests (Tab. 1).

3.3 Diversity patterns and Red List statuses

The accumulation curves showed well-covered ground-dwelling communities above 95 % (total fauna) and above 90 % (Araneae). The highest faunal diversity was found for the meadow edges ('M') when using the highest taxonomic resolution, and the ecotones ('E') for Araneae (Fig. 4); at family level the forest plots ('FF') had the highest faunal diversity (Fig. A4).

At the highest taxonomic resolution, we could not find any significant differences in the mean diversity indices (i.e. taxa richness, Shannon, and Simpson diversity, Fig. 4 and Tab. A1); however, the edge plots 'M' and 'F' had the highest values. On average, we identified 21 taxa for the meadows, while the ecotones ('E') and forest edge ('F') harboured 27 and 26 taxa, respectively ($F_{4,40} = 3.275$, $p = 0.021$).

At family level, all mean diversity indices were significantly lower in the meadow plots ('MM'), while the ecotones ('E') and the forest plots ('F', 'FF') showed higher values (Fig. A4 and Tab. A2). In detail, 14 families were found exclusively and rarely in only one of the plots: seven of them were Coleoptera (e.g. Brentidae in 'MM', Silphidae and Byrrhidae in 'FF'), and six Arachnida (e.g. Pisauridae in 'MM', Hahniidae in 'M', Trogulidae in 'E').

Looking at the Araneae only, we found a high species richness for the central transect section spanning from 'M' to 'F' (Fig. 3), but only the forest edges 'F' were significantly more divers than the meadows 'MM' (Tab. A2). At species level, 22 out of the 70 Araneae species were found in only one habitat plot type (e.g. 9 in the meadow edges 'M'), while this was the case for 9 of the 17 Formicidae species (Tab. A2).

Most of the identified Araneae and Formicidae species (i.e. 87 in total) belonged to the Red List category 'Least Concern LC' (62 species, 71.26 %), followed by the category 'Near Threatened NT' (9, 10.34 %); eight species had no Red List status assessed. We found six threatened Formicidae and one Araneae species belonging to the categories 'Vulnerable VU' (i.e. five Formicidae) and 'Endangered EN' (i.e. one Araneae and one Formicidae), mostly present in the meadow plots 'M' and the ecotone plots 'E' (Fig. A5 and Tab. B1).

4. Discussion

Here we present data on activity densities and community composition of ground-dwelling macro-invertebrates along short ecological transects with a sharp and shrub-free boundary from temperate mountain meadows to mixed forests in South Tyrol, Italy. Although we only sampled these faunal communities during a relatively short period, namely in spring, we found all major invertebrate groups inhabiting the soil

Table 1. Top five indicator taxa of ground-dwelling macro-invertebrates from montane meadows and mixed forests in South Tyrol, Italy. Family level data come from pitfall traps along linear transects from extensively managed hay meadows ('MM', 'M') across sharp and narrow ecotones ('E') towards mixed forest stands ('F', 'FF'). Taxa per habitat were ranked according to the IndVal values (percent, given in parentheses along the p-values).

Ranking [IndVal]	'MM'	'M'	'E'	'F'	'FF'
1	Tetragnathidae 66.28 %, p < 0.001	Lycosidae 36.74 %, p = 0.008	Formicidae 51.02 %, p = 0.003	Staphylinidae 39.59 %, p = 0.070	Amaurobiidae 31.91 %, p = 0.011
2	Thomisidae 46.61 %, p = 0.001	Philodromidae 34.57 %, p = 0.005	Julidae 42.11 %, p = 0.001	Porcellionidae 36.60 %, p = 0.002	Carabidae 26.14 %, p = 0.008
3	Lycosidae 42.94 %, p = 0.002	Auchenorrhyncha 26.90 %, p = 0.082	Latridiidae 34.30 %, p = 0.015	Polyxenidae 35.09 %, p = 0.002	Sclerosomatidae 22.22 %, p = 0.036
4	Auchenorrhyncha 32.58 %, p = 0.035	Thomisidae 25.20 %, p = 0.063	Staphylinidae 31.11 %, p = 0.944	Dysderidae 32.67 %, p = 0.013	Agelenidae 21.46 %, p = 0.128
5	Chrysomelidae 26.39 %, p = 0.024	Heteroptera 25.12 %, p = 0.023	Gnaphosidae 30.92 %, p = 0.024	Lithobiomorpha 31.58 %, p = 0.004	Monotomidae 20.74 %, p = 0.050

Table 2. Mean activity densities (ind./day) and standard deviation (in parentheses) of ground-dwelling macro-invertebrates from montane meadows and mixed forests in South Tyrol, Italy. Family level data come from pitfall traps along linear transects from extensively managed hay meadows ('MM', 'M') across sharp and narrow ecotones ('E') towards mixed forest stands ('F', 'FF'). Abundances were standardised by dividing them by 31 (i.e. sampling days). Results of a negative binomial GLM and Tukey's HSD tests are given for significant differences (i.e. superscript letters). n = 9. A full list of the fauna can be found in Tab. B1, Appendix B.

[A]	'MM'	'M'	'E'	'F'	'FF'
GASTROPODA	**0.072** (0.113)	**0.018** (0.023)	**0.018** (0.036)	**0.108** (0.103)	**0.043** (0.046)
ARANEAE	**3.057** (1.757)[a]	**1.645** (0.732)[b]	**1.097** (0.413)[bc]	**0.864** (0.129)[c]	**0.717** (0.291)[c]
Dysderidae	**0.007** (0.014)[a]	**0.007** (0.014)[a]	**0.057** (0.070)[ab]	**0.075** (0.062)[b]	**0.032** (0.023)[a]
Linyphiidae	**0.211** (0.154)	**0.251** (0.237)	**0.330** (0.178)	**0.247** (0.129)	**0.211** (0.129)
Tetragnathidae	**1.487** (1.863)[a]	**0.204** (0.289)[ab]	– [ab]	**0.018** (0.054)[b]	**0.036** (0.108)[b]
Araneidae	–	–	**0.004** (0.011)	–	–
Lycosidae	**1.068** (0.544)[a]	**0.914** (0.641)[a]	**0.294** (0.284)[b]	**0.151** (0.141)[bc]	**0.061** (0.096)[c]
Pisauridae	**0.004** (0.011)	–	–	–	–
Miturgidae	–	**0.004** (0.011)	**0.004** (0.011)	**0.004** (0.011)	**0.004** (0.011)
Agelenidae	**0.004** (0.011)[a]	**0.032** (0.053)[ab]	**0.097** (0.088)[b]	**0.093** (0.071)[b]	**0.086** (0.101)[b]
Cybaeidae	**0.007** (0.014)[a]	**0.004** (0.011)[a]	**0.007** (0.022)[ab]	**0.004** (0.011)[ab]	–
Hahniidae	–	**0.004** (0.011)	–	–	–
Amaurobiidae	**0.036** (0.075)[ab]	**0.029** (0.063)[a]	**0.168** (0.190)[bc]	**0.215** (0.176)[c]	**0.251** (0.149)[c]
Clubionidae	**0.007** (0.014)	**0.004** (0.011)	**0.007** (0.014)	–	**0.004** (0.011)
Gnaphosidae	**0.029** (0.025)	**0.032** (0.046)	**0.115** (0.156)	**0.050** (0.061)	**0.022** (0.046)
Philodromidae	**0.043** (0.067)[a]	**0.050** (0.063)[ab]	**0.004** (0.011)[b]	– [ab]	– [ab]
Thomisidae	**0.154** (0.219)[a]	**0.111** (0.153)[a]	**0.011** (0.023)[b]	**0.011** (0.023)[b]	**0.007** (0.014)[b]
Salticidae	–	–	–	–	**0.004** (0.011)
OPILIONES	**0.004** (0.011)[a]	**0.186** (0.162)[b]	**0.247** (0.220)[b]	**0.165** (0.218)[b]	**0.165** (0.251)[b]
Nemastomatidae	–	–	**0.014** (0.023)	**0.018** (0.023)	**0.014** (0.033)
Phalangiidae	**0.004** (0.011)	**0.186** (0.162)	**0.229** (0.219)	**0.147** (0.226)	**0.143** (0.258)
Trogulidae	–	–	**0.004** (0.011)	–	–
Sclerosomatidae	–	–	–	–	**0.007** (0.014)
CHILOPODA	–	–	**0.029** (0.030)	**0.036** (0.030)	**0.014** (0.023)
Lithobiomorpha	–	–	**0.022** (0.016)	**0.032** (0.028)	**0.014** (0.023)
Geophilomorpha	–	–	**0.007** (0.022)	**0.004** (0.011)	–
DIPLOPODA	**0.011** (0.023)[a]	**0.014** (0.023)[a]	**0.093** (0.073)[b]	**0.090** (0.053)[b]	**0.086** (0.091)[b]
Julidae	**0.011** (0.023)[ac]	**0.007** (0.014)[a]	**0.086** (0.076)[b]	**0.036** (0.041)[ab]	**0.065** (0.068)[bc]
Blaniulidae	–	–	–	**0.004** (0.011)	–
Polyxenidae	–	**0.004** (0.011)	**0.007** (0.014)	**0.043** (0.048)	**0.014** (0.043)
Glomeridae	–	**0.004** (0.011)	–	**0.007** (0.014)	**0.007** (0.022)
ISOPODA (Oniscidea)	**0.014** (0.017)	**0.018** (0.028)	**0.036** (0.044)	**0.057** (0.039)	**0.025** (0.045)
Porcellionidae	– [a]	**0.004** (0.011)[a]	**0.014** (0.017)[a]	**0.029** (0.019)[b]	**0.014** (0.028)[a]
Oniscidae	–	–	**0.014** (0.033)	**0.014** (0.023)	**0.007** (0.014)
Ligiidae	**0.014** (0.017)	**0.014** (0.023)	**0.007** (0.014)	**0.014** (0.023)	**0.004** (0.011)

Table 2 continued.

[B]	'MM'	'M'	'E'	'F'	'FF'
COLEOPTERA	**0.466** (0.443)[a]	**0.509** (0.256)[ab]	**1.050** (0.608)[bc]	**1.147** (1.113)[c]	**0.785** (0.345)[abc]
Carabidae	**0.168** (0.244)	**0.237** (0.172)	**0.348** (0.261)	**0.351** (0.278)	**0.391** (0.242)
Silphidae	–	–	–	–	**0.004** (0.011)
Ptiliidae	–	–	–	**0.004** (0.011)	–
Staphylinidae	**0.147** (0.143)[ac]	**0.118** (0.136)[a]	**0.434** (0.447)[bc]	**0.552** (1.047)[b]	**0.143** (0.106)[a]
Pselaphidae	**0.004** (0.011)	–	**0.004** (0.011)	–	–
Cantharidae	–	–	**0.004** (0.011)	–	**0.007** (0.014)
Elateridae	–	**0.004** (0.011)	–	–	–
Buprestidae	**0.022** (0.046)	**0.007** (0.022)	–	–	–
Dryopidae	**0.007** (0.014)	**0.004** (0.011)	–	–	–
Byrrhidae	–	–	–	–	**0.007** (0.022)
Nitidulidae	**0.025** (0.035)	**0.047** (0.086	**0.014** (0.023)	**0.032** (0.051)	**0.025** (0.022)
Kateretidae	–	**0.004** (0.011)	–	–	–
Monotomidae	**0.011** (0.023)	**0.007** (0.014)	**0.014** (0.023)	**0.025** (0.039)	**0.050** (0.078)
Cryptophagidae	–	**0.004** (0.011)	**0.004** (0.011)	**0.011** (0.016)	**0.007** (0.014)
Latridiidae	– [ab]	**0.011** (0.023)[a]	**0.190** (0.264)[b]	**0.100** (0.143)[b]	**0.068** (0.050)[ab]
Zopheridae	–	–	–	**0.004** (0.011)	–
Ptinidae	–	**0.004** (0.011)	**0.025** (0.045)	**0.007** (0.014)	**0.004** 0.011)
Geotrupidae	–	**0.007** (0.022)	–	**0.004** (0.011)	–
Scarabaeidae	**0.004** (0.011)	–	–	**0.018** (0.054)	**0.025** (0.064)
Chrysomelidae	**0.068** (0.089)[a]	**0.050** (0.065)[a]	**0.004** (0.011)[a]	**0.007** (0.014)[a]	**0.014** (0.023)[a]
Brentidae	**0.004** (0.011)	–	–	–	–
Curculionidae	**0.007** (0.022)	**0.007** (0.022)	**0.011** (0.023)	**0.032** (0.048)	**0.039** (0.096)
COLEOPTERA L.	**0.022** (0.028)[ab]	**0.032** (0.046)[ab]	**0.118** (0.237)[a]	**0.032** (0.051)[ab]	**0.007** (0.014)[b]
Carabidae L.	–	**0.007** (0.022)	**0.004** (0.011)	**0.004** (0.011)	–
Staphylinidae L.	**0.011** (0.023)	**0.004** (0.011)	**0.104** (0.216)	**0.022** (0.053)	–
Lampyridae L.	–	**0.004** (0.011)	**0.004** (0.011)	–	–
Cantharidae L.	**0.011** (0.023)	**0.014** (0.028)	–	–	–
Curculionidae L.	–	**0.004** (0.011)	**0.004** (0.011)	–	**0.004** (0.011)
FORMICIDAE	**0.143** (0.194)[a]	**0.190** (0.173)[a]	**2.703** (2.916)[b]	**0.832** (2.132)[b]	**0.254** (0.704)[a]
HETEROPTERA	**0.007** (0.014)	**0.047** (0.076)	**0.022** (0.028)	**0.007** (0.022)	–
STERNORRHYNCHA	–	**0.004** (0.011)	**0.007** (0.022)	**0.004** (0.011)	**0.004** (0.011)
AUCHENORRHYNCHA	**0.233** (0.368)[a]	**0.165** (0.264)[a]	**0.047** (0.033)[ab]	**0.018** (0.043)[b]	**0.014** (0.023)[b]
DERMAPTERA	**0.014** (0.043)[ab]	**0.011** (0.016)[a]	**0.072** (0.060)[b]	**0.054** (0.048)[ab]	**0.047** (0.058)[ab]
LEPIDOPTERA L.	**0.025** (0.031)	**0.047** (0.054)	**0.072** (0.113)	**0.054** (0.048)	**0.082** (0.114)
CAELIFERA	**0.011** (0.023)	**0.004** (0.011)	**0.004** (0.011)	–	–
ENSIFERA	**0.004** (0.011)	**0.004** (0.011)	**0.014** (0.017)	**0.004** (0.011)	**0.007** (0.022)
Total fauna	**6.037** (2.189)[ab]	**4.307** (1.075)[ac]	**8.344** (4.553)[b]	**5.159** (4.397)[abc]	**3.328** (1.272)[c]

surface. This was confirmed by the accumulation curves, which show a well-covered sampling effort for spring with values exceeding 90 %. We were able to detect significant effects of these abrupt habitat shifts affecting the distribution and diversity patterns of several macro-invertebrate groups. By looking at three different taxonomic resolutions (total fauna, family, and species level), we were able to distinguish between different habitat effects at community and species level.

4.1 Patterns in macro-invertebrate communities

Our results revealed two well-separated faunal communities for the meadows and the forests, and the community of the narrow ecotone lines clustering with the forests. This separation was mainly driven by two major animal groups: Araneae were highly active and predominant in the meadows, while saprophagous Diplopoda and Isopoda were mainly found in the ecotones and forests (Figs 3 and 4).

For example, spider specimens of Tetragnathidae (all individuals belonging to the species *Pachygnatha degeeri* Sundevall, 1830) were abundant indicator species in the meadows which prefers low vegetation habitats and is characteristic spider of xeric fields, meadows, but also forests (Heimer & Nentwig 1991). Another dominant family in the meadows were Lycosidae (i.e. the mainly diurnal genera *Alopecosa*, *Pardosa*, and *Trochosa*), which hunt in the low vegetation and herb layers. These surface-living predators were also the dominant Araneae family in a related study covering the same sampling plots (Plunger et al. 2022). In general, mountain grasslands have been shown to support a high diversity of Araneae (Lessard-Therrien et al. 2018), and rare and specialist species (Hilpold et al. 2018). We were able to confirm this in our case study as we found the highest proportion of threatened Red List species of spiders and ants in the 'M' meadow plots (Fig. A5).

Most Diplopoda as well as terrestrial Isopoda (i.e. Oniscidea) are classified as detritivores that feed on and process litter and other dead organic material (Hauser & Voigtländer 2019, Potapov et al. 2022) and are therefore
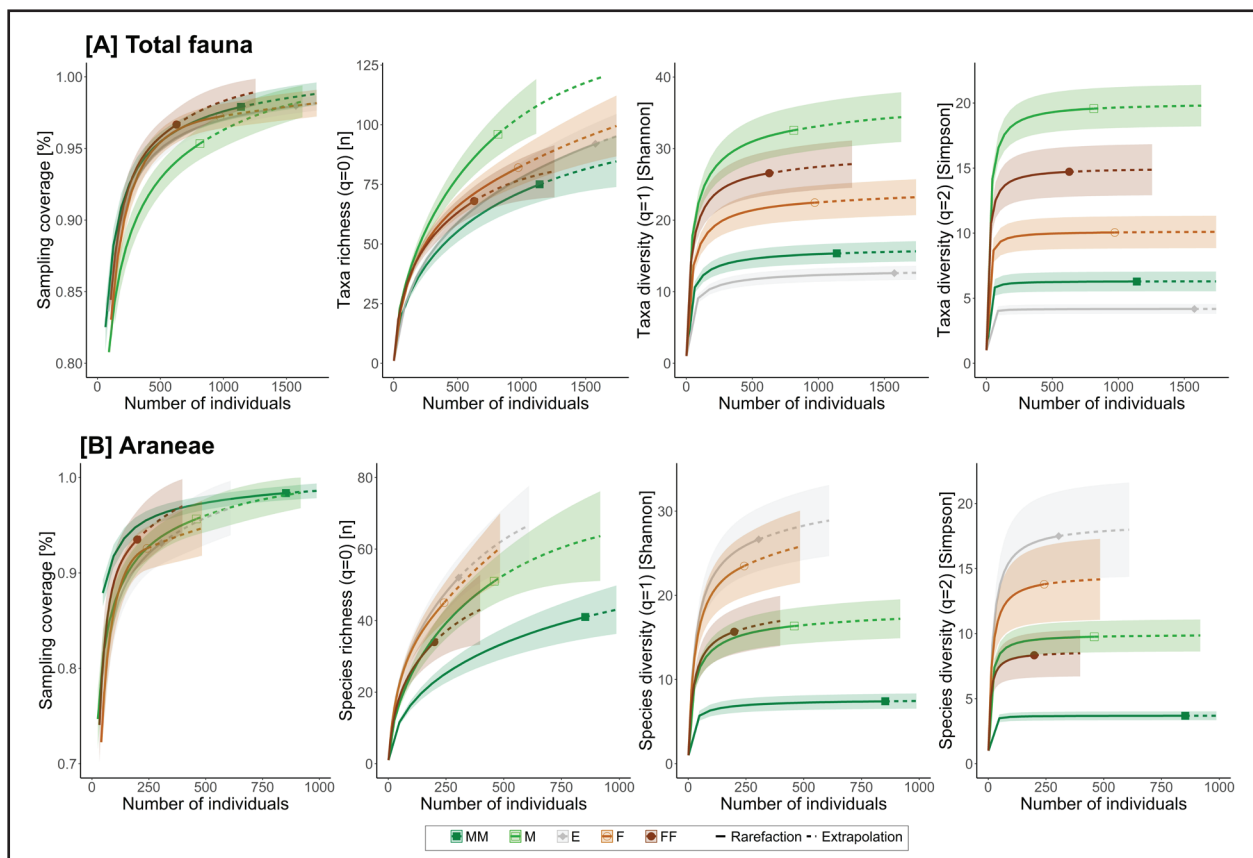

Figure 4. Abundance-based accumulation curves for ground-dwelling macro-invertebrates from montane meadows and mixed forests in South Tyrol, Italy. The data come from pitfall traps along a linear transect from extensively managed hay meadows ('MM' and 'M', squares) across an abrupt ecotone ('E', diamonds) towards mixed forest stands ('F' and 'FF', circles). The curves show from left to right: the sampling coverage, taxa and species richness (Hill number q = 0), Shannon (q = 1) and Simpson diversity (q = 2). Plot [**A**] shows the total faunal community data at the highest taxonomic resolution, plot [**B**] the Araneae data at species level.

typical forest floor taxa. Recent studies from Europe have found that mixed stands (i.e. of broadleaved and coniferous species) – similar to the forest plots in our study here – provide a wide variety of food sources and can therefore support a higher and broader detritivore community than pure deciduous and conifer stands (Ganault et al. 2021, David et al. 2023). Mixed forests are characterised by a high humidity and a thick litter layer composed of several leaf types, which creates multiple ecological niches compared to more dry meadows with little or no litter layer. De Smedt et al. (2016) found that such dry conditions make meadows unfavourable for these decomposer groups due to a low desiccation tolerance (though being species-specific), which was confirmed in our study (see Fig. 3 and Tab. 2). In a previous study comparing subalpine grasslands with coniferous forests, we found similar results for the soil fauna, where Diplopoda were highly abundant in relatively open European Larch (*Larix decidua*) stands, but were scarce in extensively grazed dry pastures and even absent in intensively managed hay meadows (Damisch et al. 2020).

Coleoptera are a highly diverse insect order that includes a variety of habitat preferences and functional groups (e.g. predators, detritivores, and herbivores, Potapov et al. 2022). In our study, they were significantly more abundant in the ecotones and forest edges, but were present in high numbers in all five plots; specimens of the agile Staphylinidae and Carabidae families dominated and were found in almost all 45 pitfall trap samples. These two abundant Coleoptera families were also among the indicator taxa for the ecotones and forests (Tab. 2), indicating a preference for wetter and heterogeneous habitats with a distinct litter layer that can host prey and detritus as food sources. However, we believe that we detected only minor differences between the habitats due to the rather low taxonomic resolution for Coleoptera (i.e. family level), and would expect clearer preferences when using species level for this species-rich and heterogenous order (as shown for Araneae).

4.2 Habitat-specific drivers

Deciduous (and mixed) forests and extensively managed meadows have become rare in South Tyrol (as in many other regions of the European Alps). Our study highlights the importance of such semi-natural and low-input/low-impact habitat types – which are considered to be of high cultural and agronomic value – in supporting and preserving diverse ground-dwelling macro-invertebrate communities (e.g. Guariento et al. 2020, Hilpold et al. 2018). Diversity is crucial for maintaining essential (soil) ecosystem functions such as the decomposition of dead organic matter (Diplopoda, Isopoda) and the top-down control of herbivores (Araneae, Lithobiomorpha, several Coleoptera), which in turn can directly and indirectly influence plant performance and competition, and thus the plant community composition in grasslands (Perner et al. 2005, Eisenhauer et al. 2011).

Boundaries and field margins between two different habitats or successional stages are characterised by strong biotic and abiotic gradients and have been reported to support a high diversity of ground-dwelling invertebrates due to greater structural heterogeneity (Lövei et al. 2006, Ewers & Didham 2008, Marshall & Moonen 2002). Therefore, we expected that our forest–grassland ecotones – even though they are narrow – to be highly diverse plots, as it has been shown, for example, for grasshoppers at grassland edges, where they seek shelter from mowing (Rada et al. 2014, Schwarz et al. 2023), but not for millipedes (Bogyó et al. 2015). However, our narrow forest–grassland ecotones did not support an exceptionally high invertebrate diversity, most likely due to the lack of a true broad transition zone with an abundant shrub layer. Therefore, we do not expect such sharp ecotone areas and shifts between forests and grasslands to act as an effective spill-over zone in times of disturbance (e.g. mowing of the grassland) and would not necessarily have a positive impact on local biodiversity.

5.   Conclusions

Mountains are considered as biodiversity hotspots, but their rugged topography limits the amount of land available for agriculture, increasing land-use conflicts and the pressure for efficient use. In our study area of South Tyrol, this has often led to sharp and narrow habitat shifts from, for example, extensively managed meadows to mixed and coniferous forests. Here we show that such narrow shrub-free ecotones clearly separate ground-dwelling macro-invertebrate communities. Both meadow and forest habitats – even if shaped by human activities – support a high invertebrate diversity, with mixed forests (and in our case also the similar ecotone lines) supporting a particularly high number of taxa (i.e. Diplopoda, Isopoda, partly Coleoptera), whereas the meadows support a higher proportion of threatened Red List species (i.e. Araneae, Hemiptera). Therefore, both extensively managed habitat types should be specifically promoted by farmers and policy makers for their high conservation value.

However, our ecotone communities clearly resembled forest communities and did not form a mixed and intermediate community as would be expected in a

broad transition zone, and therefore did not enrich local biodiversity by providing additional ecological niches. The lack of such a buffering shrub strip, as would be present in a gradual transition between grasslands and forests (i.e. field margins) where more land is available, may impede the movement of ground-dwelling macro-invertebrates between the habitat types, especially when seeking shelter during management activities (e.g. mowing, logging). Our results will help local and regional decision-makers to update their mountain grassland and forest management plans to include more sustainable and biodiversity-supportive recommendations such as the inclusion of buffering shrub strips. Our results are also useful for rugged mountain regions and elsewhere, where agricultural land is limited but necessary. Agricultural land use, in addition to generating economic income, could considerably contribute to the restoration and preservation of semi-natural habitats that support a diverse above-ground wildlife and thus ensure ecosystem functioning (Watts & Jump 2022).

6.   Supplementary online material

Appendix A
Figure A1: Additional photos of the study area of Barbian/ Barbiano, South Tyrol (Italy).
Figure A2: DCA plot of log-transformed ground-dwelling macro-invertebrate abundances at family level.
Figure A3: Overview of indicator taxa of ground-dwelling macro-invertebrate abundances at family level.
Figure A4: Abundance-based accumulation curves for ground-dwelling macro-invertebrates at family level.
Figure A5: Proportion of Red List status of Araneae and Formicidae species.
Table A1: Results of PERMANOVAs of the five ground-dwelling macro-invertebrate communities.
Table A2: Results of diversity indices at different taxonomic levels.

Appendix B
Table B1: Full table of the fauna activity densities (absolute and standardised as ind./day).
Table B2: Full table of the plant species from the extensively managed meadows.

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9.   Author Contributions

Conceptualisation, J. S., H. B., J. P. and M. S.; Methodology, J. S., H. B., J. P. and M. S.; Validation, H. B., J. P. and M. S..; Formal Analysis, M. S.; Investigation, H. B.; Resources, H. B.; Data Curation, H. B., J. P. and M. S.; Writing – Original Draft Preparation, M. S., J. S., J. P. and H. B.; Writing – Review & Editing, M. S., J. S., J. P. and H. B.; Visualisation, M. S.; Supervision, J. S. and M. S.; Project Administration, J. S.

10. Conflicts Of Interests

The authors declare no conflicts of interests.

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