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Soil Macroinvertebrate Distribution Along a Subalpine Land Use Transect

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Little is known about the complex processes within the soil ecosystem and especially about soil animals and their role in supporting and sustaining ecosystem functioning in alpine soils. Currently, environmental and socioeconomic changes, such as climate change and the cessation of traditional cultivation, are influencing mountain ecosystems. Epi- and endogeic animals play an essential role in litter decomposition, humus formation, and pedogenesis and in improving resistance to natural hazards. Therefore, knowledge about the diversity of soil macroinvertebrates is of immediate importance. To test the effect of different management techniques on soil macroinvertebrates, we took 144 soil monoliths from 4 different land use types (with 3 replicates each) in a subalpine area. The land use types were (1) extensively grazed dry pastures, (2) intensively used hay meadows, (3) larch forests, and (4) spruce forests. All sites were comparable in terms of bedrock and exposition. Additionally, we measured pH, organic matter content, and C and N content, as well as soil temperature and soil moisture. We found the highest abundances of macroinvertebrates on the intensively used hay meadows, followed by larch forests, spruce forests, and dry pastures. Diptera larvae and Lumbricidae were predominant in hay meadows, while we found the highest number of Coleoptera larvae, Araneae, and Symphyla in larch forests. In comparison to the other land use types, the dry pastures harbored the most Gastropoda individuals. No unique taxa were observed in the spruce forests. At species level, larch forests had the highest number of species (73), followed by hay meadows (44), spruce forests (42), and dry pasture (36). Despite showing lower biodiversity, we found more rare and specialist species in the extensive dry pastures compared to the more generalist species assemblages in the other habitats, supporting the high conservation value of extensively managed alpine landscapes.

Keywords: *climate change; European Alps; LTSER; soil biodiversity; South Tyrol; traditional low-input land use.*

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Introduction

A main characteristic of the European Alps is their subalpine pasturelands. These landscapes, which can often be considered as seminatural grasslands (Dengler et al 2014; Hilpold, Tasser, et al 2018), are highly interesting to farmers and tourists (Schirpke et al 2013). They provide important ecosystem services, such as erosion prevention, carbon storage and sequestration, water purification, and many others (Villoslada Peciña et al 2019). Few people are aware of the fact that these scenic landscapes exist only because of human activities (often grazing and low-input farming over several centuries; Simonneau et al 2013; Steinwandter 2019). However, the agricultural landscapes in the Central European Alps are in a state of change, not only because of external influences, such as climate change (Dellar et al 2018), but also because of intensification and abandonment of subalpine grassland, which have significantly increased since the postwar decades (Mottet et al 2006; Tasser et al 2007; Niedrist et al 2009; Graf et al 2014; Egarter Vigl et al 2016).

In general, intensification and abandonment were found to reduce biodiversity, but how these land use changes will affect the complex processes within the alpine soil ecosystem and their inhabitants has rarely been studied (Tsiafouli et al 2015; Steinwandter et al 2017; Hilpold, Seeber, et al 2018; Montagna et al 2018). Epi- and endogeic animals have adapted over centuries to this traditional low-input management (Spehn et al 2006) and play essential roles in ecosystem processes, such as litter decomposition, humus formation (Seeber and Seeber 2005), pedogenesis, and resistance to natural and human-made hazards like soil erosion, the last through positive effects on soil stability (Lavelle et al 2006). Therefore, knowledge of the diversity and functionality of the soil macroinvertebrates is of immediate importance.

Little is known about soil macroinvertebrates in subalpine ecosystems, the complex processes they contribute to, and the role they play in supporting and sustaining ecosystem functioning (Decaëns 2010; Hiiesalu et al 2012). Additionally, the effects of ongoing land use changes on soils and their faunal inhabitants are not yet fully understood (Rikhari et al 1993; Seeber et al 2005; Seeber and Seeber 2005). A few studies have shown differences in the abundances of soil invertebrates between meadows and pastures, as well as between different forest types (Salmon et al 2006; Negro et al 2010; Wang et al 2018). Compared to intensively managed meadows, which are dominated by earthworms and have high abundances of dipteran larvae, extensively managed pastures were found to have lower mean abundances of soil macroinvertebrates but had more rare and specialist species (Steinwandter et al 2017; Hilpold, Seeber, et al 2018). In alpine coniferous forests, taxa such as myriapods (mainly centipedes) and dipteran larvae are abundant, while earthworms show relatively low numbers, mainly due to the unfavorable soil conditions (thick litter layer of conifer needles; Schneider et al 2019). However, management measures, such as regular fertilization and mowing, irrigation, plowing, or reforestation after abandonment, might have more profound consequences on soils in montane and subalpine regions than in the valley bottom. For example, decreases in below- and aboveground biodiversity resulting from land use changes increase soil erosion and surface runoff and cause higher risks of avalanches and other natural hazards (Tasser et al 2003; Spehn et al 2006; Steinwandter et al 2017; Orgiazzi and Panagos 2018).

In a case study area in the Central European Alps (Matsch Valley, South Tyrol, Italy), we identified soil macroinvertebrates from 4 land use types representative of the subalpine region—grazed dry pastures, intensively used hay meadows, larch forests, and spruce forests—to assess the effect of different management practices on soil macroinvertebrate communities in subalpine grasslands. The European Union gave high priority to the conservation of low-input grasslands by including them in the Habitat Directive (European Commission 1992; Hilpold, Seeber, et al 2018), and the Aichi Targets also focused on preserving subalpine areas (CBD 2018; Institute for Biodiversity 2019). Here, we focus on soil macroinvertebrates to answer the question of how management affects belowground biodiversity. We expected profound differences in community composition and species richness between habitats depending on the land use. In particular, we expected lower species numbers in hay meadow soils compared to the 3 other habitats, due to intensive management. We also expected higher species numbers and a more diverse soil invertebrate community in larch forests, which are a successional stage after abandonment of formerly managed grasslands, while spruce forests as a climax stage with very specific soil characteristics (eg high amount of litter material, low pH values) were expected to harbor fewer soil macroinvertebrate species. The results of our study will be a basis for further studies of the effect of land use changes on (sub)alpine grasslands and will be an important contribution to recommendations on sustainable agricultural practices in these sensitive alpine landscapes.

Materials and methods

Compliance with ethical standards

Eurac Research has a general permit to conduct scientific research in the Val Mazia/Matschertal LTSER (Long-Term Socio-Ecological Research) area. The study design was carefully planned to ensure that no populations of soil macroinvertebrates were endangered.

Study area

The study sites at Muntatschinig/Montescino belong to the Val Mazia/Matschertal LTSER area, which is located in a side valley of the Vinschgau/Val Venosta in South Tyrol, Italy (Figure 1, site code IT25 and LTER_EU_IT_097; 46.6840°N, 10.5860°E; DEIMS.iD: https://deims.org/11696de6-0ab9-4c94-a06b-7ce40f56c964). It is located in the south of the Central Eastern Alps and has a subcontinental climate with a mean annual precipitation of 525 mm and an air temperature ranging between −15.29°C and +27.79°C (at 1500 masl; Hilpold, Seeber, et al 2018; *Supplemental material*, Appendix S1: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1), thus representing one of the driest valleys in the Alps. We selected 4 different land use types with 3 replicates each at an elevation of 1500 m within a study area of approximately 1.50 km^2 (Figure 1). These were (1) extensively grazed dry pastures (P1–P3), (2) intensively used (ie fertilized and irrigated) hay meadows (H1–H3), (3) larch forests (*Larix decidua* Mill., L1–L3), and (4) spruce forests (*Picea abies* (L.) H.Karst., S1–S3). For more details see Hilpold, Seeber, et al (2018).

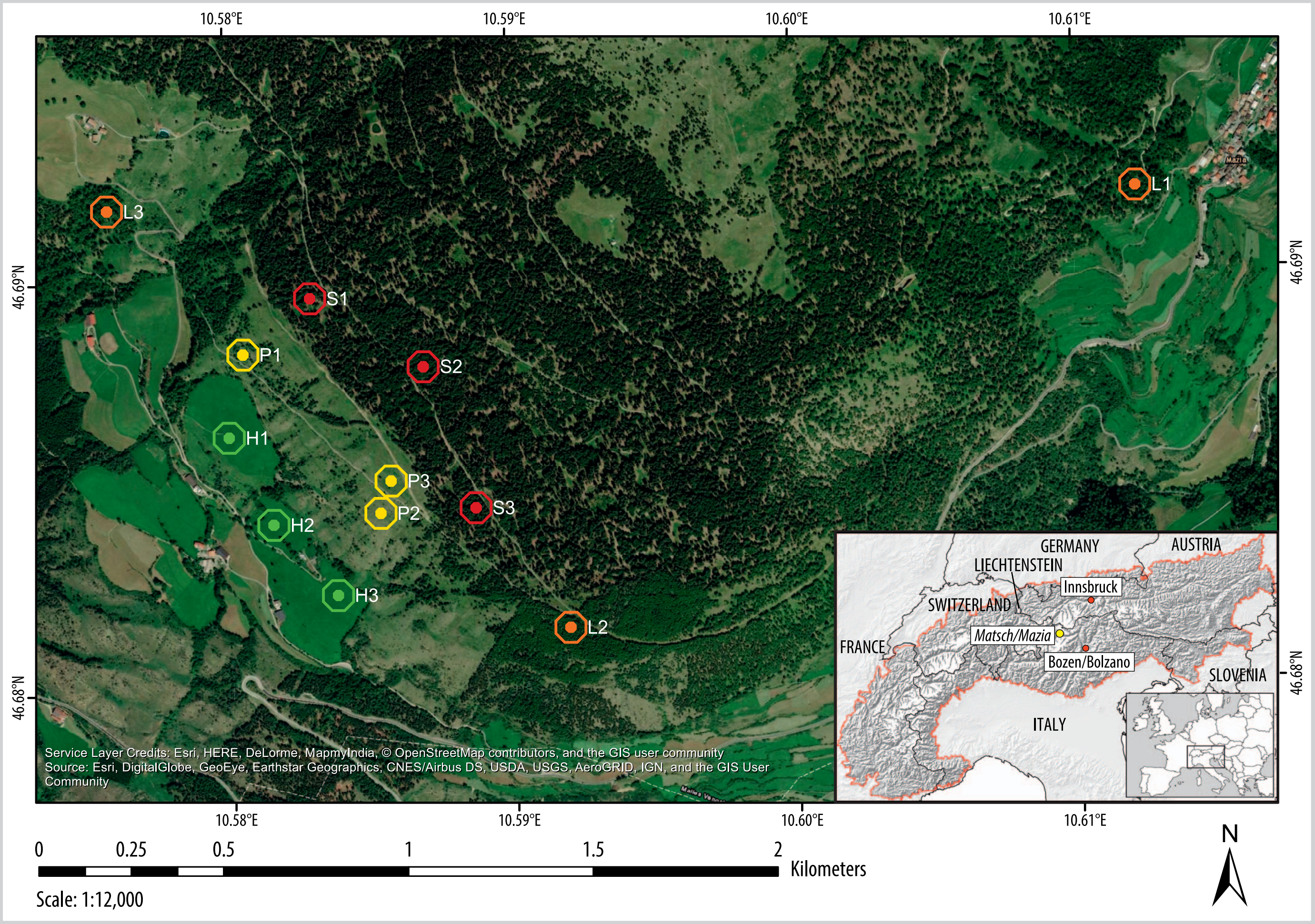
In short, the hay meadows belong to the alliance of Trisetetum flavescentis, the dry pastures as Sub-Pannonian steppic habitats are part of the EU Habitats Directive (code 6240*), the larch forests were afforested and are successional stages of montane mixed forests (Larici-Piceetum), and the spruce forests are part of the Directive habitat 9410 Acidophilous Picea forests of the montane to alpine levels (Vaccinio-Piceetea) (European Commission 2007). All sites are comparable in terms of bedrock, which belongs to the Matsch Nappe (biotite-rich crystalline schists, paragneiss, phyllite, and phyllonite (Geographie Innsbruck 2019), inclination, and exposition (Tables 1, 2).

Soil macroinvertebrates

To account for seasonal variations in soil macroinvertebrate distribution, we took soil monolith samples at 4 sampling dates from April to October 2016 (in total 144). The specific sampling dates were (1) 18 April 2016, (2) 16 June 2016, (3) 10 August 2016, and (4) 19 October 2016. From each of the 12 plots, we took soil monoliths (20 × 20 × 15 cm, if the depth of the soil allowed) randomly with a minimum distance of 5 m between any two. Before taking the soil monoliths, the plant cover was cut to 1 cm. On the same day, the 36 soil monoliths were transferred to cotton bags and taken to the soil laboratory. They underwent heat extraction for 12 days using a modified Kempson extractor (Kempson et al 1963), starting with 50% light and heat intensity for the first 6 days, which was then continuously increased to 100%. The animals were collected in propylene glycol and stored in 75% ethanol in urine cups until identification using a stereomicroscope (M205c, Leica Microsystems, Wetzlar, Germany).

Adult specimens of macroinvertebrates (>2 mm) were determined, if possible, to species level using the following identification keys: for Lumbricidae, Christian and Zicsi (1999); Coleoptera, Freude et al (1999); Staphylinidae, Assing and Schülke (2012); Araneae, Nentwig et al (2019), Diptera larvae, Smith (1989); for all other taxa, we followed Schaefer (2018). Taking soil samples is a destructive method; however, to minimize impact on the sensitive alpine habitats, the desiccated soil monoliths were taken back to the study sites.

FIGURE 1 Aerial photograph of the study area at Muntatschinig/Montescino belonging to the Val Mazia/Matschertal LTSER area. P1–P3, dry pastures; H1–H3, intensively used hay meadows; L1–L3, larch forests; and S1–S3, spruce forests.



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Site and soil parameters

From each site, at each sampling date, we took additional soil samples to analyze soil properties (Tables 1, 2; *Supplemental material*, Appendix S2: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1). These samples were air-dried for 1 week at room temperature before being sieved to 2 mm. The pH was determined by dissolving 20 mL soil in 50 mL 0.1 M $CaCl_2$ solution, stirring it for 2 hours, and then measuring with a pH multimeter (HI2020 edge, Hanna Instruments, Woonsocket, Rhode Island).

To determine the soil organic matter (SOM) content, the soil samples were dried for 24 hours at 105°C in a drying chamber (BD 240, Binder, Tuttlingen, Germany). Afterwards, they were weighed and combusted at 440°C for 4 hours in a muffle furnace (Carbolite ELF1114, Carbolite, Hope Valley, United Kingdom) and weighed again to calculate the SOM (ie the percentage of the organic compounds that were combusted). For the total C and N content, oven-dried soil material was powdered in a ball mill (Pulverisette 0, Fritsch, Idar-Oberstein, Germany). The total C and N content was determined in an organic element analyzer (TruSpec® CHN, Leco, St. Joseph, Michigan); the C:N ratio was then calculated.

Furthermore, at each plot at each sampling date, we recorded the soil moisture and temperature, coordinates, inclination, exposition, and elevation. Soil moisture was measured as volumetric soil content (percentage and μS) using a water-content sensor (HydroSenseII, Campbell Scientific, Logan, Utah) and soil temperature with a thermistor sensor (ML3 ThetaProbe, Delta-T Devices, Cambridge, United Kingdom). We are aware that soil temperature and soil moisture were only point measurements at the single sampling dates; however, we believe the mean values and standard deviations of these 4 measurements per plot are well representative for the respective land use types.

Statistical analyses

All statistical calculations were conducted in the open-source statistical programming language R (version 3.6.0, R Core Team 2019) in RStudio (version 1.2.1335, RStudio Team 2019). Differences in soil parameters between land use types were calculated using one-way analyses of variance (ANOVAs) followed by Tukey's honest significant difference (HSD) post-hoc tests. The Shannon–Wiener index was calculated using the *diversity* function in the R package VEGAN (version 2.5-6; Oksanen et al 2019), and differences in Shannon–Wiener diversity between habitats and between sampling dates were calculated with a factorial ANOVA followed by Tukey's HSD post-hoc tests. The effect of

TABLE 1 Characteristics and soil parameters of 4 alpine habitats differing in land use: mean (SD) values of the study sites (ie of 36 replicate plots). The last row shows F and *P* values of the ANOVA analyzing differences between land use types.

Site ID ($n = 36$)	El (m)	Ex (°)	In (°)	Soil moist (% I/WC)	Soil temp (°C at 5 cm)	pH	SOM (%)	C:N
P	1546	232.5	17	26.33 (1.99) ^{a}	15.93 (0.46) ^{a}	5.37 (0.05) ^{a}	7.60 (0.38) ^{a}	14.28 (0.80) ^{a}
H	1444	225.0	13	36.22 (1.14) ^{b}	13.56 (0.53) ^{b}	5.82 (0.07) ^{b}	14.08 (0.39) ^{bc}	10.68 (0.15) ^{b}
L	1595	187.5	18	19.19 (2.04) ^{c}	9.68 (0.37) ^{c}	4.99 (0.06) ^{c}	10.41 (0.62) ^{ab}	17.96 (0.45) ^{c}
S	1645	225.0	25	10.77 (1.52) ^{d}	8.32 (0.32) ^{c}	4.16 (0.11) ^{d}	18.04 (2.18) ^{c}	25.91 (0.96) ^{d}
$F_{3,139}$				40.13				
$F_{3,140}$					66.38	85.87	15.20	95.37
P				<0.001	<0.001	<0.001	<0.001	<0.001

Superscript letters indicate significant differences between land use types based on Tukey's HSD post-hoc tests at significance level $P < 0.05$.
El, elevation; Ex, exposition; In, inclination; moist, moisture; temp, temperature; SOM, soil organic matter; C, carbon; N, nitrogen; P, dry pastures; H, hay meadows; L, larch forests; S, spruce forests.

environmental factors on Shannon–Wiener diversity was evaluated by linear mixed effects models with habitat as a random effect and using the R package lme4 (Bates et al 2015). The community–environment relationship was analyzed with canonical correspondence analysis (CCA) using the vegan package. Taxa with very low abundances of <10 individuals in all samples of the 4 dates ($n = 144$) were excluded from all analyses; data were log-transformed to account for high abundances of Diptera larvae. The significance of environmental parameters in the CCA was assessed using permutation tests implemented in the vegan package. Nonsignificant parameters were excluded from the analysis in a second step. Differences of community composition between habitats was tested with a PERMANOVA using the *adonis* function in vegan.

Results

For the 4 land use types we identified a total of 6754 individuals of soil macroinvertebrates belonging to 77 families and 145 species (Table 3; see Appendix S3 for the full species list and Appendix S4 for the seasonal development of taxa, both in *Supplemental material*: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1). Representatives of the class Insecta with 56 families showed the highest individual numbers (4111, ie 60.87%), followed by Myriapoda (991, in 7 families, 14.67%), Oligochaeta (822,

TABLE 2 Characteristics and soil parameters of 4 alpine habitats differing in land use: mean (SD) values of the study sites along the year-long sampling period.

Plot ID ($n = 12$)	Date	Soil moist (% I/WC)	Soil temp (°C at 5 cm)	pH	SOM (%)	C:N
P	Apr	29.01 (6.02)	14.87 (0.64)	5.38 (0.16)	8.87 (2.03)	13.66 (1.94)
	Jun	37.90 (6.29)	15.40 (0.94)	5.12 (0.29)	7.58 (2.26)	12.74 (1.68)
	Aug	28.54 (7.92)	20.22 (1.16)	5.64 (0.16)	6.69 (0.94)	13.35 (0.76)
	Oct	9.88 (3.76)	13.22 (0.50)	5.36 (0.26)	7.27 (0.94)	13.20 (0.70)
H	Apr	37.73 (5.64)	11.86 (1.03)	5.56 (0.30)	13.42 (1.19)	10.99 (0.23)
	Jun	36.46 (5.76)	13.12 (2.97)	5.98 (0.25)	16.04 (1.59)	11.09 (0.60)
	Aug	40.63 (5.54)	18.08 (1.38)	6.19 (0.19)	13.94 (1.02)	10.46 (0.38)
	Oct	30.06 (6.34)	11.19 (0.58)	5.56 (0.12)	12.90 (1.81)	10.18 (0.43)
L	Apr	20.08 (13.10)	7.47 (1.10)	4.92 (0.17)	10.30 (4.25)	19.81 (2.54)
	Jun	32.80 (4.80)	10.26 (0.99)	4.93 (0.22)	9.15 (3.33)	18.22 (2.11)
	Aug	18.10 (6.84)	12.68 (1.03)	5.42 (0.30)	10.98 (2.11)	18.62 (1.40)
	Oct	6.48 (2.53)	8.30 (0.69)	4.67 (0.27)	11.20 (3.41)	15.19 (0.93)
S	Apr	6.20 (2.18)	5.96 (0.59)	4.29 (0.27)	16.30 (5.94)	29.37 (5.09)
	Jun	20.09 (11.20)	9.86 (1.04)	4.21 (0.38)	27.11 (17.81)	28.24 (3.25)
	Aug	13.13 (7.03)	10.22 (0.40)	4.75 (0.48)	20.53 (9.38)	25.80 (2.01)
	Oct	3.67 (1.61)	7.24 (0.35)	3.40 (0.27)	8.22 (2.40)	20.22 (3.81)

moist, moisture; temp, temperature; SOM, soil organic matter; C, carbon; N, nitrogen; P, dry pastures; H, hay meadows; L, larch forests; S, spruce forests.

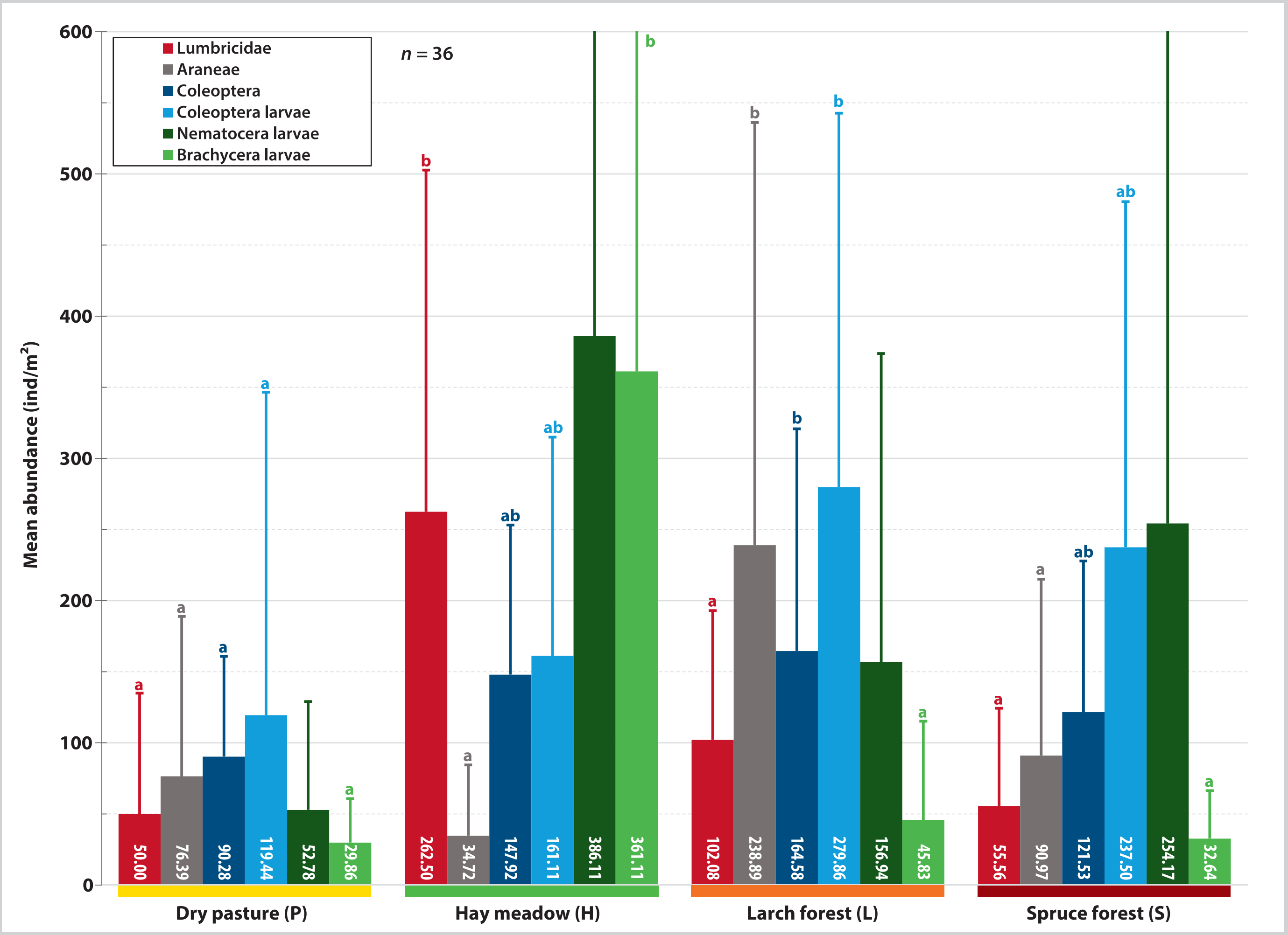
TABLE 3 Mean (SD) abundances as individuals per square meter (A) and values of the Shannon-Wiener index (B) of representative soil macroinvertebrates from 4 alpine habitats differing in land use.

(A) Species, individuals/m^2	P	H	L	S	$F_{3,32}$	P
Gastropoda	47.22 (69.64) ^{a}	11.11 (15.17) ^{b}	32.64 (52.04) ^{ab}	12.50 (27.71) ^{b}	5.04	0.002
Lumbricidae	50.00 (84.94) ^{a}	262.50 (240.20) ^{b}	102.08 (90.90) ^{a}	55.56 (68.69) ^{a}	18.28	>0.001
Chilopoda	13.19 (29.57)	25.00 (70.96)	56.25 (75.45)	42.36 (92.16)	2.58	0.056
Diplopoda	– ^{a}	1.39 (5.81) ^{b}	77.08 (102.53) ^{c}	47.22 (96.69) ^{c}	7.89	0.001
Symphyla	161.81 (276.68) ^{ac}	22.92 (56.81) ^{b}	202.08 (304.28) ^{c}	38.89 (110.91) ^{ab}	6.17	0.001
Araneae	76.39 (112.43) ^{a}	34.72 (49.74) ^{a}	238.89 (297.22) ^{b}	90.97 (124.09) ^{a}	9.60	>0.001
Linyphiidae	52.78 (79.68) ^{a}	27.78 (46.97) ^{a}	231.25 (292.91) ^{b}	89.58 (121.06) ^{a}	10.91	>0.001
Lycosidae	6.25 (21.86)	6.94 (12.83)	2.78 (9.96)	—	0.73	0.486
Gnaphosidae	9.72 (23.36) ^{a}	— ^{ab}	1.39 (5.81) ^{c}	0.69 (4.17) ^{c}	4.57	0.013
Araneae rest	7.64 (26.61)	—	3.47 (12.18)	0.69 (4.17)	1.51	0.226
Coleoptera	90.28 (70.53) ^{a}	147.92 (105.28) ^{ab}	164.58 (156.22) ^{b}	121.53 (106.26) ^{ab}	2.93	0.036
Carabidae	9.72 (16.12) ^{ab}	20.83 (26.39) ^{a}	15.28 (34.47) ^{ab}	4.17 (12.68) ^{b}	3.21	0.025
Staphylinidae	38.89 (44.50) ^{a}	98.61 (78.59) ^{b}	94.44 (81.53) ^{b}	101.39 (92.96) ^{b}	5.44	0.001
Curculionidae	30.56 (31.69) ^{a}	5.56 (12.12) ^{b}	16.67 (26.73) ^{ab}	11.81 (26.38) ^{b}	6.35	>0.001
Coleoptera rest	11.11 (30.73)	22.92 (41.57)	38.19 (134.76)	4.17 (12.68)	1.52	0.211
Coleoptera larvae	119.44 (227.10) ^{a}	161.11 (153.81) ^{ab}	279.86 (262.87) ^{b}	237.50 (242.94) ^{ab}	3.73	0.013
Carabidae larvae	2.08 (7.01)	6.94 (22.84)	11.81 (46.48)	11.11 (31.31)	0.78	0.507
Staphylinidae larvae	37.50 (54.94)	102.78 (136.9)	62.50 (62.54)	67.36 (119.94)	2.60	0.055
Cantharidae larvae	1.39 (5.81) ^{a}	10.42 (16.23) ^{a}	140.28 (174.98) ^{b}	102.08 (147.16) ^{b}	12.84	>0.001
Elateridae larvae	1.39 (5.81) ^{a}	7.64 (16.71) ^{ab}	13.89 (46.46) ^{ab}	33.33 (81.72) ^{b}	3.01	0.032
Tenebrionidae larvae	57.64 (198.01)	—	5.56 (33.33)	12.50 (26.39)	2.11	0.127
Curculionidae larvae	8.33 (26.05)	25.00 (47.43)	18.06 (51.62)	2.08 (9.21)	2.62	0.053
Coleoptera larvae rest	11.11 (19.31)	8.33 (27.39)	27.78 (63.18)	9.03 (22.48)	2.18	0.093
Nematocera larvae	52.78 (76.25)	386.11 (389.07)	156.94 (216.76)	254.17 (1150.97)	1.90	0.133
Brachycera larvae	29.86 (30.95) ^{a}	361.11 (295.53) ^{b}	45.83 (69.31) ^{a}	32.64 (33.71) ^{a}	40.43	>0.001
(B) Month, Shannon-Wiener index						
April	1.48 (0.45)	1.68 (0.27)	1.69 (0.59)	1.26 (0.58)	1.51	0.231
June	1.53 (0.53)	2.05 (0.39)	1.94 (0.39)	1.55 (0.67)	2.50	0.077
August	1.83 (0.43) ^{a}	2.10 (0.38) ^{ab}	2.32 (0.26) ^{b}	2.10 (0.26) ^{ab}	3.21	0.036
October	1.88 (0.29) ^{a}	1.90 (0.32) ^{a}	2.41 (0.24) ^{b}	2.11 (0.26) ^{ab}	7.06	0.001
Overall	1.68 (0.45) ^{a}	1.92 (0.37) ^{ab}	2.09 (0.48) ^{b}	1.76 (0.59) ^{a}	5.31	0.002

The abundance values represent yearly means ($n = 36$). Results from ANOVA and Tukey's HSD post-hoc tests between the four habitat types are given; superscript letters represent significant differences at $P = 0.05$.
P, dry pastures; H, hay meadows; L, larch forests; S, spruce forests.

in 2 families, 12.75%), Arachnida (681, in 11 families, 10.08%), and Gastropoda (149, 2.21%). In total, we were able to identify 1008 adult individuals to species level and a further 517 to genus level. The highest mean annual soil macroinvertebrate abundance with 1518.75 individuals per m^2 was recorded for the intensively used hay meadows, followed by larch forests (1495.14 ind/m^2), spruce forests (947.92 ind/m^2), and dry pastures (736.81 ind/m^2). At species level, larch forests had the highest number (73), followed by hay meadows with 44 species, spruce forests with 42 species, and dry pasture with 36 species. Shannon–Wiener diversity was significantly higher in the larch forests ($F_{3,140} = 5.31$,

FIGURE 2 Mean abundances and standard deviations (in parentheses) of 6 soil macroinvertebrate groups from 4 alpine habitats differing in land use. Letters indicate significant differences of each taxa between land use types based on Tukey's HSD post-hoc tests at significance level $P < 0.05$, n = 36.



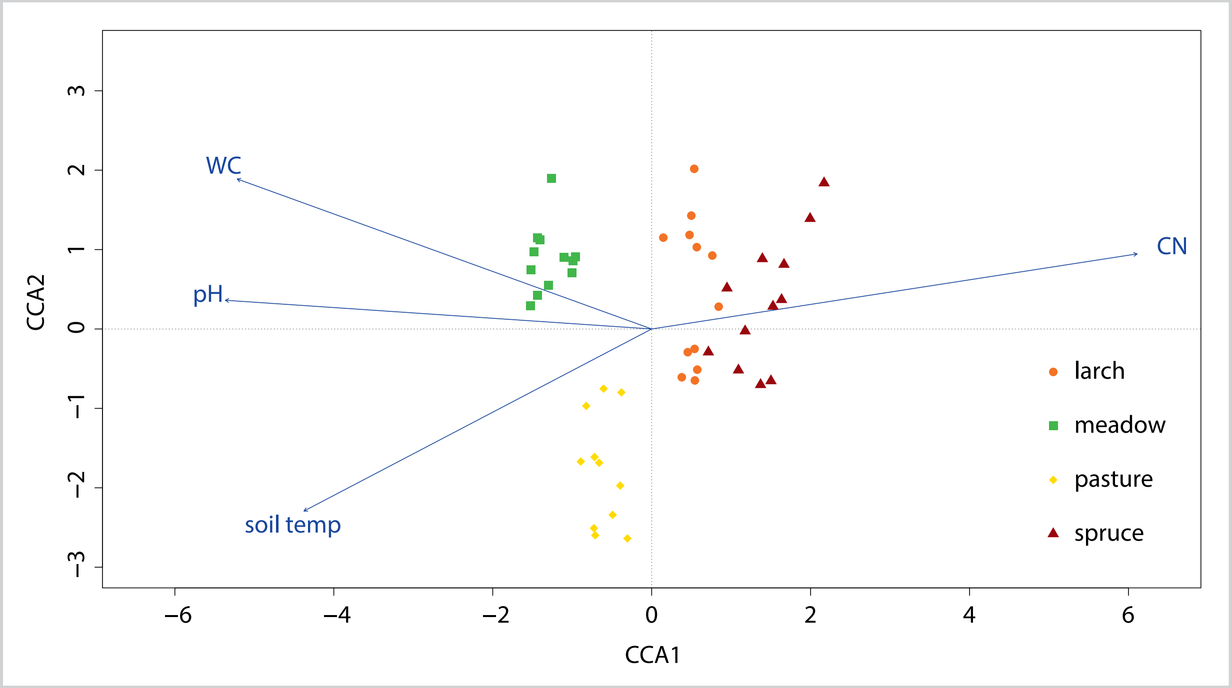
$P = 0.002$; Table 3B), and significant differences were only found between sampling dates in the 2 forest habitats ($F_{3,32} = 6.43$, $P = 0.002$ for larch forests, and $F_{3,32} = 6.99$, $P = 0.001$ for spruce forests), with the 2 later dates (August and October) being significantly different from the first one (April).

Irrespective of habitat and sampling date, Diptera (Nematocera and Brachycera) larvae were the most numerous (1319.44 ind/m^2; Table 3A), followed by Coleoptera larvae (797.91 ind/m^2), Myriapoda (Chilopoda, Diplopoda, and Symphyla; 688.20 ind/m^2), Coleoptera adults (524.13 ind/m^2), Lumbricidae (470.14 ind/m^2), and Araneae (440.97 ind/m^2). Gastropoda had the highest annual mean abundance in the dry pastures (47.22 ind/m^2), Lumbricidae in the hay meadows (262.50 ind/m^2), and Araneae in the larch forests (238.89 ind/m^2; Figure 2). Myriapoda (335.42 ind/m^2) and Coleoptera (adult and larvae combined, 378.47 ind/m^2) predominated in the larch forests, while Diptera larvae had their highest numbers in the hay meadows with 747.22 ind/m^2 (*Supplemental material*, Appendix S3: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1).

Table 3A further shows an overview of characteristic and abundant families for each habitat type. For example, the spider family Linyphiidae was most abundant in the larch forests with a mean density of 231.25 ind/m^2 (12 species identified; see *Supplemental material*, Appendix S3: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1). In contrast, Lycosidae showed the highest abundances in the hay meadows (6.94 ind/m^2; 2 taxa identified: 1 species and 1 genus) and Gnaphosidae in the dry pastures (9.72 ind/m^2).

Within the Coleoptera, the Staphylinidae predominated, with 51 species identified in sum (plus 6 to genus level) and were most abundant in the spruce forest with a mean of 101.39 ind/m^2 (16 taxa: 15 species and 1 genus identified), followed by Curculionidae (16 species in total) peaking in the dry pastures (30.56 ind/m^2 with 7 species, *Supplemental material*, Appendix S3: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1). The family Carabidae (16 species in total) showed their highest densities in the hay meadows, with 20.83 ind/m^2 (and 6 species). The highest proportion of Coleoptera larvae were Staphylinidae larvae and peaked, in contrast to the adults, in the hay meadows with 102.78 ind/m^2. Cantharidae larvae with 140.28 ind/m^2 were most abundant in the larch forests. Tenebrionidae larvae with 57.64 ind/m^2 were predominant in the dry pasture, while Elateridae larvae with 33.33 ind/m^2 peaked in the spruce forests. Finally, Curculionidae larvae with 25.00 ind/m^2 were most abundant in the hay meadows and Carabidae larvae with 11.81 ind/m^2 in the larch forests.

FIGURE 3 Canonical correspondence analysis (CCA) plot for the soil community composition of 4 alpine habitats differing in land use. The arrows represent significant parameters: soil temperature (soil temp), soil water content (WC), pH, and C:N ratio (CN).



The Myriapoda were most abundant in the larch forests with 56.25 ind/m^2 for Chilopoda, 77.08 ind/m^2 for Diplopoda, and 202.08 ind/m^2 for Symphyla, while Diptera (Nematocera and Brachycera) larvae showed the highest abundances with 747.22 ind/m^2 in the hay meadows (Figure 2).

The CCA (Figure 3) showed a clear separation of the hay meadows and the pastures from the forests in terms of their community composition (PERMANOVA $F_{3,44} = 6.03$, $P = 0.001$). Significant parameters for this separation were soil temperature ($P = 0.001$), soil moisture (as soil water content, $P = 0.001$), pH ($P = 0.002$), and C:N ratio ($P = 0.001$). Linear modeling of the Shannon–Wiener index confirmed the importance of soil temperature ($P = 0.012$) and soil moisture ($P = 0.024$) for species diversity.

Discussion

Here, we report on differences in soil macroinvertebrate species diversity and composition in intensified hay meadows, extensively grazed dry pastures, abandoned pastures covered by larch forests, and spruce forests to evaluate the effect of different management techniques on the soil fauna. By analyzing soil macroinvertebrates from 144 soil monoliths covering an entire vegetation period, we were able to show clear differences in community composition between 4 land use types (Table 3; Figure 3). Intensively managed hay meadows were found to be well separated from extensively grazed dry pastures and both forest types ($P = 0.001$; Figure 3), thus confirming our first hypothesis that community composition in the hay meadows differs from the other habitats. Replicate plots from the dry pastures were the most variable (as seen from the distance between single points in the CCA plot; Figure 3), while larch forests are the most similar. However, larch and spruce forests had similar community composition and could not be well distinguished, probably due to similar habitat structures in forests (eg well-developed litter layers). Interestingly, parameters determining the distinction between land use types in terms of species diversity and community composition were primarily climatic ones (ie soil temperature and soil moisture as results of CCA and linear mixed effects models). These seem to be more important than abiotic ones (eg organic matter content [SOM], pH; Tables 1, 2), since many soil invertebrates are sensitive to low soil moisture and high soil temperatures (Christenson et al 2017; Zagatto et al 2019).

Looking in detail at the community composition, the highest abundances were recorded from the hay meadows, which was mostly due to the high abundance of Diptera larvae (Table 3A; Figure 2). Nematocera larvae, in particular, were dominant, finding ideal living conditions on the irrigated and fertilized, and thus humid, hay meadows (Frouz 1999; Delettre 2000). Moreover, Lumbricidae (and within these the burrowing genus *Lumbricus*) characterized this land use type, which is plausible because of the high soil moisture levels (Figure 3) and deep soils (cambisols; J. Seeber, personal communication). Looking at the species level, there were distinct Coleoptera such as Apionidae (*Apion cruentatum* Walton 1844, *Catapion seniculus* (Kirby 1808), *Ischnopterapion virens* (Herbst 1797), *Protapion apricans* (Herbst 1797), and *Protapion fulvipes* (Geoffroy 1785)), which are phytophagous and were found exclusively in hay meadows rich in graminoids (Niedrist et al 2016; *Supplemental material*, Appendix S3: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1). In sum, we found 24 unique species (2 Araneae, 22 Coleoptera) in the hay meadows, the same number as in the dry pastures (5 Araneae, 16 Coleoptera, 3 Heteroptera). Therefore, our expectation that hay meadows would show a low biodiversity was not met. In contrast to the humid, irrigated hay meadows (Tables 1, 2; Figure 3), dry pastures were characterized by sporadic grazing by horses and cows, as well as very dry, shallow, and sandy soils, all reasons for the low abundances in the dry pastures (only Gastropoda had the highest occurrence in the dry pastures). However, one highlight was the carabid beetle *Amara infima* (Duftschmid, 1812), found in the dry pastures, which represents a new finding for South Tyrol (M. Kahlen, personal communication). These are exceptional habitats, and according to Hilpold, Seeber, et al (2018), dry pastures represent the most species-rich habitats with the highest rates of rare and specialist species after larch forests. In part, our data confirm this, because from 9 recorded Araneae families 7 were found in the dry pastures and 6 in the larch forests, whereas only 2 occurred in the spruce forests and the hay meadows (*Supplemental material*, Appendix S3: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1; Hilpold, Seeber, et al 2018). However, in our study, the highest biodiversity was found in the larch forests with 73 different species (of which 42 were unique). The reason could be that the successional and afforested larch forests are the most heterogeneous habitats due to different stand ages and variable understory, resulting in the lowest number of within-habitat shared species (Hilpold, Seeber, et al 2018). Still, Myriapoda and Coleoptera (adult and larvae) predominate in the larch forests. Within the Staphylinidae, 15 species—the highest number among all habitats—were found exclusively in this habitat as well as 5 curculionid species (*Brachysomus echinatus* (Bonsdorff, 1785), *Otiorhynchus carinatopunctatus* (Retzius 1783), *Otiorhynchus ovatus* (Linnaeus, 1758), *Otiorhynchus raucus* (Fabricius 1777), and *Phyllobius arborator* (Herbst 1797)) (Germann et al 2017; Schneider et al 2019; *Supplemental material*, Appendix S3: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1). Myriapoda had the highest abundances and diversity in larch forests, especially the Glomeridae; *Glomeris hexasticha* Brandt 1833 was found only in this habitat. The spruce forests exhibited no characteristic specialist species (in sum 20 unique species); 7 Staphylinidae and 7 other Coleoptera species (eg *Byrrhus fasciatus* Forster 1771 (Byrrhididae) and *Hylastes cunicularius* Erichson 1836 (Curculionidae)) were found exclusively in this forest type with its acid soil and high SOM content. However, we could only partially prove our third hypothesis, stating that larch forests have higher species numbers and a more diverse soil community, especially compared to spruce forests. Larch forests did harbor the most species compared to all other habitats (73), but according to the CCA the community composition was similar to that of the spruce forests (Figure 3). Even though larch forests also harbored the most unique species (42), these occurred only in very low abundances.

In reference to the Aichi Biodiversity Targets, Target 3 states that until 2020 impacts that are harmful to biodiversity should be minimized or even avoided (CBD 2018; Institute for Biodiversity 2019). In our case, this means prohibiting intensification and maintaining extensive and traditional farming. Extensive (ie low-input) management, as practiced in the dry pastures of the Val Mazia/Matschertal LTSER area, supports the development of a distinct and specialized community (Steinwandter et al 2019), as has been shown in a recent multi-taxon study including above- and belowground taxa (Hilpold, Seeber, et al 2018). Even though we could not confirm this for the soil macroinvertebrate community, since the dry pastures showed the lowest abundances and the fewest species compared to the other 3 land use types, this recommendation still holds, since above- and belowground biodiversity are closely connected and affect each other (Bardgett and van der Putten 2014; Lukac 2017). We assume that the low numbers are connected primarily to abiotic (ie shallow, hot, and dry soils) and not to land use parameters. In particular, intensification (H) of these pastures leads to a decline of biodiversity and to a composition of more generalist species. Reasons for this include intensive land use, such as larger flocks and heavy machines, and frequent compacting and disturbance of the soil structure (Schon et al 2008; Bueno and Jiménez 2014). Also, abandonment and afforestation with only spruce trees for silvicultural purposes (which results in dense spruce forests such as ours) might have negative impacts on biodiversity and should be avoided (as stated in Aichi Biodiversity Target 5). Instead, natural succession processes should be supported (as seen in the larch forest sites, which are the most species-rich habitats).

Conclusions

Extensively managed grass- and pasturelands in the European Alps and elsewhere have been found to harbor high biodiversity. In our case study, we were able to partly confirm this for soil macroinvertebrate communities, as the dry pastures did not harbor many species, but those found were new and rare. We found the highest biodiversity in the heterogeneous larch forests and the most individuals in the intensively managed hay meadows. Despite this, we still can consider the traditionally and extensively managed dry pastures as landscapes of high belowground biodiversity and conservational value, as they additionally provide vital ecosystem services.

Landscapes have always been, and will always be, changed by human activity (eg land use) and natural processes (eg soil erosion). To better understand how these changes affect soil macroinvertebrate assemblages, more studies on their structural and functional properties are urgently needed. We conclude that in subalpine pastureland, if abandonment is inevitable, a scattered afforestation with larch trees should be favored over intensive planting of spruce monocultures, which leads to lower (belowground) biodiversity. For the future, it is important to promote and keep sustainable forms of land use to maintain high biodiversity and essential ecosystem services.

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Supplemental material

APPENDIX S1 Monthly mean air temperature and cumulative precipitation in the study area at Muntatschinig/Montescino within the LTSER area of Val Mazia/Matschertal, Italy.

APPENDIX S2 Characteristics and soil parameters of the sampled plots.

APPENDIX S3 Mean abundance of soil macroinvertebrates from soil monoliths from 4 alpine habitat types.

APPENDIX S4 Seasonal development of mean abundances of 6 soil macroinvertebrate groups from four alpine habitat types.

Found at: https://doi.org/10.1659/MRD-JOURNAL-D-19-00057.1.S1.