

A comparison of Alpine soil macro-invertebrate communities from European larch and Swiss pine forests in the LTSER area “Val Mazia/Matschertal”, South Tyrol

Abstract

In the Central Alps the treeline is formed by the European larch (*Larix decidua* Mill.) and the Swiss pine (*Pinus cembra* L.), shaping the alpine plant community Larici-Cembretum. Currently, alpine pastures, which are increasingly abandoned in the European Alps, are colonised, after a phase of shrub encroachment, by the European larch, while a Swiss pine forest will establish once the undergrowth becomes too dense for larch trees. Former studies on tree growth rates indicate that the European larch will react positively to increasing temperatures at the treeline and will grow faster in the future. The Swiss pine has in general slower growth rates and will likely be less affected by higher temperatures. Thus, there might be a change from Swiss pine to European larch forests at the tree line.

This change in the dominating tree species might have profound impacts on the soil macro-invertebrate community, particularly due to differing chemical and physical compositions of larch and pine needle litter. To investigate potential effects of this change, we took soil core and litter samples and further installed pitfall traps in pure European larch and Swiss pine forests, as well as in mixed forests.

We found no explicit differences in species composition between forests, presumably due to highly variable site and environmental parameters between and within forest types. The larch forests showed the highest number of taxa in general and the highest number of taxa found exclusively in this habitat. The pine forests were inhabited by the highest number of characteristic taxa while mixed forests harboured the most stable and consistent soil macro-invertebrate community.

Zusammenfassung

In den Zentralalpen wird die Baumgrenze von der Europäischen Lärche (*Larix decidua* Mill.) und der Zirbe (*Pinus cembra* L.) gebildet und prägt die alpine Pflanzengemeinschaft Larici-Cembretum.

In den europäischen Alpen besiedelt die Lärche aufgelassene Almflächen. Sobald das Unterholz für Lärchen zu dicht wird, bildet sich ein Zirbenwald. Frühere Studien zu den Wachstumsraten der Bäume deuten darauf hin, dass die Lärche positiv auf steigende Temperaturen an der Baumgrenze reagieren und in Zukunft schneller wachsen wird. Die Zirbe zeigt allgemein langsamere Wachstumsraten und wird voraussichtlich weniger von höheren Temperaturen betroffen sein. So könnte es zu einem Wechsel von Zirben- zu Lärchenwäldern an der Waldgrenze kommen.

Diese Veränderung der dominierenden Baumarten könnte tiefgreifende Auswirkungen auf die Makro-Invertebratengemeinschaft im Boden haben, insbesondere aufgrund der unterschiedlichen chemischen und physikalischen Zusammensetzung der Lärchen- und Zirbennadelstreu. Um die möglichen Auswirkungen dieser Veränderung zu

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untersuchen, wurden Boden- und Streuproben in reinen Lärchen- und Zirbenwäldern sowie in Mischwäldern aus beiden Arten entnommen. Weiters wurden in allen Waldtypen Barberfallen zur Erfassung der bodenoberflächenaktiven Invertebraten aufgestellt. Wir fanden keine expliziten Unterschiede in der Artenzusammensetzung zwischen den Wäldern, vermutlich aufgrund von sehr unterschiedlichen Standort- und Umweltparametern sowohl zwischen als auch innerhalb der beiden Waldtypen. Die Lärchenwälder zeigten die höchste Anzahl von Taxa im Allgemeinen und die höchste Anzahl von Taxa, die ausschließlich in diesem Lebensraum vorkommen. Die Zirbenwälder waren von der höchsten Anzahl charakteristischer Taxa bewohnt, während Mischwälder die stabilste Makro-Invertebratengemeinschaft des Bodens beherbergten.

Introduction

In the Alps the larch-pine forests are important ecosystems at the treeline (ELLENBERG 1963; NAGY & GRABHERR 2009). The European larch *Larix decidua* MILL. and the Swiss pine *Pinus cembra* L. are two trees which can defy harsh conditions such as low temperatures, soil freezing, high UV-radiation and low growth periods (KÖRNER 2012). These forest ecosystems have important influences on alpine plants and animals but also on humans. They provide several ecosystem services, like protection from soil erosion and rock fall (MAYER 1976; PRICE et al. 2011), provision of drinking water, carbon sequestration and scenic beauty (JANDL & PRICE 2011), and are a habitat for specialised above- and below-ground animals (RIEF et al. 2017 and citation therein). Former studies on tree growth rates indicate that the European larch and the Swiss pine might benefit from increasing temperatures due to climate change at higher elevations, while at lower elevation decreases in growth rates due to lower mean annual precipitation are expected. However, the Swiss pine has generally slower growth rates and will thus likely not be as strongly affected as the European larch. This might lead to a shift from pine to larch forests at the treeline (OBOJES et al. 2016, 2018). Furthermore, the densification of trees as a result of climate change might additionally affect the treeline ecosystems (HAGN & PEER 2010).

Litter quality is an important factor for decomposition (GARCÍA-PALACIOS et al. 2016) and species composition of soil fauna (MA & YIN 2019). It influences available nutrients and minerals (FROUZ 2017) and usually differs between tree species (NICKMANS et al. 2019). A change from evergreen pine needles containing a high amount of phenols and other secondary plant products to deciduous larch needles will likely cause a shift in litter quality and thus different feeding conditions for soil animals. In previous studies, the soil macrofauna of various forest types has been assessed and trophic shifts of soil animal species with forest type have been observed. Further, earthworm communities as well as soil organism abundance and diversity were affected by tree species identity (KLARNER et al. 2014; SCHWARZ et al. 2015; KORBOULEWSKY et al. 2016).

Several studies concerning the impact of climate change on either tree species or the corresponding ecosystem exist (JANDL et al. 2018; OBOJES et al. 2018; BERNIER & GILLET 2012; SILES et al. 2017; STEINWANDTER & SEEGER 2017, HILPOLD et al. 2018), however, there are no studies dealing with the soil macro-invertebrate communities and how they differ between larch and pine forests. It has been shown that soil animals are important for ecosystem functioning (HÄTTENSWILER 2005) as they play a key role in litter decomposition via physical fragmentation of litter, chemical digestion and changing activity of microorganisms (MA et al. 2019). Thus, knowledge on their community composition is of immediate importance.

In this study we determined the communities of soil macro-invertebrates of larch and pine forests to test if their compositions differ due to differences in litter and soil characteristics. Further, we calculated characteristic taxa for each forest type.

Material and Methods

Study area

The study took place in the LTSEr area “Val Mazia/Matschertal”, representing a side valley of the dry inner-Alpine Vinschgau valley in South Tyrol, Italy (46.6876° N, 10.6411° E). The village of Mazia/Matsch (1570 m a.s.l.) has an annual precipitation of 528 mm and an average annual temperature of 6.6 °C (Obojes et al. 2018). Geologically, it is part of the paragneis and phyllitgneis zone of the Central Alps, belonging to the subgroup Ötztal Alps (Tirol ATLAS 2019). We used forest sites on the orographic left side of the valley with mountain slopes exposed to the west (Fig. 1). The study area has an expansion of approximately 4 km length and 2 km width, and spans from 2000 to 2150 m elevation. The undergrowth consists of varying mixtures of grasses and dwarf shrubs, with areas of bare soil and rocks.

To ensure a sound study design, we selected three plots of each pure European larch forests (L100), pure Swiss pine forests (Z100) and plots of a mixed forests with larch and pine (LZ50). Each sampling plot consisted of an area of approximately 300 m² (i.e. 10 m within the plot centre). Distances between all plots were at least 400 m (except for Z100_1 and LZ50_2 where it was 300 m).

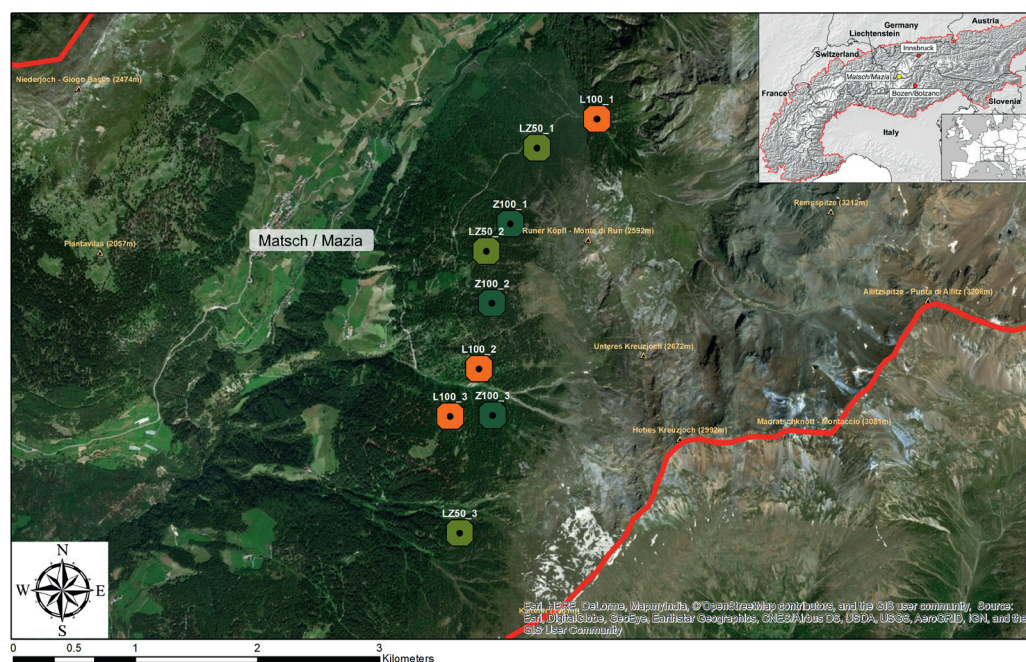


Fig. 1: Aerial photo of the study site in the LTSEr area “Val Mazia/Matschertal”. The orange points represent the sampled European larch forests (L100), the dark green the Swiss pine forests (Z100) and the bright green the mixed larch-pine forests (LZ50). The red line delineates the LTSEr boundary.

Sampling of soil macro-invertebrates

In each sampling plot, each three samples of the three sampling types soil core samples, litter samples and pitfall traps were randomly taken, resulting in a total of 81 samples. On 05.09.2017 we installed each three pitfall traps consisting of plastic cups with an opening diameter of 8.5 cm and a transparent polycarbonate roof for rain protection. The pitfall traps were filled with propylene glycol as preservation fluid and emptied after three weeks in the field (i.e. 20 days).

We took litter and soil core samples with a size of 20 × 20 cm on 26.09.2017. The thickness of the sample depended on the litter and soil depth but was 10 cm at maximum for each layer. To extract the animals from litter and soil samples, we used a modified Kempson apparatus (KEMPSON et al. 1963). Samples were heat-extracted for 12 days

with continuous light exposure; as collection fluid we used again propylene glycol. All collected animals were stored in 75 % ethanol until identification.

Site and soil parameters

The GPS coordinates, inclination, exposition, elevation, soil and litter depth, were noted at each soil and litter sampling point (Table 1). Soil moisture at the time of sampling was measured as volumetric soil content (percentage and μS) using a HydroSenseII (Campbell Scientific, Logan, Utah). Soil material was taken in the laboratory of the Institute for Alpine Environment, Eurac Research for further analyses.

The pH-value was determined by dissolving 20 ml of air-dried soil in 50 ml of 0.1 M CaCl_2 solution. After 2 hours the pH-value was measured with a pH-multimeter (HI2020 edge, Hanna Instruments, Woonsocket, Rhode Island) after short stirring. For the soil organic matter content (SOM), soil material was dried for 24 hours at 105 °C in a drying chamber (BD 240, Binder, Tuttlingen, Germany), weighted and combusted at 400 °C for 4 hours in a muffle furnace (Carbolite ELF1114, Carbolite, Hope Valley, United Kingdom). Afterwards, the sample was re-weighted, and SOM was calculated (i.e. dried material minus muffled material).

The total C and total N content was determined using a TruSpec® CHN elemental analyser (Leco, St. Joseph, Michigan) and then the C:N ratio was calculated.

Table 1: Mean and standard deviation (in parentheses) of study site and environmental parameters of soil from Alpine European larch and Swiss pine forests. Results of univariate Analyses of Variance (ANOVA) are shown in the last row. Superscript letters indicate significant differences between the sites as indicated by Tukey's HSD post-hoc tests at significance level $p < 0.05$. L100... European larch, LZ50... mixture, Z100... Swiss pine; $n = 9$.

Plot	Elevation	Inclination	Exposition	Moisture	Litter layer	Soil layer	pH	SOM	C/N
	[m a.s.l.]	[°]	[°]	[% I/WC]	[cm]	[cm]		[%]	
L100	2035	20	WNW 292.5	18.60 (9.68)	3.00 (1.00)	8.33 (1.32) ^a	3.75 (0.59)	26.06 (16.33)	25.43 (7.56)
LZ50	2075	20	WNW 292.5	20.26 (8.62)	3.00 (1.22)	6.88 (0.64) ^b	3.50 (0.43)	36.15 (23.44)	22.87 (3.23)
Z100	2140	20	WNW 292.5	15.93 (4.97)	2.56 (1.24)	7.00 (1.22) ^b	3.66 (0.49)	28.49 (21.75)	21.82 (5.18)
				$F_{2,24} = 0.666$ $p = 0.523$	$F_{2,24} = 0.441$ $p = 0.648$	$F_{2,23} = 5.736$ $p = 0.021$	$F_{2,24} = 0.585$ $p = 0.548$	$F_{2,23} = 0.545$ $p = 0.587$	$F_{2,24} = 0.995$ $p = 0.384$

Identification of animals

Most of the animals from our samples were identified to family level (Myriapoda, Araneae, Coleoptera and Diptera larvae), while others were determined to genus (Pseudoscorpiones) or species level (Lumbricidae, Opiliones, Table 2). Hymenoptera, adult Lepidoptera and Diptera, and representatives of the mesofauna (i.e. Acari and Collembola) were excluded from the analyses. Animals were identified under a stereomicroscope (MZ8, Leica Microsystems, Wetzlar, Germany,) using different identification keys. The determination of Lumbricidae followed CHRISTIAN & ZICSI (1999), that of Diptera larvae SMITH (1989), of Opiliones KÖHLER (2015), and of all other taxa ZETTEL (1999) and SCHÄFER (2018).

Data analyses

Most statistical analyses were conducted with the open-source program R (version 3.6.1, R CORE TEAM, 2019) in RStudio (version 1.2.5001, R STUDIO TEAM 2016), using the packages VEGAN (version 2.5-6 from OKSANEN 2019), TIDYVERSE (version 1.2.1, WICKHAM 2017) and CORRGRAM (version 1.13, WRIGHT 2018). In order to compare the environmental and soil parameters between the forests, ANOVAs (Analysis of Variance) were calculated.

Table 2: Mean densities (ind./m² with standard deviation in parenthesis) and abundances (ind./sampling day) of Alpine soil macro-invertebrates from European larch and Swiss pine forests. L100... European larch, LZ50... mixture, Z100... Swiss pine; n = 9.

1/2	L100					LZ50					Z100				
	Soil		Litter		Surface	Soil		Litter		Surface	Soil		Litter		Surface
	ind/m ²	(sd)	ind/m ²	(sd)	ind/d	ind/m ²	(sd)	ind/m ²	(sd)	ind/d	ind/m ²	(sd)	ind/m ²	(sd)	ind/d
Gastropoda	–		–		0.05	–		5.56	(7.86)	0.50	–		–		0.25
Lumbricidae	75.00	(85.80)	19.44	(38.69)	0.20	47.22	(41.57)	50.00	(100.0)	0.20	25.00	(42.49)	100.00	(196.1)	0.40
<i>Aporrectodea rosea</i> (SAVIGNY, 1826)	2.78	(7.86)	–		–	–		–		–	–		–		–
<i>Aporrectodea</i> sp.	13.89	(39.28)	–		–	5.56	(15.71)	–		–	–		–		–
<i>Dendrobaena octaedra</i> (SAVIGNY, 1826)	–		5.56	(10.39)	–	2.78	(7.86)	2.78	(7.86)	–	2.78	(7.86)	2.78	(7.86)	–
<i>Dendrobaena</i> sp.	19.44	(46.81)	5.56	(15.71)	–	2.78	(7.86)	–		–	2.78	(7.86)	5.56	(15.71)	–
<i>Lumbricus rubellus</i> (HOFFMEISTER, 1843)	5.56	(15.71)	–		0.05	–		–		0.05	–		–		0.10
<i>Lumbricus</i> sp.	8.33	(16.67)	–		0.15	–		–		0.15	–		5.56	(10.39)	0.30
<i>Octolasion lacteum</i> (ORLEY, 1885)	2.78	(7.86)	–		–	–		–		–	2.78	(7.86)	–		–
<i>Octolasion</i> sp.	16.67	(33.33)	–		–	16.67	(16.67)	2.78	(7.86)	–	2.78	(7.86)	5.56	(15.71)	–
juvenile / indet.	5.56	(10.39)	8.33	(16.67)	–	19.44	(30.68)	44.44	(93.38)	–	13.89	(23.90)	80.56	(176.3)	–
Enchytraeidae	8.33	(11.79)	2.78	(7.86)	–	–		–		–	–		2.78	(7.86)	–
Isopoda	–		5.56	(15.71)	–	–		–		0.05	–		–		0.25
Chilopoda: Lithobiidae	38.89	(48.75)	5.56	(10.39)	0.05	83.33	(124.7)	27.78	(29.92)	0.55	66.67	(92.80)	8.33	(16.67)	0.25
Diplopoda	–		–		0.75	2.78	(7.86)	5.56	(10.39)	1.35	2.78	(7.86)	–		0.70
Pollyxenidae: <i>Polyxenus lagurus</i> (LINNAEUS, 1758)	–		–		0.10	–		–		–	–		–		–
Julidae	–		–		0.50	2.78	(7.86)	5.56	(10.39)	1.10	2.78	(7.86)	–		0.65
Craspedosomatidae	–		–		0.15	–		–		0.25	–		–		0.05
Opiliones	–		–		11.10	–		–		11.70	–		–		7.55
Nemastomatidae	–		–		0.25	–		–		0.30	–		–		0.20
<i>Histicostoma dentipalpe</i> (AUSSERER, 1867)	–		–		0.15	–		–		0.10	–		–		0.10
<i>Mitostoma chrysomelas</i> (HERMAN, 1804)	–		–		–	–		–		0.20	–		–		0.10
<i>Paranemastoma quadripunctatum</i> (PERTY, 1833)	–		–		0.10	–		–		–	–		–		–
Phalangidae: <i>Mitopus morio</i> (FABRICIUS, 1799)	–		–		10.60	–		–		11.40	–		–		7.20
juvenile / indet.	–		–		0.25	–		–		–	–		–		0.15
Araneae	5.56	(10.39)	38.89	(41.01)	10.10	30.56	(45.30)	22.22	(29.92)	10.80	50.00	(70.71)	41.67	(48.59)	10.00
Theridiidae	–		–		0.55	–		–		0.35	–		–		–
Linyphiidae	5.56	(10.39)	36.11	(39.28)	7.30	25.00	(45.64)	11.11	(23.90)	7.75	38.89	(66.78)	33.33	(44.10)	7.00
Lycosidae	–		–		0.60	2.78	(7.86)	2.78	(7.86)	0.70	2.78	(7.86)	2.78	(7.86)	0.50
Miturgidae	–		–		0.05	–		–		–	–		–		–
Agelenidae	–		–		–	–		–		–	–		–		0.10
Cybaeidae	–		–		1.30	2.78	(7.86)	8.33	(11.79)	1.70	5.56	(10.39)	2.78	(7.86)	1.90
Gnaphosidae	–		2.78	(7.86)	0.25	–		–		0.25	2.78	(7.86)	–		0.25
Thomisidae	–		–		0.05	–		–		0.05	–		2.78	(7.86)	0.25
Pseudoscorpiones	13.89	(26.64)	19.44	(25.86)	0.05	5.56	(10.39)	22.22	(36.22)	–	36.11	(44.27)	16.67	(20.41)	–
Neobisidae	5.56	(15.71)	13.89	(26.64)	0.05	5.56	(10.39)	22.22	(36.22)	–	36.11	(44.27)	16.67	(20.41)	–
Chernetidae	8.33	(23.57)	5.56	(10.39)	–	–		–		–	–		–		–

2/2	L100					LZ50					Z100				
	Soil		Litter		Surface	Soil		Litter		Surface	Soil		Litter		Surface
	ind/m ²	(sd)	ind/m ²	(sd)	ind/d	ind/m ²	(sd)	ind/m ²	(sd)	ind/d	ind/m ²	(sd)	ind/m ²	(sd)	ind/d
Dermaptera	–		–		1.25	–		–		1.15	–		2.78	(7.86)	0.65
Thysanoptera	8.33	(23.57)	25.00	(28.87)	–	–		11.11	(23.90)	0.05	5.56	(10.39)	19.44	(25.76)	–
Hemiptera	25.00	(35.36)	55.56	(79.74)	3.95	66.67	(106.1)	138.89	(147.7)	1.25	127.78	(227.4)	227.78	(311.7)	0.65
Sternorrhyncha	19.44	(36.85)	36.11	(62.48)	0.05	58.33	(109.3)	97.22	(136.6)	0.35	116.67	(215.1)	180.56	(295.3)	0.30
Auchenorrhyncha	2.78	(7.86)	8.33	(16.67)	3.90	2.78	(7.86)	27.78	(29.92)	0.80	8.33	(16.67)	13.89	(26.64)	0.35
Heteroptera	2.78	(7.86)	11.11	(17.12)	–	5.56	(15.71)	13.89	(39.28)	0.10	2.78	(7.86)	30.56	(77.98)	–
Coleoptera	19.44	(25.76)	13.89	(12.42)	4.50	22.22	(24.85)	16.67	(20.41)	5.95	44.44	(52.41)	25.00	(37.27)	4.75
Carabidae	–		–		2.15	2.78	(7.86)	2.78	(7.86)	3.60	–		–		1.75
Cholevidae	–		–		0.20	–		–		0.05	–		–		0.25
Leiodidae	–		–		0.05	–		–		–	2.78	(7.86)	–		0.10
Staphylinidae	11.11	(17.12)	13.89	(12.42)	2.00	13.89	(20.79)	13.89	(17.12)	2.00	11.11	(12.42)	5.56	(10.39)	2.60
Cantharidae	5.56	(15.71)	–		–	–		–		–	–		–		–
Cryptophagidae	–		–		0.05	–		–		0.15	–		–		0.05
Lathrididae	–		–		–	–		–		0.05	–		–		–
Monotomidae	–		–		–	–		–		0.10	–		–		–
Tenebrionidae	2.78	(7.86)	–		0.05	–		–		–	5.56	(15.71)	–		–
Scarabaeidae	–		–		–	5.56	(10.39)	–		–	–		–		–
Curculionidae	–		–		–	–		–		–	25.00	(45.64)	19.44	(38.69)	–
Coleoptera Larvae	72.22	(71.15)	94.44	(94.12)	0.70	75.00	(116.7)	111.11	(134.4)	1.65	177.78	(207.0)	100.00	(90.52)	0.80
Carabidae L.	5.56	(15.71)	–		0.15	–		–		–	2.78	(7.86)	–		0.15
Staphylinidae L.	22.22	(21.87)	19.44	(32.87)	0.15	41.67	(92.80)	13.89	(23.90)	0.10	19.44	(22.91)	11.11	(12.42)	0.05
Cantharidae L.	38.89	(57.87)	61.11	(89.06)	0.35	16.67	(26.35)	88.89	(119.1)	1.45	94.44	(173.5)	69.44	(99.85)	0.60
Melyridae L.	–		–		0.05	–		–		0.10	–		–		–
Cleridae L.	5.56	(15.71)	5.56	(15.71)	–	2.78	(7.86)	–		–	–		–		–
Tenebrionidae L.	–		5.56	(10.39)	–	11.11	(12.42)	8.33	(11.79)	–	50.00	(108.7)	19.44	(36.85)	–
Scarabaeidae L.	–		–		–	–		–		–	2.78	(7.86)	–		–
Curculionidae L.	–		2.78	(7.86)	–	2.78	(7.86)	–		–	8.33	(11.79)	–		–
Nematocera Larvae	38.89	(50.15)	55.56	(105.9)	0.10	91.67	(93.54)	350.00	(608.5)	–	88.89	(125.3)	288.89	(480.8)	0.05
Chironomidae L.	5.56	(10.39)	8.33	(23.6)	–	50.00	(92.04)	–		–	5.56	(10.39)	2.78	(7.86)	0.05
Sciaridae L.	2.78	(7.86)	–		–	–		–		–	8.33	(16.67)	–		–
Cecidomyiidae L.	30.56	(45.30)	19.44	(22.9)	–	11.11	(17.12)	88.89	(71.79)	–	30.56	(62.85)	122.22	(196.3)	–
Ceratopogonidae L.	–		25.00	(70.7)	–	22.22	(54.57)	238.89	(562.6)	–	38.89	(68.83)	144.44	(382.7)	–
Tipulidae L.	–		2.78	(7.9)	0.10	8.33	(16.67)	22.22	(46.31)	–	5.56	(15.71)	19.44	(46.81)	–
Brachycera Larvae	25.00	(28.87)	13.89	(17.12)	0.05	27.78	(41.57)	25.00	(31.18)	0.05	27.78	(36.22)	8.33	(16.67)	–
Dolichopodidae L.	25.00	(28.87)	5.56	(10.39)	–	22.22	(36.22)	16.67	(31.18)	–	19.44	(25.76)	5.56	(15.71)	–
Empididae L.	–		–		–	5.56	(10.39)	2.78	(7.86)	–	–		–		–
Therevidae L.	–		–		–	–		–		–	2.78	(7.86)	–		–
Tabanidae L.	–		8.33	(16.67)	–	–		–		–	2.78	(7.86)	–		–
Heleomyzidae L.	–		–		–	–		5.56	(15.71)	0.05	2.78	(7.86)	2.78	(7.86)	–
Fannidae L.	–		–		0.05	–		–		–	–		–		–
Lepidoptera Larvae	–		–		0.05	11.11	(23.90)	–		0.15	13.89	(31.43)	2.78	(7.86)	0.40

To analyse the community-environment relationship, Constrained Correspondence Analyses (CCA) were calculated using the multivariate data exploration software Canoco 5 (version 5.12, TER BRAAK & ŠMILAUER 2018). Data from pitfall traps were analysed separately from soil core and litter samples due to different data specifications.

To find characteristic taxa of each forest type and layer, we applied the indicator species method by DUFRENE & LEGENDRE (1997): “For each species i in each site group j , we computed the product of A_{ij} , which is the mean abundance of species i in the sites of group j compared to all groups in the study, by B_{ij} , which is the relative frequency of occurrence of species i in the sites of group j , as follows:

“ $A_{ij} = N_{\text{individuals}_{ij}} / N_{\text{individuals}_i}$, $B_{ij} = N_{\text{sites}_{ij}} / N_{\text{sites}_j}$, $\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$, where IndVal is the indicator value of species i in site cluster j .”

The threshold for IndVal is set at 25 % indicating that this characteristic species is present in at least 25 % of replicate samples and its relative abundance in that group reaches at least 25 %.

Results

General results

Altogether, we identified 3130 soil macro-invertebrate specimens, 526 from soil core samples, 709 from litter samples and 1895 from pitfall traps (Table 2). In total, 69 taxa were identified, 55 of them were in the larch, 50 in the pine and 48 in the mixed forests. Some taxa were found exclusively in one of the forest types (Table 2): six for L100 (*Aporrectodea rosea* (SAVIGNY, 1826), *Polyxenus lagurus* (LINNAEUS, 1758), Miturgidae, Chernetidae, Cantharidae larvae and Fanniidae larvae), five for LZ50 (*Mitostoma chrysomelas* (HERMAN, 1804), Lathrididae, Monotomidae, Scarabaeidae and Empididae larvae), and four for Z100 (Agelenidae, Curculionidae, Scarabaeidae larvae and Therevidae larvae). The highest number of individuals was collected in the mixed forests (1155), the most abundant taxa were spiders (686, whereof 495 were from the family Linyphiidae), followed by harvestmen (607, 584 of these belonged to the species *Mitopus morio* (FABRICIUS, 1799)), beetles (356 adult individuals, of which 157 were Staphylinidae, and 291 larvae), and nematoceran larvae (331, of which 116 were Cecidomyiidae).

Community composition

Soil macro-invertebrate communities collected from soil core and litter samples (Fig. 2A) and pitfall traps (Fig. 2B) differed between forest types. In general, replicates of mixed forests were more similar than replicates from pure forests and seem to occupy an intermediary position between larch and pine forests. For soil and litter, the plots of the pure forests are disjoint, with single replicates being closer to the mixed forests than to other replicates (i.e. L100_1 and Z100_3), while they are more clustered for the surface communities (Fig. 2B). Exposition is a main driver for communities sampled from litter and soil as well as from the soil surface, while pH and elevation are also affecting community composition in soil and litter.

Characteristic taxa

Characteristic taxa, as derived from DUFRENE & LEGENDRE (1997), are taxa that are frequent (i.e. found in many replicate samples) and abundant (i.e. in high individual numbers) in a certain habitat (Table 3). The highest number of characteristic taxa were observed from the soil and litter layer in Swiss pine forests (16 taxa). When looking at soil, litter and the soil surface collectively, the mixed forests showed the highest number (20 taxa). More characteristic taxa were discernible from soil and litter layers (24 taxa) than from the soil surface (13 taxa).

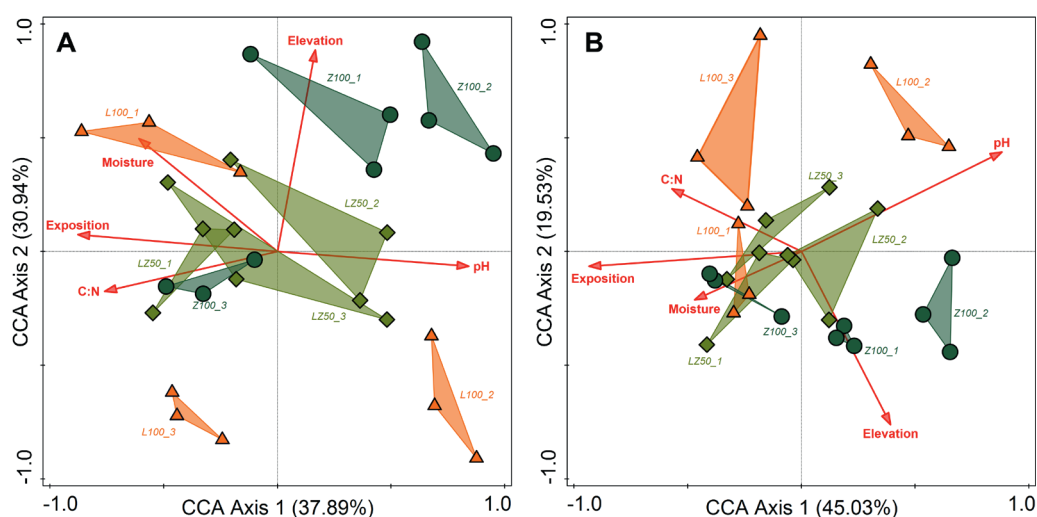


Fig. 2: Canonical Correspondence Analyses (CCA) of soil macro-invertebrate communities in Alpine coniferous forests. The figure shows the correspondence of five environmental factors with the soil fauna on family level or higher in soil core and litter samples (A) and pitfall traps (B). Rare taxa (i.e. less than three individuals) were excluded. L100... European larch, LZ50... mixture, Z100... Swiss pine; n = 3.

Table 3: Characteristic Alpine soil taxa from the soil and litter layer and the surface from European larch and Swiss pine forests. The shown values represent the indicator value of soil taxa calculated after the method described in Dufrene & Legendre (1997). All values above 25 were highlighted, with the highest numbers per layer each being the darkest (four categories). The last row summarizes the number of characteristic taxa.

1/2	Soil + Litter			Surface		
	L100	LZ50	Z100	L100	LZ50	Z100
Gastropoda	0.00	22.22	0.00	0.69	34.72	10.42
Lumbricidae: <i>Aporrectodea rosea</i> (SAVIGNY, 1826)	16.67	0.00	0.00	–	–	–
Lumbricidae: <i>Dendrobaena octaedra</i> (SAVIGNY, 1826)	38.60	10.53	23.39	–	–	–
Lumbricidae: <i>Lumbricus rubellus</i> (HOFFMEISTER, 1843)	31.75	0.00	12.70	–	–	–
Lumbricidae: <i>Octolasion lacteum</i> (ORLEY, 1885)	23.33	60.00	13.33	–	–	–
Isopoda	0.00	0.00	0.00	0.00	5.56	16.67
Lithobiidae	25.70	64.26	43.37	0.69	27.78	0.00
Polyxenidae: <i>Polyxenus lagurus</i> (LINNAEUS, 1758)	–	–	–	11.11	0.00	0.00
Julidae	0.00	50.00	5.56	7.58	42.42	0.00
Craspedosomatidae	–	–	–	6.67	33.33	0.00
Nemastomatidae: <i>Histicostoma dentipalpe</i> (AUSSENER, 1867)	–	–	–	9.52	3.17	3.17
Nemastomatidae: <i>Mitostoma chrysomelas</i> (HERMAN, 1804)	–	–	–	0.00	44.44	0.00
Nemastomatidae: <i>Paranemastoma quadripunctatum</i> (PERTY, 1833)	–	–	11.11	0.00	11.11	–
Phalangidae: <i>Mitopus morio</i> (FABRICIUS, 1799)	–	–	–	32.27	39.04	0.00
Dermaptera	0.00	0.00	22.22	27.32	33.52	4.74
Thysanoptera	42.67	7.11	40.00	0.00	11.11	0.00
Sternorrhyncha	9.71	27.20	51.97	0.79	16.67	42.86
Auchenorrhyncha	11.59	53.14	23.19	77.23	8.80	0.00
Heteroptera	18.52	6.48	33.33	0.00	22.22	0.00
Theridiidae	–	–	–	40.74	12.96	0.00
Linyphiidae	43.21	26.75	53.50	33.11	35.15	0.00
Lycosidae	0.00	22.22	22.22	11.11	21.60	18.52

2/2	Soil + Litter			Surface		
	L100	L250	Z100	L100	L250	Z100
Miturgidae	–	–	–	11.11	0.00	0.00
Cybaeidae	0.00	38.10	28.57	17.69	30.84	38.78
Gnaphosidae	0.00	0.00	11.11	18.52	11.11	11.11
Thomisidae	0.00	0.00	22.22	1.59	1.59	15.87
Neobisidae	8.64	24.69	82.10	11.11	0.00	0.00
Chernetidae	44.44	0.00	0.00	–	–	–
Carabidae	0.00	0.00	0.00	9.56	5.33	0.00
Cholevidae	–	–	–	4.44	0.00	11.11
Leioididae	0.00	0.00	111.11	22.22	0.00	66.67
Staphylinidae	56.00	0.00	0.00	0.00	0.00	13.13
Cantharidae	22.22	0.00	0.00	–	–	–
Cryptophagidae	–	–	–	0.00	6.67	0.00
Lathrididae	–	–	–	0.00	22.22	0.00
Tenebrionidae	7.41	0.00	0.00	0.00	0.00	0.00
Curculinonidae	0.00	0.00	22.22	–	–	–
Carabidae larvae	14.81	0.00	37.04	16.67	0.00	0.00
Melyridae larvae	–	–	–	0.00	0.00	0.00
Cleridae larvae	17.78	22.22	0.00	–	–	–
Tenebrionidae larvae	2.61	0.00	16.34	–	–	–
Scarabaeidae larvae	0.00	0.00	66.67	–	–	–
Chironomidae larvae	12.82	0.00	5.13	0.00	0.00	0.00
Sciaridae larvae	5.56	0.00	83.33	–	–	–
Cecidomyiidae larvae	18.35	14.68	33.64	–	–	–
Ceratopogonidae larvae	1.18	49.44	26.04	–	–	–
Tipulidae larvae	1.06	81.48	47.62	11.11	0.00	0.00
Dolichopodidae larvae	35.95	27.45	0.00	–	–	–
Therevidae larvae	0.00	0.00	22.22	–	–	–
Heleomyzidae larvae	0.00	0.00	44.44	–	–	–
Tabanidae larvae	19.05	0.00	0.00	0.00	0.00	0.00
Fannidae larvae	–	–	–	11.11	0.00	0.00
Sum of characteristic taxa	9	11	16	5	9	3

Discussion

The soil macrofauna is quite understudied in alpine ecosystems. This study shows first results of a comparison of the soil macro-invertebrates between *Larix decidua* and *Pinus cembra* forests in the Central Alps near the treeline based on our hypothesis that differences in soil characteristics and litter quality would affect the community compositions.

Site and environmental parameters were similar between the forests (Table 1). The soil depth at these sites is low (between 5 and 10 cm) and the immediate proximity of the bedrock could have a stronger influence on the pH-value and other parameters than litter (HILLER et al. 2005). In our analysis exposition is the environmental parameter with the strongest influence on community composition (Fig. 2). Although it varies only between 200–340°, it exhibits different pH-values. pH is higher the more the plot is exposed to the south which is comprehensible, since higher solar radiation and temperature increase the activity of microorganisms in the soil and decomposition rates (FRAVOLINI et al. 2016), which leads to higher pH-values (MALKOMES 1991, SALMON et al. 2008; McCAY et al. 2013; SALMON 2018). Most of the other site and environmental parameters could not be used to differentiate between forest types.

In our study we could not confirm our hypothesis stating clear differences in species composition between forest types, however, we observed a trend (Fig. 2). Replicates of pure forests are quite dissimilar, irrespective of the layer sampled. Interestingly, mixed forests form a well-defined group and assume a central position between the pure larch and pine forest plots. Studies in other forest systems showed that tree species identity and the understory vegetation are the main factors for soil species composition (MITCHELL et al. 2011; LORANGER-MERCIRIS et al. 2007; STAŠIOV et al. 2012), and that litter quality strongly influences the soil fauna (KOOCH et al. 2018; STAŠIOV et al. 2012). As already mentioned, environmental parameters were quite variable in our case study area, also differing within forest type (as observed from very high standard deviations, Table 1). The understory of each site, even though not recorded in detail, differed highly among and between forests types, especially pronounced in the pure forests, and could not be allocated to a specific forest type. Therefore, also soil community structures, since influenced by these factors, varied between study plots and no specific community could be determined for either larch or pine forest. Still, the more uniform mixed forests seemed to reconcile and attenuate the high variabilities in environmental and site parameters of the pure forests and thus harboured a more stable soil invertebrate community.

The method of DUFRENE & LEGENDRE (1997) has been developed to find taxa that are frequent and abundant in and thus characteristic for a certain habitat (Table 3). Taxa that have been identified as characteristic in our study are taxa that are commonly known to inhabit the respective layers. For soil and litter, earthworms, millipedes, and insect larvae have primarily been corroborated, all of them demonstrably inhabitants of the soil ecosystem. For the surface, millipedes and spiders have been confirmed. When comparing forest types, it is most notable that the mixed forests harbour not only the most stable soil invertebrate community, but also the highest number of characteristic taxa (all three layers collectively). It has been widely recognized that the number of tree species is positively correlated with habitat heterogeneity and thus with epigeic species richness (e.g. RODRIGUES et al. 2017, MAGURA et al. 2006), confirming the need to support natural, native forests composed of several tree species.

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