

## Short- and long-term effects of fire on the Collembola communities of a sub-alpine dwarf pine ecosystem in the Austrian Alps

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### Abstract

We compared the Collembola communities of three sub-alpine sites in the Limestone Alps to evaluate the short- and long-term effects of natural forest fires. SITE 1 was burned in August 2003, SITE 2 was burned 50 years ago and sampled to assess the long-term effects of fire and the recovery of soil animals. A reference site (REF) was sampled to represent the undisturbed dwarf pine community. All sites are close to each other on a steep slope between 1 400 and 1 650 m above sea level. We found a total of 41 species of Collembola, as well as clear differences in the species composition and abundance between the sites. Most species (29) were found on the REF site. The highest abundance was found on SITE 1 (48 960 individuals\*m<sup>-2</sup>, 22 species). We assume that some species survived the fire in deeper soil layers and others migrated or were passively dispersed from unburned patches and surrounding sites. The lowest abundance and species number (8 160 individuals\*m<sup>-2</sup>, 18 species) were found on the 50-year-old site. This site was covered with a typical community for moving substratum, consisting mainly of alpine grasses, yet the dwarf pine vegetation had not yet recovered. The soil layer was still very thin and we therefore assume that a recovery of the Collembola community will take much longer than 50 years.

### Profile

Protected area

Kalkalpen National Park

Mountain range

Alps

Country

Austria

### Introduction

Fire is a common and destructive disturbance in terrestrial ecosystems. Large wildfires can destroy the above-ground vegetation and also change the belowground physical, chemical and biological properties. Secondary effects like enhanced erosion may result in a further loss of plant biomass and soil nutrients. However, fire is not deleterious for all organisms: some animals and plants are well adapted to this disturbance, for example in the Mediterranean regions and in Australia. Pyrophilous species of insects or fungi may even depend on it to thrive.

Certini (2005) reviews the effects of fires on the forest soil and distinguishes between 1) low to moderate fires and 2) severe fires. Most prescribed fires are of low intensity and can be used as a management tool without long-term effects on organism density and composition. Wildfires, on the contrary, are often of high intensity, occur during dry periods and have much larger and even irreversible effects on the ecosystem. Certini (2005) concludes that if plants succeed in recolonizing a burned site soon after the fire, the pre-fire conditions can recover within a short time. Neary et al. (1999) give a general review on the effects of fire on belowground systems and describe the physical, biogeochemical and biological effects. Low impact fires can encourage herbaceous flora, increase plant available nutrients and thin out overcrowded forests. Severe fires, on the contrary, change the mineralization rate, alter C to N ratios, influence above- and belowground species composition, decrease the micro- and macro-



Field work on a burned site in the Austrian Alps. © Erich Weigand, Kalkalpen National Park

fauna and alter the microbial population. Recovery time depends on fire intensity, the effects on key ecosystem processes and components, but also on previous land-use practices. Neary et al. (1999) conclude that the impact of fires can vary greatly and therefore is not predictable. Wildfire occurrences might increase in the future through a global increase in temperature and decrease in rainfall (McKenzie et al. 2004; Brennan et al. 2009; Lutz et al. 2009). Therefore, their importance in disturbance ecology will increase and their impact on ecosystems like national parks should be investigated further.

Collembola (springtails) are small, soil inhabiting, wingless insects. Like other edaphic arthropods, they may be especially affected by fires because they cannot escape the heat and generally depend on moist and

Table 1 – Species abundance table of the Collembola found in soil samples of three investigation sites of a study on wildfire. SITE 1 is a disturbed site that burned in 2003, SITE 2 burned in 1950 and REF is an undisturbed reference site. Values are individuals \* m<sup>2</sup>.

Species	SITE 1	SITE 2	REF
<i>Allacma fusca</i> (Linnaeus, 1758)	0	0	80
<i>Anurophorus laticis</i> (Nicolet, 1842)	0	0	40
<i>Bourletiella</i> (B.) <i>pistillum</i> (Gisin, 1946)	0	0	40
<i>Ceratophysella</i> sp1.	40	0	0
<i>Ceratophysella</i> sp2.	0	480	0
<i>Desoria</i> sp.	1 520	0	0
<i>Entomobrya nivalis</i> (Linnaeus, 1758)	0	0	40
<i>Entomobrya</i> sp.	240	0	560
<i>Folsomia penicula</i> (Bagnall, 1939)	1 680	1880	3440
<i>Heterosminthurus</i> sp.	160	240	0
<i>Hypogastrura cf assimilis</i> (Krausbauer, 1898)	17 320	560	0
<i>Isotoma</i> sp.	0	440	0
<i>Isotomiella minor</i> (Schäffer, 1896)	2 360	320	7 040
<i>Kalaphorura burmeisteri</i> (Lubbock, 1873)	520	0	480
<i>Lepidocyrtus cyaneus</i> (Tullberg, 1871)	2 880	0	40
<i>Lepidocyrtus</i> sp.	120	0	200
<i>Lipothrix lubbocki</i> (Tullberg, 1872)	0	0	120
<i>Mesaphorura sylvatica</i> (Rusek, 1971)	3 280	1 640	15 720
<i>Mesaphorura</i> sp.	200	0	1 120
<i>Neanura parva</i> (Stach, 1951)	0	40	0
<i>Odontella armata</i> (Axelson, 1903)	360	0	0
<i>Oligaphorura absoloni</i> (Börner, 1901)	0	360	0
<i>Onychiroides pseudogranulosus</i> (Gisin, 1951)	1 760	280	80
<i>Onychiurus fimetarius</i> (Linnaeus, 1767)	920	0	0
<i>Onychiurus vontoernei</i> (Gisin, 1957)	1 040	40	2 040
<i>Onychiurus</i> juv.	2 440	40	80
<i>Orchesella montana</i> (Stach, 1960)	0	160	0
<i>Parisotoma notabilis</i> (Schäffer, 1896)	10 040	1 280	2 320
<i>Pseudachorutes subcrassus</i> (Tullberg, 1871)	0	240	80
<i>Pseudanurophorus boernerii</i> (Stach, 1922)	200	0	1 520
<i>Pseudisotoma sensibilis</i> (Tullberg, 1876)	0	0	160
<i>Seira</i> sp.	0	0	40
<i>Sminthurides</i> sp.	40	80	120
<i>Sminthurus maculatus</i> (Tömösvary, 1883)	0	0	40
<i>Tetracanthella stachi</i> (Cassagnau, 1959)	560	0	1 040
<i>Thaumanura oniscooides</i> (Latzel, 1917)	0	0	120
<i>Tomocerus minor</i> (Lubbock, 1862)	1 280	40	800
<i>Tullbergiinae</i> sp.	0	40	0
<i>Willemia anophthalma</i> (Börner, 1901)	0	0	160
<i>Willemia denisi</i> (Mills, 1932)	0	0	200
<i>Xenylla</i> sp.	0	0	5 360
<b>Total number of individuals * m<sup>2</sup></b>	<b>48 960</b>	<b>8 160</b>	<b>43 080</b>
<b>Total number of species per site</b>	<b>22</b>	<b>18</b>	<b>30</b>

cool conditions in the litter and upper soil layers. The high temperatures of an intense fire usually reach these strata and may destroy the life therein. Most studies investigating the effects of fire on Collembola have been conducted in habitats where fires are a common disturbance, e.g. in Australia (Greenlade 1997; Driessen & Greenlade 2004) or Finland (Koponen 1988, 1989, 1995; Huhta et al. 1967, 1969). They found recovery times varying between a few to over 20 years, depending on the intensity of the fire.

In the Central Alps, fires are less frequent and a rarely studied disturbance. Gimmi et al. (2004) investigated

the fire frequency and Wohlgemuth et al. (2002, 2005) the ecological resilience of the plant and animal communities in the Swiss Alps after a large fire of 300 ha in 2003. Some species there may benefit from the disturbance. Early successional or ruderal species are able to colonize burned sites and species-rich mosaics of spatial patches may develop. Very few species are truly fire-dependent but the rare carabid beetle *Agonum bogemanni* is an example (Peter Zulka, Vienna Univ., oral comm., September 2006). If the occurrence of wildfires will increase in the future because of climate warming, the Alps will also be affected. This should be con-

Table 2 – Species (Sørensen Index) and dominance similarity (Bray-Curtis Index) of the Collembola faunas in soil samples of three investigated sites of a study on wildfire. For site codes, see Table 1.

Bray-Curtis Index		
	REF	SITE 2
SITE 2	21.39	–
SITE 1	29.38	21.29
Sørensen Index		
	REF	SITE 2
SITE 2	42.55	–
SITE 1	62.75	55.00

sidered in conservation and management of protected areas, especially in nature reserves and national parks. A recent wildfire in the Austrian Alps offered the opportunity to investigate the short-term (1 year) and long-term (50 years) effects of high intensity burning in a sub-alpine habitat and to compare the recovery times of the vegetation and the Collembola to studies in other parts of the world. Both sites are close to each other and to an undisturbed reference site, so we assumed that all three had a similar dwarf pine vegetation and Collembola community prior to the fires. As large natural wildfires are rare in the Eastern Alps, no comparable sites were found to replicate the experiment.

## Material and Methods

### Study area

The study area is situated in the north-eastern Limestone Alps in the Sengsengebirge (Kalkalpen National Park; Upper Austria). This mountain range stretches in a roughly east-west direction and rises up to 2000 m. Sub-alpine dwarf pine vegetation (*Erico-Pinion mugi* Leibundgut 1948) covers its steep south-facing slopes above the timber line. Dwarf pines (*Pinus mugo*) are dominant here and form an impenetrable thicket, with Winter Heath (*Erica carnea*) and Hairy Alpine Rose (*Rhododendron hirsutum*) underneath. Individual larch (*Larix decidua*) and Norway spruce trees (*Picea abies*) are interspersed among the dwarf pines. The soil is a Tangelrendzina (Austrian soil classification: Kilian 2002), covered with a 15–20 cm layer of raw humus. We selected three sites on the slope, all close to each other, at altitudes ranging from 1400 to 1650 m.

### SITE 1

In August 2003, an area of 15 ha (centre of the site: 14°18' E, 47°46' N; SW exposition; slope: 35°) burned for 8 days (August 17 to 24) during a very dry weather period, probably due to natural lightning. The fire was fought from the ground and with helicopters, but no retardant was used. During the fire, all dwarf pines, most of the larch trees and large parts of the raw humus layer burned. The rainfall of autumn 2003 and the snow melt in spring 2004 eroded large parts of the remaining soil and ash. The result was a patchy

mosaic of soil remnants, rock and scree. At the time of sampling (10 months after the fire), the vegetation was very sparse and consisted only of a few remaining or colonizing species (*Funaria hygrometrica*, *Campanula cochlearifolia*, *Calamagrostis villosa*, *Erica carnea*, *Galium anisophyllum*, *Heleborus niger*).

### SITE 2

Close to SITE 1, a similar dwarf pine stand of 12 ha (S exposition; slope 30–40°) burned for three weeks from 29 June 1950. We used this area to investigate the long-term effects of fire and the subsequent succession of Collembola for 50 years.

The plant community was dominated by grasses, all other plants appeared in low coverage. Sociologically, it belonged to the association of *Athamanto-Trisetum distichophyllum* (Jenny-Lips 1930) which is typical for moving limestone scree (Seibert 1974; Englisch et al. 1993). In addition, *Carex sempervirens* and *Sesleria albicans* were found in high coverage. These two species are typical of the formation of *Seslerio-Caricetum sempervirentis* (Beger 1922) (Grabherr et al. 1993; Oberdorfer 1974/76) which grows on reposing limestone scree and is often associated and interspersed with the *Athamanto-Trisetum distichophyllum* (Ellenberg 1996).

The dwarf pines, larch trees and Norway spruce trees were not fully recovered and the vegetation was generally patchier than SITE 1. The soil layer was still shallow, probably due to heavy erosion over the last 50 years and the movements of the limestone scree.

### REF

A reference site north of SITE 1 was sampled to represent the undisturbed Collembola fauna. We assume that the Collembola fauna of the REF site was identical to the fauna of SITE 1 and SITE 2 prior to the fire. The tree, shrub and herb layers were well developed at the site. A sparse moss layer was also found. The tree layer consisted of two species, *Picea abies* and *Larix decidua* (2.35 stems \* 100 m<sup>-2</sup>). The shrub layer was dominated by *Pinus mugo*. Within the herb layer, the acidophilus species *Vaccinium myrtillus*, *V. vitis-idea* and *Erica carnea* dominated in high coverage and constancy. The plant association was a *Homogyno-Piceetum* (Zukrigl 1973), which is often found along the timberline in the Northern Alps (Seibert 1988; Mertz 2002).

### Field sampling

Collembola were sampled at the three sites on 26 June 2004, shortly after snowmelt. On each site, ten soil cores were taken with a 57 x 57 mm<sup>2</sup> steel tube (Bruckner 1998) to a depth of 100 mm, stored in plastic bags and cooled until extraction. The cores were taken at random positions with a minimum spacing of 5 m, wherever sufficient substratum was available and within an area of 1000 m<sup>2</sup> each site. The samples were taken to the laboratory and extracted in a modified Macfadyen-Extractor for seven days into 10% benzoic acid solution. The Collembola were transferred

to 70% ethanol, counted and identified using the keys of Babenko et al. (1994), Bretfeld (1999), Gisin (1960), Potapow (2001), Stach (1960, 1963), Thibaud et al. (2004) and Zimdars & Dunger (1994).

#### Data treatment

With the full data set, the species similarity of the faunas on the three sites was calculated with the Sørensen Index, and similarity of the dominant species with the Bray-Curtis index. The dominance structure of the communities was compared graphically with rank-abundance plots.

Prior to the multivariate data analyses, species with less than three individuals per core were removed from the data (25 species remained); accordingly, two samples (one in SITE 1 and one in REF) were classified as outliers ( $> 2$  SD average distance longer than overall mean multivariate distance) and not included in the analysis. Non-metric multidimensional scaling (NMDS, Bray-Curtis-similarity, McCune & Grace 2002: 125ff) was performed to ordinate the individual samples along axes in multidimensional species space and separate the three sites. We tested for significant differences between the three faunas in ordination space with a nonparametric procedure (MRPP; multi-response permutation procedure, McCune and Grace 2002: 188ff). We used PRIMER 5.2.9 (Clarke & Gorley 2001) for the calculation of the Sørensen and Bray-Curtis Index, and PC-ORD 4.25 (McCune & Mefford 1999) for the multivariate analyses.

#### Results

We collected 2505 Collembola specimens in the soil samples. They belonged to 41 species (Table 1). Clear differences were found in total Collembola abundance and species richness among the three sites: SITE 1 had the highest abundance of 48 960 individuals  $\cdot$  m<sup>-2</sup> and 22 species. *Hypogastrura cf. assimilis*, *Parisotoma notabilis* and *Mesaphorura sylvatica* were the most abundant species. SITE 2 showed the lowest number of individuals (8160  $\cdot$  m<sup>-2</sup>) and also the lowest species richness (18). *Folsomia penicula*, *Mesaphorura sylvatica* and *Parisotoma notabilis* were the most abundant species.

The highest species richness was found on the REF site with 29 species and a high abundance of 43 080 individuals  $\cdot$  m<sup>-2</sup>. *Mesaphorura sylvatica*, *Xenylla sp.* and *Isotomiella minor* were the most abundant species.

Species similarity (Sørensen Index, Table 2) was moderately high between the REF and SITE 1 faunas; lower between the SITE 1 and SITE 2 faunas; and lowest between REF and SITE 2. The similarity of the dominants (Bray-Curtis Index, Table 2) was low between REF and SITE 2 and between SITE 1 and SITE 2; and slightly higher between REF and SITE 1. The rank-abundance plots of the three sites are approximately linear and very similar (Figure 1). A small number of dominant species makes up a large proportion of the catch. Most other species occur in inter-

mediate to low abundance. Therefore, the fire did not affect the dominance structure of the site faunas.

The ordination of the 28 samples with the non-metric multidimensional scaling (NMDS) did not reveal a strong multivariate gradient separating the three sites along any of the axes. Indistinct site clusters are evident, however, in plots of the first three axes (Figure 2). This clustering was significant (MRPP;  $T = -11.17$ ,  $p = 2 \cdot 10^{-8}$ ).

#### Discussion

We found substantial compositional differences between the Collembola faunas of the three investigated sites. This shows that fires may have significant short- and long-term effects on the Collembola communities in sub-alpine habitats.

The result of low abundance and species richness at SITE 2, compared to the reference site, is initially surprising, as we would have expected extensive recovery of the Collembola community after 50 years of post-fire succession. Other authors found much faster recovery times: Sgardelis & Margaris (1993), Majer (1984), Metz & Farrier (1973) and Seastedt (1984) estimated short recovery times (3–4 years) after controlled and less destructive fires. Jahn et al. (1970) investigated the succession of Collembola on another burned alpine site (Tyrol, Austria, 1 600–2 137 m), the only other study investigating the effect of fire on Collembola in the Alps. They found that the number of individuals and species declined in the first year and was still lower eleven years after the fire, but had recovered after twenty years. Koponen (1988, 1989 and 1995) found lower densities of springtails and mites, instable and divergent communities four years after a fire in Finland. Similar results were presented by Huhta et al. (1967, 1969) in central Finland, where seven years were insufficient for the communities to recover. But Koponen and Huhta et al. only investigated short-term effects and did not sample after longer recovery times. Long-term effects (8–11 and 27 years) were investigated by Driessen & Greenslade (2004) in Australian lowland grasslands. They found some differences in the species composition in the younger regrowth site but not in the older site. Shaw (1997) found depauperate communities on two sites that burned twenty years ago and again five years prior to sampling. He also described a strong rise of Collembola densities three months after a shallow fire and accounted for this with enhanced egg germination due to the fire. The recovery times of Collembola communities found by other authors varied greatly and probably depended mainly on the intensity of the fire but also on the seasonality of the fire and the local adaptation of the habitat to this disturbance.

However, if secondary effects of the fire are considered, the reasons for the slow recovery of the fauna on SITE 2 are obvious and correspond to the development of vegetation. The soil was probably denuded

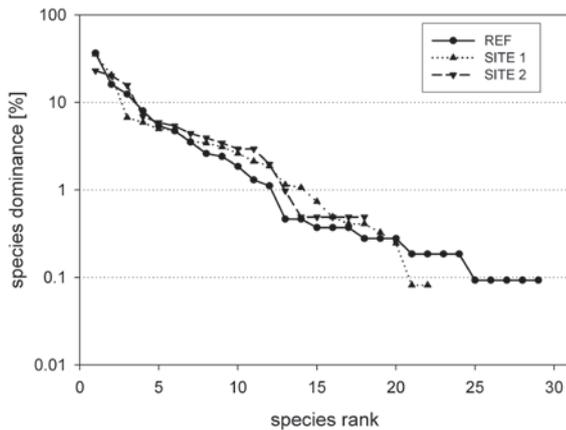


Figure 1 – Rank-abundance curve for the *Collembola* from three investigation sites of a wildfire study. For site codes, see Table 1.

after the fire of 1950 and, because of the steep inclination, heavy rains and intensive snow melt each spring, the soil developing processes were retarded afterwards. A shallow soil layer discourages the development of larger plants, which by itself would stop erosion more effectively. As a result of the missing humus layer, the rocks become destabilized (Conedera 2005), creating a moving substratum on the steep slopes. This also prevented the original vegetation from recolonizing the site. Limestone and the shallow humus body below the rock contain sufficient nutrients (Zöttl 1952) but only few plant species can survive on moving rubble. This substratum can only be colonized by species able to dam up moving rocks, wander downward or overgrow the moving scree. A change to alpine grassland and later to the original dwarf pine is only possible when rock fall has stopped. This succession is not expected within the next centuries due to the very short vegetation period each year (June to September).

In our case we found a long-term reduction in the quality of the ecosystem. But small and short fires might also improve the quality of the whole ecosystem when a larger area, such as the entire national park, is considered. Small wildfires can enhance the total species

richness when new species can establish themselves at the site and a more diverse mosaic of microhabitats can develop. In contrast, long and large fires should be prevented by the management of the national park as they favour erosion processes. We found a severe impact on the soil animal community that could result in a lower soil quality.

The short grass vegetation and shallow soil layer of SITE 2 exhibit a more extreme microclimate than the dwarf pine stand and can affect the *Collembola* community indirectly: 1) higher temperatures occur in summer due to the steep inclination and southern exposition, 2) colder temperatures occur in winter due to lack of a buffering dwarf pine layer, and 3) drought occurs because the soil layer is too thin to store significant amounts of humidity and limestone itself does not hold water. 4) Wind action can be expected to be another major factor. This also coincides with the hypothesis of Certini (2005) and Webb (1994) that the recovery time of the animal assemblages after fires depends very much on the recovery of the vegetation. As a result of these secondary effects, we predict a decline of the number of species and abundance for SITE 1 over the next 50 years towards a community similar to that of SITE 2. These results contradict those of Wolgemuth et al. (2005) and Schönenberger & Wasem (1997) who reported a rather fast recovery of the plant cover of burned sites in Wallis (southern Switzerland). Especially *Calamagrostis varia* was found within one year in their sites. This plant may derive from surviving rhizomes below the ash layer (Wolgemuth et al. 2005). On the site in Austria, the soil layer was almost completely destroyed by the fire of 2003 and we do not expect a recovery from the seed bank or surviving rhizomes.

The recently burned SITE 1 exhibited high *Collembola* abundance and species number. This was unexpected, since the fire severely reduced the humus layer, and we expected it to have a devastating impact on the soil fauna. *Hypogastrura cf. assimilis*, *Parisotoma notabilis* and *Mesaphorura sylvatica* were the dominant species at this site and seem to benefit from the disturbance or were

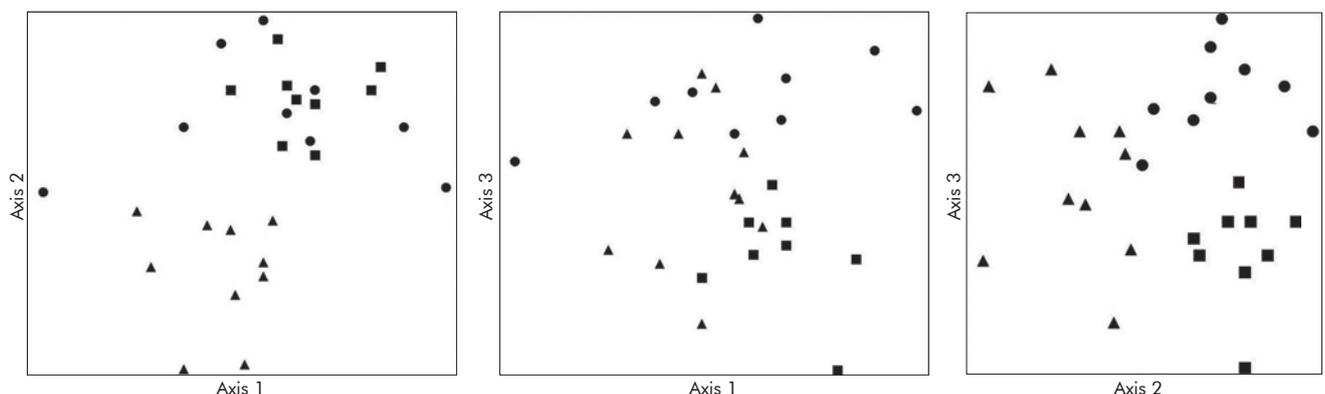


Figure 2 – Ordination of 25 samples along (a) axes 2 and 1, (b) axis 3 and 1 and (c) axis 3 and 2 in a multidimensional space (non-metric multidimensional scaling; NMDS). SITE 1 (▲) is a disturbed site that burned in 2003, SITE 2 (■) burned in 1950 and REF (●) is an undisturbed reference site.



Effects of fire on a sub-alpine dwarf pine ecosystem in the Austrian Alps. © Erich Weigand, Kalkalpen National Park

the first to recolonize the site. *Hypogastrura cf. assimilis* is described as a eurytopic species, *Parisotoma notabilis* is one of the most ubiquitous species and *Mesaphorura sylvatica* also occurs widely, both are found in all kinds of habitats. None of these species is specific to the early stages of the succession (few studies have investigated succession of Collembola in the Alps). *Folsomia penicula*, *Mesaphorura sylvatica* and *Parisotoma notabilis* were the dominant species of the 50-year old burned site. In the future it should be investigated if this is a stable climax community. *Folsomia penicula* is described as mesophilic, is mostly a forest species and usually found in high abundances. *Mesaphorura sylvatica*, *Xenylla sp.* and *Isotomiella minor* are the dominant species of the undisturbed site and this should be part of a stable climax community. *Xenylla sp.* was not identified to species level (it may be a new species) so we cannot say anything about its ecology. Both *Mesaphorura sylvatica* and *Isotomiella minor* are not typical Alpine species. *Isotomiella minor* is also described as one of the most ubiquitous species and occurs in all kinds of habitats. After Deharveng (oral comm. at the Aperygota conference in Siena, September 2010), *Parisotoma notabilis* and *Isotomiella minor* each are probably a group of species.

Our findings indicate that survival of resident species and immigration from outside may have a role in this: 1) Collembola may have survived the fire in deeper soil layers. They are known to migrate into deeper soil layers (up to 10 cm) during unfavorable conditions, for example heat or drought (Hopkin 1997: 168). As the fire occurred in a very hot and dry summer period, animals might have survived within the site. Webb (1994) showed in experimental fires that the heat does not penetrate deeper than 5 cm into the soil and that microarthropods can survive. 2) Active migration/recolonization over short distances from the small unburned patches within the site (as proposed by Bellido 1987 or Shaw 1997) and/or from the surrounding unharmed dwarf pine stands is possible, since microarthropods can migrate a few meters within a short time (Hågvar 1995). 3) Passive dispersal of animals with water and soil substrate after heavy rains and snowmelt from upslope areas was probably

the most important factor. As Collembola can be active under the snow cover (Aitchison 1979, 1984) and reproduce fast (Hopkin 1997: 133), they had enough time to recover during the ten months after the fire. Our results underline the fact that identification to species level provides much deeper ecological insights than the mere counting of individuals. We found similar abundances on SITE 1 and the REF site, but the species compositions were significantly different. Conclusions in the literature on the recovery times, based on abundances only, do not account for the potential extinction of certain species, recolonization by others and compositional changes in the community as a whole. Even the identification of morpho-species, as done in Australia by Greenslade & Driessen (1999), can give a better resolution.

We are aware that the successional stages in our investigation were not replicated, so that the generality of the results is debatable. Larger studies with a detailed resolution of chronosequences are needed to investigate further the long-term effects of fires on Collembola in the Alps and to test the prediction of a species loss within 50 years after the fire. Sites older than 50 years could reveal the time needed to reach an ecological climax. The only study in the Alps sampling a large number of sites at different successional stages was done by Moretti et al. (2004), who sampled 22 sites in the southern Alps of Switzerland to investigate the effects of single and repeated forest fires on the species richness of ground beetles, hoverflies, bees, wasps, spiders, bugs and lacewings. In Australia, Greenslade & Driessen (1999) sampled 27 Buttongrass moorland sites for the Collembola communities with a chronosequence ranging from one month to 64 years since the last fire.

Friend (1996) suggested in his review six invertebrate groups (spiders, butterflies, isopods, Isoptera, Thysanoptera and Blattodea) as indicator groups for fire disturbances.

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