Ecological responses of semi-natural grasslands to abandonment: case studies in three mountain regions in the Eastern Alps

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Abstract Semi-natural, extensively managed, grasslands are among the most species-rich agroecosystems in Europe. However, they are threatened by abandonment. We investigated the response of semi-natural grasslands to cessation of mowing at ten sites in three UNESCO Biosphere Reserves in Switzerland and Austria. We assessed vegetation characteristics, topsoil properties and microbially mediated soil processes by comparing once-a-year mowed with adjacent long-term abandoned grasslands on semi-dry, nutrient-poor, base-rich soils. Plant litter decomposition was determined using standardized substrates (Tea Bag Index). Soil microbial community composition was assessed by

phospholipid fatty acid analysis. Abandonment altered floristic composition by replacing shade-intolerant or low-growing grassland species, in particular character species of the alliance *Bromion erecti*, with medium- to tall-sized grasses (e.g. *Brachypodium pinnatum*) and tall herbs (e.g. *Laserpitium latifolium*). Time since abandonment had an influence on the magnitude of successional changes after abandonment. Cessation of mowing increased above-ground phytomass but decreased plant species richness and evenness. Abandonment increased soil microbial biomass, promoted litter decomposition and led to an increased soil organic carbon, C:N ratio, and inorganic N supply. Our findings also showed that abandoned grasslands dominated by grasses remained shrub- and treeless for several decades.

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Introduction

Mountain regions are worldwide of utmost importance to biodiversity (MacDonald et al. 2000). In the Eastern Alps and in many other European mountain regions, unfavourable topographical and climatic conditions preclude an intensive agricultural land use. Thus, the agricultural landscape is characterized by a high proportion of extensive grasslands. Extensively managed grasslands (one cut each year in mid-summer without organic or inorganic fertilization, no over-sowing or herbicide

treatment) in the montane and subalpine regions represent low productive, species-rich, semi-natural plagioclimax communities. Especially semi-natural, dry, calcareous grasslands belong to the most species-rich agroecosystems in Europe, and thus have a great nature conservation value (Poschlod and Wallis De Vries 2002). During the twentieth century, the number and area of this habitat type decreased dramatically due to intensification of grassland management, abandonment, afforestation or conversion to other land-use types. Nowadays, semi-natural calcareous grasslands are threatened throughout Europe (Poschlod and Wallis De Vries 2002). The maintenance of these species-rich grasslands by extensive management is therefore an important conservation target in Europe.

Several studies have investigated the ecological consequences of grassland abandonment (Moog et al. 2002; Niedrist et al. 2009; Walcher et al. 2017; Hussain et al. 2018). However, little information is available on concurrent changes of soil properties (Köhler et al. 2001; Oelmann et al. 2017; Zeller et al. 2001).

From a climate change point of view, information on alterations in litter decomposition and soil organic carbon (SOC) sequestration after abandonment are important because of their feedbacks on climate processes. Also, from an environmental and nature conservation viewpoint, more detailed information on soil and vegetation changes induced by abandonment are desirable because alterations in plant diversity, composition and structure of grassland communities as well as changes in soil physical, chemical and microbiological properties may have long-term consequences for the provision of ecosystem services (ESs).

Litter decomposition in the soil influences build-up of soil organic matter (SOM) and provides the primary source of inorganic N for plants and soil organisms in semi-natural grasslands (Parton et al. 2007). Soil N supply, in turn, plays a major role in determining species composition, plant diversity and productivity of the grassland vegetation, thereby influencing the rate and pattern of successional changes in grassland communities after abandonment (Tilman 1987). Litter decomposition is mainly controlled by microclimate, litter quality and by the diversity, composition and activity of the soil decomposer community (Scherer-Lorenzen 2008). Soil microbial communities are strongly influenced by climate (especially precipitation), vegetation, soil properties and land use (De Vries et al. 2012). Abandonment may alter the size, activity and composition of the soil microbial biomass through vegetation changes (plant biomass production, rhizodeposition,

vegetation composition, species dominance, plant diversity) and soil changes (pH, N supply, quantity and quality of SOM, soil temperature and moisture).

For landscape management it is important to know whether the environmental impacts of abandonment are primarily site- or habitat-specific. If semi-natural grasslands from different mountain regions in the Eastern Alps respond to abandonment consistently, we would be able to identify a general successional pattern and to predict the environmental impacts of abandonment more generally. This, in turn, is important for setting priorities in species and habitat conservation as well as for developing general landscape management recommendations.

The objective of this study was to evaluate the ecological responses of semi-natural grasslands to abandonment in different mountain regions in the Eastern Alps. We hypothesized that abandonment leads to consistent changes of vegetation, soil and microbial properties within the same habitat type under different climatic conditions, which in turn influences major ecosystem processes (plant biomass production, litter decomposition, SOC sequestration, N cycling) in a similar vein. We focused on extensively managed grasslands on semi-dry, nutrient-poor, base-rich soils because this habitat type is threatened throughout Europe by land-use change.

Material and methods

Study regions and study sites

The study was conducted in three mountain regions (Val Müstair, Central Ennstal, Great Walsertal) in the Swiss and Austrian Alps representing low-, intermediate- and high-rainfall areas, respectively (Fig. 1, Table 1). Within each study region, we compared long-term (> 30 years) extensively managed grasslands with immediately neighbouring abandoned grasslands. Altogether, we surveyed ten regularly managed (mown) and ten abandoned (unmown) grasslands at various sites in different regions. At each study site, managed and adjacent abandoned grasslands did not differ in their abiotic site conditions (topography, bedrock, soil type, soil thickness). The study sites were particularly suited for this ‘paired-site’ study because they enabled the use of chronosequences (space-for-time substitution) to study the long-term ecological consequences of grassland abandonment (Walker et al. 2010).

Fig. 1 Location of the study regions in the Swiss and Austrian Alps

The study sites were located in the montane and subalpine belt on south-facing slopes. Altitude varied from 660 to 1,800 m a.s.l. (Table 1). Soil types were nutrient-poor, well-aerated Rendzinas and calcic Cambisols developed over limestone or marl with mull humus and a loose, porous crumb structure in topsoil. Thickness of A horizon varied from 20 to 90 cm. The managed grasslands were mown once a year, usually between mid-July and the beginning of August, and received neither farmyard manure nor mineral fertilizers. None of the traditionally managed grassland sites was grazed, re-seeded or irrigated. Before cessation of mowing, the abandoned grasslands were also used as extensively managed grasslands. Therefore, we assume that the initial plant species composition, species

richness, soil properties and soil microbial community composition of both land-use types were similar. The time elapsed since abandonment varied from 15 to 60 years. During the successional time, there was no human-mediated disturbance at the studied abandoned grassland sites. However, localized natural biotic disturbance through the activity of small rodents (e.g. voles) or browsing by wild animals (e.g. deer) cannot be ruled out. Phytosociologically, the managed grasslands belonged to the alliance *Bromion erecti*, which is widely distributed throughout Europe (Mucina et al. 2016; Willner et al. 2019). The plant communities within this alliance are characterized by a restricted water and nutrient supply (lack of plant available nitrogen and phosphorus), low productivity and high vascular plant

Table 1 Characteristics of the study regions and study sites

Environmental variables and management history	G. Walsertal (Vorarlberg, Austria)	V. Müstair (Graubünden, Switzerland)	C. Ennstal (Styria, Austria)
Geographic location of the study sites	47°14' – 47°15' N 9°57' – 9°58' E	46°36' – 46°37' N 10°21' – 10°25' E	47°31' – 47°40' N 14°04' – 14°35' E
Number of study sites	3	3	4
Years since abandonment	35–60	15–20	20–40
Altitude of the study sites [m a.s.l.]	1,180–1,250	1,740–1,800	660–790
Mean annual air temperature [°C]	+5.7	+5.9	+6.9
Mean air temperature January [°C]	–2.4	–2.8	–3.9
Mean air temperature July [°C]	15	16	17
Mean annual precipitation [mm]	1,637	811	1,219

species richness (Köhler et al. 2001). The abandoned grasslands represented plant communities in a successional stage characterized by the dominance of tall grasses (*Brachypodium pinnatum* stage). The surrounding vegetation of the study sites were forests, hedgerows, shrub communities and more intensively managed permanent meadows.

Vegetation survey and phytomass harvest

Vegetation surveys were carried out in June 2015. At each site an area was selected which was fairly uniform with respect to topography, soil type and vegetation. Within this area, four plots (1×1 m), each spaced 5 m apart, were placed side by side (Fig. 2). The choice of the plot size (1 m^2) for the measurement of vegetation characteristics was governed by the need to compare our results with data from literature. To avoid edge effects, at each study site the spatial distance between managed and abandoned plots was at least 20 m. Vegetation surveys were carried out with a modified Braun-

Blanquet scale for species cover consisting of three subdivisions per cover class (Supplementary Table S1; Braun-Blanquet 1964). Only vascular plant species were recorded. Taxonomy and nomenclature follows Fischer et al. (2008). All plots were revisited in August 2015 to ensure that late-flowering species had not been missed. For vegetation analyses, means of the minimum and maximum of modified Braun-Blanquet cover-class-ranges were used.

To assess vegetation changes due to abandonment, the following plant parameters were analysed (i) total vegetation cover, cover of plant functional groups (grasses, herbs, legumes) and individual cover of all vascular plant species; (ii) species richness (number of species per plot), Shannon index and evenness; (iii) flower traits (colour, abundance, cover); (iv) plant strategy types according to (Grime 1977) and four plant traits (life span, type of reproduction, Raunkiaer life form, type of rosettes, unweighted in each case); (v) unweighted Ellenberg indicator values for light, soil moisture and nutrient availability (Ellenberg et al. 2001).

Fig. 2 Schematic overview of the study and sampling design

Total vegetation cover, flower cover and cover of plant functional groups were recorded as percentage cover per m². The flower cover was estimated both in June and August 2015, reflecting different phenological stages of the plant community. Plant traits were selected based on field experience and from information in the literature (Prévosto et al. 2011). Plant strategy types, plant traits and flower colour were abstracted from the BIOLFLOR database (Klotz et al. 2002). Both plant traits and Ellenberg indicator values were not weighted by abundance because in species-rich vegetation types weighted and unweighted averages usually give similar results (Diekmann 2003).

Standing phytomass was assessed on a 50 × 50 cm area of each plot in June 2015 (Fig. 2). The plants were clipped by hand shears at the soil surface. The harvested phytomass was sorted into five categories: grasses, herbs, legumes, necromass and biomass. In this study, we distinguished between biomass (living green plant tissue), necromass (dead tissue on the plant), phytomass (biomass plus necromass) and plant litter (dead plant material at the soil surface). Plant samples were dried at 60°C for 72 h.

Soil sampling and soil analysis

At each study site, six individual soil samples were taken randomly outside of each vegetation plot at a distance of 1 m with a soil corer (4 cm diameter). Soil sampling was performed in June and August 2015 from the main rooting zone of the plants (0–10 cm depth). Samples were mixed to obtain one composite sample per site and sampling date (Fig. 2). We only sampled the uppermost 10 cm of the soil because this soil layer responds most sensitively to changes in grassland management (Bohner et al. 2016). Soil samples were transported to the laboratory in cool boxes and stored at –20°C until analyses. An aliquot of each sample was air-dried and passed through a 2-mm sieve for the analysis of basic soil parameters. Total carbon (C_{tot}) and total nitrogen (N_{tot}) were determined by dry combustion (1,250°C) using an elemental analyser (LECO TruMac, LECO Corp., St. Joseph, USA). Carbonate was measured gas-volumetrically. Organic carbon (C_{org}) was calculated as the difference between total C and carbonate C. Soil pH was measured in 0.01 M CaCl₂ solution at a soil-to-solution ratio of 1:2.5 using a glass electrode. NH₄-N and NO₃-N were determined colourimetrically

after extraction with 1 M KCl (Hood-Nowotny et al. 2010). Soil microbial community composition was assessed in June and August 2015 by analysing the microbial phospholipid fatty acid (PLFA) composition (Hackl et al. 2005). Therefore, soil (1.5 g fresh weight) was extracted with a buffer mixture consisting of chloroform:methanol:citrate buffer (1:2:0.8, v/v/v). The lipids were separated into neutral lipids, glycolipids and phospholipids on a silicic acid column. After a mild alkaline methanolysis the phospholipid methyl esters were separated on an Agilent 6890 gas chromatograph equipped with a flame ionization detector (Agilent Inc., Santa Clara, CA, USA). Methyl non-adeconoate fatty acid (19:0) was added as internal standard in order to quantify peak areas. A standard qualitative bacterial acid methyl esters mix (BAC mix) and a standard qualitative fatty acid methyl esters mix (FAME mix; both Sigma Aldrich Co., St. Louis, MO) were also measured to allow identification of the fatty acid peaks. In total, 31 PLFAs were identified. The total amount of PLFAs was used as a measure of the active soil microbial biomass (Zeller et al. 2001).

At each study site, in June and August 2015 gravimetric soil water content was determined using four soil cores (0–10 cm depth, diameter 4 cm) and soil temperature was measured in 5 cm depth using four insertion thermometers (Votcraft DET3R, Conrad Electronic SE, Hirschau, Germany). The measurements were taken outside of the vegetation plots at a distance of 1 m (Fig. 2).

Litter decomposition

Litter decomposition was determined using the ‘tea bag index’ (TBI; Keuskamp et al. 2013). The TBI consists of two parameters: litter decomposition rate (k) expresses the velocity of decomposition, while litter stabilization factor (S) expresses the inhibiting effect of environmental conditions on the decomposition. Both parameters are based on weight loss of litter material. Two tea types with contrasting decomposition characteristics were used: green tea (*Camellia sinensis*; Lipton, EAN 87 22700 05552 5) with high cellulose content and expected fast decomposition and rooibos tea (*Aspalathus linearis*; Lipton, EAN 87 22700 18843 8) with high lignin content and expected slow decomposition (Keuskamp et al. 2013). At each study site, ten pairs of green and rooibos tea bags were buried in June 2015 in

8 cm soil depth outside of the vegetation plots at a distance of 1 m (Fig. 2). The tea bags were retrieved after a field incubation period of 52 and 79 days. The tea bags were cleaned from adhered soil particles and roots, dried at 70°C for 48 h and weighed. Stabilization factor *S* and decomposition rate *k* were calculated using the hydrolysable fraction of green tea (0.842 g·g⁻¹) and rooibos tea (0.552 g·g⁻¹).

Statistical analysis

Normal distribution of residuals was checked with qq-plots and Shapiro-Wilk tests, homogeneity of variances with histograms and Bartlett-tests. When assumptions were met, we performed analyses of variances (ANOVAs) with management, sampling date and region (block) as factors. When sampling date was not significantly different, means between the two sampling dates were analysed. If assumptions for parametric statistics were not met we applied Box-Cox transformations or performed non-parametric Kruskal-Wallis tests. For post-hoc comparisons of ANOVAs, we used Tukey tests. Correlations were tested with Pearson's correlation coefficient. Differences in plant species composition were analysed by principal coordinate analyses (PCO) using PerMANOVA by applying a Bray-Curtis distance matrix and 9,999 permutations. The assumption of homogeneity of multivariate dispersions among treatments for PerMANOVA was checked. PerMANOVA was carried out with Primer (Primer6 and Permanova+ 2003), all other statistical analyses with R (version 3.1.1; R Development Core Team 2014). All results were stated as statistically significant if $P < 0.05$.

Results

Vegetation characteristics

In all study regions, mean species richness, Shannon-Index and evenness were significantly lower on abandoned than on managed plots (Tables 2 and 3). Across study regions, species composition of the vegetation was significantly affected by abandonment. Abandoned plots were clearly separated from managed plots by the first axis in the PCO-plot (Fig. 3). In each study region, vegetation composition differed considerably between

Table 2 ANOVA and Kruskal-Wallis results for the effects of management and region on vegetation characteristics

Parameter	Treatment	Region	Treatment × region
	$F_{1, 78}$	$F_{2, 77}$	$F_{2, 77}$
Total vegetation cover	41.921*	39.440*	6.846*
Ag phytomass	25.451*	5.807*	2.242
Ag plant biomass	5.054*	18.099*	1.241
Necromass	34.853*	2.631	
Species richness	135.320*	12.962*	3.196*
Shannon-Index	84.779*	1.621	3.456*
Evenness	56.534*	0.580	5.575*
EIVI	40.322*	1.994	1.722
EIVm	5.714*	1.978	0.437
EIVn	0.408	7.306*	6.169*
Legumes	27.984*	4.974*	8.107*
Herbs	13.670*	6.190*	4.340*
Grasses	0.055	4.812*	0.492

*After values refer to significant differences ($P < 0.05$). Ag – Above-ground, EIVI – Ellenberg light indicator, EIVm – Ellenberg soil moisture indicator, EIVn – Ellenberg nutrient availability indicator

abandoned and managed plots but was quite similar within the abandoned and managed plots (Fig. 3).

The dominant species in managed plots was *Bromus erectus*. In abandoned plots, however, *Brachypodium pinnatum* was dominant (Supplementary Table S2). Most of the plant species in abandoned plots were common and widespread species whereas character species of the alliance *Bromion erecti* were scarce. Only a few species were restricted to abandoned plots (*Trifolium medium*, *Vicia sepium*, *Cephalanthera damasonium*, *Epipactis atrorubens*, *Galeopsis tetrahit*, *Anthericum ramosum*, *Lilium bulbiferum* subsp. *bulbiferum*, *Hypericum perforatum*, *Rubus idaeus*, *Rosa* species). Most of them are usually found in forests, forest edges and forest clearings. In abandoned plots, seedlings of *Fraxinus excelsior* were the most abundant woody plants (cover: always less than 0.5 %, frequency: 15%).

Managed plots were dominated by light-demanding and drought-tolerant, low soil fertility grassland species. The mean Ellenberg indicator value for light was significantly lower on abandoned than on managed plots whereas that for soil moisture was significantly higher. The mean Ellenberg indicator value for nutrient availability, however, showed no consistent trend in response to abandonment (Tables 2 and 3).

Table 3 Vegetation parameter of the managed and abandoned grasslands under study

Parameter	Region	Managed grasslands	Abandoned
Total vegetation cover [%]	G. Walsertal	98.3 ± 1.3	99.0 ± 0.0
	V. Müstair	97.1 ± 1.9	99.4 ± 0.5
	C. Ennstal	92.6 ± 6.8	97.8 ± 1.4
Above-ground phytomass [g·m ⁻² ·DM]	G. Walsertal	391.8 ± 138.3	559.8 ± 116.0
	V. Müstair	298.1 ± 81.1	428.5 ± 219.0*
	C. Ennstal	520.5 ± 115.2	560.4 ± 112.8*
Above-ground plant biomass [g·m ⁻² ·DM)	G. Walsertal	258.2 ± 57.9	266.2 ± 61.6
	V. Müstair	143.4 ± 40.4	166.6 ± 83.6
	C. Ennstal	189.9 ± 66.8	248.1 ± 63.6*
Necromass (g·m ⁻² ·DM)	G. Walsertal	4.1 ± 2.3	27.9 ± 35.7*
	V. Müstair	2.3 ± 2.8	95.4 ± 78.6*
	C. Ennstal	12.0 ± 21.2	63.5 ± 55.5*
Species richness	G. Walsertal	30.8 ± 3.6	13.7 ± 2.4*
	V. Müstair	25.0 ± 5.1	12.6 ± 3.1*
	C. Ennstal	31.3 ± 7.1	20.3 ± 6.1*
Shannon index	G. Walsertal	2.21 ± 0.2	1.38 ± 0.2*
	V. Müstair	2.48 ± 0.2	1.11 ± 0.4*
	C. Ennstal	2.46 ± 0.6	1.51 ± 0.5*
Evenness	G. Walsertal	64 ± 0.1	53 ± 0.1*
	V. Müstair	78 ± 0.1	44 ± 0.2*
	C. Ennstal	72 ± 0.1	50 ± 0.1*
Ellenberg light indicator	G. Walsertal	7.2 ± 0.2	6.7 ± 0.2*
	V. Müstair	7.2 ± 0.1	6.8 ± 0.5*
	C. Ennstal	7.1 ± 0.2	6.8 ± 0.2*
Ellenberg soil moisture indicator	G. Walsertal	4.1 ± 0.2	4.4 ± 0.4*
	V. Müstair	4.1 ± 0.2	4.2 ± 0.4
	C. Ennstal	4.3 ± 0.5	4.4 ± 0.4
Ellenberg nutrient availability indicator	G. Walsertal	3.7 ± 0.3	3.1 ± 0.3*
	V. Müstair	3.1 ± 0.4	3.6 ± 0.8
	C. Ennstal	4.0 ± 0.8	4.0 ± 0.9

*After values refer to significant differences within a region ($P < 0.05$). Means ± *SD*, $n = 3$ for G. Walsertal and V. Müstair, $n = 4$ for C. Ennstal, DM – dry mass

Grasses were the dominant functional group across all sites. The proportion of both herbs and legumes was significantly lower on abandoned than on managed plots (Table 4). Vegetation on all plots was dominated by perennials which accounted for more than 90% of the total vegetation cover. Proportion of perennials was significantly higher on abandoned than on managed plots, while that of biennials was significantly lower. Proportion of species reproducing by seeds only was significantly lower on abandoned than on managed plots. Proportion of hemicryptophytes was significantly

lower and that of chamaephytes was slightly lower on abandoned than on managed plots, while the proportion of both geophytes and phanerophytes was comparatively higher; proportion of therophytes was similar in both land-use types. Proportion of erosulate plants was significantly higher on abandoned than on managed plots, while that of hemirosette plants was significantly lower. Proportion of competitors was significantly higher on abandoned plots compared to managed plots whereas that of ruderals was significantly lower. Proportion of stress-tolerators was unaffected.

Fig. 3 Principal coordinate analysis (PCO) showing plant species composition in managed and abandoned grasslands in three different regions in the Eastern Alps. $n = 3$ for G. Walsertal and V. Müstair, $n = 4$ for C. Ennstal

At peak season, total vegetation cover, above-ground phytomass, above-ground plant biomass and necromass were significantly higher on abandoned than on managed plots (Table 2). Biomass to necromass ratios varied from 2 to 10 in abandoned and from 16 to 63 in managed plots. In both land-use types, the necromass was mainly composed of dead grass leaves, which were concentrated in the lower canopy layer.

At peak flowering season in June, the percentage of flowering species and the flower cover were significantly lower on abandoned than on managed plots whereas in August after mowing both parameters were comparatively higher, though not significantly, on abandoned plots (Table 4). In both land-use types, the prevalent flower colours of blooming plants were yellow and white. On managed plots, the flower colours were more evenly distributed than on abandoned plots.

Table 4 Vegetation parameter of the managed and abandoned grasslands under study

Parameter	Managed grasslands	Abandoned grasslands
Plant functional groups		
Grasses [%]	64	76
Herbs [%]	28	21*
Legumes [%]	8	3*
Life span		
Annual [%]	3.8	3.1
Biennial [%]	3.7	0.5*
Perennial [%]	92.5	96.4*
Type of reproduction		
Only by seed [%]	24.8	17.4*
Mostly by seed, rarely vegetatively [%]	23.0	24.6
By seed and vegetatively [%]	50.4	53.9
Mostly vegetatively, rarely by seed [%]	1.8	4.1
Raunkiaer life form		
Therophytes [%]	3.3	3.2
Hemicryptophytes [%]	83.2	77.9*
Geophytes [%]	5.1	8.2
Chamaephytes [%]	4.2	3.0
Phanerophytes [%]	4.2	7.7
Type of rosettes		
Erosulate plant [%]	24.9	36.8*
Hemirosette plant [%]	63.6	53.0*
Rosette plant [%]	11.5	10.2
Plant strategy types		
Competitors [%]	53	60*
Stress-tolerators [%]	26	26
Ruderals [%]	21	14*
Flower colour (flowering plants)		
Blue [%]	10.5	2.5*
Brown [%]	1.2	0.8
Yellow [%]	35.8	48.2
Green [%]	2.8	1.6*
Red [%]	17.6	16.3*
White [%]	32.1	30.6
Flower abundance (June)		
Flowering species [%]	30.7	17.7*
Flower cover [%]	3.85	0.80*
Flower abundance (August)		
Flowering species [%]	3.6	7.1
Flower cover [%]	0.28	0.29

*After values refer to significant differences ($P < 0.05$)

Topsoil properties

Across study regions, both the concentration of C_{org} and the C:N ratio in topsoil were significantly higher on abandoned than on managed plots (Table 5). The soil organic C (SOC) accumulation as a result of abandonment was associated with N_{tot} enrichment in all study regions, except V. Müstair. At the sampling date in June, the NH_4 -N concentration in topsoil was significantly higher on abandoned plots compared to managed plots (Table 5). In the uppermost soil layer of both land-use types, the concentration of NO_3 -N was significantly lower than that of NH_4 -N. The topsoils (0–10 cm depth) of both land-use types were in the carbonate buffer range (pH $CaCl_2$: > 6.2 ; Table 6). Soil temperature in 5 cm depth at the two sampling dates in June and August 2015 was significantly lower on abandoned than on managed plots in V. Müstair and C. Ennstal (Table 6). In all study regions, except V. Müstair, soil moisture in the layer 0–10 cm tended to be higher in abandoned than in managed plots.

Soil microbial community composition varied considerably among study regions. The total amount of PLFAs and the relative proportions of the functional groups of soil microorganisms revealed no significant differences between managed and abandoned plots (Table 5). In all study regions, the soil microbial community was dominated by bacteria (Supplementary Table S3). Generally, gram-negative bacteria represented the largest proportion of total PLFAs. In each study region, the proportions of gram-positive bacteria, gram-negative bacteria and arbuscular mycorrhizal fungi (AMF) were slightly higher in abandoned than in managed plots. For other functional groups, no consistent trend was observed. The ratio of gram-positive to gram-negative bacteria was only slightly affected by abandonment. The ratio of bacterial to fungal PLFA was higher, though not significantly, in abandoned than in managed plots. The total amount of PLFAs correlated positively with concentrations of C_{org} ($\rho_{sumPLFA, C_{org}} = 0.900$, $P < 0.001$), N_{tot} ($\rho_{sumPLFA, N_{tot}} = 0.887$, $P < 0.001$), NH_4 -N in August ($\rho_{sumPLFA, NH_4-N} = 0.789$, $P < 0.001$), NO_3 -N in August ($\rho_{sumPLFA, NO_3-N} = 0.663$, $P = 0.003$) and soil moisture ($\rho_{sumPLFA, moisture} = 0.805$, $P < 0.001$).

Table 5 ANOVA results for the effects of management and region on soil physical and chemical parameters, soil microbial community composition and litter decomposition

Parameter	Treatment <i>F</i>	Region <i>F</i>	Treatment × Region <i>F</i>
Soil physical and chemical parameters ¹			
Soil temperature [°C]	22.870*	52.230*	1.800
Soil moisture [% of pore volume]	1.921	46.711*	2.405
pH (CaCl ₂)	1.236	1.859	0.794
C _{org} [g kg ⁻¹]	7.922*	23.394*	2.103
N _{tot} [g kg ⁻¹]	1.963	27.333*	1.733
C:N ratio	15.622*	10.447*	0.796
NH ₄ -N [μg·g ⁻¹ dry soil] – June	11.906*	2.805	1.181
NO ₃ -N [μg·g ⁻¹ dry soil] – June	1.238	0.670	0.090
NH ₄ -N [μg·g ⁻¹ dry soil] – August	3.135	8.504*	2.329
NO ₃ -N [μg·g ⁻¹ dry soil] – August	0.002	11.828*	0.435
Soil microbial community ¹			
Total PLFAs [nmol·g ⁻¹ dry soil]	3.271	19.596*	0.183
Gram ⁺ bacteria [%]	0.526	12.375*	0.010
Gram ⁻ bacteria [%]	0.270	2.419	0.158
Fungi [%]	0.094	25.780*	1.243
Arbuscular mycorrhizal fungi [%]	0.544	12.848*	0.044
Actinomycetes [%]	0.016	15.356*	0.522
Unspecific bacteria [%]	0.003	4.207*	0.002
Protozoa [%]	0.007	9.793*	0.004
Others [%]	3.716	50.242*	0.451
Bacteria:fungi ratio	1.005	30.520*	0.126
Litter decomposition ²			
Litter decomposition rate <i>k</i>	51.042*	18.128*	6.453*
Stabilization factor <i>S</i>	42.841*	141.984*	7.371*

*After values refer to significant differences ($P < 0.05$). ¹: *d.f.* treatment: 1, 16; region: 2, 15. ²: *d.f.* treatment: 1, 190; region: 2, 189

Litter decomposition

Across study regions, litter decomposition rate and stabilization factor were significantly higher on abandoned than on managed plots. Both parameters varied considerably among study regions, being highest at the subalpine site V. Müstair (Table 5, Fig. 4). Decomposition rate and stabilization factor correlated positively with necromass ($\rho_{k,necromass} = 0.638$, $P = 0.006$; $\rho_{S,necromass} = 0.521$, $P = 0.030$). Stabilization factor correlated negatively with N_{tot} in the topsoil ($\rho_{S,N_{tot}} = -0.537$, $P = 0.022$).

Discussion

Vegetation changes due to abandonment

Abandonment caused a marked decrease in species richness, Shannon-Index and evenness on all study sites, illustrating the importance of regular mowing for the maintenance of high plant species richness in semi-natural grasslands (Ryser et al. 1995; Böhner et al. 2012). Our findings also suggested that the similarity in plant species composition between abandoned and adjacent managed grasslands decrease with increasing

Table 6 Basic soil physical and chemical properties of the studied managed and abandoned grasslands. Mean values from two sampling dates in June and August 2015

Parameter	Region	Managed grasslands	Abandoned
Soil temperature [°C] ^x	G. Walsertal	15.8 ± 0.7	14.9 ± 1.0
	V. Müstair	13.9 ± 0.5	11.9 ± 0.9*
	C. Ennstal	20.6 ± 1.8	16.9 ± 1.9*
Soil moisture [% of pore volume] ^x	G. Walsertal	80.0 ± 8.8	83.4 ± 15.4
	V. Müstair	45.5 ± 4.7	42.5 ± 7.4
	C. Ennstal	29.8 ± 13.0	43.6 ± 14.3
pH [CaCl ₂] ^x	G. Walsertal	6.4 ± 0.8	7.0 ± 0.2
	V. Müstair	6.4 ± 1.3	6.3 ± 0.8
	C. Ennstal	6.7 ± 0.9	7.1 ± 0.2
C _{org} [g kg ⁻¹] ^x	G. Walsertal	107.9 ± 20.2	138.1 ± 42.1*
	V. Müstair	62.6 ± 5.0	62.2 ± 7.9
	C. Ennstal	55.2 ± 21.3	90.7 ± 22.6*
N _{tot} [g·kg ⁻¹] ^x	G. Walsertal	10.6 ± 1.9	11.8 ± 3.9
	V. Müstair	5.2 ± 0.4	4.5 ± 0.9
	C. Ennstal	5.2 ± 2.0	7.7 ± 1.2
C:N ratio ^x	G. Walsertal	10.2 ± 0.2	11.9 ± 0.8
	V. Müstair	12.0 ± 0.4	14.2 ± 2.3
	C. Ennstal	10.7 ± 0.4	11.7 ± 1.3
NH ₄ -N [μg·g ⁻¹ dry soil] – June ^y	G. Walsertal	15.9 ± 1.1	24.9 ± 7.4
	V. Müstair	19.9 ± 5.0	21.5 ± 1.0
	C. Ennstal	13.5 ± 1.6	20.0 ± 4.7
NO ₃ -N [μg·g ⁻¹ dry soil] – June ^y	G. Walsertal	1.3 ± 0.6	2.1 ± 1.7
	V. Müstair	0.9 ± 0.5	1.7 ± 1.6
	C. Ennstal	0.6 ± 0.6	1.2 ± 0.6
NH ₄ -N [μg·g ⁻¹ dry soil] – August ^y	G. Walsertal	39.5 ± 3.1	44.9 ± 9.1
	V. Müstair	34.8 ± 3.4	33.0 ± 4.6
	C. Ennstal	26.4 ± 3.1	35.1 ± 4.8
NO ₃ -N [μg·g ⁻¹ dry soil] – August ^y	G. Walsertal	10.8 ± 3.4	10.1 ± 0.7
	V. Müstair	6.7 ± 0.8	6.1 ± 0.8
	C. Ennstal	6.1 ± 1.3	6.8 ± 0.7

*After values refer to significant differences within a region ($P < 0.05$). Means ± *SD*, ^x: $n = 6$, ^y: $n = 3$

successional age. After cessation of mowing the dominant species shifted from the tussock-forming grass *B. erectus* to the vegetatively propagating grass *B. pinnatum* with extensive rhizomes and therefore highly competitive in abandoned grasslands (Grime et al. 1988).

Only a few plant species were restricted to abandoned grasslands, indicating a low habitat-specific species pool of grass-dominated successional communities. With just a few exceptions (e.g. *L. bulbiferum* subsp. *bulbiferum*), regionally rare or endangered plant species

did not benefit from abandonment. Abandonment favoured tall and broad-leaved grasses (*B. pinnatum*, *Arrhenatherum elatius*) at the expense of small- to medium-sized, fine-leaved grasses (*Festuca rupicola*, *F. rubra*). A few legumes (*T. medium*, *V. sepium*) also benefited from abandonment. *Vicia sepium* is a scrambling legume with leaf tendrils, which is advantageous on abandoned sites. Tall herbs (especially *Laserpitium latifolium*) and clonally proliferating species such as *Galium album* were also promoted by abandonment. Based on results from this study and in accordance with

Fig. 4 Litter decomposition rate (k) and stabilization factor (S) in managed and abandoned grasslands in three different regions in the Eastern Alps. Means $\pm$ SD, $n = 3$ for G. Walsertal and V.

Müstair, $n = 4$ for C. Ennstal. * denotes significant differences between managed and abandoned grasslands (Tukey-HSD, $P < 0.05$), n.s. no significant differences

other studies (Böhner et al. 2012; Prévosto et al. 2011), the following plant attributes appear to be important in grassland succession: tall stature, leaves evenly distributed along the erect stem (erosulate plants), broad leaves, competitive strategy, perennial life cycle, below-ground reserve organs (geophytes), vegetative propagation via rhizomes (rhizomatous species), scrambling life form (leaf tendrils), tolerance to low light availability at different stages.

In the abandoned grasslands under study, there was no significant invasion of shrubs and trees even after 60 years of secondary succession. We assume that the germination and establishment of woody plants is impeded by a virtually closed sward and by accumulated necromass, retarding further succession to shrub communities. This finding is supported by several other studies (Böhner et al. 2012; Moog et al. 2002).

The managed and abandoned grasslands studied differed greatly in physiognomy and flowering phenology, which might also affect insects (Walcher et al. 2017; Hussain et al. 2018).

Topsoil changes due to abandonment

Across study regions, abandoned grasslands had significantly higher soil C_{org} concentrations than managed grasslands primarily due to higher rates of soil C inputs

resulting from greater above-ground phytomass. Across study regions, abandonment increased soil C:N ratio, indicating that the cessation of mowing favours accumulation of less humified organic matter in topsoil. Since SOC accumulation generally involves the sequestration of soil N (Stevenson and Cole 1999), grassland abandonment frequently leads to enrichment of N_{tot} in the surface soil layer. In abandoned grasslands, the soil N supply was higher than in managed meadows because of higher rates of N inputs to the soil resulting from plant litter decomposition. At all study sites, NH_4^+ was the major form of inorganic soil N at the time of sampling, indicating a low nitrifying capacity of the studied semi-dry, nutrient-poor grassland soils. Similar effects of grassland abandonment on topsoil properties were observed in many other studies (Knops and Tilman 2000; Köhler et al. 2001; Tilman 1987; Zeller et al. 2001). The higher above-ground plant biomass and the denser surface layer of necromass at abandoned sites reduced average soil temperature and increased soil moisture (Facelli and Pickett, 1991).

Soil microbial community composition (PLFA) differed significantly among study regions but was not significantly affected by abandonment. This indicates that functional groups of soil microorganisms are more strongly influenced by local abiotic site conditions than by species composition of the vegetation (litter quality), plant community productivity (litter quantity) and plant

species richness (litter diversity). This finding is in agreement with that of other studies (De Vries et al. 2012; Zeller et al. 2001). For most of the functional groups of soil microorganisms no consistent response to abandonment was obvious except for gram-positive bacteria, gram-negative bacteria and AMF, which slightly benefited from the cessation of mowing. Abandonment increased the bacteria:fungi ratio, presumably because of an enhanced soil water and inorganic soil N supply (De Vries et al. 2012; Hackl et al. 2005). The results of our correlation analysis suggested that microorganisms benefit from a high concentration of C_{org} in topsoil, from an enhanced inorganic soil N supply and improved soil water availability, indicating that resource availability (nutrients, water) has a strong influence on soil microorganisms (De Vries et al. 2012).

Changes in litter decomposition due to abandonment

The decomposition rate of both litter types was significantly higher on abandoned than on managed plots, indicating more favourable soil environmental conditions for decomposer microorganisms in abandoned semi-dry grasslands (Zhang et al. 2008). Thus, abandonment may accelerate litter decomposition in the topsoil at least during dry periods through increased soil water availability, leading to a faster N cycling and hence higher grass cover (Tilman and Downing 1994) in abandoned grasslands. Under semi-dry soil conditions, the positive effect of higher soil water availability after abandonment on microbial litter decomposition might be stronger than the negative effect of lower soil temperature (Butenschoen et al. 2011; Garcia-Palacios et al. 2016). Across study regions, litter stabilization factor, which is indicative for long-term C storage (Keuskamp et al. 2013), was significantly higher on abandoned plots compared to managed plots. We assume, that abandonment of semi-natural grasslands promotes SOC sequestration in the topsoil despite higher litter decomposition rates because a higher proportion of plant litter presumably enters the permanent (passive) SOM pool (Schulze et al. 2000). Our results demonstrate that abandonment of semi-natural grasslands promotes SOC sequestration in the topsoil not only by increasing plant litter inputs to the soil (Bohner et al. 2006), but also by converting more plant litter into SOM.

Ecosystem services

The cessation of mowing promotes SOC sequestration but can have detrimental effects on ESs linked to aesthetic values, if abandonment leads to grass-dominated, less colourful plant stands and can even affect human health aspects (Arnberger et al. 2018a, b). A high aesthetic value of semi-natural grassland communities as a result of great herb diversity is hardly compatible with SOC sequestration because annual mowing without manuring over a long period together with removal of the mown biomass inevitably leads to C losses in the topsoil (Bohner et al. 2016). To optimize the provision of ESs at the landscape scale, a mosaic of different land-use types and management intensities, including abandoned grasslands of different successional age, seems necessary.

Conclusions

Contrary to our hypothesis, the results show that several vegetation, soil and microbial parameters display no consistent trend during secondary succession in semi-natural grasslands on semi-dry, nutrient-poor, base-rich soils under different climatic conditions. Our study shows that vegetation parameters in general respond more sensitively and less site-specific to abandonment than soil and microbial parameters at the plant community scale, making the former a more reliable indicator of successional changes. Among the studied soil parameters, C:N ratio in topsoil seems to be the best parameter for monitoring successional changes due to abandonment.

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