



Using diatoms and physical and chemical parameters to monitor cow-pasture impact in peat cores from mountain mires

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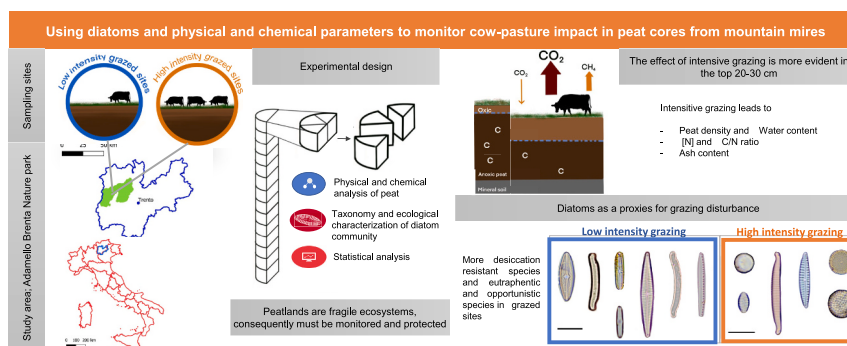
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HIGHLIGHTS

- The effects of cattle grazing on mires were assessed using chemistry and diatoms.
- Grazing increased dewatering and N, primarily in the top part of the peat.
- Diatoms can serve as reliable proxies for grazing-induced disturbance.
- More eutraphentic and aerial diatom species in grazed sites.
- Even if impacted, Alpine peatlands can host threatened Red List species.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:

Grazing
C cycle
C/N ratio
Bioindicator
Red list
Eutraphentic diatoms
Aerial diatoms

ABSTRACT

Peatlands play a crucial role in carbon (C) sequestration and biodiversity conservation. However, these environments are highly vulnerable, and Europe has lost >60 % of its peatland habitat in recent decades. Cattle grazing and trampling contribute to peatland degradation, which generally result in a shift from moss-dominated vegetation to vascular plants and in lower C sequestration rates. Overgrazing poses also a significant threat to habitat integrity and biodiversity, especially in the Alpine area, where close-to-pristine mires with high ecological integrity are becoming extremely rare. Thus, a more in depth understanding of how cattle grazing and trampling are threatening Alpine mires is strongly needed for a sustainable management and conservation of these habitats. The objective of this study was to examine the impact of grazing on the physical, chemical, and biological characteristics of peat, with a focus on diatoms. To answer such a question, seven 50-cm deep cores were collected from mires located in the Adamello-Brenta Nature Park (North of Italy) along a grazing-induced disturbance gradient. Results indicated that grazing primarily affected at least the upper 15 cm of the peat, resulting in increased density and reduced water content, due to compaction, and lower C-to-nitrogen ratio,

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<https://doi.org/10.1016/j.scitotenv.2024.171779>

Received 22 November 2023; Received in revised form 14 February 2024; Accepted 15 March 2024

Available online 18 March 2024

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possibly caused by both cow manure inputs and increased peat mineralization. Moreover, almost 200 diatom taxa were recorded across the 7 cores, with several of them falling under threat categories in the Red List for central Europe. The higher percentage of eutraphentic species in highly-grazed areas was related to the increase in nutrients caused by cattle manure. Finally, intense grazing increased the share of taxa that are more likely to survive in environments with unstable water availability (= aerial species). We showed that diatom data, supported by physical and chemical parameters, can be a refined tool to inform mire protection and rehabilitation.

1. Introduction

Peatlands are terrestrial waterlogged ecosystems formed when the production of organic matter (OM) exceeds its decomposition. This is generally due to challenging conditions such as acidic pH, often low nutrient levels, water saturation, reduced oxygen (O₂) availability, and low temperatures (Clymo, 1991), which prevent plant material from complete decomposition and lead to the formation of peat (Clymo, 1983). Actually, the upper section of a peat profile (generally referred to as the acrotelm), undergoes oxidation processes, while in deeper layers (catotelm) only anoxic decay occurs. At the same time, while on one side the top peat layers are exposed to oxidation for decades or centuries, water table level is highly dynamic, thus meaning that a drop in its level may 'move' peat layers that are currently part of the catotelm to become again part of the acrotelm (van Bellen et al., 2020).

Under undisturbed conditions, peat may sum up 90–95 % water by weight, thus making peatlands a unique kind of natural OM-rich water system (Shotyk, 1988; Zaccone et al., 2009, 2017). The OM content in peat is generally >65 %, with carbon (C) ranging between 50 and 60 % (Zaccone et al., 2007; Loisel et al., 2014); consequently, despite their limited global extent (~3 %), peatlands play a crucial role in the global C cycle, serving as the largest net terrestrial reservoir of C worldwide and encompassing about 21–25 % (610–644 PgC) of the global soil organic C stock (Loisel et al., 2021).

At the same time, peatland ecosystems are highly vulnerable to changing climatic conditions and human activities, particularly because of global warming and altered precipitation patterns. Historically, peatlands have acted as significant C sinks, but the rising temperatures associated with climate change and human disturbance are elevating net primary production (NPP) and ecosystem respiration, thereby impacting their role in the C cycle (Gong et al., 2013; Bragazza et al., 2016). Moreover, changes in precipitation patterns result in decreased water table depths and in more surface aerobic conditions, that accelerate the decomposition of OM; this is causing a shift in the C balance of peatlands, i.e., from being primarily C sinks to potential C sources (Wellock et al., 2011). Peatland degradation represents a significant portion of global annual emissions of atmospheric CO₂ (Parish et al., 2008). Europe, which has historically undergone extensive peatland drainage for agriculture and forestry, has experienced a substantial peatlands loss. More than 75 % of peatland areas are degraded in 20 European countries, underscoring the widespread and growing anthropogenic pressure on these ecosystems (Tanneberger et al., 2021). Human activities, primarily agriculture and forestry, cover >25 % of the global peatland area and have opposite impacts on C dynamics according to the different management practices carried out (Laine et al., 2009; Schrier-Uijl et al., 2011). Moreover, human-induced disturbances often yield cumulative effects that exceed the impacts of individual disturbances. This amplification of disturbances is evident in the synergy among drought, drainage, OM mineralization, and the increasing susceptibility and incidence of fires in peatlands (Page et al., 2002; Zaccone et al., 2014; Page and Baird, 2016). These complex interactions underscore the urgent need for comprehensive understanding and management strategies to safeguard the critical role of peatlands in the global C cycle as well as their ecosystem stability.

Grazing livestock on peatlands is a traditional practice worldwide. However, intensive grazing has detrimental effects, causing physical, chemical, and biodiversity degradation. Overgrazing leads to trampling,

compacting and eroding peat, and lowers the capacity of the biomass to grow and regenerate (Joosten et al., 2012). Cattle manure deposition provides nutrients, including nitrogen (N), which are often limited in oligotrophic mires. N enrichment may cause nitrous oxides (N₂O) release, accelerate peat decomposition, alter the vegetation composition, and favour disturbance-tolerant species while diminishing sensitive and rare bryophytes (Bragazza et al., 2004, 2006; Parish et al., 2008; Spitale, 2021).

Diatoms, microalgae in the Bacillariophyta division, are crucial indicators of aquatic ecosystem health due to their sensitivity to various factors like temperature, light, and nutrients. The diverse morphology of diatoms, supported by their resilient silica frustules, contributes to their taxonomic differentiation. Among the organisms colonizing mires, algae play an important role, despite being scarcely visible (e.g., Poulíčková et al., 2003; Ammann et al., 2013). Diatoms, even if less studied, are also usually relevant in mires (e.g., Watanabe et al., 2000), that can host communities with very high percentages of threatened species (Cantonati et al., 2011). Diatoms are widely represented in all types of peatlands; they are highly diverse, and their taxonomy is well-known. The diversity of diatoms in the peatlands of Europe is very high, with around 403 recorded taxa, and a major representation of the genera *Pinnularia* (14 %), *Eunotia* (10 %) and *Navicula* (10 %) with respect to the total number of taxa (Mutinová et al., 2017). Diatoms in mires have been very scarcely investigated in Italy (Dell'Uomo, 1992), and especially in the south-eastern Alps, where only two studies took place, i.e., a general hydrobiological investigation of the Fivè mire by Marcuzzi et al. (1971), and a more recent study on the taxonomy and ecology of diatom communities of shallow pools of the Danta di Cadore mires by Cantonati et al. (2011). Peatlands can host a high percentage of threatened and rare diatom species (Cantonati and Lange-Bertalot, 2011) according to the Red List (Hofmann et al., 2018). Cantonati et al. (2022) reported that endangered species are concentrated in dystrophic and oligotrophic environments. Moreover, diatoms and testate amoebae are strongly associated with the variation from dry to wet peat conditions, thus making them particularly suitable for quantitative reconstruction of water table depth associated to climate change and human disturbance (Mitchell et al., 2008; van Bellen et al., 2018; Fracasso et al., 2024). Thus, while these microorganisms may serve as useful paleo-bioindicators in mires due to both their sensitivity to environmental changes and their good preservation in peat (Fukumoto et al., 2012; Vidaković et al., 2016; King, 2020), there is a pronounced lack of studies about the ecology of diatoms in overgrazing-affected mires.

The aim of the present study is to provide evidence to address specific research questions related to the impact of overgrazing on mountain mires and the effects of livestock trampling and 'manuring' on the dynamics of both peat and diatom communities, in order to identify chemical and diatom proxies of the degree of peatland disturbance.

2. Materials and methods

2.1. Study area, site selection and peat sampling

The study was conducted in Adamello-Brenta Nature Park (Southern Alps, Autonomous Province of Trento, Italy). The Park has an area of 620.5 km², ranging in elevation from 477 to 3558 m a.s.l. Established in 1967, the Adamello-Brenta Nature Park became part of the European and World Geoparks Network of UNESCO in 2008, and is the largest

protected area in the Trentino Alto-Adige Region. This Park exhibits distinct lithological characteristics in its two sectors: the eastern region, known as the Brenta Dolomites, originated from sedimentary processes and consists of limestones and dolomite formations, whereas the western sector, dominated by the Adamello-Presanella mountain group, is primarily composed of volcanic rocks, which contribute to a lower permeability and the occurrence of alpine peatlands, including those investigated in this study.

The studied peatlands are located near the town of Madonna di Campiglio, and are part of the so-called Alta Val Rendena mires (Fig. 1). Here, a variety of peatland types, such as bogs, poor and rich fens, can be found. In a previous study, Spitale (2012) reported that bogs cover 177 ha, which correspond to 0.3 % of the total area of the park; however, in most of the cases, these peatlands exhibit signs of disturbance, predominantly attributed to either livestock trampling or drainage.

In order to discern the contrasting effects of intensive versus low grazing on peatlands, the quantification of cow trampling intensity was carried out by counting hoof prints within a circular area with a 5-m radius (Spitale, 2021). A gradient of grazing intensity was then established through the selection of seven sites, encompassing varying levels of disturbance.

Among the selected sites, all of them characterized by similar vegetation and formation patterns, the Canton Ritorto mire exhibited varying grazing intensity; here, two cores were collected in July 2020 along a grazing gradient, one representative of a highly grazed area (T1P) and the other a barely grazed area (T1C). In July 2021, an additional core was collected from the same mire (T3P) and one core from the Zeledria mire (ZEL), both featuring intensive grazing and degradation; peat cores were also collected from the Malghette (MAL1 and MAL2) and Patascoss (PAT) mires and identified as slightly grazed. Main features of the study sites are summarized in Table 1.

Peat sampling was carried out using a stainless-steel Belarus corer. Once collected, the 50-cm deep cores were photographed, wrapped in polyethylene film, and placed in half-cut PVC tubes to avoid compression. The cores were stored at -18°C , cut while frozen into 3 cm slices,

and each of them divided into sub-samples to allow physical, chemical and biological analyses.

2.2. Physical and chemical characterization

Bulk density was determined by dividing the dry weight (obtained at 105°C for 24 h) by the volume of each peat slice. The ash content, expressed as a percentage of the original dry weight, was determined by combustion in a muffle furnace at 550°C for 5 h. The water content was determined using Eqs. (1) and (2):

$$WC = \frac{W_w - D_w}{W_w} \times 100 \quad (1)$$

where WC is the water content (in %), while W_w and D_w are the wet and the dry weight (at 105°C), respectively;

$$GWC = W_m/D_w \quad (2)$$

where GWC is the gravimetric water content (as $g_{\text{water}}/g_{\text{peat}}$), W_m is the mass of water and D_w is the weight of dry peat.

Total C, hydrogen (H), N and sulfur (S) concentrations were determined by flash combustion using an elemental analyzer (CHNS vario MACRO cube, Elementar, Germany).

pH and electrical conductivity (EC) were determined on unfiltered porewater samples collected by squeezing following the method proposed by Shoty and Steinmann (1994). Due to the low availability of samples, porewater was extracted only from the first 6 cm of the peat cores, at 3 cm resolution, and from the layer at 12–15 cm of depth.

The thermal stability, often used as an indicator of OM recalcitrance (Zaccone et al., 2018), was assessed using a thermogravimetric analyzer coupled with simultaneous differential scanning calorimetry (TGA-DSC3+, Mettler Toledo, Switzerland). An aliquot of selected samples was placed in an alumina crucible and heated from 30 to 700°C at $10^{\circ}\text{C min}^{-1}$ under air using a flow rate of 100 mL min^{-1} . Several thermal proxies were obtained, including TG-T₅₀, which represent the

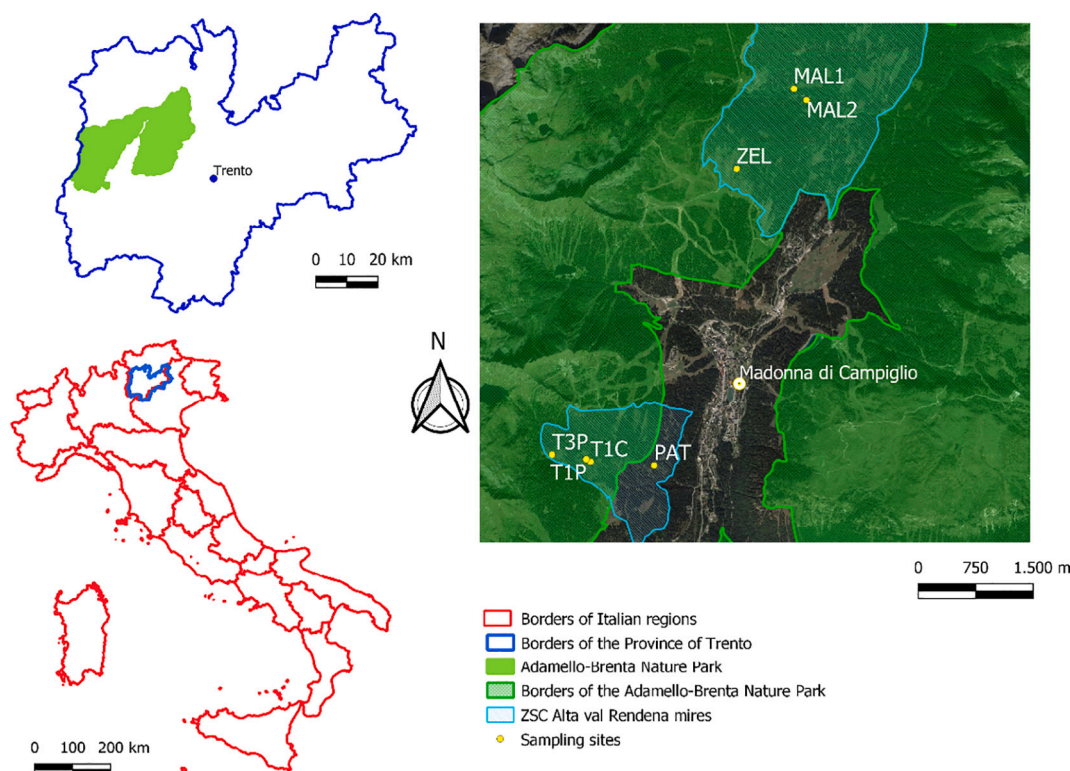


Fig. 1. Geographical location of the study area (Adamello-Brenta Nature Park, Italy), with a zoom on the sampling sites (see also Table 1).

Table 1
Main features of the sites studied.

	Site name	Core code	Coordinates	Elevation (m a.s.l.)	Sampling date	Main plants and bryophytes	Hoof prints
Low grazed sites	Canton di Ritorto	T1C	639106 E; 5120000 N	1777	2020-07-30	<i>Eriophorum vaginatum</i> , <i>Carex pauciflora</i> , <i>Drosera rotundifolia</i> , <i>Trichophorum cespitosum</i> , <i>Sphagnum angustifolium</i> , <i>S. subnitens</i> , <i>S. warnstorffii</i>	12
	Malghette	MAL1	641766 E; 5124927 N	1718	2021-08-26	<i>Andromeda polifolia</i> , <i>Carex echinata</i> , <i>C. nigra</i> , <i>C. pauciflora</i> , <i>Drosera rotundifolia</i> , <i>Menyanthes trifoliata</i> , <i>Sphagnum subnitens</i> , <i>S. angustifolium</i>	11
	Malghette	MAL2	641930 E; 5124780 N	1711	2021-08-26	<i>Andromeda polifolia</i> , <i>C. pauciflora</i> , <i>C. rostrata</i> , <i>Drosera rotundifolia</i> , <i>Trichophorum cespitosum</i> , <i>Sphagnum subnitens</i>	0
	Patascoss	PAT	639944; 5119938 N	1702	2021-08-26	<i>Molinia caerulea</i> , <i>Trichophorum cespitosum</i> , <i>Drosera rotundifolia</i> , <i>Carex nigra</i> , <i>Sphagnum angustifolium</i> , <i>S. subnitens</i>	5
High grazed sites	Canton di Ritorto	T1P	639050 E; 5120032 N	1782	2020-07-30	<i>Potentilla erecta</i> , <i>Eriophorum vaginatum</i> , <i>Drosera rotundifolia</i> , <i>Trichophorum cespitosum</i> , <i>Sphagnum subnitens</i>	65
	Canton di Ritorto	T3P	638603 E; 5120093 N	1782	2021-07-29	<i>Potentilla erecta</i> , <i>Trichophorum cespitosum</i> , <i>Drosera rotundifolia</i> , <i>Molinia caerulea</i> , <i>Sphagnum subnitens</i> , <i>S. subfulvum</i>	37
	Zeledria	ZEL	641017 E; 5123869 N	1953	2021-08-26	<i>Trichophorum cespitosum</i> , <i>Carex magellanica</i> , <i>Cladopodiella fluitans</i> , <i>Odontoschisma elongatum</i> , <i>Sphagnum subnitens</i> , <i>S. subsecundum</i>	51

temperature at which 50 % of the SOM mass is lost, and ratios between weigh loss (WL) occurring in specific temperature ranges ($WL_{350-450/250-350}$ and $WL_{400-500/200-300}$).

2.3. Biological analysis

An aliquot (~1 g) of peat material was removed from each slice. Peat samples were then treated with hydrogen peroxide, potassium dichromate, and hydrochloric acid, and cleaned valves were mounted in Naphrax® (Phyco Tech, St. Joseph, MI, USA). Slides, prepared material, and aliquots of the original samples were deposited in the diatom collection of the Science Museum of Trento (MUSE), Italy.

Permanent mounts were prepared for each sample, and a total of about 400 valves were counted at x1000 magnification considering the exact number of valves for each species and the number of fields of view observed. Relative and absolute abundances were calculated following Cantonati et al. (2023a). Identification and nomenclature were based on the following taxonomic references: Lange-Bertalot and Metzeltin (1996), Lange-Bertalot et al. (2011, 2017), and Krammer (1997, 2000, 2002). The most updated taxonomic concepts and nomenclature were applied in accordance with AlgaeBase (Guiry, 2023), DiatomBase (Kociolek et al., 2021), and Diatoms of North America (Spaulding et al., 2020). Light microscope observations and micrographs were conducted using a Zeiss Axioskop 2 microscope (Zeiss, Jena, Germany) equipped with phase-contrast and with an Axiocam digital camera. SEM observations were made at the Science Museum of Trento using a ZEISS EVO 40 XVP Scanning Electron Microscope at high vacuum on gold-coated prepared material.

2.4. Data processing and statistical analyses

The main factors tested in this work were grazing (low and high), defined on the base of trampling disturbance (see Section 2.1), and depth (0–15 and 15–45 cm), established according to the influence on main physical and chemical parameters of peat. One-way ANOVAs followed by Tukey tests were performed to assess significant differences in peat properties *i*) between low and high grazed sites at a fixed depth, and *ii*) between depths, within sites characterized by the same intensity of grazing. Results were considered significant with $p < 0.05$.

Non-metrical multidimensional scaling (NMDS) with Bray–Curtis dissimilarity matrix was used for exploring patterns of diatom species composition. The NMDS is a common approach for graphically represent relationships among samples in a multidimensional space (Legendre and Legendre, 1998). The sample units showed in the plot are in the same rank order as in the original distance matrix. Thus, similar samples are placed close in the plot, whereas dissimilar samples are far away from one another. In order to test for differences between low and high

grazing in the diatom assemblages, the permutational multivariate analysis of variance was used. The analysis (also known as *Adonis* in the R package *vegan*; Oksanen et al., 2019) is used to compare groups of objects and test the null hypothesis that the centroids and dispersion of the groups are equivalent. The multivariate analysis of variance was conducted using the Bray–Curtis dissimilarity matrix and the F test was assessed by random permutations of the samples between the two groups (high and low grazing).

All the statistical analyses were performed using R ver. 4.32 (R Core Team, 2023).

A threat status was assigned to all diatom species according to current Red List data (Hofmann et al., 2018). Ecological indicator values for pH, trophic state and moisture were reported following van Dam et al. (1994).

3. Results and discussion

3.1. Variation of physical and chemical properties of peat with grazing

Main physical and chemical properties of peat across all sites investigated are summarized in Table 2. The pH of the porewater ranges between 5.3 and 6.4, while the EC from 5.3 up to 107 $\mu\text{S cm}^{-1}$; this suggests that the studied mires are mainly poor-to-rich fens. Bulk density has been commonly reported to increase with depth, because of the weight of the overlying peat column (Zaccone et al., 2018). Average values of this parameter range from 0.078 ± 0.03 (living layer) to 0.173 ± 0.04 g cm^{-3} (at 36–39 cm of depth) in highly grazed sites, and from 0.049 ± 0.02 to 0.135 ± 0.03 g cm^{-3} in low grazed sites (Fig. S1). Thus, bulk density increases as a function of grazing intensity; in fact, high grazed sites show a significantly higher density compared to low grazed ones in both surface (0.177 and 0.120 g cm^{-3} , respectively) and deeper (0.131 and 0.082 g cm^{-3} , respectively) peat layers (Fig. 2a). This suggests the possible occurrence of mineralization processes, resulting in an enrichment of ash, and/or an increase in peat compaction.

In both high and low grazed sites, the content of water in peat decreases with depth (Fig. 2b,c; Fig. S1). However, high grazed sites are always characterized by a significant lower WC than low grazed in both surface (83 vs. 90 %, respectively) and deeper layers (80 vs. 84 %, respectively) (Fig. 2b). The same trend is observed also for the GWC (Fig. 2c). This lower water retention is possibly due to the physical degradation of peat caused by trampling which, in turn, results in an increase of peat compaction and density, and in a decrease of porosity (McCarter et al., 2020; Liu et al., 2022). In fact, a negative correlation is generally observed between WC and bulk density, as also reported in previous studies (Zaccone et al., 2009, 2018; Poto et al., 2013). Thus, peat from highly grazed sites is more degraded, decomposed and dense and therefore retains less water. If the WC decreases significantly, it

could lead to an increase of O₂ concentration within the peat profile and, therefore, to higher mineralization rates due to microbial respiration. Moreover, the decomposition rate could also be speed up by the N inputs in form of manure, being N generally a limiting nutrient in peatlands (Bragazza et al., 2004, 2006). Higher O₂ and N concentrations would therefore lead to an increase of the amount of mineral matter (i.e., ash) in peat, whose average and median content is much higher in peatlands characterized by high grazing intensity (Table 2), and promote more minerotrophic conditions.

Total organic C concentration in low intensity grazed sites is significantly smaller in the surface layers than in deeper ones (Fig. 2d); no significant differences are observed between low and high grazed sites at a fixed depth, and between depths in sites characterized by elevated grazing pressure (Fig. 2d). The same trend is observed for total N, with concentrations in low grazed sites significantly smaller in surface than in deeper layers (Fig. 2e). However, in such a case, the absence of significant differences between grazing intensities is due to the extremely high variability of N concentrations found (Table 2), especially in the top 9 cm (Fig. S1). In pristine peatlands, N is mostly retained by the vegetation and its belowground turnover is dominated by organic forms (Hemond, 1983; Urban and Eisenreich, 1988). At low background N deposition rates, the NPP of peatland forming mosses can temporarily increase as a response to an increased N deposition level (Blodau, 2002). However, such a response does not always occur (Williams et al., 1999; van der Heijden et al., 2000); in fact, manure results in increased N deposition levels that can even be detrimental to the *Sphagnum* NPP because nutrient imbalances develop (van der Heijden et al., 2000).

The C/N ratio, often used as a proxy of OM inputs and decomposition (Stevenson, 1982; Kuhry and Vitt, 1996), decreases with depth and clearly mirrors the effect of grazing. In particular, the average C/N ratio in surface peat (0–15 cm) is significantly higher in sites characterized by low intensity grazing (28.9) compared to that characterizing high grazed sites (20.6); no significant differences in C/N ratio in the deeper layer (15–45 cm) are found comparing low and high grazed sites (Fig. 2e; Fig. S1). The influence of grazing is also evident comparing C/N variation as a function of depth; in fact, while a significant difference between surface and deeper layer occurs in low grazed sites, in the high grazed ones the C/N ratio is extremely similar (Fig. 2e). This may suggest more decomposed surface OM in high grazed sites, with peat features resembling that of deeper layers. In fact, decomposed peat generally shows lower C/N ratios (Zaccone et al., 2007, 2018; Leifeld et al., 2020) due to a relative enrichment of total N with respect to organic C, as well as a residual enrichment of more recalcitrant compounds (Stevenson, 1982). These results are in agreement with a previous study comparing undisturbed and degraded peatlands, where lower C/N ratios were found in the degraded site due to higher microbial activity and decomposition processes occurring in the upper layers (Krüger et al., 2015).

On the opposite, the C/H ratio, generally mirroring the humification degree (Stevenson, 1982; Zaccone et al., 2018), increased with depth independently of the grazing intensity, ranging from ~7.5 to ~9.0 (Fig. S1). Actually, higher C/H ratio values were expected in peat samples from sites showing high grazing intensity; however, comparing the mean values of the sites with different grazing intensity, no

Table 2
Main physical and chemical properties (min, max, avg. ± st. dev, median) of peat samples collected in both low- and high- grazed sites.

		Density	WC	GWC	Ash	N	C	S	C/N	C/H
		(g cm ⁻³)	(%)	($\frac{1}{g_{water} g_{peat}}$)	(%)	(%)	(%)	(%)		
Low grazed sites										
T1C	min	0.054	81.7	4.5	3.9	0.79	42.5	0.07	18.3	8.0
	max	0.172	92.6	12.4	16.7	2.67	50.0	0.54	57.5	10.5
	avg	0.103	87.3	7.7	11.5	1.82	46.7	0.28	28.6	8.9
	st.dev.	0.043	4.0	2.9	4.9	0.57	2.5	0.14	10.9	0.6
	median	0.082	88.8	8.0	12.3	2.03	46.2	0.25	24.4	8.9
MAL1	min	0.069	82.0	4.5	7.2	0.88	42.1	0.19	14.7	7.1
	max	0.164	91.9	11.3	15.0	2.98	53.4	0.51	48.2	8.5
	avg	0.129	84.7	6.0	9.3	2.29	46.2	0.32	22.6	7.8
	st.dev.	0.033	3.3	2.2	2.8	0.65	3.9	0.11	9.5	0.5
	median	0.139	83.4	5.0	8.5	2.49	45.1	0.33	20.9	7.9
MAL2	min	0.034	70.0	2.3	2.0	1.10	32.2	0.09	12.1	7.4
	max	0.240	94.0	15.6	35.2	3.49	50.3	0.42	40.2	8.7
	avg	0.116	84.9	6.9	9.4	2.58	42.5	0.24	18.6	7.9
	st.dev.	0.049	6.2	4.0	13.0	0.74	5.7	0.09	8.6	0.4
	median	0.117	85.2	5.7	3.1	2.87	43.8	0.25	15.4	7.8
PAT	min	0.032	83.2	4.9	2.2	1.55	41.3	0.10	15.5	6.9
	max	0.144	93.0	13.4	11.3	3.08	52.3	0.63	27.3	8.7
	avg	0.109	87.6	7.4	6.7	2.20	48.2	0.34	22.5	8.1
	st.dev.	0.027	2.4	2.1	3.6	0.40	3.7	0.14	3.7	0.5
	median	0.112	87.3	6.9	7.1	2.09	49.9	0.34	23.6	8.1
High grazed sites										
T1P	min	0.067	77.0	3.3	5.4	1.52	40.5	0.24	15.2	8.0
	max	0.222	85.8	6.0	28.2	3.23	54.3	0.36	29.0	9.7
	avg	0.158	81.4	4.5	14.0	2.34	48.1	0.28	21.4	8.8
	st.dev.	0.044	2.8	0.9	6.8	0.50	4.5	0.04	4.6	0.5
	median	0.173	80.4	4.1	13.5	2.27	50.7	0.28	20.3	8.8
T3P	min	0.038	68.4	2.2	6.3	0.99	16.2	0.07	13.9	6.7
	max	0.327	91.1	10.2	20.0	3.31	46.2	0.36	31.3	7.9
	avg	0.178	77.8	4.1	13.0	2.16	35.9	0.17	17.5	7.4
	st.dev.	0.072	6.6	2.4	4.9	0.79	10.3	0.07	5.1	0.4
	median	0.184	78.4	3.6	16.3	2.08	42.7	0.16	15.9	7.4
ZEL	min	0.065	81.0	4.3	13.1	1.74	39.2	0.49	21.2	7.7
	max	0.180	89.3	8.4	34.6	2.11	53.1	0.90	26.3	8.5
	avg	0.134	83.6	5.3	20.1	1.97	46.6	0.61	23.6	8.1
	st.dev.	0.032	2.5	1.3	8.6	0.12	3.9	0.13	1.4	0.3
	median	0.140	82.8	4.8	14.2	2.01	46.1	0.58	23.6	8.1

significant differences were observed.

3.2. Peat organic matter stability

During the peat decomposition, a loss of OM and a change in the primary chemical composition occur. However, this process may evolve in different directions mainly depending on differences in peat-forming vegetation, climatic conditions, peat depth, trophic status, pH, and age (Zaccone et al., 2018). Selected thermal proxies, mirroring peat chemical complexity, are summarized in Table 3. The TG-T₅₀ index generally increases with depth in all sites, thus suggesting that a higher temperature is needed to degrade half the sample mass (higher thermal stability due to more recalcitrant molecules). Moreover, it is also possible to observe small differences across the grazing gradient, with TG-T₅₀ values slightly higher in peat samples from intensively grazed sites with respect to those from sites with a lower grazing intensity.

The same trend was observed comparing WL occurring within different ranges of temperature (Table 3). Analysing peat and plant materials, Lévesque and Diné (1978) found a WL region between 275 and 325 °C, associated to readily oxidizable compounds like sugars and cellulosic materials, and another in the 360–460 °C region, due to more recalcitrant structure including lignin. Samples from highly grazed sites show generally higher values of both WL_{400-500/200-300} and WL_{350-450/250-350} ratios than samples from low grazed sites, thus suggesting an OM enriched in residual recalcitrant molecules.

3.3. Diatom assemblage composition

In total, 190 diatom taxa, belonging to 47 genera, were found in 56 layers out of 62 analyzed. The 6 samples in which no diatoms were observed corresponded to deeper layers of peat cores from highly grazed areas. The poor preservation of the frustules is generally due to the chemical dissolution of the diatom valves; in fact, according to Bennett (1991), dissolution and solubility of silicate minerals (including diatom valves) is greatly enhanced under environments that are anoxic and highly organic with a circum-neutral pH, conditions that are common in

Table 3

Thermal indices reported for the shallower (living layer, LL), intermediate, and deeper samples across the sites studied.

Sample	Average depth (cm)	TGA-T ₅₀	WL _{350-450/250-350}	WL _{400-500/200-300}
Low grazed sites				
T1C_#LL	1.5	308	0.40	0.23
T1C_#6	-16.5	329	0.70	0.71
T1C_#13	-37.5	343	0.92	0.73
Ma1_LL	1.5	319	0.38	0.60
Ma1_#6	-16.5	336	0.84	0.62
Ma1_#13	-37.5	339	0.83	0.39
Ma2_LL	1.5	317	0.49	0.45
Ma2_#6	-16.5	344	0.83	1.02
Ma2_#13	-37.5	325	0.66	0.44
High grazed sites				
T1P_#LL	1.5	307	0.50	0.37
T1P_#6	-16.5	349	1.04	0.90
T1P_#13	-37.5	354	1.12	1.03
T3P_#LL	1.5	310	0.53	0.05
TEP_#6	-16.5	339	0.82	0.93
T3P_#13	-37.5	348	0.87	1.19
ZEL_LL	1.5	320	0.56	0.58
ZEL_#6	-16.5	356	0.96	1.26
ZEL_#13	-37.5	340	0.81	0.94

fens and are generally a function of depth (Shotyk, 1988). The taxa found belong to pennate diatoms with the exception of 9 species of centric diatoms belonging to the genera *Aulacoseira* (6), *Cyclotella* (1), *Orthoseira* (1), and *Pantocsekiella* (1). As expected for acidic sites also showing low EC, the genera with the highest number of taxa were *Eunotia* (38) and *Pinnularia* (20), followed by *Gomphonema* (19), *Encyonema* (9), *Cymboplectra* (6), and *Nitzschia* (6).

In cores from sites with low grazing pressure 164 taxa were found, while 118 were found in cores from sites with high grazing pressure. To point out overgrazing effects, only uppermost layers were considered, i. e., from the living layer to 15 cm of depth.

The less grazed areas are characterized by a total of 125 out of 164

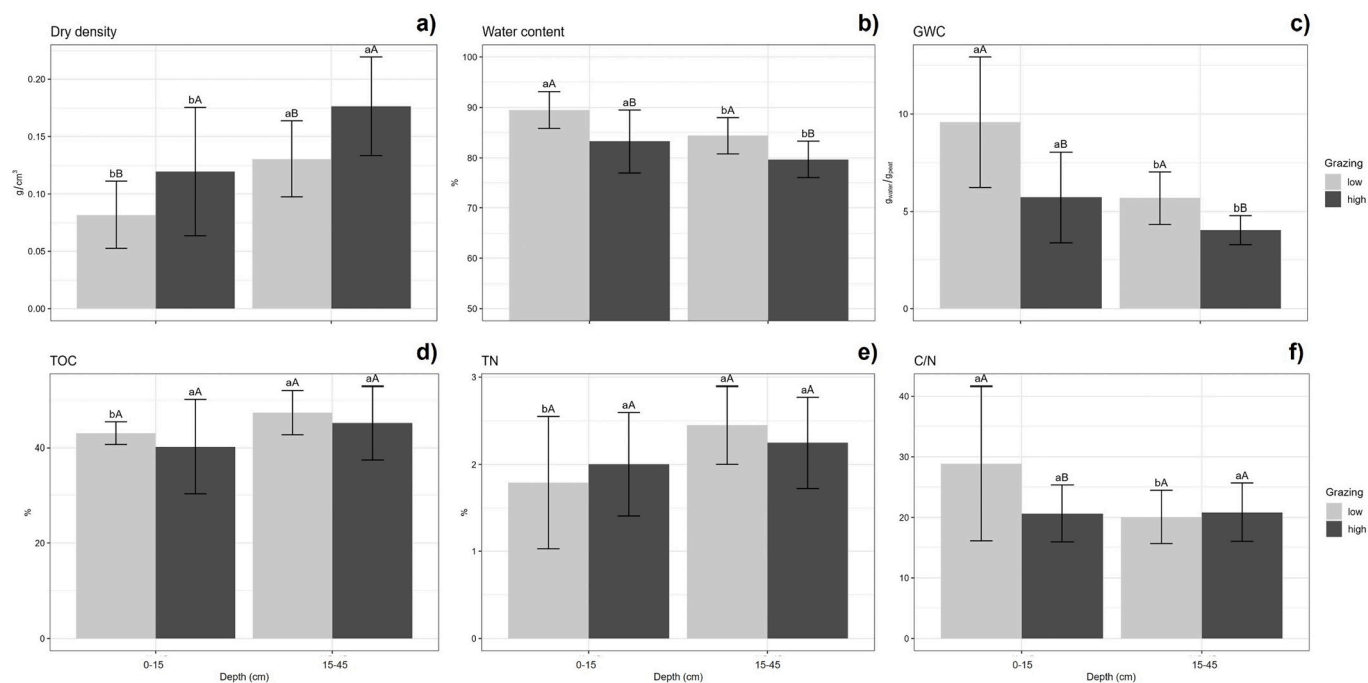


Fig. 2. Average values of bulk density (panel a), water content (panel b), gravimetric water content (panel c), total organic carbon (panel d), total nitrogen (panel e), and C/N ratio (panel f) in top (0–15 cm) and deep (15–45 cm) peat layers from low- and high- grazed peatlands. For each depth (0–15 and 15–45 cm), different uppercase letters indicate differences between grazing intensities, while lowercase letters indicate differences between depths within the grazing intensity ($p < 0.05$).

taxa belonging to 33 genera. Among them, those with a higher number of taxa are: *Eunotia* (30), *Pinnularia* (15), *Gomphonema* (12), *Encyonema* (9), *Chamaepinnularia* (5), and *Aulacoseira* (4). The most frequent taxa found in barely grazed sites are *Encyonema perpusillum*, *Eunotia boreoalpina* and *Kobayasiella micropunctata*. The species reaching the highest maximum relative abundances (MRA) is *Kobayasiella micropunctata*, with an MRA >96 %, followed by *Eunotia paludosa* (MRA = 71.7).

The higher intensity grazed areas show a total of 100 out of 118 taxa belonging to 31 genera; among them, those with a higher number of taxa are: *Eunotia* (30), *Pinnularia* (7), *Gomphonema* (6), *Encyonema* (6), *Aulacoseira* (4), and *Chamaepinnularia* (3). The most frequent taxa in high grazing intensity cores are *Eunotia paludosa* and *Kobayasiella micropunctata*. *Kobayasiella micropunctata* had the highest MRA (76.5), followed by *Aulacoseira alpigena* (68.7).

Only for 25 % of the taxa found environmental preferences were available in van Dam et al. (1994). In detail, 51 % of the taxa for which data are available belong to categories 1 (acidobiontic) and 2 (acidophilous) of the R index (“pH”); 84 % belong to the cat. 2 and 3 (acidophilic or circumneutral); 44 % of the taxa are mainly present in water bodies or regularly present in humid places (cat. 3 of the M index, “moisture”), and 57 % of the species are oligotraphentic or oligomesotraphentic (T index, “trophic state”).

The higher percentage of eutraphentic and hypereutraphentic species in highly grazed areas is related to the increase in nutrients (mainly N) caused by cattle manure and urine. Moreover, intense grazing increases the share of taxa that are more likely to survive in environments with unstable water availability (= aerial species).

3.4. Diatom diversity

More than 90 % of the taxa found in barely grazed areas are found in the Red List by Hofmann et al. (2018). Of these, 58 % belonged to some threatened category (1, 2, 3, G, R, V), and included 5 species in category 1 “threatened with extinction”, *Eunotia bactriana*, *E. cisalpina*, *E. faba*, *E. hexaglyphis*, and *E. superpaludosa*; 12 taxa belong to the category 2 “Severely endangered”, and 15 taxa to the category 3 “endangered”.

In the highly grazed sites, 90 % of taxa found that are included in the Red List. Three species are reported as category 1 “threatened with extinction” (*Eunotia bactriana*, *E. hexaglyphis*, and *E. superpaludosa*), 9 taxa belong to category 2 “Severely endangered”, and 10 taxa to the category 3 “endangered”.

Thus, the percentage of threatened species is very high both in slightly and in highly grazed sites, thus suggesting that even grazed mires are overall still able to host sensitive species. Previous studies had obtained similar results, observing high percentages of rare and threatened species (according to the Central European Red List) in different environments (Cantonati et al., 2011; Stanković et al., 2022). It should also be noted that the percentage of Red List species belonging to threatened categories might be overemphasized by the relevant occurrence of aerial diatom species in heavily grazed sites. As noted also by Cantonati et al. (2023b) studying small springs with highly variable discharge in southern Germany, many aerial species are less known in their distribution and ecology and therefore can be found on the Red List with a degree of threat that does not necessarily correspond to their real condition.

3.5. Diatom communities

Grazing has a significant impact on the diatom species composition present in the top 15 cm of the peat cores. The assemblages on the control sites were significantly different from the grazed sites ($F = 3.01$, $p = 0.013$) according to the permutational multivariate analysis of variance (Table 4). The ordination of samples performed with the NMDS, and based on the Bray-Curtis dissimilarity index, showed a clear partitioning of the diatom assemblages collected in low vs high grazed areas (Fig. 3a). The most characteristic species for low and high grazing

Table 4

Significance of the factors analyzed using dissimilarity matrices. Permutation: free. Number of permutations: 999. Significant code: 0.01 “**”.

	Df	Sum of Sqs	F. Model	R ²	Pr (>F)	
gc	1	0.820	3.0074	0.079	0.013	*
Residuals	35	9.54		0.921		
Total	36	10.36		1.00		

sites were identified by means of the IndVal procedure and depicted in the Fig. 3b and Fig. 3c. Using a cut-off alpha value of 0.01 for the statistical significance, *Brachysira confusa*, *Eunotia tenella*, *Chamaepinnularia schaupiana*, *C. muscicola*, *Eunotia nymmaniana* were selected as characteristic of low grazing sites, and *Aulacoseira alpigena*, *A. islandica*, *Eunotia fallax*, *Encyonema perpusillum* and *Staurosira spinarum* were indicators of high grazed mires (Table 5). We used a lower than usual alpha level to avoid possible problems of multiple testing when we make community-level statements.

Red List species in threat categories occur with higher percentages in the less grazed mires, indicating that this disturbance causes the disappearance of the most sensitive and at-risk species. However, also the most grazed sites host a relatively high percentage of endangered Red List species. Consulting the current diatom Red List, it comes to light that the species acting as indicators of highly grazed sites do have a certain value in terms of nature conservation. Consequently, Alpine peatlands, even if they may be partially degraded by grazing, are still able to host threatened species according to the Red List of Central Europe (Hofmann et al., 2018). For instance, *Encyonema perpusillum* is considered as a threatened species (Category 3 “endangered”) by the Red List of Central Europe, but it is a very common species in peatlands (Kulikovskiy et al., 2010; Chen et al., 2014). It should be noted that the Red List, that tries to cover all main types of inland waters, considers mires as fragile environments overall, because they represent a small surface of the European area, and their peculiar, extreme conditions make their biodiversity very specific. Thus, if *E. perpusillum* is correctly classified as an endangered species when dealing with the diatom microflora of the inland waters of central Europe, it should probably be considered as an opportunistic, common, and widespread peatland species when dealing specifically and solely with mires. To assess the status of mires, it would be necessary to create a Red List of diatoms specific for such a particular environment (Cantonati et al., 2022). Future metrics allowing to evaluate the impact of grazing on mires and to differentiate sites with different grazing intensities will have to take this into consideration, in order to protect these environments when degradation is still in its early stages.

From an applied standpoint, only two approaches are known to preserve the mires with the most valuable and sensitive biota from the detrimental effects of grazing: building fences to exclude livestock (Wahren et al., 2001; Cabezas et al., 2015), and revoking grazing licenses (Good and Johnston, 2019). We showed that diatom data, supported by physical and chemical parameters, can be a refined tool to single out the mires with the most sensitive biota, and thus to inform mire protection and rehabilitation.

4. Conclusions

Grazing causes physical, chemical, and biological disturbances in mires. Overgrazing leads to an increase in peat density and a decrease in WC (and GWC), due to compaction caused by trampling, and to a higher OM mineralization rate, due to both N inputs and O₂ occurrence. This increased decomposition of peat in overgrazed areas is supported by the lower C/N ratio, the higher ash content and the higher thermal stability observed. The effects of intensive grazing on peat are generally noticeable in the top 15 cm, while no significant differences were observed below this depth for most of parameters. Diatom taphocoenoses have been proved to serve as a reliable proxy for grazing-induced disturbance.

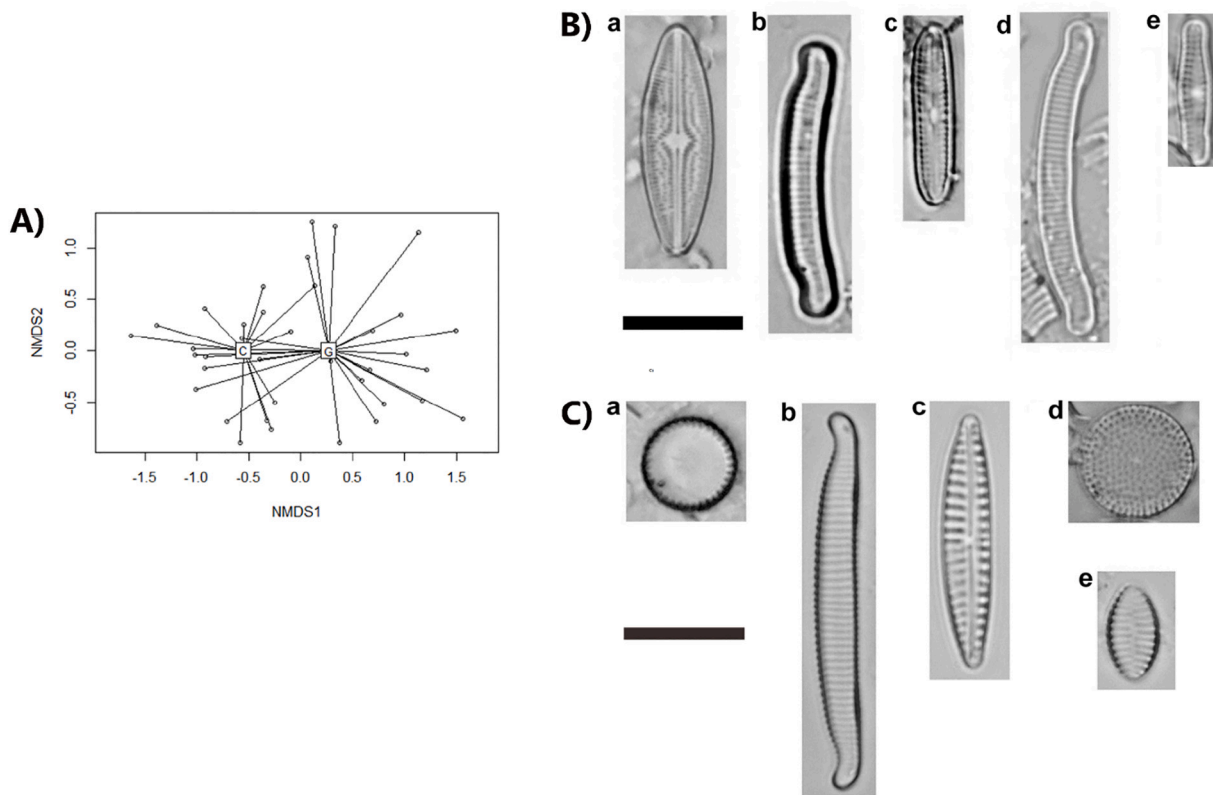


Fig. 3. Separation of control (C) and grazed (G) sites as obtained by NMDS carried out on the diatom taphocoenoses (panel A), and potential indicator taxa of C (panel B) and G (panel C). Two-dimensional plot of the NMDS obtained from the Bray-Curtis similarity matrix and using the absolute abundances of the species in the top 15 cm of depth (panel A). Light-microscopy images of potential indicator taxa for mildly grazed sites (panel B): a. *Brachysira confusa*, b. *Eunotia tenella*, c. *Chamaepinnularia schaupiana*, d. *Eunotia nymanniana*, e. *Chamaepinnularia muscicola*. Light-microscopy images of potential indicator taxa for highly grazed sites (panel C): a. *Aulacoseira alpigena*, b. *Eunotia fallax*, c. *Encyonema perpusillum*, d. *Aulacoseira islandica*, e. *Staurosira spinarum*.

Table 5
Statistically significant indicator species of barely and highly grazed sites.

	Stat	P value
Barely grazed sites		
<i>Brachysira confusa</i>	0.838	0.005
<i>Eunotia tenella</i>	0.810	0.005
<i>Chamaepinnularia schaupiana</i>	0.769	0.005
<i>Eunotia nymanniana</i>	0.666	0.010
<i>Chamaepinnularia muscicola</i>	0.577	0.005
Highly grazed sites		
<i>Aulacoseira alpigena</i>	0.896	0.005
<i>Eunotia fallax</i>	0.864	0.010
<i>Encyonema perpusillum</i>	0.863	0.015
<i>Aulacoseira islandica</i>	0.771	0.010
<i>Staurosira spinarum</i>	0.721	0.010

The presence of more aerial diatom species in grazed sites is due to the physical impact of cattle trampling, such as peat compaction and increased density, which in turn resulted in lower WC. The increased nutrient input, particularly N, favours the presence of eutrathentic species. In high grazed peatlands, a higher number of species was found, as opportunistic and moderately sensitive species can be competitive due to increased nutrient availability. The sensitivity of diatoms to nutrient variability demonstrates their potential to track grazing impacts. In conclusion, diatom biodiversity in mires can be preserved only if increased nutrient input due to grazing are prevented, and the creation of a metric for assessing the impact of grazing with diatoms in mires would be extremely beneficial to protect the environment during the initial phases of degradation.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.171779>.

CRedit authorship contribution statement

María Cid-Rodríguez: Methodology, Validation, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Marco Cantonati:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration. **Daniel Spitale:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing, Visualization. **Giorgio Galluzzi:** Investigation, Formal analysis, Data curation, Writing – review & editing. **Claudio Zaccone:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We are grateful to the Adamello-Brenta Nature Park Authority for allowing this research. Many thanks to Nicola Angeli (MUSE—Museo delle Scienze, Trento, Italy) for useful practical suggestions in technical aspects during the realization of this project.

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