Moss flora of two Alpine glacial and periglacial sites on crystalline and carbonatic bedrock

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Abstract - Mosses are important pioneer organisms in cold and wet habitats, such as glacial and periglacial habitats of the European Alps. These habitats include glaciers and rock glaciers, respectively, and are of increasing interest for being directly threatened by climate change and for hosting a specialized and often rare and endemic biodiversity (EU Habitats Directive, habitat code 8340, Natura 2000 network). However, the moss flora of rock glaciers was never studied, and, in general, few studies were performed specifically on mosses of icerelated landforms in the European Alps. The aim of this work is to give a first comparative checklist from two Alpine sites, the rock glacier of Lazaunkar (Bolzano, Italy) and the debris-cover glacier and rock glacier of Cima Uomo (Trento, Italy), with different bedrock compositions. Threatened species (according to the International Union for Conservation of Nature red lists) and extremely specialized high-elevation species were found in both sites, but mostly on crystalline bedrock in Lazaunkar. This biodiversity is the most threatened by climate change. These findings highlight how these habitats still need to be studied and monitored in the future.

Key words: biodiversity, checklist, cold-loving organism, permafrost, threatened habitats.

Riassunto - Flora muscinale di due siti glaciali e periglaciali alpini, su basamento cristallino e carbonatico.

I muschi sono importanti organismi pionieri in ambienti freddi e umidi. Gli ambienti glaciali e periglaciali delle Alpi, come ghiacciai e i rock glacier, sono di interesse sempre crescente per essere fortemente minacciati dal cambiamento climatico e per ospitare una biodiversità estremamente specializzata e spesso rara ed endemica (UE Direttiva Habitats, codice habitat 8340, network Natura 2000). Tuttavia, la flora muscinale dei rock glacier non è mai stata studiata e, in generale, pochi lavori sono stati condotti sulle Alpi specificamente sui muschi degli am-

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Received for publication: 18 July 2024 Accepted for publication: 22 October 2024 Online publication: 3 December 2024 bienti legati al ghiaccio. L'obiettivo di questo lavoro è fornire una prima checklist comparativa di due siti Alpini, il rock glacier del Lazaunkar (Provincia di Bolzano), nonché il ghiacciaio nero e il rock glacier di Cima Uomo (Provincia di Trento), caratterizzati da diversa litologia. Sono state trovate specie minacciate (in accordo con le liste rosse dell'*International Union for Conservation of Nature*) e specie adattate all'alta quota in entrambi i siti, ma soprattutto su substrato cristallino, presso il Lazaunkar. Questa biodiversità è la più minacciata dal cambiamento climatico. Questi risultati sottolineano quanto questi ambienti debbano ancora essere studiati per poter essere monitorati in futuro.

Parole chiave: biodiversità, checklist, habitat minacciati, organismi frigofili, permafrost.

INTRODUCTION

Mosses are widely distributed organisms strictly linked to freely available water in the form of precipitation or cloud moisture, with only a few species adapted to survive in dryland areas (Geffert et al., 2013). They have an important role in facilitating habitat formation (Grims, 1982; Wheeler et al., 2011; Lett et al., 2017) and in microhabitat construction (e.g., Rusek, 2001), especially in glacial habitats (Jonsdottir, 2005; Coulson & Midgley, 2012). They also support multiple ecosystem services – mainly linked to soil carbon and nutrient cycles - especially in low-productive ecosystems where vascular plant cover is low (Eldridge et al., 2023). Ice-related landforms like glacial and periglacial (i.e., associated with permafrost) sites are extreme habitats of increasing interest for being directly threatened by climate change and for hosting specialized and often rare and endemic biodiversity (Cauvy-Fraunié & Dangles, 2019; Gobbi et al., 2021; Valle et al., 2022); for this reason, they are included in the Natura 2000 network as "Permanent Glaciers" (code 8340; Council of the European Communities, 1992). There is evidence of the role of mosses as pioneer organisms in glacial habitats (e.g., Gärtner, 2010; Hågvar et al., 2020, Crosta et al., 2024, Valle et al., 2025), even on the ice surface (Fickert et al., 2007; Belkina & Vilnet, 2015). However, to our knowledge, no studies are available that describe the moss flora of periglacial habitats, and only a few works specifically describe the moss flora of ice-related landforms, often reporting only their overall presence without identification at the species level or limiting identification to dominant species (e.g., Grims, 1982; Hyvönen & Hyvönen, 1985; Fickert et al., 2007; Gärtner, 2010).





Knowledge of this flora is fundamental for planning, monitoring, and conservation programs (e.g., Puglisi & Cataldo, 2019; Callaghan & Gadsdon, 2023). This work aims to contribute to the knowledge of mosses in periglacial and related habitats by providing a first comparative checklist of two Alpine sites, respectively differentiated by crystalline and carbonatic bedrock.

MATERIALS AND METHODS Study areas

Sampling was performed at two Alpine sites located on different bedrocks in the central-eastern European Alps. Lazaunkar site ("LAZ": 46°44'48.0"N, 10°45'19.3"E; Val Senales, Trentino-Alto Adige, Bolzano Province, Italy. Figs. 1a and c) is characterized by the presence of an active rock glacier that extends for 0.12 km², covering the altitudinal range between 2700 m and 2480 m asl (Krainer *et al.*, 2015: data from 2005). The bedrock is constituted by paragneiss and micaschists (Krainer *et al.*, 2015). Cima Uomo site ("UO": 46°24'35" N, 11°48'25" E; Valle San Nicolò, Trentino-Alto Adige, Trento Province, Italy. Figs. 1b and d) hosts both a rock glacier (between 2430 and 2400 m asl) and, just uphill, a debris-covered glacier occupying an area of 0.10 km² between 2460-2700 m asl

(Seppi *et al.*, 2015). Cima Uomo is characterized by carbonate bedrock. In both sites, the substrate of the investigated landform is constituted by stony debris of different dimensions, including 1 m and above, on Lazaunkar and isles of fine debris (Fig. 2).

Sampling design

In each site, ice-related landforms, rock glaciers and debris-covered glaciers (only at Cima Uomo) were investigated (Fig. 1). To have a more complete overview of the moss flora of these habitats, also close ice-free landforms with similar substrates were investigated. In particular, a fossil rock glacier (i.e., rock glacier without ice core) and a scree slope were investigated at Lazaunkar, and the moraine of the Little Ice Age (LIA) glacier at Cima Uomo (Fig. 1).

On each landform, identified as a sampling unit ("mesohabitat"; Vanderpoorten *et al.*, 2010), 2-6 random plots were identified. The number of plots was chosen according to the landform area (Fig. 1). Each plot consisted of a square of 50 m² where all morphological species, discriminated with the aid of a magnifier, were intensively collected. Each sample was stored and transported in a paper bag for dehydration. Samples are preserved in the collection of the Herbarium Universitatis Mediolanensis (University of Milan).



Fig. 1 – Sampling design on Lazaunkar (a) and Cima Uomo (b) and an overview of the two sites, (respectively c and d). Yellow letters indicate studied landforms: A and F) active rock glaciers (light blue dots); B) scree slope (orange dots); C) fossil rock glacier (red dots); D): moraine of the Little Ice Age (green dots); E) debris-covered glacier (blue dots). / Piano di campionamento al Lazaunkar (a) e a Cima Uomo (b) e una panoramica dei due siti (rispettivamente c e d). Le lettere gialle indicano le landform studiate: A e F) rock glacier attivi (punti azzurri); B) ghiaioni (punti arancioni); C) rock glacier relitto (punti rossi); D) morena della Piccola Età Glaciale (punti verdi); E) debris-covered glacier (punti blu).

Morphological identification

For morphological identification, each sample was hydrated and analyzed under a stereo microscope (for general morphology) and with a light microscope for microscopic characters. In particular, the gametophyte (stem, leaf, rhizoids, and cells) and, when present, the sporophyte, were analyzed following the identification keys reported in Cortini Pedrotti (2001, 2005), and in Guerra *et al.* (2021) and Ignatova *et al.* (2009) for the genus *Schistidium*. Nomenclature refers to Hodgetts *et al.* (2020). For *Bryum* sp. 2 (UO), *Dicranella* sp. and *Schistidium* sp. (LAZ) it was not possible to identify samples at the species level because of the lack of material including diagnostic parts of the plant, such as the sporophyte.

Information on ecology and the altitudinal distribution in Italy was taken from Cortini Pedrotti (2001, 2005), while information on species presence in the Trentino-Alto Adige region was from Aleffi *et al.* (2023). The International Union for Conservation of Nature (IUCN) red list categories were taken from Puglisi *et al.* (2024) for Italy and Hodgetts *et al.* (2019) for Europe and refer to both geographical Europe ("EU" in Tab. 1) and the area of the 28 Member States of the European Union ("EU 28" in Tab. 1).

RESULTS

In total, 36 species were found: 19 at Lazaunkar, and 17 at Cima Uomo (Tab. 1). A total of 22 species were found on the two active rock glaciers, 8 on a fossil rock glacier, 11 on the scree slope and on the LIA moraine. No species were found on the debris-covered glacier of Cima Uomo. Only two species were found on both sites, *Encalytpa alpina* and *Pohlia cruda*.

According to IUCN red list (Tab. 1), at Italian scale the investigated sites host a critically endangered species (*Dicranum brevifolium*), two endangered species (*Hymelonoma compactum* and *Dicranum elongatum*) and two vulnerable species (*Ptychostomum funkii* and *Grimmia incurva*).

At the European scale, the most critical taxa are *Andreaea nivalis* (near threatened, according to "EU" red list), *Hymelonoma compactum* (Data Deficient according to both



Fig. 2 – Details of the surface of the sampled sites at Lazaunkar in a general view of the active rock glacier (a), of cyclopic rocks (with a person as a comparison) (c) and fine debris island (d) and at Cima Uomo in a general view of the active rock glacier (b) and detail on its debris surface (e). / Dettaglio della superficie dei siti campionati del Lazaunkar, con una visione del rock glacier attivo (a), dei massi ciclopici (con una persona come confronto) (c), e le isole di detrito fine (d) e di Cima Uomo, con una visione del rock glacier attivo (b) e un dettaglio della superficie (e).

Tab. 1 – Species found at the two sites, with indication of the landform where they were found. No species were found on the debris-covered glacier, which is not reported in the table. / Specie trovate nei due siti, con indicazioni sulle geoforme dove sono stati rinvenuti. Nessuna specie è stata trovata sul ghiacciaio nero, per questo non è riportato in tabella.

	Site	IUCN category Italy (Puglisi <i>et al.</i> , 2024)	Europe	Micro habitat	Altitudinal belt	<u> </u>	Fossil rock glacier	Scree slope	LIA moraine
Andreaea nivalis Hook.	LAZ	LC	NT (EU) LC (EU28		*			Х	
Bartramia ithyphylla Brid.	LAZ	LC	LC	R+	**	Х			
<i>Brachythecium albicans</i> (Hedw.) Schimp.	LAZ	LC	LC	G+	***	Х			
Dicranella sp	LAZ	-	-			Х			
<i>Dicranum brevifolium</i> (Lindb.) Lindb.	LAZ	CR	LC	R-	*	Х			
Dicranum elongatum Schleich. Ex Schwägr.	LAZ	EN	LC	RHW	**		Х		
Grimmia incurva Schwägr.	LAZ	VU	LC	RS+	*		Х	Х	
<i>Grimmia montana</i> Bruch & Schimp	LAZ	LC	LC	RD+	**	Х		Х	
<i>Heterocladiella dimorpha</i> (Brid.) Ignatov & Fedosov	LAZ	LC	LC	RWS+	***	Х			
Hymenoloma compactum (Schleich. ex Schwägr.) Och	LAZ yra	EN	DD	R+	*	Х	Х		
<i>Kiaeria starkei</i> (F. Weber & D. Mohr) I. Hag	LAZ gen	LC	LC	RGVW	*	Х	Х	Х	
Paraleucobryum enerve(Thed.) Loeske	LAZ	LC	LC	RGW	*		Х	Х	
Pohlia nutans (Hedw.) Lindb		LC	LC	RG+	***	Х		Х	
Politrychastrum sexangulare (Brid.) G.L.Sm	e LAZ	LC	NT (EU) VU (EU28	RVW	*			Х	
Polytrichum piliferum Hedw	. LAZ	LC	LC	GD	***	Х	Х	Х	
Ptychostomum imbricatulum (Müll.Hal.) Holyoak & N. Pe		LC	LC	RG	***	Х	Х	Х	
Schistidium sp.	LAZ	-	-					Х	
Encalytpa alpina Sm.	LAZ, UO		LC	HR-	**	Х			
Pohlia cruda (Hedw.) Lindb.	LAZ, UO	LC	LC	HRS+	**	Х	Х	Х	
<i>Blindia acuta</i> (Hedw.) Bruch & Schimp.	UO	LC	LC	RW	*	Х			Х
Brachytecium trachypodium (Brid.) Ignatov & Huttunen	UO	LC	LC	R-	**	Х			
<i>Campylophyllum halleri</i> (Hedw.) M. Fleisch.	UO	LC	LC	R-	***				Х
<i>Distichium capillaceum</i> (Hedw.) Bruch & Schimp.	UO	LC	LC	RS-	***	Х			Х
Encalypta vulgaris Hedw.	UO	LC	LC	HR-	***				Х
Mnium thomsonii Schimp.	UO	LC	LC	HR W-	**	Х			
Orthothecium intricatum (Hartm.) Schimp.	UO	LC	LC	HRWS-	***	Х			
Bryum sp. 2	UO	-	-						
<i>Ptychostomum elegans</i> (Nees) D. Bell & Holyoak	UO	LC	LC	R W-	***	Х			Х

To be continued on next page

	Site	IUCN	IUCN	Micro	Altitudinal	Active	Fossil	Scree	LIA
	Site	category Italy (Puglisi <i>et al.</i> , 2024)	category Europe (Hodgetts <i>et al.</i> , 2019)	habitat	belt	rock glacier	rock glacier	slope	moraine
Ptychostomum funkii (Schwägr.) J.R. Spence	UO	VU	VU (EU) EN (EU28)	RG-	***				Х
Sanionia uncinata (Hedw.) Loeske	UO	LC	LC	HRW	***				Х
<i>Schistidium apocarpum</i> (Hedw.) Bruch & Schimp.	UO	LC	LC	R+	***	Х			Х
Stereodon hamulosus (Schimp.) Lindb.	UO	LC	LC	RGW-	**	Х			
Syntrichia norvegica F.Weber	UO	LC	LC	R-	**				Х
Tortella tortuosa (Hedw.) Limpr.	UO	LC	LC	RG-	***	Х			Х

Table 1 –Continued from previous page.

LAZ, Lazaunkar; UO, Cima Uomo; microhabitat preferences: R, rocks; G, sand, gravel; H, humus; V, snowbed; W, high humidity; D, aridity; S, shadow; +, acidic soil reaction; -, alkaline soil reaction; altitudinal belt: *from alpine to nival belt; **from mountain to nival belt; ***from plain to nival belt. The International Union for Conservation of Nature (IUCN) categories for Europe consider both geographical Europe ("EU") and the political Europe of the 28 Member States of the European Union ("EU 28") (Hodgetts *et al.*, 2019); where not specified, the category is the same for the two cases. / LAZ, Lazaunkar; UO, Cima Uomo; preferenze in termini di microhabitat: R, rocce; G, sabia, ghiaia; H, humus; V, vallette nivali; W, elevata umidità; D, aridità; S, ombra; +, substrato acido; -, substrato alcalino; fascia altitudinale: *dalla fascia alpina a quella nivale; ***dalla fascia montana a quella nivale; ***dalla fascia planiziale a quella nivale. Categorie dell'*International Union for Conservation of Nature* (IUCN) per l'Europa considerando sia l'Europa geografica ("EU") che l'Europa Politica dei 28 Stati membri dell'Unione Europea ("EU 28") (Hodgetts *et al.*, 2019); dove non specificato, la categoria è la stessa in entrambi i casi.

European red lists), *Politrychastrum sexangulare* (near threatened, according to "EU", and vulnerable, according to "EU 28") and *Ptychostomum funkii* (vulnerable, according to "EU", and near threatened, according to "EU 28").

Ecologically, all the species are linked to rocky, gravelly, and sandy habitats, even if some of them also colonize more organic soils (7 species, 21% of the total number of species; in Tab. 1, species with "H" microhabitat preference). A total of 12 species (36%, Tab. 1) need high levels of humidity and can be associated with water streams, while only three species (9%) are associated with dry con-

ditions and 5 species (15%) are linked to shaded places.

Excluding generalist species, mosses found on Lazaunkar are usually linked to acidic soils, apart from *Dicranum brevifolium* and *Encalypta alpina* which are usually linked to more alkaline soils. Species from Cima Uomo are usually linked to alkaline soils, except for *Pohlia cruda*.

Concerning the altitudinal distribution of species found, the Lazaunkar site shows a higher percentage of species strictly related to high-altitude environments, while in the Cima Uomo site, only one high-altitude species was found (Fig. 3).



from alpine to nival zone from mountan to nival zone from plain to nival zone

Fig. 3 - Altitudinal distribution of species found in the two sites. / Distribuzione altitudinale delle specie trovate per i due siti.

DISCUSSION AND CONCLUSIONS

Our data indicate that the moss diversity of the investigated landforms is not high (e.g., comparing it with that of urban environments; Fojcik & Stabel, 2014) but includes several taxa that are critical from a conservation perspective. Dicranum brevifolium has been recorded in Italy since 1968 (Aleffi et al., 2023) only for the Trentino-Alto Adige region, where we have confirmed its presence in the Lazaunkar site. Dicranum brevifolium is considered critically endangered at the national level because of its ecology, being threatened by habitat shifting and alteration (Puglisi et al., 2024). Habitat shifting and alteration is a common threat for all the other taxa the conservation of which is critical at the national level: the two endangered species, Dicranum elongatum and Hymenoloma compactum, and the two vulnerable species, Grimmia incurva and Ptychostomum funkii. Other impending threats are mining, guarrying, recreational activities and the exposure to extreme drought events (Puglisi et al., 2024). Ptychostomum funkii is showing a decrease in its European range confirming its endangered status at the European scale (Hodgetts et al., 2019).

Andreaea nivalis is a circumpolar species with a relict distribution at lower latitudes on high mountains of central and southern Europe (Jenīík, 1997) and is linked to melting snow or ice (Schultze-Motel, 1970; Murray, 1988). Because of its likely high sensitivity to climate change by virtue of its ecology and its fragmented distribution, the present record from Lazaunkar is remarkable and should be considered for future monitoring. Even if this species is not considered a priority for conservation at a national scale (least concern; Puglisi *et al* 2024), it is classified as near threat-ened at the European scale (Hodgetts *et al.*, 2019). The same applies to *Politrychastrum sexangulare* (near threaten/vulnerable; Hodgetts *et al.*, 2019), a typical snowbed species, currently threatened in a global warming scenario (Carbognani *et al.*, 2012).

The great majority of these taxa of conservation concern were found on crystalline bedrock in the Lazaunkar site. Indeed, the observed biodiversity on crystalline bedrock appeared very specialized, including many exclusive high-elevation, cold-loving species. For example, Polytrichastrum sexangulare, Dicranum elongatum and Andreaea nivalis found in Lazaunkar are considered glacial relicts of subarctic species in the Alps (Fudali & Kučera, 2002). The majority of species found on both sites are typical of rocky habitats because of the dominance in all the investigated landforms of coarse stony debris. However, on the moraine originated during the last phase of glacier advance of the Little Ice Age, c. 200 years B.P., also species more exigent in terms of humus presence can grow, like Sanionia uncinata, already reported by Hyvönen and Hyvönen (1985) on Aletsch Glacier (Switzerland) as a typical species of recent moraines where a thin layer of humus occurs.

The sampled environments host both species of dry and exposed, and moist and shadowy habitats, highlighting microhabitat heterogeneity, which could be enhanced by the presence of ice influencing snow persistence and soil humidity at the surface. For example, *Andreaea nivalis* and *Grimmia incurva* prefer wet and rocky habitats of high elevations (Cortini Pedrotti, 2001), while *Politrychum piliferum* is typical of dry glacial mineral soils (Hyvönen & Hyvönen, 1985; Gärtner, 2010) but also occurs at low elevations (Cortini Pedrotti, 2001). The heterogeneous grain size distribution allows for the occurrence of species reported to be linked to vertical cliffs, like *Blindia acuta* (Hyvönen & Hyvönen, 1985). The importance of the bedrock as an ecological factor in these landforms is highlighted by the almost complete divergence between the floristic composition of the two sites, with species typical of alkaline soil, such as *Distichum capillaceum*, occurring in the Cima Uomo site.

It is noteworthy that, at least in our two sites, rock glaciers host a markedly different moss flora than that of proglacial habitats such as recently-deglaciated forelands, as dominant species reported to be highly frequent at these sites such as *Pohlia filum* and *Racomitrium canescens* are absent (Burga, 1999; Hyvönen & Hyvönen, 1985; Gärtner, 2010; Hågvar & Pedersen, 2015). No species were found on the debris-covered glacier, probably because of its high dynamicity and slope, and the frequent rockfall from the surrounding cliffs. However, further investigation is necessary to know the still understudied supraglacial moss biodiversity on the Alps, since an Arctic supraglacial moss richness would suggest a habitat suitability for hygrophilic mosses (Belkina & Vilnet, 2015).

As suggested for other taxa (Brighenti *et al.*, 2021; Gobbi *et al.*, 2021), it is possible that, in the future, in a global warming scenario, many threatened, cold-loving and hygrophilic species will retreat to periglacial refugia: Although preliminary, our findings suggest that this could also occur for mosses.

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REFERENCES

- Aleffi M., Cogoni A. & Poponessi P., 2023 An updated checklist of the bryophytes of Italy, including the Republic of San Marino and Vatican City State, *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 157 (6): 1259-1307.
- Belkina O.A. & Vilnet A.A, 2015 Some aspects of the moss population development on the Svalbard glaciers. *Czech Polar Reports*, 5 (2): 160-175.
- Brighenti S., Hotaling S., Finn D., Fountain A., Hayashi M., Herbst D., Saros J., Tronstad L. & Millar C., 2021 – Rock glacier and related

cold rocky landforms: overlooked climate refugia for mountain biodiversity. *Global Change Biology*, 27 (8): 1504-1517.

- Burga C.A., 1999 Vegetation development on the glacier forefield Morteratsch (Switzerland). Applied Vegetation Science, 2: 17-24
- Callaghan D.A. & Gadsdon S., 2023 How basic bryophyte recording provides information on major changes in key conservation localities: a case study of Epping Forest, England, an internationally significant site. *Journal of Bryology*, 45 (2): 159-171.
- Carbognani M., Petraglia A. & Tomaselli M., 2012 Influence of snowmelt time on species richness, density and production in a late snowbed community. *Acta Oecologica*, 43: 113-120.
- Cauvy-Fraunié S. & Dangles O., 2019 A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, 3 (12): 1675-1685.
- Cortini Pedrotti C., 2001 Flora dei muschi d'Italia. 1a parte. Antonio Delfino Editore, Roma.
- Cortini Pedrotti C., 2005 Flora dei muschi d'Italia. 2a parte. Antonio Delfino Editore, Roma.
- Coulson S.J. & Midgley N.G., 2012 The role of glacier mice in the invertebrate colonisation of glacial surfaces: the moss balls of the Falljökull, Iceland. *Polar Biology*, 35 (11): 1651-1658.
- Council of the European Communities, 1992 Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. ">https://eur-lex.europa.eu/eli/dir/1992/43/oj/eng
- Crosta A., Valle B., Caccianiga M., Gobbi M., Ficetola F.G., Pittino F., Franzetti A., Azzoni R.S., Lencioni V., Senese A., Corlatti L., Buda J., Poniecka E., Novotná Jaroměřská T., Zawierucha K. & Ambrosini R. 2024 – Ecological interactions in glacier environments: a review of studies on a model Alpine glacier. *Biological Review*, 100 (1): 227-244.
- Eldridge D.J., Guirado E., Reich P.B. Ochoa-Hueso R., Berdugo M., Sáez-Sandino T., Blanco-Pastor J.L., Tedersoo L., Plaza C., Ding J., Sun W., Mamet S., Cui H., He JZ, Hu HW, Sokoya B., Abades S., Alfaro F., Bamigboye A.L., Bastida F.L., de los Ríos A., Durán J., Gaitan J.J., Guerra C.A., Grebenc T., Illán J.G., Liu YR, Makhalanyane T.P., Mallen-Cooper M., Molina-Montenegro M.A., Moreno J.L., Nahberger T.U., Peñaloza-Bojacá G.F., Picó S., Rey A., Rodríguez A., Siebe C., Teixido A.L., Torres-Díaz C., Trivedi P., Wang J., Wang L., Wang J., Yang T., Zaady E., Zhou X., Zhou XQ, Zhou G., Liu S. & Delgado-Baquerizo M., 2023 The global contribution of soil mosses to ecosystem services. *Nature Geosciences*, 16: 430-438.
- Fickert T., Friend D., Gruninger F., Molnia B. & Richter M., 2007 Did debris-covered glaciers serve as Pleistocene refugia for plants? A new hypothesis derived from observations of recent plant growth on glacier surfaces. Arctic Antarctic and Alpine Research, 39 (2): 245-257.
- Fojcik B. & Stebel A., 2014 The diversity of moss flora of Katowice town (S Poland). *Cryptogamie, Bryologie*, 35 (4): 373-385.
- Fudali E. & Kučera J., 2002 Andreaea nivalis (Andraeaceae, Musci) new to the Larlonosze Mts. (SW Poland). Polish Botanical Journal, 47 (1): 45-47.
- Gärtner G., 2010 –. Glaziale und periglaziale Lebensräume im Raum Obergurgl. *Alpine Forschungsstelle Obergurgl*, 1: 145-154.
- Geffert J. L., Frahm J-P., Barthlott W. & Mutke J., 2013 Global moss diversity: spatial and taxonomic patterns of species richness. *Journal* of Bryology, 35 (1): 1-11.
- Gobbi M., Ambrosini R., Casarotto C., Diolaiuti G., Ficetola G.F., Lencioni V., Seppi R., Smiraglia C., Tampucci D., Valle B. & Caccianiga M., 2021 – Vanishing permanent glaciers: climate change is threatening a European Union habitat (Code 8340) and its poorly known biodiversity. *Biodiversity Conservation*, 30: 2267-2276.
- Grims F., 1982 Über die besiedlung der vorfelder einiger dachsteingletscher (Oberösterreich). Stapfia, 10: 203-233.
- Guerra J., Cano M.J., Martinez M., Jiménez J.A. & Gallego M.T., 2021 Schistidium apocarpum complex (Grimmiaceae, Bryophyta) in the Baetic Mountain Ranges, southern Iberian Peninsula. *Cryptogamie, Bryologie* 42 (5): 45-71.

- Hågvar S. & Pedersen A., 2015 Food choice of invertebrates during early glacier foreland succession. *Arctic, Antarctic, and Alpine Research*, 47 (3): 561-572.
- Hågvar S., Gobbi M., Kaufmann R., Ingimarsdóttir M., Caccianiga M., Valle B., Pantini P., Fanciulli P.P. & Vater A., 2020 – Ecosystem birth near melting glaciers: A review on the pioneer role of ground-dwelling arthropods. *Insects* 11 (9): 644.
- Hodgetts N.G., Cálix, M., Englefield E., Fettes N., García Criado M., Patin L., Nieto A., Bergamini A., Bisang I., Baisheva E., Campisi P., Cogoni A., Hallingbäck T., Konstantinova N., Lockhart N., Sabovljevic M., Schnyder N., Schröck C., Sérgio C., Sim Sim M., Vrba, J. Ferreira C.C., Afonina O., Blockeel T., Blom H., Caspari S., Gabriel R., Garcia C., Garilleti R., González Mancebo J., Goldberg I., Hedenäs L., Holvoak D., Hugonnot V., Huttunen S., Ignatov M., Ignatova E., Infante M., Juutinen R., Kiebacher T., Köckinger H., Kučera J., Lönnell N., Lüth M., Martins A., Maslovsky O., Papp B., Porley R., Rothero G., Söderström L., Stefánut S., Syrjänen K., Untereiner A., Váňa J. I, Vanderpoorten A., Vellak K., Aleffi M., Bates J., Bell N., Brugués M., Cronberg N., Denyer J., Duckett J., During H.J., Enroth J., Fedosov V., Flatberg K.I., Ganeva A., Gorski P., Gunnarsson U., Hassel K., Hespanhol H., Hill M., Hodd R., Hylander K., Ingerpuu N., Laaka-Lindberg S., Lara F., Mazimpaka V., Mežaka A., Müller F., Orgaz J.D., Patiño J. Pilkington S., Puche F., Ros R.M., Rumsey F., Segarra-Moragues J. G., Seneca A., Stebel A., Virtanen R., Weibull H., Wilbraham J. & Żarnowiec J. 2019 - A miniature world in decline: European red list of mosses, liverworts and hornworts. IUCN, Brussels.
- Hodgetts N.G., Söderström L., Blockeel T.L., Caspari S., Ignatov M.S., Konstantinova N.A., Lockhart N., Papp B., Schröck C., Sim-Sim M., Bell D., Bell N.E., Blom H.H., Bruggeman-Nannenga M.A., Brugués M., Enroth J., Flatberg K.I., Garilleti R., Hedenäs L., Holyoak D.T., Hugonnot V., Kariyawasam I., Köckinger H., Kučera J., Lara F. & Porley R.D., 2020 – An Annotated Checklist of Bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology*, 42 (1): 1–116.
- Hyvönen S. & Hyvönen J., 1985 Contributions to the lichen and bryophyte flora of Aletschwald Nature Reserve and its surroundings (Valais, Switzerland). *Bulletin de la Murithienne*, 103: 127-168.
- Ignatova E.A., Blom H.H., Goryunov D.V. & Milyutina I.A., 2009 On the genus *Schistidium* (Grimmiaceae, Musci) in Russia. *Arctoa*, 19: 195-233.
- Jenīik J., 1997 Anemo-orographic systems in the Hercynian Mts and their effects on biodiversity. Acta Univ. Wratislaviensis 1950. Prace Instytutu Geograficznego, Ser. C. Meteorologia i Klimatologia, 4: 9-21.
- Jonsdottir I.S., 2005 Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic Island perspective. *Proceedings of the Royal Irish Academy B*, 105: 155-165.
- Krainer K., Bressan D., Dietre B., Haas J., Hajdas I., Lang K., Mair V., Nickus U., Reidl D., Thies H., Tonidandel D., 2015 – A 10,300-yearold permafrost core from the active rock glacier Lazaun, southern Ötztal Alps (South Tyrol, northern Italy). *Quaternary Research*, 83 (2): 324-335.
- Lett S., Nilsson M.C., Wardle D.A. & Dorrepaal E., 2017 Bryophyte traits explain climate–warming effects on tree seedling establishment. *Journal of Ecology*, 105 (2): 496-506.
- Murray B., 1988 The genus Andreaea in Britain and Ireland. *Journal of Bryology*, 15 (1): 17-82.
- Puglisi M. & Cataldo D., 2019 A comparative study on the bryophyte and lichen flora for monitoring the conservation status of protected areas of Sicily (Italy) *Nova Hedwigia*, 109 (3-4): 321-343.
- Puglisi M., Campisi P., Aleffi M., Bacilliere G., Bonini I., Cogoni A., Dia M.G., Miserere L., Privitera M., Tiburtini M. & Poponessi S., 2024 – Red-list of Italian bryophytes. 2. Mosses. *Plant Biosystems - An International Journal Dealing with All Aspects of Plant Biology*, 158 (5): 1031-1056.
- Rusek J., 2001 Microhabitats of Collembola (Insecta: Entognatha) in beech and spruce forests and their influence on biodiversity. *European Journal of Soil Biology*, 37 (4): 237-244.

- Schultze-Motel W., 1970 Monographie der Laubmoosgattung Andreaea. *Willdenowia*, 6: 25-110.
- Seppi R., Zanoner T., Carton A., Bondesan A., Francese R., Carturan L., Zumiani M., Giorgi M. & Ninfo A., 2015 – Current transition from glacial to periglacial processes in the Dolomites (South-Eastern Alps). *Geomorphology*, 228: 71-86.
- Valle B., di Musciano M., Gobbi M., Bonelli M., Colonnelli E., Gardini G., Migliorini M., Pantini P., Zanetti A., Berrilli E., Frattaroli A. R., Fugazza D., Invernizzi A. & Caccianiga M., 2022 Biodiversity and ecology of plants and arthropods on the last preserved glacier of the Apennines mountain chain (Italy). *Holocene*, 32 (8): 853-865.
- Valle B., Ligi O., Moscatelli A., Onelli E. & Caccianiga M., 2025 Bryophyte colonization on an alpine recently deglaciated glacier foreland (European Alps). *Journal of Bryology*. doi: 10.1080/03736687.2025. 2456310.
- Vanderpoorten A., Papp B. & Gradstein R., 2010 Sampling of bryophytes. In: Manual on field recording techniques and protocols for all taxa biodiversity inventories. Vol 8. Eymann J, Degreef J, Häuser C, Monje JC, Samyn Y, Vandespiegel D (eds). ABC taxa, Belgium.
- Wheeler J.A., Hermanutz L. & Marino P.M., 2011 Feathermoss seedbeds facilitate black spruce seedling recruitment in the forest-tundra ecotone (Labrador, Canada). *Oikos*, 120 (8): 1263-1271.