






Original Article


Glacial biodiversity of the southernmost glaciers of the European Alps (Clapier and Peirabroc, Italy)


Barbara VALLE^{1*}  <https://orcid.org/0000-0003-4829-4776>;  e-mail: barbara.valle@unimi.it


Mauro GOBBI²  <https://orcid.org/0000-0002-1704-4857>; e-mail: Mauro.Gobbi@muse.it

Marta TOGNETTI¹  <https://orcid.org/0000-0001-8509-4998>; e-mail: marta.tognetti@gmail.com

Marina Serena BORGATTI¹  <https://orcid.org/0000-0003-3842-8646>; e-mail: marina.s.borgatti@gmail.com

Chiara COMPOSTELLA³  <https://orcid.org/0000-0002-2905-8121>; e-mail: chiara.compostella@unimi.it

Paolo PANTINI⁴  <https://orcid.org/0000-0001-8332-1915>; e-mail: paolo.pantini@comune.bergamo.it

Marco CACCIANIGA¹  <https://orcid.org/0000-0001-9715-1830>; e-mail: marco.caccianiga@unimi.it

*Corresponding author

¹ Università degli Studi di Milano, Department of Biosciences, Via Celoria 26, 20133 Milano, Italy

² MUSE - Science Museum of Trento, Research and Museum Collections Office, Climate and Ecology Unit, Corso del Lavoro e della Scienza, 3, 38122 Trento, Italy

³ Università degli Studi di Milano, Dipartimento di Scienze della Terra "A. Desio", Via Mangiagalli 34, 20133 Milano, Italy

⁴ Museo Civico di Scienze Naturali "E. Caffi", Piazza della Cittadella, 10, 24129 Bergamo, Italy

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Abstract: We applied a multi-taxa approach integrating the co-occurrence of plants, ground beetles, spiders and springtails with soil parameters (temperatures and chemical characteristics) in order to describe the primary succession along two glacier forelands in the Maritime Alps (Italy), a hotspot of Mediterranean biodiversity. We compared these successions to those from Central Alps: Maritime glacier forelands markedly differ for their higher values of species richness and species turnover. Contrary to our expectation, Maritime glacier forelands follow a 'replacement change model', like continental succession of Inner Alps and differently from other peripheral successions. We propose that the temperatures along these Mediterranean glacier forelands are warmer than those along other Alpine

glacier forelands, which promote the faster species turnover. Furthermore, we found that early and mid successional stages of the investigated glaciers are richer in cold-adapted and endemic species than the later ones: we confirmed that the 'replacement change' model disadvantages pioneer, cold-adapted species. Given the overall correspondence among cold-adapted and endemic species, the most threatened in this climate phase, our results raise new concerns about the extinction risk of these species. We also describe supraglacial habitat of Maritime glaciers demonstrating that supraglacial debris represents an environment decoupled from the regional climate and may have an important role as refugium for cold-adapted and hygrophilous plant and animal species, whose survival can be threatened by climate change and by a rapid ecological succession in the adjacent forelands.

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1 Introduction

Alpine glaciers are retreating globally due to climate change (Paul et al. 2015; Roe et al. 2017), freeing bare grounds - the glacier forelands - that are colonized by several micro- and macro-organisms (e.g. bacteria, plants, arthropods) giving an excellent opportunity to study an ecological succession triggered by climate changes (Cauvy-Fraunié and Dangles 2019; Ficetola et al. 2021).

The main driver of this succession is the time since deglaciation (Erschbamer and Caccianiga 2016; Hågvær et al. 2020), but its dynamics also depend on local climate (Matthews, 1992), biogeographic context (Tampucci et al. 2015) and by physical and chemical conditions at microscale (Castle et al. 2016; Hågvær et al. 2020). In addition, Rosero et al. (2021) recently demonstrated that the patterns of colonisation are taxa-dependent, i.e. different taxa can follow different models along to the same ecological succession.

Two main colonisation models were described (Vater and Matthews 2015; Ficetola et al. 2021): the 'addition and persistence' and 'replacement-change'. The former consists of the persistence of pioneer species (i.e. the initial colonisers) from the recently deglaciated sites (early successional stages) to late-successional stages. Conversely, with the 'replacement-change' process, mainly observed in the Alps, a group of initial colonisers (the pioneer community) is progressively replaced by other species; in this case, there is a species turnover. The two models can be distinguished through the persistence of pioneer species throughout the succession, which can be assessed by different indices (see Matthews et al. 2018) although fixed threshold values cannot be established.

A pilot study by Tampucci et al. (2015) performed in the Central Italian Alps highlighted how colonization dynamic is different in inner mountain chains with respect to peripheral ones, as a consequence of regional climate and altitude (see also Vater and Matthews 2013). In the peripheral chains of the Southern European Alps, the oceanic climate regime seems to allow the persistence of pioneer species along the glacier forelands and makes the

succession slower than on glacier forelands at the same altitude under continental climatic regime, probably because of the harsher conditions during the growing season. This phenomenon is particularly evident for plants (Tampucci et al. 2015). This observation is consistent with the autosuccession concept tested by Matthews et al. (2018) along a climatic gradient in Norway, where a 'replacement change' model could be observed in the subalpine zone, progressively replaced by a pattern characterized by a longer persistence of pioneer species, ending with an autosuccession (overlap between pioneer and late successional stages) in the most-climatically-limited sites of the high-alpine zone.

The long-lasting persistence of pioneer stages is particularly important as, in some areas, it allows the survival and extended distributional area of many endemic species (Tampucci et al. 2015).

An additional effect of climate change observed is the increase of supraglacial stony debris due to the reduction of the pressure of the ice volume on the headwalls and the amplification of frost and heat weathering that increase their erosion (Paul et al. 2007). The supraglacial debris can hosts cold-adapted species currently threatened by global warming (Caccianiga et al., 2011; Gobbi et al. 2011, 2017; Valle et al. 2020; Valle et al. 2022) and reduces the ablation rate (Nakawo and Rana 1999), thus potentially acting as refugium for these species during the current warm climatic stage.

In the context of climate change, peripheral glacial areas deserve particular attention for at least three reasons: (1) they display one of the plausible future scenarios for the whole inner chain, given their overall low altitude and the occurrence of few, small and rapidly shrinking glaciers; (2) they are characterised by high richness of endemic species (Medail and Quezel 1999), since they were partially ice-free during glacial periods, acting as refugia (Schonswetter et al. 2005); (3) they could host threatened cold-adapted species in recently-deglaciated areas and on supraglacial debris (Tampucci et al. 2015; Valle et al. 2020)

Maritime Alps (maximum altitude: 3297 m a.s.l.) are the southernmost portion of the European Alps, and border the Mediterranean Sea. They host two small glaciers, Clapier and Peirabroc, the southernmost of the whole Alpine chain (Smiraglia and Diolaiuti 2015). A large amount of rainfall mainly concentrated in spring and autumn as snowfall allows

Maritime glaciers to persist at low latitude and relatively low altitude (Hannss 1970).

Maritime Alps represent the richest area in terms of biodiversity in the European Alps (Medail and Quezel 1999; Villemant et al. 2015) due to the peripheral position with respect to the ice sheet during the Ice Ages, the proximity to the sea, the high environmental variability due to the lithological variety and the high altitude of peaks that allow species of the Alpine altitudinal belt to persist within the Mediterranean region. Because of this peculiar climatic and biogeographic context, Maritime glaciers are unique within the European Alps.

This paper aims to analyse the ecological succession of plant and arthropod (Aracnida: Araneae, Coleoptera: Carabidae and Hexapoda: Collembola) communities along the glacier foreland and on the supraglacial stony debris of the Clapier and Peirabroc glaciers. We hypothesize that: i) different taxa colonise the glacier foreland and the supraglacial habitat, in relation to soil parameters and temperature, with different colonization patterns from each other; ii) succession model in Maritime glaciers are similar to those of other peripheral glaciers as reported in Tampucci et al., 2015; iii) as a

consequence of hypothesis ii, cold-adapted species are distributed throughout the whole succession, from pioneer to late successional stages; iv) supraglacial habitat hosts cryophilic (i.e. cold-adapted and hygrophilous) species; v) supraglacial habitat of peripheral glaciers is a peculiar environment hosting a more endemic taxa with respect to supraglacial habitat of inner Alps.

2 Material and Methods

2.1 Study area

The Maritime Alps represent the southernmost part of the Alpine chain, and occur both in Italy and France. We studied Peirabroc (44°07'14" N, 7°24'53" E) and Clapier (44°06'51" N, 7°25'21" E), the last remaining glaciers of Maritime Alps (Smiraglia and Diolaiuti 2015) (Fig. 1, Appendix 1). The bedrock is siliceous, consisting of gneiss and amphibolite (Piana et al. 2017)

The studied glaciers showed an overall retreat following the end of the Little Ice Age (LIA, c. mid 19th century); an advance phase was recorded during the

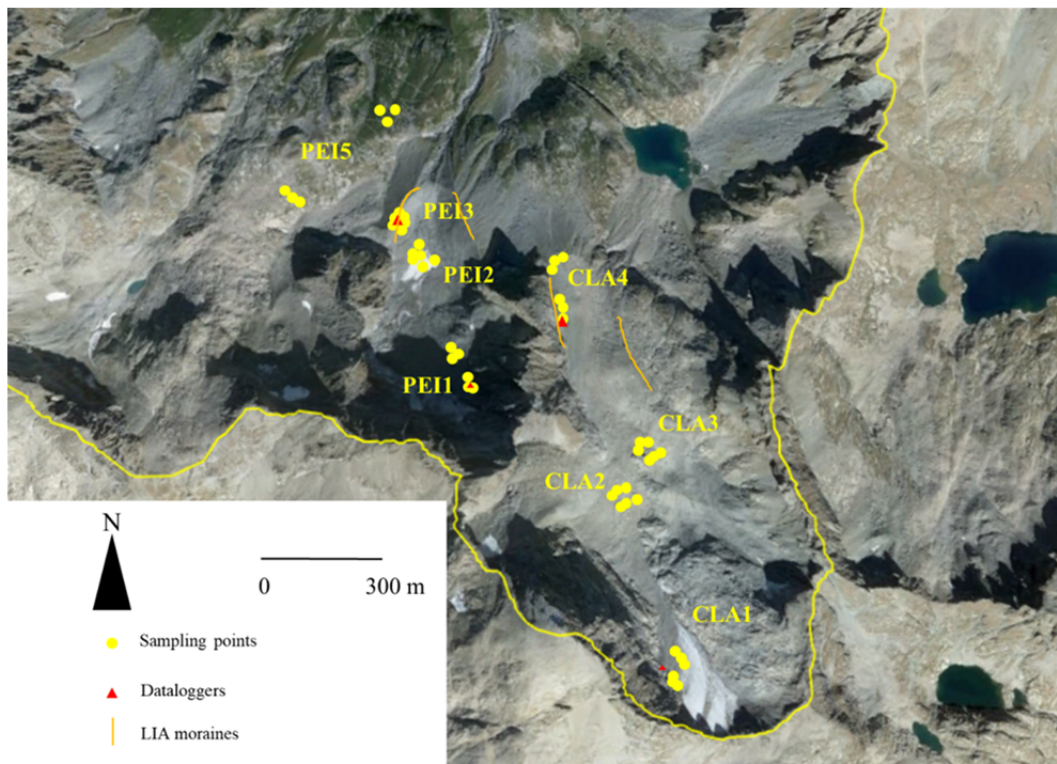


Fig. 1 Sampling plan. View of the environmental units investigated in each study area: Clapier “CLA” and Peirabroc “PEI”. Yellow line indicates national border (Italy-France). Orthophoto from Google Earth. See text for details about the sampling design.

1930s and in 1951. The retreat pace increased after 2002 (Federici and Pappalardo 1995, 2010). However, no glaciological data are available for the period 1967-1989, in correspondence to the last consistent advance of Alpine glaciers. Thus, a further possible advance phase was not recorded for these glaciers and only approximate dating of the glacial deposits is possible (Table 1).

Smiraglia and Diolaiuti (2015) reported a surface reduction of 30% for Peirabroc (from 0.1 to 0.07 km²) and of 77% for Clapier (from 0.3 to 0.09 km²) for the period 1957-2010.

Approximately 1/3 of the surface of both glaciers is covered by supraglacial stony debris, which is located in the proximal part of the ice tongue (debris cover estimated with Agea 2015 Orthophoto). The minimum altitude of the glaciers tongue recorded in 2019 was 2430 m asl for Peirabroc and 2650 m asl for Clapier; the tongue of Clapier is separated from the accumulation basin at 2750 m asl.

2.2 Sampling design

Five environmental units were selected, three occurring on Peirabroc, four on Clapier, and one common to both glaciers. The environmental units correspond to a specific deglaciation or moraine deposition age, from the glacier front to terrains ice-free since the Late Glacial Period (LG- c.10000 years BP) - (Table 1); the environmental unit corresponding to LG terrains (PEI5) is common to both glaciers, it

ideally represents the late-successional stage of the succession. Terrain age was obtained from literature data reporting previous glaciological surveys (see previous paragraph). An environmental unit was selected also on the supraglacial debris of both glaciers (Fig. 1, Table 1, Appendixes 1 and 2). Two plots were placed in each environmental unit, each one consisting of three sampling points at least 10 meters apart from each other. For each sampling point:

(1) We performed a vegetation survey in a quadrat of 5 x 5 m². The cover of rock outcrop, debris, of the whole plant cover and of every single species was estimated with a resolution of 5%; a cover value of 3% or 1%, was assigned for rare (less than 5% cover) and sporadic (one individual) species (Table 2, Appendix 3).

(2) We placed a pitfall trap, to catch and preserve arthropods, consisting of a plastic glass (diameter 7 cm) filled up with a non-toxic and frost-resistant solution made by 2:1 water and wine-vinegar, with salt and few drops of soap (Gobbi 2020); pitfall traps were collected and re-set during two sampling sessions (Harry et al. 2011; Lencioni and Gobbi 2021): 20/21 August 2019 - 10/12 September 2019.

Among the sampled taxa, ground beetles (Coleoptera, Carabidae), springtails (Hexapoda, Collembola) and spiders (Aracnida, Araneae) were chosen for the analyses, because they are ubiquitous and good ecological indicators, particularly in glacial environment (Hågvar et al. 2020).

Table 1 Plot site data. For each glacier, plot codes, their relative environmental unit and deglaciation age are reported.

Glacier	Plot code	Successional stage	Environmental unit	Deglaciation age	Mean altitude of plots (m asl)	Datalogger altitude (m asl)
Peirabroc	PEI1.1 PEI1.2	SD	SD (PEI1)	-	2500	2549
	PEI2.1 PEI2.2	Early SS	Young moraine (PEI2)	1920-1980?	2460	-
	PEI3.1 PEI3.2	Mid SS	LIA Moraine (PEI3)	ca. 1850~	2420	2465
Clapier	CLA1.1 CLA1.2	SD	SD (CLA1)	-	2780	2771
	CLA2.1 CLA2.2	Early SS	Young glacier foreland (CLA2)	1980	2630	-
	CLA3.1 CLA3.2		Young moraine (CLA3)	1920-1980?	2640	-
	CLA4.1 CLA4.2	Mid SS	LIA Moraine (CLA4)	ca. 1850	2510	2552
	Peirabroc Clapier	PEI5.1 PEI5.2	Late SS	LG terrains (PEI5)	>10.000 years BP	2450

Notes: Deglaciation age: time of deglaciation (foreland) or deposition (moraines). SD= Supraglacial debris ; SS= successional stage. See text for details about the sampling design.

Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H* = hygrophilous species, V = endemic species of Western Alps, V° = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, V° = endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70 < x < 90, green 40 < x < 60, light blue 30 < x < 40). For sporadic species see Appendix 3.

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Dor_clu	✓			p	<i>Doronicum clusii</i> (All.) Tausch (X)	.	.	.	0.2	0.5	.	.	.
Sax_aiz		✓		p	<i>Saxifraga aizoides</i> L.	0.2	.	.	1	0.5	.	.	.
Sax_ped			V*	p	<i>Saxifraga pedemontana</i> All. sbsp. <i>pedemontana</i>	0.5	.	.	1	2	.	.	.
Sax_ret	✓		V	p	<i>Saxifraga retusa</i> Gouan ssp. <i>augustana</i> (Vacc.) D.A.Webb	0.3	.	.	1	1	.	2	.
Poa_laxa	✓			p	<i>Poa laxa</i> Haenke	0.3	.	.	1	1	2	.	.
Ade_leu	✓	✓	V	p	<i>Adenostyles leucophylla</i> (Willd.) Rechb.	0.2	.	.	3	3	6	3	1
Art_gla	✓			p	<i>Artemisia glacialis</i> L.	.	.	.	0.3	1	.	0.2	.
Epi_nut		✓		p	<i>Epilobium nutans</i> F.W.Schmidt	.	.	.	0.3
Art_umb	✓			p	<i>Artemisia umbelliformis</i> Lam. ssp. <i>eriantha</i>	1	.	.	.
Hor_alp				p	<i>Hornungia alpina</i> (L.) O.Appel	.	.	.	1	1	.	.	.
Lin_alp				p	<i>Linaria alpina</i> (L.) Mill.	.	.	.	1	0.5	.	.	.
Oxy_dig	✓			p	<i>Oxyria digyna</i> (L.) Hill	.	0.3	3	3	3	.	.	.
Sax_opp	✓			p	<i>Saxifraga oppositifolia</i> L.	.	.	.	1
Alc_alp				p	<i>Alchemilla alpina</i> L.	1	.
Min_rec				p	<i>Minuartia recurva</i> (All.) Schinz & Thell.	3	.
Sax_pan				p	<i>Saxifraga paniculata</i> Mill.	.	.	.	0.3	1	.	2	.
Sil_aca	✓			p	<i>Silene acaulis</i> (L.) Jacq.	.	.	.	1	1	.	3	.
Ac_erb	✓			p	<i>Achillea erba-rota</i> All. subsp. <i>erba-rota</i>	.	.	.	0.2	0.5	2	.	.
Ara_alp				p	<i>Arabis alpina</i> L.	.	.	.	1	2	1	.	.
Car_par				p	<i>Carex parviflora</i> Host	.	.	.	0.2	.	0.2	1	.
Luz_alp_pil	✓			p	<i>Luzula alpinopilosa</i> (Chaix) Breistr.	.	0.3	.	1	.	1	2	.
Noc_cor	✓			p	<i>Nocca corymbosa</i> (J.Gay) F.K.Mey.	.	.	.	0.2	2	2	2	.
Poa_cen				p	<i>Poa centista</i> All.	.	.	.	2	1	2	1	.
Sax_bry	✓			p	<i>Saxifraga bryoides</i> L.	.	.	1	2	3	2	3	.
Sax_exa	✓			p	<i>Saxifraga exarata</i> Vill.	.	0.3	3	2	3	3	3	.
Sem_ara				p	<i>Sempervivum arachnoideum</i> L.	.	.	.	0.2	1	3	3	.
Ach_nan	✓			p	<i>Achillea nana</i> L.	.	.	+	.	.	1	.	.
Dry_vil				p	<i>Dryopteris villarii</i> (Bellardi) Woy. ex Schinz & Thell.	2	0.5	.
Eri_alp				p	<i>Erigeron alpinus</i> L.	1	2	.
Eup_alp				p	<i>Euphrasia alpina</i> Lam.	5	2	.
Fes_hal				p	<i>Festuca halleri</i> All. subsp. <i>halleri</i>	2	1	.
Hie_mor				p	<i>Hieracium pilosum</i> Schleich. ex Froel.	+	1.5	.
Gna_sup	✓			p	<i>Omalotheca supina</i> (L.) DC.	1	1	.

(-To be continued-)

(-Continued-)

Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H* = hygrophilous species, V = endemic species of Western Alps, V^o = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, U = endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70 < x < 90, yellow 60 < x < 70, green 40 < x < 60, light blue 30 < x < 40). For sporadic species see [Appendix 3](#).

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Jun_tri				p	<i>Oreojuncus trifidus</i> (Jacq.) Zav.Drabk. & Kirschner	2	2	.
Luz_spi				p	<i>Luzula spicata</i> (L.) DC.	2	3	.
Myo_alp				p	<i>Myosotis alpestris</i> F.W.Schmidt	2	3	.
Pil_lac				p	<i>Pilosella lactucella</i> (Wallr.) P.D.Sell & C.West	0.5	0.2	.
Poly_lon				p	<i>Polystichum lonchitis</i> (L.) Roth	2	.	.
Sag_sag				p	<i>Sagina saginoides</i> (L.) H.Karst. subsp. <i>saginoides</i>	1	1	.
Thy_oen				p	<i>Thymus oenipotanus</i> Heimr.Braun ex Borbas	1	2	.
Tri_theta				p	<i>Trifolium thalii</i> Vill.	4	5	.
Min_ver				p	<i>Sabulina verna</i> (L.) Rehb.	1	.
Tus_far				p	<i>Tussilago farfara</i> L.	1	.	.
Agr_rup	√			p	<i>Agrostis rupestris</i> All. subsp. <i>rupestris</i>	2	1	2
Agr_sch				p	<i>Agrostis schraderiana</i> Bech.	3	1	1
Alc_vul				p	<i>Alchemilla flabellata</i> Buser	1	4	2
Ant_alp				p	<i>Anthoxanthum nipponicum</i> Honda	6	1	6
Arm_alp				p	<i>Armeria alpina</i> Willd.	3	3	1
Cam_sch				p	<i>Campamula scheuchzeri</i> Vill.	4	2	3
Eup_min				p	<i>Euphrasia minima</i> Jacq. ex DC.	2	3	1
Fest_vio				p	<i>Festuca violacea</i> Ser. ex Gaudin subsp. <i>violacea</i>	1	.	3
Fes_var				p	<i>Festuca varia</i>	1	7	2
Lot_alp				p	<i>Lotus corniculatus</i> L. subsp. <i>alpinus</i> (DC.) Rothm.	2	3	4
Min_sed	√			p	<i>Cherleria sedoides</i> L.	1	3	2
Sen_inc	√			p	<i>Jacobaea incana</i> (L.) Veldkamp	3	.	2
Sil_rup				p	<i>Atocion rupestre</i> (L.) Oxelman	2	1	2
Tri_alp				p	<i>Trifolium alpinum</i> L.	2	5	2
Ped_ros_hel				p	<i>Pedicularis rostratospicata</i> Crantz ssp. <i>helvetica</i> (Steininger) O.Schwarz	3	1
Phy_glo_ped	√			p	<i>Phyteuma globulariifolium</i> Sternb. & Hoppe ssp. <i>pedemontanum</i> (Rich.Schulz) Becherer	1	2
Ast_min				p	<i>Astrantia minor</i> L.	1
Ave_ver				p	<i>Helictochloa versicolor</i> (Vill.) Romero Zarco subsp. <i>versicolor</i>	1	2
Car_sem				p	<i>Carex sempervirens</i>	1	25
Leo_hel				p	<i>Scorzoneroides helvetica</i> (Merat) Holub	1	4

(-To be continued-)

(Continued-)

Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H* = hygrophilous species, V = endemic species of Western Alps, V° = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, U = endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70 < x < 90, yellow 60 < x < 70, green 40 < x < 60, light blue 30 < x < 40). For sporadic species see [Appendix 3](#).

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Lig_mut				p	<i>Mutellina adonidifolia</i> (J.Gay) Gutermann							.	2
Luz_lut				p	<i>Luzula lutea</i> (All.) DC.							2	1
Meu_ath				p	<i>Meum athamanticum</i> Jacq.								1
Nar_str				p	<i>Nardus stricta</i> L.								20
Phy_mic			V	p	<i>Phyteuma michelii</i> All.								2
Ran_mon				p	<i>Ranunculus montanus</i> Willd.								3
Rho_fer				p	<i>Rhododendron ferrugineum</i> L.								10
Sol_alp				p	<i>Soldanella alpina</i> L. ssp. <i>alpina</i>							0.2	2
Vac_myr				p	<i>Vaccinium myrtillius</i> L.								2
Vac_uli				p	<i>Vaccinium uliginosus</i> L.								4
Vio_cal				p	<i>Viola calcarata</i> L.								1
Sem_mon				p	<i>Sempervivum montanum</i> L.				1	0.5			
Sem_tec				p	<i>Sempervivum tectorum</i> L.			0.2	1	1	1	1	1
Car_res				p	<i>Cardamine resedifolia</i> L.			2	2	1	1	1	2
Cir_spi				p	<i>Cirsium spinosissimum</i> (L.) Scop.			0.2	0.2	.	1		1
Fes_mel				p	<i>Festuca nigricans</i> (Hack.) K.Richt.			2	2	2	6	9	3
Leu_alp	✓			p	<i>Leucanthemopsis alpina</i> (L.) Heywood			0.3	1	0.2	0.3	2	1
Poa_alp				p	<i>Poa alpina</i> L.			1	3	3	4	5	4
Sag_gla				p	<i>Sagina glabra</i> (Willd.) Fenzl			0.3	0.3	.	1	1	1
Sed_alp				p	<i>Sedum alpestre</i> Vill.			2	2	2	3	3	2
Ver_alp		✓		p	<i>Veronica alpina</i> L.			1	1	.	1	3	1
Ore_ang	✓	✓	V*	b	<i>Oreonebria angusticollis</i> ssp. <i>microcephala</i> (K. & J. Daniels)	+							
Neb_joc				b	<i>Nebria jockischii</i> Sturm. 1815								
Cic_gal				b	<i>Cicindela gallica</i> Brullé						+	.	
Lae_jan_coe				b	<i>Laemostenus janthinus coeruleus</i> Dejean. 1828								
Ama_car	✓		V°	b	<i>Amara cardui</i> ssp. <i>psyllocephala</i> K. & L.							+	
Car_ped	✓		V	b	<i>Carabus pedemontanus</i> Ganglbauer. 1891						+	+	+
Pte_mor	✓		V*	b	<i>Pterostichus morio</i> ssp. <i>fenestrellanus</i> Csiki						+	+	+
Har_rub				b	<i>Harpalus rubripes</i> (Duftschmid. 1812)								+
Ore_mac	✓		U	b	<i>Oreonebria macrodera</i> (K. Daniel. 1903)								+
Ent_sp				s	<i>Entelecara</i> sp			+					+

(-To be continued-)

(-Continued-)

Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H* = hygrophilous species, V = endemic species of Western Alps, V° = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, V* = endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70 < x < 90, yellow 60 < x < 70, green 40 < x < 60, light blue 30 < x < 40). For sporadic species see [Appendix 3](#).

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Dip_hel	✓			s	<i>Diplocephalus helleri</i> (L. Koch. 1869)				+				
Mug_sp				s	<i>Mughiphantes</i> sp			+					
Ves_jug	✓		V*	s	<i>Vesubia jugorum</i> (Simon. 1881)				+				
Coe_pab			V	s	<i>Coelotes pabulator</i> Simon. 1875				+		+		
Coe_pic_pas	✓		V	s	<i>Coelotes pickardi pastor</i> Simon. 1875					+		+	
Par_nig	✓			s	<i>Pardosa nigra</i> (C. L. Koch. 1834)					+			
Dys_cri	✓		V	s	<i>Dysdera cribrata</i> Simon. 1882								
Xys_des	✓			s	<i>Xysticus desidiosus</i> Simon. 1875								
Zel_gal				s	<i>Zelotes gallicus</i> Simon. 1914						.	+	
Dra_pub				s	<i>Drassodes pubescens</i> (Thorell. 1856)				+				+
Cen_pab				s	<i>Centromerus pabulator</i> (O. Pickard-Cambridge. 1875)								+
Coe_ose	✓		U*	s	<i>Coelotes osellai</i> de Blauwe. 1973								+
Pal_pal				s	<i>Palliduphantes pallidus</i> (O. Pickard-Cambridge. 1871)								+
Par_bla				s	<i>Pardosa blanda</i> (C. L. Koch. 1833)								+
Orc_fro	✓		V	c	<i>Orchesella</i> cf. <i>frontimaculata</i> Gisin	+		+		+			
Iso_sp.				c	<i>Isotomidae</i> sp.	+		.	+				
Deu_pal				c	<i>Deuterosminthurus pallipes</i> (Bourlet. 1843)	+		+	.	.	+		
Lep_cur_gr				c	<i>Lepidocyrtus</i> gr. <i>curvicollis</i> (sensu (Mateos. 2012)	+		+	+	+	+		+
Orc_alt				c	<i>Orchesella alticola</i> Uzel			+	+	+			
Tom_min				c	<i>Tomocerus minor</i> (Lubbock)				+				
Smi_sp				c	<i>Sminthurus</i> sp.				+			+	
Cer_arm				c	<i>Cerathophysella armata</i> (Nicolet. 1841/1842)							+	
Fas_sau	✓		V	c	<i>Fasciosminthurus sauteri</i> (Nayrolles & Lienhard. 1990)						+		
Ent_lan				c	<i>Entomobrya lamuginosa</i> (Nicolet. 1842)						+		
Lep_cya_gr				c	<i>Lepidocyrtus</i> gr. <i>cyaneus</i> (sensu (Mateos. 2012))						+		+
Orc_qui				c	<i>Orchesella quinquefasciata</i> (Bourlet)								+

(3) We collected a soil sample of 200 g for analyse pH values, organic matter content (Walkley-Black method). In every plot (except plot CLA2, where it was not possible) a soil sample of approximately 2 kg was taken to estimate grain size distributions.

The considered taxa were identified to the species level or, whenever it was not possible, to the genus or family level. Plants were identified with Pignatti (2017), ground beetles with Pesarini and Monzini (2010, 2011), spiders with Roberts (1995), springtails with Bretfeld (1999), Gisin (1960), Jordana (2012), Mateos (2012), Thibaud et al. (2004). Only adult specimens of carabids and spiders were considered. Nomenclature follows Bartolucci et al. (2018); Jong et al. (2014) for plants and arthropods, respectively.

The sampled arthropods were preserved in ethanol and stored at Natural Science Museum of Bergamo, Italy (spiders), and at MUSE - Science Museum of Trento, Italy (ground beetles, springtails and other taxa not identified at the species level).

Two dataloggers (Tinytag plus 2) were placed, one in correspondence to supraglacial debris and one near the LIA Moraines of each glacier in order to analyse the patterns of mean daily ground surface temperature and humidity during the period 3 August 2019 - 13 September 2020. The devices were placed between stones at a depth of c. 10 cm, in order to shield them from direct solar radiation, and to obtain micrometeorological data about the substrate in which plant roots and arthropods develop. The recording was set at 30 minute intervals. Datalogger on Peirabroc supraglacial debris was downloaded in September 2019; afterwards, it was lost during winter due to avalanches and rockfalls; thus only data from one month (4 August 2019 - 11 September 2019) are available.

2.3 Data analysis

Vegetation data were expressed as cover values (%), while occurrence data of the considered ground-dwelling arthropods were expressed as presence/absence, since the second sampling session was not available for all the sampling points because many traps were damaged by snow and wild fauna. Site (altitude, slope, aspect) and soil data were standardized ($y = (x - \text{mean}) / \text{standard deviation}$; Kreyszig 1979) and aspect was normalized with $(-\cos(X))$.

We defined as “cold-adapted” all the species

strictly linked to the Alpine and Nival altitudinal belts (Table 2). In particular, concerning plants, we defined as “cold-adapted” the species with temperature index = 1 (alpine and nival) and temperature range of variation = I (temperature index variation at most ± 1) in Landolt et al. (2010); concerning arthropods, we referenced to the available descriptive literature about the ecological requirement of each identified taxon (Thaler 1988, 1999; Gisin 1960; Isaia et al. 2007; Bisio 2008; Jordana 2012; Pantini and Isaia 2019; Pesarini and Monzini 2010, 2011; Potapov 2001). Hygrophilous species are those linked to high availability of water (but not aquatic): we consider hygrophilous plant species with Landolt’s humidity index = 4 or 4.5; concerning arthropods, we referenced to the available descriptive literature about the ecological requirement of each identified taxon (as above). Species that are both cold-adapted and hygrophilous are defined cryophilic (Deharveng et al. 2008). All analyses were performed with PAST 4.05 software (Hammer et al. 2001).

2.3.1 Environmental variables

In order to calculate changes in mean annual temperature and snow persistence along the glacier foreland, micrometeorological data recorded on LIA moraines were used to estimate soil temperature on the whole glacier foreland, applying a standard adiabatic gradient of $0.6^{\circ}\text{C}/100\text{ m}$ (Rolland 2003), as tested by Tampucci et al. (2015). Data recorded by datalogger placed on the supraglacial debris of Clapier were used to describe the supraglacial environment. Temperature data obtained by the dataloggers allowed us to outline the snow cover period, where temperature remain constant and close to 0°C . (Appendix 4) The shorter series of data available for the Peirabroc supraglacial environment was compared with Clapier’s corresponding series in order to evaluate differences or homologies in trends between the two glaciers.

We used descriptive statistics (mean value and standard deviation for each environmental unit) to describe the distribution of soil parameters (soil pH, organic matter content, grain size distribution, total plant cover) along the investigated glacier forelands.

A non-parametric monotone correlation coefficient (Spearman’s *rho*) was calculated to investigate the collinearity between the soil variables, then Principal Component Analysis (PCA) was used to evaluate the association among them in order to rule out some of

the auto-correlated variables from the subsequent analyses (Hammer 1999-2021).

2.3.2 Plant and arthropod succession in relation to environmental gradients

Patterns of plant and arthropod species distribution along the glacier foreland in relation to environmental variables were described through canonical correspondence analysis (CCA; Legendre and Legendre 1998). We selected this direct gradient analysis because the response of species to the environmental variables is supposed to be unimodal due to the presence of complex ecological filtering driving the response of species occurrence and/or abundance (see Ficaretola et al. 2021); furthermore, this analysis is particularly suitable for heterogeneous datasets along long ecological gradients (Hammer et al. 2001; Zeleny 2022).

These analyses were carried out: (A) for plants, on a matrix of continuous data of plant species including 22 sampling points for 76 species on Peirabroc (20 species out of 96 were omitted since occurring in only one sampling point; 2 sampling points were omitted since no plant species was recorded in them) and 22 sampling points for 73 species on Clapier (19 species out of 92 were omitted since occurred in only one sampling point; 2 sampling points were omitted since no plant species was recorded in them); (B) for arthropods, on a binary matrix with 21 plots and 27 species on Peirabroc and 21 plots for 30 species on Clapier. Environmental variables included in all CCA analyses were slope, aspect, pH and soil organic matter; the three most correlated variables - gravel and sand, silt and clay and plant cover - were omitted, because of their ecological redundancy (Appendix 5).

For identifying typical plant and arthropod species of each environmental unit, we used Indicator Species Analysis (indicator value: IndVal; Podani & Csányi 2010), carried out on the matrix used for CCA, merging plots of the same age into the same environmental unit according to Table 1.

2.3.3 Comparative analysis of succession parameters

In order to compare the succession trend of different regions of the Alpine chain, we compared the ecological succession of the two Maritime Alps glacier foreland with one glacier from the peripheral (southern) Alps: Trobio glacier (Orobian Alps, glacier foreland above the tree line, 2350-2550 m asl,

(Tampucci et al. 2015) and with two glaciers from Rhaetian (inner) Alps: Rotmoos glacier (Rhaetian Alps, glacier foreland near the potential tree line, 2280-2400 m asl, Austrian Alps; Kaufmann 2001; Marcante et al. 2009), and Cedec glacier (Rhaetian Alps, glacier foreland above the tree line, 2694-2726 m asl, Italian Alps; Gobbi et al. 2010). All these glaciers are characterized by siliceous bedrock. The terrain age for each sampled site was taken from the original publications (literature cited above).

Specifically, for each ecological succession of the glacier forelands we calculated two indices of turnover for plants, spiders, ground beetles and springtails (springtail data were available only for Peirabroc and Clapier):

(1) Whittaker species turnover index (Whittaker 1972): $\beta_w = (\gamma - \alpha)/\alpha = \gamma/\alpha - 1$ (where γ is the total species diversity and α is the mean species diversity at the habitat level);

(2) Persistence index (Vater and Matthews 2015): $PPn = 100c/a$ (where c is the number of common species of the two sites and a the number of species of the most pioneer site).

To perform a homogeneous comparison, we merged the two pioneer stages of Clapier (CLA2 and CLA3), considering the following four deglaciation stages (Tampucci et al. 2015): 1 = pioneer (1-30 years since deglaciation); 2 = early (31-100 years since deglaciation); 3 = mid (101-170 years since deglaciation); 4 = late (c. 10.000 years old, ice-free since the LG) (Table 1). Plant and arthropod data were not available for stage 1 on Peirabroc and Clapier, because this environment was not included in our sampling design being not clearly identifiable on the field: for this reason, the total persistence index was calculated from 2 to 4 for all glacier forelands.

3 Results

3.1 Environmental gradients along the glacier foreland and on the supraglacial debris

The mean annual temperature measured on the LIA moraine was 4.2°C for Clapier (at 2510 m asl) and 3.3°C for Peirabroc (at 2420 m asl). The values calculated for the uppermost areas of the glacier forelands are 4.0°C for Clapier (at 2630 m asl) and 2.5°C for Peirabroc (at 2460 m asl). The mean annual temperature of the supraglacial debris, available only for Clapier, was -1°C.

Snow lasted on the Peirabroc LIA moraines for about 214 days and for 183 days on Clapier; on the supraglacial debris of Clapier it lasted for 295 days; considering the similarity among the thermal trends on the two glaciers we can expect similar data of snow persistence on Peirabroc glacier.

Soil parameters were not related to slope and aspect on both glaciers (Appendix 5). Soil parameters along the glacier foreland showed a progressive decrease of pH (from 7.5 to 5.5), gravel and sand fraction (from 99% to 60%) and a corresponding increase of organic matter content (from 4 to 163 g/kg), silt and clay fraction (from 1% to 40%) with increasing terrain age (Appendix 6)

PCA gave similar results for the two glaciers (Appendix 7): soil data were displaced along PCA axis 1, particularly for Peirabroc glacier, representing the main environmental gradient, while slope and aspect were related to axis 2.

3.2 Biodiversity of the southernmost alpine glacier forelands

One hundred and four plant species were found on both glacier sites; the most frequent are *Poa alpina*, *Festuca nigricans*, *Adenostyles leucophylla* (occurring respectively in 64%, 50%, 47%, of all samples), and the most abundant are *Festuca nigricans*, *Poa alpina* and *Carex sempervirens* (cumulative cover values are 124%, 101% and 96%, respectively). Among the observed species, 22 (21.2%) are “cold-adapted” and 13 (12.5%) are endemic to the Alps, including *Saxifraga pedemontana* ssp. *pedemontana*, stenoendemic of Maritime Alps and *Saxifraga retusa* ssp. *augustana*, *Adenostyles leucophylla* and *Phyteuma michelii* endemic of Western Alps. *Saxifraga retusa* ssp. *augustana* is also cold-adapted and *Adenostyles leucophylla* is also cryophilic.

Among the nine ground beetle species found on both glaciers, the most abundant are *Pterostichus morio* ssp. *fenestrellanus* (80% of all individuals sampled, 117 specimens) and *Carabus pedemontanus* (10%, 14 specimens); Five of these species (56 %) are high-mountain cold-adapted species (Table 2); five species (56%) are Alpine endemic, including one species endemic of Western Alps, *Carabus pedemontanus*, two subspecies present only in Maritime Alps, *Oreonebria angusticollis* ssp. *microcephala*, *Pterostichus morio* ssp. *fenestrellanus*,

and *Amara carduii* ssp. *psylocephala*, the latter present in Maritime and Ligurian Alps. All the cold-adapted species are also endemic. *Oreonebria angusticollis* ssp. *microcephala* is the only cryophilic arthropod found.

Fifteen spider species were found on both glaciers; the most abundant are *Pardosa blanda* (36%, 20 specimens) and *Coelotes pabulator* (9%, 5 specimens). Seven of them (47%) - *Coelotes osellai*, *Coelotes pickardi pastor*, *Diplocephalus helleri*, *Dysdera cribrata*, *Pardosa nigra*, *Vesubia jugorum*, *Xysticus desiosus* - are high mountain cold-adapted species. Five (33%) are Alpine endemic species, including *Coelotes osellai* (endemic of Maritime and Apuane Alps) and *Vesubia jugorum*, stenoendemic to Maritime Alps.

Twelve species of ground-dwelling springtails were found on both glaciers, with *Orchesella* cf. *frontimaculata* (45%, 350 specimens) and *Orchesella quinquefasciata* (25%, 195 specimens) as the most abundant. Among them only *Orchesella* cf. *frontimaculata* and *Fasciosminthurus sauteri* are high mountain and Alpine endemic species (17 %).

3.3 Plant community succession

In both Peirabroc and Clapier sites plots are arranged following two main gradients outlined by the CCA (Fig. 2): the first corresponds to soil evolution, expressed by pH value and organic matter content, that arrange plots following their chronological succession and are highly correlated with CCA axis 1 (Pearson *r* index 0.91 and -0.87 for Peirabroc and -0.71 and 0.92 for Clapier, respectively). The second gradient is related to topographic data (aspect: Pearson *r* index with CCA axis 2 0.71 and 0.65 for Peirabroc and Clapier, respectively).

The plant succession dynamic is similar along the two glacier forelands, with differences due to sporadic species occurrence. In the early successional stage of Peirabroc glacier forelands (environmental unit PEI2) we found 31 plant species (mean total plant cover for plot 32%); on Clapier this successional stage includes two different environmental units: on the young glacier foreland (CLA2) we found only six plant species (mean total plant cover for plot 2%). On the young moraine (CLA3) we found 24 species, with a mean total plant cover of 34%. According to Indval (Table 2, Appendix 8) the best indicator species of early successional stages are *Oxyria digyna*, *Arabis*

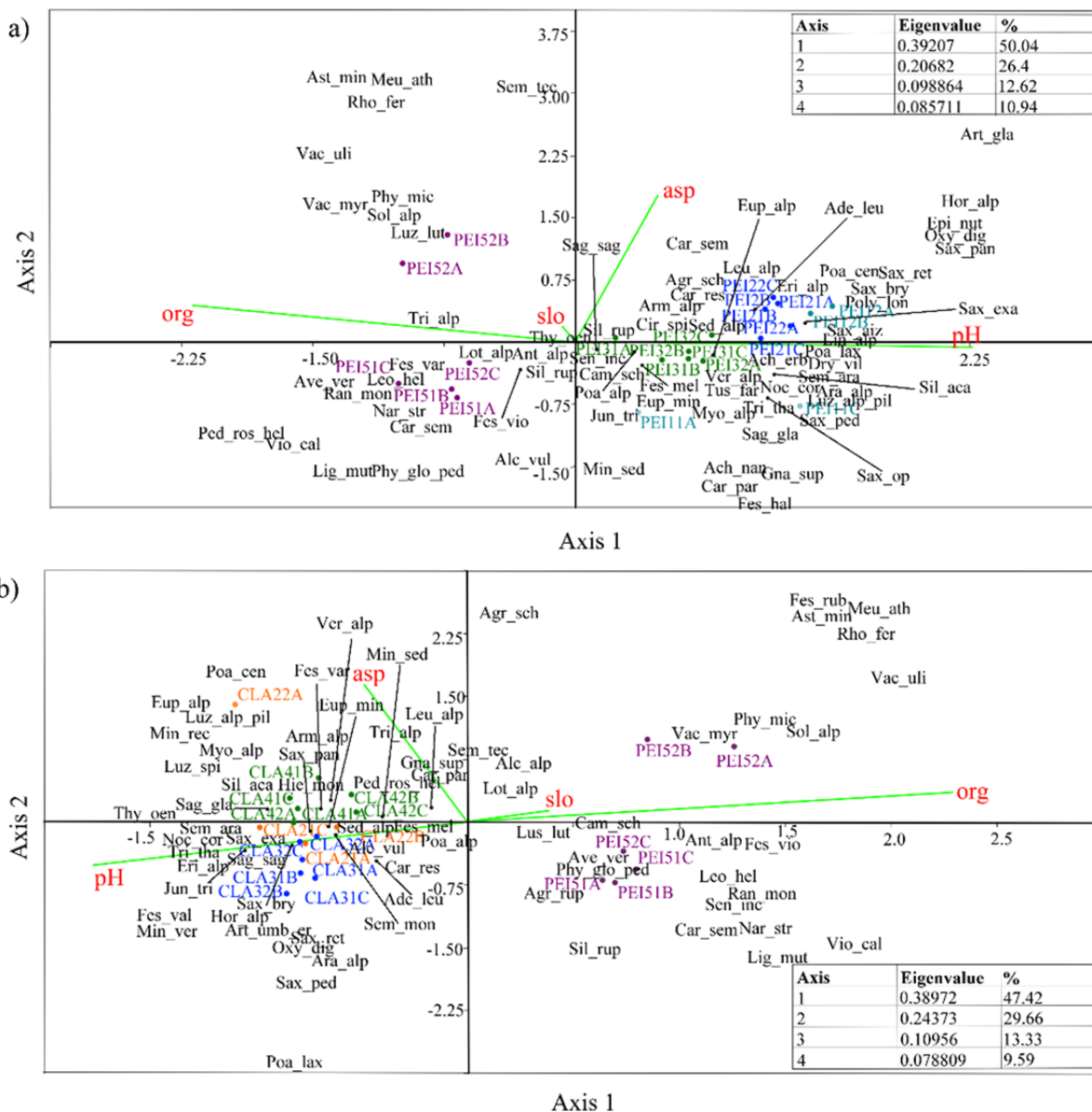


Fig. 2 Plant Canonical Correspondence Analysis (CCA) graphs for a) Peirabroc and b) Clapier. asp = aspect, slo = slope, org = organic matter, pH = soil pH.

alpina, *Saxifraga aizoides*, *Hornungia alpina* and *Linaria alpina*. In mid-successional stages on Peirabroc (PEI3, LIA moraines) eleven early colonizer species persisted, but 37 late colonizers appeared, thus reaching the highest species richness (48) with a mean total plant cover of 97%. This could be observed also in the mid-successional stage of Clapier (CLA4), with 53 species and a mean total plant cover of 115%. According to IndVal, the indicator species for this environmental unit (Table 2) are *Myosotis alpestris*, *Euphrasia alpina*, *Trifolium thalii*, *Luzula spicata* and *Armeria alpina*. Late successional stages (PEI5) showed slightly higher plant cover values (133%) with

many exclusive late successional species such as *Carex sempervirens*, *Scorzonerooides helvetica*, *Nardus stricta* and *Ranunculus montanus*, which are the best indicator species according to IndVal (Table 2).

In general, only few species are ubiquitous along all the glacier forelands: *Leucanthemopsis alpina*, *Poa alpina*, *Luzula alpinopilosa*, *Saxifraga bryoides*, *Saxifraga exarata*. Analysing the general trend of species richness (Fig. 3), plants show an increase in species richness on the mid-successional stages and then a decrease in the late successional stages.

Among the early successional species, only

Saxifraga pedemontana ssp. *pedemontana*, the hygrophilous *Saxifraga aizoides*, the cold-adapted *Saxifraga retusa*, *Poa laxa* and the cryophilic *Adenostyles leucophylla* have been found on supraglacial debris, in Peirabroc sites (PEI1); the percentage of endemic plant species is 60% (3 species among 5) and also the percentage of cold-adapted species is 60%; 2 among 3 species are both endemic and cold-adapted. On Clapier supraglacial debris (CLA1) no plant species was found.

3.4 Arthropod community succession

Along Peirabroc glacier foreland arthropod communities are arranged primarily in relation to a soil evolution gradient (Fig. 4), with CCA axis 1 highly correlated to organic matter content (Pearson *r* index = 0.83) and soil pH (Pearson *r* index = -0.92). Axis 2 is related to aspect (Pearson *r* index = -0.42). Along Clapier glacier foreland arthropod distribution follows two main gradients: the first is that of the soil organic matter (Pearson *r* index = 0.86), arranging plots and species along the CCA axis 1 and the second is that of aspect and slope, correlated to CCA axis 2 (Pearson *r* index = -0.66, Pearson *r* index = -0.58).

IndVal analysis significantly associated to early successional stage of the young glacier foreland (CLA2) the cold-adapted and endemic springtail *Orchesella* cf.

frontimaculata and the spider *Entelecara* sp. (Table 2, Appendix 8) with a total amount of two species of spiders and four of ground-dwelling springtails; only one species of ground beetle was sampled here, the cryophilic and endemic *Oreonebria angusticollis* ssp. *microcephala*.

In the early successional stages of young moraines (PEI2 and CLA2-3), one ground beetle species (*Nebria jockischii*), six species of spiders (four cold-adapted and three endemic) and three ground-dwelling springtail species were found. The spider *Coelotes pabulator* and the springtails *Lepidocyrtus* gr. *curvicollis* and *Orchesella alticola* resulted an indicator species of this successional stage according to IndVal (Table 2).

In the mid-successional stages (PEI3 and CLA4) we found five ground beetle species (three cold-adapted and endemic), seven spider species (four cold-adapted and three endemic; among these seven species, only *Coelotes pabulator* was found on Peirabroc) and seven ground-dwelling springtail species (one of them cold-adapted and endemic). The ground beetles IndVal analysis showed the *Carabus pedemontanus*, *Pterostichus morio* ssp. *fenestrellanus*, the spider *Zelotes gallicus* and the springtails *Fasciosminthurus sauteri* and *Entomobrya lanuginosa* to be indicator species for these successional stages (Table 2).

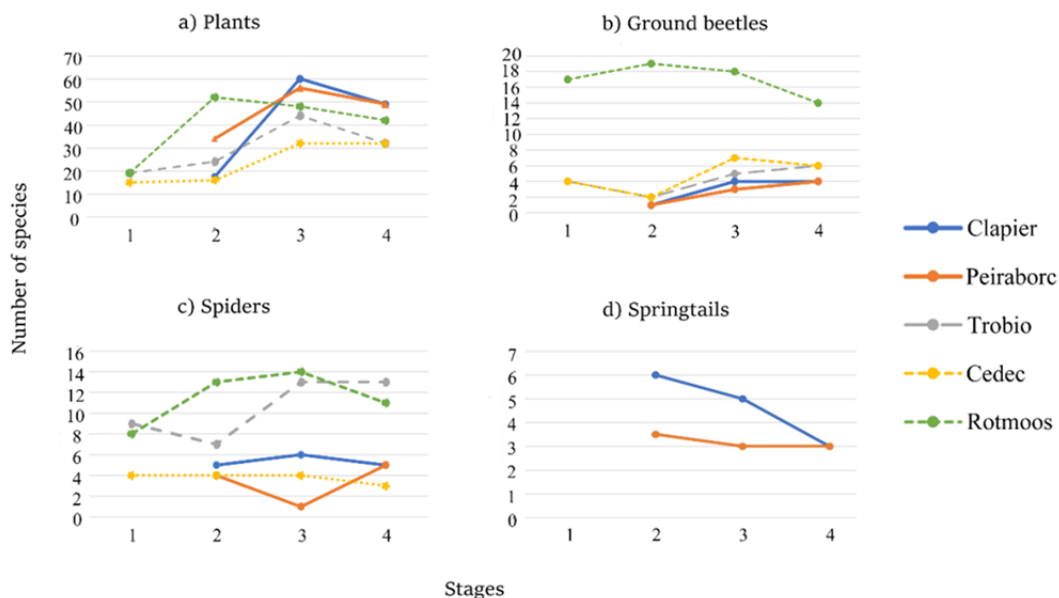


Fig. 3 Species richness for plants a), ground beetles b), spiders c) and springtails d) along the compared glacier forelands. Stages of deglaciation: 1 = pioneer stage (c. 1-30 years since deglaciation); 2 = early stage (c. 31-100 years since deglaciation); 3 = mid stage (c. 101-150 years since deglaciation, ice-free since the LIA); 4 = late stage (c. 10.000 years old, ice-free since the LG).

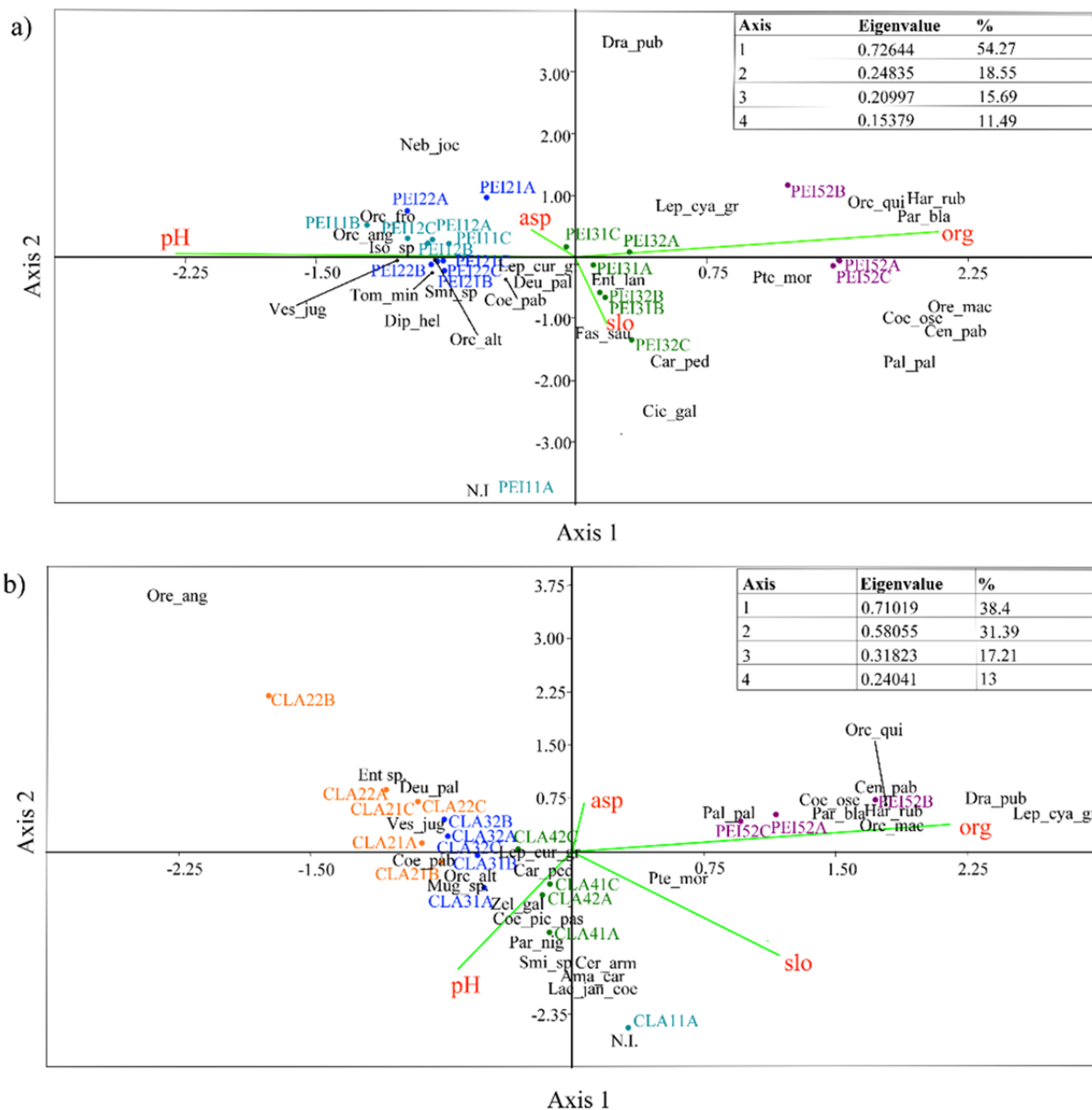


Fig. 4 Arthropod Canonical Correspondence Analysis (CCA) graphs for a) Peirabroc and b) Clapier. asp = aspect, slo = slope, org = organic matter, pH = soil reaction, pH.

The late successional stage (PEI5) hosts an arthropod community quite different from that of the previous successional stage, with four ground beetle, six spider and three ground-dwelling springtail species. According to IndVal, the indicator species linked to this successional stage are: the ground beetle *Harpalus rubripes*, the wolf spider *Pardosa blanda* and the springtail *Orchesella quinquefasciata* (Table 2).

The main difference between the two glaciers is the low number of spiders in the mid-successional stage of Peirabroc.

Analysing the general trend of species richness, arthropods and plants follow different colonization patterns, with some differences between the two glaciers (Fig. 3 b-d). Spiders show a strong decrease in total species richness in the mid-successional stages of Peirabroc but a peak on Clapier. Ground-dwelling springtails show the highest number of species in the early successional stages and then a monotonic decrease on Peirabroc. On Clapier the trend is similar but with lower initial values. Ground beetles show an increase of species during the succession until the LIA moraines, and then the

number stabilizes; only along the Clapier glacier foreland there is a positive peak in the mid-successional stages.

The supraglacial debris also hosts arthropod species. Five ground-dwelling arthropod taxa were found: the cryophilic and endemic ground beetle *Oreonebria angusticollis* ssp. *microcephala* (for the indicator species for this environment; Table 2) the springtails *Orchesella* cf. *frontimaculata* (cold-adapted and endemic species), Isotomidae sp., *Deutherosminthurus pallipes*, *Lepidocyrtus* gr *curvicollis*. No spiders were found on this environmental unit. The percentage of endemic species among arthropods in this habitat is 40%, considering ground beetles and springtails, and 100%, considering only spiders and ground beetles. The same percentages also represent the incidence of cold-adapted species, since all species are both cold-adapted and endemic.

3.5 Comparative analysis of succession patterns

The pattern of total plant species richness along the Clapier and Peirabroc chronosequence was characterised by a mid-successional maximum in correspondence to LIA moraines. Differently, an early-successional maximum was recorded for Rotmoos (Fig. 3a). A trend similar to the plant trend, with a lower maximum, was observed for ground

beetles (Fig. 3b); also for ground beetles, on Rotmoos the maximum of species richness was reached earlier than on the other glaciers. Unlike the other taxa, for spiders it is difficult to identify a general trend common among glaciers (Fig. 3c). The comparison between Peirabroc and Clapier springtail trends suggested a general decrease in species richness along the foreland (Fig. 3d).

In general, Peirabroc and Clapier are characterized by higher values of the Whittaker species turnover β_w than the other glaciers previously studied in inner and peripheral Alps. For plant succession, the highest values on Peirabroc and Clapier occurred in the transition from early to mid-successional stages (Fig. 5a), differently from other glaciers where usually the turnover lies between mid and late-successional stages. A similar trend, with different absolute values, was observed for ground beetles (Fig. 5b). For spiders, the trend is similar among glaciers, with a late peak in turnover (Fig. 5c). The comparison among Whittaker indexes in springtail succession along Peirabroc and Clapier glacier forelands suggested very different trends among the two Maritime glaciers (Fig. 5d).

The persistence index (Fig. 6a-d) showed lower values for Clapier and Peirabroc than for the previously studied glaciers, confirming an overall higher turnover. In particular, all pioneer taxa persisted to the mid-successional stage on Trobio glacier, while on Cedec and Rotmoos species persisted

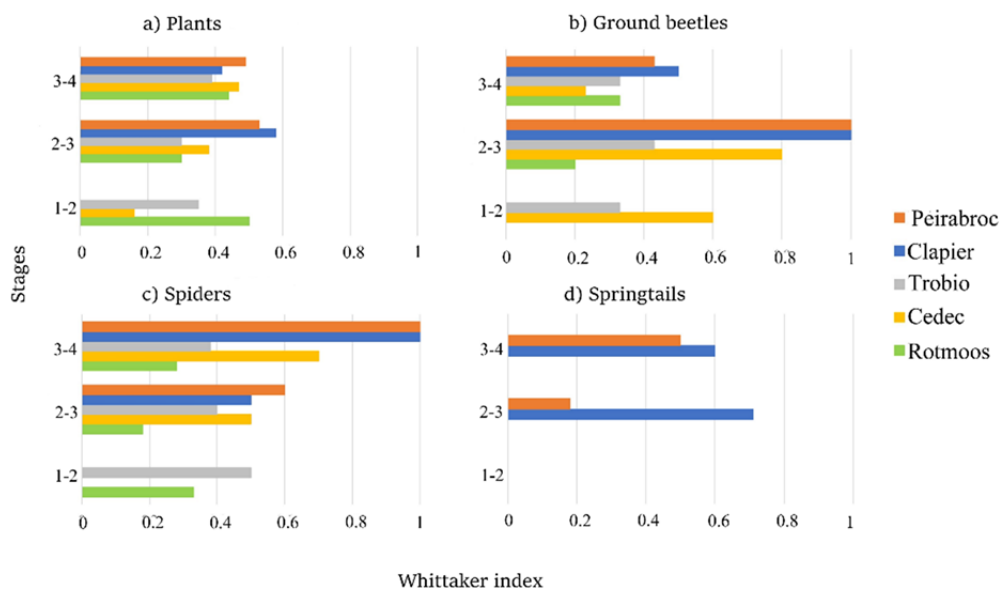


Fig. 5 Whittaker index for plants a), ground beetles b), spiders c), springtails d) along compared glacier forelands. 1-2 = from pioneer to early successional stage, 2-3 = from early to mid successional stage, 3-4 = from mid to late successional stage.

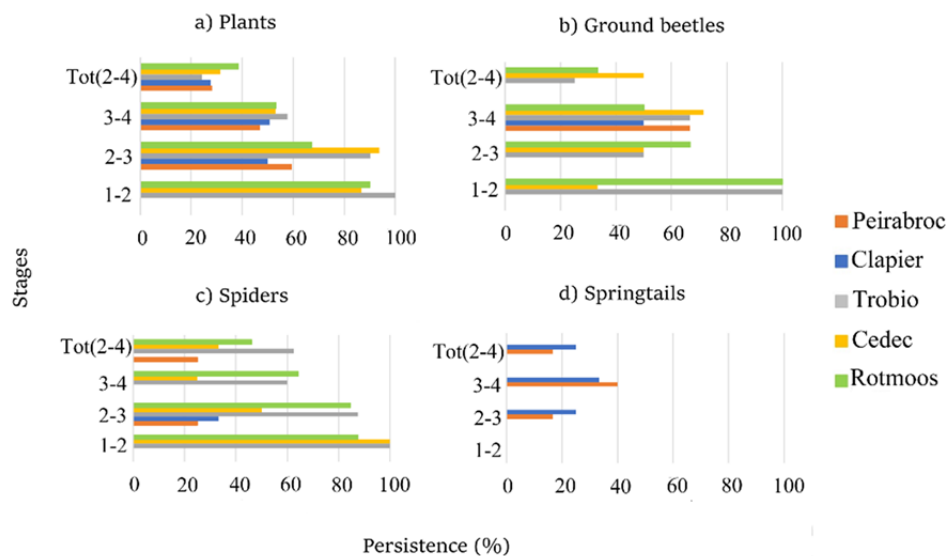


Fig. 6 Persistence index for plants a), ground beetles b), spiders c) and springtails d) along the compared glacier forelands. 1-2 = from pioneer to early successional stages, 2-3 = from early to mid successional stages, 3-4 = from mid to late successional stages. Data are not available for the passage from stage 1 to 2 on Peirabroc and Clapier: for this reason, the total persistence index was calculated from 2 to 4 for all glacier forelands.

longer through the succession. Plants (with the exception of Rotmoos) and spiders were the most persistent taxa from pioneer to mid successional stages; instead, ground beetles are persistent from mid to late successional stages. On Peirabroc and Clapier, springtail persistence index is very low in every successional stage.

4 Discussion

4.1 Thermal data

Our work is among the first to describe plant and arthropod communities colonizing the southernmost glacier forelands of the European Alps: Peirabroc and Clapier glacier forelands stand out for having remarkably higher average annual temperature (respectively 2.5° and 4.0°C) with respect to other studies in the inner (-1.8°C/-1.3°C ; Kaufmann et al. 2002a,b), and peripheral (1.7°C in Gobbi et al. 2017; from 0.5°C to 1.3°C in Tampucci et al. 2015) Central Alps, at comparable altitude. The average annual temperature recorded by our dataloggers is comparable to values reported by Federici and Pappalardo (2010) and Rapetti and Vittorini (1992) for the same area, confirming reliability of our data. The average annual temperature recorded on supraglacial debris (-1°C) is similar to those recorded on other debris-covered glaciers of the European Alps

(Gobbi et al. 2017; Valle et al. 2020).

4.2 Biodiversity of the southernmost Alpine glacier forelands

The investigated glacial environments host a remarkable biodiversity, with some noteworthy peculiarities of endemic species most of which are also cold-adapted and considered to be alpine species, but there are species of the area straddling both the Southern Alps and the Northern Apennines: the ground beetle *Oreonebria macrodera*, from Maritime Alps to Northern Apennines, and the spider *Coelotes osellai*, from Maritime Alps to Apuan Alps.

The most relevant findings include the plant *Saxifraga pedemontana* ssp. *pedemontana*, the ground beetles *Carabus pedemontanus*, *Oreonebria angusticollis* ssp. *microcephala*, *Amara carduii* sbsp. *psyllocephala*, *Pterostichus morio* sbsp. *fenestrellanus*, the spider *Vesubia jugorum*, and the springtail *Orchesella* cf. *frontimaculata*. These species have a very restricted distribution range and are strictly linked to cold environments; in particular, *Vesubia jugorum* is the only spider present in IUCN's Red List of threatened species (Mammola et al. 2016). *Vesubia jugorum* is classified as endangered because the current observed extent of occurrence (EEO 4,412 km²) and the area of occupancy (AOO 835 km²) are declining due to climate change (Isaia and Mammola 2018).

Supraglacial biodiversity is represented only by few species extremely specialised to cold and wet high-altitude environments. These include the springtail *Orchesella* cf. *frontimaculata* and the ground beetle *Oreonebria angusticollis*; both were found only in supraglacial habitat and in early successional stages, confirming for *Oreonebria angusticollis* its exclusivity for cold and wet habitats observed by Gobbi et al. (2011) and Bisio and Taglianti (2021).

Among springtail species, *Fasciosminthurus sauteri* is new for the Italian fauna; this species is an Alpine species described for Switzerland (Nayrolles and Lienhard 1990), where it was found in a scree slope vegetation and in a *Seslerio-Caricetum* grassland above 1800 m asl. Our data confirmed its presence in an open environment at high altitude; since we collected it quite far from the *locus typicus*, we can suppose that its distribution is underestimated and it may include a larger part of the Alps.

4.3 Homologies and differences among plant and arthropod successions along Peirabroc and Clapier glacier forelands

Plant and arthropod succession along Peirabroc and Clapier glacier forelands is arranged mainly in relation to soil evolution gradient driven by the time since deglaciation, as already observed in other Alpine glacier forelands (Matthews 1992; Burga 1999; Caccianiga et al. 2001; Khedim et al. 2021). However, we observed that aspect and slope also play an important role and, the latter for the arthropod communities of Clapier, suggesting that the microenvironmental variability could influence the successional pathway.

LG terrains usually host a lower number of plant species with respect to LIA moraines (Caccianiga et al. 2001; Tampucci et al. 2015); on the other hand, we cannot exclude an additional negative impact of grazing by ungulates (e.g. chamois and alpine ibex, pers. obs.) on plant species richness.

The higher values of turnover index and the lower persistence values with respects to other glacier forelands indicate that, despite some differences among taxa, plant and arthropod of Peirabroc and Clapier show the succession ‘replacement-change’ model, confirming observations by Rosero et al. (2021) and confuting our first hypothesis. In addition, Peirabroc and Clapier show some differences in their

successional patterns despite their proximity: this finding stresses the hypothesis that each succession - even on a very small scale - has its own characteristics, perhaps in relation to the limited extension of these environments and the great environmental heterogeneity (Kaufmann et al. 2002b; Mori et al. 2008). Such differences between the two proglacial successions are particularly evident for spiders and springtails. We hypothesize that the high variability of spider and springtail successions could be due to their microhabitat sensitivity and mobility (Rusek 2001; Widenfalk et al. 2016) that make pitfall traps a non-fully exhaustive sampling method for these taxa. In addition, this may have been enhanced by the short duration of the sampling, for the reasons explained in Material and Method chapter.

4.4 Successional patterns on different glacier forelands: peculiarities of peripheral glaciers with Mediterranean climate

Peirabroc and Clapier markedly differ from all the other successions we have considered in their higher species turnover and, for this reason, our results disprove hypothesis (ii) because, contrary to our expectation, Peirabroc and Clapier follow a typical ‘replacement change model’, with high turnover rates, as observed along the glacier forelands crossing the tree line in the inner Alps (Gobbi et al. 2006, 2007; Tampucci et al. 2015) as well as in Norway (Matthews et al. 2018), instead of an ‘addition and persistence model’ as observed in the other peripheral glaciers (see. Tampucci et al. 2015).

The ‘replacement change model’ of colonisation has been associated with less severe environmental conditions, such as higher mean summer temperature and lower disturbance, and to a greater species pool (Holten 2003; Walker et al. 2004; D’Amico et al. 2015; Matthews et al. 2018). Tampucci et al. (2015) associated such conditions with continental climate of the inner Alpine chain, with higher tree line position and generally warmer conditions during the growing season, whereas the oceanic climate of the peripheral chains results in more severe environmental conditions during the favourable season and ultimately in a longer persistence of pioneer species. We propose that, despite of their peripheral position, the peculiar climatic traits of Maritime Alps provide mild temperatures that could promote the rapid species turnover observed along the succession, as

pointed out by Ficetola et al. (2021).

Trends in species richness of plants and ground beetles seem to reflect the altitudinal distribution of the glacier with respect to the tree line. Peirabroc and Clapier glacier forelands are similar to Trobio and Cedec, being all above the tree line, while Rotmoos differs from the others.

With respect to all other analysed successions, Peirabroc and Clapier show the highest absolute values in species richness along plant succession, reflecting the biogeographic role of Maritime Alps as hotspot of biodiversity in the Mediterranean basin (Medail and Quezel 1999).

Early and mid-successional stages of the investigated glaciers are richer in species number and host the highest percentage and number of cold-adapted and/or endemic species, thus disproving our hypothesis (iii) that cold-adapted species are equally distributed along the succession, in contrast to results reported by Tampucci et al. (2015) in the Southern Alps. We propose that this is due directly to the considerably average higher temperatures of the proglacial habitat of Peirabroc and Clapier, which promotes the 'replacement change' model that disadvantages pioneer, cold-adapted species. Given the overall correspondence among cold-adapted and endemic species, the most threatened in this climate scenario (Tampucci et al. 2015; Cauvy-Fraunié and Dangles 2019), our results raise new concerns about the extinction risk of these species.

4.5 Supraglacial habitat, a threatened refugium for cryophilic and endemic species

The supraglacial habitat hosts well-defined plant and arthropod communities with cold-adapted and/or hygrophilous species. In particular, arthropod species with the combination of these characteristics, like *Oreonebria angusticollis* ssp. *microcephala*, are able to persist only on the glacier surface or on terrains very close to the ice tongue. Other arthropods, cold-adapted but not hygrophilous, seem to prefer either supraglacial or early-successional habitats. This is the case of *Orchesella* cf. *frontimaculata*; for this species the competition for food resources can be a factor limiting its presence in other environments, where other *Orchesella* species, such as *O. alticola* and *O. quinquefasciata*, occur. Other cold-adapted species - like the spiders *Coelotes pickardi pastor*,

Pardosa nigra, *Dysdera cribrata*, or the ground beetles *Amara carduii* ssp. *psyllocephala*, *Carabus pedemontanus*, *Pterostichus morio* ssp. *fenestrellanus* and *Oreonebria macrodera* occur also on mid- and late-successional stages. Thus, hypothesis (iv), that cryophilic species are more linked to the ice, is confirmed, and it is particularly evident for arthropods.

The incidence of endemism in this supraglacial habitat is high, as predicted in hypothesis (v), especially if we compare it to the Inner Alps where no endemic species were observed (see data from Gobbi et al. 2006).

The low average annual temperatures recorded on the supraglacial debris emphasize the specific features of such habitats in comparison to the nearby glacier forelands with their relatively warmer thermal profiles; supraglacial debris climatic profile depends on microhabitat features like ice presence, debris thickness and conductivity (Mihalcea et al. 2008; Schauwecker et al. 2015; Gibson et al. 2017). Thus, supraglacial debris represents an environment decoupled from the regional climate and may have an important role as refugium for cold-adapted and hygrophilous plant and animal species, whose survival can be threatened by climate change and by a fast ecological succession in the adjacent forelands. By now, the situation in the Maritime Alps is alarming, considering the uniqueness of these glaciers and of their biodiversity in relation to the reduced surface of Peirabroc glacier, but, especially, to the observed fragmentation of Clapier glacier's tongue.

5 Conclusions

Every primary succession is mainly driven by soil evolution - a proxy for time since deglaciation. However, differences at regional but even at local scale (i.e. between two nearby glacier foreland) could be observed, suggesting that every succession responds to regional climate, local biodiversity, microhabitat heterogeneity and extension, but also to stochastic events (Matthews 1992, Erschbamer and Caccianiga 2016; Ficetola et al. 2021); this emphasizes the important role of the scale of observation, particularly when dealing with different taxa.

The Maritime Alps represent a peripheral chain with a unique combination of specific climatic features and taxonomic richness, with particular

reference to endemic species. Due to their great variability and to the importance of glacial habitats as refugium for cold-adapted and endemic threatened species (Valle et al. 2021, 2022), it is important to expand the number of case studies in order to have a more complete vision of the phenomenon.

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Mediterranean glacial habitats, already especially threatened with disappearance for their geographical position, are further threatened by the fast species turnover, which implies that many cold adapted and endemic species, more linked to these environments, have a severe extinction risk.

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Electronic supplementary material:

Supplementary material (Appendixes 1-8) is available in the online version of this article at <https://doi.org/10.1007/s11629-022-7331-8>.

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