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Disappeared ice, vanishing life: The end of the largest glacier of the Bergamo Alps (Italy) and the consequences for its endemic biodiversity

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Abstract

To date, the direct effects of complete glacier disappearance on the specialized fauna associated with this habitat have never been investigated *in situ*. The Trobio glacier, once the largest in the Bergamo Alps (Italy), completely vanished in 2023 due to climate-induced retreat. This study reconstructs Trobio glacier's evolution from the Little Ice Age to its disappearance and assesses the impact of glacier extinction on two cryophilic endemic terrestrial arthropod species: the ground beetle *Nebria tresignore* and the springtail *Desoria orobica*. Historical maps, literature and recent field data were used to trace glacier changes, while biological surveys evaluated species occurrence to be compared with past (last 10 years) records. These data reveal a direct link between the recorded glacier retreat and species elevational shift: *Nebria tresignore* shifted upslope about 30 m a^{-1} following glacial retreat. *Desoria orobica* showed a dramatic population collapse, with average densities dropping from 80 to $<$ 4 individuals per sample since 2020, likely due to the deeply modified glacial environment. These findings highlight the vulnerability of glacier-dependent biodiversity and the urgent need to document glacier extinction and to identify and protect microrefugia for cold-adapted species in rapidly changing alpine environments.

1. Introduction

In the current dramatic scenario of worldwide glacier retreat (Rounce and others, 2023), it remains challenging to assess the effects of this phenomenon on ecosystem functioning and services at a global scale (Velasquez Casallas and others, 2025). As far as we know, the effect of glacier disappearance on the biodiversity linked to them has never been directly documented, although numerous speculations have addressed the impacts of glacier retreat on cold-adapted species (e.g., Kaufmann, 2002; Brown and others, 2007; Cauvy-Fraunié and Dangles, 2019; Ficetola, 2021). Microorganisms, plants and animals adapted to cold and humid glacial environments (i.e., cryophilic) are at risk of disappearing along with the habitat to which they are exclusively tied (Cauvy-Fraunié and Dangles, 2019; Gobbi and others, 2021), and, in general, the knowledge on alpine soil biodiversity is rare on a global scale (Praeg and others, 2025), especially in supraglacial habitat (Valle and others, 2025), posing challenges for this kind of monitoring worldwide. From this perspective, peripheral mountain ranges – like the Bergamo Alps – are of particular importance due to their high biodiversity (Medail and Quezel, 1999), which includes species that are exclusive to this area ("endemic"; Trew and Maclean, 2021). In fact, during the ice ages, the Bergamo Alps remained partially uncovered by ice caps, allowing the local survival of many plant and animal species and giving rise to a hotspot of mountain biodiversity (Tribsch, 2004).

The Trobio glacier was the most important and one of the most iconic of the Bergamo Alps ("Alpi Orobie," Lombardy, Italy), a relatively low (maximum elevation 3052 m a.s.l.) peripheral chain of the southern Alps. The high precipitation rate of this area, compared to the neighboring Alpine sectors (Luino and others, 2020), allowed the presence of glaciers even below mountains lower than 2900 m (Scotti and others, 2014).

At the peak of the Little Ice Age (LIA), the Trobio glacier was the largest glacier of Bergamo Alps (1.1 km^2) and its front extended down to 2330 m (Caccianiga and others, 1994; Scotti and others, 2014; Fig. 1). Relatively large and easily accessible, it soon became the most famous glacier of the Bergamo Alps (Fig. 1c). Afterwards, the glacier showed a steady decline until its complete disappearance in 2023 (D'Adda and Petrone, 2024; Figs 1b and 2).

In front of the Trobio glacier tongue, *Nebria tresignore* (Szallies and Huber, 2014) (Coleoptera: Carabidae), a stenoendemic ground-dwelling, surface-runner (wingless) ground beetle was observed (Tampucci and others, 2015; Gobbi and others, 2018a; Bonelli and others,

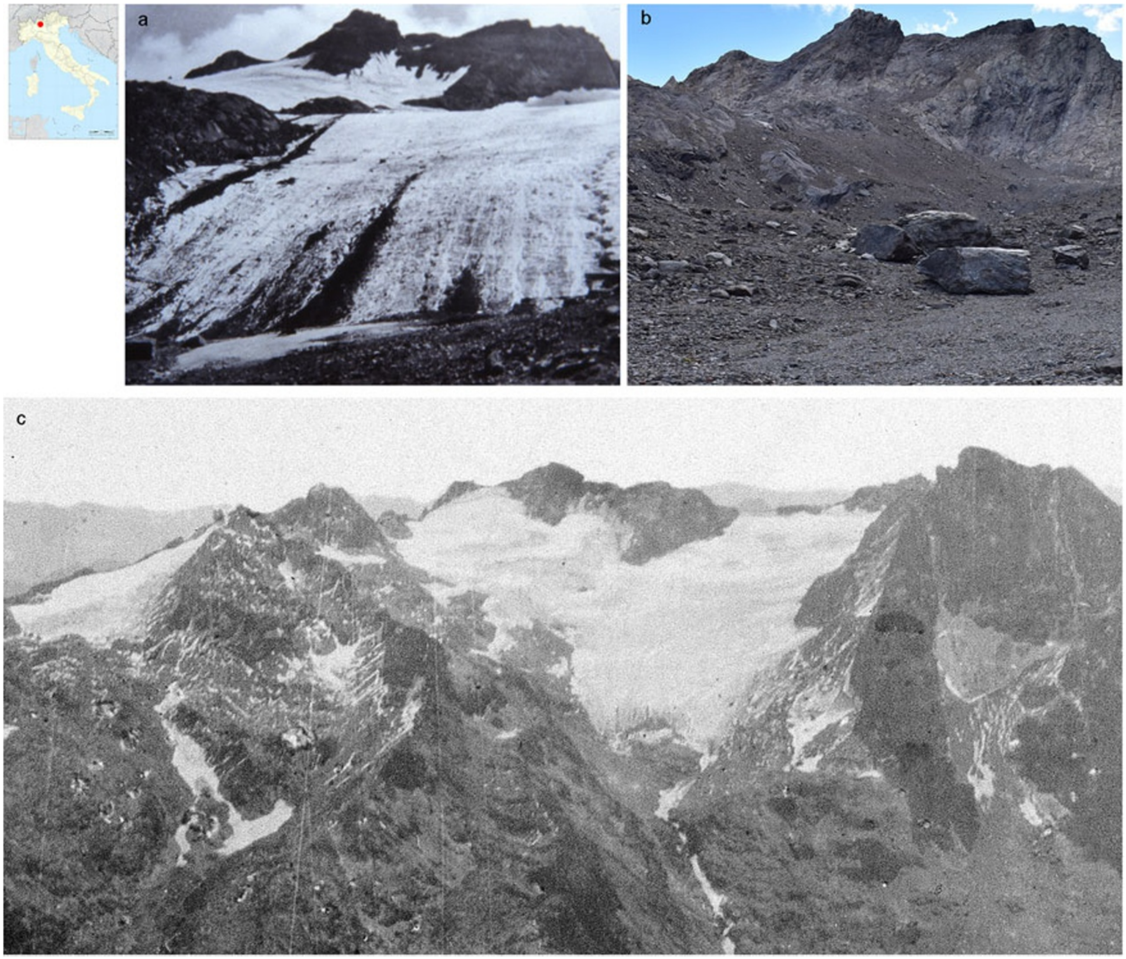

Figure 1. The Trobio glacier (Bergamo Alps, Italy) a) in 1935 and b) in 2022; c) the Trobio glacier (center) at the beginning of the 20th century. Pictures a) and b) were taken from the same viewpoint. Photographs respectively by Giuseppe Nangeroni (Comitato Glaciologico Italiano), Stefano D'Adda (Servizio Glaciologico Lombardo), Alfredo Corti (Archivio Corti, Italian Alpine Club, sez. Valtellinese).

2025). This species is closely linked to glacial environments like glacier surface, proximity of glacier tongue, glacierets, of the Bergamo Alps (Gobbi and others, 2018a; Bonelli and others, 2025). The springtail *Desoria orobica* Valle, 2025 (Collembola: Isotomidae) was discovered in 2020 and recently described for the Trobio glacier (Valle and others, 2025), but its exact distribution is still unknown (it is probably an endemic Alpine species; Valle and others, unpublished). Both organisms are cryophilic species at extremely high risk of extinction as they are strictly linked to the microhabitat conditions ensured by the presence of permanent ice and long-lasting snow cover. No data are available on *Nebria tresignore* feeding strategy and diet; it is likely an olfactory predator, similarly to the other alpine species belonging to the same genus (Wheater, 1989; Kielty and others, 1996), feeding on small arthropods like aphids, spiders, flies and springtails (Sint and others, 2018), thus probably also on *Desoria orobica*. The specific diet of *Desoria orobica* is still unknown, but it possibly consists of dead organic matter and biofilms, similarly to other springtails species of glacial and proglacial habitat (Hågvar and Pedersen, 2015).

The aims of this work are (1) reporting the glaciological trends of Trobio glacier from the LIA till its disappearance and (2) providing data about the monitoring of the abundances and distribution of the two iconic endemic indicator species, *Nebria tresignore* and *Desoria orobica*, in relation to the glacier retreat.

2. Materials and methods

2.1. Historical glaciological data

To reconstruct the past extent and dynamics of the Trobio glacier, we consulted a variety of historical sources, including cartographic records, written descriptions and photographic evidence. Early qualitative descriptions, such as those by Maironi Da Ponte (1808) and Ricci (1911), provided first-hand accounts of the glacier's characteristics and movement. Historical maps, including the 1833 Austrian military map (Caccianiga and others, 1994; Bonardi and others, 2012), offered valuable cartographic representations of its extent during the LIA.

Additionally, scientific literature detailing glaciological surveys (e.g., Caccianiga and others, 1994; Scotti and others, 2014) and inventories such as those by Porro (1925) and Nangeroni (1932) and C.N.R. – Comitato Glaciologico Italiano (1961) documented the glacier's fluctuations over time. Photographic records, including images by Alfredo Corti, further complemented our analysis by providing visual evidence of the glacier's evolution throughout the 20th century.

This comprehensive review of historical sources associated with a field-based and remote sensing geomorphological interpretation of glacier deposits and trim-lines enabled us to reconstruct the LIA

Figure 2. (a) The Trobio glacier (Bergamo Alps, Italy) in 17 September 2022; (b) The Trobio glacier in 10 August 2023 soon before the complete vanishing of the last ice patches (the red circle indicates two sampling persons as a scale). The ice patch subdivided in two parts on the bottom of (a) is the same reported in (b), where the two parts are completely separated. Photograph respectively by Stefano D'Adda and Marco Caccianiga.

glacier's maximum surface extent. By doing this, we were able to compare past glacier extents with recent field observations, facilitating a long-term assessment of the Trobio glacier retreat and disappearance.

2.2. Post-LIA glacier area change

In order to quantify post-LIA glacier change we reconstructed the glacier's extent in five different time steps. Glacier's extents in 1954, 1989 and 2003 are upgrades from Scotti and others (2014). The glacier's limits in 1954 have been formerly stereographically interpreted on paper copies of black and white aerial photographs and slightly corrected by terrestrial historical images and field surveys. Limits from 1989 rely on the 1992 Lombard glacier inventory (Galluccio and Catasta, 1992) checked on 26 September 1988 b/w orthophoto (Volo Italia 1988–89); 2003 (0.5 m grid) orthophoto mosaic and 21 August 2022 Google Earth® images have been used for the more recent time-steps, while in the year 2023 the complete glacier extinction was witnessed directly in the field.

2.3. Biodiversity monitoring

To assess the presence and distribution of the two cryophilic species *Nebria tresignore* and *Desoria orobica*, we conducted surveys during summers 2023 and 2024 verifying previous records from the years 2014 (sampling date 13 September) and 2016 (28 August) for *Nebria tresignore* (Gobbi and others, 2018a) and from the year 2020 (sampling date 18 July) for *Desoria orobica* (Valle and others, 2025) to evaluate potential shifts in species distribution and/or abundance over time. This comparison allowed us to assess population trends and habitat stability after the glacier disappearance. We also added new sampling points (A1-A2-B1-B2) where the last ice patches occurred before complete disappearance. We searched for the two species where the most favorable ecological conditions could be found, i.e. on the last ice patches (in 2023), on snowfields, and in their immediate vicinity. Observations were systematically recorded, with standardized qualitative (for *Nebria tresignore*) and quantitative (for *Desoria orobica*) sampling methods, ensuring consistency in methodology, sampling time and/or period and site conditions for a temporal comparison. *Nebria tresignore* sampling was performed by hand catching performed in nine sampling points of about 25 m^2, for 20 minutes by one experienced operator (Gobbi and others, 2018b) during the summers 2023 (10 August), 2024 (26 July and 28–29 August) (Fig. 4). Data on abundance of *Nebria tresignore* were not used for the analysis due to the different duration of the sampling performed in 2014 (1 h – Tampucci and others, 2015) with respect to those of the following sampling sessions (20 minutes), the different sampling months in each year and the low abundance of recorded individuals (average of 2 ± 1 individuals in each sampling point for each temporal session); thus only occurrence data were used. *Desoria orobica* sampling was performed in summers 2023 (10 August), 2024 (28–29 August) in the stony debris by flotation methods in three sampling points (Fig. 4, Table 3) in an area of 25 m^2 with 22 replicates in 2023 and 28 in 2024, while 17 replicates were carried out in 2020 in one sampling point. At least, three replicates for each sampling point were performed on standard volumes of soils (200 ml; Valle and others, 2023). *Desoria orobica* was also sampled by hand catching in five sampling points (Fig 4, Table 3), with 4 replicates in 2023, 12 in 2024, none in 2020, performed in each sampling point for 20 minutes by one experienced operator (Gobbi and others, 2018b; Fig. 4). Since both species, after their first identification/description for the area, could be easily identified directly on the field using a 10x lens, no individuals were collected in order not to harm the remaining population (Lencioni and Gobbi, 2021).

3. Results

3.1. Post-LIA glacier change

At the beginning of the 1800s, Giovanni Maironi Da Ponte (1808) described the Trobio glacier as a "great deposit of perpetual ice." The 1833 Austrian military map provided a plausible and consistent cartographic representation of the glacier's extent (Bonardi and others, 2012). Around 1860, the glacier likely reached its maximum extent (Fig. 3), forming the imposing moraine still visible today. A striking photograph by Alfredo Corti (Fig. 1c) shows the glacier in good condition in the early 20th century, when

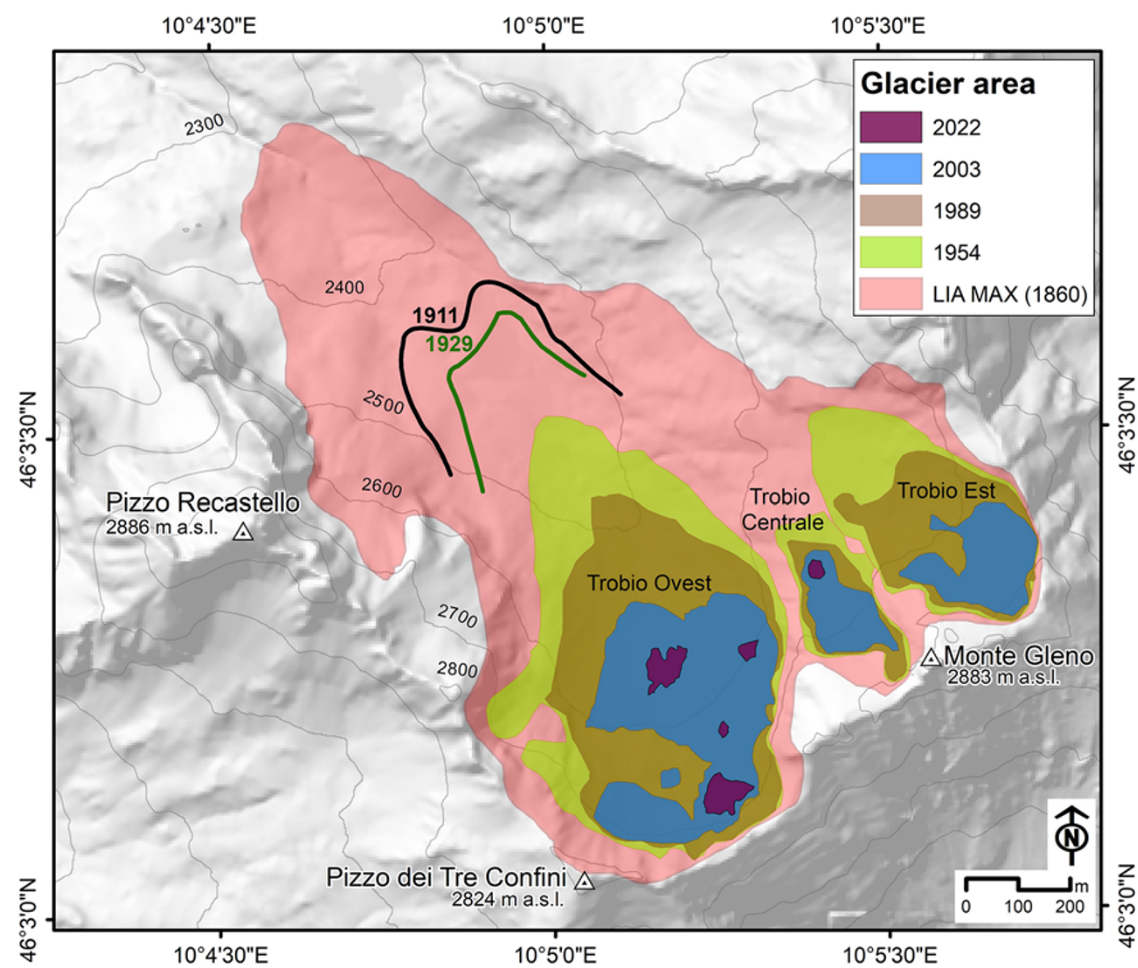

Figure 3. Reconstruction of Trobio glacier (Bergamo Alps, Italy) extents from Little Ice Age (LIA) maximum (~1860) to 2022. Front positions in 1911 and 1929 are extrapolated from Caccianiga and others (1994). Shaded relief derived from the Lombardy region 5-m Digital Terrain Model.

Table 1. Trobio glacier (Bergamo Alps, Italy) extents from Little Ice Age (LIA) maximum (~1860) to 2022. The three parts of the glacier (Trobio Est, Trobio Centrale, Trobio Ovest) are considered individually and collectively (total).

	Glacier extent (km^2)				
Glacier	LIA Max (1860)	1954	1989	2003	2022
Trobio Est		0.12	0.08	0.03	0.00
Trobio Centrale	1.11	0.04	0.03	0.02	0.00
Trobio Ovest		0.33	0.23	0.12	0.01
Trobio (total)	**1.11**	**0.49**	**0.34**	**0.17**	**0.01**

Leonardo Ricci described it in detail, providing a sketch and quantifying an "average annual displacement" of 3.75 m in its middle portion (Ricci, 1911). In the 1920s, the Trobio glacier was mentioned in Porro's first list of Italian glaciers (Porro, 1925) and later described in detail by Nangeroni (1930, 1932), who documented its subsequent fluctuations until 1952. Between 1943 and 1945 the original glacier split into two units (Trobio Ovest and Trobio Est). The glacier lost 56% of the former area between its maximum and 1954 (Fig. 3 and Table 1). Like many other Alpine glaciers, a positive phase started from the 1960s, allowing the system to regain volume and even mark a small frontal advance. Since 1987, the trend turned negative again with an average annual area decrease (AAD) that almost doubled from 0.006 km^2 a^{-1} (1860–1989) to 0.010 km^2 a^{-1} (1989–2022) until the complete vanishing of the glacier testified during the biological and glaciological surveys performed in summer 2023 (D'Adda and Petrone, 2024) (Fig. 3 and Table 2).

3.2. *Nebria tresignore* and *Desoria orobica* occurrences

In 2024, the ground beetle *Nebria tresignore* was found only in close proximity to snow patches and could not be observed in the sites of the previous observations (Fig. 4); it shifted uphill by approximately 300 m in a beeline over the last 10 years (2014–24), corresponding to a shift of approximately 30 m a^{-1}. Monitoring activity performed in 2024 revealed that *Nebria tresignore* now shares its microhabitat with the niche competitor, cold-adapted, Central Alpine endemic *Nebria lombarda* K. & J. Daniel, 1890, unlike previous observations where *N. tresignore* was the sole ground beetle occurring near the glacier front. For the springtail *Desoria orobica*, only one record was not confirmed in 2024; however, comparing abundances, very low densities were observed in 2024 with respect to the previous records. In particular, comparing average abundances recorded with flotation method, a mean value of 80.8 individuals (st. dev. 164.0) per sampling was found during 2020. The maximum values (660, 359 and 140 individuals) were all recorded within 5 cm from the snow, while the minimum values (0) were recorded at the greatest distances from the snow, from 90 to 150 cm. Conversely, during and after the disappearance of the glacier – 2023 and 2024, respectively – the maximum value recorded dropped to 3.75 (st. dev. 3.3) individuals per sampling (Fig. 4 and Table 3).

4. Discussion

Climate change is already making us witness glacier disappearance in real time. It is therefore crucial to begin monitoring this critical phase not only from a glaciological perspective, but also from a biological and ecological one. The Trobio case exemplifies a process that is occurring worldwide, where the extinction of small glaciers is advancing rapidly, with consequences that extend far beyond local landscapes.

The history of the Trobio glacier is emblematic of the broader transformations that have reshaped Alpine glacial landscapes since the end of the LIA. Despite some brief and difficult-to-quantify phases of advance, the Trobio glacier experienced an almost continuous retreat since the end of the LIA. The physical withdrawal, traced through the analysis of the Average Annual Decrement (AAD), reveals a clear climatic fingerprint: the doubling of the absolute AAD after 1989, mirroring trends observed in other mountain glaciers and sectors of the Alps (Scotti and others, 2014), clearly reflects the sharp global temperature increase occurring since the 1980s (IPCC, 2023). Notably, the European Alps have emerged as one of the most affected regions globally, with glacial recession proceeding at a markedly fast pace (Copernicus Climate Change Service (C3S) and World Meteorological Organization (WMO), 2025). A closer examination of the temporal intervals reveals that the peak of Trobio AAD occurred between 1989 and 2003 (0.012 km^2 a^{-1}). Surprisingly, despite increasingly adverse climatic conditions in the European Alps, a partial deceleration was observed in the subsequent period (0.08 km^2 a^{-1}). This partial decorrelation, seemingly at odds with the overarching trend, can be explained by glacier's progressive retreat into a more sheltered morphological niche in the last 20 years. As the ice front migrated beneath steep rock walls, it began to benefit from enhanced shading, increased wind-driven snow deposition and avalanche accumulation, factors that can temporarily buffer the glacier from climatic forcing. These peculiar morphological conditions typically lower the Equilibrium Line Altitude (ELA) of glaciers setting a local topography-driven ELA that is significantly lower than the ELA granted by climatic conditions only, i.e., Regional Climatic Equilibrium Line Altitude (ELA_{rc}). In Bergamo Alps this ELA decoupling is typically pronounced and it plays a critical role in sustaining the existence of the remaining glacial bodies (Scotti and others, 2014). However, despite the local factors offering a brief reprieve and a weak increase in glacier resilience, topographical conditions were not sufficient to halt the intensity of recent warming and the decline of the Trobio glacier. The rock walls surrounding the glacier are relatively gentle and of limited vertical extent, unable to provide the strong orographic shielding observed in other, more protected cirques in the surroundings. Conversely, the same gentle morphology, coupled with a sufficiently high elevation,

Table 2. Trobio glacier (Bergamo Alps, Italy) absolute and relative Annual Average Decrease (AAD) in multiple time-steps since LIA maximum (~1860). The three parts of the glacier (Trobio Est, Trobio Centrale, Trobio Ovest) are considered individually and collectively (total).

	Annual Average Decrease (AAD) in km^2 a^{-1} (% a^{-1})					
Glacier	1860–1954	1954–1989	1989–2003	2003–2022	1860–1989	1989–2022
Trobio Est		0.001 (0.9)	0.003 (4.2)	0.002 (5.3)	–	0.002 (3.1)
Trobio Centrale	0.007 (0.6)	0.000 (0.8)	0.001 (2.5)	0.001 (5.0)	–	0.001 (3.0)
Trobio Ovest		0.003 (0.8)	0.008 (3.5)	0.006 (4.8)	–	0.007 (3.0)
Trobio (total)	**0.007 (0.6)**	**0.004 (0.9)**	**0.012 (3.6)**	**0.008 (4.9)**	**0.006 (0.5)**	**0.010 (3.0)**

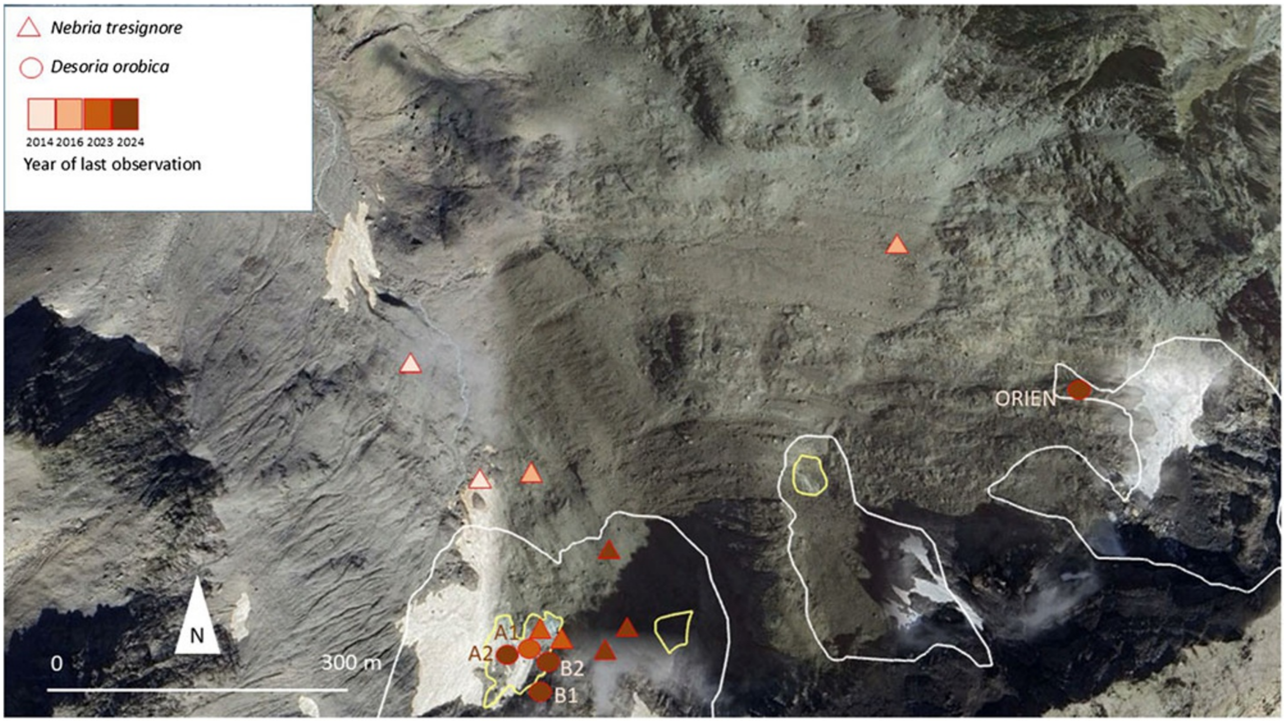

Figure 4. Temporal distribution of observation records of the cryophilic ground beetle *Nebria tresignore* and springtail *Desoria orobica* at the Trobio glacier (Bergamo Alps, Italy). *Nebria tresignore* was sampled with hand catching during the years 2014 (13 September; Gobbi and others, 2018a), 2016 (28 August; Gobbi and others, 2018a), 2023 (10 August) and 2024 (26 July and 28–29 August). *Desoria orobica* was sampled in 2020 (18 July; Valle and others, 2025), 2023 (10 August), 2024 (28–29 August) with flotation methods in the stony debris and also with hand catching (more details in the text). From left to right, Trobio Ovest, Trobio Centrale, Trobio Est glaciers. The glacier extents of 2003 (white line) and 2022 (yellow line) are shown. *Desoria orobica* abundance values are reported in Table 3 (Orthophoto from Google Earth®).

Table 3. Average abundance values and standard deviation of the cryophilic springtail *Desoria orobica* for year and sampling methods. HC = hand catching (expressed as individuals per sampling), F = flotation method (expressed as individuals 200 ml^{-1}). *Desoria orobica* was sampled in 2020 (18 July; Valle and others, 2025), 2023 (10 August), 2024 (28–29 August) with flotation methods in the stony debris and with hand catching on the ice (more details in the text). The exact year of Ice disappearance in ORIEN (Trobio Est) is unknown.

				Desoria orobica abundances during the three years of sampling					
Sampling points	Coordinates	Location	Sampling methods	2020 (average)	2020 (st.dev)	2023 (average)	2023 (st.dev)	2024 (average)	2024 (st.dev)
A1 (Trobio Ovest)	46°03′15.7″N 10°05′09.6″E	Last ice patch in 2023	HC	–	–	12	0	0	0
A2 (Trobio Ovest)	46°03′16.0″N 10°05′09.7″E	Adjacent to the last ice patch in 2023	HC	–	–	8	0	2	0
			F	–	–	3.75	3.3	–	–
B1 (Trobio Ovest)	46°03′14.8″N 10°05′10.9″E	Last ice patch in 2023	HC	–	–	–	–	4	0
			F	–	–	0.8	1.3	0	0
B2 (Trobio Ovest)	46°03′15.6″N 10°05′10.7″E	Adjacent to the last ice patch in 2023	HC	–	–	0.5	0.5	1	1
			F	–	–	0.5	0.5	1	0.5
ORIEN (Trobio Est)	46°03′24.6″N 10°05′35.2″E	Snow patch located in the place of the last remnant of ice	HC	–	–	–	–	0	0
			F	80.8	164.0	–	–	0.3	0.8

once facilitated the great expansion of the glacier at the LIA apex. During that period, a lowered ELA_{rc} favored direct snow accumulations over a vast area. In this regard, therefore, the Trobio glacier presented characteristics atypical for its size, behaving more like a large alpine glacier almost entirely fed by direct snowfall. Yet, this apparent robustness masked an underlying vulnerability. The limited elevation of the hosting cirque, combined with the absence of strongly protective topography, ultimately sealed the glacier's fate: as climate warming accelerated, these marginal conditions proved insufficient to ensure survival.

The profound physical changes observed in the Trobio glacier do not simply represent a shift in the landscape morphology. Rather, they provide a critical ecological backdrop for understanding the severe and still unfolding consequences for cryophilic fauna tightly bound to these disappearing icy habitats (Fig. 5). Although numerous speculations have addressed the impacts of glacier retreat on cold-adapted species worldwide (e.g., Kaufmann, 2002; Brown and others 2007; Cauvy-Fraunié and Dangles, 2019; Ficetola and others, 2021), the direct biological impacts of complete glacier disappearance have never been investigated in the field. Thus, the Trobio glacier offers a unique natural experiment with implications that go well beyond the Alps, shedding light on the fate of cryophilic biodiversity under accelerating global warming. Our findings show that both mobile species (i.e., ground beetles) and microhabitat-dependent taxa (i.e., springtails) exhibit rapid responses to glacial loss at fine

Figure 5. (a) *Desoria orobica* (average length: about 1.5 mm), cryophilic springtail recently described for the Trobio glacier (28 July 2024); (b) *Nebria tresignore* (length: 8.5–10 mm) dwelling on the surface of the Trobio glacier (30 July 2018). Photograph respectively by Barbara Valle and Danilo Donadoni.

temporal scale. In particular, the current occurrence of *Nebria tresignore* and *Desoria orobica* (Fig. 5) in the area once occupied by the glacier supports the hypothesis of an "extinction debt" (Kuussaari and others, 2009). This phenomenon describes a delayed biodiversity collapse, where the full impact of habitat loss becomes apparent only after a time lag.

Our data suggest that the extinction risk is particularly high for *Nebria tresignore*, whose ecological niche overlaps significantly with *N. lombarda*, a congeneric species now advancing into the glacier foreland from the surrounding slopes. Similarly to *Nebria tresignore* and other congeneric species (Raso and others, 2014), *Nebria lombarda* preys on springtails and other arthropods. In addition, intraguild predation among *Nebria* species has been documented (Raso and others, 2014; Sint and others, 2018), raising the possibility of direct competition for diminishing food resources.

Even more alarming is the striking population decline of *Desoria orobica* observed between 2020 and 2024. The combination between the final disappearance of ice and two years with below-average snow cover (namely 2022 and 2023) heavily affected the consistency of the once abundant springtail species. Its survival appears tightly linked to a microclimatic niche – cold, humid and snow-insulated – that is rapidly vanishing under the current warming trends. Yet, since the exact distribution range of this newly discovered species is still not known, the broader implications of this loss remain difficult to quantify.

Ultimately, the fate of *Nebria tresignore* and *Desoria orobica* likely depends on their ability to locate and persist in small-scale refugia: cold and humid microhabitats, such as coarse debris and/or sub-superficial ice patches. Current research efforts should aim to identify potential refugial areas where conservation and monitoring efforts can be effectively directed (Morelli and others, 2016). However, field-based evidence on fragile cryophilic biodiversity remains limited and many species still likely remain undescribed (Fjellberg, 2010; Valle and others, 2025), especially at low latitudes. Furthermore the lack of fine-scale data severely limits our ability to predict species-specific responses to the subtle but decisive role of local topography in shaping survival opportunities under climate stress. Documenting local glacier extinction is therefore not only crucial for local understanding, but also provides key evidence to understand and forecast the global consequences of glacier extinction for biodiversity and ecosystem functioning (and correlated ecosystems services, such as water regulation, nutrient cycling and habitat provision).

Data availability statement. Data are available from the authors upon request.

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Competing interests. The authors declare that they have no competing interests.

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