This is the final author copy of the peer reviewed accepted version of the following article: Brighenti S, Tolotti M, Bruno MC, Wharton G, Pusch MT, Bertoldi W (accepted 13.4.19) Ecosystem shifts in Alpine streams under glacier retreat and rock glacier thaw: a review, published in final form at doi.org/10.1016/j.scitotenv.2019.04.221. This article may be used for non-commercial purposes in accordance with Elsevier Terms and Conditions for Self-Archiving.

Ecosystem shifts in Alpine streams under glacier retreat and rock glacier thaw: a review

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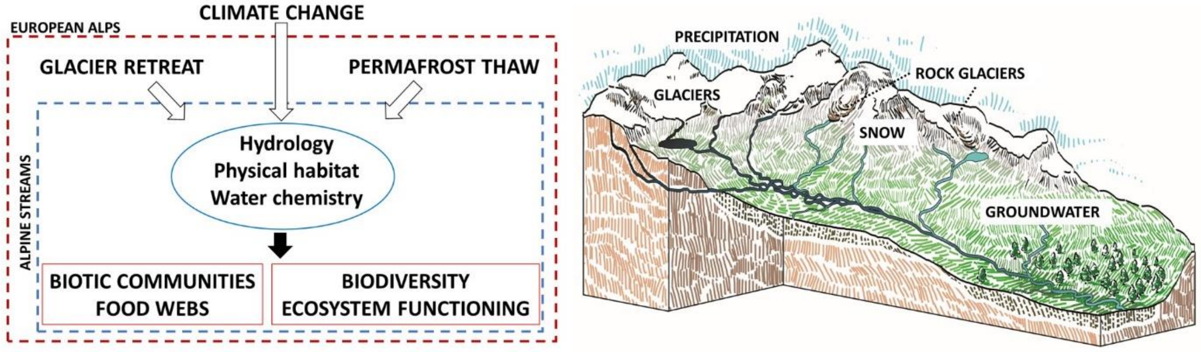
KEYWORDS: European Alps, permafrost, rock glaciers, ecosystem function, food webs
Running title: Deglaciation streams European Alps

Running title: Effects of deglaciation on Alpine stream ecosystems

Highlights

- We outline the changes in climate, glacier and permafrost occurring in the Alps
- We detail the effects of glacier retreat and rock glacier thaw on stream habitats
- We summarize the shifts in biotic communities and food webs in Alpine streams
- A conceptual model of the diverse effects of deglaciation on such streams is given
- Knowledge gaps and research priorities are examined, namely on rock glacier streams

Graphical Abstract



Abstract

This review provides a detailed synthesis of the effects of glacier retreat and permafrost thaw on stream ecosystems in the European Alps. As a working framework, we present a conceptual model developed from an integration of current knowledge and understanding of the habitat and ecological shifts in Alpine streams caused by deglaciation. In our work, we depict how climate change and the loss of cryosphere trigger complex cascading effects on Alpine hydrology, as the main water sources shift from snow and glaciers to rock glaciers, groundwater, and precipitation. The associated changes in habitat conditions, such as channel stability, turbidity, temperature, nutrient loadings, and concentrations of legacy pollutants and trace elements are identified. These changes are followed by complex ecological shifts in the stream communities (microbial community, primary producers, invertebrates) and food webs, with a predicted loss of biotic diversity. Corresponding increases in taxa abundances, biomass, functional diversity, and in the complexity of food webs, are predicted to occur in the upper reaches of Alpine catchments in response to ameliorating climatic and habitat conditions. Finally, current knowledge gaps are highlighted as a basis for framing future research agendas. In particular, we call for an improved understanding of permafrost influence on Alpine headwaters, including the ecology of rock-glacier fed streams, as these streams are likely to become increasingly important for water supply in many glacier-free Alpine valleys in the near future.

1. INTRODUCTION

Glacier retreat and permafrost thaw are among the most evident effects of current climate change (Intergovernmental Panel on Climate Change [IPCC], 2013). The global character and the speed of present deglaciation are unprecedented in the Holocene (Solomina et al., 2015), and reflect a dominant anthropogenic component (Marzeion et al., 2014). The consequences of deglaciation are a global issue, since the cryosphere provides important ecosystem services such as water provisioning, especially during hot and dry periods, climate regulation, and the global cycling and sequestration of carbon (Anesio et al., 2009; Milner et al., 2017). Mountains are acknowledged as early warning areas of global warming because of their high sensitivity to temperature changes and limited direct human impacts (Beniston, 2005; Körner et al., 2005). As they store and supply freshwater to rivers and lowland areas, with a vital importance for human societies and ecosystems (Meyer et al., 2007), mountains are considered as “water towers” of the world (see Viviroli et al., 2007). In the European Alps (hereafter referred to as “the Alps”), climate change and the accelerated reduction of the cryosphere (Vincent et al., 2017; Beniston et al., 2018) have many consequences, including summer water shortages at the whole basin scale (European Environment Agency [EEA], 2009; Huss, 2011), increased geomorphologic risk (e.g. Haeberli and Beniston, 1998; Haeberli et al., 2010; Kellerer-Pirklbauer et al., 2011; Mair et al., 2015; Haeberli et al. 2016), depletion of drinking water quality (Bogataj, 2007; Mair et al., 2015), and decline of tourism (Smiraglia et al., 2008). Long term changes also pertain to the overall Alpine mountain ecology, with a reported decrease and in places the extinction of sensitive habitats, species, and populations (e.g. Walther, 2004; Schröter et al., 2005; EEA, 2009; Dirnböck et al., 2011). Furthermore, changes in climate and deglaciation interact with local pressures, potentially multiplying the consequences. For example, water exploitation for hydropower production (e.g. Permanent Secretariat of the Alpine Convention, 2009) and drinking water supply (e.g. Klug et al., 2012), intensification of transhumance (Tiberti et al., 2014), stocking with allochthonous fish (e.g. Tiberti et al., 2013), and touristic activities and infrastructures (e.g. Rixen et al., 2011) currently represent major local stressors for freshwaters in the Alps.

Several reviews have been published to date on the effects of deglaciation on alpine freshwaters, especially during the last years. While McGregor et al. (1995) focus on the effects of hydropower generation and glacier loss specifically in the Alps, most reviews have a global perspective as they focus on the relationship between habitat changes and biotic shifts associated to glacier shrinkage at high latitudes and altitudes. Some focus on single ecosystem drivers (i.e., the importance of the ice melt: Slemmons et al., 2013); others provide different frameworks of analysis (i.e., hydroecology: Milner et al., 2009; the “multitrophic” approach: Fell et al., 2017); or focus on the organism-based research by emphasizing methods and approaches (i.e., Hotaling et al., 2017). Milner et al. (2017) provide a wider context by considering the implications of glacier loss to physical and chemical fluxes, biodiversity, and ecosystem services to lowland areas along the river continuum. However, although these reviews have been important in highlighting the significance of glacier retreat for freshwater ecosystems, they pay little attention to the thawing of permafrost. With a focus on mountain areas, only Huss et al. (2017) consider the combined loss of snow, permafrost, and glaciers, analysing the resulting changes in the overall ecology, geomorphology, and socio-economy.

Our review builds on this holistic approach to cryosphere and provides a synthesis of the consequences of both glacier retreat and permafrost thaw (hereafter referred to as “deglaciation”) on stream ecosystems in the Alps which, to the best of our knowledge, is the first synthesis for a specific mountain range. Mountain ranges around the world differ in terms of climate, topography, average elevation, geology, distribution and prevalence of glacial and periglacial forms and phenomena, sensitivity to climate change, and local and regional human pressures (e.g. Huss et al., 2017). These peculiarities likely drive unique and mountain range specific patterns of responses to deglaciation. Likewise, as the most studied mountain range in the world (Fig. 1), research on the Alps has the potential to provide insights into the effects of deglaciation elsewhere.

To synthesize the complex effects of climate change and deglaciation on stream ecosystems in the Alps, we developed a conceptual model (Fig. 2), which provides a framework for our review. Herein, stream ecosystems located above the treeline are referred to as “alpine streams”, whereas “Alpine streams” are alpine streams located in the Alps.

2. SETTING THE SCENE: THE WARMING ALPS AND THEIR DEGRADING CRYOSPHERE

The Alps (43-48°latitude, 5-17°longitude) are the highest (4,810 m a.s.l.) and largest (190,000 km^2) mountain system entirely located in Europe, covering 11% of the continental area (Treccani Enciclopedia, 2018) in one of the most densely populated areas worldwide (Huss et al., 2017). Because of their geographical location, the large-scale influences of different climate regimes (Atlantic, Mediterranean, Polar, Continental and African) interact with local features (e.g. topography, aspect, proximity to the sea), producing a large climatic variability (Beniston, 2006) that enhances biodiversity (Nagy et al., 2003; Alpine Ecological Network, 2018).

The Alps have experienced an increase in average annual temperature of 2°C between the late 19th and the early 21st Century, corresponding to more than twice the global and European averages (Auer et al., 2007; EEA, 2009). This trend is predicted to continue, as reviewed under different IPCC scenarios by Gobiet et al. (2014). On average, temperature is estimated to rise by 1.5°C during the first half of the 21st Century, and by 3.3°C during the second half, with more pronounced changes predicted at higher elevations (Gobiet et al., 2014; Kotlarski et al., 2015). Although slight average precipitation shifts were recorded during the second half of the past century depending on the Alpine sector (Auer et al., 2007), future trends are uncertain. Recent estimates support the hypothesis that, despite an overall decrease in summer precipitation in the area, high elevations may face an increased rainfall during the same season because of convective phenomena (Giorgi et al., 2016), and the seasonality and intensity of extreme precipitation events may change (Brönnimann et al., 2018).

Reductions in snow, glacier and permafrost extent are all features of the changing Alpine cryosphere (Beniston et al., 2018). The ongoing rise of the snowline is expected to continue during the 21st Century, with a decline of the snow cover and an earlier snowmelt onset during spring (Huss et al., 2017; Beniston et al., 2018,). Alpine glaciers have been receding at increasing rates during recent decades (Zemp et al., 2006; Haeberli et al., 2007; EEA, 2017). Around 75% of the Alpine glaciated surface recorded during the period 1971-1990 is predicted to vanish by 2050 (Haeberli and Hohman, 2008), while 80 to 100% of the glaciers in the Alps are expected to disappear by the end of the 21th Century (Zemp et al., 2006), with very small glaciers (< 0.5 km^2 area), representing the vast majority, vanishing over the next two decades (Huss and Fischer, 2016).

Glacier retreat is paralleled by permafrost loss. Permafrost is defined as "ground (soil or rock, including ice and organic material) that remains at or below 0 °C for at least two consecutive years" (Dobinski, 2011). Rock glaciers, defined by van Everingden (2005) as "masses of rock fragments and finer material that contains either interstitial ice or an ice core and show evidence of past or present movement", are an evident and common form of mountain permafrost (Schoeneich et al., 2011). As for glaciers, a large proportion of Alpine permafrost is located close to the melting point, and is therefore particularly sensitive to increases in atmospheric temperature. Responses to warming comprise thermal and geomorphic alterations, such as the thinning of the active layer (i.e. the upper part, seasonally freezing and thawing) and the melting of internal ice (i.e. permafrost thaw) with associated destabilization of slopes, increased frequency and magnitude of mass movements such as debris flows, rockfalls and rockslides (Schoeneich et al., 2011), and increased creeping velocity of active rock glaciers (Kääb et al., 2007; Harris et al., 2009; Kellerer-Pirklbauer et al., 2011).

Permafrost thaw triggered by increasing air temperature is much slower than glacier retreat (Beniston et al., 2018), since the active layer acts as a thermal buffer (Harris et al., 2008). Rock glaciers are thermally decoupled from external climate and are therefore less climatically sensitive than glaciers (Jones et al., 2018). For the same reason, debris covered glaciers have been reported to retreat at a slower rate than uncovered glaciers (Scherler et al., 2011), at least in the initial phases of glacial shrinkage (Banerjee, 2017). Although the present volume of the Alpine permanent cryosphere is difficult to quantify, Boeckli et al. (2012) estimated that permafrost has a larger extent (ca. 2,000-11,600 km^2) with respect to glaciers (ca. 2,000 km^2), and the shrinkage rates of the permafrost ice are estimated to be roughly 10-100-times lower than melting rates of the surface glacier ice (Haeberli et al., 2016). As a result, the relative importance of permafrost will increase during the 21st century with a shift from glacial/periglacial to paraglacial/periglacial dominated processes, and here we summarize the significant effects anticipated on the hydrology, water quality and biodiversity of Alpine freshwaters.

3. DEGLACIATION AND SHIFTING STREAM HABITAT CONDITIONS

In this section we discuss the observed and predicted shifts in hydrology, geomorphology, habitat type, and water quality of Alpine streams as a consequence of deglaciation.

3.1. Hydrology

Glaciers and snow currently represent major drivers of the Alpine hydrology, as their seasonal melting is strongly associated with surface and groundwater flows. Driven by thawing-freezing cycles, discharge can be highly variable, with seasonal maxima during summer and minima during winter, and large diel fluctuations in summer (e.g. Malard et al., 1999; Ward, 1999; Smith et al., 2001; Jansson et al., 2003). Mountain rock glaciers store large amounts of water, trapped in the form of ice, which makes them significant water reservoirs in arid regions (Rangecroft et al., 2015; Jones et al., 2018). However, rock glaciers currently contribute only little to water flow in Alpine stream networks (Geiger et al., 2014; Krainer et al., 2007). For example, Krainer et al. (2011) found that only 1.4% of the annual outflow from the Lazaun rock glacier watershed to have a permafrost ice origin, and that rock glaciers contribute only marginally (0.13%) to total runoff in the north Italian province of South Tyrol.

To assess hydrological shifts related to climate change in alpine environments, Milner et al. (2009) stress the importance of taking into account the dynamic interactions between snowmelt, ice melt, and groundwater contribution to the stream flow. In the early stages of glacier retreat, water discharge is increasing due to higher energy inputs from the atmosphere, earlier melting of reflective snow cover, and the consequent lower ice albedo

(Milner et al., 2009). For instance, Finn et al. (2010) detected hydrological changes in the Roseg Valley (Switzerland) as consequence of 52 years of glacial retreat (i.e. from 1955 to 2007). Such changes include a significant increase in short-term flow variability, higher flow maxima during summer and lower minima during winter, and an earlier onset of spring runoff. In the advanced stages of glacier retreat, glacial runoff exceeds a hydrological tipping point referred to as "peak water" (Huss et al., 2017; Huss and Hock, 2018), and decreases due to prolonged glacier shrinkage and fragmentation (Stahl et al., 2008). As glaciers retreat, split, and disappear, the importance of air warming (energy fuelling the melting process) gradually drops, whilst the progressively rising snowline and the earlier onset of the seasonal snowmelt also reduces the role of the snowpack as a natural water reservoir (Stewart, 2009; Zierl and Bugmann, 2005; Huss et al., 2017). As a result, many Alpine streams may run dry in summer in the near future, especially in warm and dry years (Zierl and Bugmann, 2005). Moreover, the marked diel and seasonal discharge fluctuations are substituted by an increased dependency on stochastic precipitation events and on groundwater sources (Milner et al., 2009), with an increased flashiness of water regime due to the decreased buffering capacity exerted by the cryosphere (Huss et al., 2017).

The contribution of rock glaciers to Alpine water flow is anticipated to increase substantially in the future. In fact, the ice loss in rock glaciers, although slower than for typical mountain glaciers, will likely increase throughout warmer and prolonged summers. In addition, new rock glaciers may form in areas left uncovered by glaciers, through different and complex mechanisms that involve e.g. the evolution of debris-covered glaciers or the accumulation of ice and detritus under favourable slope settings (Whalley and Martin, 1992; Clark et al., 1998; Zasadni, 2007; Schoeneich et al., 2011; Anderson et al., 2018). In addition, Wagner et al. (2016) stress the potential hydrological contribution from fossil rock glaciers (i.e. with no more creeping activity and no residual ice) due to their water storage capacity during dry periods and buffering potential during flood events, and suggest that in the long-term, the catchments rich in rock glaciers may be influenced by these landforms even when deglaciation has finished. Research on the contribution of permafrost to mountain hydrology has been mainly conducted on streams fed by rock glaciers. However, Rogger et al. (2017) considered also talus fans and Little Ice Age tills of a 5 km^2 catchment in the Ötztal Alps (Austria), and modelled that the complete disappearance of permafrost would reduce flood peaks by up to 19 % and increase runoff by up to 17 % during recession periods. This suggests that the water buffering capacity of Alpine slopes will likely change in the future not only due to snow cover and glacier loss but also due to permafrost thaw.

3.2. Geomorphology

Glacier-fed streams represent an important source of sediments for the river basin level, with a significant proportion transported as bedload (Gurnell et al., 2000; Mao et al., 2019). The formation and reworking of glacial deposits left uncovered after glacier retreat promotes the formation of actively braiding proglacial reaches (Church and Ryder, 1972) with high width-depth ratios (Milner and Petts, 1994). Meltwater outburst events can be a key geomorphic driver for fluvio-glacial deposits (Gurnell et al., 2000). In addition, new lakes can form in the glacial forelands, with an increased likelihood of glacier outburst floods (GLOFs) and related hazards (e.g. Emmer et al., 2015; Haeberli et al., 2016; Carrivick and Tweed, 2016; Otto, 2019). Though rare in high mountain environments, thermokarst (i.e. ice-thaw formed) lakes can occur in permafrost conditions, as reported by Kääb and Haeberli (2001) on a rock glacier in the Swiss Alps. As deglaciation proceeds and glaciers shrink, fragment, and ultimately disappear, sediment transport gradually decreases, giving way to a period of incision of previously accumulated sediments (Church and Ryder, 1972; Fleming and Clarke, 2005) and a shift to more stable forms such as single-thread channels with higher sinuosity (Milner and Petts, 1994; McGregor et al., 1995; Gurnell et al., 2000). As the rapid uplift of the vegetational belts occurring in the Alps (Rogora et al., 2018) suggests, riparian vegetation may exert an increasing hydromorphological role in stabilizing the channels in the late phases of glacier retreat. However, in glacier forelands, the succession rate from pioneer and herbaceous stages to shrubs is very slow, as it usually spans over more than a century (Gurnell et al., 2000; Eichel, 2018). Furthermore, preliminary findings from the Rocky Mountains (USA) suggest that the homogenisation of alpine vegetation will favour riparian herbaceous species at high elevations (McKernan et al., 2018), where shrubs may not act as hydromorphological drivers as they do in lower reaches.

3.3. Alpine stream habitat types

Water origin is considered the main driver of the habitat conditions in alpine streams, so that three major stream types were originally identified and described (see Ward, 1994): kryal (glacier-fed), krenal (groundwater-fed) and rhithral (snowmelt/precipitation-fed), each type characterized by different water temperature, channel form and stability, discharge patterns, turbidity, electrical conductivity and hydrochemistry (for a detailed description see Brown et al., 2003; Milner et al., 2010). Since the contribution of the different water sources to stream discharge shows high spatial heterogeneity and pronounced seasonality, a classification of stream types based on a longitudinal sub-division has been proposed (see summary by Füreder, 1999), and a more complex habitat classification based on the relative proportion of each source (snow, ice, precipitation, groundwater) to water flow has been developed by Brown et al. (2003) and Brown et al. (2009). However, a substantial gap in all these classifications is represented by the lacking inclusion of alpine permafrost as a water source. This omission needs to be addressed as active rock glacier outflows exhibit a particular set of habitat conditions, typically being clear waters (<5 NTU) at low and stable temperatures (0.5 – 1.5°C). High electrical conductivities (up to 1000 µS cm^{-1}), due to high concentrations of selected cations (Ca^{2+}, Mg^{2+}) and anions (SO_4^{2-}, NO_3^-) are also commonly observed, especially during base-flow conditions in the late summer/autumn (Williams et al., 2006; Baron et al., 2009; Thies, et al., 2013; Krainer, 2015; Carturan et al., 2016; Rotta et al., 2018). Because deglaciation causes changes in the contribution of different water sources, an increased abundance of krenal and rock glacial habitats can be anticipated, along with the uplift of kryal habitats following retreating glacier margins. However, it is very likely that the habitat framework under glacier loss will be catchment specific and dependent on local geological and geomorphological conditions interacting with the new climatic setting.

3.4. Water and sediment quality

3.4.1. Water temperature

In deglaciating alpine areas, water temperature of glacier-fed streams increases due to air warming, reduced discharge and decreased ice-melt (Milner et al., 2009). For the Alps, this was observed in nine Swiss catchments, showing a rise of 2-7°C in summer temperatures for upper stream reaches since the late 90's (Robinson and Oertli, 2009; Finn et al., 2010; Robinson et al., 2014). As rock glacier outflows (Carturan et al., 2016) and high-elevation springbrooks (von Fumetti et al., 2017) are characterized by low and constant water temperatures, they may become cold refuge areas after the glacier loss (Hotaling et al., 2017). However, deglaciation may also narrow longitudinal temperature gradients, as detected by

Finn et al. (2010) in the Roseg valley (autumn period, 1997-2007), and therefore reduce the extent of cold habitat conditions downstream.

3.4.2. Availability of carbon, nitrogen and phosphorus

Melting of the cryosphere releases carbon, nitrogen, and phosphorus to freshwaters. Glaciers accumulate and store organic carbon (OC), which derives from in-situ microbial production and atmospheric deposition of vascular plants, soil, and aerosol combustion products, as detected by Singer et al. (2012) in a study of 26 Austrian glaciers. The authors found that this ice-locked organic matter was highly labile, and demonstrated a positive correlation between DOC bioavailability and age, which ranged between 600-8,500 years BP. Glacial carbon is conveyed by glaciers and eventually released to freshwaters through the melting process (Singer et al., 2012; Hood et al., 2015), and supports kryal food webs (Fellman et al., 2015). Based on the limited research to date, rock glacier streams typically show DOC concentrations similar to those found in glacial streams, but this carbon seems to be less labile, as it was found studying three mountain areas in the USA (Fegel et al., 2016). Hence, in the initial phases of deglaciation, glacier retreat is accompanied with a boosted delivery of ancient and particularly labile carbon to freshwaters. This may have ecological consequences, since OC enhances stream metabolism via microbial uptake (Singer et al., 2012), with potential bottom-up trophic effects. However, after the “peak water” has occurred and the load of labile carbon from glaciers fades, shifts in allochthonous inputs to streams are anticipated, with enhanced loads of more recalcitrant organic carbon provided by rock glaciers (Fegel et al., 2016) and increased organic matter from vegetation colonizing upstream areas (Zah and Uehlinger, 2001).

Nitrogen pulses arising from spring snowmelt are commonly observed in Alpine catchments and are associated with dry and wet deposition and with biological processes occurring in winter (Kuhn, 2001). Deposition of nitrogen from the air in Alpine valleys is linked with intense urbanization, and agricultural and industrial activities in the surrounding areas (Rogora et al., 2006). A reduced deposition of nitrogen compounds in the Alps has been observed starting from the end of the 20th Century (Rogora et al., 2016) as a consequence of the reduction of atmospheric emissions agreed by international protocols (EEA, 2016). Nevertheless, nitrate concentrations in water >100 µg L^{-1} are commonly found in streams originating from ablating glaciers (Uehlinger et al., 2010) and active rock glaciers in the Alps

(Thies et al., 2013; Krainer, 2015; Lösch et al., 2015a) as in other mountain ranges (e.g. Barnes et al., 2013; Fegel et al., 2016). However, the causes of these high concentrations (e.g. microbial production, release from the ice melt and permafrost thaw) are still debated, and no major ecological effects have been observed worldwide (Slemmons et al., 2013). Artificially increased concentrations of nitrates and phosphates in five Swiss glacier-fed streams did not trigger any periphyton accrual (Rinke et al., 2001), suggesting that other environmental factors, such as turbidity and scouring, inhibit nutrient-driven algal growth. Since these limiting factors are commonly absent in rock glacier outflows, primary producers may be more sensitive to nitrogen inputs there, even if other features may still limit algal growth, such as low temperatures or high UV radiation. This topic, however, remains unstudied for this stream type worldwide.

Phosphorus is also supplied to alpine streams by glacier ablation, mainly through the physical erosion and weathering of rocks (Hodson, 2006). However, most of the phosphorus released by glaciers in Alpine and Arctic areas was found to be associated with clay particles, and only a minor fraction consisted of soluble reactive phosphorus (SRP) loosely aggregated with the sediment (Hodson et al., 2004). Thus, higher rates of glacier ablation likely increase the export of phosphorus to downstream environments, as detected by Robinson et al. (2014) in eight Swiss glacier-fed streams from 1998 to 2011. Even if particulate phosphorus is not bioavailable, the minerals may become dissolved under favourable conditions after the deposition of suspended sediments (Hodson et al., 2004), suggesting potential long-term effects once deposited sediments are remobilized. Notably, high loads of bioavailable SRP have been demonstrated in ice fields in Alaska (Hood and Berner, 2009) and Greenland (Hawkings et al., 2016). SRP contribution by mountain glaciers still remains understudied, although very low concentrations (<3 µg L^{-1}), consistent with those of krenal streams, have been found in kryal (e.g. Rott et al., 2006; Uehlinger et al., 2010) and rock glacial waters (Rotta et al., 2018) in the Alps.

3.4.3. Legacy contaminants

Alpine glaciers store air-borne anthropogenic contaminants and convey them to freshwaters via ice melting. These include persistent organic pollutants (POPs, i.e. industrial chemicals, pesticides, and by-products of combustion processes and chemical reactions), black carbon, i.e. dark aerosol produced from the combustion of fuels (Daly and Wania, 2005; Hodson, 2014), and trace elements (Gabrielli et al., 2008; Carling et al., 2017). The proximity of the Alps to several highly industrialized regions makes this mountain range particularly sensitive to input and accumulation of POPs, but their release from glaciers has also been observed in Himalaya and the Rocky Mountains (Miner et al., 2017). As POPs are mostly delivered through wet deposition, especially with snow, the seasonal snowmelt is an important source of these contaminants for freshwaters (Bizzotto et al., 2009). Moreover, as the accumulation zone of glaciers represents a temporary storage for snow, toxic and even banned substances can be released decades after their production. This intensifies with progressive deglaciation, with potential effects to surface water quality (Bogdal et al., 2009). Accordingly, concentrations of organochlorine chemicals and pesticides were found to be much higher in glacial compared to non-glacial streams in several Italian catchments, and concentrations increased 10-fold from snowmelt to ablation periods where seasonality was assessed (Villa et al., 2006; Bizzotto et al., 2009). Since the content of organic matter in glacier-fed streams is low and the organic pollutants can be mainly found in the dissolved phase, with a low potential for suspended sediment absorption, these compounds can be potentially bioavailable to organisms (Slemmons et al., 2013). Bizzotto et al. (2009) studied the variability in the concentrations of POPs in different macroinvertebrate feeding groups over summer, finding higher concentrations in the kryal than in krenal streams. However, bioaccumulation could not be confirmed, as the higher concentration in predators was attributed to their high lipid content, and a direct uptake from water was suggested for all organisms. The highest release of POPs from glaciers to freshwaters may be expected to coincide with "peak water", after which a gradual decrease is not necessarily accompanied by a reduced ecological effect, due to the persistence of these substances in the environment (Jones and Voogt, 1999).

3.4.4. Trace elements

Permafrost thaw is known to influence the inorganic chemistry of waters worldwide (Colombo et al., 2018a), and insights into the potential consequences of thawing rock glaciers on water quality have come from several case studies in the Alps. Acidic waters (pH=5-5.5) has been found in lakes (Ilyashuk et al., 2014) and streams (Thies et al., 2013) fed by thawing rock glaciers. Further, high concentrations of trace elements (e.g. Al, Ba, Ni, Zn, Mn, Co, Sr), often exceeding the EU limits for drinking waters, have been reported in Austrian (Thies et al., 2007; 2013) and Italian (Krainer, 2015; Nickus and Thies, 2015; Colombo et al., 2018b;

Rotta et al., 2018) rock glacial freshwaters. Even if the debate on the causes of the particular water chemistry in active rock glacier outflows is still ongoing, internal ice thaw is considered as a key driver for the enrichment of solutes and trace elements, and for the acidification of waters in catchments with sulphide-bearing lithology (see Colombo et al., 2018a).

High concentrations of trace elements (Al, Ti, Fe, Co, U, Mn, Fe) have been reported even for glacier-fed streams, in the Swiss (Brown and Fuge, 1998) and Italian Alps (Rotta et al., 2018), especially during baseflow conditions, and attributed to the rock weathering associated with the glacial/subglacial flow. However, the bulk downstream export is considered to be greater during the ablation period, when the highest discharge offsets lower concentrations (Mitchell et al., 2001). Thus, it may be expected that the highest concentrations of trace elements in Alpine streams, and the greatest associated biotic effects, will be reached during the last phases of glacier shrinkage, under decreased average discharge and ice/rock ratio from glaciers in parallel with an increased hydrological significance of thawing rock glaciers. In addition, climatic changes (e.g. more frequent dry periods, reduced snow cover) are capable of enhancing the mobilization of naturally-occurring trace metals through enhanced weathering processes in glacier-free areas, as detected in the Pyrenees (Zaharescu et al., 2016). This may cause high loads of trace elements to freshwaters, even when deglaciation has finished.

4. EFFECTS OF DEGLACIATION ON STREAM COMMUNITIES

Among the large body of literature covering different aspects of Alpine streams, we found only twenty-four published papers (hereafter identified with * at first citation) that specifically address the impact of deglaciation on stream biota (Fig. 3). Among them, three papers investigate waters affected by permafrost thaw. Eighteen studies are based on a synchronic approach that substitutes space for time in order to predict future developments and trends linked to glacier retreat. Diachronic studies based on long-term surveys are still a minority (three), but they will likely increase in the future driven by the growing interest in Alpine deglaciation, both within and outside the scientific community. Here, we briefly summarize the available knowledge on the biotic communities and the food webs of Alpine streams, identify the observed or predicted ecological effects of deglaciation, and draw comparisons - where possible - with other alpine areas.

4.1. Microbial communities

Stream microbial communities represent the trophic connection between nutrients, producers, and consumers (Battin et al., 2016). Microbes drive several biogeochemical and metabolic processes, including nitrogen uptake and transformation, methanogenesis, iron cycling, photosynthesis, and respiration (Freimann et al., 2013*), which also occur in glaciers (Anesio and Laybourn-Parry, 2012). In fact, despite their extreme habitat conditions, glaciers and ice sheets are considered as a proper biome (Anesio and Laybourn-Parry, 2012). As such, they are autotrophic systems hosting viruses, prokaryotes and algae (Anesio et al., 2017), and exporting organisms and nutrients to the heterotrophic glacier-fed streams (Anesio et al., 2009).

In Alpine streams, the strong seasonality shapes the traits of stream microbial communities, as investigated by Battin et al. (2004) in the Rotmoos (Austria) and by Freimann et al. (2013; 2014) in three Swiss catchments. During the spring snowmelt, the pulsed release of airborne organic material accumulated and processed over winter, triggers a stage of active metabolism and bacterial growth. In this phase, the enhanced hydrological linkage within the river network and between streams and groundwater, soil and vegetation results in high uptake and transport of DOC, nutrients, and microbes in freshwaters. In summer, the harsh physical conditions (e.g. high turbidity and scouring) during glacial ablation hinder microbial production in kryal habitats, which are dominated by small-sized, specialist microorganisms during this period (Freimann et al., 2013). Because of the reduced disturbance and the persistent release of labile DOC and nutrients from the melting ice, autumn represents a favourable ecological window in kryal, promoting shifts in the community composition and a dominance of larger-sized bacteria (Battin et al., 2004). Because of a less pronounced seasonality in habitat conditions, krenal and rhithral assemblages are dominated in all seasons by large and generalist bacteria that can cope with smaller changes by solely adapting cell metabolism (Freimann et al., 2013).

Research on Alpine stream sediments has shown that glacier-fed streams have lower bacterial diversity, abundance and community biomass, and bacterial carbon production compared to non-glacial streams, and these different stream types host distinct communities (Battin et al., 2001; Battin et al., 2004; Logue et al., 2004; Freimann et al., 2014*). A relatively higher abundance of α-Proteobacteria and a lower abundance of Eubacteria was found in the Rotmoos glacier-fed stream compared with rhithral and krenal habitats (Battin et al., 2004).

This difference coincides with findings from US mountains (Fegel et al., 2016), Himalaya (Liu et al., 2011), the Arctic and the Antarctic (Marghesin and Miteva, 2011; Van Horn et al., 2016). A high diversity found close to the glacier snout in the Rotmoos was attributed to bacterial inputs from the glacial environment (*Archaea*, *Proteobacteria*, *Bacteroidetes*, *Actinobacteria* and *Cyanobacteria* are typical dwellers of glaciers; Anesio et al., 2017), whereas bacterial carbon production and specific growth rates increased when proceeding downstream from the glacier snout, along with the reduction of *Archaea* abundance and in concomitance to increasing algal biomass in the biofilm (Battin et al., 2001). The progressive increase in bacterial α-diversity in water and biofilm downstream from the glacier seems to reflect the increased contribution from different sources (Wilhelm et al., 2013*), again witnessing the importance of hydrological connectivity in the catchment.

While most research on microbial communities has focused on glacial environments and streams, only few studies have been conducted to date on permafrost-fed waters in the Alps. Preliminary studies on bacterial diversity in rock glacier ponds (Mania et al., 2018) and running waters (Tolotti et al., 2018) agree with the outcomes of studies conducted in North America (Fegel et al., 2016), which show that rock glacier outflows host more abundant and diverse bacterial communities than kryal streams, with a high proportion of typical soil taxa in streambed sediments.

In addition to the loss of microbial glacier specialists (e.g. *Archea*), climate change and deglaciation may generate consequences for microbial communities by means of altered hydrological pathways. For instance, it is possible that the loss of cryosphere will also influence krenal microbial communities, due to the hydrological connection between glacial and groundwater flow in Alpine catchments (little studied, but see Ward et al., 1999; Cuffey and Paterson, 2010). After the “peak water” (i.e. maximum water flow associated with glacier loss, see 3.1), the reduced loads of organic carbon, phosphorus and nitrogen from glaciers may be paralleled by increased organic matter inputs from terrestrial vegetation and enhanced primary production in streams. Such a shift may trigger changes in the bacterial community composition and the associated functional activity, with consequent large-scale changes in the nutrient cycling and the overall ecosystem functioning. Freimann et al. (2013) claim that future stream networks in groundwater-dominated catchments will be more suitable for generalist bacterial taxa typical of krenal habitats, with a consequent loss of kryal specialists. Bacterial α-diversity is predicted to increase upstream due to the habitat amelioration (e.g. reduced scouring and turbidity), while differences between stream types and seasons will decrease, resulting in a general reduction of β-diversity (Wilhelm et al., 2013; Freimann et al., 2013). Responses to the changing physical and chemical conditions are expected to be more pronounced and complex for sediment bacteria, since microbial heterotrophs in epilithic biofilms benefit from algal exudates, while the epipsammic biofilms rely much more on external sources for DOC (Wilhelm et al., 2014).

Freshwater fungi, or “aquatic hyphomycetes” (see Bärlocher, 2016), which play a key role in the decomposition of organic matter (Gessner and Robinson, 2003), are affected differently by deglaciation when compared to other microbes. In fact, previous findings from studies in Swiss (Gessner et al., 1998; Gessner and Robinson, 2003) and Austrian Alps (Eisendler-Flöckner et al., 2013*) outlined that low allochthonous inputs rather than harsh habitat conditions (e.g. low water temperature, scouring) inhibit fungal diversity and abundance. Leaf bag experiments in the Swiss Alps, showed lower biomass (represented by concentrations of ergosterol in leaves) in kryal reaches than in the other stream types (Gessner et al., 1998; Gessner and Robinson, 2003), while a studied rock glacial stream showed similar concentrations than springbrooks (Robinson and Jolidon, 2005*). Because of the uplift of vegetational belts, fungal biomass and the associated breakdown of organic matter is expected to rise due to increased input of allochthonous material (Robinson and Jolidon, 2005). Shifts in riparian species composition may involve changes in the quality of organic matter being processed by fungi, with consequences on fungal biomass, and rates of colonization and sporulation (Gessner and Robinson, 2003). Changes in fungal communities may also trigger bottom-up effects along the food web. In fact, aquatic hyphomycetes have an important role in the nutrition of invertebrates (Bärlocher, 1985), especially in glacier-fed streams where they represent a high-quality food for meiofauna (Eisendle-Flöckner et al., 2013).

4.2. Primary producers

Alpine streams are harsh habitats for primary producers, because of intense UV radiation, low concentrations of nutrients, low temperatures and a long-lasting snow-cover. The harshest habitat conditions in kryal habitats (high turbidity and scouring) support lower periphytic biomass compared to more benign krenal habitats throughout the year, as demonstrated by Uehlinger et al. (2010*) in the Swiss Alps. A conceptual model of periphyton accrual in alpine streams based on these results points to the importance of different catchment features (e.g. climate, patterns of snow cover, and stream flow) and stream habitat conditions (light and UV, bedload, turbidity, temperature, and phosphorus availability) on a seasonal basis, and defines favourable periods (i.e. spring and autumn) as "windows of opportunity" (WO) enhancing algal productivity (Uehlinger et al., 2010). Seasonality also drives the composition of algal communities in different alpine stream types (Hieber et al., 2001). Kryal habitats are typically dominated by diatoms, whereas cyanobacteria (*Chamaesiphon sp*., *Lyngbya sp.*) and the cosmopolitan golden algae *Hydrurus foetidus* exhibit temporary blooms during low-flow periods (Ward, 1994; Uehlinger et al., 1999; Hieber et al., 2001). During summer, pioneer and stress-tolerant species with cosmopolitan distribution (e.g. *Achnantidium minutissimum*, *Hannea arcus*), characterized by reduced motility and strong adhesion to substrate, dominate the diatom community of glacier-fed streams worldwide (Cantonati et al., 2001; Hieber et al., 2001; Gesierich and Rott, 2012), while others rest in reduced form (e.g. *H. foetidus* in their basal stage, Niedrist et al., 2018).

Compared to kryal streams, communities from lake outlets, krenal, and rhithral streams, exhibit a higher algal diversity and a less pronounced seasonality, as found in the Swiss Alps, where diatoms exhibited a high diversity, and Cyanobacteria and *H. foetidus* have been found increasingly dominant over summer (Uehlinger et al., 1998; Hieber et al., 2001).

Deglaciation is anticipated to have several consequences for primary production and algal diversity. Uehlinger et al. (2010) proposed that an earlier snowmelt may open or reinforce the spring WO, since UV radiation is a limiting factor for alpine freshwater organisms (e.g. Sommaruga, 2014) and UV levels are less intense in spring. Likewise, the autumn WO could expand because of a later snowfall. Biotic interactions may represent other possible triggers for WO shifts. For instance, in glacier-fed streams the macroinvertebrate community may become increasingly abundant and diverse in an ameliorated environment, and grazers may limit periphyton growth (Milner et al., 2009; Uehlinger et al., 2010). On the other hand, changes in the stream biofilm involving primary producers may propagate to the heterotrophic component, which might benefit from algal exudates, as hypothesized by Battin et al. (2016). Glacier retreat enhances algal species richness due to the decreased environmental harshness induced by ablation (Milner et al., 2009). Fell et al. (2018*) recently studied the diversity patterns of diatoms in three Austrian valleys, where a gradient in glacier cover in the catchment was used as a proxy for glacier retreat. These authors identified several diatom taxa peculiar to high glacier cover and predict a β-diversity decline associated with glacier loss. This confirms previous research in the Hohe Tauern (Austria), where Rott et al. (2006) detected a pattern of decreasing richness as a function of increased percent glaciation in the catchment. Glacier retreat may also lead to shifts in community structure, as the increased habitat stability and temperature, and reduced scouring, potentially enhance taxa abundances of specific groups and the overall persistence of algal communities. This may favour typical rhithral cyanobacteria (e.g. *Phormidium, Oscillatoria)* and loosely attached (e.g. *Navicula*) or aggregated (e.g. *Cymbella*, *Gomphonema*) diatom taxa in previously hostile reaches. *H. foetidus*, the main kryal macroalgae, may take advantage of the improved habitat conditions and potentially anticipate its blooms because of nutrient pulses induced by earlier snowmelt (Milner et al., 2009). Due to the hydrological connectivity between glacial flow and groundwater, cascading effects of deglaciation may cause shifts in krenal communities with high conservation value. In fact, Alpine springbrooks are recognized as rich and diversified habitats hosting a significant number of peculiar, rare, and Red List diatom species (Cantonati et al., 2012). Although glacier loss will cause local extinctions of rare and stenoecious diatoms, other threatened or rare species may benefit from the pristine conditions of high mountains (Fell et al., 2018), thus posing a challenge for conservation policies aimed at preserving alpine sites from local pressures.

Algal communities are still poorly investigated in streams influenced by permafrost thaw worldwide. A preliminary study on two rock glacial streams (Ötztal Alps, Austria) during autumn baseflow conditions (Thies et al., 2013*), outlined higher proportions of acidophilous and acidobiontic taxa in association with lower pH values and higher concentrations of trace metals. Species richness was lower in the reference streams (rhithral) and in the rock glacial stream not affected by acidification and high metal concentrations, which were mainly inhabited by circumneutral taxa. It was found, however, that habitat diversity is the main driver for taxa richness in a community otherwise dominated by the stress tolerant *Achnantidium minutissimum.* A recent study on headwaters fed by glaciers and permafrost (rock glaciers and talus) in the Italian Central Alps confirmed pH and trace metals as key drivers for diatom diversity in streams influenced by permafrost and discovered higher richness in glacio-rhithral than in rock glacial habitats (Rotta et al., 2018*). These studies suggest that the effects of thawing permafrost on the diatomic community can be mediated by acid-rock drainage. Furthermore, catchments with low buffering capacity and streams with reduced habitat diversity may be more sensitive to chemical changes induced by rock glacier thaw, especially after the “peak water” when the decreasing glacial influence is paralleled by increased permafrost influence.

In contrast to the more widely studied diatoms and algae, relatively little is known about bryophytes in Alpine streams, despite their abundance and the presence of rare or endangered species (Gesierich and Rott, 2004). Given that mosses establish on stable substrates (e.g. Stream Bryophyte Group, 1999), they can be used as an indicator of reduced glacial influence. We propose that bryophyte colonization may trigger positive feedbacks capable of increasing channel stability in glacio-rhithral sections with ongoing glacier retreat, and thereby enhancing algal and invertebrate diversity and biomass (e.g. Lencioni and Rossaro, 2005; Rotta et al., 2018).

4.3. Macroinvertebrates

Macroinvertebrates represent the most studied biotic component of alpine streams worldwide (Fell et al., 2017). Originally, this research field developed following the review papers by Ward (1994) on alpine stream habitat classification, and by Milner and Petts (1994) on the characterisation of glacial rivers. These papers triggered an outburst of studies worldwide and especially in Europe, starting from AASER project (Castella et al., 2001; Brittain and Milner, 2001) and continuing to the present (see Milner, 2016). Despite the abundant literature on alpine stream communities, especially those of kryal and krenal habitats, to our knowledge very little is known about the macroinvertebrates dwelling in rock glacier-fed streams, and the environmental determinants of community characteristics. The project PERMAQUA (www.permaqua.eu) represents a first preliminary attempt to study the diversity and distribution of macroinvertebrates in Alpine streams (Lösch et al., 2015a) and lakes (Thaler and Tait, 2015) affected directly or indirectly by rock glacier thaw.

4.3.1. Community composition and diversity

Alpine streams host different zoobenthic communities depending on the habitat type (e.g. Ward, 1994) and season (e.g. Milner and Petts, 1994; Brittain and Milner, 2001; Milner et al., 2001). In summer, when the differences between habitats are greatest, insect larvae of the orders Ephemeroptera, Plecoptera, Trichoptera (EPT) and Diptera are usually found with different abundances and diversity in krenal, rhithral, and lake outlets, and in the mid and lower sections of glacier-fed streams (Maiolini and Lencioni, 2001; Füreder et al., 2001; Hieber et al., 2005). Chironomidae represent the most abundant and widely distributed taxon of alpine streams (Milner and Petts, 1994; Castella et al., 2001; Lods-Crozet et al., 2001a; Milner et al., 2001) and are the exclusive group dwelling in proglacial reaches in the Alps (e.g. Füreder, 1999; Lencioni and Rossaro, 2005; Niedrist et al., 2016; Lencioni, 2018*).

The chironomids of genus *Diamesa* are the most adapted to glacial conditions, especially low temperatures and low channel stability, and dwell at low abundances in harsh kryal habitats (e.g. Milner and Petts, 1994; Niedrist et al., 2016; Rossaro et al., 2016*; Lencioni, 2018). Downstream, temperature and channel stability increase so that other chironomid subfamilies (Orthocladiinae, Chironominae) gradually enter the community. These groups share their habitat with Oligochaeta, other Diptera (Empididae, Limoniidae, Simuliidae), Plecoptera and Ephemeroptera, which gradually enter the community with different patterns according to the mountain sector (e.g. for Austria see Füreder et al., 2001; for Italy see Maiolini and Lencioni, 2001; for the Switzerland see Lods-Crozet et al., 2001b).

The decrease of glacial influence when proceeding downstream from the glacier snout, leads to the amelioration of habitat conditions (Füreder, 2012), which in turn favours high abundance and diversity of benthic communities (Milner et al., 2001). However, taxa diversity commonly shows a unimodal pattern as a function of glacial influence (Füreder, 2012). For instance, in an extensive study located in the central Alps, Füreder et al. (2002) detected a peak of EPT and total number of taxa at 1-10% GCC (glacier cover in the catchment, i.e. the percentage of the catchment covered by glaciers), and Füreder (2007) recorded this diversity peak at 1-15% GCC in the Hohe Tauern Austrian Alps. Thus, the observed patterns of taxa distribution in glacier-fed streams (Brittain and Milner, 2001) provide the potential to predict shifts in zoobenthos as consequence of glacier retreat. Jacobsen et al. (2012*) conducted a meta-analysis of taxa distribution in glacier-fed streams in three world mountain regions (Alps, Alaska, Ecuadorian Andes), modelling α, β and γ diversity as a function of GCC. For the Alps, a loss of regional (γ) diversity starting from 30-50% GCC, together with a predicted loss of up to 16% species with total glacier disappearance. The authors also forecast a decrease in taxa turnover (β diversity), as the decreasing glacial influence induces a loss of habitat and biological heterogeneity between catchments (see also Lencioni et al., 2007a; Lencioni, 2018). In contrast, local taxa richness (α diversity) is predicted to increase in kryal sites, whereas diversity hotspots (i.e. maximum richness sites in the catchment), located at 5-30% GCC, move upstream following glacier retreat. Thus, maximum taxa richness in the catchment is expected to decrease along with glacier disappearance.

During the initial phases of increased runoff related to negative glacier mass-balance, Milner et al. (2009) predict a decrease in abundance and diversity with a concomitant shift towards communities dominated by Diamesinae and Orthocladiinae chironomids. After the "peak water", the decreased glacier contribution to stream discharge may cause an increase of taxa diversity and abundance. A loss of cold-stenothermal species and the colonisation by other taxa was detected by Rossaro et al. (2016) and Lencioni (2018), as typical kryal species have been found at increasingly higher altitudes in the Alps over the last decades, in parallel to the colonisation of upstream reaches by Orthocladiinae and Nemouridae (Lencioni, 2018). In general, although results from diachronic research are still scarce, they are confirming what has been predicted by models and studies that substitute space for time. In particular, shifts in biodiversity, abundance, and drift patterns have been observed in a wide range of Alpine catchments (Tab. 1), together with upstream migration of communities associated with different glacial influence. However, the ecological shifts associated with deglaciation may not be as deterministic as models predict. For instance, glacier retreat is accompanied by changes in the steepness of longitudinal gradients for community' diversity. For example, invertebrate diversity (expressed with the Shannon index) increased more steeply downstream of the Swiss Tschierva glacier during summer, following ten years of glacier retreat (Finn et al., 2010*). These steeper environmental gradients may act as ecological barriers, hindering the upstream colonisation of organisms. Under scenarios of rapid environmental change associated with fast glacier retreat, taxa with limited ability for dispersal may not be able to keep pace with the changing conditions (Brown et al., 2018*). Within this context, new insights come from the biogeographical role of rock glacial communities. Lösch et al. (2015b*) investigated five streams fed by rock glaciers in South Tyrol (Italy) and found a dominance of Diamesinae and Orthocladiinae chironomids, and the presence of Plecoptera, Ephemeroptera and Trichoptera. The authors report the presence of cold-stenothermal species (*Diamesa spp*), which suggests that rock glacial streams can act as refuge areas after the glacier loss. However, preliminary findings from the Solda valley (Italy) showed that rock glacial communities have similar composition to those of krenal and glacio-rhithral habitats, suggesting the potential for these streams to act as stepping-stones for the colonisation of upstream reaches during the last phases of glacier retreat (Brighenti et. al., 2018).

4.3.2. Ecological traits and functional diversity

As each organism exhibits a specific set of traits (e.g. maximal size, voltinism, resistance forms, attachment to substrate, feeding habits) that allow facing the habitat and community interactions, ecological communities can be analysed in terms of their functional diversity, which is strictly bound to the ecosystem functions (see Laureto et al., 2015). In this context, habitat acts as a filter for the ecological traits expressed by organisms (Poff, 1997). In Alpine settings, Ilg and Castella (2006) found an increasing functional diversity with increasing distance from the glacier and the consequential reduction of glacial influence in two Swiss (Rhone and Mutt) and one French (Romanche) glacier-fed streams. Glacial influence (GI, synthesized by combining water temperature, conductivity, suspended solids and channel stability) correlated negatively with body size, and positively with univoltinism/semivoltinism, absence of resistance forms, and abundance of crawling and deposit feeding organisms. Similarly, Füreder (2007) found that GCC correlates positively with the abundance of habitat specialists, rheobionts clingers with streamlined/flattened body, univoltinism/semivoltinism, cold adaptations, omnivory, and mobility of the adults in the Hohe Tauern (Austria).

Milner et al. (2009) predicted that a decreased glacial influence in alpine catchments will lead to stream communities dominated by generalists, with fewer taxa characterized by omnivory, flattened body shape and adaptation to low temperatures, and more taxa with low mobility. Increased nutrient availability and a more benign habitat will favour larger body size and the overall traits diversity. In an extensive study on the deterministic patterns structuring the functional responses of macroinvertebrate communities to glacier regression covering different biogeographic regions worldwide, Brown et al. (2018*) found a general pattern of increasing functional diversity with decreasing glacier cover, and selected traits exhibiting the same pattern across different regions. In contrast to the outcomes outlined for the Alps (Ilg and castella, 2006; Füreder, 2007), Brown et al. (2018) found fewer generations per year and a longer generation time associated with a lower glacial influence. These outcomes suggest that life history traits must be considered to better assess macroinvertebrates responses to changing seasonal time constraints. Studying *Allogamus uncatus* (Trichoptera) in the Roseg catchment (Switzerland), Shama and Robinson (2009) found a longer time to reach pupation, higher growth rates and a bigger adult mass along a gradient of distance from glaciers for permanent streams. Likewise, a later onset of snow accumulation, and the longer duration of favourable autumn conditions, may enhance oviposition and egg hatching, as observed by Schütz et al. (2001) in the Rotmoosache for *Baetis alpinus* in two contrasting years. Thus, deglaciation during summer and snowpack shifts during winter may interact, causing synergic effects on Alpine stream biota, with shifts in the life cycles and life histories of taxa that are known to be influenced by the seasonality of snow cover and temperature patterns (Füreder, 1999; Lencioni, 2004). We also suggest that shifts in life cycles might be reflected in the seasonality of the community composition, which was found to be pronounced in Alpine streams (Robinson et al., 2001; Schütz et al. 2001; Brown et al., 2015; Lencioni and Spitale, 2015).

4.4. Meiofauna

An important and to date poorly-investigated aspect of alpine stream ecology is the use of the hyporheic habitat by benthic taxa, which are small enough to dwell in the interstices. In fact, most of them are categorized as "meiofauna" (from Mare, 1942). The hyporheic habitat is more stable than the benthic one, and hosts more stable communities, especially in glacier-fed streams where the low substrate stability and the high streambed porosity facilitate the vertical migration of invertebrates (Malard et al., 2001*; Crossman et al., 2012; Lencioni and Spitale, 2015). Fauna exclusive to the hyporheic habitat are dominated by crustaceans, and harpacticoid copepods are typical dwellers of Alpine stream hyporheos. In addition, larval stages of insects use the hyporheic zone as a nursery, temporary refuge, and biological corridor (Malard et al., 2001; Malard, 2003; Malard et al., 2003*; Lencioni et al., 2007b), and even micro/meiofaunal invertebrates (e.g. nematodes, rotifers) dwell in kryal habitats (Eisendle, 2008; Eisendle-Flöckner et al., 2013).

Despite the paucity of published research on meiofauna in Alpine streams, there is evidence that kryal hyporheic communities change along the altitudinal gradient and depend on both glacial influence (water temperature and abundance of organic matter) and groundwater contribution/upwelling (Malard et al., 2003; Maiolini et al., 2006; Lencioni et al., 2007b; Raschioni et al., 2007; Lencioni and Spitale, 2015). In the Alps, meiofaunal cold-stenothermals were found to be strictly bound to glacier-fed streams (Husmann, 1975; Cottarelli et al., 2001; 2005; Malard, 2003; Maiolini et al., 2006; Raschioni et al., 2006;

Eisendle, 2008), and one species of Alpine copepod, so far endemic, has been described (Cottarelli et al., 2005). Thus, changes in the community structure of these smaller invertebrates can be predicted as a consequence of glacier retreat. In the benthos, Eisendle-Flöckner et al. (2013) found a decreasing taxonomic richness of Nematoda and Rotifera and a decreasing abundance and maturity of Nematoda, as a function of GI (water temperature, channel stability and conductivity as proxy). In the hyporheos, during the initial stages of increased glacial influence, meiofaunal diversity may drop in glacial floodplains, since it was found to be strictly related to groundwater upwelling contribution and habitat diversity (Malard et al., 2001; Malard, 2003). On the long-term, the decline of glacial influence may be paralleled by the loss of cold-stenothermals, and the upstream colonization by other taxa (Malard et al., 2003). Such upstream migration might be possible in the hyporheic zone, which can act as an ecological corridor. This was demonstrated by evidence of invertebrate taxa in the hyporheos far above their benthic altitudinal limit (Malard et al., 2001; Malard et al., 2003). However, the sensitivity and response of meiofauna to deglaciation, and its contribution to the biodiversity and complexity of food webs in alpine streams is still understudied and further research still needed.

4.5. Food webs

In alpine streams, autochthonous production is low because of the overall environmental harshness, which limit primary producers (Uehlinger et al., 2010). Further, allochthonous inputs are scarce because of a sparse and simplified vegetation (Zah and Uehlinger, 2001). Both limitations are highest in kryal habitats, where inputs of organic matter are mainly provided by the aeolian transport (Zah and Uehlinger, 2001; Füreder et al., 2003a) and by glacier ablation (Singer et al., 2012). In particular, the ablation process was found to be important in fuelling the food webs of streams in Alaska, where Fellman et al. (2015) demonstrated via stable isotope and radiocarbon analysis of different trophic levels that up to 36% of the carbon assimilated by consumers had a glacial origin. Although this topic remains to be investigated in the Alps, Niedrist and Füreder (2018*) speculate that glacial carbon is incorporated in the epilithic biofilm of kryal streams in the Hohe Tauern, as witnessed by $\delta^{13}C$ depletion in this matrix, which depends on glacial influence. Generally, the strong limitations in both autochthonous and allochthonous production, and the natural absence of fish in high mountains (Adams et al., 2001), result in simple alpine stream food webs, especially in proglacial reaches (Clitherow et al., 2013*). Gut content and stable isotope analyses undertaken in several streams in the Austrian (Füreder et al. 2003a; 2003b; Clitherow et al., 2013) and Swiss (Zah et al., 2001; di Cugno and Robinson, 2017) Alps revealed a widespread omnivore behaviour of invertebrates. Opportunistic feeding strategies, such as predation in the shredder *Leuctra sp.* and the filter-feeder *Prosimulium sp.*, and cannibalism in the collector *Diamesa latitarsis*/*steinboecki* were also detected. In addition, Niedrist and Füreder (2017) found that selective feeding may be more important in *Diamesa* than previously assumed. In fact, stable isotope and gut content analyses on this taxon in the Hohe Tauern revealed the selective preference for *H. foetidus* and diatoms and the avoidance of cyanobacteria. Niedrist and Füreder (2018) further demonstrated along a gradient of glacial influence that, unlike Orthocladiinae, the detritivore Diamesinae are capable of shifting their diet and feeding on the available epilithic biofilm in kryal reaches, which is demonstrated to have a higher nutritional quality in harsh than in benign streams (Niedrist et al., 2018*).

The demonstrated opportunistic feeding behaviour may represent an ecological buffer for organisms facing climate change and deglaciation in alpine streams (di Cugno and Robinson, 2017). With the progression of glacier retreat and the rise of the treeline and vegetational belts, allochthonous inputs will increase in the upper stream reaches and vegetation will gain importance for the stream metabolism. Further, even if these advantages may be initially counterbalanced by the increased environmental harshness caused by boosted glacial influence, the transiently augmented contribution of ancient and labile organic carbon from thawing glaciers may enhance stream food webs across microbial uptake in biofilms (Singer et al., 2012; Fellman et al., 2015, Niedrist and Füreder, 2018). After the "peak water" period, the habitat amelioration may support periphyton and *H. foetidus* accrual, resulting in increased autochthonous production. However, more external and internal inputs fuelling the system will not necessarily determine more complex food webs. In fact, Niedrist and Füreder (2017) suggest that the dietary quality of periphyton may change due to shifts in the taxa composition in the biofilm assemblage, resulting in non-predictable shifts in higher trophic levels. Niedrist et al. (2018) demonstrated a higher nutritional quality of periphyton in harsher kryal sites, pinpointed as an explanation for higher *Diamesa* body mass in reaches with high glacial influence, where competition with other taxa is absent. This is in line with the opinion of Fell et al. (2017), who suggested that biotic interactions rather than habitat conditions will determine the ecosystem shifts in ameliorated environments.

Very simple food webs such as those of kryal habitats may be sensitive to changes affecting single nodes, and radical shifts may be determined by local extinctions and by the entry of larger-sized taxa (Clitherow et al., 2013). The upstream colonization by predators, such as the observed colonisation of new habitats by *Siphonoperla sp.* in Roseg Valley (Finn et al 2010), may exert important top-down effects on such simple food webs and may thus affect the ecosystem functioning. This was demonstrated by the experimental introduction of a predatory stonefly (*Perla grandis*) in mesocosms set up in the French Pyrenees, where Khamis et al. (2015) found that the introduced predator caused an abundance depression of *Baetis alpinus*, together with changes in the feeding guild structure and body size spectrum.

Since no food web studies have been conducted in rock-glacier fed streams so far, it is difficult to fully appreciate how permafrost thaw influences stream food webs, with the exception of a potential uptake and bioaccumulation of heavy metals in affected headwaters. In fact, Ilyashuk et al. (2014) analysed various trace elements (Cu, Zn, Pb, Ni, Cr, Al, Fe, Ti, Mn, V) in tissues of key taxa from different trophic levels (selected from mosses, worms, chironomids and aquatic beetles) in the rock glacier influenced lake Rasass (South Tyrol, Italy) and in the adjacent non-affected pond. This assessment proved that trace element concentrations in body tissues were higher in the lake than in the pond, where concentrations in water and sediment were significantly lower.

5. ECOSYSTEM TRAJECTORIES FOR ALPINE STREAMS

Space for time studies and long-term monitoring are contributing to the understanding of shifts in Alpine stream ecosystems triggered by deglaciation, but much more specific research is needed. Our conceptual model (Fig. 2) is an attempt to illustrate the complex interactions between drivers of habitat change under scenarios of deglaciation and the predicted outcomes for Alpine stream ecosystems. In our model, glacier retreat and permafrost thaw interact with other climate-driven processes (vegetational shifts, snow cover changes) and with specific topographic, geomorphic, and geologic features at the catchment level. At this scale, interactions between global and local drivers determine changes in the hydrology and habitat conditions of streams. Progressive deglaciation gradually decreases the glacier contribution to streamflow, which in turn is partially offset by permafrost thaw and contributions from rock glacier outflows, resulting in a longer-term flow originating from degrading cryosphere. Increasingly unpredictable atmospheric precipitation may also become a significant hydrological driver after glacier loss (Milner et al., 2009).

The intermediate disturbance hypothesis (Connel, 1978) predicts that the performance of biological communities peaks under conditions of intermediate environmental stress. Accordingly, Füreder (2012) proposes that functional diversity, taxa abundance and diversity, as well as habitat diversity and food availability in alpine streams, are lowest when glacial influence is highest, reach a peak under the moderate harshness of intermediate glacier cover in the catchment, and decline again with decreasing glacial influence as habitat amelioration occurs. All changes in habitat conditions at various time scales affect the stream biota and food webs. A decrease in β and γ diversity and an increase in α-diversity have been anticipated in many studies regarding bacteria, algae, and invertebrates, and have already been observed in benthic invertebrates in long term studies (see Tab. 1). Reduction and loss of cold-stenothermal populations and the spread of krenal and rhithral species provide early warning signals of warming-triggered ecological shifts. Ecosystem responses occur at different levels of organization and thus shape the overall system functioning (Woodward et al., 2010).

The potential pathways for the colonization of glacier-fed streams by invertebrates depend on the ecological traits of each taxon and are different depending on season and hydrological connectivity in the catchment. Active migration across the terrestrial and aerial environments is essentially undertaken by the adults of insects (Bilton et al., 2001). Additional dispersal pathways by resistant forms (diapausing eggs for crustaceans) and parasite stages attached to insect adults and birds (e.g. water mite juveniles) have been proposed as potential pathways for meiofaunal colonisation in Alaskan streams (Robertson and Milner, 1999). In kryal habitats, active migration occurs upstream along the hyporheic corridor, and during winter within the benthic habitat of those reaches that do not freeze or run dry. The alpine hyporheic corridor also allows lateral migration between streams, as well as vertical shifts between the hyporheic and benthic zones (Bruno et al., 2012; Lencioni and Spitale, 2015). Within this context, the role of the catchment-specific hydrological connectivity is crucial for benthic life in alpine streams, as locations characterized by high hydrological connectivity (e.g. debris along steep slopes, abundance of alluvial plains) are potentially subject to faster colonization rates. It is, however, especially important to find out whether rock glacial streams can provide a long-lasting refuge for cold-stenothermals and/or sources of species for colonisation of surrounding streams after glacier loss.

6. CONCLUDING REMARKS AND FUTURE RESEARCH PERSPECTIVES

Our review provides a first extensive summary of the shifts in alpine stream ecosystems arising from both glacier retreat and rock glacier thaw with a focus on the European Alps. These insights inform about changes that occur across alpine systems worldwide (e.g. Himalaya, Rocky Mountains, Andes, New Zealand Alps), whilst recognising their differences in terms of climate and hydrology, glacier and permafrost cover, and local and regional human pressures.

Despite that the Alps are relatively well studied in comparison to other mountain ranges, considerable knowledge gaps still exist. To date, most studies on alpine stream biota have been concentrated in a few hotspots, e.g. the Val Roseg in Switzerland or the Hohe Tauern in Austria, but further research is needed across a wider range of catchments, especially in the Western Alps.

Very little is known on the hydrological significance of permafrost (including pervasive permafrost, talus fans, Little Ice Age till) for high mountain catchments. Despite the forecasted hydrological importance of rock glaciers for mountain hydrology, their increasing role in shaping stream ecology is still severely understudied. Research on streams fed by rock-glaciers under degrading permafrost conditions is therefore urgently needed for several key reasons. First, these freshwater habitats may serve as ecological refugia for cold-stenothermals biota and gain increasing conservation value. Secondly, permafrost thaw alters the physical and chemical properties of streams, causing water contamination and related problems for drinking waters (Sapelza, 2015). Thirdly, the so far limited studies in the Alps, supported by a few findings from outside Europe, show that streams fed by active rock glaciers are characterized by peculiar habitat conditions, which differ from those of other alpine stream types recognised so far. As a consequence, the role of rock glaciers in driving and modulating Alpine stream ecology is likely to become even more important in the near future.

Based on the review of existing knowledge on ecosystem shifts in alpine streams under glacier retreat and rock glacier thaw, we identify several key research priorities, and provide suggestions on how knowledge gaps may be addressed:

1. We advocate the need for an understanding of the interactions between the autotrophic and the heterotrophic components of biofilms, and on their relative importance and role in nutrient cycling. This will provide important insights into the food quality for primary consumers and allow predictions of future situations. In particular, there is the need for a deeper understanding of the ecological role of fungi and bacteria in alpine stream food webs.
2. Further investigations on community composition of primary producers in different stream types, and an understanding of the drivers and limiting factors for algal accrual during windows of opportunity, will lead to better predictions of future shifts in abundance and biomass increase and timing. Little is known about aquatic mosses diversity in alpine streams, and about their importance as hydromorphological drivers and detritus traps.
3. Invertebrate meio/microfauna, such as Copepoda, Ostracoda, Nematoda, Rotifera and Tardigrada, remain understudied in Alpine streams. Further work is particularly needed on species distribution, their autoecology, and their sensitivity to deglaciation, which helps in recognizing their functional and ecological role in Alpine stream ecosystems.
4. For macroinvertebrates, interest in the intraspecific diversity loss linked to climate change has been increasing in recent years (e.g. Finn et al., 2013; 2014). Despite a recent study on *Baetis alpinus* diversity (Leys et al., 2016), no specific research has been published so far on the loss of cryptic species related to deglaciation in the Alps. In addition, the phenotypic plasticity of organisms, and their physiological responses to environmental changes deserve further investigation (e.g. Lencioni et al., 2013).
5. For future food web studies, we call for better knowledge about the trophic and functional role of species in Alpine contexts, also based on molecular fingerprinting combined with stable isotope analysis and Bayesian mixing modelling (Niedrist and Füreder, 2018). Considering smaller invertebrates in food web studies, when possible, will also give a more comprehensive picture on the ecological role of hyporheos. Studies of the effects of POPs pollution and nutrient (P, N, OC) loads from glaciers into the food web are also limited. To the best of our knowledge, the ecological effects (e.g. uptake, biomagnification) of metals in both rock glacier- and glacier-fed streams have not been investigated so far.

In conclusion, our current understanding of the impacts of deglaciation on alpine stream ecology is largely based on fragmented data. A combination of high frequency logging and remote sensing would provide datasets with increased spatial and temporal resolution and the potential to derive valuable insights into the processes underpinning habitat and stream ecosystem changes in response to deglaciation. Advances in the analysis of such large datasets are currently creating collaborative opportunities for interdisciplinary and international research groups working on permafrost (International Permafrost Association, https://ipa.arcticportal.org). Such innovative scientific networks and novel approaches are needed to advance knowledge on the significance of mountain permafrost loss for freshwater ecosystems and place the resulting ecological impacts in the global context. International scientific networks can also provide a vital role in guiding management and policy making at the local, regional, and global scales.

7. ACKNOWLEDGEMENTS

This work was carried out within the Erasmus Mundus Joint Doctorate Program SMART (Science for the Management of Rivers and their Tidal Systems) funded by the Education, Audiovisual and Culture Executive Agency (EACEA) of the European Commission. We thank Vanessa Arrighi for drawing and digitizing the graphical abstract and for the contribution to the development/design of the conceptual model (Fig. 2). We are grateful for the comments of anonymous reviewers, which helped to greatly improve the manuscript.

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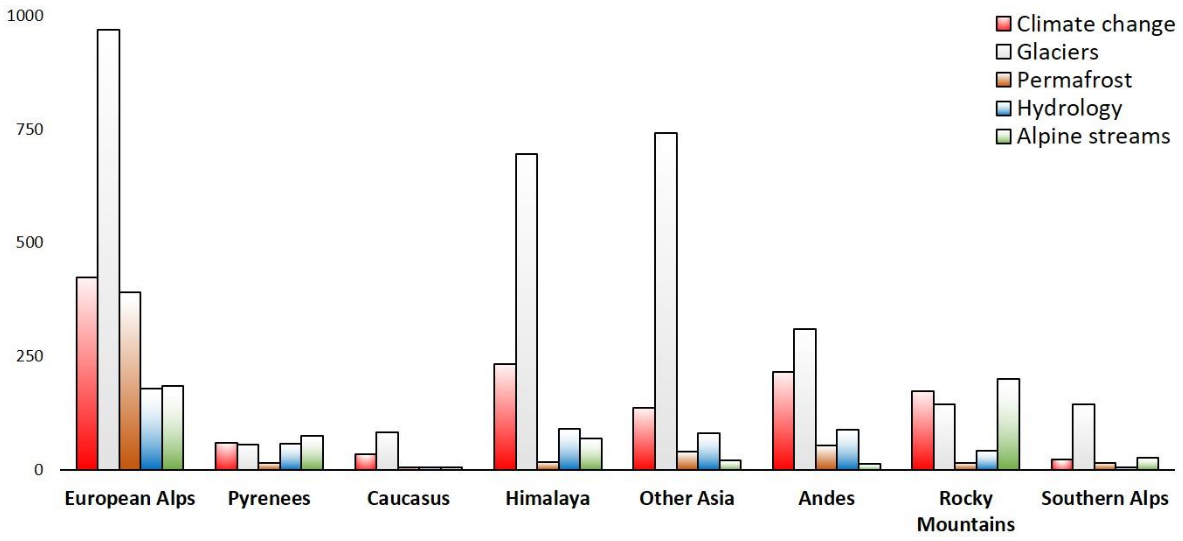

Fig. 1. Number of scientific studies published on the topics of climate change, glaciers, permafrost, alpine hydrology and alpine streams for the major world mountain regions at temperate latitudes (30-60°) and with an appreciable cryosphere extent (UNEP, 2008). NOTE: We selected in Web of Science (www.webofknowledge.com, last access 25/01/2019) searches on each region (keywords: "Alps" NOT "New Zealand", "Pyrenees", "Caucasus", "Himalaya", "Karakoram", "Tienshan" OR "Tien Shan" OR "Tian Shan" OR "Tianshan", "Kunlun Shan" OR "Kunlun mountains" OR "Kunlunshan", "Andes", "Rocky Mountains" OR "Rockies", "New Zealand" AND "Alps") as TOPIC (word included at least in title, abstract, or keywords), and crossed with each subject (keywords: "climate change" OR "global warming", "glacier" OR "glaciers" NOT "rock glacier" NOT "rock glaciers", "permafrost" OR "rock glacier" OR "rock glaciers", "hydrology" OR "hydrological", "stream" OR "streams") as TITLE (only included in the title). In the graphic "Other Asia" = Kunlunshan, Tienshan, Karakoram.

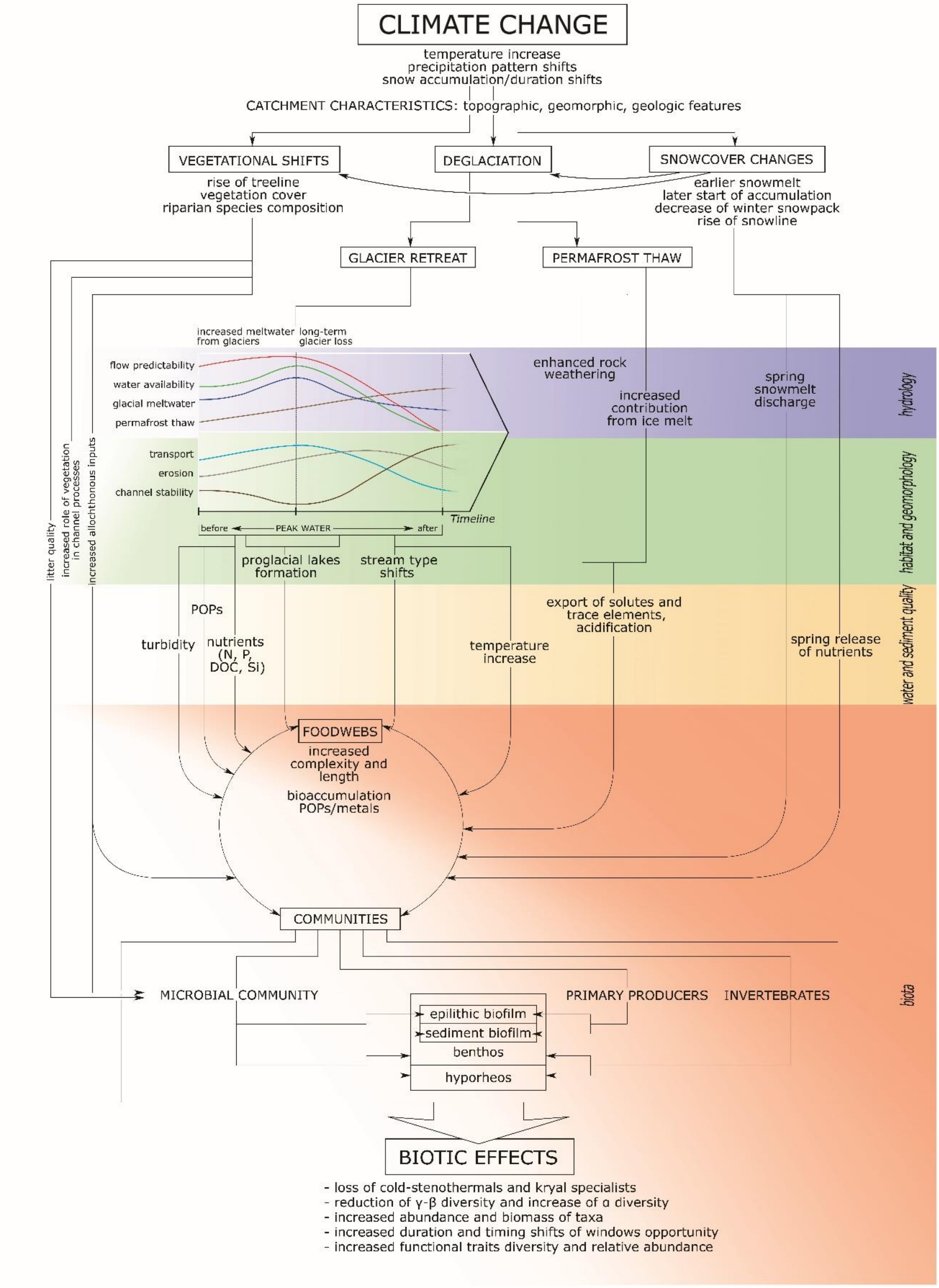

Fig. 2. Conceptual model of the effects of climate change and deglaciation on Alpine stream ecosystems. Lines with arrows: direct influence. Climate change interacts with catchment-specific features in determining deglaciation and shifts in snow cover and vegetation. These

key catchment changes and their interactions have distinct consequences on the hydrology, geomorphology and habitat, and on the quality of water and sediment (different layers). Different time scale impacts of glacier retreat are summarized in the specific chart, showing the trend of key hydrological and geomorphological parameters over the two identified phases, i.e. before and after the “peak water” period governed by glaciers. All the specified abiotic changes have different consequences for the stream biota, i.e. the different interacting communities resulting in an altered food webs (cycle). “Microbial community” is meant here as Archaea, Eubacterial heterotrophs and Fungi, and “Primary producers” include Algae, Cyanobacteria and Bryophytes. The resulting key biotic effects of deglaciation on Alpine streams are summarized in bullet points.

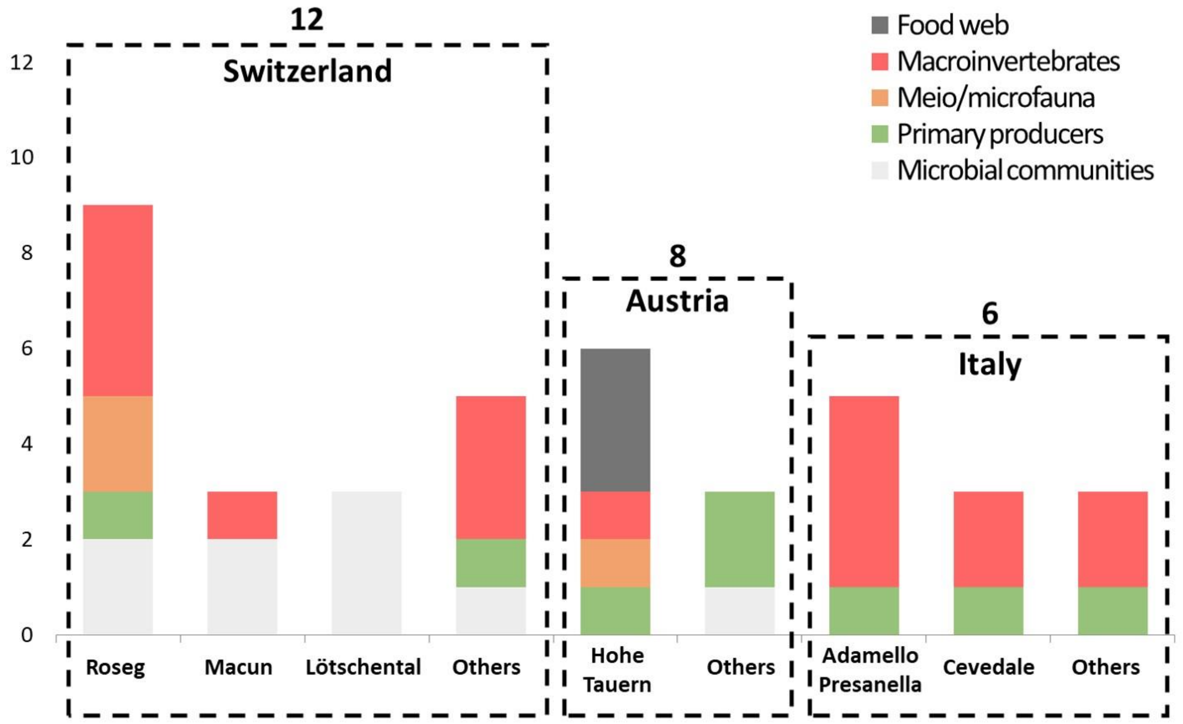

Fig. 3. Distribution of 24 research papers specifically focusing on the effects of deglaciation on alpine stream biota in the European Alps, ordered by study area/country and the investigated biotic component. Articles covering more than one catchment/country have been split into different counts. The papers have been chosen as they specifically address the topic at least in the scope of the research or treat it extensively in the discussion or conclusions. Considered papers are marked in the main text with * the first time of citation.

Table 1. Observed changes in zoobenthos diversity specified by cited references on studies in Italian and Swiss catchments.

Area	Time series and reaches	Biodiversity of zoobenthic community	References
Carè Alto (Adamello Massif)	1996, 1997, 2005 and 2013	No observed changes in α-diversity for Chironomidae community. Observed reduction of β and γ diversity. Newly-formed reaches rapidly colonized by *Diamesa sp.*	Rossaro et al. 2016
Conca, Niscli, Cornisello, Amola, Careser, Noce Bianco, Trobio catchments	1997-2013 summer campaigns covering different glacial influence reaches	Upstream migration of cold stenothermal (*Diamesa sp*) and eurieucious (*Baetis alpinus*, Orthocladiinae, Nemouridae, Limoniidae, Empididae, Oligochaeta) taxa. Concomitant increase of functional diversity and redundancy.	Lencioni, 2018
Morteratsch, Steinlimi, Tschierva, Roseg, Lang, Stein, Oberaletsch, Fiesch catchments	1998 - 2009 - 2011 (mid-summer samples) Upstream reaches flowing over deglacierized forelands	Newly-formed reaches rapidly colonized by *Diamesa sp.* β-diversity increase associated with reduction of Chironomidae and expansion of Ephemeroptera and Plecoptera taxa in the communities. Increase of γ-diversity with the entry of Diptera Blephariceridae and Trichoptera in the community	Robinson et al., 2014
Roseg Valley	1997 - 2007/08 (spring-summer-autumn campaigns)	Newly-formed reaches rapidly colonized by *Diamesa sp* and other Diamesinae (increased α-diversity). Increase of γ-diversity with the entry of *Syphonoperla sp* (Plecoptera), *Ecdyonurus sp* (Ephemeroptera Heptageniidae) *Liponeura sp.* (Diptera Blephariceridae) and *Ryacophila torrentium* (Trichoptera)	Finn et al., 2010

Swiss National Park (Macun catchment)	2001/2008 complete series of mid-summer samplings in ponds and streams	Decrease of zoobenthos densities and taxa richness (α-diversity) in rock glacier influenced streams between 2001-2004 and 2005-2008, with similar trend for lake outlets and krenal	Robinson and Oertli 2009*
Swiss National Park (Aqua and Fuorn streams)	1999/2013 complete series of monthly samplings from spring to late autumn Downstream reaches at 1707-1750 mt, with low glacial contribution	No observed changes in α-diversity but shifts in the community composition and abundance. Observed increase in abundance of Simuliidae and *Leuctra sp.* and decrease of Heptageniidae for the glacier fed river (Fuorn) and of *Protonemoura sp* for the rock glacier fed (Aqua) stream	Sertić-Perić et al., 2015*
Roseg Valley	1997/98 – 2008/09 (monthly all year campaigns)	In the downstream sections (glacio-rhithral) of the retreating glacier stream, drift densities of Chironomidae (and overall community) decreased (especially in spring and autumn) and Ephemeroptera/Plecoptera drift density increased (especially in spring and winter)	Sertić Perić and Robinson, 2015*