Trophic ecology of alpine stream invertebrates: current status and future research needs

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Abstract: Community structures of benthic invertebrates in different alpine stream types have been well documented and modeled against environmental conditions and change. However, community structure cannot be linked directly to community functions or processes, and this problem prevents clear estimation of functional consequences of environmental changes. In this article, we highlight the need to focus research efforts on the trophic ecology of alpine streams for several reasons. 1) The trophic ecology of invertebrates is remarkably understudied in the field of alpine stream ecology (only 7% of published studies), but the trophic ecology of invertebrates underlies crucial functions in these ecosystems. 2) Classifications of species into functional feeding groups, traits often used to express the functionality of invertebrate communities, are missing for several alpine species or have been deduced from classifications based on higher taxonomic levels. 3) Most investigators focused on a few trophic levels, whereas use of new analytical methods, such as Bayesian stable-isotope mixing models could provide statistically sophisticated estimations of multiple food-source contributions to consumers' diets. 4) Out-dated ideas need to be revised; e.g., we demonstrate that *Diamesa* species can actively select their food, which is against the established assumption that animals in harsh environments are forced to feed on everything they can get. Based on literature studies, we summarized most critical research needs on the trophic ecology of alpine stream invertebrates. Our goal is to promote ways to understand the ecological function of alpine stream invertebrates and the potential effects of alteration of their trophic relationships by ongoing environmental changes like glacier retreat, water exploitation, or immigration of invasive species.

Key words: functional feeding groups, functional ecology, food preference, food sources, stable isotope mixing modeling

Streams are common but diverse in landscapes situated above the montane vegetation altitude (alpine). Based on their predominant water source, associated water temperature, or glacial influence, Steffan (1971), Ward (1994), and Füreder (1999) distinguished among kryal (glacier-fed), crenal (spring-fed), and rhithral (dominated by seasonal rain and snowmelt) alpine streams. However, alpine stream networks are complex and include all of these stream types (McGregor et al. 1995). Moreover, confluences of different sources produce mixed types, e.g., glacio-rhithral streams (Füreder 1999). In this framework, we consider streams above the treeline and, thus, in the alpine vegetation zone as alpine streams (Table 1). Environmental conditions can vary laterally (different types of streams), longitudinally according to the river continuum concept (Vannote et al. 1980) with increasing contributions of other stream types with progression downstream, or temporally (e.g., intra- and interannual variability of conditions related to snow cover or glacier melt activity or as a long-term effect of source change, such as reduced glacial influence) (Milner et al. 2001, Smith et al. 2001). Environmental variability can lead to adaptation of macroinvertebrate species to particular local conditions. Furthermore, stream morphological characteristics, such as slope or exposition, can lead to species sorting in these en-

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Table 1. Glossary of terms used in this study.

Term	Definition
Alpine streams	Running waters of the alpine vegetation zone between the treeline and the permanent snow line anywhere in the world.
Trophic ecology	Examines the interaction of bottom-up and top-down forces and presents a synthesis of trophic interactions within and across ecosystems. Here it is the study of feeding relationships among organisms in communities and ecosystems, like alpine streams and not the cycling of nutrients or energy transfer.
Trophic levels	The positions that organisms occupy in a food chain (for example photosynthetic producers, herbivorous grazers, detritivores, predatory carnivores, or decomposing microorganisms); each level through which the energy proceeds through an ecosystem.
Trophic cascades	Propagation of indirect effects between nonadjacent trophic levels in a food chain or food web (for example a predatory fish decreases the abundance of herbivore fish that in turn leads to increasing biomass of producers).
Trophic structure	Refers to the number of trophic levels or feeding relationships in a community or an ecosystem.

vironments (Ceola et al. 2013). Species sorting in alpine streams has been well studied (Milner et al. 2001, Füreder et al. 2001, Lods-Crozet et al. 2001, Khamis et al. 2014, Niedrist and Füreder 2016), and significant changes in species composition resulting from anthropogenic environmental changes, such as water use (Brown et al. 2015) and glacial retreat, have been detected (Füreder 2012, Jacobsen et al. 2012) or are expected (Cauvy-Fraunié et al. 2015).

In harsh and dynamic alpine-stream ecosystems, the most important function of invertebrates in maintaining stream integrity is their feeding strategy. Invertebrate assemblages are essential to the flow of energy in alpine streams, either as primary consumers of algae or as processors of in-stream (e.g., autochthonous biofilm) or allochthonous products (allochthonous coarse particulate organic matter [CPOM] and detritus) (sensu Cummins and Klug 1979). As the sole consumers of basal resources in headwater reaches, they can affect energy flow to consumers in downstream reaches (analogous to Wallace and Webster 1996), which are the most important food resource for resident fish populations in downstream regions (Milner et al. 2009). Macroinvertebrates also are an important link between basal producers (e.g., algae), detritus, or microbial communities and higher trophic levels (Table 1). In short, they are essential for linking most compartments in aquatic habitats and regulating energy transfer along aquatic food webs (Wallace and Webster 1996). Classic examples include the role of shredding organisms in breaking down coarse particulate organic matter (CPOM), such as leaves, wood, etc., which contributes to the process of organic decomposition and, thereby, generates fine particulate organic matter (FPOM), which supplies the need of other consumers, such as collectors or filterers (Cummins and Klug 1979).

In alpine streams, grazers or scrapers feed on autochthonous food sources, such as algae, cyanobacteria, and diatoms (periphyton), which is their most important food because input from outside the stream is limited. However, the composition of periphyton species is related to environmental conditions and can differ strongly among alpine streams (Rott et al. 2006). This variability might be important because the nutritional benefit of the main periphytic components (diatoms, cyanobacteria, green algae, etc.) varies (Taipale et al. 2013, Guo et al. 2016). However, very little is known about resources available to other feeding groups (e.g., shredders) in alpine streams or about the quality and quantity of allochthonous inputs under current and future climate conditions. Overall, potential alterations of food quality and quantity and their effect on invertebrate primary consumers are totally unknown in alpine stream habitats.

Much is known about the relationship between environmental conditions and structural community metrics of alpine stream invertebrates. However, we think that our understanding of the functional responses of alpine stream invertebrates to environmental change is confounded by an inadequate understanding of the biotic interactions within invertebrate communities and of the qualitative and quantitative relationship between producers and consumers. Indeed, knowledge about invertebrates' function in streams is scarce in general.

To aid in understanding the roles of macroinvertebrates in stream ecosystems, much effort has been devoted to collecting and combining data related to feeding modes and affiliations of stream insects to certain functional feeding groups/guilds (FFG) in classification databases (Moog 1995, AQEM consortium 2002, Janecek et al. 2002) based on modifications of classification systems published by Cummins (1973, 1974), Cummins and Klug (1979), Merritt and Cummins (1996), and on experts' assignments. These traits were deduced mainly from observations of animals' mouthparts and feeding behavior, and to a lesser degree, on data from feeding observations and analyses of consumed food. Nevertheless, they enable indirect and empirical assessment of the composition of diverse feeding guilds, reflect in-stream processes, and can indicate changes in the ecological status of streams. Classification of insects by FFG is based on behavioral mechanisms (scrapers/grazers consume algae and associated material, shredders consume leaf litter or other CPOM, collectors/gatherers collect FPOM from surfaces, filterers remove FPOM from the water column, and predators feed on other invertebrate consumers; Merritt and Cummins 1996) rather than on taxonomic groups. This scheme enables investigators to study organisms collectively as members of a small number of groups based on the way they function and process energy in the stream habitat.

FFGs are in daily use, e.g., as a method in river monitoring in the implementation of the European Water Framework Directive (WFD). However, the classification of species to FFGs and their verifications for the use of FFGs are based mostly on studies from streams at mountain or lower elevations and often are not available for alpine species. The appropriateness and accuracy of a classification or assumptions about species' feeding behavior is unclear when applied in extreme environments like alpine streams. Thus, use of such classifications in alpine environments could lead to over- or underestimation of animals' realized feeding performance and misinterpretations of organic matter processing in alpine streams.

Our lack of knowledge of functional species properties in alpine stream ecosystems, which are expected to undergo considerable environmental change in the near future (Milner et al. 2009), calls for enhanced research activity in the field of alpine stream trophic ecology. In this perspective we will: 1) explain the importance of a functional understanding of alpine streams, 2) review the completeness of classifications of invertebrate species into FFGs, 3) provide an up-to-date quantification of the published literature available on trophic ecology (Table 1) of alpine aquatic invertebrates, 4) assess how studies on feeding ecology in alpine streams have improved our knowledge of functional relationships and strategies, and 5) conclude with a list of the most critical research needs for understanding trophic ecology in these stream ecosystems.

COMMUNITY STRUCTURE DOES NOT EQUAL COMMUNITY FUNCTION

The complex relationships among producer, consumer, and decomposer communities and the abiotic environment underlie ecosystem functions. These functions comprise important services, such as organic-matter processing, natural purification of water, or provision of food for other inhabitants; i.e., the transfer of energy between trophic levels. Water resources and ecosystem services (e.g., natural filtration of water by filter feeders) are critical to the well-being of human populations, and a thorough understanding of the effects of environmental change on headwater streams is needed to guide management and policy decisions.

The authors of many recent influential papers and reports have taken a structural approach to understanding alpine stream communities. In this approach, the taxonomic composition of and the presence of indicator taxa in (e.g., Khamis et al. 2014) benthic communities are linked to key environmental conditions (Milner et al. 2001, Lencioni and Rossaro 2005, Niedrist and Füreder 2016). In alpine streams, as in other streams, the prevailing environmental conditions filter invertebrate species that are not suited to the environment from the community leaving the remaining species to fill trophic roles (producer, consumer, and decomposer) and to provide ecosystem services. Thus, taxonomic information is used to predict future community structures (Jacobsen et al. 2012) and to forecast potential effects on ecosystem functions and services based on functional traits of species (Bonada et al. 2007). However, the trophic role (e.g., grazers, collectors, etc.) of taxa bearing certain ecosystem functions might change in response to environmental change (i.e., variable trophic strategies; Füreder et al. 2003b). Similarly, the same invertebrate species might grow at different rates in cold- and warm-water streams, leading to differing productivities among stream ecosystems (Hannesdóttir et al. 2013). Thus, whether and how information about changes in invertebrate community structure will allow us to understand, predict, and model ecosystem functions and processes is not clear because ecosystem alterations and species exchanges resulting from environmental change could alter community structure and ecosystem functions and processes performed by remaining taxa simultaneously (e.g., Milner et al. 2009, Khamis et al. 2014, Brown et al. 2015).

Species diversity of communities often is used as a general proxy for ecosystem functioning. However, the unclear relationship between species diversity and ecosystem functioning could potentially lead to a general misunderstanding that species losses harm ecosystems (Worm and Duffy 2003). Higher species diversity is a proxy for community stability, but does not necessarily imply better or more diverse processes within the ecosystem (McCann 2000). Ecosystem-level processes are affected by the functional characteristics of the organisms involved, rather than by taxonomic identity or species diversity per se. That is, the composition and degree of functional diversity, rather than species diversity, influence ecosystem processes and stability (Odum 1969, Tilman 1997, McCann 2000, Gagic et al. 2015, Lefcheck and Duffy 2015). The structure of a community may not be clearly linked to the functions or processes it performs (Schimel and Schaeffer 2012, Bier et al. 2015). Therefore, functional attributes of species, e.g., feeding roles, must be considered when evaluating ecosystem-level processes of communities. The composition and activity of omnivorous invertebrates or specialized grazers, filter feeders, collectors, shredders, and predators in a community influence the trophic structure, ecosystem production, and consequently, ecosystem stability (Wallace and Webster 1996).

INCOMPLETE CLASSIFICATION OF INVERTEBRATE SPECIES TO FFGS

Use of FFGs facilitates investigation of macroinvertebrates' functions in aquatic ecosystems. However, studies of ecosystem processes are limited by incomplete information on FFG assignments because knowledge about organisms feeding behavior and morphology is often lacking. A scan of the present classification databases FAA (Fauna Aquatica Austriaca) and AQEM (Assessment System for the Ecological Quality of Streams and Rivers throughout Europe using Benthic Macroinvertebrates; Janecek et al. 2002, AQEM expert consortium 2002) was summarized on the internet platform freshwaterecology.info (Schmidt-Kloiber and Hering 2015). The analysis of these databases revealed that all mayfly species have been assigned to FFGs, but this autecological information is known for only 60 and 72% of Chironomidae and Trichoptera, respectively (Fig. 1). Moreover, we think it likely that this information, which is based primarily on morphological traits of individuals from lowland streams, was assumed for a considerable number of species, when at least one representative of the genus was known (i.e., similar classifications for species belonging to the same genus). The use of FFGs might be an imprecise way to monitor the ecological status in alpine streams given missing or assumed classifications of species to FFGs and uncertainty regarding appropriateness of applying classifications based on individuals collected from lowland streams in alpine stream environments. Insecure trait information for species could hinder correct deduction of trophic function from invertebrate community structure and could render incorrect translation of community structure into community function in alpine streams. Studies of feeding preferences of alpine stream invertebrates are rare. Thus, little is known about the trophic ecology of organisms in alpine streams.

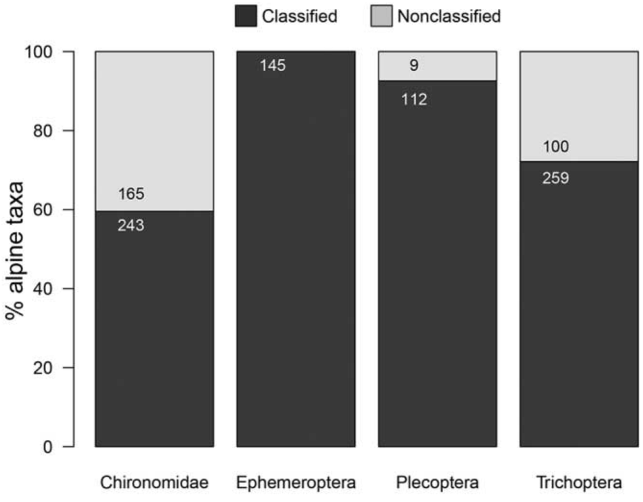

Figure 1. Relative and absolute (numbers in bars) numbers of stream invertebrate species from Austria, Germany, France, and Switzerland occurring in ecoregion 4 (Alps) with (classified) and without (not classified) information on their feeding type. Data were obtained from freshwaterecology.info (Schmidt-Kloiber and Hering 2015).

STUDIES ON ALPINE STREAMS AND TROPHIC ECOLOGY

We reviewed the published literature available on the ISI Web of Knowledge (Thomson Reuters, Philadelphia, Pennsylvania) between the year 1860 and 2015 for ecological research on 'alpine streams', determined the fraction of studies involving 'invertebrates', and identified studies on 'trophic ecology' (Appendix S1). This search may not have included all target studies, but we think it is a representative subset for illustrating patterns of research priority in alpine streams.

Our search identified 465 articles published from 1937 until the end of 2015 with a current mean of 42 publications/y, but only 198 studies of these involved invertebrates (Fig. 2). In general, we observed a significant increase in the articles published dealing with invertebrates in the early 1990s in conjunction with an increase in alpine stream studies. The most articles/y on alpine stream invertebrates was published in 2005 (15 publications). In contrast, only 7% (15) of all invertebrate studies had either 'trophic ecology' or 'feeding' in the title, abstract, or key words (summarized as 'topic' on Web of Knowledge). The first alpine invertebrate trophic study was published in the year 2001 (Zah et al. 2001) followed by studies in 2003 based on gut-content and stable-isotope analyses to infer trophic relationships (Füreder et al. 2003a, b). The scope of these pioneering studies was general and holistic, whereas subsequent work focused on the feeding habits of single species (Maiolini and Silveri 2005, Silveri et al. 2008a, b, 2009). Two teams of researchers investigated the magnitude of bioaccumulation of organic pollutants (POPs) in different feeding guilds (Bizzotto et al. 2009, Morselli et al. 2014), whereas others basically used functional feeding traits to draw trophic conclusions from structural assessments (Dražina et al. 2013, Xu et al. 2014). Clitherow et al. (2013) characterized the food-web structure of a glacier-fed river in the Austrian Alps by analyzing gut contents and were able to show interannual dynamics within these simple networks. Khamis et al. (2015) used a more experimental approach in the French Pyrenees to show the effect of the introduction of a single predator species to a 1st-order stream. They illustrated the effect of an invasive predator on the invertebrate community by analyzing community structure and size distribution

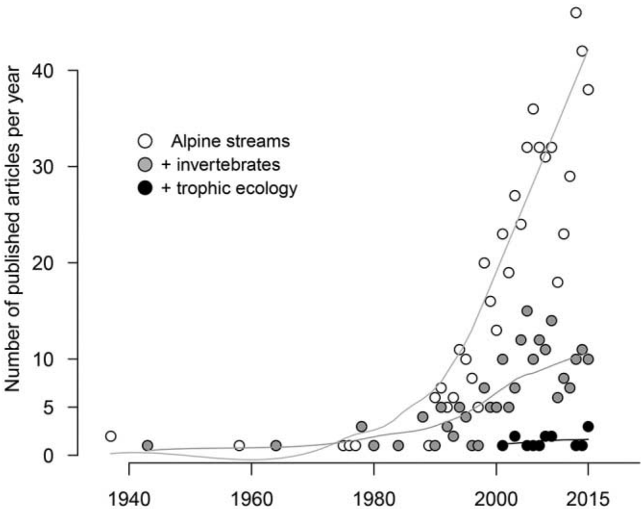

Figure 2. Number of international peer-reviewed research articles on alpine streams (alpine stream studies), with specific focus on aquatic invertebrates (studies on invertebrates) and their feeding ecology (trophic studies) from 1937–2015. The curves are loess smoothed (span = 0.8) (Source: ISI Web of Knowledge).

and predator gut contents. Last, in very recent studies, Robinson et al. (2015) assessed macroinvertebrate trophic structure of streams in an alpine catchment, and Fellman et al. (2015) used naturally occurring stable and radioactive isotopes to show the influence of ancient glacial organic C on food webs fed by a glacier.

These results show the degree of underrepresentation of trophic ecology of alpine stream invertebrates (15) among available studies of invertebrates (198) (Fig. 2). General assessments of trophic ecology in alpine stream ecosystems are even more limited because the studies were focused primarily on single watersheds or one or a few species. A very few recent publications based on experimental studies (e.g., Khamis et al. 2015) have made an interesting contribution to understanding the potential effects of species shifts consequent to environmental change and subsequent immigration of species from lower stream habitats.

RECENT CONTRIBUTIONS TO TROPHIC ECOLOGY OF INVERTEBRATES IN ALPINE STREAMS

We use the studies highlighted above to describe our knowledge of the trophic ecology of alpine macroinvertebrates (Fig. 3, Table 2). Authors of these works used various techniques to measure, assess, and interpret food sources, characterize trophic relationships and their variability in dynamic environments, present basic principles and future prospects of feeding modalities and predator effects, and provide basic knowledge about 'who eats whom' in different stream types and environmental conditions. In general, our state of knowledge about the quality and quantity of the relationships of invertebrates with primary producers is incomplete. Studies that have been published were focused on individual groups (algae, invertebrates, fish), with only a very few investigations of trophic interactions among groups (but see Fellman et al. 2015).

Autochthonous vs allochthonous food sources in alpine streams

Numerous species of epilithic diatoms, cyanobacteria, and filamentous algae are present in various alpine stream types (Hieber et al. 2001, Rott et al. 2006, Gesierich and Rott 2012) and are available for consumption by herbivorous invertebrates (Zah et al. 2001, Füreder et al. 2003b). The chrysophyte *Hydrurus foetidus*, other epilithic algae, and autochthonous detritus are generally preferred over terrestrial sources (allochthonous material) by aquatic organisms in alpine headwater streams (Zah et al. 2001) because substantial input of external energy is often missing in these systems (Zah and Uehlinger 2001). In high glacial streams, where riparian vegetation is present, high current may lead to low retention of this terrestrial material, thereby preventing its consumption by invertebrates. However, larger side-slope tributaries to glacial and alpine streams can have dense riparian vegetation, and investigators have reported variable importance of allochthonous C sources (Füreder et al. 2001, Zah et al. 2001, Robinson et al. 2015), which can consist of leaf litter, wood, grass, etc. The direct and lateral (e.g., wind-transported) input of allochthonous organic matter increased with distance from the glacier along a glacial stream. The allochthonous material was mainly in the form of grass (Zah and Uehlinger 2001), but generally occurred at a very low level (<4 g m^{-2} y^{-1} in reaches above the treeline). The available quality and quantity of allochthonous and autochthonous organic matter are expected to influence the feeding habits of invertebrates. However, potential effects of increasing riparian input on the composition of FFGs and invertebrate communities in general are unclear for alpine streams and remain to be studied.

Biofilm/periphyton quality Only a few authors differentiated between algal groups or even genera when analyzing the gut contents of alpine invertebrates (e.g., Clitherow et al. 2013). Periphyton is composed of several groups (including cyanobacteria, chrysophytes, other algae, and detritus) and numerous species, and periphyton community structure is related to in-stream environmental conditions (Rott et al. 2006). Therefore, a change of food particles for invertebrates in the periphyton can be expected as alpine river systems shift along a harsh-to-benign continuum (e.g., when glaciers retreat). Thus, a general consideration of biofilm as a potential food can be problematic when investigating trophic relationships along a continuum of environmental change (e.g., environmental harshness, glaciality index [Ilg and Castella 2006], degree of meltwater contribution) because such generalization neglects varying biochemical food

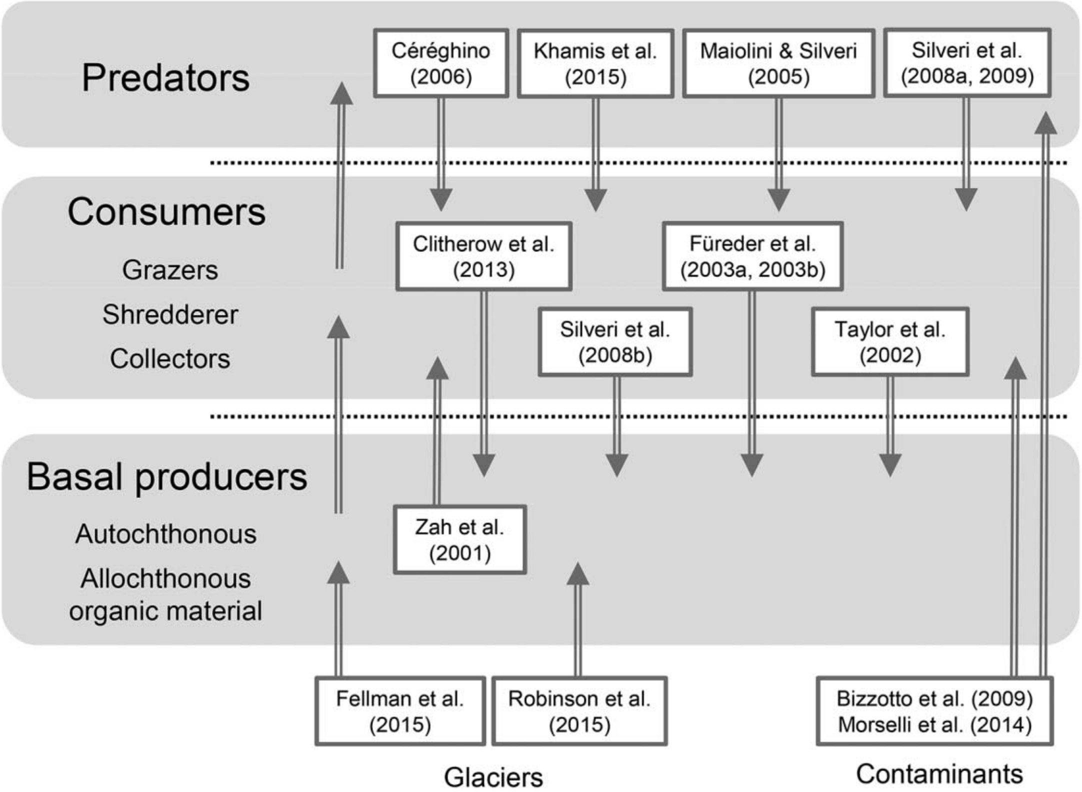

Figure 3. Conceptual diagram of published studies from alpine streams that were focused on trophic relationships of producers, consumers, predators and considered external influences (e.g., glaciers or contaminants). Locations of boxes indicate main study groups (producers, consumers, predators, etc.), arrows show the relationship(s) investigated or the affected trophic group.

quality, as has been shown for different algal groups (Taipale et al. 2013, Guo et al. 2016). To our knowledge, no study on the relationship between food quality and invertebrate grazers in alpine stream environments has been published. However, the differing biochemical quality of epilithon-forming groups (diatoms, chrysophytes, cyanobacteria, chlorophytes) might directly influence growth and reproduction of grazing invertebrates, in a manner analogous to the influence of the relative content of polyunsaturated fatty acids in phytoplankton on herbivorous zooplankton in freshwater (Kilham et al. 1997, von Elert 2002, Taipale et al. 2011). Thus, the physical condition of animals in glacier-fed streams might depend on the quality of the food available, which would change as the degree of glaciated catchment decreases (Rott et al. 2006). However, such cascading effects of environmental change on producers and consumers are not yet known for alpine headwater systems.

Influence of glaciers on the relative abundance of food resources Some potential food sources for invertebrates in glacier-fed streams can be found in the form of detritus (dissolved organic matter [DOM], FPOM, or CPOM). Such compartments can be quantified in gut-content analyses, but assigning them to the original food sources by microscopic observation is impossible (Füreder et al. 2003b). Mixing models based on stable isotopes can provide important insights to the contribution of original food sources (Parnell et al. 2013). Robinson et al. (2015) suggested that C sources for basal consumers in a glacial stream in Wyoming, USA, show a glacial signature at sites near the glacier, then shift to in-stream C sources (via algal CO_2-fixation) farther downstream, and finally become allochthonous in character in stream reaches below the treeline. This finding was supported by Fellman et al. (2015), who reported strong ^{14}C-depletion of biofilm, reflecting the assimilation of ^{14}C-depleted (highly fractionated and thus old) C, and its subsequent detection in consumers in glacially but not in nonglacially influenced streams during the period of highest glacier runoff in Alaska, USA. Singer et al. (2011, 2012) suggested that ancient and bioavailable DOC released from melting glaciers is metabolized by heterotrophic bacteria and then consumed by invertebrates feeding on epilithon. Füreder et al. (2003b) and Clitherow et al. (2013) observed high levels of fine glacial rock fragments in the guts of invertebrates. The fragments suggested unintentional uptake of bacteria by invertebrates grazing on biofilm or filtering sestonic particles, which could be an adaptive mechanism to consume bacterial biomass. In this way, melting glaciers

Table 2. Examples of trophic studies in high-altitude streams.

Approach	Objective	Target species	Reference
Experimental	Grazers effect on periphyton	Multiple	Taylor et al. (2002)
	Effect of predator invasion on stream communities	Multiple	Khamis et al. (2015)
Stable-isotope studies	Importance of allochthonous food sources	Multiple	Zah et al. (2001)
	Influence of ancient C on a glacial stream food web	Multiple	Fellman et al. (2015)
	Trophic structures of invertebrates in alpine streams	Multiple	Robinson et al. (2015)
Stable isotopes/ gut content analysis	Autochthony, feeding strategies of invertebrates	Multiple	Füreder et al. (2003a, b)
Gut content studies	Feeding habits of *Dictyogenus fontium*	Single	Maiolini and Silveri (2005)
	Effects of life history on feeding habits of stoneflies	Single	Céréghino (2006)
	Feeding habits of *Nemoura mortoni* and Perlodidae	Single	Silveri et al. (2008a, b)
	Feeding habits of *Chloroperla susemicheli*	Single	Silveri et al. (2009)
	Characterization of foodweb metrics at snout of glacier-fed river	Multiple	Clitherow et al. (2013)
Contaminant concentration	Bioaccumulation of contaminants	Multiple	Bizzotto et al. (2009)
	Quantifying and modelling stream invertebrates	Multiple	Morselli et al. (2014)

can be viewed as sources of ancient C that accelerate biomass production of invertebrates in a nutrient-poor environment.

Trophic interactions and structures of food webs in alpine streams

Interactions between producers and consumers Primary consumers in different types of alpine streams at high altitudes and latitudes are mainly chironomids, which numerically dominate different stream types above the montane vegetation level (Milner et al. 2001, Lods-Crozet et al. 2001, Lencioni and Rossaro 2005, Niedrist and Füreder 2016). In harsh ecosystems, they are the first colonizers (Milner et al. 2001). Thus, they can be considered as first consumers along the river continuum. Generally, their occurrence seems to be closely related to algal sources, given their algal isotopic C signatures (Zah et al. 2001, Füreder et al. 2003b). In inhospitable environments like glacier-fed streams, where the degree of competition is generally low, species seem to be forced into opportunistic omnivorous (Füreder et al. 2003b, Maiolini and Silveri 2005) or even cannibalistic (Clitherow et al. 2013) feeding behavior to survive. This feeding strategy is indicated by overlapping δ^{13}C and highly variable δ^{15}N signatures of invertebrates (Zah et al. 2001, Füreder et al. 2003b). In contrast, stable conditions in nonglacial streams allow the existence of various food sources for herbivores (e.g., mosses, macrophytes) and considerable input of allochthonous organic matter from the riparian vegetation (Zah and Uehlinger 2001) and, thus, enable existence of invertebrates with distinct and narrow feeding preferences (Füreder et al. 2003b). However, invertebrate feeding habits have been better studied in glacial alpine streams than in other stream types, so the relationship of feeding strategies along a gradient of environmental conditions has not been demonstrated.

More species or families of invertebrates are found in stream beds when conditions moderate in downstream reaches of glacier-fed streams and in nonglacial streams (see concept of Milner et al. 2001). Mayfly species (e.g., *Baetis alpinus*, *Rhithrogena loyolaea*, *Rhithrogena nivata*) that are characterized as collector/gatherers and grazers/detritivores (Moog 1995, Merritt and Cummins 1996) scrape epilithon and feed on detritus (Füreder et al. 2003a), but whether grazing species actively select compartments of high food quality (diatoms and chrysophytes) or consume bulk epilithon is not clear.

In general, it is not known whether invertebrates living in harsh environments can choose the most nutritious food sources or must feed on anything they can get (Füreder et al. 2003b). Species within the genus *Diamesa* (Diptera: Chironomidae) are likely to prefer *H. foetidus* during summer (Fig. 4, Appendix S1), but the growth of this alga is inhibited in summer (Hieber et al. 2001). This information indicates lower importance of detritus and bulk biofilm in glacier-fed streams and selective feeding of these larvae despite the harsh environmental conditions. Microscopic analysis of gut contents of same *Diamesa* species showed a predominance of diatoms, a high-quality food source (Fig. 5, Appendix S1). With respect to the available food sources, invertebrate grazers seem to actively ingest high-quality food, based on their relative content of polyunsaturated fatty acids (Taipale et al. 2013) and to avoid low-quality food sources like cyanobacteria (Fig. 5). However, the benefit of high-quality food for invertebrates has never been tested in alpine streams. This information would be of highest interest because a potential bottom-up effect

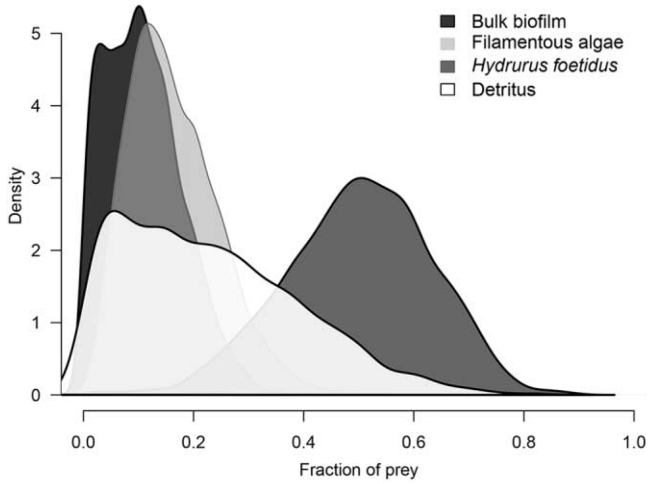

Figure 4. Density plot of Bayesian estimates of the proportions of 4 basal food sources (filamentous algae, bulk biofilm, the chrysophyte *Hydrurus foetidus*, and detritus) contributing to the diet of *Diamesa* species in 6 glacier-fed streams. Most frequent estimations (highest density of same estimates) display the most likely contribution of the respective food source. Broad peaks indicate an uncertain estimate (Detritus). The mixing model was performed using a personalized MixSIAR model (Stock and Semmens 2013) resulting in final 3000 simulations.

of primary producers on the success of invertebrates would be a new perspective for alpine stream ecology.

Bayesian mixing models, which are being newly applied in this area of research, enable demonstration of consumers' preferences for certain algal components of the epilithon of glacier-fed streams in analyses of C and N isotopic signatures of consumers and their food sources (bulk biofilm, detritus, *H. foetidus*, and other filamentous algae) (Appendix S1). In contrast to linear mixing models (Philips 2001), the Bayesian approach precisely models the contribution of different food sources and provides likelihood for the resulting dietary contribution. The benefit of using Bayesian models becomes especially evident when back-tracking the contributions of >3 different food sources or when sample sizes are small, as these models acknowledge variability in the isotopic signal of different food sources, can incorporate prior information, and execute thousands of runs (Parnell et al. 2013).

Predators Stonefly (*Dictyogenus* spp.), some caddisfly (e.g., *Rhyacophila* spp.), and certain chironomid species (Tanypodinae spp.) are major predators in alpine and subalpine streams. Predatory stoneflies in alpine habitats seem to feed preferentially on chironomids relative to other macroinvertebrates in streams in the western Italian Alps (Maiolini and Silveri 2005, Silveri et al. 2008a). In dynamic and cold alpine streams, Zah et al. (2001) and Füreder et al. (2003b) reported high feeding plasticity of invertebrates and found evidence of predatory activity of species that usually graze. Chironomid taxa classified as detritivores/grazers might even be forced into cannibalistic feeding habits during the high summer discharge in glacier-fed streams (Clitherow et al. 2013). Knowledge about the relationship between feeding plasticity or opportunistic predatory and environmental conditions in alpine streams is still scarce, but predatory activity by generalists seems to depend on environmental conditions (Füreder et al. 2003b).

Predators generally feed on scraping and grazing species and control their density through direct consumption or prey-avoidance mechanisms (Lancaster 1990). However, a study in streams in Utah revealed that predators can influence the processing of leaf litter (Oberndorfer et al. 1984) by efficiently controlling the number of shredders in the system, which in turn, led to a reduction in leaf-breakdown rates and an increase in the persistence of leaves in the water body. The magnitude of top-down effects and trophic cascades (Table 1) in different alpine stream types (e.g., glacier-fed vs groundwater-fed) is unknown and should be considered in future experiments.

Expected changes of environmental conditions in glacially influenced stream ecosystems under scenarios of future hydrological change (Milner et al. 2009) will make upstream habitats more favorable to predatory species from downstream regions and will allow their upstream colonization (e.g., Brown et al. 2007). Such 'invaders' could have tremendous effects on simple food webs of low-order streams, comparable to cascading effects of invaders, such as the zebra mussel, in other aquatic habitats (Noonburg et al. 2003, Gallardo et al. 2016). Stream-channel experiments illustrated potential effects on body-size spectra and foodweb interactions when the predator *Perla grandis* 'invaded' alpine stream habitats (Khamis et al. 2015). These effects could include negative shifts in body size and a general intensification of biotic interactions. Besides potential intraguild predation effects known from other systems (Polis et al. 1989) (when *P. grandis* is feeding on *Rhyacophila* spp.), the presence of this more efficient predator might lead to a decreasing prey abundance of *Baetis* spp. by increased drift rate and predation. Furthermore it might also evoke prey body-size reductions and potential trophic cascades as a consequence of its size-selective predation (Peckarsky 1985, Wooster 1994, Khamis et al. 2015). Khamis et al. (2015) acknowledged probable bias in their results caused by high prey turnover rates or low statistical power and made an appeal for further research on these effects. In lower-altitude stream habitats, predator body-size is an essential determinant of trophic niche overlap and intraguild predation (Woodward and Hildrew 2002), as is potentially the case in alpine streams.

Food webs Trophic structures (Table 1) in alpine stream environments generally are simple (only few taxa) and con-

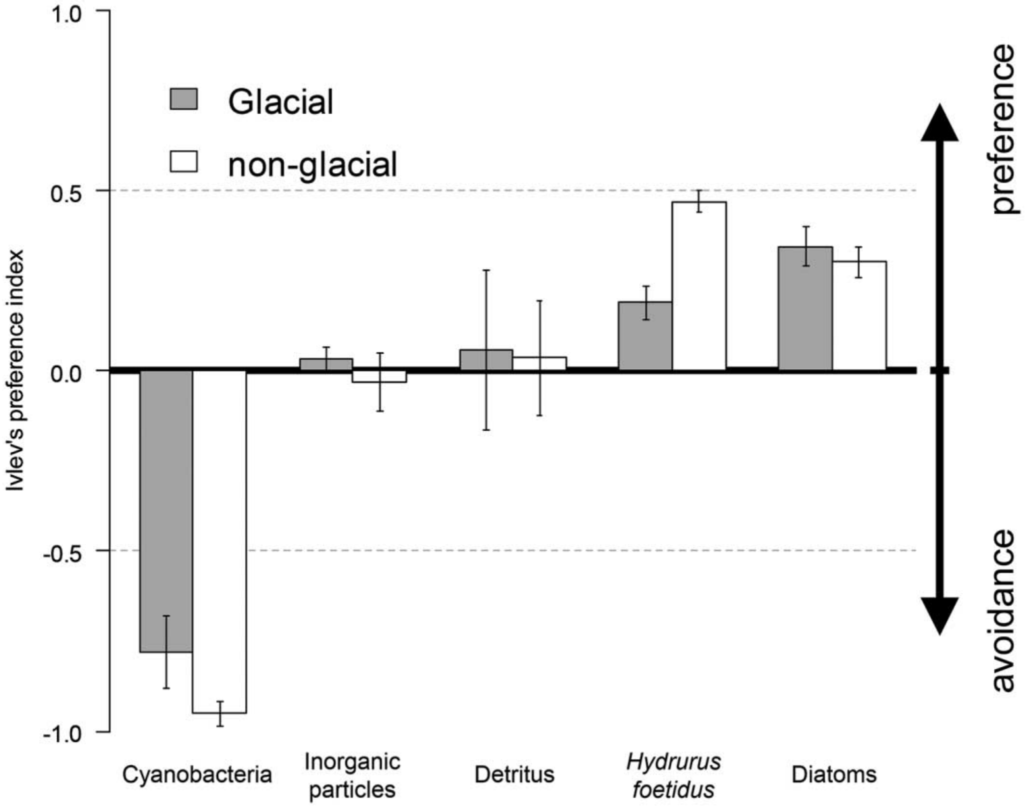

Figure 5. Mean (±SE, $n = 48$) food preference (Ivlev's preference; Ivlev 1961) of *Diamesa* larvae (*D. steinboecki* and *D. latitarsis* gr. A) for 5 food items relative to food abundance in high-elevation glacial and nonglacial streams in the Hohe Tauern Nationalpark. Positive values indicate preference for a source, negative values indicate avoidance, 0 indicates food source was taken in proportion to its abundance in the ecosystem.

sist of primary producers (diatoms, filamentous algae, heterotrophic bacteria, cyanobacteria, and mosses), primary consumers, and omnivores/predators (Zah et al. 2001, Füreder et al. 2003b). In harsh stream ecosystems with a low input of allochthonous organic matter and restricted primary production during extreme summer runoff, invertebrates seem to be forced to a general feeding habit (Füreder et al. 2003b). However, specific studies on such strategies of invertebrates in alpine environments are rare. Short food-chain lengths (mostly linking only 2 trophic elements) and high connectance characterized a food web at a glacier snout in Austria (Clitherow et al. 2013). In less harsh and less disturbed environments, such as groundwater-fed streams, food chains are considerably longer (see results from nonalpine streams; Parker and Huryn 2006, Sabo et al. 2010), and food webs possess more trophic levels. Despite the tight relationships among species living in alpine streams, no study has been published that addresses the potential weakness and low stability of their food webs in response to prospective environmental change. Furthermore, the potential dependence of consumers on the structure of producer communities has not been assessed. Zah et al. (2001) observed more distinct trophic levels in spring-fed than in glacier-fed streams, where feeding interactions were less intense. Thus, increased intensity of species interactions could be expected as the influence of glaciers on alpine streams decreases in the near future (Milner et al. 2009). The effect of more diverse communities on intraguild competition is barely known. An increasing number of cohabitating species might evoke competitive communities and lead to trophic niche differentiation and species' specialization as known from classical ecological principles (Armstrong and McGehee 1980) and recent studies of microbial communities (DeLong and Vasseur 2012, Livingston et al. 2012, Wilhelm et al. 2015). On the whole, more diverse communities might increase resource exploitation in alpine stream systems (Finke and Snyder 2008). However, any prognoses about the consequences of environmental change on foodweb properties and stability are speculative because of the information gap about foodweb properties of alpine stream types (but see Clitherow et al. 2013 for a glacier-fed stream). Understanding foodweb properties (connectance, chain lengths, trophic levels, etc.), resource availability, and resource exploitation in different stream types should be a research priority in alpine stream ecology. Such information is needed to forecast responses to environmental change.

FUTURE PROSPECTS AND RESEARCH NEEDS

Significant advances have been made during the last decades to evaluate structural community patterns of biotic components and their relationship with environmental conditions in alpine stream ecosystems (e.g., Füreder et al. 2001, Lencioni and Rossaro 2005, Brown et al. 2007, Khamis et al. 2014, Cauvy-Fraunié et al. 2015, Giersch et al. 2016, Niedrist and Füreder 2016), but our understanding of consequential functional shifts in alpine streams is still limited. Alpine stream ecosystems will experience physicochemical alterations resulting from human activities including water use, climate change, and glacial recession. Alterations of diurnal, seasonal (annual differences in snow-pack or the timing of snow and ice melt), and long-term hydrological dynamics will alter the habitat template for benthic communities (Milner et al. 2009), which will change according to species tolerances. In addition to the general up-valley movement of plants (Rosenzweig et al. 2008), missing discharge dynamics will increase the presence of the riparian vegetation and its connection to the rivers. Inputs of allochthonous material probably will be used by invertebrates (Füreder et al. 2003b), but specific roles, adaptations, strategies, feeding plasticity, or the trophic niches of alpine species are barely known. Hence, predictions are difficult to make regarding the functional consequences of structural shifts in alpine stream invertebrate communities subsequent to environmental change.

We suggest key research needs and priorities that would enhance our understanding of functional strategies, relationships, and services of invertebrate species in alpine stream ecosystems when considering climate-change scenarios:

1. Broader knowledge of the structural changes in invertebrate communities is needed to gain a better understanding of functional responses to environmental conditions and to estimate the future services of these ecosystems.
2. The effects of key environmental variables that change during glacier retreat on the composition of the epilithon, including bacterial groups, and the input of allochthonous organic matter, principal food sources for invertebrates in alpine streams, must be clarified.
3. The effects of food quality on the fitness, development, and body-size/mass of benthic invertebrates require additional study (Guo et al. 2016). Bottom-up trophic cascades can influence consumers' success in harsh environments, but also can provoke changes in community structure.
4. Studies of invertebrates' potential to use allochthonous food sources in different types of alpine streams are needed to evaluate the influence of riparian vegetation on stream inhabitants. Allochthonous sources might become more available to invertebrates in benign habitats with low currents, such as small springs.
5. Tests of the trophic roles of invertebrate species are needed to ensure the applicability of functional traits and the characterization of invertebrate species in alpine stream ecosystems according to FFGs (e.g., Füreder 2007).
6. Identifying the feeding strategies of dominant invertebrates in relation to prevailing and changing environmental conditions will enhance our understanding of invertebrates' potential to adapt to changing environments.
7. The relationships among primary and secondary producers should be quantified for a wide range of streams in cold environments (high altitude and latitude) to understand the implications of glacier retreat and increasing riparian input for both compartments (Lamberti and Resh 1983, Rosemond et al. 1993, Feminella and Hawkins 1995, Wellnitz and Ward 2000, Taylor et al. 2002).
8. Alpine streams are critical sites for organic matter processing (sensu Wallace 1997), nutrient cycling (Bernhardt et al. 2005), and food production for fish (Milner et al. 2009). The potential of shredding invertebrate species to adapt to a higher input of allochthonous material into alpine streams in the future should be addressed in the form of manipulative experiments (Robinson and Jolidon 2005, Milner et al. 2009).

The above-mentioned research gaps must be addressed to understand the trophic relationships and functions of alpine streams. The effects of environmental change are now becoming evident. Addressing these points is urgently important to estimate consequences of glacier retreat on invertebrate functions.

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