

Long-term monitoring of high-elevation terrestrial and aquatic ecosystems in the Alps – a five-year synthesis

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Abstract

Whether and how alpine organismic communities respond to ongoing environmental changes is difficult to assess quantitatively, given their intrinsically slow responses, remote locations and limited data. Here we provide a synthesis of the first five years of a multidisciplinary, highly standardized, long-term monitoring programme of terrestrial and aquatic ecosystems in the Austrian Hohe Tauern National Park and companion sites in northern Italy and the central Swiss Alps. The programme aims at evidencing the ecological state and trends in largely late-successional, high-elevation ecosystems. We present the conceptual framework, the study design and first results. Replicated over five regions, different sites and a multitude of permanent plots, the abiotic (microclimate, physics and chemistry of soils and water bodies), biodiversity (plants, animals, microbes), and productivity data (alpine grassland, lakes, streams) provide a representative reference for future re-assessments. The wide spectrum of biological baseline data presented and their spatial and temporal variation also illustrate the degree of uncertainty associated with smaller-scale and short-term studies and the role of stochasticity in long-term biological monitoring.

Introduction

The alpine life zone above the climatic treeline often represents the last wilderness at continental scale, where organismic assemblages reflect the outcome of evolutionary selection and the requirements of the abiotic environment. Biological communities are nature's long-term answer to climatic and geochemical conditions; they also reflect natural biotic interactions (i.e. when there is no or hardly any human influence). If conditions change, the assemblages of organisms are expected to change as well. These changes are often slow, subtle and not obvious to an observer, unless long time series of standardized observations are available. Here we report on a broad, interdisciplinary, long-term monitoring programme of terrestrial and aquatic alpine biota in the Alps, with the intention of providing a reference point for future re-assessments. We present the conceptual framework and a summary of the initial years' findings for both terrestrial and associated aquatic ecosystems.

Long-term monitoring

It has long been noted that assessing environmental influences on biota requires long-term data series in analogy to meteorology, where day-to-day weather reveals climatic trends only once decades of standardized observations are available (for a high-elevation application of climatic trends in ecology, see e.g. Kittel et al. 2015). Standardization requires tools and procedures agreed upon initially by the research teams involved, as well as continuous recordings at a given location. These ideas stimulated the foundation of Long-Term Ecosystem Research (LTER) in North

America in the 1980s, which was developed into an international platform in 1993 (iLTER), with European (eLTER) networks launched in 2003 (Mirtl et al. 2018). Pioneer long-term monitoring projects at high elevation are those for aquatic systems (Miller and McKnight 2015) and terrestrial systems (Williams et al. 2015) in the Niwot Ridge region in the Rocky Mountains. The international GLORIA programme (Global Observation Research Initiative in Alpine environments) is a successful worldwide initiative that monitors summit floras and is best exemplified by the work carried out to date in Europe (Pauli et al. 2007; Gottfried et al. 2012; Lamprecht et al. 2018).

Data collection of all LTER-related activities rests on the permanent plot concept (Bakker et al. 1996; Blonder et al. 2018). A permanent plot can be a defined piece of land, a lake, part of a river system, or a specific ocean area. Once such permanent plots have been established, long-term observations or experiments help understand long-term ecological responses. A famous example is the ongoing Rothamsted Park Grass experiment, which started in 1856 in the UK. Its immense archive of stored samples became a treasure for modern analytical procedures (Silvertown et al. 2006). Snow manipulation experiments have a long tradition in alpine settings (Williams et al. 1998; Walker et al. 1999; Mark et al. 2015). Decades of observation (up to 52 years) of both experimental (Wipf & Rixen 2010) and natural observations (Frepaz et al. 2012) are available for snowmelt gradients, for simulating effects of climatic warming (Hansen et al. 2006), and for monitoring grazing effects on alpine plant communities (Virtanen et al. 1997; Mayer & Erschbamer 2017).

Some observations can become *long-term* post-hoc, by using natural archives such as dendrochronology or sediment cores of lakes, which may permit reconstructing life conditions and biota over millennia (e.g. Lotter et al. 2006 for alpine chronologies). Another type of post-hoc *monitoring* is revisiting locations for which very old but credible observation data are available, although the critical issue here is identifying of the original location. Here, we present examples from mountains. By identifying the original plots, a grassland experiment in the Swiss Alps could be re-visited 60 years after its foundation, and the fingerprints of past fertilizer treatments could be identified half a century later (Hegg et al. 1992). Thanks to their obvious geographical identity, very high and precipitous mountain peaks offer a unique opportunity for re-assessing inventories of plant species a hundred years later, with clear evidence for a rise in the number of species over the 20th century (Pauli et al. 2001; Stöckli et al. 2011; Wipf et al. 2013). Inevitably, summit research is confined to exposed habitats, often dominated by raw substrates and pioneer species that spread well, and yield rapid responses to climatic warming (early *warning*). In late successional vegetation on mature soils, such responses will be slower and not so easy to identify, given the dominance of long-lived clonal plant species (Vittoz et al. 2009). Clonal plants do not depend on regular sexual reproduction, and their genets may become thousands of years old (Steinger et al. 1996; de Witte & Stöcklin 2010; de Witte et al. 2012). However, their vigour and spreading, but also their mortality, depend on micro-environmental conditions.

So, why monitor? If we were to ask meteorologists, they would be perplexed by that question, because it seems obvious that society needs information about ongoing weather patterns, and only long time series of data will allow climatic trends and the magnitudes of extreme events to be revealed in a historical context. However, the justification seems less obvious when it comes to monitoring biotic communities. Some reasons to carry out biological long-term monitoring are incontrovertible (e.g. Franklin et al. 1990; Silvertown et al. 2010; Fischer et al. 2010): (1) Changes in organismic assemblages cannot be traced by our senses, because the changes are often too subtle or too slow (exceptions are the disappearance or arrival of large animals or obvious neobiota). Hence, monitoring the state of such assemblages will allow the visualization of changes for both science and society. (2) If monitoring includes potential drivers of change, we may be able to explain the changes. (3) Such changes can have conservation implications (e.g. the local disappearance of rare species). (4) If associated with specific drivers of global change, such changes allow the identification of nature's responses, and thus provide information on the long-term consequences of the environmental changes (e.g. the response of Chironomids to palaeotemperature, Ilyashuk et al. 2011). (5) Stochastic phenomena, such as extreme drought (Craine et al. 2012),

freezing or extreme snow-cover scenarios, all of which potentially exert lasting effects, are not adequately captured by long-term means or single site visits. (6) When documented in a protected area, evidencing such changes helps the respective protecting agency to estimate conservation implications.

Why monitor mountain ecosystems?

In addition to the general motives listed above, others relate to mountains more specifically. At low elevation, almost all land has undergone some anthropogenic transformation, most dramatically in the temperate and subtropical zones, making it hard to distinguish between consequences of ever-changing land use and changing atmospheric conditions. This applies even more to aquatic systems, which are typically very dynamic. Remote mountainous regions are exceptional, often hosting the last remaining wilderness areas in a wider subcontinental or even continental range. Representing c. 12% of the terrestrial surface outside Antarctica (Körner et al. 2011), mountains also host a disproportionate fraction of global biodiversity, because they stretch across contrasting climates over short geographical distances. At low latitude, the elevational stratification of mountain biota can include humid tropical forests and glacial forelands, all closely tied to the elevation-specific temperature regime. Roughly a third of all terrestrial protected areas are associated with mountains (Körner & Ohsawa 2005).

Within sufficiently high mountains, the alpine belt is defined as the land above the climatic treeline; it covers c. 2.6% of the global land surface outside Antarctica. Its plant species richness was estimated to be as high as 4% of the global total (Körner 1995) – almost double what is expected by area only, in particular when one takes into account that much of the area consists of bare rock and ice. In mountainous countries such as Austria and Switzerland, the alpine land area may reach 20% of the total land area, with even higher species richness. The high biodiversity in what is commonly considered a harsh environment reflects the diversity of microhabitats across short distances (Körner 2004, 2021). Above the climatic treeline, life conditions are defined by topography and plant stature, rather than elevation (Körner & Hiltbrunner 2021). The mean temperature of the growing season across such alpine (or arctic) mosaics of thermal habitats was found to differ by more than 8 K over a few tens of metres (Scherrer & Körner 2009). In addition to exposure and topographic shelter, plant stature is key, because a dense, low plant canopy traps solar heat, with plant and topsoil temperatures often approaching those found 1,000 to 2,000 m lower. In other words, above the treeline, the actual life conditions for terrestrial biota can be substantially warmer than assumed from measured air temperature; they cannot therefore be deduced from weather service data, but must be measured *in situ*. These strongly varying life conditions at very small spatial scales result in alpine biota

in general being rather robust against climatic change (Körner & Hiltbrunner 2021). However, if one captures the micro-scale transitions from one microhabitat to the next, these mosaics of alpine life also provide extremely sensitive indicators of change over short distances (Smith et al. 2012; Körner 2021).

Alpine aquatic systems may be substantially cooler than local air temperature during snow- or ice-melting and early in the growing season, but may warm up more and store heat during clear weather in summer, depending on wind and lake characteristics such as water depth, lake size and fetch, and discharge from and into streams. But, compared to terrestrial systems, aquatic systems are thermally far more buffered, and life conditions are often dominated by the nutrients provided by the surrounding terrestrial ecosystems and the lithography. As such, small alpine lakes and small rivers serve as signal integrators of the terrestrial conditions in the catchments from which they drain (Füreder 2010; Williams et al. 2011). Because of their integrating role, such aquatic systems, streams in particular, also have the potential for up-stream genetic diversity to be assessed using novel molecular tools (e.g. Deiner et al. 2016).

Because of the often cm-scale differences of life conditions, the terrestrial alpine world provides unrivalled opportunities to study effects of temperature on life in what might be seen as *experiments by nature*. The current distribution patterns of terrestrial alpine species in a varied topography reflect long-term selective pressures, with ranges and range limits of species across microclimatic gradients reflecting these conditions. Over very short distances, soils bear a location-specific *memory* of millennia of topography-biota interactions. In contrast, biota of aquatic systems are likely to track year-to-year variations in water quality and weather. The planktonic basis of the food web can change within a few days, or benthic biofilms in stream habitats may change in weeks, whereas the annual biomass production is buffered to some degree in terrestrial systems by the large below-ground biomass and reserves. In both systems, multi-year data are required in order to achieve an acceptable signal-to-noise ratio and elaborate a reference database that is not biased by stochasticity (see the stochasticity section). The initial phase of such long-term monitoring must be continued until robust means are established. A time span that will cover the range of year-to-year signal variation will be somewhere between 5 and 10 years, as a minimum. Thereafter, a longer interval between monitoring periods may be appropriate, with any later re-assessment again requiring multiple years of continuous monitoring. The change in species' range limits, of clonal plant species in particular, may yield trustworthy evidence only over census intervals of several years. Yet, even 21 years of monitoring of plant communities in contrasting habitat types on Niwot Ridge, in the Rocky Mountains, revealed considerable non-directional scatter, causing the authors to urge for fine-scale

observations along defined environmental gradients (as explored here for that reason) in order to cope with the intrinsic heterogeneity of alpine vegetation (Spasojevic et al. 2013).

What should be monitored?

In an ecosystem approach, a number of abiotic and biotic conditions and parameters need to be monitored for several reasons. First, it is not *a priori* clear how responsive different organisms are; second, a mechanistic explanation needs to build on cause-and-effect relationships; and third, no monitoring should be conducted that does not meet basic scientific standards, which means collecting information beyond its mere documentary value, in order to advance the theory of ecosystem functioning. Various environmental drivers may exert interactive effects. For instance, snow cover, lake ice and the dynamics of both may interact with atmospheric nitrogen deposition or the nutrient cycle in general (Baron & Cambell 1997; Williams et al. 1998). Species identity may matter for entire-community responses. Hence, knowing traits of organisms and the functions of these traits can guide towards understanding and explaining whole-system responses (see e.g. Matteodo et al. 2013).

The environmental parameters and organismic groups to be included in long-term monitoring are likely to exert different responses at different time scales. Soil physics, soil chemistry and certain aquatic parameters (pH, bedrock chemistry) can be characterized by a single initial assessment and are unlikely to change over decades. Plant species' ranges or abundance may vary significantly over 5 to 10 years only (Spasojevic et al. 2013; Mayer & Erschbamer 2017); aquatic and terrestrial productivity and associated biogeochemical cycles (nutrients, carbon) will differ from year to year. The species composition of soil arthropods and soil microbiota may be rather stable, but the relative abundance of certain taxa may vary over very short periods. Influences other than weather data need to be recorded, such as wild or domestic ungulate presence. In addition, the actual micro-environmental conditions need to be recorded at sub-diurnal (e.g. hourly) resolution, because it is the frequency distribution of these conditions rather than their long-term mean that matters for life (e.g. temperature in the most active soil layer or water in aquatic systems, presence/absence of snow cover or ice on water etc.).

Because the spatial variation can be so large, replication at regional and larger scales is required to arrive at a representative picture, even when similar types of ecosystems are selected. At each site, replicated permanent plots are required, best aligned with a series of typical and well-documented local life conditions (e.g. topographic snowmelt gradient). Combining subject-specific temporal and spatial replication can cause such monitoring to become logistically overwhelming. Deciding on a certain sampling/observation design and census frequency, one has to take into account the

long-term nature of the proposed monitoring. What might seem feasible to accomplish in one or two years could be beyond the realms of what can be done over multiple years in a consistent manner.

Stochasticity and disturbance

There are periods or entire years with exceptional conditions. Embedded in a continuous series of observations, such events can help to test theory, but they are unsuitable as a reference point for long-term monitoring. This is a problem with re-visitations of sites dominated by short-lived pioneer plant species, where the stochasticity of weather conditions can affect both the historical reference records and the new data, making it hard to identify trends. Perennial flowering plants from later-succession habitats that are likely to persist over a couple of years under varying weather conditions would be more robust in this respect. Further, it is hard to account for shifts in species-specific range limits, because species that have arrived at a new location may still be operating far from their outer limits (niche boundary), and may have moved in over large distances (Körner 2011) during once-in-a-century climatic events. In contrast to re-visitations, long-term monitoring reveals fine-grain temporal responses, permitting a separation of long-term trends from noise (year-to-year variation). Continuous monitoring will thus cover and evidence short-term variability that must not be confused with long-term trends (Walker et al. 1994; Körner 2018a; Dai et al. 2019).

One of the biggest problems of ecosystem monitoring is natural and anthropogenic disturbances. Major natural disturbances are erosion, rock fall, flooding, avalanches, fire, dust storms or rodent invasions, and major anthropogenic disturbances are related to pastoralism, tourism, hydroelectric installations, road, hiking trail, powerline, cable car construction, or the introduction of fish into remote lakes (Körner & Ohsawa 2005; Körner 2014). The natural hazards can be minimized by careful site selection. Further, publicly protected areas provide a certain safeguard against anthropogenic disturbance that private land ownership cannot guarantee. National parks offer the highest level of protection. In addition, they are designed to be institutionally stable over the long term. They therefore offer the greatest likelihood that observations will be repeatable in a century's time, making them the preferred hosts for long-term monitoring. Research institutions, but also other public institutions, are inherently unstable, depending on political *weather conditions*, changes in personnel and shifts in interest. However, national parks need external research partners who agree on and document a high degree of standardization in their approaches, so that a change in research staff does not put the long-term task of monitoring at risk of inconsistency.

The current monitoring programme

The programme was initiated and is coordinated by the Austrian Hohe Tauern National Park (NPHT; see also Körner 2014; Körner et al. 2020). It uses sites in three regions of the NPHT (Innerschloß, IN; Seebachtal, SE; Untersulzbachtal, UN), and terrestrial partner sites in Northern Italy (South Tyrol; Oberettes, OB) and Switzerland (Furka pass, FU). The programme is carried out by researchers associated with the universities in Graz, Innsbruck, Salzburg and Vienna, and a private lab in Salzburg. The partners for South Tyrol are from Eurac research, Bozen; those for Switzerland are from the University of Basel (Table 1, Figure 1).

This coordinated long-term monitoring programme aims at producing a baseline for future reassessments of the state of typical alpine ecosystems in the central Alps at 260 to 400 m above the regional mean elevation of the current climatic treeline (Table 1). The programme started in 2016, with the first data becoming available in 2017. Our aim is to provide a summary of the abiotic site conditions as a reference for future thematic publications. Further, we will synthesize the evidence that is currently available in the biotic inventory (and the methods employed) for these sites, including plant species diversity and productivity, soil meso-fauna, soil microbiome, lake zooplankton diversity, and benthic fauna of streams in micro-catchments. Documentation of the initial monitoring phase has been produced by the NPHT and is available online (Körner et al. 2020; in German).

In what follows, we will explain the design of the programme, which aims to optimize spatial and temporal replication, cover key organismic groups and habitat types, and discuss feasibility (methods, logistics, personnel).

Methods: study design, sites and techniques employed

Five test sites were selected on siliceous bedrock only, in the regions listed in Table 1. The sites cover different weather regimes ranging from more frontal NW weather (Salzburg), more southern or mixed weather regimes (Carinthia, Swiss site), and more continental inner Alps weather (East Tyrol, South Tyrol). In East and South Tyrol, the weather combines with the climatic *mass elevation effect*. The programme as a whole thus covers a great deal of variation along the main divide of the Alps, over a geographical distance of 360 km, at roughly 47°N, in a cool temperate climate that is under the pronounced influence of the Gulf Stream (for its latitude, Europe has a comparatively warm climate). The terrestrial site in Salzburg (UN) belongs to a wilderness region that was never under human land use; the sites in Carinthia (SE), East Tyrol (IN) and the Swiss Furka pass (FU) show marginal land use (episodic sheep, minor tourism); the site in South Tyrol (OB) is not only by far the highest, but

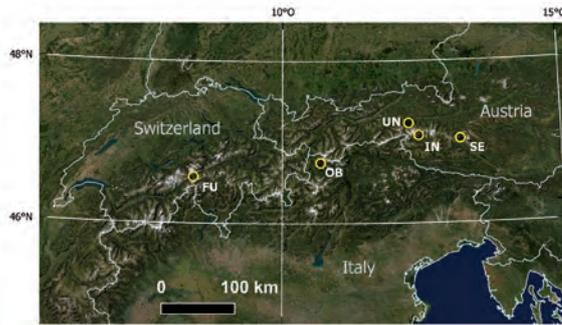


Figure 1 – Location of the long-term monitoring sites in the Alps. Yellow circles: Terrestrial site locations: IN = Innerschlöss, SE = Seebachtal, UN = Untersulzbachtal, FU = Furka pass, OB = Oberettes). Basemap source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

also the only site under heavy, traditional grazing pressure from sheep.

The terrestrial data originate from five regions (three in NPHT, plus OB and FU), specifically from monitoring sites in the alpine grassland belt dominated by *Carex curvula* and *Nardus stricta*. In each of the five terrestrial test sites, a transect approach is employed (Körner 2018b) (see below for explanation). The aquatic data are based on six small alpine lakes for each of the three NPHT regions within 8 km of IN, UN and SE (total of 18 lakes), and streams discharging from each of these three terrestrial sites. Since no lakes exist at UN itself, the 6 lakes for that region were chosen from the adjacent Obersulzbachtal.

Terrestrial sites

As mentioned earlier, environmental gradients that are tied to topographic features represent a sort of long-term experiment by nature itself, because topography does not change over time scales that are relevant for monitoring purposes. The biota associated with such gradients can be assumed to reflect long-term selective pressure – that is, nature's

response to the life conditions along the gradients. Among the ecologically most powerful gradients are snowmelt gradients, which impose similar yearly spatial melting patterns on biota (related to topography) but with variable timing (Friedel 1961; Körner 2018b, 2021). Along a snowpack gradient, microhabitats vary from those least affected by snow at exposed edges or ridges (longest growing season) to the most affected microhabitats (snowbeds) which are released from snow only late in the season (shortest growing season). For the terrestrial part of the current monitoring programme, we selected 3–6 gradients per site, the gradients ranging from the locally highest to the locally lowest in terms of plant biomass production over a distance of 7–10 m. We address these season-length gradients as transects and in what follows will frequently refer to H (top), M (middle) and L (bottom) sections along the transects (Figure 2).

Each of the transects is composed of three adjacent, 1-m wide strips that go from the bottom to the top of the snowmelt gradient. The central strip is reserved for non-destructive assessments; the other two are used for sampling biological material in a way that prevents resampling the same location for the next 6 to 8 years (Figure 3). Strips are divided into a grid of 1 m² quadrats (*plots*), each subdivided into 4 smaller quadrats of 50 cm x 50 cm (*subplots*), the identity of which is recorded during each sampling. Transects are georeferenced, marked with pegs and permanent metal geo-reference points at either end. Since alpine terrain is never homogeneous, a list of criteria was developed for subplots to be included or excluded from sampling. For instance, bare ground, stones or rock, isolated massive tussocks, and areas that are bare because of the activity of mice are excluded (see Figure 3). In total, the terrestrial teams are surveying 22 transects, each with 18–27 permanent quadrats (depending on transect length), yielding a total of c. 500 permanent quadrats (1 m grid cells) and c. 2000 subplots (0.5 m x 0.5 m), two thirds of which are available for invasive sampling. While sampling is strictly confined to individual permanent plots, the plots were assembled post-hoc into the three

Table 1 – Terrestrial site locations and their macro-climate. Treeline elevation is presented as a bioclimatological reference*. On-site seasonal mean air temperatures are calculated for two slightly differing summer periods for a total of three years (2017–2019) and show that the atmospheric conditions are very similar across the sites. Aquatic sites are located within a few km (alpine lakes) or <0.5 km (riverine sites) of the terrestrial sites. NPHT = Hobe Tauern National Park.

Location name (code)	Region (country)	Geographical coordinates	Site elev. (m)	Mean treeline elev. (m)	Maximal treeline elev. (m)	Seasonal mean T (°C) 16/6–15/9	Seasonal mean T (°C) 1/7–30/9
Innerschlöss (IN)	East-Tyrol (A), NPHT	47°06'40.1"N, 12°25'35.5"E	2,350	2,020	2,070	8.65	8.01
Seebachtal (SE)	Carinthia (A), NPHT	47°02'21.9"N, 13°10'58.1"E	2,303	2,040	2,160	8.15	7.84
Untersulzbachtal (UN)	Salzburg (A), NPHT	47°09'58.2"N, 12°19'51.1"E	2,380	1,980	2,050	8.19	7.72
Furka pass (FU)	Switzerland (CH)	46°34'40"N, 08°25'12"E	2,467	2,080	2,150	8.26	7.52
Oberettes (OB)	South-Tyrol (I)	46°45'59.9"N, 10°42'38.2"E	2,700	2,320	2,360	8.38	7.59

* These google-earth-based elevations are provided for an estimated mean elevation (repeatedly recorded treeline position within 5 km of the site), while maxima refer to the position of the uppermost groups of trees > 2 m in height in the same region in the early 21st century.

sections: bottom (least productive, L), middle (M), and top (most productive, H). Although high in number, and although grid positions resemble a random initial selection along the climatic gradient, repeated sampling of these permanent plots and subplots cannot be randomized. The reason is that each year certain additional *blind areas* are defined by the previous year's sampling. Hence sampling-locations require a plan that will ensure that the entire subplot provides enough space for new sampling to take place until traces of past sampling have faded (this takes a few years in alpine grasslands such as those in our study areas). Each subplot is potentially suitable for 4 plant biomass harvests on a 20 cm x 20 cm sampling area, yielding theoretically c. 5,000 locations for an annual plant biomass harvest of 132 samples (6 samples for each of the 22 transects). The variable alpine topography did not allow wider or longer transects without including terrain that does not match our definition of a consistent L-M-H snowmelt gradient (Körner 2018b).

Aquatic sites

The lakes team chose 18 small natural lakes. The maximum depths of the lakes vary from 1 to 42 m (with most in the 5–10 m range); the areas of the lakes range between 0.03 and 15 ha (with most measuring around 1 ha). Measurements and samples were taken from the entire depth profile in a stratified manner. In the larger lakes, a small inflatable boat was used. Except for the few periglacial lakes, each lake is surrounded along at least half of its shoreline by alpine vegetation. It was expected that these lakes would continue to exist for many years. They were chosen for being as close to the terrestrial sites as possible and at different alpine elevations within each valley. Logistical constraints also played a role in site selection (e.g. location within hiking distance from a road or hut). In three of the 18 lakes, we noticed fish (Seebachsee, Löbbensee and its adjacent lake); all other lakes are currently fish-free, to the best of our knowledge.

For each terrestrial site, the stream team selected a small stream that drained from adjacent land (< 200 m away). The stream at SE dried up almost completely under summer heat-wave conditions (2018, 2019). All abiotic conditions were assessed upstream and downstream of a reference location within 100 m of the source at IN, UN and SE. Streams are < 2 m wide, have a sandy or rocky bed, and are surrounded by closed-cover alpine vegetation; none of the streams originates directly from a retreating glacier or permanent snowfield.

Sampling concept: what, how often, for how long?

For the *terrestrial* systems, it was decided to monitor snow dynamics and the temperature of the topsoil, and to cover different organismic groups that typically occur across snowmelt gradients: assemblages of flowering plants and their biomass production, soil

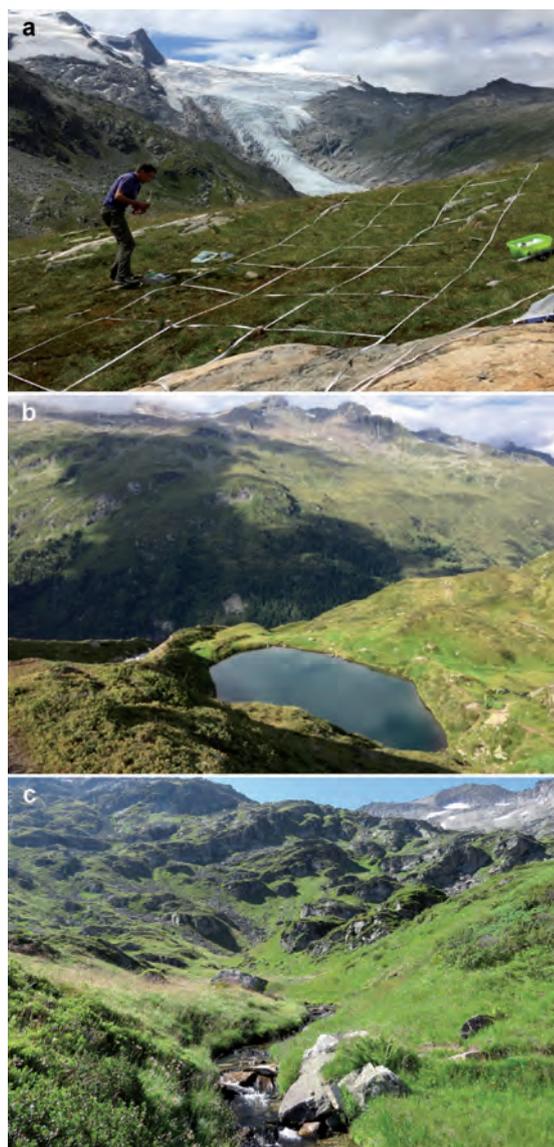


Figure 2 – Examples of study sites. a) Terrestrial snowmelt gradients with a grid of permanent plots in Innerschlöss (IN) with the 3,700 m Venediger massif in the background); b) example of an alpine lake (Salzbodensee, IN); c) micro-catchment with a stream explored in East Tyrol (IN). © C. Körner

mesofauna, and soil microbiome (bacteria and fungi). A detailed physical and chemical characterization of soils across the transects is an obvious starting point.

In the *aquatic systems* monitored, the lake team assessed the water's chemical characteristics and temperature (including ice dynamics), phytoplankton biomass (via chlorophyll-a estimated from *in situ* algal fluorescence), as well as zooplankton abundance and species richness. The stream team monitored water chemistry, pH, water temperature, flow rate, biofilms and benthic invertebrate communities.

Different abiotic and biotic parameters require different sampling and observation intervals. Among the abiotic conditions, most aspects of soil physics (density, porosity, grain-size spectra, water-holding capacity) require only a single initial assessment, because such



Figure 3 – Fieldwork at the terrestrial and aquatic sites. a) 20 cm × 20 cm plot after peak season biomass harvest; b) measurement of reference air temperature (here at Untersulzbachtal); c) soil coring for physical soil data, microbiome and soil-mesofauna; d) automatic monitoring of large herbivores; e) digital imaging device; f) sampling at an alpine stream (Innerschlöss); g) filtering scraped and washed biofilm; h) plankton sampling at defined depth at Seebachtal. © a–d) C. Körner, e) R. Kaiser, f–g) G.H. Niedrist, h) E. Hainzger

characteristics are not going to change. This also holds for basic chemical characteristics of soil such as buffer capacity, pH, concentration of soil organic matter, and total and available cations and anions. Cations and anions may require re-assessments after a few decades. In contrast, temperature and snow or ice cover require records at a resolution of 1–3 h for as long as other

observations are continued. Such data need to account for microclimatology (upper soil-layer temperature across the snowmelt gradient *versus* air temperature on terrestrial sites, water depth in lakes, in situ records in streams).

Some of the biological assessments are comparatively simple (harvesting above-ground plant biomass, collecting lake or stream water), while others are extremely laborious (e.g. identifying and counting collembola and mites in soil samples). The data reported in this paper also reflect such pragmatic criteria. The presence of organismic groups and species (or operational taxonomic units [OTUs], in the case of microbes) is unlikely to change over a couple of years (plants, for instance, are sessile). However, individual abundance or biomass of entire communities or certain taxa (or OTUs) may change rapidly (from year to year, for instance, depending on the weather). This means that inventory data (presence / absence) need to be collected repeatedly over longer periods. Annual data are required for the abundance of key organismic groups, plant biomass, lake plankton and stream biota.

For how long? As in meteorology, data have to be collected continuously over a long enough period, so that short-term variability (or *noise*) is recorded with sufficient detail while permitting longer-term trends to be distilled (this is when *weather* becomes *climate* in meteorology). Since it is not clear *a-priori* how large the intrinsic variability is, one of the results of the initial period of long-term monitoring is to identify variance with at least 95% confidence. For some of the biological indicators, we can provide initial guidance for year-to-year variance, and we recommend that variance assessments are repeated so that the duration of the initial phase can be planned. Earlier attempts to assess time series of grassland productivity in the Rocky Mountains and on the Tibetan plateau (Walker et al. 1994; Dai et al. 2019) suggest a minimum duration of 7–10 years for the initial recording phase.

For the synthesis we present here, the specific methods applied by the various teams will be presented as succinctly as possible, together with the first findings. A detailed description of the methods used will be provided in the individual thematic publications to come, and can be found in the online manual of methods (Ecosystem Monitoring Team 2021).

Results

Abiotic conditions

Macro-climate

Using waterproof, single-channel data loggers in standard radiation screens, we obtained year-round air temperature data, illustrating that we were successful in selecting locations that were thermally fairly similar (Table 1). Data gathered over three years revealed that, for the period 15 June to 15 September, which covers most of the growing season at the top

of each transect (position H), the air temperature differed by only 0.4 K across the five sites (0.5 K for July to September). Hence the differences in site elevation account for regional climate in such a way that the mean air temperatures during the growing season are almost identical. The warmest month is commonly July. At FU, for example, the mean air temperature in July varied from 6.6°C (2014) to 11.0°C (2015), and the July mean over 8 years (2013–2020) was 8.9°C. From precipitation data recorded at regional weather stations, all five sites can be characterized as humid, receiving > 1,000 mm precipitation annually: the on-site annual mean for FU is 1,140 mm for 2013–2020, with a range of 1,020–1,280 (of which 240–500 mm fell from June–August); for OB we estimated precipitation from data collected at the nearby village of Match at 2,000 m asl using a 30 mm / 100 m rise as elevation lapse rate, arriving at a mean of 1,080 mm at 2,750 m asl (the driest of all sites).

All sites may experience moderate drought during midsummer, which may cause small streams to dry up, as was shown for SE in 2018 (see abiotic conditions in streams). Although snow may fall on any day during the year, snowmelt outside snowbeds commonly occurs in mid-June (see microclimate), with substantial year-to-year variations and local variations between early May and mid-July. The season ends with vegetation browning in mid- to late September, resulting in a growing season of 8–12 weeks (shorter in snowbeds).

Terrestrial microclimate

For 25 to 75 days from snowmelt (variable date) until 31 August, and for day-time hours (09–18h) only, the mean temperature 3 cm below the soil surface was 3–5 K warmer than the air temperature at 2 m (Figure 4). A depth of 3 cm was chosen because this is

roughly where apical shoots, basal leaf meristems of the dominant graminoids, rhizomes, and peak microbial activity are found.

Remarkably, there are no significant differences in temperature between the bottom (L) and top (H) of the transects, indicating that the differentiation in life conditions reflected so obviously in vegetation composition and seasonal productivity (see biological results below) largely rests on the length of the season. Season length ranges from 49 to 122 days across sites, years and positions along transects. Averaged across years and sites, the length of the growing season is roughly 3 months at H, and 20 days shorter, on average, at L (Table 2).

These mean temperature differences between topsoil and air correspond to a difference in air temperature over a change in elevation of c. 700 m (applying a mean atmospheric temperature lapse rate of 0.55 K per 100 m). Importantly, these means include all types of weather conditions. The main driver of topsoil (and bottom canopy) warming is solar radiation (Figure 4) modulated by wind speed. On bright days, the topsoil-air difference exceeds 10 K, reflecting a substantial decoupling of microclimate and macroclimate. If we compare temperatures for H and L positions for such bright days only, we still do not see a thermal differentiation during daylight hours. However, soils cool faster (become more similar to air temperature) at L during the night, presumably as a result of the lower plant cover at L, and thus greater radiative and convective heat loss.

Water temperature was recorded every 6 hours at a depth of c. 40 cm using two data loggers installed in each lake. The mean temperature of the ice-free period across all lakes was 8.8°C, which was surprisingly similar to the seasonal mean air temperature (Ta-

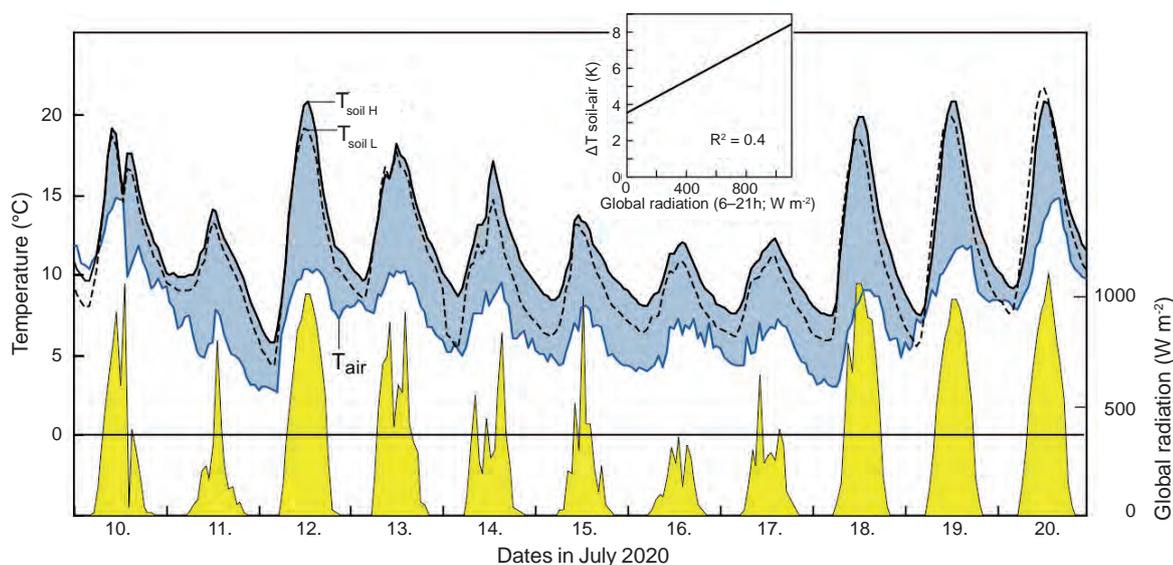


Figure 4 – A comparison of topsoil and air temperature at positions bottom (L) and top (H) across the five snowmelt gradients at Furka pass (FU) during a typical summer period, including both clear sky (12, 18–20 July) and overcast conditions (16, 17 July). Note the effect of solar radiation (regressed for H during daytime; inset diagram). L and H differed little, but a little more at night under cloudy skies, when soils lose less of the stored heat by radiative cooling at H, presumably because of higher plant cover.

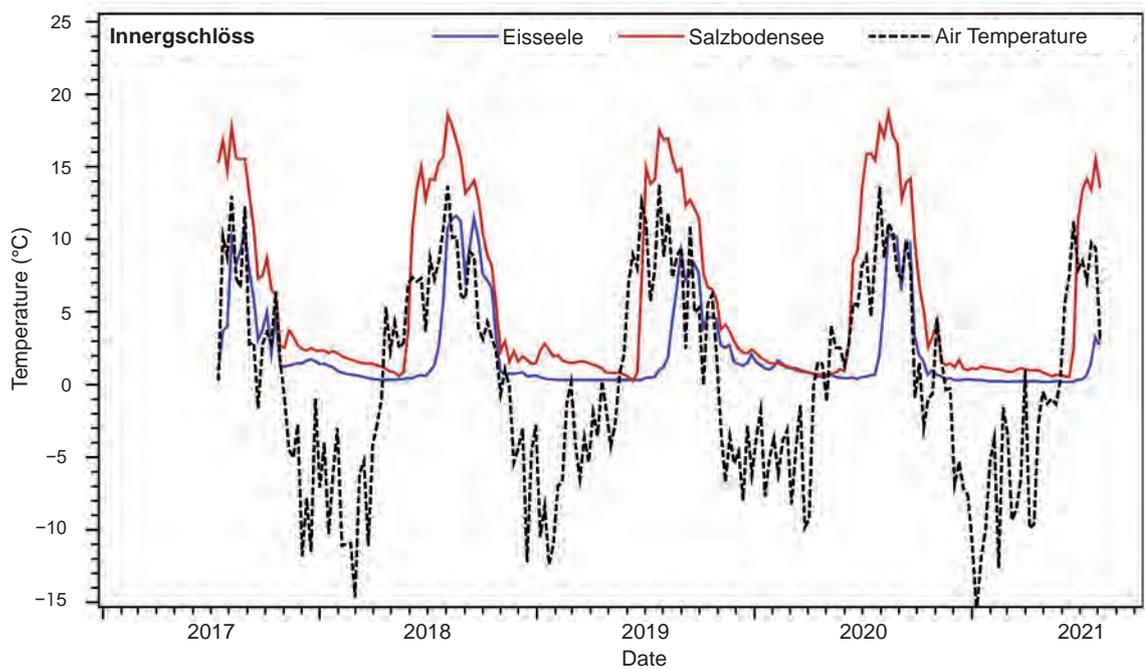


Figure 5 – Air (2 m) and water temperatures (at 40 cm depth) in two lakes in Innergsschlöss (IN): Eisseele (2,550 m) and Salzbodensee (2,138 m; horizontal distance 2.2 km). 6-hourly data for the lakes, and 6 h means for air temperature at 2,350 m (IN, Table 1), with lines smoothed by loess fits. Note the sharp rise of lake temperature at melt-out.

ble 1). However, the ice-free period and temperatures varied substantially among and within lakes. For instance, we recorded seasonal means of 5.4°C in Sulzsee (Obersulzbachtal valley, next to UN) *vs.* 12.5°C in Salzbodensee (IN), which can be partly explained by differences in lake size, elevation and exposure. Lake Eisseele has a much shorter ice-free period (the ice-out occurs almost two months later than on Sulzsee and Salzbodensee), and also has a much cooler mean temperature during the ice-free period (8°C) than Salzbodensee from the same region (Figure 5). As would be expected, water temperature differences in winter are small, irrespective of elevation; in this respect,

Table 2 – Effective season length (days) across sites (a year effect) and across years (b site effect) for the L (bottom) *vs.* H (top) positions at Seebachtal (SE), Untersulzbachtal (UN), Innergsschlöss (IN), Oberettes (OB) and Furka pass (FU). Means for 5 years (4 at UN and OB). The season is counted from day of snow melt to 15 September, when communities are commonly senesced.

a)	2017	2018	2019	2020	2021
H	106	109	81	102	84
L	92	89	67	83	68
H-L	14	20	14	19	16

b)	SE	UN	IN	OB	FU
H	104	106	90	104	82
L	101	92	62	84	65
H-L	3*	14	28	20	17

* SE turned out to show minor H-L gradients, with snow drift caused by wind dominating over topographical effects.

lakes are similar to terrestrial ecosystems under snow. The lakes investigated were all well oxygenated (68–81% saturation, averaged over all measured depths) and nutrient-poor, with nitrate levels of 0.2–1.1 mg NO₃-N L⁻¹ (P data are not yet available). The highest nutrient levels were found in the hypolimnion of stratified lakes, particularly those with a deep chlorophyll maximum (DCM) in this zone. The pH range in the lakes was narrow (pH 6.7–8.2, again averaged over depth).

Abiotic conditions in streams

Stream temperatures ranged between 0 and 1.9°C in winter, warming to mean summer temperatures (July, August and September) of between 4.6°C (UN) and 7.8°C (IN) – that is, they were mostly cooler than the concurrent mean air temperatures (Table 1, Figure 6). Higher temperatures were recorded in SE, which are related to very low discharge and dry periods (see gaps in Figure 6). Based on longer time series (2010–2017) of water temperatures from multiple rivers (18) in the NPHT (Niedrist & Füreder 2021), the summers of 2017 and 2018 can be rated as exceptionally warm.

The streams differ in the concentration of transported plant nutrients. The highest mean nitrogen levels (NH₄-N and NO₃-N) were recorded in SE, with 155 ± 50 µg L⁻¹ (2019–2021, n=12), followed by UN (89 ± 19 µg L⁻¹, n=8), and IN with 36 ± 7 µg L⁻¹ (n=16). Phosphorus concentration was also highest in SE (2.2 ± 1.0 µg L⁻¹) and lower in the other streams (1.8 ± 1.0 µg L⁻¹ in IN and 1.6 ± 0.8 µg L⁻¹ in UN). Compared to the other sites, IN exported the highest concentrations of dissolved organic carbon (776

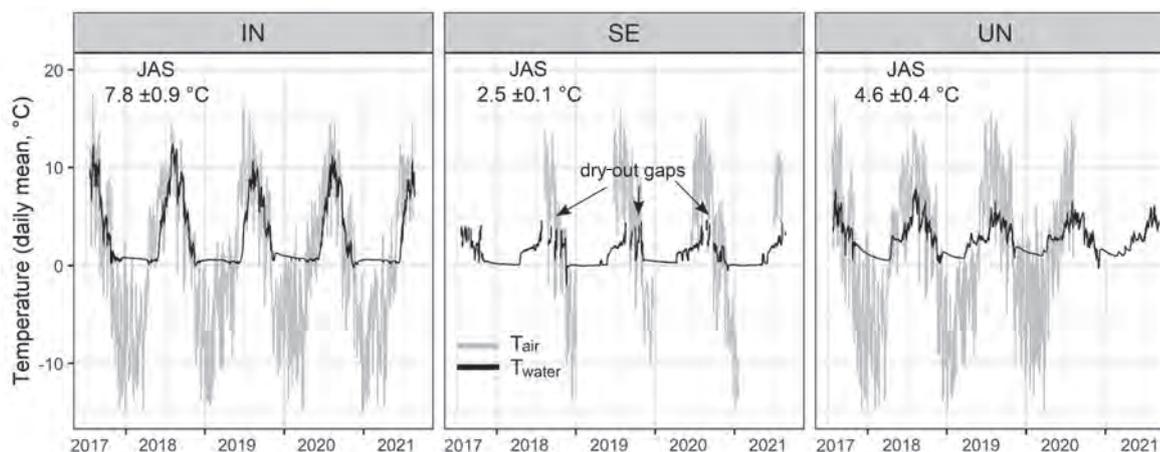


Figure 6 – Daily means of water temperature (based on hourly measurements) in the three study streams (IN = Innergschlöss, SE = Seebachtal, UN = Untersulzbachtal) from July 2017 to July 2021. Mean water temperatures for summer (JAS: July, August, September) \pm SD are given for each plot (the data from SE has multiple gaps during summer, when the stream became almost dry).

$\pm 230 \mu\text{g L}^{-1}$), caused by the well-developed peat bog areas in the catchment. As expected for non-glacial streams, concentration of suspended solids was moderate (highest in UN with 3.9 ± 2.3 , and lowest in IN with $1.2 \pm 1.1 \text{ mg d.m. L}^{-1}$) and linked to slope and discharge of the streams.

Soils

Our attempts to avoid as far as possible any confounding variations in soil properties among the sites and transects were successful: for KCl extracts, we arrived at very similar soil pH (3.8) across sites, with very little variation (3.4 the single lowest value in a peat layer at SE). There is one exception to this pattern: of the five transects at FU, one showed a pH of 5 and 6 at positions M and L, due to an unexpected, small pocket of carbonate-rich glacier deposits. The overall low pH reflects both the acidic bedrock and the high soil organic matter (SOM), across transect means, for topsoil 8–13% dry matter (d.m.) (FU, UN and IN); 23–25% (OB and SE). Soils contain on average c. 8% and 4% d.m. soil organic carbon (SOC) at depths of 0–5 and 5–10 cm respectively, with a consistent topsoil (0–5 cm) C/N ratio of around 15 across sites (at 5–10 cm; values are consistently lower, at around 12). With a mean soil density of 1 g cm^{-3} , the soil pore volume is substantial (c. 50% vol.: c. 60% top 5 cm, c. 40% 5–10 cm). With a mean plant wilting point reached at 15% vol. soil water content, a maximum of c. 35% of the soil water content is available to plants in the top 10 cm (35 mm over a 10 cm soil profile). Assuming a typical mean daily evapotranspiration of 3 mm under bright weather conditions, these reserves would last for 12 days only. Hence rooted profiles must be substantially deeper (as they commonly are) to cope with longer dry periods, as during the 2018 heatwave. Given the well-known decline in SOM along snowmelt gradients (from 20 to 10% d.m. from H to L in FU, IN, UN), local summer drought effects are more likely to impact L-biota. The gradients are reversed at

OB, where there is an accumulation of fines at L as a result of up-slope trampling by sheep (erosion). At SE the mineral soil fraction is very low in some plots at L, with peat (43% SOM) overlaying bare rock.

As an indication of the rate at which nitrogen cycles through soils, we obtained $^{15}\text{N}/^{14}\text{N}$ soil signals (expressed as $\delta^{15}\text{N}$). The most abundant N isotope, ^{14}N , is metabolically more active, and thus mineralized more quickly from plant debris, causing the rare, heavier and metabolically discriminated ^{15}N to accumulate in the SOM pool. The more ^{15}N accumulates, the older the recalcitrant N-pool in the soil. We found very similar $\delta^{15}\text{N}$ signals across all sites, and no difference along snowmelt gradients in topsoil SOM ($\delta^{15}\text{N}$ of 3.4, 3.7 and 3.2‰ for H, M and L across all sites; $\delta^{15}\text{N}$ is 2–5, mostly 3, across H, M, L sites, with s.d. between 0.5 and 1‰). The accumulation of ^{15}N almost doubles in 5–10 cm soil depth, and thus N is older ($\delta^{15}\text{N}$ 5.8, 6.4, 5.7‰ for H, M, L across sites; again, the differences are not statistically significant). This indicates that the smaller annual biomass production at L compared to H is in balance with smaller annual recycling, and thus arrives at similar $\delta^{15}\text{N}$, with longer residence times of ^{15}N in deeper layers (Yang et al. 2015). For a summary of the physical conditions in the top 5 cm of soil, see Seeber et al. (2021).

As one moves from H to L, soil nutrients (liquid extraction by BaCl for cations) change little when expressed per unit of sieved-soil dry matter (soluble forms of Ca, Na, Mg, K, Fe, Al). There is a small but not significant trend for lower concentrations at L. The only exception, and with surprising consistency, is the decline of Mn^{++} from H to L in the most-active top 5 cm of the profile (not at a depth of 5–10 cm, where extractable concentrations were less than one tenth of those at 0–5 cm). However, the absolute concentrations of Mn^{++} extracted by the BaCl solution vary substantially among sites, reaching 4–6 mmol kg^{-1} at FU and $< 0.4 \text{ mmol kg}^{-1}$ at IN. We have no explanation for these trends in Mn^{++} , nor is it clear whether

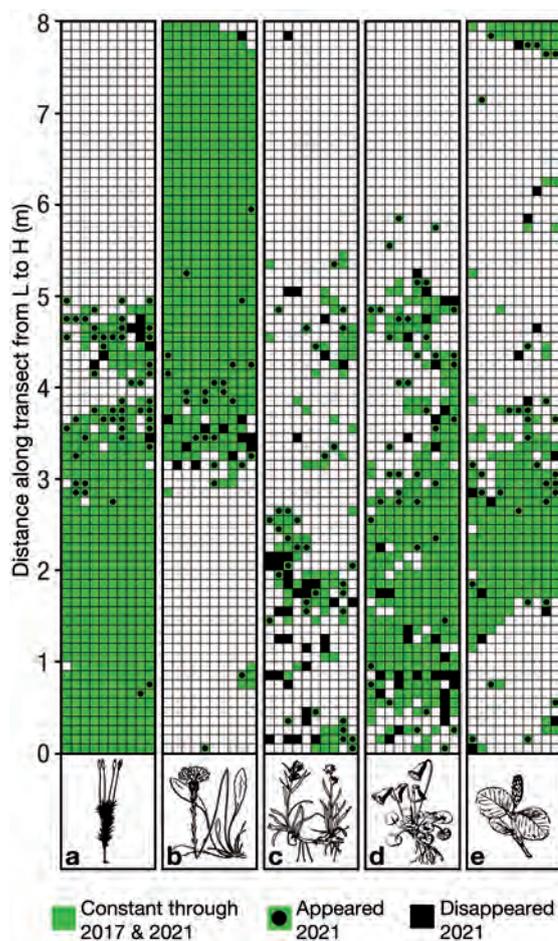


Figure 7 – Examples of species distributions along the bottom (L) to top (H) snowmelt gradients as captured by digital image analysis (H at the top). Note the sharp range limits for a) *Polytrichum sexangulare* and b) *Leontodon belveticus*, and the more diffuse or even bimodal patterns in others (c) *Gnaphalium supinum*, d) *Soldanella pusilla*, e) *Salix herbacea*. Data from transect 4 at site Innergschlöss (IN) for 2017 and 2021 with differences at the 10 cm × 10 cm grid level highlighted by different symbols. Note that turnover tends to be more intense near the range edge.

this is of ecological relevance. High concentrations of Mn^{++} are toxic to some species (even more so Fe^{++} and Al^{+++} , neither of which exhibits such a trend). As a reference for future research, we archived (in glass jars) 100–200 cm³ of air-dried samples from the 2 mm soil fraction from all transects at the Tyrolian Landesmuseum Ferdinandeum, Innsbruck, Austria.

Biological results

Plant species diversity

Vegetation transects were monitored with a close-range image acquisition system that uses standardized illumination (exclusion of daylight). The images provide a resolution of ca. 0.1 mm that not only permits species identification but also facilitates automatic image analysis using machine learning and computer vi-

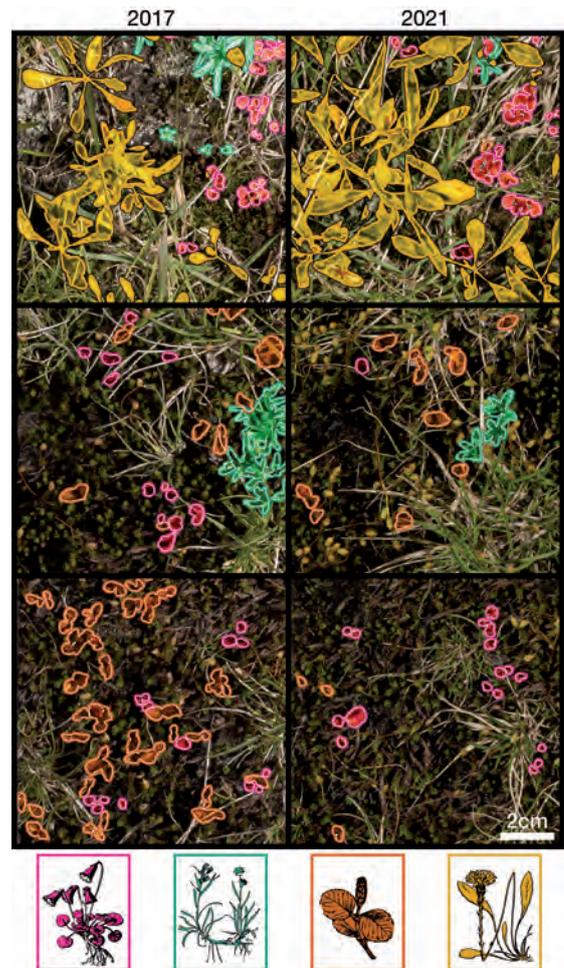


Figure 8 – Examples of 10 cm × 10 cm image pairs from transect 4 at site Innergschlöss (IN) from mid (M) to low (L) position: 4.9–4.8 m, 2.3–2.2 m, 1.2–1.1 m (lowest position = 0 m) for the years 2017 (31 July) and 2021 (11 August, a year with a late season start). Outlined shapes of four selected species as used in the training of machine learning algorithms (for species see Figure 7).

sion algorithms to classify, outline shapes, and count individual plants or plant organs. However, overlapping plant canopies constrain the analysis in dense communities. The strengths of the technique are its high precision, adjustable scale of analysis, reproducibility, and the absence of classical sources of error in fieldwork such as subjectivity, and varying degrees of attention and botanical expertise. In a year-by-year image comparison, individual plants, especially long-lived clonal species and tussock grasses, can literally be *watched growing*. By capturing numbers and sizes of individuals or ramets of clonal plants, population dynamics can be assessed. Since data are digitally archived, it will be possible to re-evaluate them in the future. Conventional photographs and ground-truth species lists are available for all 1 m² plots from OB and FU.

The distribution of indicator species reflects the H to L environmental gradient across the 14 transects

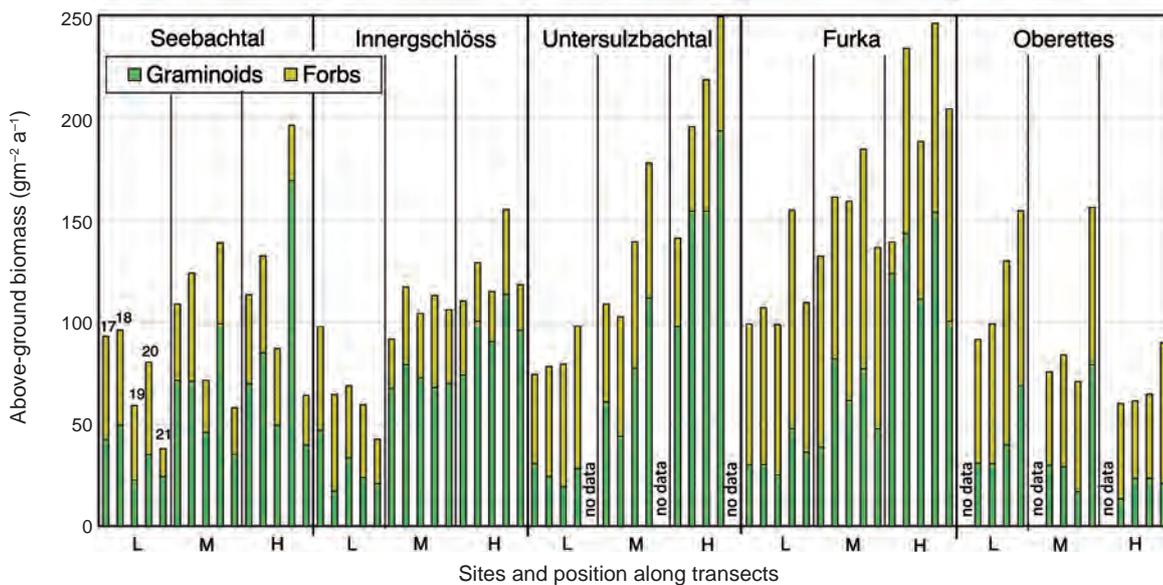


Figure 9 – Seasonal plant biomass production for five years and three positions along snowmelt gradients (L for bottom snowbed, M for middle, H for high, earliest melting; missing data: no site access to Untersulzbachtal in 2021 because road closed by mudslides, and a late start in Oberettes). Means for 3–6 transects per site, separated into graminoids (grasses, sedges and rushes) and forbs. Note that the H-to-L difference comes largely from graminoids, pointing to these as potential indicator species for climate warming.

monitored (Figure 7). A future lengthening of the growing season in a warmer climate would cause a decline in snowbed species and favour grassland species. Moss communities, which are currently important in L, may also lose ground. Our survey so far has encountered 85 species of flowering plants. We have also obtained data for the dominant (i.e. most abundant) moss species (*Polytrichum sexangulare*) and two lichen species that have very high indicator power (*Solorina crocea*) or wide distribution (*Cetraria islandica*) across all sites (*S. crocea* is not found in OB). Of the flowering plant species, 19 were found in all 5 sites; 13 occur in the Hohe Tauern region only (SE, IN, UN). In total, 45 species occurred at one site only (of these, 22 alone at FU, and 10 at OB). Species lists from these sites indicate that the most abundant taxa typically found in either H or L co-occur at all 5 sites: *Helictotrichon versicolor* [= *Avenula versicolor*], *Leontodon helveticus* [= *Scorconeroides helvetica*] in H; *Gnaphalium supinum*, *Leucanthemopsis alpina*, and *P. sexangulare* in L. The current data suggest that *G. supinum*, *P. sexangulare*, *Salix herbacea*, *Soldanella pusilla*, and *H. versicolor* are the most promising species for identifying climatic warming effects, because these taxa show clear position preferences along the transects and are widely distributed. We also identified a few species with a known preference for warmer locations that are promising candidates for future range expansion (*Anthoxanthum alpinum*, *L. helveticus*, and *Geum montanum*). Our comparison of the 2017 and the 2021 data in the Hohe Tauern (Figure 8) reveals a down-slope (H to L) shift for *L. helveticus*, signs of grass encroachment in L, and reduced abundance (number of ramets) of *G. supinum* and

S. pusilla in L. Based on 50 random samples, a pairwise comparison for transect 4 in IN results in mean differences in cover: -25 cm^{-2} (-29% change), -23 cm^{-2} (-33%), -26 cm^{-2} (-29%), and $+145 \text{ cm}^{-2}$ ($+119\%$) for *Soldanella*, *Gnaphalium*, *Salix* and *Leontodon*, respectively, between the 2017 and 2021 surveys (Figure 8). However, it will require a longer time series to distinguish any such trend from stochastic events and the effects of micro-environmental heterogeneity.

Plant biomass production

Harvested at peak season, live (green), annual, above-ground biomass production varied between 40 and 250 g m^{-2} across all sites, transect positions and years (Figure 9). The date of harvest, commonly around mid-August, was chosen depending on the year-specific snowmelt regime and the phenology, so that communities at H had not yet entered seasonal senescence (leaf browning), while the communities released from snow latest at L had just reached their seasonal peak. We found end of flowering / onset of fruiting (stalk elongation stage) in the typical snowbed species *Gnaphalium supinum* to be the most suitable pheno-marker at L for the compromise in sampling date (repeated site visits were logistically impossible in all sites except FU). Attached dead parts (necromass) and litter were discarded. Bryophytes (mainly tiny *Polytrichum* sp.), fruticose lichens (commonly very small amounts) and earlier years' woody stems (again tiny fractions) were also dismissed, because they cannot be attributed to a given year's productivity. Biomass was sorted into dicots (herbs) and monocots (graminoids).

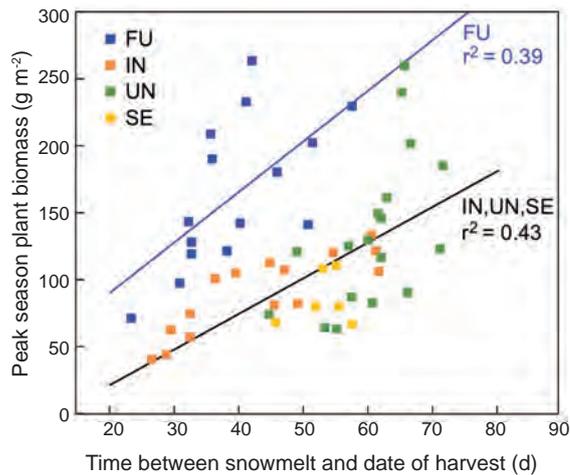


Figure 10 – Mean seasonal peak biomass for 5 years plotted against the 5-year mean of the time between snowmelt and harvest. Given the obvious difference between Furka pass (FU) and the three sites in the Hobe Tauern National Park, we show two regressions. The variance reflects a combination of (a) the 5-year period not yet capturing the long-term mean season length to which communities are adapted, (b) the spatial variation of biomass at the scale of the 20 cm × 20 cm harvest plots.

High-intensity traditional grazing at our highest site, at OB, reversed the soil conditions (best in depressions, worst at the top), causing the biomass production to reverse as well, despite caging the harvest plots in the year of harvest. The effect of the soil quality was therefore greater than the effect of the shorter season at L. With means of 100 g m⁻² at L and 60 g m⁻² at H, this was also the least productive site, despite the similar growing season temperatures. At all other sites, productivity showed a significant decline from H (mean 160 g m⁻²; range 120 at SE to around 200 g m⁻² at UN and FU) to c. 80 g m⁻² at L, across sites and years (range 70 at SE and IN to 110 g m⁻² at FU). Year-to-year variation was substantial, and in part also reflected the 20 cm × 20 cm plots that happened to be harvested in a given year at a given site, illustrating the importance of site replication for arriving at a typical mean annual pattern. Across sites and transect positions, productivity rose from 2017 to 2021, with the highest biomass for H at all four sites occurring in 2020 (up to 250 g m⁻² at UN and FU). This trend was less pronounced at L and even reversed at SE and IN. Productivity rose in the sequence SE, IN, UN, FU, which seems to be unrelated to temperature or snowmelt regimes but rather to reflect the greater soil depth at UN and particularly at FU, with thinner soils overlying glacial cuttings at SE and IN. Overall, annual biomass production correlates with the mean L-M-H-related duration of the growing season across sites (Figure 10).

In a linear multivariate statistical model, year (n=5), site (n=5), and position on transect (n=3; L, M, H) for 22 transects explain 47% of the variance. Excluding OB because of the intense pressure caused by traditional grazing, and transect 2 at site SE which turned

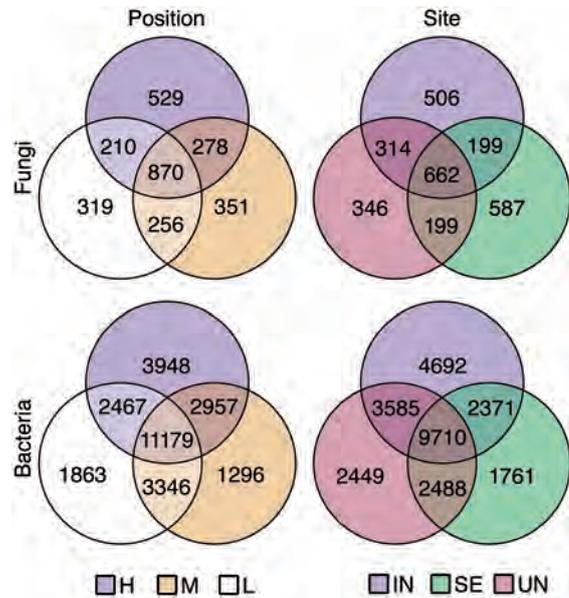


Figure 11 – Operational taxonomic units (OTUs) of the fungal and bacterial communities in top soil separated by site (Innerschblöss, Seebachtal, Untersulzbachtal) and by position (H=top, M=middle, L=low) with the overlaps illustrating commonness. The total number of fungal OTUs is 2,813 and that of bacteria 27,056.

out to have neither a snowmelt nor a soil or vegetation gradient, the model explains 56% of the variance, with site (21%) and L-M-H position on transect (29%) showing the largest influences, each with high statistical significance. Year explains only 6% of the variance, because a single year's weather conditions exert little influence on cover in these perennial systems. Much of the above-ground spring growth is produced from *stored growth*, using reserves mobilized from the large below-ground biomass fraction (> 80% of total). This is also why we averaged the time to peak biomass in Figure 10. As the regression in Figure 9 illustrates, the 3 sites in the NPHT (SE, IN, UN) form a cluster distinct from the Swiss site (FU). As mentioned above, the most likely reason for this is deeper soil profiles at FU (the soil chemistry itself does not hold an obvious answer). The remaining unexplained variance is largely associated with the patchiness of biomass at the 20 cm × 20 cm sampling scale.

Soil mesofauna

Vertically stratified samples collected using a split-core sampler were used to evaluate the abundance and diversity of soil microarthropods (mainly collembolans and oribatid mites). These small invertebrates (body size < 2 mm) are abundant and important members of high-alpine soil animal communities and are well adapted to life in cold environments. They can also use the intra-nivean space for moving during snow cover (Hågvar 2010) and prolong their life cycles to compensate for the shorter growing season (e.g. Søvik et al. 2003). Due to these adaptations, micro-scale

distribution and community composition of snowbed microarthropods might be affected above-average by climate warming.

Most individuals (> 95%) were obtained from the litter layer and the upper 5 cm of the soil profile via heat extraction in a Macfadyen high-gradient apparatus. Across all sites and transects, 25 species of collembola and 49 species of oribatid mites were found (see Seeber et al. 2021). Transects at FU harboured the highest mean number of microarthropod individuals (c. 15,660 individuals m^{-2}); SE exhibited the highest species diversity (17 collembolan and 25 oribatid mite species). Most individuals belonged to a few widespread species which occurred in at least three out of the five sites. Consequently, community composition, which was driven mainly by soil organic matter content and soil porosity, showed little variation across the study sites. Mean snowpack duration between bottom and top of the transect generally differed by 1-3 weeks, causing drastic changes in vegetation. However, unlike in other studies (e.g. Green & Slatyer 2019), our currently available data do not reveal any significant effect of snowpack duration on the abundance and species numbers of soil microarthropods. To what extent potential differences in individual longevity contribute to the small abundance gradient from H to L remains unresolved.

Soil microbiome

Culture-independent, high-throughput genome sequencing of soil samples from the terrestrial transects yielded a total of 27,056 bacterial and 2,813 fungal OTUs (note the order of magnitude difference). We observed a general decrease in OTU richness towards the nutritionally poorer, lowest parts of the gradients. Among bacteria, taxa known for their preference for drier habitats dominated the top (H), and taxa affiliated with moister conditions dominated near the bottom (L). Among fungal taxa, such trends were not as pronounced, but first data show a stronger presence of Basidiomycota in snowbeds (L), including ectomycorrhizal and saprobic taxa, while at L, microfungi are more abundant, including AM mycorrhizae. There is a remarkable site and position specificity of OTU communities (Figure 11). For comparison, 10,406 bacterial and 6,291 fungal taxa were recorded across 10 summit sites of the GLORIA programme by Adamczyk et al. (2019). In their study (on much less developed soils), bacterial diversity was positively correlated with increasing (less acidic) soil pH, but negatively with increasing elevation, whereas fungal α -diversity remained more or less the same. Yao et al. (2013) mapped fungal diversity in the rhizosphere of the ectomycorrhizal plant species *Bistorta* (*syn. Polygonum vivipara*) along ridge-to-snowbed gradients in alpine Norway, and found taxonomic differentiation between ridges (with Sebaciniales-related OTUs) and snowbeds (harbouring specific *Tomentella* and *Cortinari* OTUs).

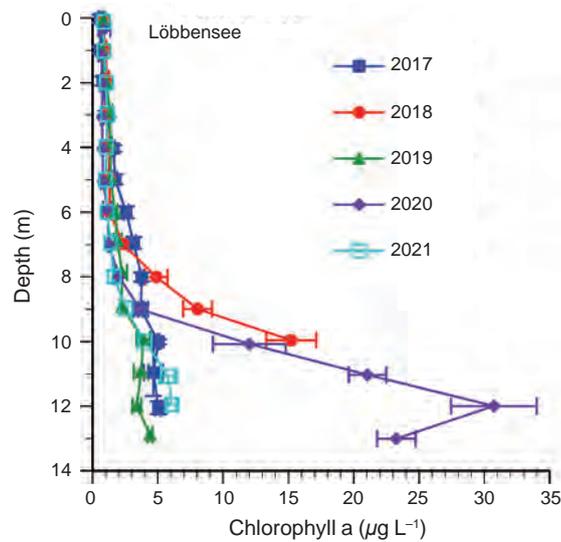


Figure 12 – The 5-year variation in vertical chlorophyll-a concentration exemplified by lake Löbbensee (2,226 m, region Innerschläss). Note the high chlorophyll maxima very deep in the profile in 2018 and 2020 only.

In addition to the influences of topography, microbial abundance patterns are also affected by seasonality. Lazzaro et al. (2015) found a clearly reduced bacterial abundance in winter (as measured by detected gene copy numbers) and a rise after snowmelt to a summer maximum. In contrast, there was much less seasonality in fungal OTUs, with a trend towards higher abundances in winter. Broadbent et al. (2021) found that bacterial and fungal lineages responded differently to experimental snow-removal in alpine grassland, which corresponds to our H position: among bacteria, Acidobacteria increased and Actinobacteria decreased after snow-removal; among fungi, Gemibasidiales increased and Pleosporales decreased. Shifts included functional ones (assessed by quantifying corresponding genes). Notably, microbial genes associated with N-cycling increased significantly in summer. It is therefore important *when* in the course of a year standardized samples are obtained in long-term monitoring. The timing of snowmelt triggers the composition, abundance and activity of the soil microbiome, but unlike plant and animal activity, microbial activity remains high under snow, explaining why most of the annual net ecosystem production is recycled over winter (Scholz et al. 2017).

Lake biota

Like the abiotic parameters, the vertical chlorophyll-a profiles also differ from year to year (Figure 12), with some lakes exhibiting similar patterns, while some neighbouring lakes may differ substantially, underlining the importance of microclimate and replication. Covering a wide range of habitats is key to identifying regionally representative trends in the context of environmental change (e.g. nitrogen deposition; Elser et al. 2020). The monitoring of plankton (30 μm

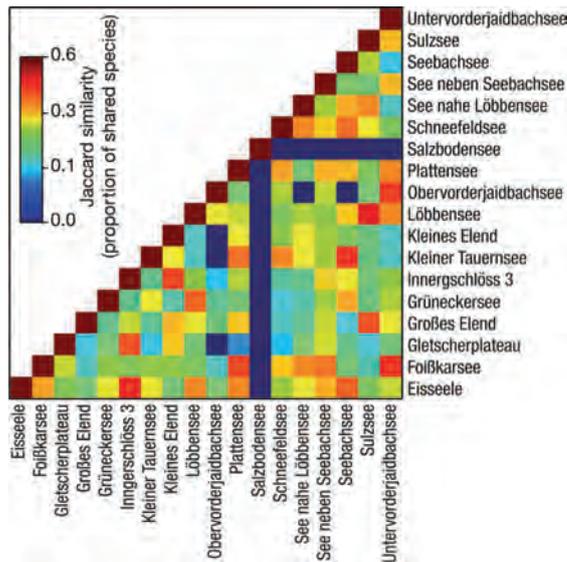


Figure 13 – Jaccard similarity between the zooplankton communities of the 18 sampled lakes. Data for four years (2017–2020). Warmer colours indicate greater similarity. The blue bar for Salzbodensee indicates that this lake has no taxa in common with any other lake (two unique and large omnivorous species).

plankton net samples for metazoan zooplankton and large ciliates, whole water samples for phytoplankton and smaller ciliates) has also revealed a wide variety of responses to environmental conditions. Zooplankton alpha diversity differs strongly among lakes (1–11 species per lake). The lakes have remarkably few species in common, and even neighbouring lakes may differ greatly – i. e. beta diversity in zooplankton is high (Figure 13). Only 3 species (two rotifers, *Keratella quadrata* and *Polyarthra dolichoptera*, and one ciliate, *Bursaridium* sp.) were found to be common to at least one third of all lakes. This result is supported by analysis of the total molecular diversity of the lakes (R. Ptacnik, unpublished results). These contrasts can only partly be explained by abiotic differences, but may result also from strong dispersal limitations (Allen et al. 2012) or other factors. Species composition in most lakes has remained stable over the last five years, with few lakes showing establishment of new species. Young lakes (≤ 30 years) that have emerged since the retreat of glaciers are probably still in a colonization phase, and can be expected to become more species-rich in the future (Cauvy-Fraunié & Dangles 2019). There is a positive relationship between phytoplankton and zooplankton biomass, but there are clearly more drivers of zooplankton biomass and diversity than simply primary production. In lakes with fish, for example, there is higher zooplankton diversity, particularly in rotifers, compared with fish-free lakes, where large crustacean zooplankton dominates. The lakes with the lowest zooplankton diversity tend to be young, cold and turbid, indicating that both colonization rates and hostile abiotic conditions contribute to driving zooplankton

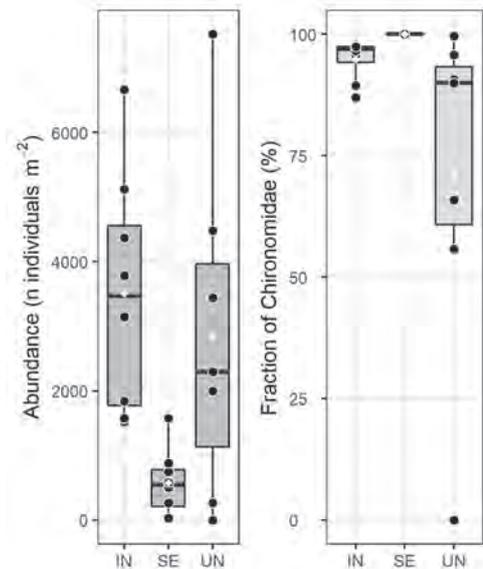


Figure 14 – Abundance of stream invertebrates and the fraction of Chironomidae (non-biting midges) in all samples per site from July 2017. Bold horizontal lines for median; white dots are means. Single dots (=individual samples) indicate the microhabitats along each stream. IN=Innerschlöss, SE=Seebachtal, UN=Untersulzbachtal.

diversity. The picture we have after five years of data collection is one of unexpectedly high abiotic and biotic diversity among these small alpine lakes. It is still too early to formulate hypotheses for future trends. The data illustrate that the long-term monitoring of alpine lakes requires more than five years of initial data collection to overcome stochastic effects.

Life in streams

The biofilm biomass on stones averaged 0.135 ± 0.02 mg cm⁻² (2017–2018, n=90), with a maximum of 0.43 mg cm⁻² at UN late in the season. However, seasonal changes were generally small (no increase during the growing period, in contrast to terrestrial plant biomass), except for low-water and dry conditions at SE in August, followed by a green algal bloom when the water flow decreased and then returned. Generally, biofilm biomass increased from upstream to downstream. Biofilms are largely composed of periphytic groups (cyanobacteria, diatoms and green algae) and other bacteria and fungi (these other bacteria and fungi are not studied here), with cyanobacteria contributing 49–55% of the cover in all three streams studied, followed by diatoms (18–42%) and green algae (5–16% only, predominantly after low-water conditions). Cyanobacteria profit from a stable environment and thus are barely present in glacier-fed streams, which benefit diatoms (Niedrist et al. 2018). As alpine streams warm, we expect an increase in cyanobacteria, especially in non-glacial streams (Niedrist & Füreder 2021; Lürding et al. 2018).

Benthic invertebrate abundance was highest during the early alpine summer (July), and declined by more

than 50% later in the season. In July, we recorded densities of $3,503 \pm 655$ individuals m^{-2} at IN, 577 ± 180 individuals m^{-2} at SE, and 2857 ± 984 individuals m^{-2} at UN (Figure 14); the highest taxa richness was found at IN and UN (48 and 46, respectively; 12 at SE). The low taxa number at SE reflects periodic stream-drying, where only a selection of tolerant organisms can reproduce. As expected, the dipteran family Chironomidae dominates (commonly >80% of all individuals) at all sites (Figure 14), which also corresponds to observations in other rivers of the NPHT (e.g. Niedrist & Füreder 2021), and underlines the adaptation of this family to harsh living conditions (Füreder 1999).

Large herbivores

Since the terrestrial monitoring part of our research aims at identifying changes in plants and associated soil biota and ecosystem processes in response to environmental change (climate change, changes in atmospheric chemistry), it is important to identify all potentially confounding influences, including changes in the abundance and activity of herbivores. We monitored the presence of, and habitat use by, large herbivores and marmot using automatic wildlife camera traps with 10 s photo intervals over a distance of up to 200 m. The cameras were operated at IN, UN and SE each year, at FU (which revealed almost no wild animals) during one season only, and not at all at OB (because of the very intense and high sheep stocking). We documented (in descending frequency) *Rupicapra rupicapra* (chamois), *Marmota marmota* (alpine marmot), *Capreolus capreolus* (roe deer), *Capra ibex* (alpine ibex), *Cervus elaphus* (red deer), and *Ovis gmelini aries* (domestic sheep, at IN and FU). In our image analysis, we distinguished states of grazing, movement or resting, for July, August and September (daytime only). At IN, there are mainly sheep; at UN and SE, mainly chamois. The total land area covered by each camera was used to calculate the overall grazing time per m^2 weighted by the number of animals (Table 3). Animal presence was generally low at IN, UN, SE and FU, but varied substantially among study sites and years. The comparatively low incidence at SE is probably a consequence of the proximity of a popular hiking trail. The decline in presence at IN in 2019 is probably due to the reduction in the sheep-flock size (a yearly random effect). Animal presence may affect the composition of vegetation and ecosystem processes through grazing (e.g. Meier et al. 2017) or dung (e.g. Iravani et al. 2011; Williams & Haynes 1995); it may also affect the actual standing crop of plant biomass. Thus, where sheep are present traditionally (not at UN or SE; low frequency at IN and FU; very high stocking at OB), a given year's targeted micro-plot for plant biomass harvest had to be fenced (IN) or caged (FU, OB) in the early part of the season (i.e. until harvest).

Within an elevational transect from the climatic treeline up to (or slightly above) the permanent plots (SE 1900–2300 m; IN 2080–2350 m; UN 1730–

Table 3 – Large herbivore presence at the study sites Innerschlöss (IN), Seebachtal (SE), Untersulzbachtal (UN) (data for the biomass sampling sites only, not for elevation transects) in the Hohen Tauern National Park region. Note: the generally low $s\ m^{-2}$ mean grazing-time values for the total land area covered by the camera may result from local hotspots of use in otherwise hardly impacted terrain (presence in hours was calculated as presence time \times number of animals for a 14.8 h mean of total daylight monitoring time).

Study site	Weighted sum of presence (h)*				Grazing time ($s\ m^{-2}$)			
	2017	2018	2019	2020	2017	2018	2019	2020
IN	304	306	51	73	0.79	0.78	0.13	0.19
SE	159	38	48	53	0.27	0.06	0.08	0.09
UN	436	143	361	n.d.	0.24	0.20	0.20	n.d.

* Data for FU are available for the first half of the 2017 season only (a total of 92 h of weighted presence of either marmot or sheep, up to 12 August 2020). This represents a low presence when scaled to the entire season.

2400 m), 10 regularly spaced cameras documented the general wildlife presence in open terrain in these test regions. Roe deer was documented up to 2,160 m only; chamois and marmot were documented everywhere, but in densities that increased rapidly with elevation. These animals are heat-sensitive and shift to higher (cooler) regions when it gets too warm (which is a likely scenario for the future, leading to habitat shrinkage).

Discussion and conclusion

After five years of fieldwork, this interdisciplinary long-term monitoring programme of alpine ecosystems in the central Alps has arrived at a first consolidated database and has established working routines. For both terrestrial and aquatic ecosystems, the teams provide datasets that allow the study sites to be characterized in a comparative way, and the data illustrate the spatial and temporal variability of the parameters monitored. Macroclimatic, water and soil data provide evidence that site selection was successful in terms of achieving the maximum possible standardization of terrestrial sites in an alpine context, or of covering the small-scale spatial variation which is intrinsic to aquatic systems. These are essential pre-requisites to identify effects of environmental changes that act on top of local influences.

For the terrestrial sites, we evidence a surprisingly similar (almost identical) macroclimatic situation, as characterized by a mean air temperature of $8^{\circ}C$ during the main growing season. This high temperature for sites at 260–400 m above the treeline reflects late snowmelt and a short growing period, confined to the two warmest months of the year (after the summer solstice). The main finding from microclimate monitoring is that the H vs L contrast along the snowmelt gradients is the duration of the snow-free period as such, whereas differences in temperature after snow melt were negligible. The critical temperatures in the

topsoil, where meristems are nested and most mesofauna and microbial activity occur, are on average 4 K warmer than the air temperature (consistent across sites), with midday peaks exceeding 10K on bright summer days. Lakes and streams, in contrast, show more pronounced spatial variability and sharp influences of the local ice dynamics. Nitrate loading in streams is an order of magnitude lower than in lakes; overall, the concentrations obtained are relatively low, as would be expected for alpine systems, but with exceptions. According to Swiss sources (Kosonen et al. 2019), current rates of total N-deposition (wet plus dry) in the central Alps is close to $7 \text{ kg ha}^{-1} \text{ a}^{-1}$, with rates at UN likely to be higher than in all other sites (exposed to front range weather). $4\text{--}6 \text{ kg N m}^{-2} \text{ a}^{-1}$ were reported by Bowman (1992) and Baron and Campbell (1997) for the Rocky Mountains in Colorado, placing the rates in the central Alps at the high end for temperate alpine sites. Such rates of N-deposition are likely to exceed critical loads for alpine vegetation (i.e. loads to which vegetation responds) (Kosonen et al. 2019).

One major message from the biological data collected annually so far is a pronounced year-to-year variation at all sites (up to a factor of 2), while the spatial differences (both along transects and among sites, as well as across lakes or streams) have largely been conserved over the years. The monitoring has not yet reached a point where we can separate long-term trends from stochasticity. Therefore, we refrain from attributing the steady rise in terrestrial productivity to climatic change. The data captured some exceptionally warm summers (2018–2020); data for further years are clearly needed to arrive at a consolidated mean that can serve as a reference for future re-assessments. Averaged across years, the terrestrial productivity at FU and UN is similar to the 200 g m^{-2} reported in the literature for H-type alpine grasslands (Körner 2021), but is only half as high at SE, IN and OB, suggesting that these sites operate within more limiting growth conditions. At SE and IN, the probable explanation is shallow soil on solid bedrock, while at OB the long-term grazing pressure has reduced the carrying capacity of the system, particularly at H, where trampling appears to have caused fines to become washed out to L.

Digital vegetation surveys open up an arena for fine-scale monitoring of *populations at the edge*. The technique allows the identification of seedlings and clonal expansion or retraction at the mm scale. Our data confirm the power of very detailed assessments of well-defined, small-scale permanent plots for assessing high-alpine vegetation dynamics (Blonder et al. 2018). Most species that have been newly identified by us downslope on the H to L transects belong to the typical grassland flora, suggesting that the recent exceptionally warm years facilitated their establishment. The fact that a quarter of the flowering plant species co-occur at all sites underlines the importance of selecting sites with similar environmental starting

conditions, a practice which holds promise for future site comparisons and for identifying species-specific responses to environmental change.

Similar to flowering plants, initial data for soil biota (mesofauna and microbiota) suggest that less than a third of all species or OTUs occur at all sites studied. To date, neither of these assessments reveals clear H to L abundance shifts. Since a large proportion of the mesofauna was found in the litter layer and top mm of soils, high mobility may be one answer. Another reason might be a greater longevity of individuals at the cold end, balancing a potentially reduced rate of reproduction. Among microbiota, there is a shift in the abundance of some fungal taxa from H to L, while among bacteria there is a shift in functional groups, pointing to higher moisture at L. A repeat assessment is urgently needed in order to identify taxonomic groups that can serve as focal organisms for future re-assessments and for validating the initial data.

Thanks to our monitoring of site visits by large herbivores, we can conclude that the grazing pressure by these animals on plant biomass is very low (except in OB) and is unlikely to affect our productivity data as long as the pre-harvest protection of designated sampling plots is ensured (IN, FU). But it is important that land-use effects are accounted for, even for areas where they are expected to be small, and particularly where they can be intrinsic, as in mountain biosphere reserves (Becker et al. 2007). At the whole-mountain scale, thus including montane elevations, the effects of changes in land use are likely to be significantly greater than the effects of climate change (Spehn et al. 2006; Körner 2014; Caro et al. 2022). This also relates to the presence of fish, which can completely restructure the food web in alpine lakes (Manca & Amiraglio 2002; Schabetsberger et al. 2009).

In terms of the further development of this monitoring project, the teams conclude that the following schedule for the completion of the base-line data acquisition is required: (1) soil physics and chemistry: no need for repetition within the next decade; (2) macro- and microclimate, lake and stream chemistry: continue as long as regular field sampling is under way; (3) plant biomass, lake and stream biota: current data suggest an obvious need for more than 5 years to consolidate site-specific means (e.g. up to 2027); (4) soil mesofauna and microbiota: a second survey is urgently needed (2022), and a third one might ideally be conducted around 2027; (5) large herbivore monitoring: reduce to plant biomass sampling sites at IN and UN for as long as these surveys are continued. Given the great impact and stochasticity of mice activity on vegetation, the group suggests expanding the monitoring work to rodents.

The methods and field experience of the various teams will hopefully encourage other researchers or conservation managers to initiate similar programmes elsewhere in comparable alpine habitat types. In this way, an interdisciplinary network of alpine ecosystem

monitoring sites could increase the confidence in ongoing ecological changes at high elevations at even larger geographical scale. The results obtained here for late successional vegetation on well-developed soils complement the outcome of the summit monitoring programme for largely pioneer biota in exposed habitats by the world-wide GLORIA programme (see Introduction). By combining the terrestrial with the aquatic biota, the monitoring programme provides a holistic view of alpine life under change.

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References

- Adamczyk M., F. Hagedorn, S. Wipf, J. Donhauser, P. Vittoz, C. Rixen, A. Frossard, J.-P. Theurillat & B. Frey 2019. The soil microbiome of Gloria Mountain summits in the Swiss Alps. *Frontiers Microbiology* 10: 1080.
- Allen, M.R., R.A. Thum, J.N. Vandyke & C.E. Caceres 2012. Trait sorting in *Daphnia* colonising man-made lakes. *Freshwater Biology* 57: 1813–1822.
- Bakker, J.P., H. Olf, J.H. Willems & M. Zobel 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science* 7: 147–156.
- Baron, J.S. & D.H. Campbell 1997. Nitrogen fluxes in a high elevation Colorado Rocky Mountain basin. *Hydrological Processes* 11: 783–799.
- Becker, A., C. Körner, J.J. Brun, A. Guisan & U. Tappeiner 2007. Ecological and land use studies along elevational gradients. *Mountain Research and Development* 27: 58–65.
- Blonder, B., R.E. Kapas, R. Dalton, B. Graae, J. Heiling & O. Opedal 2018. Microenvironment and functional-trait context dependence predict alpine plant community dynamics. *Journal of Ecology* 6: 1323–1337.
- Bowman, W.D. 1992. Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arctic, Antarctic, and Alpine Research* 24: 211–215.
- Broadbent, A.A., H.S. Snell, A. Michas, W.J. Pritchard, L. Newbold, I. Cordero, T. Goodall, N. Schallhart, R. Kaufmann, R.I. Griffith, M. Schloter, M. Bahn & R.D. Bardgett 2021. Climate change alters temporal dynamics of alpine soil microbial functioning and biogeochemical cycling via earlier snow melt. *The ISME Journal* 15: 2264–2275.
- Caro, T., Z. Rowe, J. Berger, P. Wholey & A. Dobson 2022. An inconvenient misconception: Climate change is not the principal driver of biodiversity loss. *Conservation Letters*: e12868. Doi: 10.1111/conl.12868
- Cauvy-Fraunié, S. & O. Dangles 2019. A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology and Evolution* 3: 1675–1685.
- Craine, J.M., J.B. Nippert, A.J. Elmore, A.M. Skibbe, S.L. Hutchinson & N.A. Brunsell 2012. Timing of climate variability and grassland productivity. *Proceedings of the National Academy of Sciences of the USA* 109: 3401–3405.
- Dai, L., X. Ke, X. Guo, Y. Du, F. Zhang, Y. Li, Q. Li, L. Lin C. Peng, K. Shu & G. Cao 2019. Responses of biomass allocation across two vegetation types to climate fluctuations in the northern Qinghai-Tibet Plateau. *Ecology and Evolution* 9: 6105–6115.
- de Witte, L.C., G.F.J. Armbruster, L. Gielly, P. Taberlet & J. Stocklin 2012. AFLP markers reveal high clonal diversity and extreme longevity in four key arctic-alpine species. *Molecular Ecology* 21: 1081–1097.
- de Witte, L.C. & J. Stöcklin 2010. Longevity of clonal plants: why it matters and how to measure it. *Annals of Botany* 106: 859–870.
- Deiner, K., E.A. Fronhofer, E. Mächler, J.C. Walser & F. Altermatt 2016. Environmental DNA reveals that rivers are conveyor belts of biodiversity information. *Nature Communications* 7: 12544. Doi: 10.1038/ncomms12544
- Ecosystem Monitoring Team 2021. *Manual of methods/Methodenhandbuch*. Hohe Tauern National Park - Research (Matsch in East-Tyrol) and Academy of Sciences (Vienna). Available at: <https://hohetauern.at/de/forschung/langzeitmonitoring.html> (accessed 17/03/2022)
- Elser, J.J. et al. 2020. Key rules of life and the fading cryosphere: Impacts in alpine lakes and streams. *Global Change Biology* 26: 6644–6656. Doi: 10.1111/gcb.15362
- Fischer, M., O. Bossdorf, S. Gockel, F. Hansel, A. Hemp, D. Hessenmoller, G. Korte, J. Nieschulze, S. Pfeiffer, D. Prati, S. Renner, I. Schoning, U. Schumacher, K. Wells, F. Buscot, E.K.V. Kalko, K.E. Linsenmair, E.D. Schulze & W.W. Weisser 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology* 11: 473–485.

- Franklin, J.F., C.S. Bledsoe & J.T. Callahan 1990. Contributions of the long-term ecological research program. An expanded network of scientists, sites, and programs can provide crucial comparative analyses. *BioScience* 40: 509–523.
- Freppaz, M., M.W. Williams, T. Seastedt & G. Filipa 2012. Response of soil organic and inorganic nutrients in alpine soils to a 16-year factorial snow and N-fertilization experiment, Colorado Front Range, USA. *Applied Soil Ecology* 62: 131–141.
- Friedel, H. 1961. Schneedeckendauer und Vegetationsverteilung im Gelände. *Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn (Vienna)* 59: 317–369.
- Füreder, L. 1999. High alpine streams: cold habitats for insect larvae. In: Margesin, R. & F. Schinner (eds.), *Cold-Adapted Organisms*: 181–196. Springer, Berlin.
- Füreder, L. 2010. Hochalpine Flusslandschaft Rotmoos. In: Koch, E.M. & B. Erschbamer (eds.), *Glaziale und periglaziale Lebensräume im Raum Oberegurgl*: 185–202.
- Gottfried, M. et al. 2012. Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2: 111–115. Doi: 10.1038/nclimate1329
- Green, K. & R. Slatyer 2019. Arthropod Community Composition along Snowmelt Gradients in Snowbeds in the Snowy Mountains of South-Eastern Australia. *Austral Ecology* 45: 144–157.
- Hägvar, S. 2010. A review of Fennoscandian arthropods living on and in snow. *European Journal of Entomology* 107: 281–298.
- Hansen, A.H., S. Jonasson, A. Michelsen & R. Jukonen-Tiitto 2006. Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs. *Oecologia* 147: 1–11.
- Hegg, O., U. Feller, W. Dahler & C. Scherrer 1992. Long term influence of fertilization in a Nardetum. *Vegetatio* 103: 151–158.
- Ilyashuk, E.A., K.A. Koinig, O. Heiri, B.P. Ilyashuk & R. Psenner 2011. Holocene temperature variations at a high-altitude site in the Eastern Alps: a chironomid record from Schwarzsee ob Sölden, Austria. *Quaternary Science Reviews* 30: 176–191. Doi: 10.1016/j.quascirev.2010.10.008
- Iravani, M., M. Schütz, P. Edwards, A. Risch, Ch. Scheidegger & H. Wagner 2011. Seed dispersal in red deer (*Cervus elaphus* L.) dung and its potential importance for vegetation dynamics in subalpine grasslands. *Basic Applied Ecology* 12: 505–515. Doi: 10.1016/j.baae.2011.07.004
- Kittel, T.G.F., M.W. Williams, K. Chowanski, M. Hartman, T. Ackerman, M. Losleben & P.D. Blanken 2015. Contrasting long-term alpine and subalpine precipitation trends in a mid-latitude North American mountain system, Colorado Front Range, USA. *Plant Ecology and Diversity* 8: 607–625.
- Körner, C. 1995. Alpine plant diversity: a global survey and functional interpretations. In: Chapin, F.S. III & C. Körner (eds.), *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences*. Ecological Studies 113: 45–62. Springer, Berlin.
- Körner, C. 2004. Mountain biodiversity, its causes and function. *Ambio Special Report* 13: 11–17.
- Körner, C. 2011. Coldest places on earth with angiosperm plant life. *Alpine Botany* 121: 11–22.
- Körner, C. 2014. Mountain ecosystems in a changing environment. *eco.mont - Journal on protected mountain area research and management* 6(1): 71–77.
- Körner, C. 2018a. Concepts in empirical plant ecology. *Plant Ecology and Diversity* 11: 405–428.
- Körner, C. 2018b. Comparative, long-term ecosystem monitoring across the Alps: Austrian Hohe Tauern National Park, South-Tyrol and the Swiss central Alps. *Conference Volume, 6th Symposium for research in protected areas. Nationalpark Hohe Tauern*: 331–337. Available at: http://www.parc.at/npa/pdf_public/2018/36275_20180523_093027_ConferenceVolume_6thSymposium_FINAL_corr.pdf (accessed 17/03/2020)
- Körner, C. et al. 2020. *Langzeitmonitoring von Ökosystemprozessen im Nationalpark Hohe Tauern: Synthese der Startphase 2016–2018*. Available at: http://www.parc.at/npht/pdf_public/2020/38764_20200901_115652_WEB_Synthesebericht.pdf (accessed 17/03/2020) Doi: 10.1553/GCP_LZM_NPHT_Synthese
- Körner, C. 2021 *Alpine plant life*. Cham
- Körner, C. & E. Hiltbrunner 2021. Why is the alpine flora comparatively robust against climatic warming? *Diversity* 13: 383 Doi: 10.3390/d13080383
- Körner, C. & M. Ohsawa 2005. Mountain Systems. In: Hassan, R., R. Scholes & N. Ash (eds.), *Ecosystems and human well-being: current state and trends*: 681–716. Volume 1. Washington DC.
- Körner, C., J. Paulsen & E.M. Spehn 2011. A definition of mountains and their bioclimatic belts for global comparison of biodiversity data. *Alpine Botany* 121: 73–78.
- Kosonen, Z., E. Schnyder, E. Hiltbrunner, A. Thimonier, M. Schmitt, E. Seitler & L. Thöni 2019. Current atmospheric nitrogen deposition still exceeds critical loads for sensitive, semi-natural ecosystems in Switzerland. *Atmospheric Environment* 211: 214–225.
- Lamprecht, A., P.R. Semenchuk, K. Steinbauer, M. Winkler & H. Pauli 2018. Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. *New Phytologist* 220: 447–459.
- Lazzaro, A., D. Hilfiker & J. Zeyer 2015. Structures of Microbial Communities in Alpine Soils: Seasonal and Elevational Effects. *Frontiers in Microbiology* 6: 1330. Doi: 10.3389/fmicb.2015.01330
- Lotter, A.F., O. Heiri, W. Hofmann, W.O. van der Knaap, J.F.N. van Leeuwen, I.R. Walker & L. Wick 2006. Holocene timber-line dynamics at Bachalpsee, a lake at 2265 m a.s.l. in the northern Swiss Alps. *Vegetation History and Archaeobotany* 15: 295–307.
- Lüring, M., M. Mendes-Mello, F. van Oosterhout, L. de Senerpont-Domis, M.M. Marinho 2018. Response of natural cyanobacteria and algae assemblages

- to a nutrient pulse and elevated temperature. *Frontiers in Microbiology* 9: 1851. Doi: 10.3389/fmicb.2018.01851
- Manca, M. & M. Armiraglio 2002. Zooplankton of 15 lakes in the Southern Central Alps: Comparison of recent and past (pre-ca 1850 AD) communities. *Journal of Limnology* 61(2). Doi: 10.4081/jlimnol.2002.225
- Mark, A.F., A.C. Korsten, D.U. Guevara, K.J.M. Dickinson, T. Humar-Maegli, P. Michel, S.R.P. Halloy, J.M. Lord, S.E. Venn, J.W. Morgan, P.A. Whigham & J.A. Nielsen 2015. Ecological responses to 52 years of experimental snow manipulation in high-alpine cushionfield, Old Man Range, south-central New Zealand. *Arctic, Antarctic, and Alpine Research* 47: 751–772.
- Matteodo, M., S. Wipf, V. Stöckli, C. Rixen & P. Vittoz 2013. Elevation gradient of successful plant traits for colonizing alpine summits under climate change. *Environmental Research Letters* 8: 24043–24053.
- Mayer, R. & B. Erschbamer 2017. Long-term effects of grazing on subalpine and alpine grasslands in the Central Alps, Austria. *Basic and Applied Ecology* 24: 9–18.
- Meier, M., D. Stöhr, J. Walde & E. Tasser 2017. Influence of ungulates on the vegetation composition and diversity of mixed deciduous and coniferous mountain forest in Austria. *European Journal of Wildlife Research* 63: 1–10. Doi: 10.1007/s10344-017-1087-4
- Miller, M.P. & D.M. McKnight 2015. Limnology of the Green Lakes Valley: phytoplankton ecology and dissolved organic matter biogeochemistry at a long-term ecological research site. *Plant Ecology and Diversity* 8: 689–702.
- Mirtl, M., E.T. Borer, I. Djukic, M. Forsius, H. Haubold, W. Hugo, J. Jourdan, D. Lindenmayer, W.H. McDowell, H. Muraoka, D.E. Orenstein, J.C. Pauw, J. Peterseil, H. Shibata, C. Wohner, X. Yu & P. Haase 2018. Genesis, goals and achievements of Long-Term Ecological Research at the global scale: A critical review of ILTER and future directions. *Science of the Total Environment* 626: 1439–1462.
- Niedrist, G.H., M. Cantonati & L. Füreder 2018. Environmental harshness mediates the quality of periphyton and chironomid body mass in alpine streams. *Freshwater Science* 37: 519–533.
- Niedrist, G.H. & L. Füreder 2021. Real-time warming of Alpine streams: (re)defining invertebrates' temperature preferences. *River Research and Applications* 37: 283–293.
- Pauli, H., M. Gottfried & G. Grabherr 2001. High summits of the Alps in a changing climate. The oldest observation series on high mountain plant diversity in Europe. In: Walther, G.-R., C.A. Burga & P.J. Edwards (eds.), *"Fingerprints" of climate change. Adapted behaviour and shifting species ranges*: 225–231. Kluwer Academic/Plenum, N.Y.
- Pauli, H., M. Gottfried, K. Reier, C. Klettner & G. Grabherr 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* 13: 147–156.
- Schabetsberger, R., M.S. Luger, G. Drozdowski & A. Jagsch 2009. Only the small survive: monitoring long-term changes in the zooplankton community of an Alpine lake after fish introduction. *Biological Invasions* 11: 1335–1345. Doi: 10.1007/s10530-008-9341-z
- Scherrer, D. & C. Körner 2009. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* 16: 2602–2613.
- Scholz, K., A. Hammerle, E. Hiltbrunner & G. Wohlfahrt 2018. Analyzing the effect of growing season length on the net ecosystem production of alpine grassland using model data fusion. *Ecosystems* 21: 982–999.
- Seeber, J., C. Newesely, M. Steinwandter, C. Körner, U. Tappeiner & E. Meyer 2021. Soil invertebrate diversity across steep high elevation snowmelt gradients in the European Alps. *Arctic, Antarctic, and Alpine Research* 53: 288–299. Doi: 10.1080/15230430.2021.1982665
- Silvertown, J., J. Tallwin, C. Stevens, S.A. Power, V. Morgan, B. Emmett, A. Hester, P.J. Grime, M. Morecroft, R. Buxton, P. Poulton, R. Jinks & R. Bardgett 2010. Environmental myopia: a diagnosis and a remedy. *Trends in Ecology and Evolution* 25: 556–561.
- Silvertown, J., P. Poulton, E. Johnston, G. Edwards, M. Heard & P.M. Biss 2006. The Park Grass experiment 1856–2006: its contribution to ecology. *Journal of Ecology* 94: 801–814.
- Smith, J.G., W. Sconiers, M.J. Spasojevic, I.W. Ashton & K.N. Suding 2012. Phenological Changes in Alpine Plants in Response to Increased Snowpack, Temperature, and Nitrogen. *Arctic, Antarctic, and Alpine Research* 44: 135–142.
- Søvik, G., H.P. Leinaas, R.A. Ims & T. Solhøy 2003. Population dynamics and life history of the oribatid mite *Ameronothrus lineatus* (Acari, Oribatida) on the high Arctic archipelago of Svalbard. *Pedobiologia* 47: 257–271.
- Spasojevic, M.J., W.D. Bowman, H.C. Humphries, T.R. Seastedt & K.N. Suding 2013. Changes in alpine vegetation over 21 years: Are patterns across a heterogeneous landscape consistent with predictions? *Ecosphere* 4: 117.
- Spehn, E.M., M. Liberman & C. Körner 2006. *Land use change and mountain biodiversity*. CRC Press, Boca Raton.
- Steinger, T., C. Körner & B. Schmid 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of *Carex curula*. *Oecologia* 105: 94–99.
- Stöckli, V., S. Wipf, C. Nilsson & C. Rixen 2011. Using historical plant surveys to track biodiversity on mountain summits. *Plant Ecology and Diversity* 4: 415–425.
- Virtanen, R., H. Henttonen & K. Laine 1997. Lemming grazing and structure of a snowbed plant community - a long-term experiment at Kilpisjärvi, Finnish Lapland. *Oikos* 79: 155–166.
- Vittoz, P., C. Randin, A. Dutoit, F. Bonnet & O. Hegg 2009. Low impact of climate change on sub-

alpine grasslands in the Swiss Northern Alps. *Global Change Biology* 15: 209–220.

Walker, M.D., D.A. Walker, J.M. Welker, A.M. Arft, T. Bardsley, P.D. Brooks, J.T. Fahnestock, M.H. Jones, M. Losleben, A.N. Parsons, T.R. Seastedt & P.L. Turner 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes* 13: 2315–2330.

Walker, M.D., P.J. Webber, E.H. Arnold & D. Ebert-May 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology* 75: 393–408.

Williams, M.W., R.T. Barnes, J.N. Parman, M. Frepaz & E. Hood 2011. Stream water chemistry along an elevational gradient from the continental divide to the foothills of the Rocky Mountains. *Vadose Zone Journal* 10: 900–914.

Williams, M.W., P.D. Brooks & T. Seastedt 1998. Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, USA. *Arctic, Antarctic, and Alpine Research* 30: 26–30.

Williams, M.W., T.R. Seastedt, W.D. Bowman, D.M. McKnight & K.N. Suding 2015. An overview of research from high elevation landscape: the Niwot Ridge, Colorado Long Term Ecological Research program. *Plant Ecology and Diversity* 8: 597–605. Doi: 10.1080/17550874.2015.1123320

Williams, P.H. & R.J. Haynes 1995. Effect of sheep, deer and cattle dung on herbage production and soil nutrient content. *Grass and Forage Science* 50: 263–271. Doi: 10.1111/j.1365-2494.1995.tb02322.x

Wipf, S. & C. Rixen 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research* 29: 95–109.

Wipf, S., V. Stöckli, K. Herz & C. Rixen 2013. The oldest monitoring site of the Alps revisited: accelerated increase in plant species richness on Piz Linard summit since 1835. *Plant Ecology and Diversity* 6: 447–455.

Yang, Y., R.T.W. Siegwolf & C. Körner 2015. Species specific and environment induced variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in alpine plants. *Frontiers in Plant Science* 6: 429. Doi: 10.3389/fpls.2015.00423

Yao, F., U. Vik, A.K. Brysting, T. Carlsen, R. Halvorsen & H. Kausrud 2013. Substantial compositional turnover of fungal communities in an alpine ridge-to-snowbed gradient. *Molecular Ecology* 22: 5040–5052.

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