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Assessment of climate change effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines.

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50 Abstract

51 Mountain ecosystems are sensitive and reliable indicators of climate change. Long-term studies 52 may be extremely useful in assessing the responses of high-elevation ecosystems to climate change 53 and other anthropogenic drivers from a broad ecological perspective. Mountain research sites within 54 the LTER (Long-Term Ecosystem Research) network are representative of various types of 55 ecosystems and span a wide bioclimatic and elevational range.

Here, we present a synthesis and a review of the main results from long-term ecological studies in mountain ecosystems at 20 LTER sites in Italy, Switzerland and Austria covering in most cases more than two decades of observations. We analyzed a set of key climate parameters, such as temperature and snow cover duration, in relation to vascular species composition, plant traits, abundance patterns, pedoclimate, nutrient dynamics in soils and water, phenology and composition of freshwater biota.

The overall results highlight the rapid response of mountain ecosystems to climate change, with 62 63 site-specific characteristics and rates. As temperatures increased, vegetation cover in alpine and subalpine summits increased as well. Years with limited snow cover duration caused an increase in 64 soil temperature and microbial biomass during the growing season. Effects on freshwater 65 ecosystems were also observed, in terms of increases in solutes, decreases in nitrates and changes in 66 67 plankton phenology and benthos communities. This work highlights the importance of comparing 68 and integrating long-term ecological data collected in different ecosystems, both terrestrial and freshwater, for a more comprehensive overview of the ecological effects of climate change. 69 Nevertheless, there is a need for (i) adopting co-located monitoring site networks to improve our 70 71 ability to obtain sound results from cross-site analysis, (ii) carrying out further studies, in particular short-term analyses with fine spatial and temporal resolutions to improve our understanding of 72 73 responses to extreme events, and (ii) increasing comparability and standardizing protocols across networks to clarify local patterns from global patterns. 74

75 Key-words: long-term research, climate change, vascular plants, freshwater, soil, snow cover,
76 alpine lifezone, Alps, Apennines.

77

78 1. INTRODUCTION

Mountains represent unique areas to detect climate change and assess climate-related impacts. One reason they are unique is that, as the climate rapidly changes with altitude over relatively short horizontal distances, so do vegetation and hydrology (Whiteman, 2000). Therefore, because of the complex topography in alpine environments, mountains exhibit high biodiversity (Winkler et al., 2016).

84 According to climate change projections, global warming will not be uniform but will vary considerably between different regions; in particular, climate change will be greater over land and 85 at high latitudes and elevations (Auer et al., 2007; Gobiet et al., 2014). The high sensitivity of 86 87 mountain areas with respect to climate change was clearly highlighted by the IPCC in its latest report (IPCC, 2014). Mountain ecosystems are indeed increasingly threatened by climate change, 88 causing biodiversity loss, habitat degradation, deterioration of freshwater quality and landscape 89 modifications (e.g., Körner, 2003), which poses a serious threat to the ecological integrity of 90 91 terrestrial and freshwater ecosystems and the services they provide (Stoll et al., 2015; Huss et al., 92 2017). The response of mountain ecosystems may differ according to the rate of climate change, the ecological domain and the biogeographical region (Beniston, 2003; Müller et al., 2010). 93

94 High mountains in Europe contain 20% of the native flora of the continent (Väre et al., 2003) and 95 are centers of plant diversity, hosting highly specialized vascular plants (Myers et al., 2000; 96 Barthlott et al., 2005) and many endemic species (Langer & Sauerbier, 1997; Dirnböck et al., 2011; 97 Stanisci et al., 2011). Climate change is considered one of the main threats to plant diversity above 98 the tree-line. Recent model projections using climate change scenarios predicted a dramatic 99 reduction of suitable habitats for high-elevation herbaceous plants (Engler et al., 2011) even if 100 thermal microhabitat mosaics offer alpine species both refuge habitats and serve as stepping stones 101 as atmospheric temperatures rise (Scherrer, Körner 2011). The slow growth rates of long-lived 102 alpine plants may lead to a delayed decrease in the ranges of species, creating an extinction debt 103 (Dullinger et al., 2012). Mountain forests are also particularly vulnerable to climate change due to 104 their long rotation cycles that may hinder their adaptation capacity (Lindner et al., 2010). However, 105 forests can also benefit from global change, as increasing concentrations of CO₂ and nitrogen 106 deposition should increase photosynthesis rates and forest growth (e.g., Matyssek et al., 2006).

107 Freshwater ecosystems in mountain areas are of paramount importance as high-quality water resources and biodiversity hotspots because they host specialized aquatic biotas (Körner, 2004). 108 Mountain lakes are particularly sensitive to the effects of global change, such as the deposition of 109 110 atmospheric pollutants and increasing temperatures (Battarbee et al., 2009; Catalan et al., 2009). Mountain lakes are usually small ($< 0.5 \text{ km}^2$), relatively shallow and generally ice-covered for 111 prolonged periods (from 3-4 to 8-9 months per year). Organisms living in these lakes face harsh 112 environmental conditions, low nutrient availability, and extreme changes in light conditions during 113 the year (Sommaruga, 2001). Riverine habitats in glacier catchments are also among the most 114 115 vulnerable habitats with respect to climate change. River community structure (species composition, abundance, and ecological traits) is related to geomorphological features, which are in 116 turn affected by glacier dynamics (Füreder, 2007; Finn et al., 2010) that are strongly affected by 117 118 climate change.

Increased air temperatures due to climate change resulted in shorter snow cover seasons due to later 119 accumulation and earlier meltdown (Klein et al., 2016). A general decrease in the spatial extent of 120 spring snow cover in the Northern Hemisphere has been reported (IPCC, 2014) as well as an 121 upward shift of the rain-snow line (Lundquist et al., 2008). In the Alps, mean snow depth, snow 122 cover duration and number of snowfall days have decreased since the early 1980s, although with 123 large regional and altitudinal variations (Laternser and Schneebeli, 2003). Changes in snow cover 124 may in turn affect mountain ecosystem hydrology (Gobiet et al., 2014), biogeochemical processes 125 in soil and water (Magnani et al., 2017), plant composition, phenology and structure (Grabherr et al. 126

127 1995). The insulating properties of snow influence the underlying soil temperature regime and the 128 extent to which soil is directly exposed to cold air temperatures in the winter (Edwards et al., 2007). 129 Indeed, mountain soils typically experience freezing conditions only during the early winter. After 130 the deposition of snow cover that insulates the underlying soils from low air temperatures, soils 131 remain unfrozen during most of the winter season (Jones, 1999).

A valuable volume of long-term ecological data that can be used for defining and testing the 132 consequences of climate change on mountain ecosystems is available from the LTER Network 133 (Long Term Ecosystem Research; http://www.lter-europe.net/). The LTER is an international 134 monitoring network that gathers multiyear high-quality ecological data that are periodically 135 136 collected to assess the impacts of global change on ecological processes. The operation of several 137 LTER sites distributed along the Apennines and the Alps offers an excellent resource to develop and test the effects of climate change on different types of mountain ecosystems. Indeed, long-term 138 ecosystem research has been successfully carried out adressing the impact of climate change in the 139 different high elevation ecosystems, and very interesting results have been found (Müller et al., 140 141 2010). However, these results have often been determined only at a site-specific or regional level. Based on the urgent demands for long-term research with comparative ecological analysis (Müller 142 et al. 2010), a comprehensive overview accounting for the effects of climate change in different 143 144 mountain ecosystems needs further attention and research efforts.

In this context, this paper presents a new analysis of existing ecological data for many LTER sites, both terrestrial and freshwaters, and aims to summarize the complex information obtained from the long-term observations of different mountain ecosystems in response to climate change. We aimed to assess and possibly synthetize the response of the main ecological processes in different mountain ecosystems to climate change. In particular, the ecological changes we tested with our analyses were: (i) the change in vegetation cover and C-uptake; (ii) the alteration of biogeochemical cycles in soils and water; and (iii) the change in phenology and biological diversity.

- 152 We focused on the following compartments and ecological parameters:
 - 6

soil: the interannual variability in soil temperature and nutrient cycling was investigated at one
 LTER site in the Alps in relation to snow cover duration and pedoclimatic conditions;

vegetation: we assessed changes in vegetation cover over time considering both regional scale
and elevation belts, using newly collected data from LTER high-elevation sites;

freshwater: we assessed interannual variability and long-term changes in selected chemical and
 biological variables in response to climate drivers at some LTER lake and river sites representative
 of different mountain areas.

160 In addition, we discuss previous and on-going studies in LTER mountain sites dealing with the 161 effects of climate drivers on additional ecological parameters, including grassland ecosystem 162 productivity, forest carbon storage and animal population dynamics.

163

164 2. RESEARCH SITES AND DATA ANALYSIS

165 2.1 Study area and climate driver description

We considered 20 research sites, representative of the Alps, from west to east (Italy, Switzerlandand Austria) and of the Apennines (Italy) (Tab. 1, Fig. 1).

The sites are located between 1300 and 3212 m a.s.l. The sites are not directly affected by 168 anthropogenic disturbance, or are natural sites under sustainable management or under mild 169 170 pressure (e.g., land abandonment, reduced grazing, sustainable forest management). Fourteen sites are terrestrial sites (forests, grasslands, alpine tundra and nival areas), and six are freshwater sites 171 (lakes and rivers). Details on site characteristics, the purpose and history of the research site and on-172 173 going studies can be found at the specific links in the DEIMS-DSR portal (Dynamic Ecological Information Management System - Site and dataset registry; https://data.lter-europe.net/deims/) 174 provided in Tab. 1. Long-term ecological data collected at the selected sites were used in this paper 175 for assessing decadal changes in soil properties, vegetation cover and chemical and biological 176 features of freshwater ecosystems. 177

178 Tab. 1 - LTER mountain sites considered. June anomaly refers to the air temperature anomaly (1995-2015) with respect to a 1961-1990 base period (see 179 180 Fig. 1).

| Site code | Site name | Elevation - average m a.s.l. | June anomaly | Site type | Parent site | Established | Site description in DEIMS |
|----------------|--|------------------------------------|-----------------|-------------|--|-------------|--|
| LTER_EU_IT_021 | Central Apennines: Gran Sasso d'Italia | 2210 | 1.46 | Terrestrial | IT01- Apennines - High elevation Ecosystems | 1986 | https://data.lter-europe.net/deims/site/lter_eu_it_021 |
| LTER_EU_IT_025 | Central Apennines: Velino Duchessa (VEL) | 2145 | 1.36 | Terrestrial | IT01- Apennines - High elevation Ecosystems | 1993 | https://data.lter-europe.net/deims/site/lter_eu_it_025 |
| LTER_EU_IT_022 | Central and southern Apennines: Majella-Matese (MAJ -MAT) | 2400 | 1.22 | Terrestrial | IT01- Apennines - High elevation Ecosystems | 2001 | https://data.lter-europe.net/deims/site/lter_eu_it_022 |
| LTER_EU_IT_023 | Northern Apennines (NAP) | 1900 | 3.02 | Terrestrial | IT01- Apennines - High elevation Ecosystems | 2001 | https://data.lter-europe.net/deims/site/lter_eu_it_023 |
| CH-VAL | W-Alpes: Alps of Valais-Entremont (Switzerland) (VAL) | 2777 | 1.11 | Terrestrial | Project GLORIA site, not yet in LTER network | 2001 | |
| IT-ADO | S-Alps, Dolomites (Italy) (ADO) | 2705 | 1.45 | Terrestrial | Project GLORIA site, not yet in LTER network | 2001 | |
| LTER_EU_IT_073 | W-Alpes: Mont Avic (MAV) | 2340 | 1.41 | Terrestrial | IT19 - High elevation sites in the NWAlps | 2001 | https://data.lter-europe.net/deims/site/lter_eu_it_073 |
| LTER_EU_AT_007 | E-Alps: Hochschwab (HSW) | 2100 | 0.85 | Terrestrial | LTES Platform Eisenwurzen (EW) | 1998 | https://data.lter-europe.net/deims/site/lter_eu_at_007 |
| LTER_EU_IT_074 | W-Alps: Cime Bianche | 3100 | 1.30 | Terrestrial | IT19 - High elevation sites in the NW Alps | 2006 | https://data.lter-europe.net/deims/site/lter_eu_it_074 |
| LTER_EU_IT_077 | W-Alpes: Torgnon grassland Tellinod | 2100 | 1.30 | Terrestrial | IT19 - High elevation sites in the NW Alps | 2008 | https://data.lter-europe.net/deims/site/lter_eu_it_077 |
| LTER_EU_IT_076 | W-Alpes: Istituto Scientifico Angelo Mosso | 2700 | 1.28 | Terrestrial | IT19 - High elevation sites in the NW Alps | 1928 | https://data.lter-europe.net/deims/site/lter_eu_it_076 |
| LTER_EU_IT_031 | Central Apennines: Collelongo-Selva Piana ABR1 | 1500 | 1.36 | Terrestrial | IT03-Forest of the Apennines | 1991 | https://data.lter-europe.net/deims/site/lter_eu_it_031 |
| LTER_EU_IT_033 | Central Apennines: Montagna di Torricchio | 1260 | 0.99 | Terrestrial | IT03-Forest of the Apennines | 1971 | https://data.lter-europe.net/deims/site/lter_eu_it_033 |
| LTER_EU_IT_109 | W- Alps: Gran Paradiso National Park | 2500 | 1.34 | Terrestrial | IT23 - Gran Paradiso National Park - Italy | 1922 | https://data.lter-europe.net/deims/site/lter_eu_it_109 |
| LTER_EU_IT_089 | W-Alps: Lake Paione Superiore | 2269 | 1.41 | Freshwater | IT09-Mountain Lakes | 1978 | https://data.lter-europe.net/deims/site/lter_eu_it_089 |
| LTER_EU_IT_088 | W-Alps:Lake Paione Inferiore | 2002 | 1.41 | Freshwater | IT09-Mountain Lakes | 1978 | https://data.lter-europe.net/deims/site/lter_eu_it_088 |
| LTER_EU_IT_047 | Northern Apennines:Lake Scuro Parmense | 1527 | 2.21 | Freshwater | IT09-Mountain Lakes | 1986 | https://data.lter-europe.net/deims/site/lter_eu_it_047 |
| LTER_EU_IT_046 | Northern ApenninesLake Santo Parmense | 1507 | 2.21 | Freshwater | IT09-Mountain Lakes | 1952 | https://data.lter-europe.net/deims/site/lter_eu_it_046 |
| LTER_EU_AT_012 | E-Alps: Gossenköllesee | 2417 | 1.24 | Freshwater | LTSER Platform Tyrolean Alps (TA) | 1975 | https://data.lter-europe.net/deims/site/lter_eu_at_012 |
| LTER_EU_IT_100 | E-Alps: Saldur River | 2000 | 1.46 | Freshwater | IT25 - Val Mazia/Matschertal | 2008 | https://data.lter-europe.net/deims/site/lter_eu_it_100 |



Fig. 1. Location of the LTER sites. The map shows the June temperature anomaly (1995-2015) with respect
to a 1961-1990 base period (map prepared from data provided by E-OBS, Haylock et al. 2008, resolution
0.25°; Coordinates are in ETRS-LAEA/ETRS89 – EPSG: 3035).

In the Northern Hemisphere, the IPCC (2014) indicated that the period between 1983 and 2012 was the warmest of the millennium. Moreover, the IPCC reported recent changes in precipitation patterns due to an increase in the atmospheric moisture content.

189 Extensive studies on alpine climate showed that air temperature increases were quite homogeneous190 over the Alps (EEA, 2009). The long-term climatic data available for the alpine tundra (LTER site

191 LTER_EU_IT_076 "Istituto Mosso", time span 1928-2013, station "Gabiet") showed an increase in 192 maximum air temperature equal to 0.015° C y⁻¹ (Fratianni et al., 2015). In the Ossola Valley, 193 Western Alps, where some LTER lake sites are located (LTER_EU_IT_088, LTER_EU_IT_089), 194 long-term air temperature data (since the 1930s) showed an average increase rate of 0.011° C y⁻¹ 195 (0.015° C y⁻¹ in the summer) (Rogora et al., 2004). In the central Apennines, an average temperature 196 increase rate of 0.027° C y⁻¹ occurred during the period 1950-2014 (Evangelista et al., 2016).

The research sites considered in this paper all experienced an increase in air temperature over the 197 past two decades, as shown by the June temperature anomaly (1991-2015) with respect to a 1961-198 1990 base period (Fig. 1). The increments range from 0.85°C at Hochschwab (LTER_AT_007) to 199 200 3.02°C in the Apennines (LTER_IT_023). We considered June temperatures because June represents a key month for mountain ecosystem phenology. For instance, June coincides with the 201 202 first part of the growing period, which is the most relevant for plant growth (Gottfried et al., 2012). 203 Moreover, at high elevations in the Alps and Apennines, June temperatures strongly influence snow melting rates, with significant effects on the beginning of the growing season (e.g., Sedlacek et al., 204 2015). June temperatures may also be critical for high-elevation lakes and rivers, because they also 205 affect the timing of ice-break (Preston et al., 2016) and can drive the onset of lake water 206 stratification and stream water discharge. Finally, June represents a crucial month for many 207 208 mountain vertebrates, including ungulates, because it corresponds to the birthing season and, at lower elevation (1300 – 1800 m a.s.l.), this month is also crucial for forest carbon sequestration. 209

Precipitation trends are more spatially variable compared to trends in air temperature (IPCC, 2014).
Climate warming is predicted to cause changes in the seasonality of precipitation, with an expected
increase in intra-annual variability, more intense precipitation extremes, and more potential for
flooding (Gobiet et al., 2014). Projected changes in precipitation, snow cover patterns and glacier
storage in the Alps will also alter runoff regimes, leading to more droughts in the summer (EEA,
2009).

Snow cover duration (SCD) is also an important driver of change in mountain ecosystems. A
reduction in the snow cover amount and extent has been described for areas in the Alps below 2000
m a.s.l. Specifically, the delayed onset of snow and the anticipated snowmelt contribute to an
overall decrease in SCD (Klein et al., 2016). A decrease in snow cover depth and SCD has been
specifically recorded in some of the analyzed LTER lake sites (Western Alps) over the last 30 years
(Rogora et al., 2013).

222

223 2.2 Data collection and analysis

224 The data analyses were partly performed on already existing datasets, developed in the framework of previous and on-going research projects (e.g., GLORIA: GLobal Observation Research Initiative 225 in Alpine environments; http://www.gloria.ac.at), and partly on datasets specifically developed for 226 this paper (e.g., lake chemistry). Information about the datasets for each site, their availability and 227 the methods used for generating the data are provided in DEIMS-DSR (Tab. 1). Some of the sites 228 included in our analysis are also part of the NEXTDATA special project "Data-LTER-Mountain" 229 (http://www.nextdataproject.it/). Within this project, a distributed system of archives and access 230 231 services to data and metadata of the Italian LTER sites located in mountain regions has been developed. 232

233

234 2.2.1 Snow cover duration and soil properties

To analyze the regional pattern of SCD and of the snow melting date we used soil temperatures 235 collected different LTER research sites (LTER_EU_IT_031, LTER_EU_IT_022, 236 at LTER_EU_IT_077 and LTER_EU_IT_076). We used thermistors combined with data loggers 237 placed at a soil depth of 10 cm for the measurement of the hourly soil temperature (instrument 238 sensitivity of \pm 0.1°C). The SCD at each study site was calculated based on the daily soil 239 240 temperature amplitude (Schmid et al. 2012). When the daily soil temperature amplitude remained within a range of 1 K, the day was defined as a "snow cover day" (Danby and Hik, 2007). The SCD 241

was calculated as the sum of the snow-covered days. When the daily mean soil temperature dropped
below and rose above 0°C, it was considered as a freeze/thaw cycle (FTC) (Phillips and Newlands,
2011) that approximately corresponded to the melting period. Then, the snow melting date (DSO1:
day since October 1st) was assessed.

To assess the impact of SCD changes on soil properties, i.e., temperature and moisture during the 246 growing season, microbial carbon, microbial nitrogen, ammonium, nitrate, dissolved organic carbon 247 248 and dissolved organic nitrogen, we used both meteorological and physico-chemical soil data recorded in 2008-2016 at the LTER site LTER_EU_IT_076, located close to Monte Rosa Massif. 249 The study was conducted at three high-elevation subsites located in the upper part of a glacial 250 251 valley, at an elevation ranging between 2500 and 2800 m a.s.l. (Table S1). Each subsite consisted of three plots. Soil temperatures collected by data loggers and thermistors were used for calculating 252 the beginning of the growing season that was defined as the time when weekly topsoil temperature 253 254 reached 3°C (Paulsen and Körner, 2014). For soil characteristics, a soil sampling campaign was performed in mid-September, approximately at the end of the growing season. Every year (2008-255 256 2016), three soil samples (A horizon, 0-10 cm depth) were collected at each subsite, which in turn consisted of three subsamples in each plot. Samples were homogenized by sieving at 2 mm within 257 24 h of collection. At each sampling time, subsamples were dried at 100°C overnight to obtain the 258 259 gravimetric water content. An aliquot of 20- g of fresh soil was extracted with 100 mL K₂SO₄ 0.5 M as described by Brooks et al. (1996), whereas a 10-g aliquot was subjected to chloroform 260 fumigation for 18 h before extraction with 50 mL of K₂SO₄ 0.5 M. Dissolved organic carbon was 261 determined with 0.45 µm membrane-filtered K₂SO₄ extracts (extractable DOC) with a total organic 262 carbon (TOC) analyzer (Elementar, Vario TOC, Hanau, Germany). Microbial carbon (Cmicr) was 263 calculated from the difference in DOC between fumigated and non-fumigated samples and was 264 corrected by a recovery factor of 0.45 (Brookes et al., 1985). The ammonium in the K₂SO₄ extracts 265 (extractable N-NH4⁺) was diffused into a H₂SO₄ 0.01M trap after treatment with MgO (Bremner, 266 1965), and the trapped NH₄⁺ was determined colorimetrically (Crooke and Simpson, 1971). The 267

nitrate (extractable N-NO₃⁻) concentration in the same extracts was determined colorimetrically as NH₄⁺ after reduction with Devarda's alloy (Williams et al., 1995). Total dissolved nitrogen (TDN) in the extracts was determined as reported for DOC. Dissolved organic nitrogen (extractable DON) was determined as the difference between TDN and inorganic nitrogen (N-NH₄⁺ + N-NO₃⁻) in the extracts. Microbial nitrogen (Nmicr) was calculated from the difference in TDN between the fumigated and non-fumigated samples and was corrected by a recovery factor of 0.54 (Brookes et al., 1985).

275

276 2.2.2 Vegetation cover

277 We used vegetation data that were collected in 2001 and 2015 in permanent plots at eight high mountain study areas of the LTER and GLORIA networks and distributed in the Italian Apennines 278 and Alps and in the Austrian and Swiss Alps (Tab. S2). According to the GLORIA sampling design 279 280 (Pauli et al., 2015), each site comprises 2-4 summits along an elevation gradient. For each summit, a 3×3 m² grid was established for each cardinal direction at 5 m below the summit peak. In the four 281 282 $1-m^2$ corner plots (4 quadrats) of the grids, the percentage cover for each plant species was estimated. At one site (Velino: VEL), the plant species cover was collected on permanent plots 283 placed along an elevational gradient that was divided into six 100 m elevation bands (from 1800 to 284 285 \sim 2400 m a.s.l.; Theurillat et al., 2007). For each band, four to six 2 m x 2 m vegetation plots were sampled. 286

We analyzed vegetation cover change over time (T1 - T2) for mountain sites (i.e., considering all the plots grouped by site) and vegetation belts (i.e., grouping plots by vegetation belt). The vegetation belts present in the analyzed sites were defined according to Pignatti (1979) and Theurillat et al. (1998).

We analyzed changes in vegetation cover by first calculating the total vegetation cover per plot as the sum of the cover estimates of the individual plant species as a proxy, non-destructive measure, of aboveground biomass (Fry et al., 2013). Then, we quantified vegetation change for each site and

vegetation belt, by calculating the effect size obtained by computing the weighted average of the 294 295 standardized difference (based on pooled variance measures) between the mean cover values on the two sampled dates (T1 and T2; unbiased estimator Hedge's g; Hedges, 1981). This standardized 296 difference, which estimates the effect size as the difference between T2 and T1, provides an 297 estimate of the magnitude of an effect, i.e., the cover change between the sampled dates, when data 298 collection varies among studies (e.g. Elmendorf et al., 2012). The effect size is positive when the 299 300 vegetation cover increases over time and is negative when the cover decreases. We randomly chose one of the four plots in each cardinal direction for the GLORIA sites and one from each band for 301 the Velino site. For each randomly extracted plot, we calculated the difference between cover 302 303 values on the two dates (T2-T1), and based on these differences, we computed the median and the 95% confidence intervals of Hedge's g by using the BootES package (Kirby and Gerlanc, 2013) in 304 the R statistical software (R Development Core Team, 2011). In addition to the weighted median 305 306 effect size, we also reported the median percent change in all the studies.

307

308 2.2.3 Freshwater chemistry and biology

The high elevation LTER lakes considered in this paper (Tab. S3) are located both in the Alps (Italy 309 and Austria) and in the Apennines (Central Italy). They have different origin, morphometry and 310 surrounding land cover characteristics. However, they share some common features, such as an 311 312 oligotrophic status, diluted waters with low solute content and relatively simple food webs compared to lowland lakes (Rogora et al., 2013; Sommaruga 2001). To test for common trends 313 duting 1980-2016, the following variables were considered: conductivity, alkalinity, sulphate and 314 nitrate ions. Because data have been collected with different sampling methods (e.g., vertical 315 316 profiles at the deepest points, sampling of lake outlets or at the lake shores) and frequency, we 317 selected surface data representative of the late summer or early autumn period, when lakes are more stable and uniform from a chemical point of view. Chemical analyses were performed according to 318

standard methods for freshwater (APHA AWWA WEF, 2012). We assessed trend significance and 319 320 slope by the Mann-Kendall test (Hirsch et al., 1982) and Sen's method (Sen, 1968), respectively. In addition to chemical trends, long-term biological data available for two lakes in the Apennines 321 were analyzed (SCU and SAN; Tab. S3). The two lakes are characterized by different size, trophic 322 structure, and level of anthropogenic disturbance. Extensive information on the lakes' chemico-323 physical and biological characteristics can be found in Bondavalli et al. (2006) and Bertani et al. 324 325 (2016). Monthly values of water temperature throughout the water column, chlorophyll-a concentrations and zooplankton species abundance during the open-water season (May-October) are 326 available for these two lakes for the following periods: SAN, 1971-1975 and 2012 and SCU, 1986-327 328 2012. Monthly average air temperatures duting 1971-2012 were derived from a weather station near the two lakes (Passo della Cisa: 44°26' N, 9°25' E) (data downloaded from the National Oceanic 329 and Atmospheric Administration (NOAA) website; www.climate.gov). From the same website, we 330 also downloaded monthly values of the East Atlantic pattern (EA) climatic index, a teleconnection 331 that influences climate in the Mediterranean region throughout the year (Kutiel and Benaroch, 332 2002). For both air temperature and EA we calculated seasonal averages for the winter (December 333 through February), spring (March through May), summer (June through August) and autumn 334 (September through November). We hypothesized that positive values of the EA climatic index 335 336 would be associated with higher air and water temperatures and earlier seasonal plankton development. 337

For the two lakes, we analyzed interannual changes in the phenology of chlorophyll-a (a proxy for phytoplankton abundance) and zooplankton taxa by calculating different phenology metrics. Specifically, we estimated the timing of the seasonal phytoplankton peak each year by calculating the "center of gravity" for monthly chlorophyll-a values across the open-water season (Edwards and Richardson, 2004; Thackeray et al., 2012). For each of the dominant zooplankton taxa, we characterized population phenology each year by calculating the date of its first appearance and the date of its peak population abundance (Adrian et al., 2006).

We tested for relationships between large-scale climatic patterns (EA) and interannual variability in both local climate features (air and water temperature) and plankton phenology by calculating correlations (Spearman's correlation coefficient) between the average seasonal EA values and 1) corresponding average seasonal air and water temperature values and 2) phyto- and zooplankton phenology metrics.

Benthic community structure was evaluated at the LTER river site LTER EU IT 097 350 Matsch/Mazia Valley (Tab. S3) in the upper Vinschgau/Venosta Valley (South Tyrol, Italy). The 351 Saldura Stream, draining the Matsch/Mazia Valley, one of the driest valleys of the Alps, represents 352 an ideal site to focus on climate change impacts. The Matsch/Mazia Valley is characterized by the 353 354 presence of a glacier that is rapidly melting. The glacier extends from 2,800 m to 3,500 m a.s.l. To evaluate the influence of the glacier and the spatial patterns of the macrobenthic assemblage, three 355 sampling stations were selected along the main stream at increasing distances from the source 356 357 (located from 2400 m a.s.l. to 1500 m a.s.l.). The macrobenthic community was analyzed by applying the multi-habitat sampling methodology using a standard Surber Sampler. The biological 358 359 samples were integrated by chemico-physical analyses of the running water to correlate community composition and diversity with environmental variables. We assessed temporal and spatial 360 distribution patterns of the macroinvertebrate community and related the biological results with the 361 362 changing abiotic conditions.

363

364 3. RESULTS AND DISCUSSION

365 3.1 Snow cover duration and effects on soil properties and animal population dynamics

The SCD and melting date calculated from the soil temperature data greatly varied across elevational and latitudinal gradients, from short SCD (~100 days) and early snow melting dates (DSO1~ 200) in the lower altitudes (~1500 m a.s.l.) and latitudes (Lat. 41 N) to long SDC (~250 days) and late snow melting dates (DSO1~300) in the higher altitudes (~2800 m a.s.l.) and latitudes 370 (Lat. 46 N) (Fig. 2). Our results agree with previous studies reporting a strong relation between the
371 SCD and the snow melt day for the Swiss Alps (Klein et al., 2016).

372



373 374

Fig. 2 - Melting dates in DSO1 (Day Since October 1st) (above) and SCD (days) (below) calculated from soil
temperature data at selected LTER sites across elevation and latitude gradients. Yearly average values for the
period 2008-2015. For more details about analyzed LTER sites see Tab. 1.

378

The analysis of soil temperature data collected at the research site Istituto Scientifico Mosso 379 380 (LTER_EU_IT_076) demonstrated that the mean soil temperature of the snow cover season is - $0.19^{\circ}C$ (±0.31). The beginning of the snow cover season showed lower temporal variability than the 381 382 end of the SCD, ranging between October 27 (± 15 days) and June 24 (± 20 days), respectively. The analysis of the relation among SCD and both soil temperature and microbial biomass recorded 383 during the growing season showed the occurrence of significant negative correlations (r=-0.621, 384 p<0.01 and r=-0.566, p<0.01, respectively; Fig. 3). As observed by Magnani et al. (2017), a short 385 SCD may increase soil temperature and substrate availability during the subsequent growing 386 387 season, favoring soil microbial biomass. 388 Soil N-NH₄ (r=-0282; p<0.05), DOC (r=-0.427; p<0.01) and N_{micr} (r=-0.403; p<0.01) were

Soll N-NH₄ (r=-0282; p<0.05), DOC (r=-0.427; p<0.01) and N_{micr} (r=-0.403; p<0.01) were inversely correlated with SCD, while N-NO₃ showed a sharp increase during 2008-2009,

characterized by rather extreme meteorological conditions; in particular, the 2007-2008 winter 390 391 season was characterized by a thinner snow depth (max approximately 200 cm) than the average snow depth value (289 cm, time-span 2008-2016), while the 2008-2009 winter season had a thicker 392 snow depth (max of 560 cm). The little snowpack in 2007-2008 caused a large number of soil 393 394 FTCs, which could have contributed to the destruction of the soil aggregates and the release of previously unavailable organic N (Freppaz et al., 2007). The thick snowpack recorded during the 395 next winter season could have released a greater N-NO₃ input into the soil than average during 396 397 snow melt.



398

Fig. 3 - Scatterplots between SCD and soil mean temperature (r = -0.62, p < 0.01) (left panel) and between SCD and C_{micr} (r=-0.57, p < 0.01) (right panel) measured in the growing season considering all the study subsites of LTER_EU_IT_076 (site 1, site 3, and site 5; Table S1) during 2008-2016 (n = 79).

Snow cover is also an important driver for animal population dynamics. Long-term studies that 403 have been performed at the LTER site LTER_EU_IT_109 Gran Paradiso National Park since the 404 405 1950s showed how the dynamics of the Alpine ibex (*Capra ibex*) prior to 1980s was mainly driven by the average winter snow depth that represented a limiting factor for population growth (Jacobson 406 et al., 2004). In general, the snow cover effect on Alpine ibex survival was not linear and not equal 407 408 for all sex and age classes, and the snow effect was amplified during years of high animal densities (Mignatti et al., 2012). Snow precipitation patterns proved to also be important for vegetation 409 growth and consequently for resource availability (Pettorelli et al., 2007). 410

412 **3.2** Vegetation cover at high elevations and carbon sequestration in mountain forests

The analysis of vegetation cover changes showed positive effect size estimates for all high mountain sites (Fig. 4) but with site-specific magnitudes. In particular, the Majella site (CAM) had the largest positive and significant effect size (Hedge's g=0.70, 95% CI, 1.45 - 0.08), followed by Dolomites (ADO) (Hedge's g=0.55, 95% CI, 0.86 - 0.29).



417

Fig. 4. Median effect sizes (Hedge's g) of temporal change on vegetation cover for each site separately (sites are arranged from south to north). Error bars show 95% confidence intervals. An effect size is significantly different from zero when its 95% confidence interval does not overlap zero. Median percent change recorded over all plots is shown above the corresponding bar. Abbreviations refer to Table 1. The number of plots per site is indicated in parenthesis.

423

A general tendency towards increased vegetation cover was also observed in Matese (SAM), Velino
(VEL), Northern Apennines (NAP), Mont Avic (MAV), Hochschwab (HSW) and Valais-Entremont
(VAL).

The analyses of plant cover changes per vegetation belt showed a positive effect size for treeline, subalpine and alpine belts and no effect for the nival belt (Fig. 5). The increase in plant cover over the last fifteen years is most likely related to a greening process (Carlson et al., 2017), which reduced vegetation gaps and was promoted by the expansion of the most thermophilic species already present in the plots and/or to the immigration of species from lower elevations (Gottfried et 432 al., 2012).



433

Indeed, global warming affects high mountain ecosystems by increases in temperature, early 438 439 snowmelt and a prolonged growing season (Pauli et al., 2012). These factors might have played a 440 key role in the observed increase in plant cover. In fact, the air temperatures before snowmelt and after the meltdown (i.e., the May/June temperatures) are the main factor affecting plant growth in 441 these ecosystems (Jonas et al., 2008; Rammig et al., 2010; Carbognani et al., 2016). However, 442 climate change probably interacted with land-use change, which can exacerbate the effects of 443 444 climate warming on mountainous vegetation (Theurillat and Guisan, 2001), although such an issue is still largely unexplored (Chelli et al., 2017). 445

On European mountain summits, increasing atmospheric temperatures already have resulted in a measurable expansion of thermophilic species that increased their cover in situ and migrated from lower elevations into the alpine lifezone (Grabherr et al., 1995; Gottfried et al., 2012; Jiménez-Alfaro et al. 2014). Our results agree with recent local research that provided evidence of an

<sup>Fig. 5. Median effect sizes (Hedge's g) of temporal change on vegetation cover grouped by vegetation belt.
Error bars show 95% confidence intervals. An effect size is significantly different from zero when its 95%
CI does not overlap zero. The number of plots per vegetation belt is indicated in parenthesis.</sup>

increase in caespitose hemicryptophytes and suffruticose chamaephytes frequencies on CAM
summits (Stanisci et al., 2016) and an overall increase in species frequency on ADO summits
(Erschbamer et al., 2011; Unterluggauer et al., 2016).

The temporal analysis of vegetation belts at the LTER and GLORIA mountain sites highlighted a 453 significant increment in vegetation cover at these alpine sites, followed by the subalpine ones, 454 whereas sites located at the treeline belt showed negligible variation, and vegetation cover at the 455 456 nival belt did not show any change. The specific behavior of vegetation cover on each elevational belt probably reflects the natural structure patterns of plant communities across the elevation 457 458 gradient. For instance, the cover of subalpine and alpine sparse/open vegetation in ridge habitats 459 significantly increased, appearing more prone to a greening process. This process is likely due to the expansion of plant species already present at the site and to colonization events, which have 460 been recorded in previous papers based on long-term vegetation analysis in alpine environments 461 462 (Walther et al., 2005; Vittoz et al., 2009b; Matteodo et al., 2016; Carbognani et al., 2014).

463 Conversely, although nival ridges experienced changes in species composition (e.g., Pauli et al.
464 2012), this did not seem to result in an increase in vegetation cover. The environmental constraints
465 at these elevations likely do not allow a greening process, at least until now, but only plant species
466 turnover.

467 Previous vegetation studies carried out at high-elevation LTER and GLORIA sites in the Alps and Apennines indeed revealed changes in plant community structure and composition. Specifically, an 468 increase in species richness (Erschbamer et al., 2008; Erschbamer et al., 2011; Pauli et al. 2012; 469 Unterluggauer et al., 2016) and changes in community compositions (Petriccione, 2005; 470 Erschbamer et al., 2008; Erschbamer et al., 2011; Stanisci et al. 2016) were observed in response to 471 472 temperature increases and changes in precipitation patterns (Petriccione, 2005). For instance, Unterluggauer et al. (2016) observed a 9% to 64% increase in species richness over a period of 14 473 years in the Southern Alps (Dolomites). Similarly, Petriccione (2005) observed a 10 to 20% 474 increase in species richness at the research site Gran Sasso d'Italia (LTER_EU_IT_021) over a 475

476 period of nine years.

As observed on other European summits (Gottfried et al., 2012), a thermophilization process also 477 occurred at the Apennine and Alps LTER and GLORIA sites (Theurillat and Guisan, 2001; Pauli et 478 al., 2007; Holzinger et al., 2008; Parolo and Rossi 2008; Engler et al., 2011, Erschbamer et al., 479 480 2008, 2011; Matteodo et al., 2013; Cannone and Pignatti, 2014; Stanisci et al., 2016) and the arrival of new species typical of lower elevation belts was registered (Petriccione, 2005; Vittoz et al., 2008; 481 482 Erschbamer et al., 2009; Pauli et al., 2012; Evangelista et al., 2016; Unterluggauer et al., 2016). In the central Apennines, a general increase of chamaephytes, drought-tolerant species (Petriccione, 483 2005) and graminoids (Stanisci et al., 2016) was recorded too. Furthermore, graminoids 484 485 demonstrated better growth performance under a warm and dry climate, which is most likely related to their strategy to allocate resources to belowground parts (Wellstein et al. 2017). 486

487 Our results, based on plant cover data recorded in permanent plots, highlight that the observed 488 changes in species composition and structure in alpine and subalpine ridge habitats of the Alps and 489 Apennines are causing a greening trend. Our results are largely consistent with those determined 490 through remote sensing studies (Carlson et al. 2017), which identified on-going greening trends in 491 over half (67%) of the above treeline habitats in the French Alps.

As vegetation cover may be considered a proxy of standing biomass (Fry et al. 2013), its increase
affects ecosystem productivity and services in mountain landscapes.

Indeed, climate warming effects, changes in rainfall seasonality and water availability have been proven to be important for ecosystem productivity (Rammig et al., 2010). This issue has been investigated at the Forests of the Apennines (LTER_EU_IT_003 site; Tab. 1) research site where changes in aboveground net primary productivity (ANPP) in response to a shift in the precipitation regime have been detected (Chelli et al., 2016).

499 Ferretti et al. (2014), in a study including LTER forest sites in the Alps and Apennines, 500 demonstrated that an increase in nitrogen deposition had a positive effect on tree growth (measured 501 as basal area increment) and on aboveground net primary productivity (ANPP), thus promoting

carbon sequestration. However, reduction in rainfall can override such positive effects (Chelli et al. 502 503 2017). Long-term studies performed at a beech forest in the Apennines (LTER EU IT 031; table 1) showed that carbon (C) sequestration depends on both water availability (precipitation) and air 504 temperature. Lower C sequestration in the beech forest was detected in the years characterized by 505 below-average summer precipitation especially when there was also warmer temperatures 506 (Scarascia and Matteucci, 2014; Mazzenga, 2017). Furthermore, in these beech forests, a significant 507 508 increase in the growing season length and a general increase in the annual net C sequestration were detected from remotely sensed data during 2000 – 2015 (Mazzenga, 2017). 509

510

511 **3.3** Long-term changes in water chemistry

The studied mountain lakes (Tab. S1) are representative of varying levels of solute content and buffer capacities, from very diluted water (LPS, LPI: conductivity < 10 μ S cm⁻¹ at 20°C; alkalinity 20-50 μ eq L⁻¹) to moderately diluted waters (GKS, SCU: conductivity 25-30 μ S cm⁻¹; alkalinity 100-150 μ eq L⁻¹) or highly mineralized water (LBS: 60 μ S cm⁻¹; alkalinity 400-500 μ eq L⁻¹). All of the lakes are oligotrophic or ultraoligotrophic systems (total phosphorus < 10 μ g P L⁻¹).

All the lakes showed an increase in alkalinity values (Fig. 6). These trends were highly significant 517 (p<0.001) according to the Mann-Kendall test. Slopes varied from 0.8-0.9 μ eq L⁻¹ v⁻¹ (LPI, LPS, 518 GKS) to 3.9 μ eq L⁻¹ y⁻¹ (LBS). In the LPS and LPI, the alkalinity trend was mainly a sign of 519 acidification recovery in response to a decrease in acid deposition after a period of acidification in 520 the 1980s (Rogora et al., 2013). Conductivity also increased over time in the GKS and LBS 521 (p<0.001; slopes 0.16 and 0.56 μ S cm⁻¹ y⁻¹, respectively), whereas it slightly decreased in the LPI 522 and LPS. Lake Scuro showed high interannual variability in both conductivity and alkalinity, with a 523 tendency towards increasing values for the latter variable (from 100-120 to 200 μ eg L⁻¹). 524

Highly significant negative trends in SO₄ concentrations were observed in the LPI and LPS (-6.5 μ eq L⁻¹ y⁻¹), due to a sharp decrease in SO₄ deposition that occurred throughout Europe over the last three decades (Rogora et al., 2006). In contrast, SO₄ increased significantly in the GKS and LBS

(slopes of 3.7 and 6.0 μ eq L⁻¹ y⁻¹, respectively). These trends may be ascribed to an enhanced 528 release of sulphate from the rocks and soils in the catchments of those two lakes. Both lakes also 529 showed positive trends in base cation (calcium and magnesium) concentrations. This increase in the 530 content of major ions in lake water (sulphate, bicarbonate, base cations) has been reported 531 532 elsewhere in the Alps (Sommaruga-Wögrath et al., 1997; Rogora et al., 2013; Thies et al., 2013; Ilyashuk et al., 2014) and in other remote regions (Williams et al., 2006; Kokelj et al., 2009; Preston 533 et al., 2016; Salerno et al., 2016) where it was ascribed to climate drivers, including a decrease in 534 the amount and extent of snow cover, a shift in ice-off dates, glacier retreat, and permafrost 535 thawing. Low rates of runoff in the summer of dry and warm years may also contribute to 536 537 concentrated solutes in the runoff water and in the lake (Preston et al., 2016).



538

Fig. 6 – Time series of selected water chemical variables at LTER lake sites in the Italian and Austrian Alps
and in the Northern Apennines, Italy: a) conductivity at 20°C; b) nitrate; c) alkalinity; d) sulphate. For the
lake acronyms, see Tab. S3.

⁵⁴³ The study sites in the Alps showed a common trend in decreasing nitrate concentrations over the

past decade (Fig. 6). The trend was significant at the GKS, LPS (p<0.01), LPI and LBS (p<0.05)

sites. The trend slopes varied between $-2.0/-2.5 \ \mu g \ L^{-1} \ y^{-1}$ in the LPI and LBS and $-2.8 \ \mu g \ L^{-1} \ y^{-1}$ in the GKS and LPS. Lakes in the Apennines showed a high interannual variability (e.g., NO₃ in Lake Scuro varied from 20-30 to 200 $\mu g \ N \ L^{-1}$), without any evidence of a trend.

The negative temporal trends observed for NO₃ concentrations could be related to an increase in 548 primary productivity in the lakes in response to climate warming, promoting nitrogen uptake 549 (Sommaruga-Wögrath et al., 1997). Nitrogen uptake also occurs in lake catchments and is regulated 550 551 by the extent of soil and vegetation (Marchetto et al., 1995). No specific studies have been performed at the lake sites to assess potential changes in plant cover in the catchments. However, it 552 may be hypothesized that the increase in plant cover observed during the last two decades at the 553 554 LTER vegetation sites (see paragraph 3.2) has taken place in the lake areas too, contributing to the increase in N retention and decrease in NO₃ export to the surface waters. Furthermore, changes in 555 depth and extent of snow cover have been shown to affect soil nutrient dynamics (see paragraph 556 557 3.1), thereby regulating N release to the water compartment. In general, soil, vegetation and water are strongly interconnected with each other in these high-altitude environments (Magnani et al., 558 559 2017); the observed changes in lake water NO₃ are probably the result of several interacting processes. Besides climate, a decrease in N input from the atmosphere is likely to have played a role 560 in the observed trend in NO₃, especially for acid-sensitive lakes in the Alps; atmospheric deposition 561 562 of inorganic nitrogen has recently decreased as an effect of decreasing emissions of N compounds, mainly in the oxidized form (Waldner et al., 2014; Rogora et al., 2016). The effects of decreasing N 563 deposition on NO₃ levels in rivers and lakes have been widespread, with several monitoring sites in 564 Europe showing a significant negative trend in NO₃ concentrations (Garmo et al., 2014). 565

566

567 **3.4 Biological response in lakes and rivers**

568 *3.4.1 Large-scale patterns*

The effect of a large-scale climatic pattern (EA: East Atlantic pattern climatic index) on plankton
phenology was tested in two Apennine lakes (LTER_EU_IT_046 and LTER_EU_IT_047; Tab. S3).

In Lake Santo, we found a positive correlation between the spring EA values and June water 571 temperatures (Spearman's rho=0.66, p < 0.05; not shown in tables), while in Lake Scuro, the spring 572 EA was positively correlated with May water temperatures (Spearman's rho=0.67, p < 0.05; not 573 shown in tables). In Lake Santo, we observed significant negative correlations between the spring 574 EA values and the center of gravity calculated for chlorophyll-a at the surface, intermediate, and 575 bottom layers, respectively. We also found significant negative correlations between the spring EA 576 577 values and the date of the first appearance of several of the most abundant zooplankton taxa, including the dominant microcrustaceans (Daphnia longispina, Bosmina longirostris, and 578 579 *Eudiaptomus intermedius*) (Tab. 2).

We did not find significant relationships between the proxies of phytoplankton and zooplankton phenology (chlorophyll-*a* center of gravity, date of peak of chlorophyll-*a* concentration, dates of first seasonal appearance of zooplankton taxa) in Lake Santo. In Lake Scuro, the dates of the first seasonal appearance of several zooplankton taxa were positively related to the corresponding dates of peak chlorophyll concentrations (Tab. 2), while both the phytoplankton and zooplankton phenological proxies did not show any relationship with the EA values.

Our results for Lake Santo suggest that large-scale climate variations may be associated with 586 changes in lake plankton phenology, likely because of changes in local climate (e.g., air 587 588 temperature) and lake thermal dynamics. Specifically, in Lake Santo, we observed that years with positive spring EA values were characterized by higher spring air temperatures, warmer June water 589 temperatures, and earlier seasonal development of both phytoplankton (represented by chlorophyll-590 a) and key zooplankton taxa. The lack of similar climatic signatures on plankton dynamics in Lake 591 Scuro is most likely due to the relatively small size and substantially reduced thermal inertia of this 592 lake, resulting in a markedly higher sensitivity of Lake Scuro to local meteorological variability and 593 thereby masking the potential impacts of large-scale climatic patterns when compared to Lake 594 Santo. On the other hand, we found significant correlations between the phytoplankton and 595 zooplankton proxies in Lake Scuro, indicating a stronger influence of interspecific interactions in 596

597 this lake.

Tab. 2 - Spearman's correlation values between: a) spring EA values and plankton phenology metrics for
Lake Santo; b) phyto- and zooplankton phenology metrics for Lake Scuro. CG: chlorophyll-a center of
gravity calculated for the surface (sur), intermediate (int) and bottom (bot) layers of the water column;
ChlaMax: date of peak chlorophyll-a concentration; C1, 2, 3: 1st, 2nd, and 3rd copepodite stages; ns: not
significant.

603

| | EAspr | ChlaMax |
|--------------------------------------|-------|---------|
| | (SAN) | (SCU) |
| Phytoplankton | | |
| CGsur | -0.68 | - |
| CGint | -0.70 | - |
| CGbot | -0.75 | - |
| Zooplankton (date of 1st appearance) | | |
| Eudiaptomus intermedius ovigerous F | -0.79 | ns |
| Eudiaptomus intermedius nauplii | -0.80 | ns |
| Eudiaptomus intermedius C1 | ns | 0.77 |
| Eudiaptomus intermedius C2 | ns | 0.68 |
| Eudiaptomus intermedius C3 | ns | 0.68 |
| Cyclopoid copepodites | ns | 0.66 |
| Mesocyclops leuckarti | ns | 0.69 |
| Conochilus gr. unicornis-hippocrepis | ns | 0.66 |
| Daphnia longispina | -0.80 | ns |
| Bosmina longirostris | -0.76 | ns |
| Ascomorpha ecaudis | -0.69 | ns |
| Kellicottia longispina | -0.69 | ns |
| Keratella quadrata | -0.69 | ns |
| Synchaeta gr. stylata-pectinata | -0.69 | ns |
| Zooplankton (date of peak) | | |
| Eudiaptomus intermedius nauplii | ns | 0.87 |
| Eudiaptomus intermedius C2 | ns | 0.62 |
| Keratella cochlearis | ns | 0.57 |
| Cyclopoid nauplii | ns | 0.69 |
| Pleurata sp. | ns | 0.17 |

604 605

Overall, these results indicate that large-scale climate indices can be useful indicators of climate
variation at a local scale. The EA, in particular, was confirmed as a relevant index for the
Mediterranean area (Salmaso et al., 2012). However, the response of lakes to large-scale climatic

patterns is largely dependent on the thermal structure and mixing regime of lakes (Gerten andAdrian, 2001).

611 3.4.2 Local patterns

The effects of local patterns, mainly abiotic parameters, on benthic communities were investigated 612 613 at the LTER site Matsch/Mazia Valley (LTER_EU_IT_100). Long-term data showed clear seasonal distribution patterns; the increased discharge at snowmelt during June and July led to a sharp 614 615 decrease of faunal density and number of taxa (Fig. 7). A significant negative correlation was found between the monthly discharge and number of individuals (r = -0.73; p<0.001). The presence of a 616 glacier within the drainage basin also played a role, by affecting abiotic parameters (primarily water 617 618 discharge) over a wide range of time scales, with fundamental implications for the whole river 619 system.

620





<sup>Fig. 7 – Time series of monthly mean discharge and number of macrobenthic individuals at one sampling
station located at 2340 m a.s.l. on the Saldur Stream (Matsch/Mazia Valley; LTER_EU_IT_100).</sup>

624

These results demonstrate that, in addition to large-scale patterns, minor changes in environmental conditions can also have significant consequences on biological communities in mountain lakes and streams (Wallace and Webster, 1996). In particular, the snow melting process significantly modifies the biological communities of stream invertebrates in the Saldur stream (Fig. 7). Benthic

community structure in mountain streams is a result of complex environmental interactions (Milner 629 630 et al. 2001; Zemp at al., 2009; Lencioni and Spitale, 2015; Niedrist and Füreder, 2017). Therefore, the understanding of hydro-ecological relationships is essential for the development of effective 631 conservation strategies for alpine rivers. Long-term observations on benthic invertebrate 632 communities may enable assessments of the potential impacts of global change on stream 633 ecosystems (Jourdan et al., 2018). In particular, the community composition of the numerous small 634 alpine valleys, which are often not investigated from the faunistic point of view, may be an 635 important proxy for environmental changes, including climate change. 636

Besides the long-term effects of climate change, high-elevation ecosystems may also be affected by 637 638 extreme climatic events such as heat waves, droughts, heavy rainfall and floods (Jones, 2013). Studies at the survey lakes in the Western Alps, Italy, belonging to the parent site 639 LTER EU IT 009 Mountain Lakes, showed that climatic factors, particularly air temperature and 640 641 SCD, interact with atmospheric deposition and determine short-term changes in lake water e.g., heavy rainfall or snowy winters caused a temporary decrease in the alkalinity pool in the lakes by 642 dilution and a simultaneous pulse of NO3 to the lake, with an overall acidification effect (Rogora et 643 al., 2013). The impact of extreme climatic events on ecological processes was also addressed at the 644 LTER site LTER_EU_IT_047 Lake Scuro Parmense; Bertani et al. (2016) observed a shift from an 645 646 unvegetated to a macrophyte-dominated regime as a result of the 2003 heat wave. Some of the observed changes in the lake food web persisted after 2003, suggesting that abrupt and long-lasting 647 ecosystem-level reorganizations may occur in small mountain lakes as an effect of extreme events. 648

649

650 Conclusions

651 The long-term ecological analysis we performed, based on data obtained from permanent plots, 652 provided evidence that mountain ecosystems in the Alps and Apennines, both terrestrial and 653 freshwater, show varying levels of effects in response to climate change.

654 The results of our analyses and the review of the results gathered at the study sites from previous

and on-going studies highlight that climate change effects are mainly indirect and result from multiple, interacting processes. To assess these changes, there is a need for strong partnerships in mountain ecosystem observation and research and for multidisciplinary approaches, encompassing the distinction between different types of ecosystems (Mirtl et al., 2018).

The observed long-term ecological changes include the increase in vegetation cover and in soil 659 microbial biomass in alpine and subalpine summits, and the increase in C uptake in mountain 660 661 forests. The interannual variability in snow cover duration plays a relevant role in nutrient cycles, both in soils and in surface waters, and snow cover change, when coupled with climate-related 662 vegetation phenology, was also proven to affect animal population dynamics, namely, some glacial 663 664 follower species, such as the alpine ibex. Snow- and ice-melting processes also affect biological communities of glacier-fed streams by interacting with abiotic parameters such as water discharge 665 and turbidity. 666

In addition to long-term changes, short-term episodes or extreme events also proved to be relevant for mountain ecosystems, causing, for instance, a regime shift in response to heat waves, pulses of nutrient or chemicals to lake water at snowmelt and sudden changes in the nutrient dynamics in soils.

The joint analyses we provided demonstrate that long-term research is essential to understanding mountain ecosystem complexity and dynamic. The results also highlighted the great potential for further scientific advances that rely on international collaboration and integration. From this perspective, the LTER is an ideal network for improving our knowledge on sensitive ecosystems such as mountain soils, vegetation and freshwater lakes and streams.

Our effort of combining a huge amount of data gathered from different ecosystem types also demonstrates the limits of such an approach; there is a strong need for adopting co-located monitoring site networks (Haase et al. 2018) to improve our ability to obtain sound results from cross-site analysis. Moreover, a useful tool would consists of the adoption of site and dataset registries, providing access to site metadata and information on existing collaborative networks and

681 research platforms.

682 Nevertheless, there is a need for further studies, in particular, short-term analyses with fine spatial 683 and temporal resolutions to improve our understanding of the response to extreme events and an 684 effort to increase comparability and standardize protocols across networks to clarify local patterns 685 from global patterns.

The outcomes of this paper demonstrate that LTER mountain sites would gain additional value from the development and improvement of joint networks, indicators, and methodologies. This approach would take advantage of mountain ecosystems as early warning indicators in monitoring frameworks.

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701 **Conflict of interest**

The authors certify that there is no actual or potential conflict of interest in relation to this article.

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