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Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1692263> since 2023-01-27T10:32:03Z

Published version:

DOI:10.1007/s00027-019-0629-0

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(Article begins on next page)

Aquatic Sciences

If Alpine streams run dry: the drought memory of benthic communities

--Manuscript Draft--

Manuscript Number:	AQSC-D-18-00123R4	
Full Title:	If Alpine streams run dry: the drought memory of benthic communities	
Article Type:	Research Article	
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Corresponding Author's Institution:	Universita degli Studi di Torino Dipartimento di Scienze della Vita e Biologia dei Sistemi	
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Order of Authors Secondary Information:		
Funding Information:	Ministero dell'Istruzione, dell'Università e della Ricerca (201572HW8F)	Prof. Pierluigi Viaroli
Abstract:	<p>Several mountain streams are currently changing from perennial to temporary due to increasing water abstraction and global climate change with expected detrimental effects on stream biodiversity and functionality. We here examined whether macroinvertebrates and diatoms, experiencing recurring non-flow periods, show alterations even after complete flow resumption in 13 mountain streams in SW Italian Alps. Benthic communities were sampled after complete flow resumption in April 2017 in a control section, with permanent flow, and an intermittent section, which experiences a non-flow period during summer, in each stream. We tested for differences in terms of taxonomic and functional composition, diversity and functional group composition between permanent and temporary sections. Our results showed a significant alteration of benthic invertebrate, but not diatom communities in temporary sections. Different species composition and low diversity values in temporary sections were due to the replacement of monovoltine taxa, with aquatic respiration, preferring medium to fast flowing, oligotrophic waters by plurivoltine taxa, with aerial respiration preferring lentic habitats. Such results provide some insights into the mechanisms by which non-flow periods impact Alpine streams, and further investigations in mountain areas are required in the future to better unravel the repercussions on stream ecosystem processes.</p>	
Response to Reviewers:	Dear Dr. Piano,	

We have received the reports from our advisors on your manuscript, "If Alpine streams run dry: the drought memory of benthic communities", submitted to Aquatic Sciences. I haven't send the manuscript for external review, but instead I've read and edit/comment the abstract. You'll see my comments in the attached document, mainly referring to terminology. Please, address these minor issues and submit it again. I won't take you more than 10 minutes and the manuscript will be accepted directly.

I am looking forward to receiving your revised manuscript before 01 Mar 2019.

Thank you very much.

With kind regards,
Vicenc Acuna
Associate Editor
Aquatic Sciences

Response to the Editor:

Dear Editor,

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Our very best regards,
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IF ALPINE STREAMS RUN DRY: THE DROUGHT MEMORY OF BENTHIC COMMUNITIES

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Acknowledgements

The authors wish to thank M. Apostolo, R. Bolpagni, M. C. Bruno, G. Burgazzi, C. Garetto, A. Laini, D. Melchio, D. Morandini and B. Palmia for their assistance and contribution during the field and laboratory activities. Marco Baltieri (Associazione Tutela Ambienti Acquatici e Ittiofauna) is greatly acknowledged for his help in the identification of temporary sampling stretches. This work was realized within the framework of the PRIN NOACQUA "Risposte di comuNità e processi ecOsistemici in corsi d'ACQUA soggetti a intermittenza idrologica" - code 201572HW8F, funded by the Italian Ministry of Education, University and Research. This research is original and has a financial support of the Università del Piemonte Orientale.

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Abstract

Several mountain streams are currently changing from perennial to temporary due to increasing water abstraction and global climate change with expected detrimental effects on stream biodiversity and functionality. We here examined whether macroinvertebrates and diatoms, experiencing recurring non-flow periods, show alterations even after complete flow resumption in 13 mountain streams in SW Italian Alps. Benthic communities were sampled after complete flow resumption in April 2017 in a control section, with permanent flow, and an intermittent section, which experiences a non-flow period during summer, in each stream. We tested for differences in terms of taxonomic and functional composition, diversity and functional group composition between permanent and temporary sections. Our results showed a significant alteration of benthic invertebrate, but not diatom communities in temporary sections. Different species composition and low diversity values in temporary sections were due to the replacement of monovoltine taxa, with aquatic respiration, preferring medium to fast flowing, oligotrophic waters by plurivoltine taxa, with aerial respiration preferring lentic habitats. Such results provide some insights into the mechanisms by which non-flow periods impact Alpine streams, and further investigations in mountain areas are required in the future to better unravel the repercussions on stream ecosystem processes.

Keywords

Diatoms, macroinvertebrates, hydrological intermittency, functional traits

INTRODUCTION

1 Stream ecosystems have been recognized as extremely sensitive to climate change, because of the raising
2 of water temperatures and the disruption of hydrologic cycles (Heino et al. 2009; Whitehead et al. 2009;
3 Fenoglio et al. 2010). Changes in precipitations, temperature and evaporation determine shifts in river flow
4 regimes and groundwater recharge (IPCC 2013), with consequences for the temporal and spatial
5 distribution of biodiversity and ecosystem processes in streams and rivers (Acuña and Tockner 2010; Datry
6 et al. 2016). This climatic alteration can lead to extreme flow events, like floods and non-flow events, which
7 can be exacerbated by anthropogenic activities (e.g. deforestation, water capture, streambed alterations;
8 Fenoglio et al. 2010; Ledger and Milner 2015). Among flow regime alterations, riverbed desiccation is one
9 of the most pressing environmental issues related to climate change (Wilhite 2000). In Mediterranean
10 streams, non-flow events represent natural component of their hydrologic cycle. Therefore, freshwater
11 biota in temporary streams is physically, chemically and biologically shaped by sequential, predictable and
12 seasonal events of non-flow periods (Boulton et al. 2014). Therefore, freshwater biota of periodically
13 temporary environments shows adaptations and strategies to survive dry periods (e.g. desiccation-resistant
14 stages or colonization of hyporheic environment; Boulton and Lake 1992; Fenoglio et al. 2006; Bonada et al.
15 2007a; López-Rodríguez et al. 2009a; Souffreau et al. 2010). This is in accordance with the *natural flow*
16 *regime paradigm*, which states that the structure and function of a lotic ecosystem, and the adaptation of
17 its constituent aquatic species, are determined by the pattern of temporal variation in river flows (Poff et
18 al. 1997; Lytle and Poff 2004). However, consequences of desiccation on aquatic organisms are expected to
19 be different in temperate streams, where this phenomenon is quite recent and communities are still not
20 adapted (Calapez et al. 2014; Elias et al. 2015).

21 Among these, Alpine and in general mountain streams are becoming increasingly affected by intermittent
22 flow (Beniston 2012; Chiogna et al. 2016). In the Alpine areas, low flows normally occur during winter and
23 are caused by snow accumulation and freezing processes (Veza et al. 2010; Fenoglio et al. 2015). However,
24 summer non-flow periods are becoming more common since mountainous regions in the mid-latitudes are
25 warming at a rate two to three times faster than the global average (Hansen et al. 2005; Pederson et al.
26 2010), causing rapid shrinkage of glaciers and snowpack (Hall and Fagre 2003; Rauscher et al. 2008).
27 Moreover, these lotic ecosystems are suffering the heavy flow regulation, hydropower and increased water
28 abstraction aimed to fulfill local human needs (e.g. agricultural use, drinking water, etc). As a consequence,
29 mountain streams are changing from perennial to temporary systems with expected long-term detrimental
30 effects on stream biodiversity and functionality (Durance and Ormerod 2007; Fenoglio et al. 2007; Leigh et
31 al. 2016a; Pinna et al. 2016).

32 From an evolutionary perspective, by influencing mortality rates, desiccation represents a primary selective
33 pressure on aquatic communities (Lytle and Poff 2004). These strong environmental filters are expected to
34 differentially affect species from the regional pool by either favouring species that can tolerate drying

1 conditions and/or disfavoured species lacking resistance or resilience mechanisms to the disturbance, in
2 accordance with the *habitat templet theory* (Southwood 1977, 1988; Townsend and Hildrew 1994). On one
3 hand, in naturally intermittent Mediterranean streams, stretches experiencing drying likely have, on
4 average, less diverse communities than those of nearby perennial sites (e.g. Datry et al. 2014), because of
5 the exclusion of the most sensitive species (but see Bonada et al. 2007a for contrasting results in a large
6 scale analysis). On the other hand, such environmental filtering is expected to cause turnover among
7 perennial and intermittent stretches due to substitution of non-adapted taxa by disturbance-tolerant
8 species (Myers et al. 2015). Both phenomena may result in biotic homogenisation of temporary streams
9 due to the loss of rare and specialised species and the gain of tolerant species (Socolar et al. 2016).
10 Selection process due to desiccation is likely to favour particular traits (Webb et al. 2010; Luck et al. 2012)
11 conferring resistance (i.e. set of traits that enable organisms to survive during non-flow periods) and/or
12 resilience (set of traits that enable organisms to recolonize and recruit after non-flow events). A trait is
13 defined as a characteristic that reflects a species adaptation to its environment (Menezes et al. 2010) which
14 can be morphological or physiological attributes measured at the individual level (Violle et al. 2007; Webb
15 et al. 2010), or aspects of the realized niche of the species (Bowler et al. 2015). Exploring shifts in the
16 functional profile of a community could therefore shed light into species-disturbance relationships (McGill
17 et al. 2006) but also into their repercussion on the ecosystem functionality. Depending on which traits are
18 extirpated, such trait shifts may, in fact, have severe effects on ecological functions, with a wide range of
19 potential impacts on functional processes (Hooper et al. 2005; Cardinale et al. 2012).

20 Alterations in community diversity and functional traits might be temporary, depending on the recovery
21 capacity of aquatic organisms: species highly resilient or resistant to drying are able to recover within a few
22 weeks or months, therefore limiting long-term effects of desiccation (Rincon and Cressa 2000; Fritz and
23 Dodds 2004; Vander Vorste et al. 2015). However, some taxa might not be able to recover so quickly, with
24 cumulative detrimental effects on diversity and functionality over the years. For instance, Datry et al.
25 (2011), in the Albarine river (France), found persistent differences in shredder density among intermittent
26 and permanent sections long after flow resumption, underlying the so-called “drying memory” of the
27 system. Therefore, the assessment of non-flow effects needs to consider not only immediate but also long-
28 term impacts.

29 We here investigate the long-term effects of drying events (“drying memory”) on benthic organisms, in
30 thirteen Italian Alpine streams, where summer non-flow events, lasting two months, have been recorded
31 since 2011. In particular, we compared the response of two different communities, i.e. macroinvertebrates
32 and diatoms, to highlight potential differences in their recovery capacity, since they are known to exhibit
33 differential responses to stream alteration, like metal pollution (Hirst et al. 2002; De Jonge et al. 2008),
34 physical alterations (Bona et al. 2008) or siltation (Bona et al. 2016). In each of these streams, we sampled
35 and compared an intermittent and a perennial stretch during baseflow conditions to quantify differences as

1 a result of eventual cumulative effects of non-flow events. We here assumed that aquatic communities in
2 intermittent sites would have reached a complete recovery if their composition and diversity is comparable
3 to that of communities sampled in perennial sites. Such comparison allowed us to investigate differences
4 between diatoms and macroinvertebrates as well as underlying selection mechanisms, i.e. species loss vs
5 species replacement, due to filtering of non-adapted species and/or gain in generalist species. In this
6 context, we hypothesized that: i) recovery capacity differs between benthic invertebrates and diatoms due
7 to their different reproduction rates and dispersal capacities (Elias et al. 2015); ii) cumulative effects of non-
8 flow events on benthic communities mainly result in species loss processes and iii) species loss is due to the
9 depletion of non-adapted taxa.
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17 **MATERIALS AND METHODS**

18 **Sampling design**

19 This study was conducted in thirteen low order streams belonging to the SW Alps hydroecoregion (HER 4,
20 Piemonte, NW Italy; Wasson et al. 2007, Fig 1), therefore comparable in terms of geology, climate and
21 altitude to reduce confounding factors. Such hydroecoregion includes Cottian and Maritime Alps, whose
22 streams are characterized by a nivo-pluvial regime. In consequence, several stretches are already facing
23 seasonal hydrological alterations in summer because of reduction in precipitations and the following
24 increase in water abstraction for human needs.
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31 We selected two sampling sections for each stream, with different levels of hydrological disturbance: i) a
32 control section, with permanent water during the whole year (hereinafter CON section); ii) an intermittent
33 section, which experiences non-flow periods during summer (hereinafter DIS section). CON sections were
34 consistently located upstream, therefore representing a potential source of organisms for DIS sections after
35 flow resumption. In particular, selected streams were chosen based on interviews to fishermen
36 (Associazione Tutela Ambienti Acquatici e Ittiofauna) and on the data provided by the ARPA -
37 Environmental Protection Agency of Piedmont, according to which these streams have been already facing
38 seasonal summer non-flow events lasting two months since 2011, with the riverbed almost completely dry
39 in their DIS sections, as a combination of climatic factors and anthropogenic pressures (A.A. V.V. 2011;
40 Borroni 2011; ARPA 2013). CON sections were identified within 10 km upstream of the DIS section to
41 reduce environmental variability between the two stretches (Fig. 1). To verify if a “drying memory”
42 phenomenon occurred in benthic invertebrate and/or in diatom communities after the complete flow
43 resumption, we performed our sampling campaign in April 2017 (6 months after the drying period), under
44 moderate flow ($Q_{\text{mean}} = 3.98 \pm 4.56 \text{ m}^3/\text{s}$) occurring in both sections. Water flow in DIS sections had
45 resumed in November 2016 after a heavy rain event, interrupting the dewatering period of the streams
46 (Hydrological bulletins, www.arpa.piemonte.it).
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Data collection

1 In each sampling stretch, we collected a set of 13 local environmental variables. Water physical and
2 chemical parameters (water dissolved oxygen, oxygen saturation, pH, water temperature, conductivity)
3 were measured with a multiparametric probe (Hydrolab mod. Quanta). Additionally, to check the water
4 quality, water samples were collected from the middle of the water course in each sampling section. The
5 samples were then analysed with standard spectrophotometric (Perkin Elmer, Lambda 35) methods for
6 soluble reactive and total phosphorus (APHA 1998), ammonium (Koroleff 1970), nitrate (APHA 1998) and
7 total nitrogen (APHA 1998).

8 In each stretch we defined five microhabitats spaced at least 5 m apart, where we measured flow velocity
9 (0.05 m from the bottom) and water depth with a current meter (Hydro-bios Kiel) and we visually
10 estimated the % of six classes of substratum (boulders, cobbles, pebbles, gravels, sand and silt). These
11 microhabitats were selected following the Italian multihabitat sampling method (Buffagni and Erba 2007).
12 One sample of macroinvertebrates was collected in each microhabitat, for a total of five samples in each
13 stretch, using a Surber sampler (250 μm mesh size; 0.062 m^2 area). Collected samples were conserved into
14 plastic jars with 75% ethanol. In the laboratory, all benthic invertebrates were identified according to
15 Campaioli et al. (1994, 1999) to the family or genus level and counted. Based on their trophic strategies and
16 their biological and ecological requirements, macroinvertebrates were classified into the Functional
17 Feeding Groups (FFGs - Merritt et al. 2017) and biological and ecological groups (Usseglio-Polatera et al.
18 2000) respectively. Macroinvertebrates are classified into Functional Feeding Groups based on their
19 morpho-behavioral mechanisms of food acquisition (Merritt et al. 2017). Biological and ecological groups
20 were defined by Usseglio-Polatera et al. (2000) by grouping together taxa displaying similar biological (e.g.
21 size, life-cycle, respiration, reproduction, dispersal, locomotion) and ecological (transversal and longitudinal
22 distribution, preferred substrate and current velocity, trophic status) traits respectively.

23 For benthic diatoms, one sample for each stretch was collected, brushing 3 different cobbles, covering at
24 least an area of 10 cm^2 (European Committee for Standardization, 2003), chosen in correspondence of
25 three of the five microhabitats and merged together in a unique sample for subsequent analyses (see
26 Falasco et al. 2018). Diatoms were identified mainly according to reference floras Krammer and Lange-
27 Bertalot (1986–1991) as well as on recent bibliography including series of Diatoms of Europe Iconographia
28 Diatomologica and relevant scientific papers (Krammer and Lange-Bertalot 1986-1991 a, b; Krammer 1997
29 a, b, 2002, 2003; Reichardt 1999; Lange-Bertalot 2001; Werum and Lange-Bertalot 2004; Blanco et al. 2010;
30 Hofmann et al. 2011; Bey and Ector 2013; Falasco et al. 2013; Ector et al. 2015). Diatom species were then
31 assigned to one category of life-form based on classification provided by Rimet and Bouchez (2012) and to
32 one eco-morphotype, which combines the ecological guilds with size classes, based on the classification
33 provided by B-Béres et al. (2017).

Data analysis

To test whether aquatic communities completely recovered after desiccation, we here compared the composition and diversity of aquatic communities between DIS and CON sections. We assumed that aquatic communities in intermittent sections would have reached a complete recovery if their composition and diversity was comparable to that of communities sampled in perennial sections. All statistical analyses were performed using R software (R Core Team 2017).

Environmental variables at CON and DIS stretches. To explore potential differences between CON and DIS stretches with respect to environmental conditions, we performed a Principal Component Analysis (PCA) using the 13 habitat variables. A Permutational Multivariate Analysis of Variance PERMANOVA (Anderson 2001) was then applied to the environmental dissimilarity matrix based on Euclidean distances to test for differences between CON and DIS stretches with the function “adonis” in the *vegan* package (Oksanen et al. 2015). Statistical significance was tested via 9999 random permutations with the ID of each stream as stratum.

Community composition. We first visually inspected whether taxa dissimilarity differs among CON and DIS sections by means of a Principal Coordinate Axes (PCoA) using the Bray-Curtis dissimilarity index. We then tested whether dissimilarity in taxa composition between CON and DIS was significantly different from a random distribution with a PERMANOVA. Statistical significance was tested via 9999 random permutations with the stream identity as stratum. Both analyses were conducted with the *vegan* package (Oksanen et al. 2015). We then performed the Indicator Species Analysis (Dufrêne and Legendre 1997) with the function “multipatt” in the *indicspecies* package (De Caceres and Legendre 2009) to identify which taxa are more specifically linked to CON and DIS stretches for both diatoms and benthic invertebrates.

α -, β - and γ -diversity. To test whether differences between CON and DIS sections were due to taxa loss (α - and γ -diversity) or species replacement (β -diversity), we followed the approach proposed by Xiao et al. (2018). We then decomposed taxa richness of benthic invertebrates and diatoms into local (α) and total (γ) diversity, wherein local diversity is obtained as the average value of taxa richness at each sampling section and total diversity is given by the total number of encountered taxa in the entire sampling area. Beta diversity was calculated with the Whittaker’s multiplicative formula as the ratio between gamma and alpha diversity. Statistical significance was calculated through a non-parametric, randomization test, where the null expectation of each metric is defined by permuting sampling sections between treatments and recalculating the taxa richness for each permutation. Significant differences between treatments can thus be obtained by comparing the observed value of the taxa richness to the null expectation when treatments are randomly permuted across the sampling sites (Legendre and Legendre 1998). At the α scale where there are replicate plots to summarize over, we calculate the ANOVA F -statistic as our test statistic for the observed values compare it with the distribution of F -statistics obtained for each permutation. At the γ scale, for which we only have a single value for each treatment (and therefore cannot use the F -

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statistic) we compare the observed absolute difference between the treatments with the distribution of those obtained from permutations (see McGlenn et al. 2018 for further details). These statistical analyses were performed with the R package *mobr* (Xiao et al. 2018).

Functional profile of benthic communities in CON and DIS sections. To check whether differences between CON and DIS sections were due to selective environmental filtering of some functional traits, we considered functional feeding groups (FFGs), ecological and biological groups (Usseglio-Polatera et al. 2000) for benthic invertebrates, whereas for diatoms we evaluated life-forms (Rimet and Bouchez 2012) and ecomorphotypes (B-Béres et al. 2017). We calculated this set of functional metrics as the community-level weighted means of trait values, with the function “functcomp” of the *FD* package (Laliberté and Legendre 2010; Laliberté et al. 2014). This function builds a site-by-trait matrix by multiplying the site-by-species matrix with a species-by-trait matrix. For continuous and ordinal traits, like diatom body size, this function calculates the mean trait value of all species present in the community weighted by their relative abundances. For nominal and binary traits, like FFGs, ecological and biological groups for benthic invertebrates and life-forms and ecological guilds for diatoms, the relative abundance of taxa belonging to each individual class is returned. In addition, such comparison was applied also to those taxa potentially most threatened by desiccation. For benthic invertebrates, we focused on the EPT (Ephemeroptera, Plecoptera, Trichoptera) taxa richness because they are a key component of benthic assemblages in Alpine streams and sensitive to flow variability (Laini et al. 2018). For benthic diatoms, we considered the Red List (RL) taxa richness because it showed to be negatively affected by desiccation in Mediterranean streams (Falasco et al. 2016a). Significant effects of hydrological conditions on functional metrics were tested by means of a one-way ANOVA with the stream identity as error stratum. Data were log-transformed to achieve normal distribution and homoscedasticity of residuals.

RESULTS

Environmental parameters (Tab. S1) were comparable across the investigated streams and between the two sampling sections. The first two axes of the PCA explained 40.5% of the total variance in the environmental variables across all sites (Fig. 2). The first axis (22.8%) represents a gradient of rheophily, being positively correlated with flow velocity, % cobbles, oxygen saturation and dissolved oxygen, and negatively with % pebbles and temperature. The second axis (17.7%) represented a streambed sediment gradient, being negatively correlated with % pebbles, % sand and positively correlated with % cobbles and pH. PERMANOVA showed that environmental variables did not differ between CON and DIS sections (PERMANOVA, $P = 0.1107$, Table 1).

The PCoA depicted differences in species composition between CON and DIS sections for benthic invertebrates (Fig. 3a), whereas this pattern was not evident for diatoms (Fig. 3b). These patterns revealed

1 significant differences between CON and DIS sections for benthic invertebrates (PERMANOVA, $F_{1,128} = 5.84$;
2 $P < 0.001$) but not for diatoms (PERMANOVA, $F_{1,25} = 0.692$; $P = 0.072$).

3 The Indicator Species Analysis identified 12 indicator taxa in CON sections and 1 indicator taxon of DIS
4 sections for benthic invertebrates (Tab. 1), whereas no indicator species were identified for diatoms.

5
6 The results of the diversity partitioning showed significant effects of the hydrological conditions on
7 macroinvertebrate taxa richness at both alpha and gamma scale (Fig. 4a), which drops from an average
8 value of 11.6 in CON stretches to 8.58 in DIS stretches. Conversely, we did not find statistical differences in
9 any of the diversity metric considered between CON and DIS sites for diatoms (Fig. 4b).

10
11 Considering the community functional profile of benthic invertebrates, we found significant effects of the
12 hydrological conditions on EPT richness (Tab. 2 and Fig. 5a) and FFG composition (Tab. 2 and Fig. 6), with
13 particularly evident impacts on predators, scrapers and shredders. In CON sites, the abundances of
14 predators, scrapers and shredders are on average 4%, 8% and 9%, respectively, but drop to 3%, 6% and 3%
15 in DIS sites. Conversely, results showed a significant effect of hydrological conditions on collector-gatherers
16 (Tab. 2 and Fig. 6), with higher values in DIS (70%) compared to CON sites (59%), whereas no significant
17 effects (Tab. 2 and Fig. 6) were recorded for filter-feeders (20% in CON sites and 18% in DIS sites).
18 Significant negative effects of non-flow hydrological conditions were observed for organisms preferring
19 medium to fast flowing, oligotrophic waters and living on coarse mineral substrata and vegetation
20 (ecological groups A and C ; Tab. 2 and Fig. 6). Percentages of individuals belonging to ecological groups A
21 and C showed significant lower values in DIS than in CON stretches, dropping from 12% and 21% to 6% and
22 13% respectively. For taxa preferring lentic habitats (ecological group F), we observed a significant increase
23 from CON (36%) to DIS (48%) sites (Tab. 2 and Fig. 6). Significant effects of hydrologic conditions were also
24 recorded for several biological groups (Tab. 2 and Fig. 6). Percentages of semivoltine organisms, large-sized
25 predators and crawlers (biological group d), monovoltine organisms, medium-sized shredders and crawlers
26 with aquatic respiration (biological group f), and small to medium-sized swimmers or crawlers, with aerial
27 respiration (biological group g), showed a significant decreasing pattern (Tab. 2 and Fig. 6) from CON (2%,
28 15% and 9% respectively) to DIS (1%, 8% and 4% respectively) stretches. Conversely, plurivoltine, small-
29 sized organisms (biological groups h and e) showed significant higher values in the DIS (11% and 76%
30 respectively) than in CON (5% and 64% respectively) sites (Tab. 2 and Fig. 6).

31
32 Considering the community functional profile of benthic diatoms, we could not detect any significant effect
33 of hydrological conditions on red list species abundance (Tab. 2 and Fig. 5b) and on functional groups (Tab.
34 2), except for high profile species of size class 4, which resulted more abundant in DIS than in CON sites.

35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 **DISCUSSION**

57
58 Alpine and mountainous streams are affected by multiple pressures that often cause the alteration and
59 sometimes even the almost complete destruction of these ecosystems (Wohl 2006). In particular,
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1 increasing water abstraction (for hydroelectric power generation, drinkable waters, irrigation and snow
2 generation) combined with the global climate change effects have severe repercussions on Alpine streams,
3 with increasing non-flow events in previously perennial systems (Fenoglio et al. 2010). Such events are
4 expected to affect biotic communities, whose composition changes substantially during non-flow periods,
5 but recover quite rapidly after water returns (Lake 2003; Fowler 2004). However, this might not be true in
6 recently temporary streams, where biotic communities still lack adaptations to such extreme events.
7 Although environmental variables in permanent and intermittent sites were similar in our study, we
8 recorded differences in benthic community diversity and composition, which could be ascribed to the long-
9 term effects of desiccation. This result clearly strengthens the role of biological communities in assessing
10 ecological conditions as their response integrates temporal aspects. Our results revealed that in recently
11 temporary alpine streams benthic macroinvertebrates, but not diatoms, reflect a negative effect of water
12 intermittency, confirming earlier findings in Mediterranean (Boix et al. 2010) and other temperate regions
13 (Calapez et al. 2014; Elias et al. 2015).

23 *Benthic invertebrate response*

24 Our results depicted how river reaches experiencing non-flow periods supported different and less species-
25 rich communities compared to perennial reaches. These results suggest that the shift in macroinvertebrate
26 community composition was partly determined by a species filtering process, such that only a limited set of
27 species — with particular trait combinations — can survive in the intermittent sections, similarly to Giam et
28 al. (2017).

29 To further investigate whether desiccation favours tolerant-disturbance species or species that share
30 particular traits, we tested whether communities in perennial and intermittent river reaches differed in
31 their functional trait composition. In accordance with literature (Dewson et al. 2007; Datry et al. 2014), we
32 observed that taxa depletion in intermittent sites was mainly driven by the loss of the EPT (Ephemeroptera,
33 Plecoptera and Trichoptera) taxa, which represent the dominant group in the alpine streams and the most
34 sensitive taxa as well. Likewise, several EPT taxa can be found almost exclusively in perennial sections, as
35 demonstrated by the Indicator Species Analysis. Consistent results were obtained by Doretto et al. (2018)
36 who conducted a manipulative experiment in artificial flumes located in Eastern Italian Alps. In the cited
37 work, taxonomic richness of benthic invertebrates and EPT richness decreased after two consecutive non-
38 flow events.

39 Considering the response in terms of biological groups of benthic invertebrates, large semivoltine taxa with
40 long larval life, such as *Dinocras* sp., *Perla* sp. and Athericidae, which are unable to survive in periodically
41 dry environments, showed lower values in intermittent than in perennial sections. Conversely, small, fast
42 growing, plurivoltine organisms, such as Chironomidae, Simuliidae and *Baetis* sp., showed an opposite
43 trend. Voltinism has been recognized as one of the most sensitive traits (Bonada and Doledec 2018) and a
44 shift from multivoltinism to semivoltinism has been observed from perennial to intermittent hydrological

1 regimes in Mediterranean streams (Corbet et al. 2006; López-Rodríguez et al. 2009a, b): in particular, these
2 authors demonstrated that species inhabiting temporary habitats complete their life cycle in less than one
3 year, emerging just before the loss of surface water. However, in Alpine streams, where non-flow events
4 are human-induced, the match between life-history adaptation and non-flow periods might be lost with
5 severe consequences for species survival. Similarly, small body size is also a common attribute of
6 macroinvertebrate taxa living in temporary Mediterranean streams, since reduced dimensions allow fast
7 development and population growth (Bonada et al. 2007b). These attributes assure higher survival rates in
8 temporary watercourses, where life-cycle has to be completed before water disappears.

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14 When looking at ecological niches, we could observe that rheophilous taxa preferring coarse substrata,
15 such as *Epeorus* sp. and *Rithrogena* sp., decreased from perennial to intermittent sites, while there was an
16 increase of lentic taxa, mainly Chironomidae, able to survive in environments with fluctuating water levels.
17 This is in accordance with Acuña et al. (2005), Pace et al. (2013) and Chessmann et al. (2015), who depicted
18 negative effects of desiccation on rheophilous taxa in Mediterranean streams.

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23 Our results on macroinvertebrates confirm early findings of Fenoglio et al. (2007) who observed similar
24 responses along a gradient of desiccation in a study on the Po river. However, as they developed their work
25 during the lentification phase, it remained less clear to what extent such functional alteration of benthic
26 invertebrate community was transient or persistent in time. Since we here sampled intermittent sections
27 six month after water returned, our data strongly suggest the long-term effect of non-flow events on
28 macroinvertebrate communities in alpine streams. Moreover, with the analysis of functional groups, we
29 could reveal that desiccation does not only filter non-adapted taxa, but this taxonomic loss is at least partly
30 compensated by positive selection of tolerant species. This desiccation-driven replacement of species
31 mirrors the effects of climatic change, whose impacts have been reported for many taxonomic groups
32 (Parmesan and Yohe 2003; Hickling et al. 2006).

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41 Our results also demonstrate that non-flow events in Alpine streams alter macroinvertebrate functional
42 feeding groups, with possible repercussions on the ecosystem functionality. We here highlighted how
43 specialised functional feeding groups, such as shredders and scrapers, mainly represented by Limnephilidae
44 and Heptageniidae respectively, decreased from perennial to intermittent sections. Conversely, the
45 generalist group of collector-gatherers, including *Baetis* sp. and Chironomidae, increased. This suggests that
46 drying events can persistently alter the composition of macroinvertebrate assemblages in streams and this
47 might be particularly true for non-adapted alpine communities. The absence of water disrupts some
48 ecological processes, such as the microbial breakdown of allochthonous inputs (Boulton and Lake 1992). In
49 this context, Wenisch et al. (2017) demonstrated how the loss of shredder benthic taxa may significantly
50 alter the decomposition rate of leaf litter in streams with consequent alteration of ecosystem functionality.
51 Such results are critical also because flow reduction and desiccation are strictly associated with heavy fine
52 sediment accumulation (i.e., clogging), since lower water velocity enables more sediment to settle out of
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1 suspension (Dewson et al. 2007; Rolls et al. 2012). Such phenomenon is also responsible for altering the
2 organic material decomposition (Doretto et al. 2016; Doretto et al. 2017), exponentially increasing the
3 negative effect of non-flow events on stream nutrient cycling. Although intermittent flow might prevent
4 the establishment of permanent periphytic biofilms (Wood and Petts 1999), this explanation is not
5 plausible to justify the strong reduction of scrapers in intermittent sections observed in our study, since we
6 could not record any clear response of benthic diatoms. However, in our sites, scrapers are mainly
7 represented by the family Heptageniidae, which includes extremely rheophilous organisms (Usseglio-
8 Polatera et al. 2000). Therefore, they are probably negatively affected more by flow reduction than by
9 trophic processes. In addition, desiccation promotes heterotrophy (Acuña et al. 2015) and alter fatty acid
10 composition (Sanpera-Calbet et al. 2017) in the biofilm, likely affecting scrapers (Guo et al. 2016). Further
11 investigations in this sense could unravel mechanisms behind this pattern.
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19 *Benthic diatom response*

20 Diatoms show a rapid recovery after non-flow regime in this study, given that after 6 months since the
21 water returned diatom community in intermittent stretches is comparable to that found in perennial sites.
22 This result was also confirmed by the analysis of the most sensitive taxa, i.e. Red List taxa, since we could
23 not find any significant pattern. Within biofilm, diatoms are probably the most sensitive component since
24 other groups, such as cyanobacteria and green algae, better cope with desiccation (Piano et al., 2017a). In
25 this context, in Mediterranean streams a clear response of diatoms to stream lentification and
26 fragmentation processes occurring during non-flow periods has been highlighted: for instance, river
27 shrinkage causes the loss of Red List diatom taxa (Falasco et al. 2016a), with increasing proportions of
28 motile (Falasco et al. 2016b) and tolerant (Piano et al. 2017b) species, and similar results were also
29 reported by Falasco et al. (2018a) in Alpine streams. Considering colonization processes during rewetting
30 phases, Artigas et al. (2012) observed a faster recolonization on bare substrates in a Mediterranean
31 temporary stream, in comparison to a slow gradual recovery in a Central European river. Similarly,
32 Souffreau et al. (2010) demonstrated that acclimatization increases the tolerance of diatom strains to
33 desiccation, underlying how non-flow events can have a stronger negative impact on diatom communities
34 in recently temporary rivers than in Mediterranean regions. Despite recovery might take more than 90 days
35 in pristine streams (Falasco et al. 2018b), diatom communities recovered faster after a non-flow event in
36 comparison with macroinvertebrates, probably due to their shorter life cycles and higher physiological
37 adaptation to dryness (Calapez et al. 2014). Moreover, the high dispersal capacity of diatoms (Robson et al.
38 2008) combined with their fast reproduction rates guarantee a rapid recovery after desiccation (i.e. mass
39 effect, Mouquet and Loreau 2003). The analysis of their functional groups confirmed results obtained from
40 diversity and community composition, since communities in intermittent sites showed no significant
41 variations in ecological guilds, size and lifeforms compared with the perennial stretches.
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1 Although changes in species diversity and composition as well as in functional groups were more clearly
2 detected for benthic invertebrates than for diatoms, translating these observations as stronger
3 invertebrate versus diatom response to long-term desiccation effects should be interpreted with caution.
4 Although diatoms and invertebrates were sampled in an equal number of sites, the higher number of
5 replicates within each site collected for macroinvertebrates could potentially lead to higher statistical
6 power to detect invertebrate versus diatom responses. Further investigations should be therefore
7 performed to shed light on this point.
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12 *Conclusions*

13 Our results emphasize how the functional-based approach can help in help in unravelling the ecological
14 responses of streams to non-flow events. Our predictions of a persistent effect of desiccation on benthic
15 communities was rejected for diatoms, but was confirmed for macroinvertebrate assemblages. Moreover,
16 we disentangled the additive effect of two mechanisms on benthic invertebrates, which may act with
17 varying intensities depending on the considered functional aspects. Species loss represents the dominant
18 mechanism, since non-adapted species are filtered out, that as confirmed by a reduction in species
19 richness. On the other hand, species replacement also plays a role since small, plurivoltine taxa, preferring
20 lentic habitats and feeding on streambed sediment are favoured in intermittent sections. Such results
21 underlay how benthic communities in intermittent sections of alpine streams are currently facing
22 alterations caused by flow intermittency and further investigations in mountain areas are required in the
23 next future to better unravel these processes. In particular, even if we did not record significant differences
24 between permanent and intermittent sites in terms of environmental parameters, results of the PCA
25 showed how intermittent sites are slightly warmer than permanent ones. Temperature increasing values
26 likely associated with low flows might also represent a disrupting mechanism, especially in cold arctic
27 streams, as highlighted by Heino et al. (2009). The effect of water warming on benthic communities should
28 be investigated in Alpine streams, which are in some respect environmentally similar to arctic streams.
29 Moreover, since alterations in benthic invertebrate functional groups could possibly have repercussions on
30 periphyton composition (e.g. scraper decrease), despite at present no alterations were recorded for diatom
31 community, monitoring both benthic communities will be essential to disentangle functional changes in the
32 lotic food web.
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Figure captions

1
2 Figure 1. Map of the thirteen study streams with respective sampling sites (circles = CON sites; squares =
3
4 DIS sites)

5
6 Figure 2. Result of the PCA. Points represent each single sample while arrows represent the loadings of
7
8 each environmental variable included in the analysis. Ellipses represent standard deviations around the
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10 centroids of the two groups.

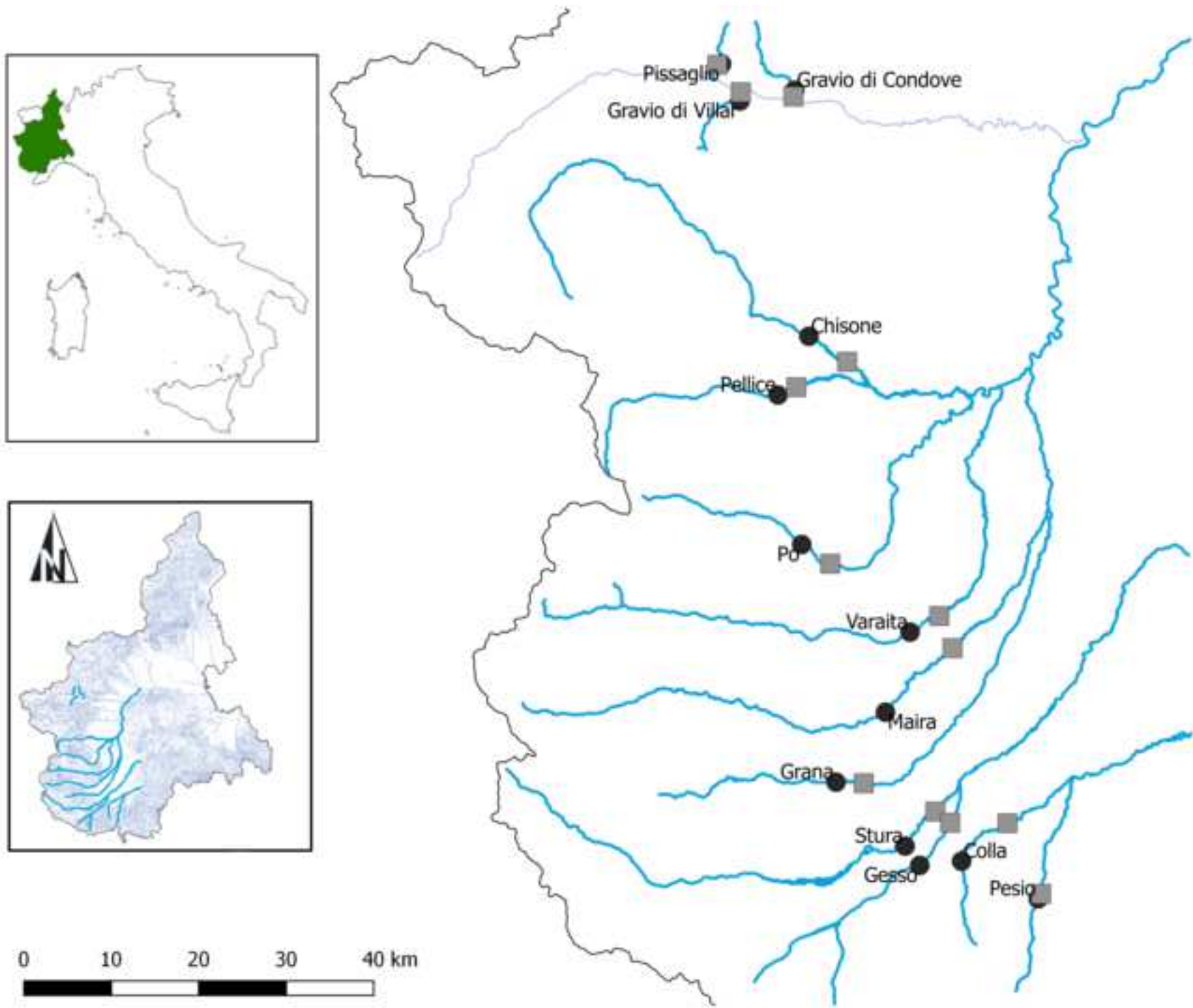
11
12 Figure 3. Ordination of the sampled benthic invertebrate (a) and diatom (b) communities according to the
13
14 first two PCoA axes (Dark grey circles = CON sites; light grey squares = DIS sites). Ellipses represent standard
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16 deviations around the centroids of the two groups.

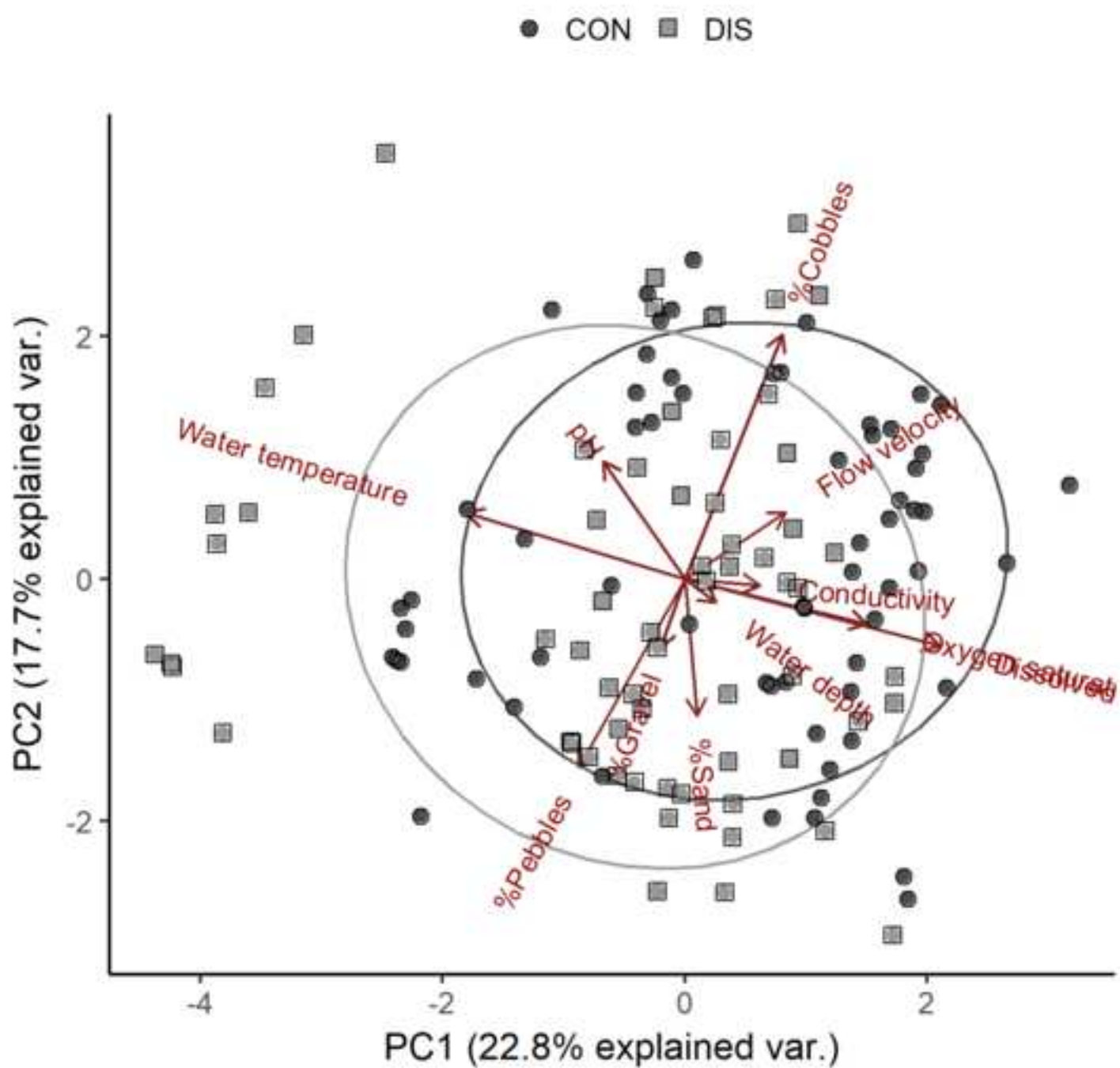
17
18 Figure 4. Diversity metrics for benthic invertebrates (a) and diatoms (b) at the α (i.e., single stretch), beta
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20 (i.e., between stretches), and γ (i.e., all stretches) scales. The p -values are based on 999 permutations of
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22 the treatment labels.

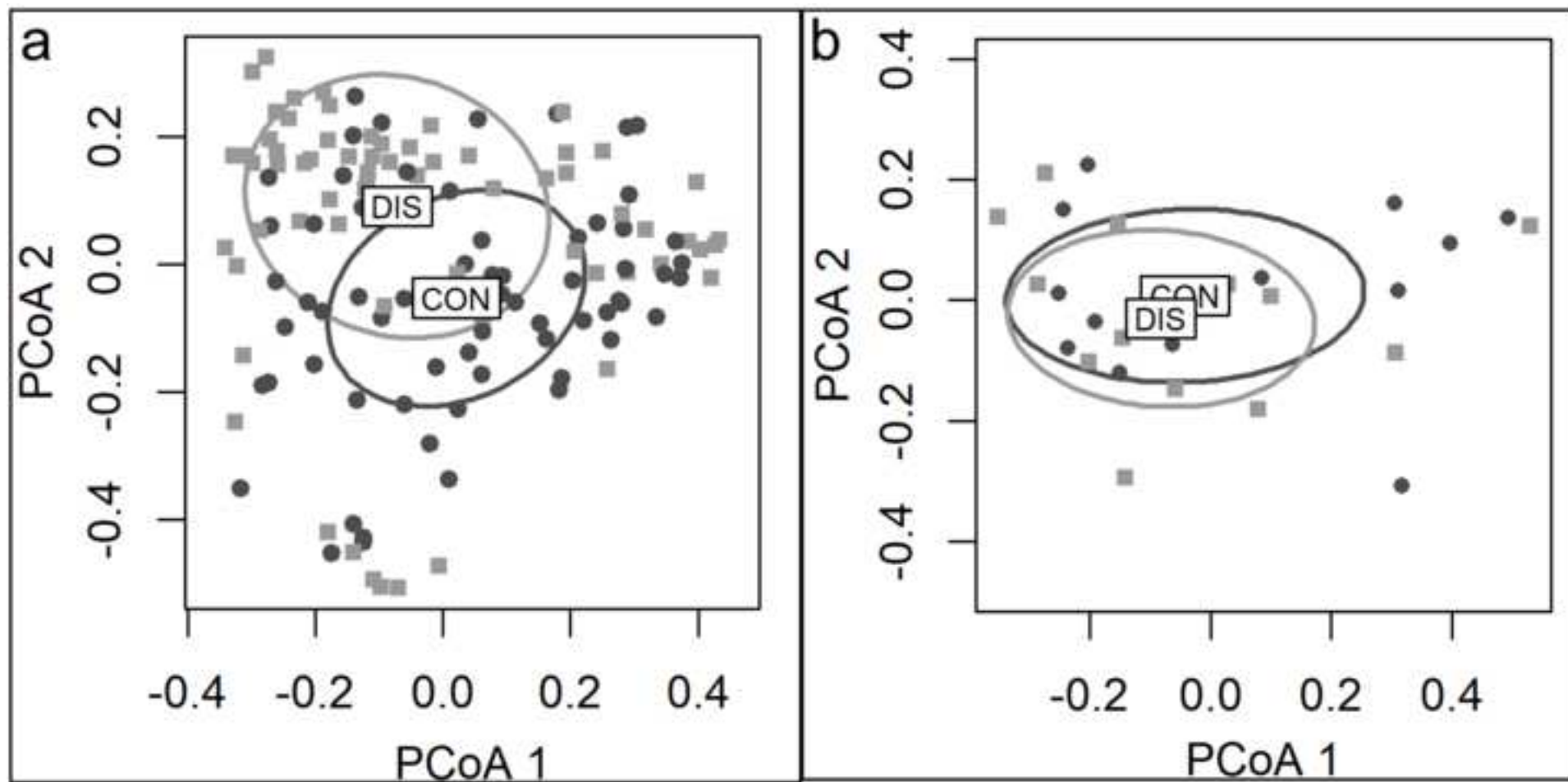
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24 Figure 5. Boxplots representing differences in EPT richness (a) of benthic invertebrates and Red List species
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26 abundance (b) of diatoms between CON and DIS sites.

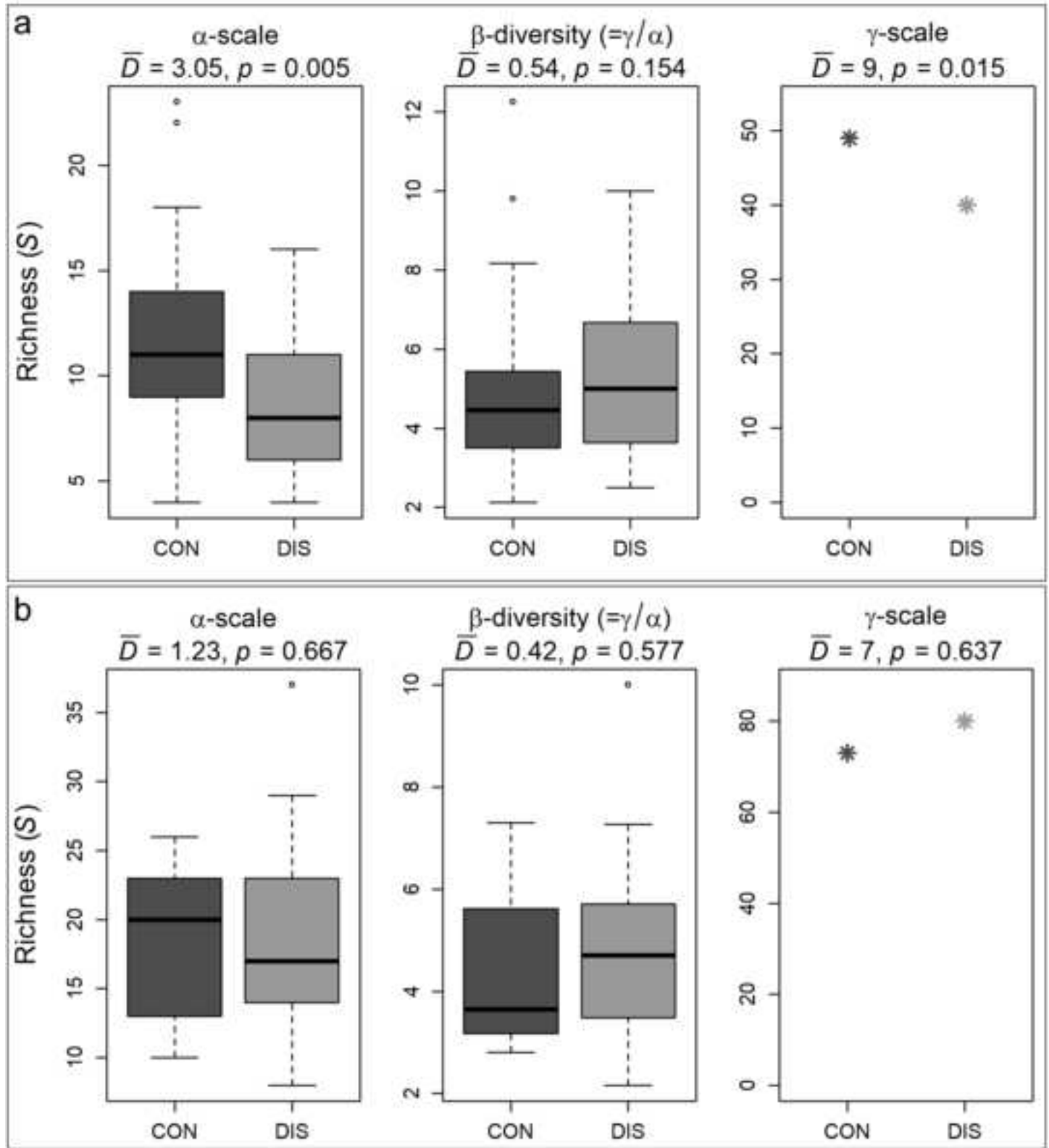
27
28 Figure 6. Boxplots representing differences in functional groups between CON and DIS sites for benthic
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30 invertebrates. Only significant results are reported. Ecological group A: rheophilous organisms preferring
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32 coarse mineral substrates in oligotrophic and cold waters; ecological group C: organisms living on mineral
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34 substrates or vegetation at slow or medium current velocities; ecological group F: organisms living in lentic
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36 and stagnant habitats. Biological group d: semivoltine, large-sized predators and crawlers, with aerial
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38 dispersal; biological group e: small to medium-sized plurivoltine crawlers with aquatic respiration; biological
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40 group f: monovoltine, medium-sized shredders and crawlers with aquatic respiration; biological group g:
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42 small to medium-sized swimmers or crawlers, with aerial respiration; biological group h: monovoltine
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44 burrowers, deposit-feeders.

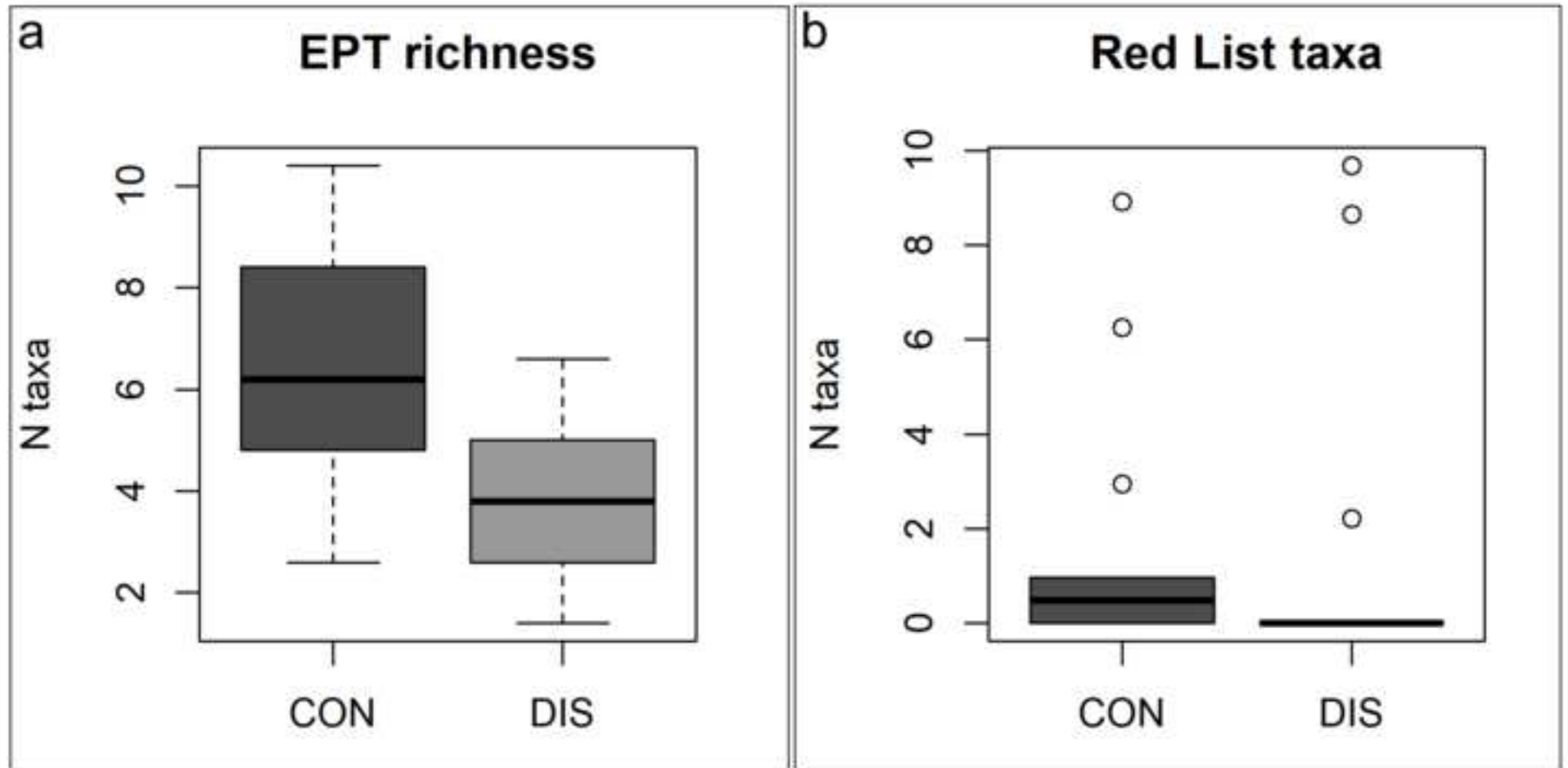
Figure 1











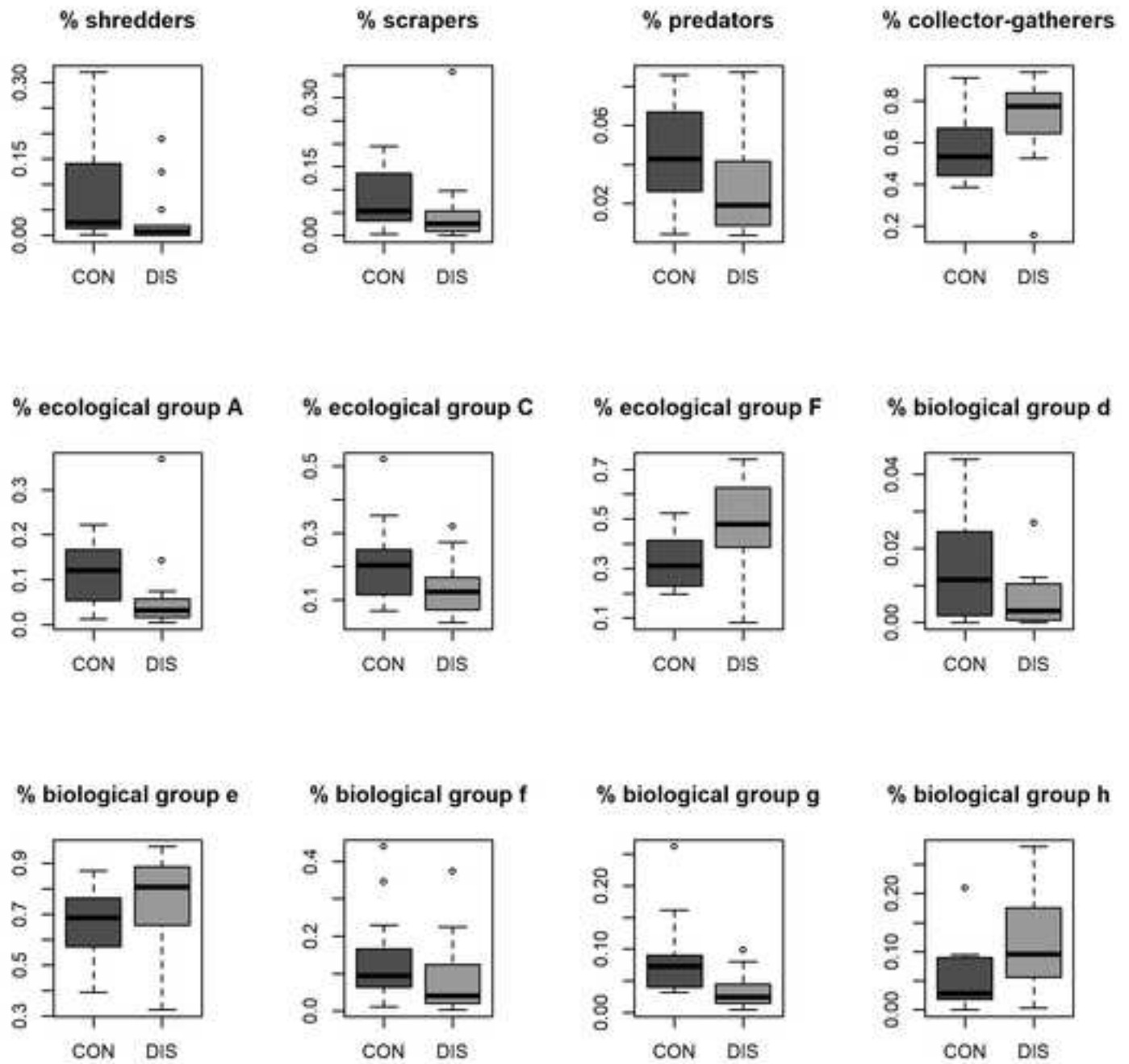


Table 1. Results of the Indicator Species Analysis for benthic invertebrates.

CON sites	IndVal	P
Rhyacophilidae	0.645	0.001
<i>Epeorus</i> spp.	0.639	0.001
<i>Ecdyonurus</i> spp.	0.586	0.001
<i>Amphinemura</i> spp.	0.575	0.001
<i>Leuctra</i> spp.	0.524	0.017
<i>Protonemura</i> spp.	0.492	0.011
<i>Isoperla</i> spp.	0.487	0.007
Sericostomatidae	0.460	0.002
<i>Dinocras</i> spp.	0.445	0.011
Blephariceridae	0.416	0.001
Odontoceridae	0.313	0.034
<i>Perla</i> spp.	0.304	0.036
DIS sites	IndVal	P
Naididae	0.762	0.001

Table 2. Results of the one-way ANOVA performed on functional traits. Significant results are reported in bold.

<i>INVERTEBRATES</i>				<i>DIATOMS</i>			
	Metric	F_{1,116}	P		Metric	F_{1,12}	P
	EPT richness	57.33	<0.001		RL taxa	0.732	0.409
FFG	Shredders	17.4	<0.001	Life-forms	Mucous	3.22	0.098
	Scrapers	4.32	0.040		Adnate	0.082	0.779
	Predators	8.93	0.003		Pad	1.69	0.219
	Coll-gath.	10.8	0.001		Stalk	0.129	0.726
	Filterers	1.42	0.237		Free	0.071	0.794
Ecological groups	Eco A	18.2	< 0.001	Solitary	0.295	0.597	
	Eco B	1.78	0.185	Colonial	0.261	0.619	
	Eco C	13.0	< 0.001	Low1	1.61	0.228	
	Eco D	0.366	0.546	Low2	2.57	0.135	
	Eco E	1.81	0.181	Low3	0.900	0.362	
	Eco F	20.5	< 0.001	Low4	0.923	0.356	
Biological groups	Bio b	1.53	0.219	Low5	0.147	0.708	
	Bio c	0.116	0.734	High1	0.732	0.409	
	Bio d	7.88	0.006	High2	0.928	0.354	
	Bio e	5.70	0.019	High3	4.48	0.056	
	Bio f	17.1	< 0.001	High4	10.63	0.007	
	Bio g	23.7	< 0.001	High5	2.43	0.145	
	Bio h	9.01	0.003	Motile1	0.172	0.686	
				Motile2	1.28	0.281	
			Motile3	0.456	0.512		
			Motile4	2.53	0.138		
			Motile5	2.08	0.175		

Table S1. Stream characterization in terms of dominant substratum, hydrological, physical and chemical parameters and land use. For flow velocity and water depth, mean values \pm SD are displayed since multiple measures were repeated in each stretch. Percentage of different land uses were calculated in a buffer of 1 km of diameter around each sampling stretch.

STREAM	DISTURBANCE	PHYSICAL AND CHEMICAL PARAMETERS							
		Substratum	Flow velocity (m/s)	Water depth (m)	Temperature (°C)	DO (mg/L)	%DO	pH	Conductivity (μ S/cm)
Chisone	CON	Pebbles	0.50 (\pm 0.28)	0.31 (\pm 0.09)	8.70	11.5	101	7.82	214
Chisone	DIS	Boulders	0.55 (\pm 0.22)	0.32 (\pm 0.07)	11.7	11.2	114	8.73	206
Colla	CON	Cobbles	0.44 (\pm 0.21)	0.20 (\pm 0.09)	11.4	9.50	90.0	7.13	62.0
Colla	DIS	Cobbles	0.11 (\pm 0.04)	0.07 (\pm 0.02)	15.8	9.50	90.0	8.32	NA
Gesso	CON	Cobbles	0.73 (\pm 0.37)	0.29 (\pm 0.09)	8.17	12.0	102	7.82	216
Gesso	DIS	Cobbles	0.64 (\pm 0.20)	0.26 (\pm 0.08)	9.20	11.0	95.2	7.75	202
Grana	CON	Boulders	0.65 (\pm 0.15)	0.29 (\pm 0.07)	8.20	11.0	93.1	7.96	255
Grana	DIS	Cobbles	0.50 (\pm 0.25)	0.39 (\pm 0.13)	8.33	11.4	96.8	7.99	253
Gravio di Condove	CON	Boulders	0.44 (\pm 0.29)	0.16 (\pm 0.11)	8.57	10.8	92.2	8.44	175
Gravio di Condove	DIS	Boulders	0.76 (\pm 0.60)	0.27 (\pm 0.08)	9.77	11.0	95.3	8.52	193
Gravio di Villar	CON	Boulders	0.55 (\pm 0.40)	0.29 (\pm 0.04)	8.59	10.8	92.3	8.74	216
Gravio di Villar	DIS	Boulders	0.51 (\pm 0.34)	0.39 (\pm 0.05)	9.37	10.9	95.3	8.26	204
Maira	CON	Boulders	0.44 (\pm 0.19)	0.17 (\pm 0.09)	7.80	11.5	100	8.4	377
Maira	DIS	Cobbles	0.70 (\pm 0.20)	0.43 (\pm 0.10)	7.93	11.0	95.0	7.97	390
Pellice	CON	Boulders	0.52 (\pm 0.22)	0.41 (\pm 0.15)	7.63	12.2	101	7.98	116
Pellice	DIS	Boulders	0.52 (\pm 0.16)	0.36 (\pm 0.17)	6.79	10.7	86.9	7.69	117
Pesio	CON	Boulders	0.26 (\pm 0.19)	0.23 (\pm 0.10)	5.35	12.0	100	7.91	122
Pesio	DIS	Cobbles	0.26 (\pm 0.12)	0.32 (\pm 0.05)	5.01	12.0	100	7.68	117
Pissaglio	CON	Cobbles	0.48 (\pm 0.25)	0.18 (\pm 0.08)	10.1	10.2	90.6	8.89	221
Pissaglio	DIS	Boulders	0.33 (\pm 0.23)	0.15 (\pm 0.03)	12.5	9.17	86.0	9.04	220
Po	CON	Boulders	0.70 (\pm 0.42)	0.39 (\pm 0.15)	11.9	10.3	94.8	7.6	103
Po	DIS	Cobbles	0.46 (\pm 0.18)	0.35 (\pm 0.13)	9.86	11.0	101	7.63	117
Stura	CON	Boulders	1.03 (\pm 0.25)	0.35 (\pm 0.15)	7.20	11.5	94.5	7.68	287
Stura	DIS	Cobbles	0.59 (\pm 0.23)	0.24 (\pm 0.07)	7.76	11.4	96.1	7.55	280
Varaita	CON	Cobbles	0.53 (\pm 0.27)	0.33 (\pm 0.11)	6.45	12.2	111	7.95	226
Varaita	DIS	Boulders	0.76 (\pm 0.28)	0.28 (\pm 0.06)	8.59	10.2	86.1	8.08	226

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STREAM	DISTURBANCE	NUTRIENTS					LAND USE		
		SRP (µg/L)	TP (µg/L)	N-NH4+ (µg/L)	N-NO3- (µg/L)	TN (µg/L)	%Natural	%Agricultural	%Urban
Chisone	CON	3.942	56.75	32.15	385.3	578.2	2.03	97.8	0.132
Chisone	DIS	9.398	12.86	15.71	183.6	540.5	25.73	74.3	0.00
Colla	CON	6.825	4.670	20.90	338.3	560.0	0.00	98.1	1.90
Colla	DIS	12.72	27.35	13.32	27.83	220.9	0.00	100	0.00
Gesso	CON	4.655	9.535	33.34	352.2	448.0	63.6	36.4	0.00
Gesso	DIS	6.887	7.680	24.99	227.7	487.4	44.16	55.4	0.437
Grana	CON	7.011	14.37	45.60	708.5	819.5	13.5	39.5	47.0
Grana	DIS	17.74	64.45	42.45	578.9	899.4	0.00	100	0.00
Gravio di Condove	CON	5.988	4.075	41.34	188.0	625.7	37.5	54.9	7.59
Gravio di Condove	DIS	4.221	5.440	27.97	548.7	580.3	4.68	85.7	9.60
Gravio di Villar	CON	3.694	6.455	21.24	629.5	964.3	57.3	20.3	22.4
Gravio di Villar	DIS	4.717	31.73	14.17	972.0	1054	100	0.00	0.00
Maira	CON	3.260	4.390	21.58	529.1	750.2	51.6	28.6	19.7
Maira	DIS	7.104	11.57	29.51	473.0	559.2	22.23	77.2	0.545
Pellice	CON	22.41	31.24	16.98	977.5	1166	23.83	76.2	0.00
Pellice	DIS	10.90	17.15	20.39	798.8	932.3	70.6	29.4	0.00
Pesio	CON	8.499	11.46	10.51	173.4	306.9	68.0	32.0	0.00
Pesio	DIS	5.306	13.81	27.04	425.7	467.1	70.7	29.3	0.00
Pissaglio	CON	5.120	11.18	15.11	391.8	779.4	69.5	0.00	30.5
Pissaglio	DIS	3.167	3.445	19.80	494.5	636.6	76.2	11.9	12.0
Po	CON	15.58	36.94	68.94	656.1	1229	97.9	2.08	0.00
Po	DIS	2.495	6.515	11.70	759.5	845.5	100.0	0.00	0.00
Stura	CON	4.190	26.02	24.22	327.8	432.6	0.00	100	0.00
Stura	DIS	5.120	20.11	29.25	344.5	474.8	43.7	56.3	0.00
Varaita	CON	6.064	17.59	43.64	760.2	1152	30.5	23.4	46.0
Varaita	DIS	3.911	12.37	33.08	704.9	776.6	11.51	88.5	0.00