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Anthropogenic-driven transformations of dragonfly (Insecta: Odonata) communities of low elevation mountain wetlands during the last century

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Running title: Impacts on Alpine odonate communities

Abstract

1. Freshwater environments are experiencing high rates of species extinction due to human impacts, with aquatic insects thought to be strongly threatened by these changes; however, long-term research on this topic is scant. Among aquatic insects, dragonflies are considered valuable indicators of human disturbance at multiple scales.
2. This study addresses transformations of odonate communities of low elevation mountain wetlands in the Alps over the last century, comparing historical and present assemblages based on past records derived from scientific collections or literature and present data derived from site resurveys.
3. 32.6% of species have been extirpated or strongly declined in the area (mostly temporary lentic and lotic water specialists, or cold-adapted species). Conversely, only 12.2% of species were new or considerably increased (mostly permanent lentic specialists and warm-adapted species). Nearly half of historical populations have been lost. The great majority of species which disappeared from all the study sites also disappeared (or strongly declined) at the regional scale.
4. Although gamma species richness was higher in the historical period compared with the present, mean alpha species richness does not significantly differ between the two, likely suggesting homogenization of communities from historical to the present period.
5. Present communities of dragonflies show a significantly higher Community Temperature Index compared with historical ones.
6. These patterns are putatively explained by the joint effects of land-use change (drainage and reclamation), land-use intensification or abandonment, environmental pollution, and anthropogenic-driven climate warming.

Keywords – global change; Community Temperature Index; freshwater ecosystems; insect crisis; larval habitat; scientific collections; temporary wetlands

Introduction

Freshwater ecosystems are among the most impacted natural systems worldwide (Sala *et al.*, 2000) and, due to human activities, an estimated half of the original global wetland area has been lost (Mitsch & Gosselink, 2000). Consequently, freshwater environments are experiencing high rates of species extinction (Ricciardi & Rasmussen, 1999; Dudgeon *et al.*, 2006). However, the effects of global change on the diversity and distribution of many freshwater organisms remain poorly understood (e.g., Heino *et al.*, 2009; Ball-Damerow *et al.*, 2014). Among freshwater organisms, invertebrates represent a relevant share; however, only a small fraction (probably less than 10%) of research has focused on them (Strayer, 2006).

A relevant portion of freshwater invertebrates are insects (Sánchez-Bayo & Wyckhuys, 2019). In recent years, increasing concern on the rapid decline of insect populations started to animate the scientific debate (Hallmann *et al.*, 2019; Thomas *et al.*, 2019). Sánchez-Bayo & Wyckhuys (2019) suggested that insect decline is even higher among aquatic insects compared with terrestrial species, with generalist species (e.g. pollution-tolerant) rapidly replacing specialists (see also Ball-Damerow *et al.*, 2014; Delpon *et al.*, 2019). The global decline of insects is expected to result in cascading effects on their predators, and thus on food webs and ecosystem services worldwide (Hallmann *et al.*, 2014; Assandri *et al.*, 2017a; Bowler *et al.*, 2019).

Among aquatic insects, odonates are considered as valuable indicators of human disturbance, ecological integrity, and land-use/climatic changes at multiple spatial scales. This is due to their complex life-cycle, which includes both a terrestrial and an aquatic phase, fully predators habits, which position them at a high level of the trophic web, and wide variability in life-history traits across species, e.g. dispersal ability, habitat and micro-habitat preferences, and water-pollution tolerance (Flenner & Sahlén, 2008; Hassall, 2015; Rocha-Ortega *et al.*, 2019). Many temperate odonate species have experienced dramatic declines in range and abundance during the second half of the 20th century due to a variety of factors, i.e. habitat loss and fragmentation, anthropogenic climate change, intensification of land uses, canalization of waterways, eutrophication, pollution, and acidification of their freshwater habitats (Kalkman *et al.*, 2007, 2018; Clausnitzer *et al.*, 2009; Rapaciuolo *et al.*, 2017).

In Europe, the Alpine region is considered the area with the highest diversity of dragonflies due to the co-occurrence of Mediterranean species in the lowland and boreal species at higher elevations within a restricted geographical range (Kalkman *et al.*, 2018). During the 20th century, the Alps experienced great socio-economic and environmental changes. In many areas, there has been severe depopulation and thus a strong decline of direct human influence on the landscape. Specifically, less accessible areas, especially pastures, were largely abandoned and re-colonized by forest. Conversely, few areas characterized by good climatic conditions and accessibility (e.g. valley bottoms) were intensified, and traditional heterogeneous crops were converted into specialized crops. The same areas also experienced infrastructure development and urbanization, also in response to the growth of tourism (Sergio & Pedrini, 2007; Zimmermann *et al.*, 2010; Schirpke *et al.*, 2017; Tappeiner & Tasser, 2019). These transformations resulted in altered landscape patterns and deep impacts on biodiversity (Chemini & Rizzoli, 2003; Fischer *et al.*, 2008; Marini *et al.*, 2011; Assandri *et al.*, 2017b, 2019a). Considering its relative cover, the wetland area in the Alps is negligible; however, these biotopes harbour disproportionately rich biodiversity (Montagna *et al.*, 2012; Moradi *et al.*, 2012). Unfortunately, studies on the effects of landscape-scale anthropogenic impacts on Alpine aquatic fauna are scant (Scotti *et al.*, 2019), and none focus on dragonflies. Similarly, long-term studies on freshwater environments are globally rare, especially when compared with the terrestrial realm (Bowler *et al.*, 2017).

When long-term studies are lacking, historical resurveys of organisms over time can provide a useful assessment on the effect of global change on biota; however, this kind of studies are limited by the availability of historical data of sufficient quality, and mostly focus on terrestrial habitats and vertebrates (Vellend *et al.*, 2013; Fourcade *et al.*, 2019). Aquatic insects, and specifically dragonflies, can be optimal models for historical comparisons aimed at assessing the impacts of freshwater ecosystem transformations (Ball-Damerow *et al.*, 2014), but to date, very few studies encompassing a long time span exist on this taxon (but see, Korkeamaki & Suhonen, 2002; Suhonen *et al.*, 2010, 2014; Brim-Box *et al.*, 2014; Ball-Damerow *et al.*, 2014; Piché & Hutchinson, 2016; Cerini *et al.*, 2020).

In order to address transformations in Alpine dragonfly assemblages in low elevation mountain areas over the past 100 years, I compared communities at the same sites and in two different time frames (one “historical” and one representing the present state). Historical Odonata occurrences were derived from literature and collections, whereas present communities were resurveyed for this purpose.

Specifically, the operational questions of this study were: i) did (and how) Odonate communities of low elevation mountain wetlands change in term of species richness and composition over the last century? ii) if they changed, were these changes related to two particular species traits (i.e. larval habitat and temperature preference), which so far received little attention compared to other traits (e.g. dispersal ability, Flenner & Sahlén, 2008; Ball-Damerow *et al.*, 2014; Cerini *et al.*, 2020)? iii) did these community patterns go in parallel with the major anthropogenic pressures/drivers which acted in the Alps?

Methods

Study area and sampling site selection

This study was performed in Trentino, covering about 6200 km² in the south-eastern Alps (NE Italy; approximately: 45.67-46.51° N; 10.51-11.96° E; Fig. S1 in supplementary materials). Trentino territory encompasses a wide altitudinal belt (67 - 3764 m), its territory being mainly mountainous, with only 31.1 % of the area below 1000 m asl and 19.9% higher than 2000 m asl. Lowland areas are mostly occupied by intensive agriculture and infrastructures, that replaced most of the natural and semi-natural habitats (Assandri *et al.*, 2017b, 2018). Mountainsides are covered by woodlands, interspersed with permanent crops (up to 1000 m asl) and anthropogenic grasslands (patchy distributed from 300 m to 2000 m; Assandri *et al.*, 2019a). The areas above 2000 m are covered by alpine grasslands, rocks, and glaciers. Trentino hosts a great variety of aquatic ecosystems, generally of reduced size, quite well preserved in the mountains and strongly human-impacted in the valley bottoms.

Low elevation mountain wetlands (most of which located on valley bottoms) were the focus of this study. The choice of the sampling sites was necessarily driven by the criterion that sites had to be clearly defined because it was essential to attribute historical records to specific sites (in fact labels from old collection specimens and localities cited in old studies are often quite general and unprecise). Based on this, ten suitable study sites (Fig. S1 in Supporting information), which are representative of the low-elevation (170-1260 m asl) aquatic environments of the study area, were selected (details on Tab. S1). All the sampling sites are now totally or partially subjected to legal protection, although of different typology. Six sites became Province Reserve between 1988-1994. Additionally, those plus other two sites entered the Natura2000 network, and since 2010 were considered Special Protection Areas (ratified 2014). The remaining two sites are part of Local Reserves since 1986 (Tab. S1).

Period delimitation and odonate data collection

Two time periods were compared (historical vs present). The historical period lasted 60 years between 1928 and 1988. The choice of this long time span was determined by the necessity to include a proper number of historical records (which are scant) for the sites selected. However, it should be noted that, for most sites, records refer to a much shorter time frame (1928-1951). Several data referred to a second later period (1977-1988) were added to include the two sites at a higher elevation (BR and LG, see Table S1), which are needed to correctly represent the global characteristics of the low elevation mountain wetlands of the study area. Although it can be agreed that this time frame might not have been completely stable in terms of Odonata assemblages due to its quite long duration, the most severe pressures which impacted the study area considered in this study (see below) acted during the last 30 years, especially at higher elevations, thus after the conclusion of the historical period (Pedrotti, 2006). Odonate data for this period were retrieved from literature and collections and were all recently critically reviewed by Assandri (2019). Collection data represent 67% of total records available, the great majority of which are specimens preserved in the collection of the MUSE of Trento (Assandri *et al.*, 2019c). The remaining 33% derived from 12 publications (e.g. faunistic site inventories, faunistic notes; see supporting information for a list).

The second period (2017-2019) represents the present status of the communities occurring in the study area. During this period three to six surveys were performed at each site. As the area and habitat complexity of sites differed considerably, the number of surveys per site was based on a statistic approach aimed at defining a minimum adequate sample coverage while optimizing the sampling effort (see statistical analyses). Visits were distributed as homogeneously as possible during the flight period of dragonflies in the study area (from May to October) for each site, guaranteeing at least one visit during the early flight period (before the 30th June), another in the middle (1st July - 31st August), and one in the late flight period (from 1st September).

When addressing dragonfly diversity, biases are possible both when only adults or only exuviae (or larvae) are sampled (Raebel *et al.*, 2010; Bried *et al.*, 2012). Here adults were censused for the sake of comparability between the two periods, as only data on imagos were available for the historical period. Adult presence/absence was assessed during each visit following the same predefined route, which enables to inspect all the micro-habitats occurring at a site. Visits were carried out in days characterized by good weather conditions (i.e. cold, windy, rainy, or overcast days were avoided) and during the peak Odonata activity hours (10.30– 17.00). Visit duration was proportional to the site area and habitat complexity (mean \pm sd = 88 \pm 43 min).

Dragonflies were identified visually with the aid of a 10x42 binoculars. Species not easily identifiable from distance were captured with an aerial insect net and examined in hand (Suhonen *et al.*, 2010). Captured individuals were generally released after examination. In a few cases, voucher specimens were retained, examined with a stereomicroscope (10-40x) and conserved in the author's collection.

Anthropogenic pressures

For each site, a list of the anthropogenic pressures which have acted on odonate aquatic habitats from the end of the historical period onward was compiled. Those data were derived from literature, Natura2000 documentations, personal observations, and comparing aerial photographs taken in the year 1973 (historical period) and 2014 (present). The pressures classification was based on the “List of pressures and threats” provided for the reporting under Article 17 of the Habitats Directive (release 2.4 - 07.05.2018; available online at http://cdr.eionet.europa.eu/help/habitats_art17). Climate change is not listed here as it is likely to impacts on all sites homogeneously as they are all located in the same region and within a restricted altitudinal range. However, to explore possible effects of anthropogenic climate change on dragonfly assemblages, the odonate community temperature index for both periods was calculated (see analyses for details). A list of anthropogenic pressures for each study site is given in Figure 2.

Data analyses

Species selection criteria and categorization

I excluded from the analyses and for further considerations *Sympetrum meridionale* and *Lestes barbarus* for which there is no evidence of reproduction in the study area (i.e. they occur in the region exclusively as migrant/erratic; based on Assandri (2019)). *Sympetrum fonscolombei* was similarly excluded as, although this species is known to reproduce in the study area, its presence strongly depends on migration waves that determined a mostly stochastic presence in the sampling sites in both periods. Additionally, *Cordulegaster boltonii* and *Cordulegaster bidentata* were excluded as no suitable habitats for the reproduction of these species occur in the sampling sites and their occasional presence depend on local movements from near suitable areas.

Additionally, considering the present period, species observed only once, outside the suitable habitats, and not displaying a clear reproductive behaviour were excluded. Such considerations are much more difficult to make for the historical period, thus (if the available literature did not state explicitly that a given species was erratic/not reproducing) all records were retained.

Species were classified according to their larval habitat preference into three categories: i) “lotic”: species which prefer running waters; ii) “lentic permanent”: species which prefer permanent standing (or very slow running) waters; iii) “lentic temporary”: species which prefer seasonally standing waters (see Fig. 1). These trait data have never been synthesized for Italy, thus they were derived from large review studies (Dijkstra and Lewington 2006; Grand and Boudot 2006; Powney et al. 2014; Boudot and Kalkman 2015; <http://dragonfly-database.eu/>) and in a few cases adapted to the study area according to personal observations.

Statistical analyses

All the analyses were performed with the software R (R Core Team, 2019). To define the minimum number of visits needed to adequately sample each site in the present period, the sample completeness was calculated (i.e., the proportion of the diversity sampled). Sample coverage, the percentage of total estimated species richness in a sample, was used to measure sample completeness with the iNEXT package (Hsieh et al., 2016). A site survey was considered sufficient when the sampling completeness resulted to be $\geq 70\%$, though in most cases much higher (mean \pm sd: $84 \pm 6\%$, $n=10$). Since data used to define historical Odonata communities are based on opportunistic surveys carried out by several collectors/researchers, it was not possible to address sampling effort or imperfect detection issues and estimate sample completeness for this period. However, it was possible to calculate two global species accumulation curves (i.e. total species richness), one for each period, in order to verify that regional species richness was adequately assessed in both surveys. Basing on species occurrence in the two periods, for each site it was calculated the number of species belonging to the following three categories: i) confirmed (observed in both periods); ii) new (absent in the historical period, observed in the present period); iii) disappeared (observed in the historical period, not confirmed in the present one).

Species richness and Community Temperature Index (CTI) were calculated at each site for both periods. Community temperature index (CTI) has been commonly used to describe the species turnover that occurs as a result of human-induced climate warming (Devictor et al., 2008; Fourcade et al., 2019). It is a measure of the relative proportion of cold- and warm-adapted species in a community, or, in other words, a community weighted mean of species’ temperature preferences, as it is calculated as the mean Species Temperature Index (STI) of all co-occurring species at a site. STI is considered as a proxy for species’ dependence on temperature and represents the average temperature experienced by a species within its geographical range (Devictor et al., 2008; Fourcade et al., 2019). STI for European dragonflies was recently provided by Teermat et al. (2019) and defined as the average temperature of the European part of the species’ range (excluding Russia). Subsequently, it was tested whether species richness and CTI differ in the two periods controlling for elevation. For this purpose, generalized linear mixed models were used, with either species richness and CTI as response variables, and the period of survey (historical vs present) plus

elevation and their interaction as explanatory variables. The identity of sampling sites was included as a random intercept effect. For species richness, a Poisson error distribution (with a log link) was used, while for CTI a gaussian one (with identity link) was used. Models were fitted using the package *glmmADMB* (Skaug *et al.*, 2016). Following Bolker (2008), not significant interactions were discarded, and models refitted and presented without them. Model marginal (R^2_m) and conditional (R^2_c) pseudo R squared for each model were calculated with the delta method in package *MuMIn* (Barton, 2019). R^2_m represents the variance explained by the fixed effects, whereas R^2_c is interpreted as a variance explained by the entire model, including both fixed and random effects (Nakagawa *et al.*, 2017).

Finally, to assess variation in community composition between the two periods, also considering STI and larval habitats, a multivariate analysis was conducted. The analysis was based on Jaccard dissimilarity index, which is suited for incident data, calculated from the site by species presence-absence matrix (Q-mode). First, an ordination through non-metric multidimensional scaling (NMDS) was performed. The analysis was conducted in two and three dimensions choosing as final configuration the one which minimized the stress value. Additionally, the results' quality was evaluated by stressplots (Borcard *et al.*, 2018; Chiarucci *et al.*, 2019).

Analysis of similarities (ANOSIM) was applied to test differences in the community compositions between periods (Clarke, 1993). Additionally, it was tested whether species co-occurrence patterns differ based on larval habitat preference applying again ANOSIM on R-mode (i.e. on transposed species by site matrix) using Jaccard distances (Borcard *et al.*, 2018). Pairwise ANOSIM comparisons between the three categories of habitat preference were thus performed. R is the ANOSIM statistic and can range from -1 to 1. Positive values indicate the separation between groups. $R > 0.75$ indicate sharp separability between groups, $0.5 < R \leq 0.75$ good separability, $0.25 < R \leq 0.5$ partial overlapping, $0 < R \leq 0.25$ important overlapping (Chiarucci *et al.*, 2019). Significance of ANOSIM comparison was computed based on 9999 permutations. Multivariate analyses were conducted with the package *vegan* (Oksanen *et al.*, 2019).

Results

Overall, 836 useful records (483 historical, 353 present) were available. They referred to a total of 49 breeding species. This represents the 84.4% of the species which reproduce/reproduced in the study area (Assandri 2019 and pers. obs.) and the 51.5% of the 95 species recorded at least once in Italy (<http://www.odonata.it/libe-italiane/>). Global accumulation curves (Fig. S2) and global sample completeness (98% for the historical period and 96.4% for the present period) suggest that in both periods the overall dragonfly communities were adequately assessed.

Overall, 11 species were contacted in the historical period only (thus disappeared from all the sites), 5 disappeared from more than the 50% of the sites in which they previously occurred, 4 were confirmed at all sites, 9 were confirmed in more than 50% of the sites, 3 were new in more than 50% of the sites and 3 were new at all sites. The remaining 14 species showed mixed patterns depending on sites (Fig. 1).

On average, 48.5% (SD = 40; range 0–100%) of the historical populations (defined by the presence of a species in a site in the historical period) had become extinct, whereas only 39.9% (SD = 35; range 0–100%) of the present populations are new.

Species loss at sites was comprised between 15.4% and 51.5%, species gain accounted for 12.1%–46.9%, and confirmed species between 23.1% and 61.5%. At sites which experienced the greatest species loss (the rightmost four in Fig. 2), acted pressure mostly related to the conversion of wetland for agricultural and settlement/recreational purposes, agricultural intensification and abandonment, hydropower, and pollution from industrial and urban areas.

Mean site species richness did not significantly differ between historical and present periods and along the elevation gradient, although a negative trend is observed (Tab. 1, Fig. 3a). Mean CTI index was significantly higher in the present period than in the historical one (Tab. 1, Fig. 3b) and negatively related to elevation. This last relationship was comparable between the two periods, as the interaction between the two variables was not significant (Tab. 1, Fig. 3c). According to pseudo R-squared, the species richness model had a poor explanatory power ($R^2_m = 0.10$; $R^2_c = 0.33$), whereas the CTI model a very high one ($R^2_m = 0.73$; $R^2_c = 0.89$).

For multivariate analysis, an NMDS ordination on three dimensions was selected because it has a lower stress value than that on two dimensions (0.10 vs 0.18). Stress values ≤ 0.1 can be considered good (Clarke & Warwick, 2001). This configuration had a high non-metric ($R^2=0.995$) and linear fit ($R^2=0.949$). The visual interpretation of the NMDS plot (Fig. 4) indicated a large overlap between the communities in the two periods, this because the present community appears to be nearly a subset of the historical one (11 vs 3 unique species, see above). This was confirmed by ANOSIM, which suggested that, although the historical and present communities are distinct, they largely overlap (R-statistic = 0.17; $p = 0.02$). Mean (\pm sd) dissimilarity between historical vs present communities is 56 ± 13 %.

Many species characteristic of the historical period (more "extern" in Fig. 4a, except for *Aeshna affinis*), which disappeared or strongly declined, are generally those which prefer temporary lentic habitat, and, to a lesser extent, lotic waters (e.g. *Onychogomphus forcipatus*, *Calopteryx virgo*) (see also Fig. 1). Pairwise ANOSIM comparison on species co-occurrence patterns based on larval habitat preference confirmed that the three groups (i.e. lotic, lentic permanent, and lentic temporary) defined on a priori knowledge are consistent; however, lentic permanent species

overlaps considerably with lentic temporary (R-statistic = 0.2; $p = 0.04$), and lotic (R-statistic = 0.23; $p = 0.02$), whereas lentic temporary less markedly with lotic (R-statistic = 0.49; $p = 0.001$). Finally, species more related to the historical communities have, in general, lower STI (blue and purple colours in Fig. 4b).

Discussion

This study documents relevant transformations of odonate communities of low elevation mountain wetlands over nearly a century. These transformations resulted in a negative balance for the local fauna; in fact, comparing historical and present surveys, 22.4% of the species disappeared and 10.2% disappeared from more than a half of the sites at which they previously occur. Conversely, only 6.1% of the species were completely new for the study area and an additional 6.1% new at more than half of the sites. Additionally, 8.2% of the species were confirmed at all sites, and 18.7% at more than half of the sites (and thus remained substantially stable).

The great majority of species which disappeared from all the study sites also disappeared (or strongly declined) at the regional scale (Assandri 2019). This suggests that the selected sites are representative of the wider study area, also given the limited sample size constrained by historic data availability. However, a limit of this study is that no abundance data are available for comparisons, and thus it is impossible to infer whether the species confirmed in the second period also remained stable in population size.

The 48.55% of the historical populations (individual species present at a given site) went loss. In a similar study carried out in Finland (comparing 1930-1975 and 1995-2003), a less severe mean decline (about -30%) was observed (Suhonen *et al.*, 2010, 2014), whereas in a shorter period (1996-2002 vs 2006-2011), in two forested and farmed areas in Sweden, the population loss was comprised between 38-43%, but with a double or triple colonization rate, mostly explained by climate change (Koch *et al.*, 2014).

Although regional (gamma) species richness was higher in the historical periods compared with the present (46 vs 38 species), mean site (alpha) species richness does not significantly differ between the two, likely suggesting that an overall lower number of more widespread and common species are shaping present communities, this meaning an overall homogenization of community composition from historical to the present period. This result is consistent with others resurvey studies on Odonata (Ball-Damerow *et al.*, 2014; Piché & Hutchinson, 2016) and other groups of insects (e.g. bumblebees in Norway; Fourcade *et al.*, 2019). However opposite results were obtained on freshwater fishes, which showed a long-term stable gamma diversity at drainage scale, but a decrease of local diversity at lower levels of scale (Patton *et al.*, 1998).

Putative drivers of dragonfly community transformations

The dragonfly community transformation drivers which acted in the last century, and more markedly in the last about 30 years, are undoubtedly complex, interacting, and difficult to disentangle due to the fragmentary nature of historical records. Additionally, any quantitative approach aimed at correlating community shift in composition to individual pressures resulted unfeasible due to the impossibility of adequately quantify pressures at a given site acting in the past. However, considering major pressures which impacted freshwater ecosystems in the Alps in this last century (Pedrotti, 2006) and the list of pressures acting locally (this study), it is worthful to qualitatively describe them, recognizing that no direct cause-effect relationship can be inferred from the results of this study.

Wetland drainage and reclamation was likely the most severe pressure which impacted dragonfly communities in the study area, as in the whole northern hemisphere, determining substantial habitat loss (Kalkman *et al.*, 2007; Elo *et al.*, 2015; Delpon *et al.*, 2019). Before 1850, the main valley bottoms of the region were extensively covered by wetlands, as in other parts of Europe (Gimmi *et al.*, 2011); reclamation started in the XIX century and had continued almost without interruption till the almost complete conversion of all preexisting wetlands in the second half of XX century, with the partial exclusion of the small areas to which was accorded a protection status starting from the second half of the '80s (Rossi, 2005). Reclamation was initially aimed at increasing arable land, but, starting from about the second half of 1900, also settlement and infrastructure creation considerably contributed. With the development of tourism, several aquatic environments (e.g. lakes) started to be seen as pleasant places (Perlik, 2006) and this determined further development of infrastructures (e.g. bathing establishments) aimed to support recreational activities in these areas. To make possible the comparison, for this study were selected sites which have been, at least partially, preserved. Much more sites completely disappeared, suggesting that the magnitude of impacts should have been much stronger.

Transformations of agricultural practices, including both intensification and abandonment, is one of the main causes of global biodiversity loss (Green *et al.*, 2005; Norris, 2008; Tscharnke *et al.*, 2012). Considering dragonflies, there is increasing evidence that this taxon is substantially impacted by intensive farming practices, which determine deterioration of the matrix in which their freshwater habitats are found (Lee Foote & Rice Hornung, 2005; Raebel *et al.*, 2012; Koch *et al.*, 2014). In the study sites, and generally, in the Alps, intensive agriculture impacted freshwater

biodiversity by: i) active abstraction of water for irrigation, which influences water levels and hydroperiod; ii) the dramatic increase in the use of fertilizers (both natural and chemical), determined by the intensification of livestock farming in the last fifty years (Marini *et al.*, 2011; Scotton *et al.*, 2014), which determined the eutrophication of water bodies; iii) the use of pesticides, which are washed and taken up to water bodies (Zedler & Kercher, 2005; Bartzen *et al.*, 2010).

Agricultural abandonment at the studied sites, as in other parts of the Alpine region, impacted wet meadows and fens, which, when traditional husbandry ceased, they were abandoned and converted into other ecosystems (e.g. reedbeds, shrublands, woods) by the secondary succession (Pedrotti, 2006).

In the Alpine region, hydropower generation has high economic importance but also determines major environmental disturbance, including canalization of watercourses, changes in flow regime, disruption of the river continuum, and thermal modifications, which, in turn, have major impacts on aquatic ecosystems, both lentic and lotic (Fette *et al.*, 2007; Bruno *et al.*, 2010; Spitale *et al.*, 2015). Although few of the sites included in this study were directly impacted by the creation of hydropower energy, this should be considered a relevant pressure impacting dragonfly communities (Chovanec & Waringer, 2001; Chovanec *et al.*, 2004).

Finally, pollution caused by the discharge of urban and touristic facilities wastewaters into aquatic ecosystems, and, to a lesser extent, heat pollution on water from industries, were likely to have further impacted local communities of dragonflies, as in other industrialized areas (Clausnitzer *et al.*, 2009; Ferreras-Romero *et al.*, 2009).

Putative impact of anthropogenic climate change on dragonfly communities

Several authors argued that the effects of human-induced climate change might be more severe in freshwater environments than in terrestrial realm (e.g. Flenner & Sahlén, 2008; Hassall & Thompson, 2008), although this is not always the case (Bowler *et al.*, 2017). Dragonflies are considered valuable macroecological indicators of climate change (Bush *et al.*, 2013; Hassall, 2015) as it is known to affect odonates by influencing their distribution (e.g. determining northwards range shifts in the Northern hemisphere, or upward shifts in mountain ranges), advancing their phenology, and filtering local assemblages based on species dispersal ability (Hickling *et al.*, 2005; Hassall *et al.*, 2007; Ott, 2010; Rapaciuolo *et al.*, 2017). Such strong selective pressure can bring to the loss of populations and, potentially, species, at the regional scale (Hassall & Thompson, 2008).

A relevant finding of this study is that the present communities of dragonflies show a significantly higher Community Temperature Index than the communities existing in the same sites in the past. The CTI is calculated as the mean of the individual Species Temperature Index, thus this pattern could be explained by the disappearance or decline of cold-adapted species, or by the increase of warm adapted ones, or by both causes. In the study area, both patterns were observed. Considering Odonata, so far, only one recent study applied this index (Termaat *et al.*, 2019). Those authors observed only a limited CTI increase at European level (1990-2015), although variable according to the different countries considered. This was explained by the relatively positive response of cold-dwelling species to temperature increase. However, the present study suggests that, in the Alps, many cold-adapted species (e.g. *Sympecma paedisca*, *Lestes sponsa*, *Coenagrion hastulatum*, *Erythromma najas*, *Aeshna grandis*, *Sympetrum flaveolum*, and *Sympetrum danae*) are among the species which locally disappeared or greatly decreased in the last century. Conversely, among those which are doing well, many warm-adapted species are found (e.g. *Chalcolestes viridis*, *Anax imperator*, *Anax parthenope*, *Aeshna isosceles*, and *Aeshna mixta*). Noteworthy, similar results were obtained in various part of Europe for other taxa, including plants, birds, butterflies, beetles, stream invertebrates, and bumblebees (Devictor *et al.*, 2008, 2012; Roth *et al.*, 2014; Thomsen *et al.*, 2016; Fourcade *et al.*, 2019; Haase *et al.*, 2019).

Loss or decline of temporary lentic and lotic habitat specialists

Most of the species whose larval habitat is represented by temporary lentic waters disappeared or declined between the two periods (contrasting with those inhabiting permanent lentic waters). Emblematic in this sense is the case of the family Lestidae. Of the four species reported in the study area, the two most dependent on temporary wetlands (i.e. *Lestes dryas* and *Lestes virens*, see Boudot & Kalkman (2015)) disappeared from the region. Additionally, *Lestes sponsa*, which is a species often found in temporary habitat, but that can be found also in more permanent systems, considerably declined in the valley bottoms of the region (being still abundant in the mountains, where habitats were less impacted, *pers. obs.*). Conversely, *Chalcolestes viridis*, which do not depend on temporary waters, apparently increased in the study area.

The decline of dragonfly species adapted to temporary waters can be explained by considering that, in temperate climates (including the study region), temporary wetlands often occur when lakes and streams are free to naturally flood during the humid season; however, most of these habitats have been altered and their water regime changed. For example, in Europe, *Sympetrum pedemontanum* (one of the species completely disappeared in the study area), before the second half of the Twentieth Century was largely confined to temporary wetlands and wet meadows flooded by melting snow such as the flood plains of mountain valleys and foothills. It almost disappeared together

with these habitats and now it mostly occurs in artificial habitats with variable water levels and maintained at early successional stages (Boudot & Kalkman, 2015). Notably, the decline of temporary habitat specialist (e.g. genus *Lestes* and *Sympetrum*) seem to be consistent at a Holarctic scale (Ball-Damerow *et al.*, 2014).

Temporary wetlands represent unique environments of high ecological, hydrological, biogeochemistry, and socioeconomic relevance (Williams *et al.*, 2001). At the landscape scale, they have the fundamental role of nodes in the hydrological network connecting permanent waters. They are threatened by human population growth resulting in urbanization, agriculture, and livestock increase, as a result of which they are reclaimed or converted into permanent systems (Jeffries *et al.*, 2016; Calhoun *et al.*, 2017).

Considering lotic water specialists, at least two species related to well preserved riverine habitats (i.e. *Onychogomphus forcipatus* and *Calopteryx virgo*) disappeared from the study sites (but not from the study region; Assandri, 2019), whereas other species which are not strictly specialists of running waters and have a wider tolerance for less well-preserved environments (i.e. *Platycnemis pennipes*, *Erythromma lindenii*, and *Calopteryx splendens*) remained stable. Globally, rivers and streams are among the most threatened of all ecosystems, being heavily exploited natural resources. They are impacted by intensive land use in their catchments, channel modification, flow regulation, and human-induced climate change (Wohl, 2006; Vörösmarty *et al.*, 2010; Scotti *et al.*, 2019). Although in western Europe water quality improved substantially during the last few decades, in the course of the XX century aquatic macroinvertebrates communities were deeply impacted by anthropogenic perturbations (Vaughan & Ormerod, 2012; Outhwaite *et al.*, 2020), also in the Alps (Maiolini *et al.*, 2006; Bona *et al.*, 2008). These impacts also affected riverine odonates (Kalkman *et al.*, 2007, 2018), being the species inhabiting lotic waters generally considered to be at greater risk than those of lentic ones (Clausnitzer *et al.*, 2009; Delpon *et al.*, 2019), or compared with species found in both (Korkeamaki & Suhonen, 2002).

Results like those presented here were obtained in Canada, where, comparing historical and present assemblages, eight species associated with streams, rivers or temporary wetlands declined or disappeared (Piché & Hutchinson, 2016). The same is true for the neighbouring Switzerland and South-Tyrol, where most of the species disappeared/declining in the study area are listed in a higher threat category by the local Red Lists or are considered regionally extinct (Gonseth & Monnerat, 2002; Lösch *et al.*, 2018). In contrast, case studies in the U.S.A, Africa, and Sweden, showed a not so harsh decline of lotic species (Ball-Damerow *et al.*, 2014; Cerini *et al.*, 2020).

Conclusions

In a recent assessment of European dragonfly occurrence trends across a period of 25-years, Termaat *et al.* (2019) observed that 55 of the 87 odonate species considered increased in occupancy at European level, 32 species remained stable, and none declined. This remarkably positive outcome was explained by the positive effect of climate change, which determined range expansion in warm-dwelling species -and a not so harsh impact on cold-dwelling one-, by the recent improvements in water quality, and by increasing efforts in wetland restoration. However, the results from Termaat *et al.* (2019) seem to find scarce accordance with the European IUCN red list, which show that 15% of the European Odonata species are threatened, a quarter of all species are declining in population abundance and distribution, and about half are stable, whereas only 10% of them are increasing (Kalkman *et al.*, 2010). The results presented here are much nearer to the latter figure, with a reported 32.6% species loss or strong decline at low elevation Alpine wetlands over the nearly last century. The most impacted species are temporary water specialists and cold-adapted ones, and, to a lesser extent, lotic specialists. Additionally, as in other studies (e.g. Flenner & Sahlén, 2008; Ball-Damerow *et al.*, 2014; Cerini *et al.*, 2020), a homogenization of the odonate community is evident. These patterns are possibly explained by the joint effects of land-use change, land-use intensification, environmental pollution, and anthropogenic climate warming.

Although it is clear that this study is limited in spatial extent, it should be stressed that it refers to a dragonfly biodiversity hotspot at the European scale (Kalkman *et al.*, 2018) from which few reports on the conservation status of Odonata exist. Recent evidence from other groups (e.g. birds) suggest that mountain ranges (including the Alps) are no more considerable mountain refugia for lowland species impacted by global change (Archaux, 2007; Korner *et al.*, 2017; Assandri *et al.*, 2019b; Fourcade *et al.*, 2019), and this is likely to be true also for dragonflies. In the last 30 years, the legal protection accorded to all sites investigated probably allowed to slow down species loss, but, based on this study, it is clear that the impacts of human activity on dragonfly communities are much more deeply rooted in time. The limited area of these protected sites in a highly human-exploited matrix, till now, prevented the recolonization of the previously lost sensitive species, and allowed only limited new colonization by widespread generalists, supporting the worrying evidence that the global biodiversity crisis is far to be sparing Alpine dragonflies.

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Conflicts of Interest

There is no conflict of interest to declare.

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Tab. 1 Results of mixed model testing for the effects of period and elevation on species richness and Community Temperature Index (CTI). In both cases, the one-way interaction resulted to be not significant and thus removed from the final model. The covariate significance was assessed by means of Wald's chi-square tests performed with the R package car (Fox and Weisberg, 2011). N=20

| | Species richness | | | | CTI | | | |
|-----------|-------------------------|-----------|----------|----------|-------------------------|-----------|----------|----------|
| | $\beta \pm s.e.$ | <i>df</i> | χ^2 | <i>p</i> | $\beta \pm s.e.$ | <i>df</i> | χ^2 | <i>p</i> |
| Period | | 1 | 0.07 | 0.78 | | 1 | 27.53 | < 0.001 |
| elevation | - 0.00026 \pm 0.00019 | 1 | 1.70 | 0.19 | - 0.00121 \pm 0.00023 | 1 | 26.49 | < 0.001 |

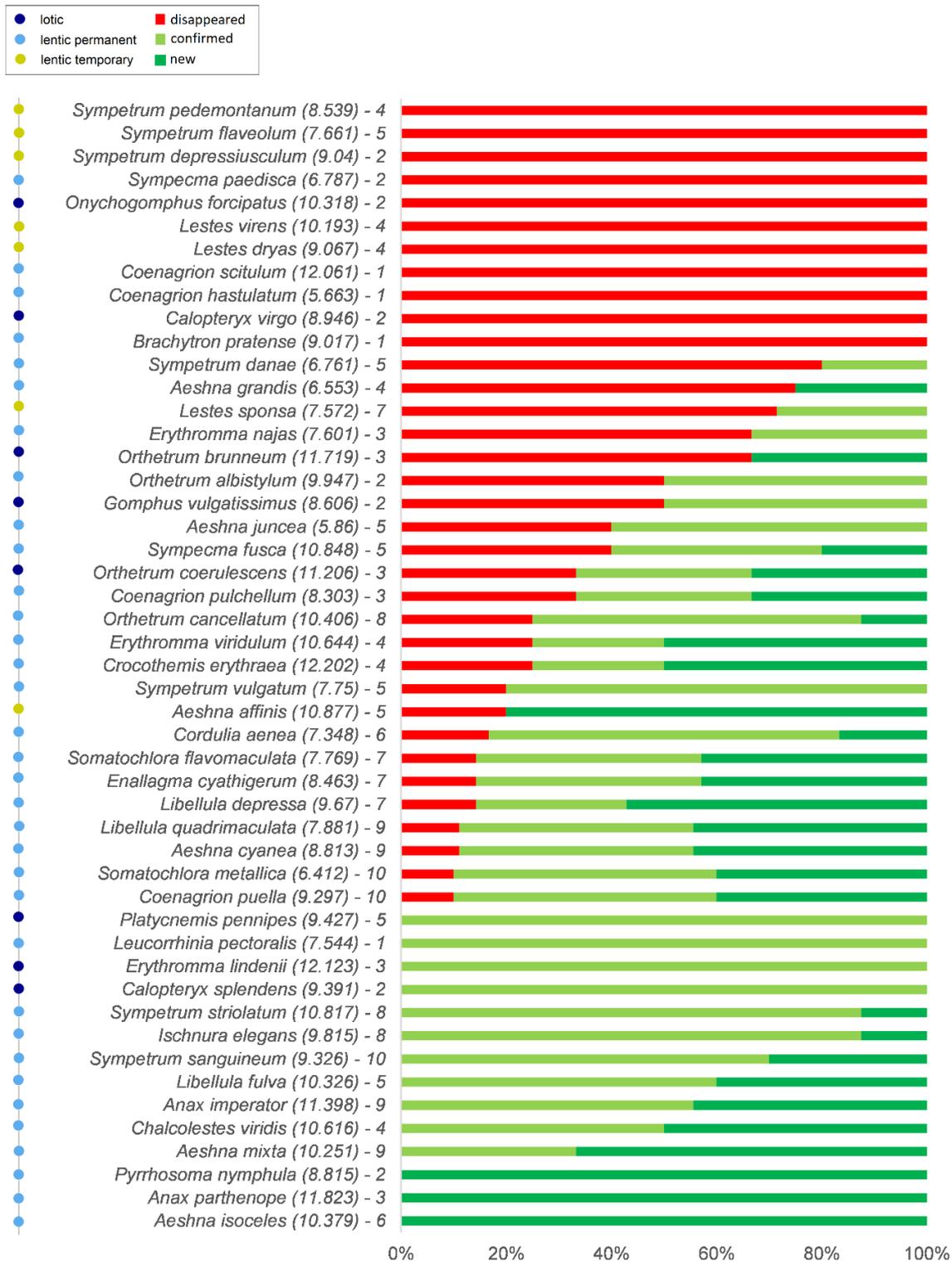
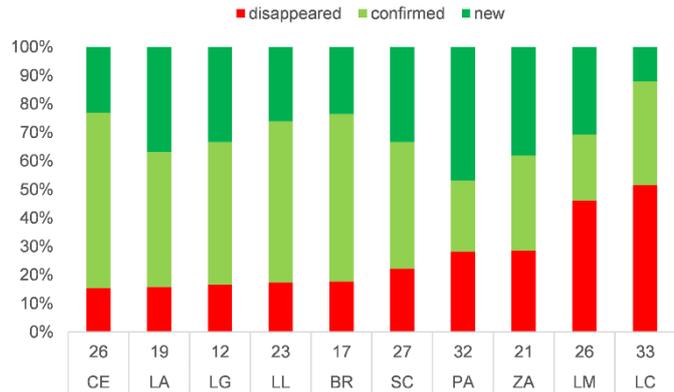


Fig. 1 Percentage of sites in the study area at which a species was confirmed (observed in both periods), new (absent in the historical period, observed in the present period), or disappeared (observed in the historical period, not confirmed in the present one). The total number of occurrence sites is also given. Larval habitat classification (see legend) and STI value (in brackets) are also given for each species.



| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| A06: Abandonment of grassland management | | | ✓ | | ✓ | ✓ | ✓ | | ✓ |
| A14: Livestock farming (without grazing) | | | | | | | | | |
| A19: Application of natural fertilisers on agricultural land | | ✓ | | | ✓ | | ✓ | | |
| A20: Application of synthetic fertilisers on agricultural land | | | | | | ✓ | ✓ | | ✓ |
| A21: Use of plant protection chemicals in agriculture | | | | | | ✓ | ✓ | | ✓ |
| A30: Active abstractions of water for agriculture | | | | | | | ✓ | ✓ | |
| D02: Hydropower | | | | | | ✓ | ✓ | | |
| A31: Drainage for use as agricultural land | | | | ✓ | | ✓ | ✓ | | ✓ |
| F26: Conversion of wetlands to settlement or recreational areas | ✓ | ✓ | | ✓ | | ✓ | | | ✓ |
| F07: Sport, tourism and leisure activities | ✓ | ✓ | | ✓ | | ✓ | | | ✓ |
| F12: Discharge of urban waste water | ✓ | ✓ | | ✓ | | ✓ | | | ✓ |
| F25: Noise, light, and heat pollution from industrial processes | | | | | | | | ✓ | |
| J04: Solid waste | | | | | | ✓ | | | |

Fig. 2 Percentage of dragonfly species confirmed (observed in both periods), new (absent in the historical period, observed in the present period), or disappeared (observed in the historical period, not confirmed in the present one) at the ten samples sites surveyed in the study area. The global species richness assessed at each site is also given. For each site, a list of anthropogenic pressure which acted starting from the end of the historical periods onward is provided. The pressures classification was based on the “List of pressures and threats” provided for the reporting under Article 17 of the Habitats Directive (release 2.4 - 07.05.2018; available online at http://cdr.eionet.europa.eu/help/habitats_art17; details on Tab. S2). For site code legend, see Tab. S1.

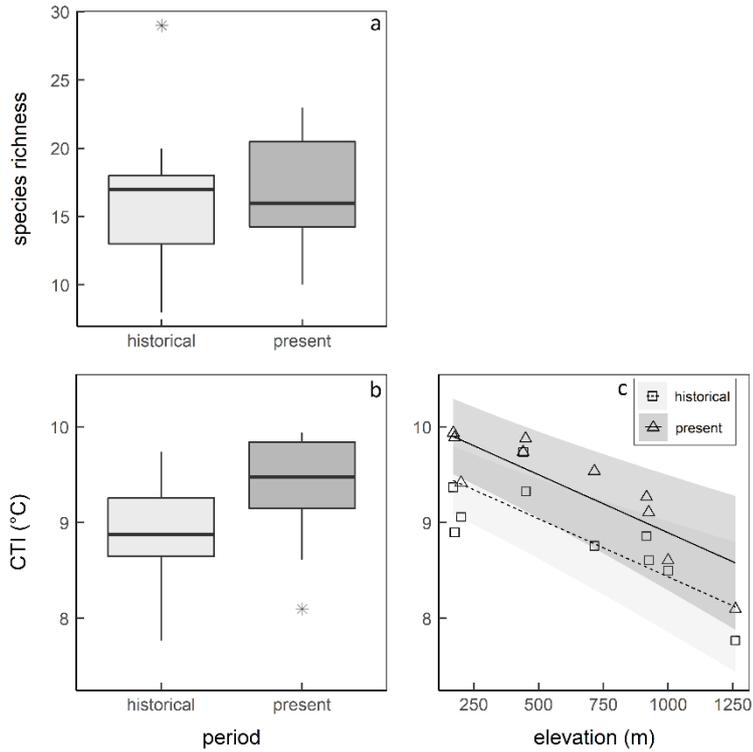


Fig. 3 Variation of species richness and Community Temperature Index (CTI) between historical and present periods (a-b), and CTI trend as a function of elevation in the historical and present period (c). In the third plot, predictions for the mean (lines) and 95% confidence intervals (in shaded grey) are derived from a gaussian GLMM. N=20.

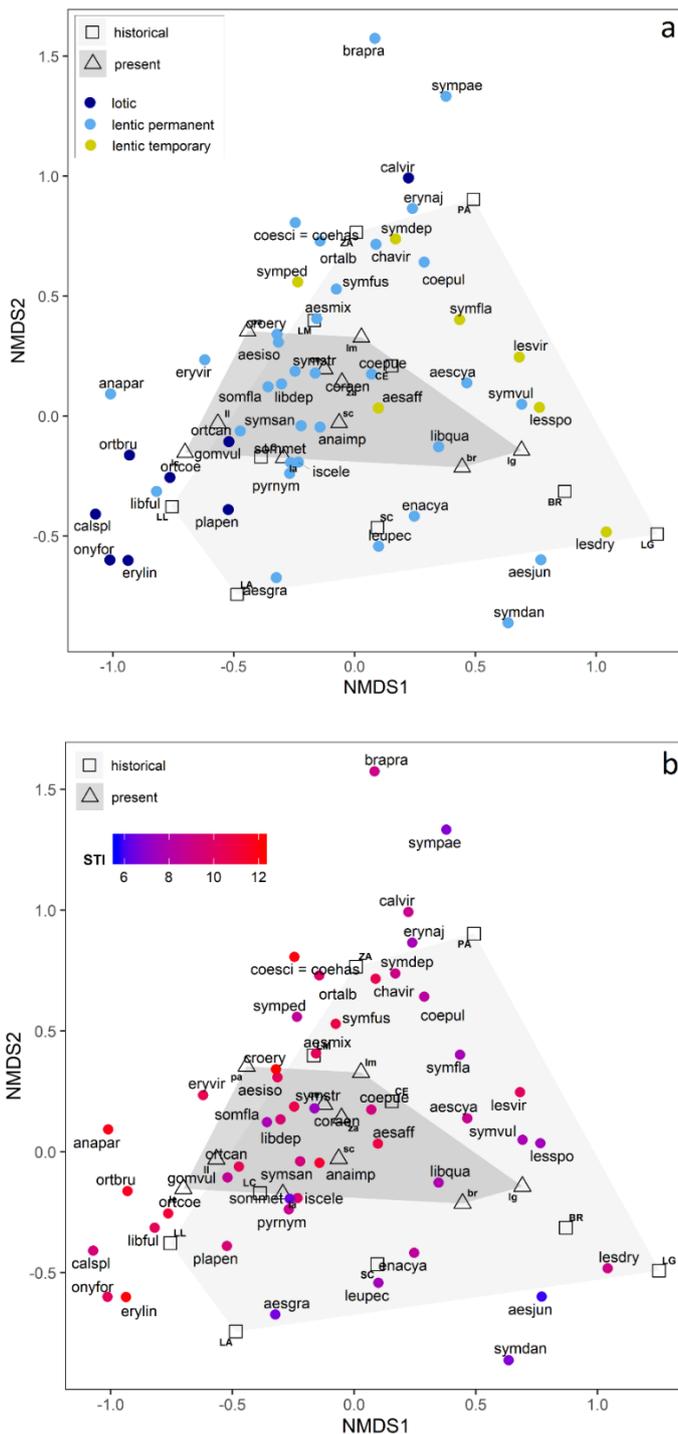


Fig. 4 Ordination plots of the first two axes of a tridimensional NMDS representing the ordering relationship amongst sites and species in the assemblage; the distance between them in the ordination plots can be directly interpreted as dissimilarity value. Function *metaMDS* in *vegan* automatically rotates the final result of the NMDS using PCA to make axis 1 correspond to the greatest variance and the second axis to the second biggest gradient (Oksanen *et al.*, 2019). Sites are depicted with empty square (historical period) and triangles (present period). Convex hulls were superimposed to represent the two periods considered. Species are shown with coloured full circles. In a) larval habitat preference of dragonflies are shown, in b) Species Temperature Index of each species is presented (Termaat *et al.*, 2019). For site label legend refer to Tab. S1 (sites; capital letters refer to the historical periods, lowercase letters refer to the present period) and for species label to Tab. S3