

A trait-based approach to assess the vulnerability of European aquatic insects to climate change

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Abstract Aquatic insects are the dominant taxon group in most freshwater ecosystems. As temperature is the main driver of their life cycle development, metabolic activity, and geographic distribution, these macroinvertebrates are particularly suitable for large scale and comparative studies of freshwater community responses to climate change. A dataset of bio-ecological traits of 1,942 Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa was used to analyze (1) the relationships among traits, (2) the potential vulnerability of EPT species to climate change, and (3) the geographical occurrence patterns of these potentially endangered species at the scale of European

ecoregions. By means of a fuzzy correspondence analysis (FCA), two gradients emerged: (1) a longitudinal gradient, describing successive upstream–downstream features, and (2) a biogeographical gradient, separating endemic and micro-endemic species from widely distributed taxa. Moreover, aquatic insects of southern European ecoregions emerged as those most endangered in terms of potential vulnerability to climate change. Comparative multi-taxon studies provide important new insights into freshwater ecosystem functioning and responses to climate change, and could be the first step toward developing integrative monitoring or assessment tools (e.g., trait-based indicators at the species level) by means of non-arbitrary statistical methods.

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Introduction

Freshwater ecosystems, like their terrestrial and marine counterparts, are facing pressure from overexploitation, pollution, habitat destruction or degradation, and alien species invasions (e.g., Allan & Flecker, 1993; Naiman & Turner, 2000; Jackson et al., 2001; Rahel, 2002; Revenga et al., 2005). Synergies and tradeoffs between these diverse impacts are also subjected to large scale and global patterns,

such as climate change and acid deposition (Dudgeon et al., 2006; Brown et al., 2009). Biodiversity in inland waters exposed to these multiple stressors is declining faster than in their terrestrial and marine counterparts (Sala et al., 2000; Jenkins, 2003), and freshwater ecosystems turn out to be among the most endangered ecosystems in the world (Dudgeon et al., 2006).

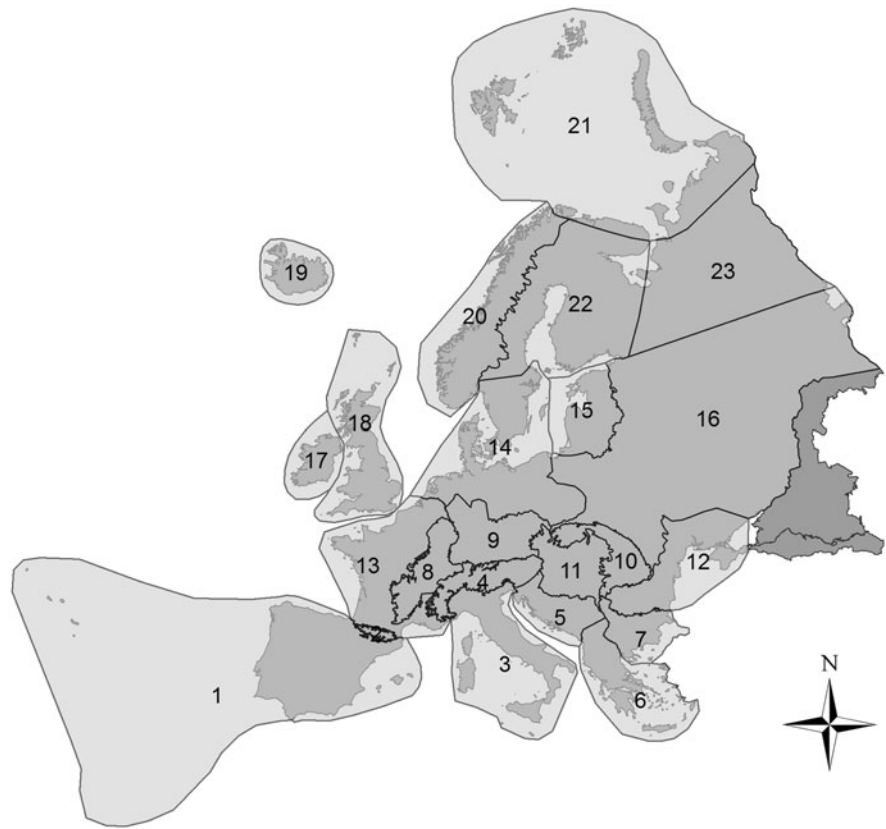
The influence of these stressors on the structure and functioning of ecosystems can be addressed at several different spatial scales (from local to global) and levels of biological organization (from individuals to communities). In this context, large-scale studies provide a better understanding of geographic patterns and a general framework within which regional (and local) conservation and management actions can be implemented. At the same time, a multi-species approach, taking into account different components of the ecosystems, may contribute to a comparative understanding of specific responses (e.g., of a single order), as well as providing a synthetic assessment of the impact of a changing environment on the ecosystem.

Macroinvertebrates, and particularly insects, are the dominant taxon group in most running waters (Resh & Rosenberg, 1989). Aquatic insects are profoundly affected by temperature at all stages in their life cycle (eggs, larvae, pupae, adults) and temperature changes are the main drivers of embryonic development, nymphal growth, emergence metabolism, survivorship, and geographic distribution (e.g., Brittain, 1980; Lillehammer et al., 1989; Marten, 1990; Watanabe et al., 1999; Sweeney et al., 2001; Zwick, 2002; Haidekker & Hering, 2008). Given that their emergence (i.e., conversion into the ephemeral and aerial adult phase) is driven mainly by photoperiod and temperature (Tobias, 1967, 1971; Perkins et al., 2010), the responses of aquatic insects to warming could be substantial.

Predicted changes in temperatures and precipitation variability are not uniform over space (Johns et al., 2003; IPCC (Intergovernmental Panel on Climate Change), 2007), and inland waters are already experiencing the effects of increasing temperatures and variability of the hydrologic regime (Rouse et al., 1997; Schindler, 2001). These modifications of the local environment select for specific adaptations, which subsequently lead to more or less extensive changes in the functional and taxonomic diversity of the resident communities (e.g., Durance & Ormerod, 2007). The biological trait approach has been

demonstrated to be a particularly effective way to describe the functional changes that occur in biological communities exposed to ecosystem variability (e.g., Statzner et al., 2001; Baird et al., 2008; Culp et al., 2011) and anthropogenic disturbances (Dolédec & Statzner, 2008; Feio & Dolédec, 2012). Differences in morphological, behavioral, and physiological traits of individual species are common along climatic gradients, i.e., regions with similar characteristics should host organisms with similar biological traits, whereas regions with differing climatic conditions can be expected to host organisms with adapted and consequently differing traits. Consequently, climate change will probably alter both trait and species compositions, although taxonomic variation is expected to outweigh functional change (Bonada et al., 2007), due to the redundancy of functional profiles among the species in a community (Tilman, 2001). During periods of rapid environmental change, certain species traits will be beneficial. For example, eurytherm (i.e., temperature tolerant) aquatic insects with long egg development, asynchronous egg hatching and nymphal development, small and cylindrical nymphal size or a multivoltine life cycle all have an increased chance of survival (Brittain, 1991; Kotiaho et al., 2005). Generalists can be expected to do better in changing environments (Townsend & Hildrew, 1994), whereas specialists with strict environmental requirements and low dispersal capacity may face range contractions or even extinctions (Brittain, 2008). Following these general assumptions, freshwater researchers began to use macroinvertebrates as species-level indicators of the potential impacts of climate change in aquatic ecosystems (e.g., Hodkinson & Jackson, 2005; Durance & Ormerod, 2007; Hannah et al., 2007; Collier, 2008; Kazanci & Dügel, 2008; Lawrence et al., 2010). Other studies provide a general framework within which invertebrate species are classified as sensitive or vulnerable to a changing environment (e.g., increasing temperatures) (e.g., Hering et al., 2009; Tierno de Figueroa et al., 2010), or model present and future climatic suitability of European macroinvertebrates under climate change scenarios (Domisch et al., 2011). The term ‘vulnerability’ is used to refer to the degree of likelihood that a system will suffer harm due to exposure to a hazard (Turner et al., 2003). Using this definition, the potential vulnerability of aquatic insects (i.e., *system*) to climate change (i.e., *hazard*) (Füssel, 2007) was addressed in these studies by analyzing the

Fig. 1 The 23 European ecoregions (sensu Illies, 1978) analyzed in the study. (1) Iberic-Macaronesian Region, (2) Pyrenees, (3) Italy, Corsica and Malta, (4) Alps, (5) Dinaric Western Balkan, (6) Hellenic Western Balkan, (7) Eastern Balkan, (8) Western Highlands, (9) Central Highlands, (10) The Carpathians, (11) Hungarian Low Lands, (12) Pontic Province, (13) Western Plains, (14) Central Plains, (15) Baltic Province, (16) Eastern Plains, (17) Ireland and Northern Ireland, (18) Great Britain, (19) Iceland, (20) Borealic Uplands, (21) Tundra, (22) Feno-Scandian Schield, and (23) Taiga



ecological preferences and life history traits of selected species. Over the last decade, and within the framework of two EU-funded projects [Euro-limpacs (2004–2009) and Refresh (2009–2013)], scientists have constructed a coherent and open-access database of freshwater biological communities, which is available at www.freshwaterecology.info (Schmidt-Kloiber & Hering, 2012). This database contains taxonomic and ecological information about European freshwater taxa, ranging from biogeography to biological and ecological traits, and information about rarity and sensitivity at species level.

In this study, the potential vulnerability of the species belonging to three orders of aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera; EPT) was assessed by means of a multivariate analysis of their ecological preferences and biological characteristics. We used a selection of traits for 1,942 species to investigate (i) the relationships among traits, (ii) the vulnerability of EPT species to increasing temperatures, and (iii) the geographical patterns of occurrence of these potentially endangered species at the scale of European Ecoregions (ERs).

Methods

Data description

Thirty-five variables describing the distribution, ecological preferences and life history traits of European aquatic insects were extracted from the www.freshwaterecology.info database (Graf et al., 2006, 2007, 2008a, b, 2009a; Buffagni et al., 2007, 2009; Graf & Schmidt-Kloiber, 2011) (see Appendix I in Supplementary data). Information was available for 1,942 taxa (i.e., species and sub-species, referred to below as either taxa or species) at the scale of ERs sensu Illies (1978) (Fig. 1), encompassing 344 Ephemeroptera, 461 Plecoptera, and 1,137 Trichoptera species. Data from 23 out of 25 ERs were used for the analyses, the Caucasus (ER 24) and the Caspic Depression (ER 25) being excluded because their species lists are still incomplete.

In the database, the occurrence of different trait modalities was coded as presence/absence, single category assignment, or by fuzzy coding (in most cases using a 10-point assignment system) (Appendix

I in Supporting data). The fuzzy coding procedure (Zelinka & Marvan, 1961; Usseglio-Polatera, 1991; Chevenet et al., 1994; Moog, 1995) allows the taxon–trait relationship to be described using the scores assigned to each modality of each trait. The score reflects the affinity of the taxon with that particular modality of each trait, e.g., ‘0’ indicates no affinity and ‘10’ high affinity. The ten-point assignment system considers gradients of habitats, feeding types, and other relevant parameters and is based on the known (or estimated) average distributions, occurrences or behaviors of a taxon within the environmental gradient under consideration (for more information on the coding system applied in the database see www.freshwaterecology.info).

Fuzzy correspondence analysis

To analyze the relationships among traits we used a fuzzy correspondence analysis (FCA; Chevenet et al., 1994). This analysis can be interpreted as a correspondence analysis of a taxon using a modality array in which the affinities of the taxon for the different modalities are indicated by frequency distributions (Usseglio-Polatera et al., 2000). Aquatic insect taxa are thus arranged along the axes on the basis of the best compromise obtained by comparing the data on modalities for each species trait. In other words, the FCA, like other multivariate ordination techniques, makes it possible to reduce the n -dimensional space represented by all the modalities of species traits into a reduced-dimension plot, summarizing the complex patterns embedded in the original dataset. Trends in the distribution of modalities within traits were quantified by correlation ratios (RS), which allowed the identification of traits that were best explained by the considered axes (only values above 10% were further discussed). RS represent proportions of the total variance explained by each axis to depict the separation among modalities of a variable (Chevenet et al., 1994), and are computed following a maximization criterion, for which the first coordinate of correspondence analysis (FCA axis 1) maximizes the average RS among the traits.

The multivariate analysis was performed on a selection of 23 biological or ecological traits (Table 1) and 113 modalities, using the *ade4* package in the R statistical environment (R Development Core Team, 2011). Nine other traits available at www.freshwaterecology.info

[freshwaterecology.info](http://www.freshwaterecology.info) were excluded from the analysis, because of the small number of species coded (<10%) (these were: sensitive species, salinity preference, indicator species for thermal regime/hydrological regime/drought resistance, climate change affected species, resistance form, dissemination strategy, dispersal capacity, r-K strategy, and occurrence in large quantities). Habitat specialists, rare and red-list species were also excluded as the ‘0’ assigned for these traits corresponds to ‘unavailable information’ rather than to a real absence of the trait. Similarly, modalities not coded or coded as ‘0’ for all 1,942 species analyzed were eliminated from the final dataset (e.g., ‘miners’ and ‘parasites’ from the trait ‘feeding type’, and ‘plastron’ and ‘extension/excursion to surface’ from the trait ‘respiration’). Finally, the parameter ‘feeding specialism’ was—if not already available per se (as in the case of Trichoptera)—derived from the ‘feeding type’ trait, and comprised all the species that scored more than 5 for the grazer, active filter feeder or passive filter feeder modalities. Shredders and predators were not considered to be feeding specialists, as they are less specialized on a specific food item.

Classification of species potentially endangered by climate change

The ecological preferences of aquatic insects have been widely used as a proxy for sensitivity. For instance, Hering et al. (2009) proposed a classification of sensitive Trichoptera based on the assignment of a species to a selection of sensitivity criteria (i.e., ecoregion endemism, preference for springs, preference for cold water temperatures, short emergence period, and restricted ecological niches in terms of feeding type). According to these authors, species potentially endangered by climate change were classified as endemic species presenting at least one more sensitivity parameter. In order to verify the ability of the FCA approach to detect the potential vulnerability of EPT species, we followed the approach of Hering et al. (2009) to identify taxa potentially endangered by climate change and plotted the species in the space defined by the first two FCA axes (F1 and F2). A t test on the F1 scores of endangered/not-endangered species was performed. Subsequently, values on the first axis of the FCA were used as a synthetic index of the potential vulnerability of EPT species.

Table 1 Ecological traits and modalities, extracted from www.freshwaterecology.info, used for the fuzzy correspondence analysis (FCA)

Trait	No. of modalities	% of EPT coded	% of E coded	% of P coded	% of T coded
Endemism	2	100	100	100	100
Micro-endemism	2	100	100	100	100
Stream zonation preference	10	72	60	75	71
Altitude preference (WFD)	3	74	78	96	61
Altitude preference	8	68	53	94	59
Microhabitat/substrate preference	13	57	58	22	67
Hydrologic preference	5	28	78	0	18
Current preference	7	76	66	56	84
Temperature range preference	3	41	37	56	31
Temperature preference	5	24	36	40	7
pH preference	3	20	28	16	11
Feeding type	8	51	44	99	29
Locomotion type	6	27	17	63	9
Respiration	2	95	100	100	92
Resistance/resilience to droughts	5	13	6	8	8
Life duration	2	38	48	86	9
Aquatic stages	4	17	11	8	14
Larval development cycle	5	22	58	13	7
Emergence/flight period	4	68	72	96	53
Duration of the emergence period	2	69	70	83	60
Reproductive cycles per year	6	26	49	27	11
Reproduction	6	16	14	8	12
Feeding specialism ^a	2	100	100	100	100

Order-specific and overall percentage of Ephemeroptera, Plecoptera, and Trichoptera species (EPT) coded for each trait are reported

^a Not included in the www.freshwaterecology.info database

Geographical patterns of EPT potential vulnerability across European ecoregions

In order to describe the geographical patterns of potential vulnerability expressed by the EPT assemblages across Europe, an average vulnerability level was computed for each ER, i.e., the average F1 value of all the taxa occurring in the ecoregion.

Results

Fuzzy correspondence analysis: ordination of taxa and relationships among traits

According to the eigenvalues, the first two axes (F1 and F2) of the FCA explained 9.3 and 5.9% of the total variability, respectively (Fig. 2a). Successive axes

showed slightly decreasing values (explained variability of F3–F5 ranged from 4.7 to 3.9%).

EPT species in the ordination showed a partial overlap in the factorial plane, indicating similarities in ecological preferences between these orders with regard to the habitats they colonize (Fig. 2b). Ephemeroptera showed the least widespread distribution, and were mainly associated with positive values along F1, whereas Plecoptera, and especially Trichoptera, were distributed along a greater range in the ordination plot. Trichoptera species spread toward the lowest F1 values, and also displayed the widest distribution along F2, for both positive and negative values. Two distinct clusters, consisting of species of all three orders, were observed along F2.

The distances between the taxa of the three orders in the factorial plane represented the overall differences (or similarities) between the ecological

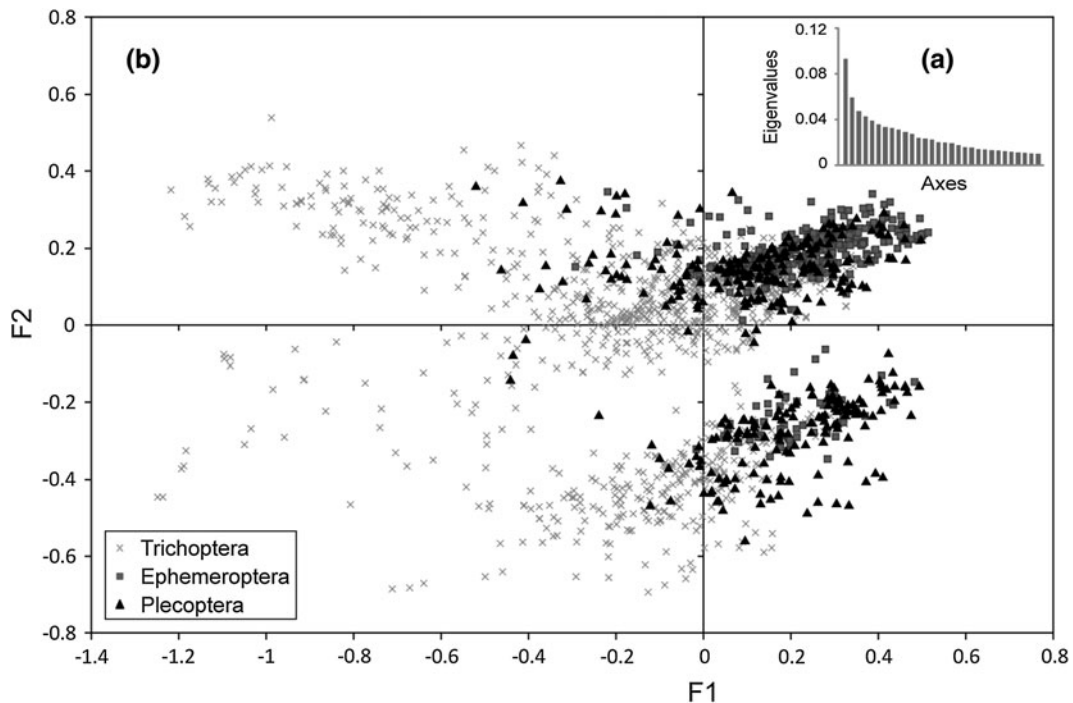


Fig. 2 Fuzzy correspondence analysis (FCA). **a** Eigenvalues of the first 30 axes of the FCA and **b** ordination of taxa belonging to the three orders according to their ecological preferences and

life history traits. Ephemeroptera (*square*), Plecoptera (*circle*) and Trichoptera (*cross*) species and sub-species are represented on the F1-F2 factorial plane of the FCA

envelopes. Trends in ecological traits were quantified by correlation ratios (Table 2). Correlation ratios greater than 10% ($RS > 0.1$) were observed for 9 out of 23 traits: in particular, 7 traits (current preference, stream zonation preference, endemism, micro-endemism, altitude preference, temperature range preference, WFD altitude preference) were more correlated with F1; one trait showed approximately the same correlation values for both F1 and F2 (microhabitat/substrate preference), and another trait was more correlated with F2 (feeding specialism). Ordination plots for these selected traits and their modalities are shown in Fig. 3a–i. Traits that were more closely correlated with F1 showed recurrent trends in their modalities (Fig. 3a–f), the positions of which along F1 described a general upstream–downstream gradient (from right to left). Preferences for higher current velocities (a), spring and upstream regions (b), high altitudes (c–d), lower temperatures (f) and hard substrates such as stones, cobbles and gravels (e) were associated with positive values along F1, whereas negative values corresponded to preferences for lowland features. Moreover, F1 positive values

were also associated with the presence of endemic and micro-endemic species (Fig. 3g–h). As for F2, the two clusters observed in the ordination (compare Fig. 2) derived from the feeding specialism of the different taxa: in particular, specialists were associated with negative values along F2, while more opportunistic species were characterized by positive values along F2 (Fig. 3i). The position of the species along the second axis was also partially explained by current preference (Fig. 3a) and microhabitat/substrate preference (Fig. 3e), following that feeding specialists seemed to be associated with preferences for limnophilic rather than rheophilic conditions, and with hygropetric habitats (i.e., thin layers of water over bedrocks, waterfalls) and algae.

FCA and potential vulnerability of EPT

When depicting on the FCA ordination taxa potentially endangered by climate change sensu Hering et al. (2009) (Fig. 4, black diamonds), a gradient of increasing vulnerability was observed along the first axis (from left to right), with potentially endangered

Table 2 Fuzzy correspondence analysis

Trait	RS1	RS2
Current preference	0.4322	0.1309
Stream zonation preference	0.3791	0.0383
Endemism	0.3404	0.0522
Micro-endemism	0.1815	0.0379
Altitude preference	0.1786	0.0218
Microhabitat/substrate preference	0.1353	0.1306
Temperature range preference	0.1127	0.0040
Altitude preference (WFD)	0.1080	0.0082
Duration of the emergence period	0.0746	0.0068
Hydrologic preference	0.0537	0.0066
Feeding type	0.0340	0.0711
Temperature preference	0.0327	0.0008
Locomotion type	0.0246	0.0028
Respiration	0.0139	0.0160
Emergence/flight period	0.0132	0.0137
Reproduction	0.0104	0.0072
pH preference	0.0074	0.0002
Resistance/resilience to droughts	0.0035	0.0006
Larval development cycle	0.0034	0.0003
Reproductive cycles per year	0.0015	0.0019
Aquatic stages	0.0013	0.0006
Life duration	0.0008	0.0046
Feeding specialism	0.0000	0.8016

Correlation ratios (RS) with F1 and F2. Traits are ordered by decreasing RS1. Plots of the traits with RS > 0.1 (bold) are shown in Fig. 3a–i

species associated almost exclusively with F1 positive values. This pattern was confirmed by the *t* test, showing that the means of potentially endangered and not-endangered species were significantly different ($t = 32.5$, $df = 1802.52$, $P < 0.001$). This trend suggested that F1 scores for the EPT species analyzed in this study could be used as a synthetic indicator of species vulnerability toward a complex of factors (e.g., temperature, hydrology, oxygen content, food resources) induced by climate change. Following this approach, the 1,942 species were ordered on the basis of their F1 scores, showing *Agraylea sexmaculata* (Hydroptilidae, Trichoptera) as the least sensitive species (-1.249) and *Leuctra vesulensis* (Leuctridae, Plecoptera) as the most sensitive species (0.512). See Appendix II in Supplementary data for a complete list of the most vulnerable species (F1 > 90th percentile).

Generally, Plecoptera showed the highest mean F1 value, with a positive value of 0.189, while Trichoptera exhibited the highest variability, with a range spanning from the overall minimum to the second highest F1 value; Ephemeroptera showed intermediate F1 values, i.e., vulnerability levels between those of the other two orders (Table 3). The three orders showed different variances in F1 values, with increasing variability of trait combinations going from Plecoptera (0.033) to Trichoptera (0.094) (Bartlett's test, $\chi^2 = 457.3$, $df = 2$, $P < 0.001$).

Comparing the percentage of vulnerable species identified following the approach of Hering et al. (2009) to the percentage of highly vulnerable species coded in this study on a continuous scale, we observed that the relative vulnerability of the three orders was preserved across the different methods: Ephemeroptera was always obviously the most tolerant order, while Plecoptera emerged as the potentially most endangered order. The high vulnerability of Plecoptera was demonstrated by the fact that 50% of the species belonging to this order occurred in the last quartile of the F1 distribution (i.e., in the 25% highest values, Table 3). Grouping species by family (Fig. 5a), all Plecoptera families showed positive medians, half of the Ephemeroptera families showed negative medians, while Trichoptera families were more widely distributed along F1. The notches overlap for Ephemeroptera families indicated that mayflies were characterized by similar ecological preferences across families, with the exception of Heptageniidae (Fig. 5a). Similarly, Plecoptera families also showed a relatively homogeneous set of preferences (exception: Perlidae), while several Trichoptera families showed contrasted combination of traits (i.e., box-and-whisker plots with non-overlapping notches). Although most Trichoptera families (11 out of 17) showed positive median values, i.e., higher potential vulnerability of species, the lower whisker extended toward extreme negative values, demonstrating a high diversity of ecological preferences among and within families (e.g., Hydroptilidae, Leptoceridae, Limnephilidae, Polycentropodidae). It follows that the widespread distribution of Trichoptera species associated with negative values along F1 in the FCA ordination plot (Fig. 2), represents an ensemble of less vulnerable species belonging to different families, rather than entire 'low vulnerability' of families (exception: Phryganeidae).

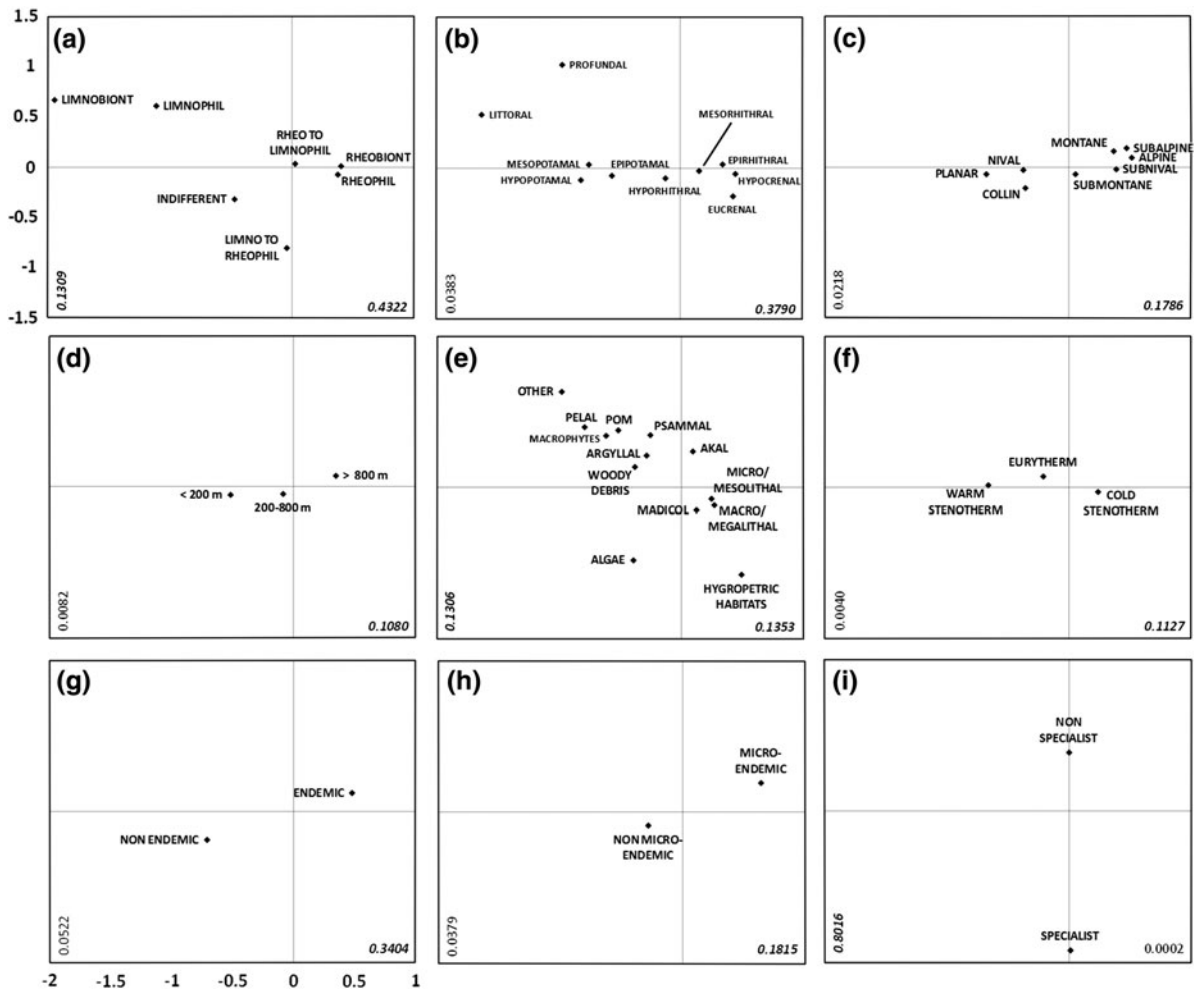


Fig. 3 Fuzzy correspondence analysis (FCA). Ordination of the modalities for the traits which presented correlation ratios (RS) > 0.1 (see Table 2 for details on RS values for each trait). RS values are reported for F1 and F2 ($RS > 0.1$ in *italic*). Eight

traits were more correlated with F1 (a–h), while the trait ‘feeding specialism’ (i) explained 80% of the variability along F2

Geographical patterns of EPT vulnerability

With regard to the ranges of vulnerability within European ERs based on the F1 values, a general trend toward lower medians emerged along a South to North gradient (i.e., ER 1 toward ER 23) (Fig. 6). Significant differences (i.e., non-overlapping notches) were observed between the median values for southern and mountainous Europe (ERs 1 to 10), and the distribution of F1 values in central (ERs 11–16) and northern Europe (ERs 19–23). The extreme values showed that tolerant species occurred in almost all ERs (lower whiskers), whereas EPT assemblages differed more with regard to the most vulnerable

species (upper whiskers): in particular, highly vulnerable species occurred mainly in southern and mountainous ERs (ERs 1–7 and ER 10).

Average F1 values for each ER were mapped for the three orders separately, and for EPT together (Fig. 7). Amongst the species assemblages in the different ERs, the Iberic-Macaronesian Region (ER 1) stood out as having the most vulnerable fauna for all three orders. This ER encompassed the second highest number of species (602 taxa), within which Plecoptera taxa accounted for 20% of total taxa (120 species), with an average F1 value amongst the highest values observed. Moreover, the average F1 value for Trichoptera species occurring in this ER

Fig. 4 Fuzzy correspondence analysis (FCA). Among 1,942 EPT taxa, 796 were assigned to the category “potentially endangered by climate change” following Hering et al. (2009) and indicated in black diamond

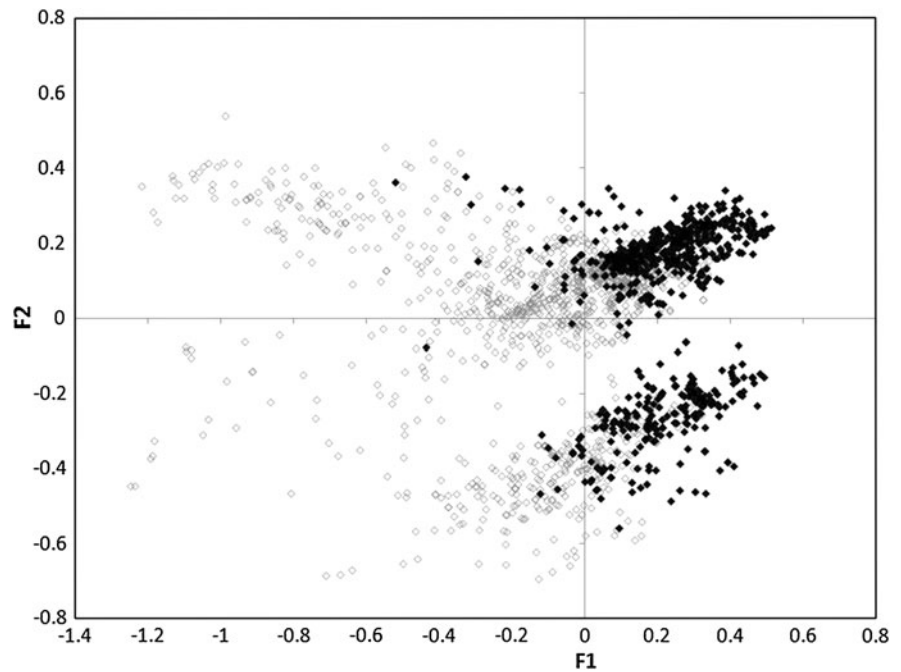


Table 3 Number of taxa (N) analyzed in the fuzzy correspondence analysis and percentage of taxa considered as potentially vulnerable

Order	N	Potentially vulnerable species (sensu Hering et al., 2009)	Potentially vulnerable species (F1 > 75th percentile)	Potentially vulnerable species (F1 > 90th percentile)	Mean F1	F1 range
Ephemeroptera	344	21% (72)	10% (34)	2% (7)	-0.0037	-0.5825–0.4167
Plecoptera	461	44% (203)	50% (231)	21% (99)	0.1891	-0.4937–0.5123
Trichoptera	1,137	41% (466)	19% (221)	8% (89)	-0.0765	-1.2487–0.4961
EPT	1,942	41% (796)	25% (486)	10% (195)	0	-1.2487–0.5123

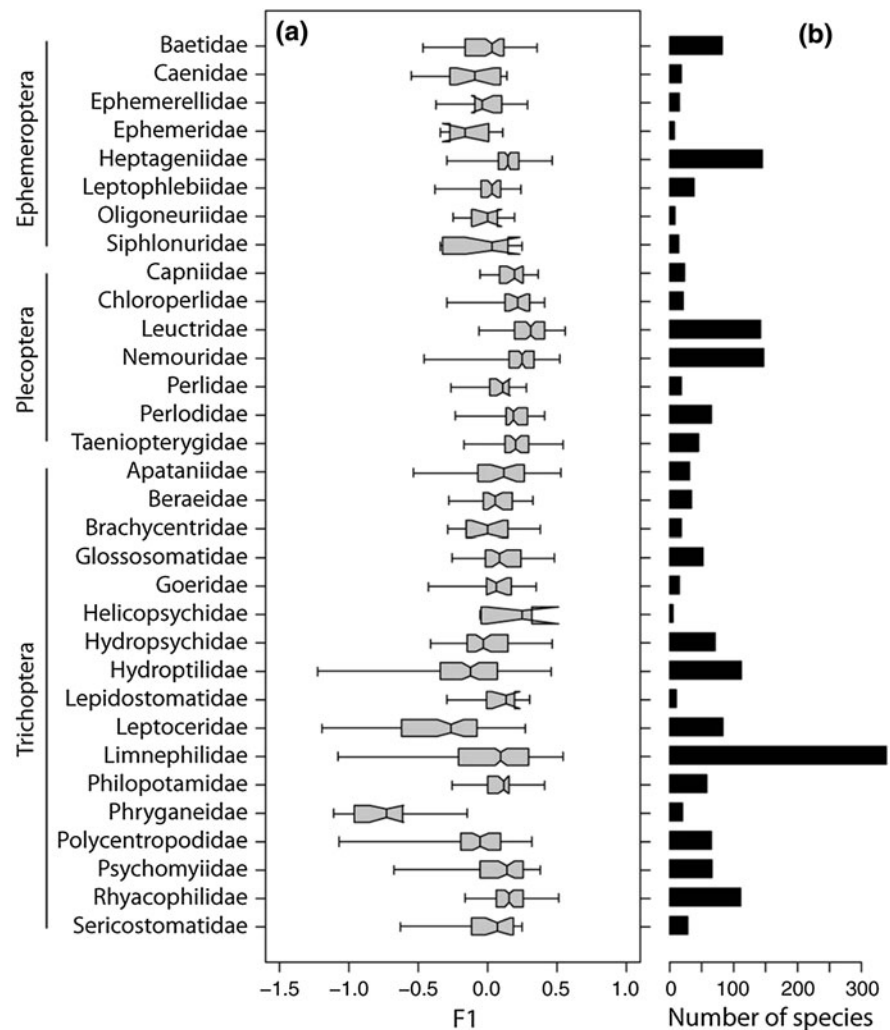
Within each order, a given taxon’s vulnerability was assessed according to its position along the first axis of the FCA using two threshold values (i.e., 75th and 90th percentile values of the taxon’s score along F1). For comparison, values from Hering et al. (2009) are also shown. The complete list of the most vulnerable EPT species (F1 > 90th percentile) is given in Appendix II in the Supplementary data

(accounting for 55% of total taxa) was highest and contributed to the overall high vulnerability of EPT in this ER (Table 4). Furthermore, southern and mountainous European regions emerged as hotspots of potential vulnerability, in particular Italy, Corsica and Malta (ER 3), the Alps (ER 4), and the Hellenic Western Balkans (ER 6). These ERs presented high numbers of EPT taxa, and all showed a similar composition in terms of the proportions of the three insect orders. Trichoptera accounted for more than half of the taxa (52–59% of total species), and Plecoptera and Ephemeroptera accounted for between 16% and 28% of the total taxa,

respectively, depending on the ER: Plecoptera were more abundant in the Hellenic Western Balkans (28%), while Ephemeroptera were more abundant in Italy, Corsica, and Malta (22%).

The geographical patterns displayed by Plecoptera (Fig. 7b) differed from those displayed by the other two orders in the northern ERs, where stonefly assemblages were generally more vulnerable than those of caddisflies and mayflies. In particular, Iceland (ER 19) emerged as a potentially endangered ER for Plecoptera, because of the high F1 value associated with the only stonefly species recorded in this region (*Capnia vidua vidua*, Capniidae).

Fig. 5 **a** Box-and-whisker plots of species' values along the first axis of the FCA (F1) among families (only families with more than five species are presented). Notches represent the 95% confidence interval. If the notches of two plots do not overlap this is 'strong evidence' that the two medians differ. **b** Number of species per family



Discussion

In this study, the ecological preferences and life history traits of three orders of aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera) were analyzed at the scale of the European ecoregions in order to assess the potential vulnerability of species to climate change. Previous studies on freshwater benthic invertebrates, using trait-based approaches, focused on the relationships between biological traits and the geographical patterns (Bonada et al., 2007) or on the biomonitoring efficiency of using traits as a tool to resolve the effects of multiple stressors on river ecosystems (e.g., Poff, 1997; Dolédec et al., 1999; Usseglio-Polatera et al., 2000; Statzner et al., 2001; Dolédec et al., 2006; Statzner & Bêche, 2010; see also

Menezes et al., 2010 for a review of the ecological background and case studies). All of these studies were based on genus level traits. Moreover, published literature dealing with geographical patterns of vulnerability generally concern only one insect order (Hering et al., 2009; Tierno de Figueroa et al., 2010). More recently, Domisch et al. (2013) modeled future suitable areas under climate change for 191 selected macroinvertebrate species belonging to 12 orders across Europe, coupling species distribution modeling with trait-based analysis. In this context, this study presents the first comparative assessment of aquatic insects' vulnerability of three organism groups based on the most comprehensive set of biological traits and ecological preferences available for macroinvertebrates species across Europe.

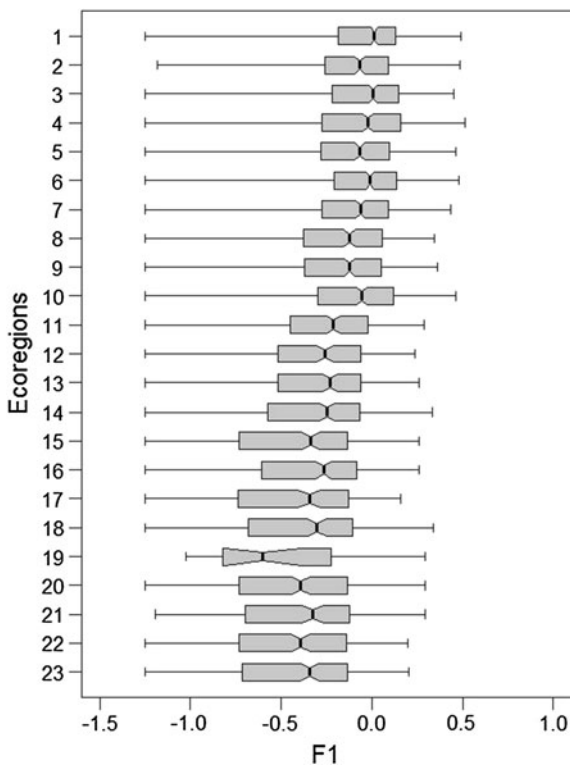


Fig. 6 Box-and-whisker plots of species' values along the first axis of the FCA (F1) among ecoregions. Notches represent the 95% confidence interval. See Fig. 1 for ecoregion coding

Relationships among traits

The analysis of relationships among biological traits and ecological preferences of aquatic insects shows that, except for feeding specialism, the most determinant traits were associated with a clear and composite gradient along the first FCA axis. This gradient arises from the underlying eco-evolutionary linkages among traits that determine recurrent combinations (also called functional trait niches, Poff et al., 2006) upon which species strategies may be defined (Verberk et al., 2013). From lower (negative) toward higher (positive) F1 values, taxa showed increasing preferences for cold, rapid, and high-altitudinal waters. This major trend describes the well-known upstream–downstream gradient that mirrors the ecological link between species occupying similar environmental conditions (Verberk et al., 2013). The co-occurrence of a second parallel gradient along F1, concerning the (micro-) endemic status of species, is related to the high incidence of endemic and micro-endemic species

in mountainous ecosystems and ERs (Graf et al., 2008b, 2009b, 2011; Waringer et al., 2011). At both extremes of these gradients, the most sensitive species *L. vesulensis* represents one of many micro-endemic, stenothermic, Alpine stonefly species (Graf et al., 2009a), while the least potentially endangered species *A. sexmaculata* is one of many European widespread Trichoptera species.

With regard to the distribution trend observed along F2, the positions of the species were explained by feeding specialism and, partially, by current and microhabitat/substrate preferences, with specialists associated with moderate flow conditions, hygropetric habitats and algae. Critical consideration suggests that this combination of preferences could in fact be an artifact resulting from the classification criteria for feeding specialists: i.e., taxa with more than 5 points for the modalities 'grazer', 'active filter feeder', or 'passive filter feeder'. In particular, species restricted to hygropetric habitats (e.g., the caddisfly genera *Stactobia* and *Tinodes*) feed nearly exclusively on epilithic algae such as diatoms. In general, the cumulative evaluation of these three insect orders may obscure the interpretation regarding functional feeding groups, as mayflies and stoneflies do not show similarly diverse preferences as caddisflies. Nevertheless, our analysis showed that 'feeding specialism'—which was also used as one of the sensitivity traits in the Hering et al. (2009) study—did not play any major role in the classification of sensitive/non-sensitive species. This descriptor was independent of the main gradient along F1 and showed no relationship with the level of potential vulnerability of taxa. While macroinvertebrates' feeding method is clearly an important component of their ecology (Wallace & Webster, 1996), we contend this functional attribute will not influence these species potential vulnerability to increasing temperatures.

The combined analysis of all available traits also highlighted some counterintuitive patterns, such as the differing contributions to the ordination of supposedly 'redundant' traits (e.g., temperature preference, and temperature range preference), which showed markedly different correlation ratios with F1 and F2. These new insights into the relationships among traits support our decision to use all the information available, and provide information about the best way to code certain ecological preferences and, ultimately, to track species vulnerability.

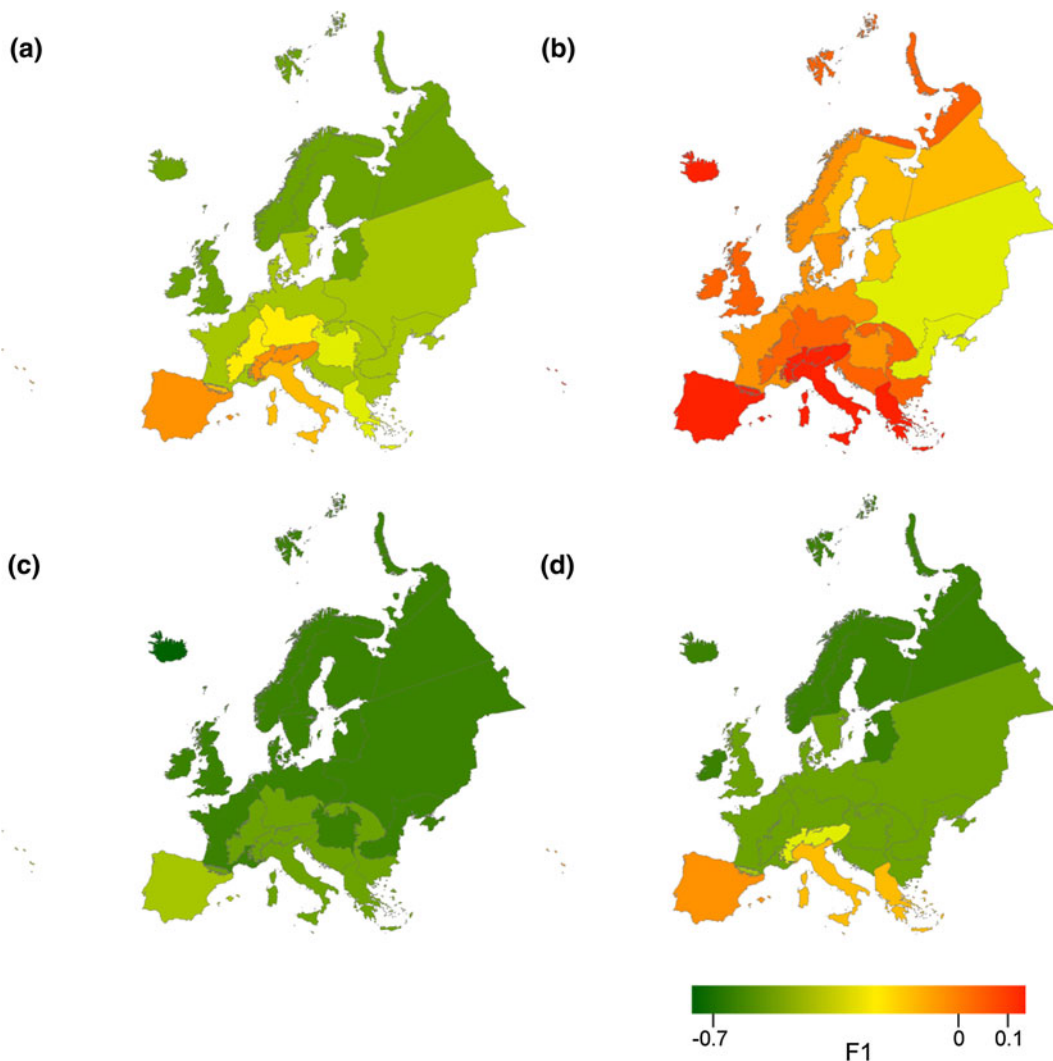


Fig. 7 Geographical patterns of taxa vulnerability to climate change. For each ecoregion, we mapped the average value of the species' positions along the first axis of the FCA for **a** Ephemeroptera, **b** Plecoptera, **c** Trichoptera, and **d** the three orders together (i.e., EPT)

Vulnerability of aquatic insects

In recent years, freshwater ecologists have proposed new methods for identifying taxa sensitive to climate change (e.g., Domisch et al., 2011, 2013); these have often been based on the ecological preferences and life history traits that are known to be related to water temperature (e.g., Hering et al., 2009; Tierno de Figueroa et al., 2010). These latter two studies assessed the sensitivity of Trichoptera and Plecoptera on the basis of the presence/absence of specific, selected criteria, leading to general patterns of vulnerability. Even though the authors provided a coherent

explanation of the selection of these 'sensitivity traits', the process represents an a priori approach. In comparison, our evaluation of EPT species' sensitivity has the advantage of using all available ecological preferences and life history traits to support an a posteriori selection of those associated with the gradient expressed along F1, which provided an integrated level of vulnerability for each taxon. The use of a robust statistical approach, such as FCA, allowed us to cope with the intrinsic weaknesses of the data set and, at the same time, to capitalize on the great amount of information available.

To summarize, vulnerability in our study was expressed along a continuous scale rather than

Table 4 Species richness and average species position along the first axis of the FCA (F1) for Ephemeroptera, Plecoptera, and Trichoptera (EPT: all species combined) in the different European ecoregions

Ecoregion		Species richness				Average F1			
No.	Name	EPT	Ephemeroptera	Plecoptera	Trichoptera	EPT	Ephemeroptera	Plecoptera	Trichoptera
1	Iberic-Macaronesian Region	602	149	120	333	-0.052	-0.033	0.145	-0.131
2	Pyrenees	384	61	97	226	-0.115	-0.061	0.147	-0.242
3	Italy, Corsica and Malta	575	124	110	341	-0.082	-0.067	0.174	-0.170
4	Alps	661	127	152	382	-0.101	-0.042	0.197	-0.240
5	Dinaric Western Balkan	475	96	104	275	-0.149	-0.113	0.103	-0.257
6	Hellenic Western Balkan	545	108	152	285	-0.071	-0.093	0.132	-0.171
7	Eastern Balkan	478	111	116	251	-0.138	-0.104	0.117	-0.270
8	Western Highlands	474	109	94	271	-0.209	-0.085	0.101	-0.366
9	Central Highlands	511	129	100	282	-0.211	-0.089	0.090	-0.374
10	The Carpathians	544	114	131	299	-0.142	-0.107	0.118	-0.268
11	Hungarian Lowlands	357	127	43	187	-0.289	-0.095	-0.027	-0.480
12	Pontic Province	211	89	12	110	-0.355	-0.117	-0.095	-0.576
13	Western Plains	371	93	39	239	-0.331	-0.132	-0.042	-0.455
14	Central Plains	419	129	45	245	-0.339	-0.119	-0.050	-0.507
15	Baltic Province	325	73	37	215	-0.425	-0.191	-0.076	-0.565
16	Eastern Plains	366	131	35	200	-0.361	-0.118	-0.096	-0.566
17	Ireland and Northern Ireland	226	36	21	169	-0.429	-0.167	-0.002	-0.539
18	Great Britain	285	53	33	199	-0.390	-0.169	0.004	-0.514
19	Iceland	20	7	1	12	-0.516	-0.264	0.296	-0.730
20	Boreallic Uplands	284	48	31	205	-0.445	-0.160	-0.032	-0.574
21	Tundra	219	40	34	145	-0.403	-0.186	-0.015	-0.554
22	Fenno-Scandian Shield	292	52	31	209	-0.446	-0.174	-0.070	-0.5706
23	Taiga	325	68	35	222	-0.426	-0.166	-0.065	-0.563

corresponding to the presence/absence of certain features, thus documenting a gradient of vulnerability. The correspondence between the sensitive species identified by the method of Hering et al. (2009) and our approach suggests that the values on the first axis of the FCA could constitute a synthetic metric of the sensitivity of aquatic insects.

This approach also suggests that in the future a ‘vulnerability index’ could be assigned to the various species. In this study, we found that *L. vesulensis* (Leuctridae, Plecoptera) was the most sensitive species, and *A. sexmaculata* (Hydroptilidae, Trichoptera) the least sensitive species from a large-scale perspective. Both species are in fact representatives of a number of other taxa with similar characteristics at either end of the F1 scale (mountainous micro-endemic species versus limnophilic lowland species with wide distribution ranges), suggesting that species could be classified using a multi-scaled vulnerability classification system. Nevertheless, this finding does

not mean that, e.g., *A. sexmaculata* populations may not be endangered locally as several of their habitats, namely wetlands, have been drastically reduced, especially in central Europe. In fact, although species fitness depends on the adaptive value of typical bio-ecological trait combinations, vulnerability is also strongly dependent on local factors such as habitat structure or water quality, but also on the availability of suitable habitats (Domisch et al., 2013) or on population sizes (Lande, 1993). Moreover, the effectiveness of species traits in supporting species persistence is strongly context-dependent and may show important variations during ontogeny or over evolutionary time (Verberk et al., 2013).

At the European scale, general patterns of vulnerability clearly emerged for Ephemeroptera, Plecoptera, and Trichoptera, with stoneflies being the most vulnerable group, due to the species’ restricted ranges in terms of thermal tolerance and altitudinal distribution, with a strong preference for upstream sections

(e.g., Zwick, 1992; Fochetti & Tierno de Figueroa, 2006). On the other hand, Trichoptera showed the widest diversity of biological traits and strategies, occurring in all ERs and all types of water bodies, revealing caddisflies to be an extremely suitable group of organisms for sensitivity assessment. Ephemeroptera displayed intermediate distribution patterns, and were generally the least vulnerable group among the orders investigated here. These findings relate to the overall characteristics of the analyzed insect orders, but do not take into account regional threats due to anthropogenic pressures or potential effects of non-indigenous species invasions, which appear to be favored by ecosystem disturbance making stressed ecosystems more susceptible (Strayer, 2010). Large lowland rivers, for example, have changed enormously during the last century as a result of human impact, at least in central European regions. The ranges of many species inhabiting these potamal rivers once covered large areas in Europe, but nearly all these species are now included in Red Lists as threatened or even extinct. There is historical information indicating that some stonefly species once occurred in very large numbers, and the rapid decline of specialized species of large rivers (e.g., *Brachyptera braueri*, *Brachyptera trifasciata*, *Isogenus nubecula*, and *Isoperla obscura*)—many of which have not been recorded for 50 years or more—is well documented (Brauer & Löw, 1857; Ausserer, 1869; Kühnreiter, 1934). Today's populations are isolated, and persist exclusively in small and severely fragmented refugia. This and other examples (e.g., Fittkau & Reiss, 1983; Russev, 1987; Sartori & Landolt, 1998; Zwick, 1992; Fochetti & Tierno de Figueroa, 2006) demonstrate the current fate of already impaired potamal communities at the edge of their ecological capability, and suggest that they might collapse due to increasing temperatures.

Geographical patterns

The vulnerability of the aquatic insects considered here displayed a general South to North gradient among the European ecoregions. This pattern has already been observed for Trichoptera (Hering et al., 2009) and Plecoptera (Tierno de Figueroa et al., 2010). Differences were observed for Plecoptera, where northern ERs also emerged as potentially endangered following the new vulnerability assessment, whereas no sensitive species were identified in these ERs by

Tierno de Figueroa et al. (2010). For example, in our study stoneflies displayed high vulnerability in Iceland which is due to the fact that there is only one species (*Capnia vidua vidua*) in this ER. Based on its restricted ecological preferences, this species could easily become extinct on this island as a result of increasing temperature. In the European context, *Capnia vidua vidua* is not endangered as it occurs in another 12 ERs (Graf et al., 2009a). However, even if there is a risk associated with the potential extinction of *Capnia vidua vidua* in Iceland, the fauna of the ER Iceland is not to be considered 'vulnerable' as a whole based on the combined assessment of all three orders.

Although no comparable latitudinal pattern was observed by Domisch et al. (2013) for projections of future macroinvertebrate distributions following climate change, our results confirm the bipolar localization of European vulnerability hotspots, restricted to Mediterranean Peninsulas and the Alps. From the trait-based analysis of 12 macroinvertebrate orders, Domisch et al. (2013) demonstrated that cold-adapted species and warm-adapted endemic species inhabiting the two extremes are highly vulnerable to the changing environment. Similar conclusions may be derived from the co-occurrence of the longitudinal and endemism gradients in our analysis, with most vulnerable species inhabiting cold headwater river reaches or being endemic of Mediterranean streams, entailing a northwards range shift of species as predicted by several authors (e.g., Bonada et al., 2007; Heino et al., 2009; Domisch et al., 2013). Nevertheless until now, we are not aware of a published invasion of a single Mediterranean element into northern areas regarding the investigated groups. Generally, vulnerability assessment must always be seen in the context of (ER) endemism. Trichoptera and Plecoptera include about 50% endemic species (Graf et al., 2008a, 2009a), whereas for Ephemeroptera only 35% of species are known to be endemic (Buffagni et al., 2009). Endemic stoneflies are associated with very low temperatures and high altitudes, whereas endemic mayflies inhabit lower mountainous areas and tend to be eurytherm. As for caddisflies, endemic species show a clear tendency to colonize springs near mountainous areas, which makes them ecologically similar to Plecoptera. On the other hand, there are also endemic caddisflies distributed in downstream areas with warmer temperatures, reflecting the high ecological variability of this aquatic insect order.

In general, the predicted range contractions may be connected with a loss of intra-specific genetic diversity, due to the reduction of effective population sizes and the extinction of regional genetic lineages (Keyghobadi, 2007), which theoretically affects the meta-population of a species negatively. Although future projections of European montane aquatic insects confirm these expectations, with the most severe biodiversity losses in the Mediterranean region (Bálint et al., 2011), the analysis of genetic diversity of refugial populations of the mayfly *Palingenia longicauda*, which has undergone severe distributional regressions, has not revealed any such effects (Bálint et al., 2012).

Knowing the geographical ranges of species is a prerequisite when attempting to analyze the effects of a changing environment as the lack of detailed distributional information hinders predictions with regard to climate change and other associated anthropogenic stressors (Heino et al., 2009). Although the ER approach presented here seems to be very coarse scale, it is the only possible approximation if detailed occurrence data are not available, e.g., compared to the occurrence information on country level. Though for all species of the investigated insect orders the ecoregional distribution is known, the results could be specified once better distributional data are available (like, e.g., for Trichoptera as collected in the BioFresh project).

Further, in order to fully understand future distribution patterns some trait information also needs more investigation. According to Travis (2003), specialized species with low colonization ability and poor dispersal rates are prone to extinction under climate change. Generally, dispersal capacity has recently gained intensive interest especially regarding conservation aspects, as it is one important trait contributing to the overall fitness of a species in a world of change. For example, Malmqvist (2000) showed a positive correlation between wing length and range size, supporting the hypothesis that low dispersal taxa are restricted to small areas. But, controversially to that, there are for example wingless (*Enoicyla*) and the smallest caddisflies (*Hydroptila*), which occupy large European areas and are among the widest spread Trichoptera (Graf et al., 2008a). Different strategies like the insufficiently understood vector “passive dispersal” may account for that. There is some general evidence that lentic or potamal species are nowadays

more widespread than crenal or rhithral ones (Hof et al., 2008; Graf et al., 2008a, 2009a) and habitat stability is discussed to be responsible for that pattern (Hof et al., 2012). In addition, Müller-Peddinghaus & Hering (2013) showed that generalists are potentially stronger dispersers than specialists. Still, long-distance dispersal is difficult to record and actual dispersal is also strongly influenced by land use characteristics (Galic et al., 2013). Although recently new insights have been gained (Bohonak & Jenkins, 2003), empirical data on dispersal abilities are still scarce and the topic is mainly approached from mechanistically driven hypotheses, whereas behavioral aspects in freshwater insects remain largely neglected.

Concluding remarks

Vulnerability is a central concept in ecological research. Our study suggests that aquatic insects exhibit a South-North gradient of decreasing vulnerability across European ecoregions, with higher potential impacts expected in the Mediterranean region. Species with narrower ecological niches, such as most Plecoptera, will also be potentially endangered at high altitudes. The identification of hotspots of potential vulnerability emerges as a crucial step toward achieving a better understanding of ecosystem responses to a warming environment, especially since the effects of climate change are expected to differ in both magnitude and direction in different geographic areas (Rijnsdorp et al., 2009). Annual mean temperatures in Europe are likely to increase more than the global mean, although the smallest increases are to be expected in the southern regions; lower precipitation is also to be expected (IPCC (Intergovernmental Panel on Climate Change), 2007). We argue that our multi-species, trait-based approach to assess freshwater macroinvertebrates highlights the importance of including integrated information about ecological preferences and life history traits in the vulnerability assessment, in order to provide a meaningful and coherent snapshot of the responses we can expect from species living in a changing world. The results obtained in this study should be considered as a first approximation of a reliable vulnerability assessment—which in an ideal scenario should address not only the effects of climate change, but also the impact

of anthropogenic pressures. Species capacities to track future changes will strongly depend on their adaptability and/or dispersal capacity, but current modeling efforts to anticipate future responses are hampered by the lack of consistent information concerning species characteristics (e.g., Domisch et al., 2013). Therefore, we expect a marked improvement in the performance of our analyses as soon as the gaps in our knowledge about important ecological features can be filled. Along with a better knowledge of general geographical patterns across Europe (i.e., detailed species occurrence records), the approach presented in this study could also provide a framework for downscaling vulnerability assessment to regional and local scales, where conservation and management priorities are defined and policies enforced.

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