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Research Article

Potential impact of climate change on aquatic insects: A sensitivity analysis for European caddisflies (Trichoptera) based on distribution patterns and ecological preferences

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Abstract. We analysed the sensitivity of European Trichoptera (caddisfly) species to climate change impacts based on their distribution and ecological preferences, and compared the fraction of species potentially endangered by climate change between the European ecoregions. The study covers 23 European ecoregions as defined by Illies (1978). For 1134 Trichoptera species and subspecies, we coded 29 parameters describing biological and ecological preferences and distribution based on the evaluation of more than 1400 literature references. Five parameters served to describe the species' sensitivity to climate change impacts: endemism, preference for springs, preference for cold water temperatures, short emergence period, and restricted ecological niches in terms of feeding types. Of the European Trichoptera species and subspecies, 47.9 % are endemic, 23.1 % have a strong preference for springs, 21.9 % are cold stenothermic, 35.5 % have a short emergence period, and 43.7 % are feeding type specialists. The fraction of endemic species meeting at least one of the four other sensitivity criteria mentioned above is highest in the Iberic-Macaronesian Region (30.2 % of all species), about 20 % in several other south European ecoregions, and about 10 % in high mountain ranges. In 15 out of 23 ecoregions (including all northern European and lowland ecoregions) the proportion is less than 3 %.

The high fraction of potentially endangered species in southern Europe is a result of speciation during the Pleistocene. Species having colonised northern Europe afterwards have generally a large geographical range and are mainly generalists and thus buffered against climate change impacts.

Key words. Ecoregions; endemism; springs; cold-stenothermy; flight periods; feeding types.

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Introduction

The earth is getting warmer at an accelerating rate. Over the coming century decreased precipitation and increased temperatures are confidently projected for southern areas of Europe, with a transition to increased and more variable precipitation and temperatures towards northern latitudes (Solomon et al., 2007). The impact of such climate change on biodiversity patterns has been investigated and predicted in a large number of recent case studies addressing mammals (Guralnick, 2007), birds (Julliard et al., 2004), amphibians (Pounds et al., 2006), terrestrial insects (Wilson et al., 2005), spiders (Gobbi et al., 2006), terrestrial plants (Fossa et al., 2004; Skov and Svenning, 2004), combinations of different taxonomic groups (Thomas et al., 2004) and hypothetical species (Travis, 2003). Frequently-used approaches for the prediction of climate change effects on the distribution and extinction of species include Population Viability Analysis (Maschinski et al., 2006), a large number of modelling techniques (recent reviews by Araujo and Rahbeck, 2006; Elith et al., 2006) ranging from the local (del Barrio et al., 2006) to the global scale (Thomas et al., 2004), the quantification of climatically suited areas under future climatic conditions (Ohlemüller et al., 2006), the use of Red List criteria (Akcakaya et al., 2006) and species traits (Svenning and Skov, 2006). Several recent studies address freshwater species, e.g., phytoplankton (Elliott et al., 2006), benthic invertebrates (Bonada et al., 2007; Brown et al., 2007; Durance and Ormerod, 2007) and fish (Xenopoulos et al., 2005). Most of the above mentioned approaches to modelling the effects of climate change require detailed knowledge of the species' population ecology and are not applicable to species, which have been less intensively investigated, such as most aquatic insects. In this study, we use an alternative approach to address the potential impact of changing climate on the European species of the aquatic insect order Trichoptera (caddisflies), based on an extensive literature survey of the species' distribution and selected ecological characteristics. The order Trichoptera includes more than 12000 described species (Trichoptera Checklist Coordinating Committee: Trichoptera World-Checklist; http://entweb.clemson.edu/database/trichopt/), more than 1000 of which occur in Europe (Malicky, 2005). Trichoptera represent a diverse range of biological and ecological traits. The feeding strategies of the aquatic larvae include the breakdown of leaves and wood, the collection of drifting materials with nets or morphological adaptations like spines, scraping of algae, sucking of algae cells and predation. Trichoptera species inhabit springs, small streams, large rivers, lakes and wetlands; some species even live in brackish water or terrestrial ecosystems. The egg, larval and pupal stages are mainly aquatic, while the adults live in the terrestrial environment. As a species-rich and ecologically diverse insect order, caddisflies are well-suited to reflect the intensity of different stressors on aquatic ecosystems. While several studies address the impact of organic pollution (e.g. Zelinka and Marvan, 1961; Dohet, 2002), hydromorphological degradation (e.g. Statzner et al., 2001; Lorenz et al., 2004), acidification (e.g. Townsend et al., 1983; Sandin et al., 2004) and pesticides (Schulz, 2004) on Trichoptera and other aquatic invertebrates, this study aims at estimating the potential impact of climate change on the occurrence and abundance of European Trichoptera. The analysis is based on the following hypotheses:

- Species with limited distribution ("endemic species") are characterised by a restricted ecological niche and limited dispersal, thus being more affected by climate change than widely distributed species as shown for vascular plants (Malcolm et al., 2006) and also supposed for benthic invertebrates (Brown et al., 2007).
- Several species inhabiting large rivers characterised by relatively high water temperatures are generally physiologically adaptive and may also react to globally rising temperatures by colonising upstream river reaches, if not restricted to large rivers for reasons other than water temperature. Species inhabiting springs cannot move further upstream, and are thus more threatened. In general, species living at high altitudes are particularly endangered by global warming (Fossa et al., 2004).
- Species adapted to low water temperatures ("cold-stenothermic species") are threatened by climate change rather than eurythermic species (compare Schindler, 2001).
- Species with short emergence periods are particularly sensitive to alterations in temperature patterns (Kotiaho et al., 2005). Species with acyclic or unsynchronised life cycles and species with several generations per year are better adapted to spates or droughts affecting mostly their aquatic stages.
- Species with restricted ecological niches (specialists), e.g. requiring special food sources, are more sensitive to large-scale changes, such as climate change, than species with broad niches (generalists) (Kotiaho et al., 2005).

We compiled all available data on ecological preferences and distribution of European Trichoptera taxa, analysed the sensitivity of the species to climate change impacts based on the above mentioned

Table 1. Percentage of available ecological information for the 1134 European Trichoptera species and subspecies.

Parameter	Coding system	Percentage of classified species
Presence in ecoregions	presence	100.0
Current preference	single category assignment	85.0
Stream zonation preference	10 points system	72.2
Substrate/microhabitat preference	10 points system	67.2
Altitude preference (WFD)	presence/absence	60.8
Altitude preference	10 points system	60.1
Duration emergence period	single category assignment	59.3
Emergence period	10 points system	52.2
Feeding specialist	presence/absence	43.7
Temperature range preference	single category assignment	31.5
Feeding type	10 points system	28.3
Respiration	presence/absence	21.5
Salinity preference	single category assignment	17.4
Hydrologic preference	10 points system	15.1
Aquatic stage	10 points system	14.5
Reproduction	single category assignment	11.9
Reproductive life cycle	single category assignment	11.5
pH preference	single category assignment	10.9
Life duration	single category assignment	9.7
Locomotion type	10 points system	8.5
Larval development cycle	10 points system	7.9
Resistance/resilience to droughts	single category assignment	7.8
Temperature preference	10 points system	6.4
Dissemination strategy	presence/absence	3.3
r-, *K*-strategy	single category assignment	2.8
Resistance form	10 points system	2.6
Dispersal capacity	single category assignment	1.0
Indicator species	single category assignment	0.9
Occurrence in large quantities	single category assignment	0.1

hypotheses, and compared the fraction of species potentially endangered by climate change between the European ecoregions.

Methods

Data compilation

We selected 29 parameters describing distribution and ecological preferences of Trichoptera species: occurrence in the individual European ecoregions, three parameters related to stream zonation, eight parameters related to habitat preferences and 17 related to life strategies (Table 1; for details see www.freshwaterecology.info). The parameters were modified from Moog (1995) and Tachet et al. (2002), and further parameters were added. In contrast to Moog (1995) we dealt with all European taxa, and in contrast to Tachet et al. (2002) coding was at the species level. For some parameters (e.g. occurrence in altitude ranges) data were coded as "present" or "absent" (presence/absence assignment). Other parameters, such as temperature range preference or reproduction techniques, were coded by selecting one category out of a given list (single category assignment). In most cases, we used a 10 point system (Zelinka and Marvan, 1961; Moog, 1995) where the ecological classification of a species is based on its average distribution within the environmental gradient under consideration. If, for example, 70 % of a species' records are located in spring brooks and 30 % in the upper trout region, 7 out of 10 points are allocated to spring brook preference and 3 points to upper trout region preference to describe the expected occurrence within the longitudinal zonation of a river. If a species is mainly a passive filter-feeder but to a lesser degree feeding as a predator and a shredder, 8 out of 10 points are allocated to the feeding type "passive filter feeder", 1 point to "predator" and 1 point to "shredder". Distribution was coded as presence assignment for each of the 27 European ecoregions defined by Illies (1978). The Illies ecoregions are widely used in aquatic ecology and for applied purposes such as lake or river typologies (Moog et al., 2004).

More than 1400 literature references on distribution and ecological preferences of European Trichoptera taxa were evaluated. The literature review covered published and "grey" literature such as Master- and PhD-theses. The data, and the literature references they are based on, were stored in an online database available at www.freshwaterecology.info (Euro-limpacs consortium, 2006; Graf et al., 2006, 2008).

Description of the database

Overall, we collected data on 1173 European Trichoptera species and subspecies (from now on referred to as “taxa”), 1134 of which are occurring in Ecoregions 1–23. Since data for Ecoregions 24, 25, X and Y were generally scarce, we limited the analysis to Ecoregions 1–23. For several ecological parameters limited information is available; between 0.1 % and 100 % of the taxa were classified for the individual parameters (Table 1). Besides the parameter “distribution in ecoregions” (100 % of all taxa occurring in Ecoregions 1–23 classified), high fractions of taxa were also coded for the parameters “current preference” (85 %), “stream zonation preference” (72.2 %) and “substrate/microhabitat preference” (67.2 %).

Data evaluation

All steps of data evaluation were related to the lowest possible taxonomic level, either species or subspecies. Based on the hypotheses given in the introduction, the following parameters were defined as indicating high sensitivity to climate change impacts (“sensitivity parameters”): endemism, preference for springs (crenal region), preference for cold water temperatures (cold stenothermy), short emergence period, and restricted ecological niches in terms of feeding types (Table 2). Due to the low proportion of classified taxa other relevant ecological parameters (for example hydrologic preference, life duration) were not regarded further. Species and subspecies, which meet the above criteria, were identified from the database by the following procedures:

- Taxa distributed in only one ecoregion were defined as “endemic” (parameter: presence in ecoregions). In addition, we defined “microendemic” taxa as being restricted, e.g., to a single mountain range in an ecoregion.
- Taxa coded with 5 or more points for “eucrenal” and “hypocrenal” were defined as specialists for springs (parameter: stream zonation preference).
- Taxa with an assignment in the category “cold-stenotherm” were defined as sensitive regarding temperature increase (parameter: temperature range preference).
- Taxa with a short emergence period were defined as sensitive regarding hydrological changes (parameter: duration emergence period).
- Taxa classified as “feeding specialist” were defined as taxa with a restricted ecological niche (parameter: feeding specialist).

For each European ecoregion the number and relative fraction of taxa meeting each of these criteria was calculated. Due to a limited amount of data, we did not consider the ecoregions Caucasus (24), Caspic Depression (25), North Africa (X) and Middle East (Y). Endemic taxa meeting at least one further sensitivity criterion were defined as “potentially endangered by climate change”.

Table 2. Ecological and distribution parameters specifically addressed in the analysis.

Parameter	Categories
Presence in ecoregions	23 ecoregions according to Illies (1978)
Stream zonation preference	eucrenal (spring region) hypocrenal (spring brook) epirhithral (upper trout region) metarhithral (lower trout region) hyporhithral (grayling region) epipotamal (barbel region) metapotamal (bream region) hypopotamal (brackish water) littoral (lake and stream shorelines, ponds, etc.) profundal (bottom of stratified lakes)
Temperature range preference	cold stenotherm (< 10°C) warm stenotherm eurytherm
Duration emergence period	short (not longer than 50 days; if differences between ecoregions occurred the longest emergence period was selected as it reflects the flexibility of a species) long
Feeding type	grazer/scraper miner xylophagous shredder gatherer/collector active filter feeder passive filter feeder predator parasite other feeding type
Feeding specialist	grazer passive filter feeder (carnivorous) passive filter feeder (FPOM) piercer sponge feeder xylophagous

Results

Sensitivity of Trichoptera species and subspecies

The number of taxa per ecoregion ranges between 12 (Ecoregion 19, Iceland) and 373 (Ecoregion 4, Alps), but lies between 200 and 300 in 15 out of the 23 ecoregions considered (Table 3). In general, there is a gradient in species richness from south to north, which is also obvious if ecoregion area is considered (Table 3).

According to the individual criteria defined, between 21.9 % and 47.9 % of the 1134 European

Table 3. Number and percentage of Trichoptera taxa meeting the sensitivity parameters in the European ecoregions. Sensitive taxa: Taxa meeting at least one sensitivity criterion (endemism, preference for springs, preference for cold water temperatures, short emergence period, and restricted ecological niches in terms of feeding types). Taxa potentially endangered by climate change: Endemic taxa meeting at least one further sensitivity criterion.

Ecoregion name	Ecoregion number	Ecoregion area (km^2)	No. of taxa	Taxa number / ecoregion area (100 km^2)	No. of endemic taxa	No. of micro-endemic taxa	No. of crenal specialists	No. of cold stenothermic taxa	No. of taxa with a short emergence period	Feeding type specialists	No. of sensitive taxa	No. of taxa potentially endangered by climate change	Percentage of taxa potentially endangered by climate change
Iberic-Macaronesian Region	1	597,127	325	0.54	142	31	59	49	85	148	268	98	30.2
Pyrenees	2	18,544	221	11.92	23	2	45	45	80	92	166	19	8.6
Italy, Corsica and Malta	3	717,330	343	0.48	118	72	81	66	103	149	278	84	24.5
Alps	4	156,069	373	2.39	52	24	104	109	159	156	288	49	13.1
Dinaric Western Balkan	5	190,930	274	1.44	32	24	62	55	102	107	201	27	9.9
Hellenic Western Balkan	6	432,671	283	0.65	76	52	53	46	109	130	220	62	21.9
Eastern Balkan	7	177,761	251	1.41	27	20	42	48	100	105	186	20	8.0
Western Highlands	8	173,108	272	1.57	6	4	56	48	110	110	196	6	2.2
Central Highlands	9	257,690	282	1.09	1	1	54	52	120	105	201	1	0.4
The Carpathians	10	158,409	297	1.87	48	17	65	60	129	101	227	37	12.5
Hungarian Lowlands	11	217,961	188	0.86	1	1	26	24	73	60	125	1	0.5
Pontic Province	12	464,423	110	0.24	1	0	10	13	30	39	66	1	0.9
Western Plains	13	582,234	239	0.41	2	1	33	30	86	93	164	2	0.8
Central Plains	14	844,503	247	0.29	4	0	25	26	80	87	157	4	1.6
Baltic Province	15	297,455	214	0.72	0	0	16	14	70	69	131	0	0.0
Eastern Plains	16	2,429,120	202	0.08	1	0	12	14	67	60	119	0	0.0
Ireland and Northern Ireland	17	199,453	170	0.85	0	0	18	17	50	75	113	0	0.0
Great Britain	18	613,973	200	0.33	3	0	24	23	67	83	135	3	1.5
Iceland	19	213,625	12	0.06	0	0	0	2	1	1	3	0	0.0
Borealic Uplands	20	647,827	206	0.32	1	0	12	15	56	66	118	1	0.5
Tundra	21	2,678,840	146	0.05	2	0	7	10	37	40	78	1	0.7
Fenno-Scandian Shield	22	959,737	211	0.22	2	0	14	16	56	70	121	2	0.9
Taiga	23	994,674	222	0.22	1	1	12	13	61	71	127	1	0.5

Table 4. Number and percentage of European Trichoptera taxa sensitive to climate change according to the sensitivity parameters.

Parameter	Number of specialised taxa (meeting the parameter)	Number of classified taxa	Percentage of specialised taxa in relation to classified taxa	Percentage of specialised taxa in relation to all taxa
Endemism	543	1134	47.9	47.9
Crenal specialists	262	819	32.0	23.1
Cold stenothermic species	248	357	69.5	21.9
Short emergence period	403	672	60.0	35.5
Feeding specialists	496	496	100.0	43.7

Trichoptera taxa occurring in Ecoregions 1–23 are sensitive to climate change (Table 4). The highest proportion is obtained for endemic taxa: 543 species and subspecies (47.9 %) are limited to a single European ecoregion, while only 121 are distributed in more than 15 ecoregions. All the widely distributed taxa are adapted to large rivers (potamal zone) or to wetland habitats. Four species occur in all European ecoregions regarded (Ecoregions 1–23): *Grammotaulius nigropunctatus*, *Limnephilus affinis*, *L. auricula* and *L. sparsus.*

A total of 262 taxa (23.1 %) have a strong preference for springs, most of which belong to the families Limnephilidae (88 taxa), Rhyacophilidae (23), Glossosomatidae (21), Hydroptilidae (20), Apataniidae (17), Beraeidae (14), Philopotamidae (13) and Psychomyiidae (12).

Among the 248 cold stenothermic taxa (21.9 % of the European taxa) most belong to the families Limnephilidae (84 taxa), Rhyacophilidae (35), Hydroptilidae (22), Philopotamidae (18), Apataniidae (16), Glossosomatidae (15) and Beraeidae (13).

The 403 taxa (35.5 %) considered to have a short emergence period mainly comprise Limnephilidae (175 taxa), Leptoceridae (35), Hydroptilidae (33), Rhyacophilidae (30), Glossosomatidae (20) and Polycentropodidae (16).

The 496 feeding type specialists (43.7 %) are mainly grazers (267 taxa), among which the Limnephilidae prevail (74), followed by Psychomyiidae (66), Glossosomatidae (52), Apataniidae (29), Hydroptilidae (20) and Goeridae (16). The 84 specialised piercers are all Hydroptilidae. A total of 73 of the passive filter feeders are carnivorous (mainly Polycentropodidae) and 58 feed on fine particulate organic matter (all Philopotamidae).

Distribution of sensitive taxa in the European ecoregions

Of the 1134 European Trichoptera taxa, 954 (84.1 %) meet at least one sensitivity criterion. The majority of those (354, 31.2 %) meet only a single parameter, 332 taxa (29.3 %) meet two, 161 taxa (14.2 %) meet three and 84 taxa (7.4 %) meet four parameters. Some 23 taxa (2.0 %) meet all five criteria.

The taxa potentially sensitive to climate change impacts are unevenly distributed between the European ecoregions (Table 3). In general, there is a strong south-north gradient, with a high number of sensitive taxa in southern Europe and a low number in northern Europe. Furthermore, an altitudinal gradient is obvious, with relatively high numbers of sensitive taxa in the Alps (Ecoregion 4), the Pyrenees (Ecoregion 2) and the Carpathians (Ecoregion 10), and low numbers in the lowland ecoregions such as the Central Plains (Ecoregion 14), the Western Plains (13) and the Eastern Plains (16). These patterns can be observed for all sensitivity parameters. Endemic taxa occur most frequently in the Iberian and Italian peninsulas (Ecoregions 1 and 3). In both ecoregions the endemic taxa mainly belong to the most species-rich families Hydroptilidae, Limnephilidae, Leptoceridae and Rhyacophilidae. No endemic taxa occur in the Baltic Province (Ecoregion 15), Ireland and Northern Ireland (17) and Iceland (19). The few endemic taxa in the central and northern European ecoregions are almost exclusively subspecies such as *Psilopteryx psorosa bohemosaxonica* (Limnephilidae) in the Central Highlands (Ecoregion 9) or various parthenogenetic *Apatania* species (Apataniidae) in the Central Plains (Ecoregion 14). The majority of taxa of northern and central European ecoregions also occur in other ecoregions, while a high fraction of the taxa occurring in the Mediterranean ecoregions is endemic or restricted to a low number of ecoregions (Figure 1). Specialists for springs (crenal) are particularly species-rich in southern Europe and in the high mountain ranges. The Alps are characterised by the highest absolute and relative number of crenal specialists (104 taxa, 27.9 % of all occurring taxa in the Alps). In contrast to the Alps, both the Carpathians (65 taxa, 21.9 %) and the Pyrenees (45 taxa, 20.4 %) hold a relatively low number of crenal specialists; however, this may partly reflect the better knowledge of ecological preferences for species occurring in the Alps.

Cold stenothermic taxa are mainly restricted to the higher and lower mountain ranges, particularly in the Alps (109 taxa, 29.2 %), Italy (66 taxa, 19.2 %) and the Carpathians (60 taxa, 20.2 %). A very limited number of cold stenothermic species occur in the northern

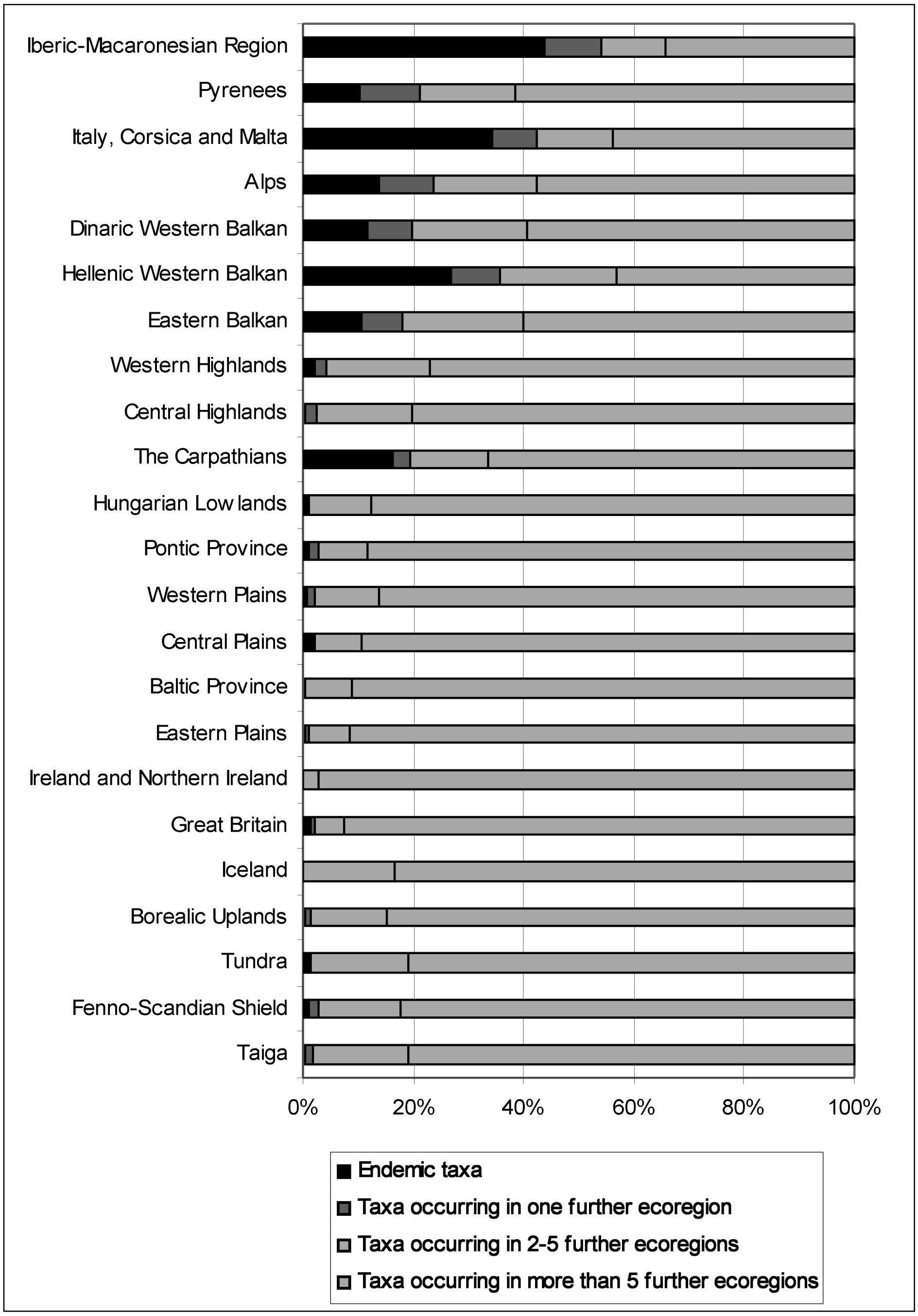

Figure 1. Fraction of endemic Trichoptera taxa and taxa occurring in additional ecoregions for Ecoregions 1–23.

European ecoregions, e.g. in Iceland only two species (*Limnephilus fenestratus* and *L. picturatus*), and 15 out of 206 species (7.3 %) in the Borealic Uplands (Ecoregion 20).

Similarly, taxa with short emergence periods mainly occur in the mountainous ecoregions: Alps (159 taxa, 42.6 %), Carpathians (129 taxa, 43.4 %) and Central Highlands (120 taxa, 42.6 %). Most of these taxa belong to the Limnephilidae (103 taxa), followed by Leptoceridae (22) and Rhyacophilidae (21). Taxa with specialised feeding types are mainly distributed in the southern European ecoregions and high mountain areas. Most taxa with specialised feeding types occur in the Alps (156 taxa, 41.8 %), while the highest fraction is observed in Ecoregion 6 (Hellenic Western Balkan, 45.9 % of all classified taxa). In the Alps, the feeding type specialists are mainly grazers (27 taxa, 16 of which are *Drusus* species).

Summing up all taxa potentially sensitive to climate change according to these parameters, a

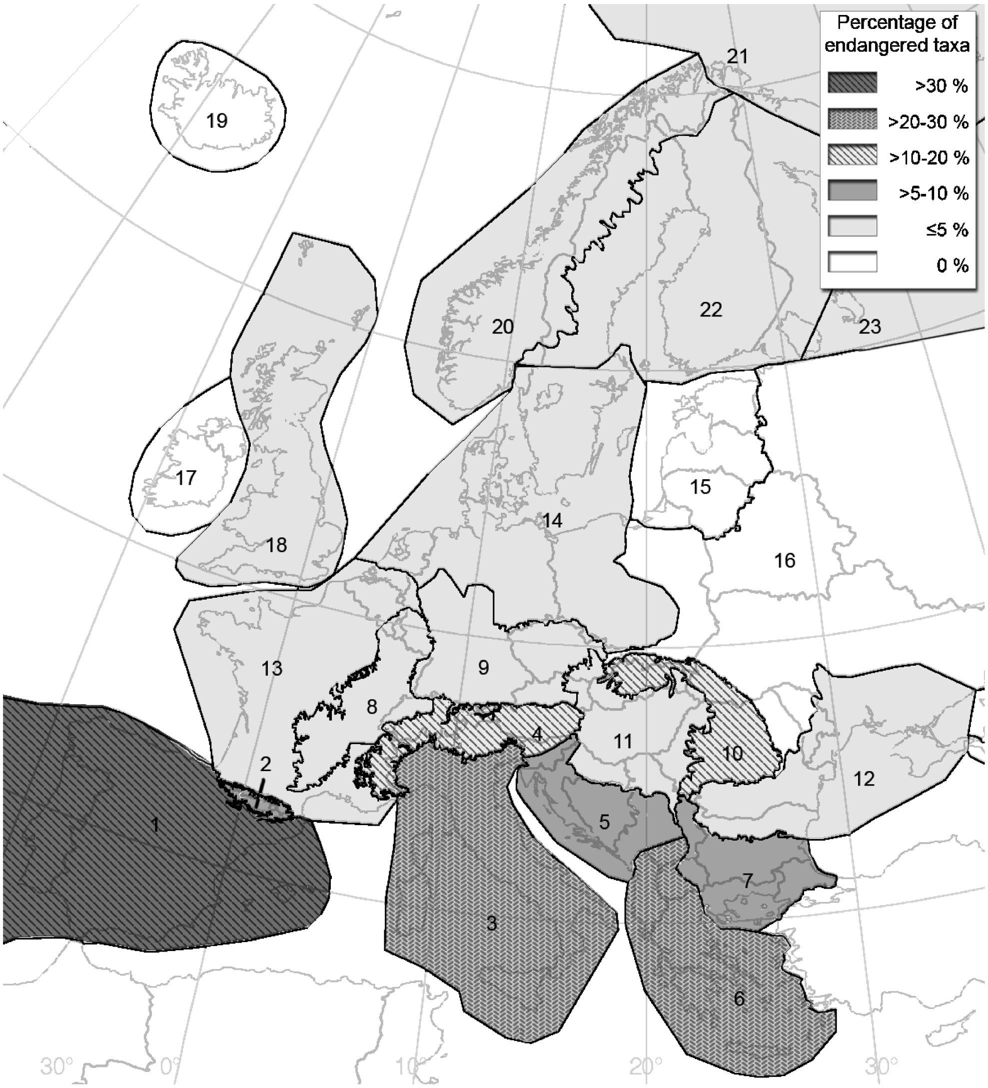

Figure 2. Fraction of Trichoptera taxa potentially endangered by climate change in the European ecoregions (endemic taxa meeting at least one additional sensitivity criterion; compare Table 3 for ecoregion name).

distinct south-east – north-west gradient is revealed. The fraction of taxa meeting at least one criterion ranges from 25 % (Iceland) to 82.5 % (Iberic-Macaronesian Region).

We defined those taxa as "potentially endangered by climate change" that are both endemic and meeting at least one additional sensitivity criterion since regionally climate change may lead to a complete loss of suitable habitats for species with a restricted distribution. The fraction of potentially endangered taxa according to this definition is below 3 % in 15 of 23 ecoregions, including all northern European and lowland ecoregions (Figure 2). Around 10 % of the species in high mountain areas are defined as endangered (Alps: 13.1 %; Pyrenees: 8.6 %; Carpathians: 12.5 %), while the fraction is highest in southern European ecoregions (Iberic-Macaronesian Region: 30.2 %; Italy: 24.5 %; Hellenic Western Balkan: 21.9 %).

Discussion

Parameters reflecting sensitivity to climate change

The majority of studies estimating the impact of climate change on biodiversity link climate scenarios to habitat requirements of selected species. This approach is generally useful for aquatic invertebrates too. However, knowledge gaps concerning distribution and ecological preferences limit the applicability of models. For Trichoptera, it is possible to generate species-lists for ecoregions or countries. A finer resolution (e.g. grids as used in several studies on vascular plants) is not feasible, since data density is too low. The alternative approach used in this study could also be applied to other taxa, for which less data are available, thus enabling a comparative sensitivity analysis of all species of larger taxonomic groups (compare Hof et al., 2008). Although relatively simple data are required, the approach is nevertheless hampered by data availability, particularly due to insufficient taxonomical knowledge, the broad definition of the term "endemism" and missing data on several relevant species traits. According to Malicky (2005) more than 300 Trichoptera species have been newly described in Europe and neighbouring areas between 1983 and 2005, most of which occur in Turkey, Greece, Italy and in the Iberic-Macaronesian Region, while only 16 new species have been described from central Europe. Thus, in northern and central Europe few additional species can be expected, in contrast to southern Europe, where many species yet unknown to science are likely to occur. Insufficient taxonomic knowledge of European Trichoptera, as for many other aquatic insect orders, is a major obstacle in analysing the impact of climate change and other emerging stressors. Several taxa are not identifiable in the larval stage, especially those occurring in southern Europe. Information on the distribution of Trichoptera species is therefore drawn mainly from the trapping of adults – the large number of benthic samples taken for river monitoring purposes do not really contribute to a better understanding of ecological preferences or distribution patterns. However, improved taxonomic knowledge will likely not change but confirm the overall endemism patterns as most of the recently described species have been found in already known hot-spots of endemism. Illies (1978, Fig. 3) and Hof et al. (2008) have described similar patterns of diversity and endemism based on the entire aquatic fauna.

For the purpose of this analysis we defined "endemism" as occurrence in only one single European ecoregion, which may cover several 100,000 km^2 (Table 3). Endemic species occurring in a comparatively large ecoregion (e.g. the Iberic-Macaronesion Region) are likely to be less endangered by climate change than endemic species occurring in a small ecoregion (e.g. the Pyrenees). Furthermore, environmental conditions are highly variable in the Mediterranean ecoregions and the high mountain areas and less variable in the lowland ecoregions of northern Europe. To compensate these factors it would be required to use the precise distributional range of each endemic species and proxies for environmental variability per ecoregion; however, such precise data are not available for Trichoptera. An alternative approach would be to focus on microendemic taxa that, e.g., occur only in a restricted mountain range. For example, members of the subfamily Drusinae are distributed in most European mountainous areas, from the Caucasus in the east to the Iberian Peninsula in the south-west; but three quarters of the Drusinae are endemic species limited to a single or very few mountain ranges, making the group an ideal model for studying speciation in connection with historical climatic processes (Marinković-Gospodnetić, 1976; Kumanski, 1988; Malicky, 2005; Sipahiler, 2002). Several taxa were classified as microendemic (Table 3); however, data are incomplete and thus not as consistent as ecoregional distribution. The definition of endemic taxa per ecoregion is therefore the best approximation presently achievable. Species distributions and taxa richness are not homogeneous within an ecoregion. Particularly in ecoregions with a long North-South extension (e.g. Italy and Fenno-Scandian Shield), responses of the caddisfly fauna to global warming within an ecoregion by northwards movements of species with southern distributions can be expected.

About 10 % (113) of all taxa are presently classified as subspecies, most of which are restricted to small and distinct areas, thus comprising a significant percentage of the endemic taxa. However, we consider it as likely that many subspecies will be ranked as species based on molecular analyses, thus not changing the overall endemism patterns.

We defined species restricted to springs as being potentially endangered by climate change impacts, since they cannot move further upstream in case of a general increase in temperature. This is despite the fact that springs are a widespread habitat type, and much more abundant than, e.g., large rivers. Species restricted to springs and at the same time being widely distributed are therefore likely to survive climatic shifts, while species restricted to this sensitive habitat and having a limited distribution are particularly endangered. Less information on thermal preferences of Trichoptera species is available, so the preference for springs, which is a well known trait, acts to some degree as a proxy for "cold stenothermy". Despite the overlap between these two parameters it is useful to consider both traits: of the 248 species known as cold-stenothermic only 176 are specialists for springs, while many others are restricted to high mountain ranges but also occur in larger streams. At a first glance, the relatively low number of cold stenothermic species in Northern European ecoregions is surprising. The majority of species occurring in Northern Europe live in Central or Southern Europe in quite different habitats than streams (e.g. larger rivers and lakes). Lentic species are generally more widespread in Europe (Hof et al. 2006). Some of them, e.g. *Limnephilus* spp., have a relatively high dispersal capacity as adults oversummer in remote places; these species have postglacially recolonised Northern Europe. They may have become adapted to colder waters and genetic analyses may reveal that they are cryptic species. We have used feeding type specialists as a proxy for niche width. Future analyses could benefit from more detailed information on food sources and feeding modes to more accurately describe the niche; however, these are presently available for very few species. Additional traits could be taken into consideration to supplement the hypotheses outlined in the introduction. Besides impacting temperature patterns, changing climate will probably alter the hydrologic regime of many rivers (Manabe et al., 2004), leading to extreme floods or the disappearance of temporary water bodies in parts of Europe, while in other areas permanent streams might be changed to temporary streams. Adaptation to floods and droughts requires populations to distribute the risk among lifestages through flexible life cycles or an extended adult phase; life cycle parameters are therefore of special importance to judge sensitivity of species. However, very limited information is available at a species level for traits such as resistance/resilience to droughts (7.8 % taxa classified) and life duration (9.7 %) (Table 1). The same is true for dispersal capacity (1.0 % taxa classified), an important parameter to judge the capability of species to colonise other areas if climatic conditions change. Most of these parameters have been classified by Tachet et al. (2002) on a genus level for several macroinvertebrate taxa (in some cases also at the species level). Particularly for Trichoptera, we expect very different adaptations of species of the same genus and therefore did not extend our investigation to an analysis at the genus level.

We restricted the parameter "niche breadth" to the analysis of feeding types; niche breadth could potentially have been extended to other parameters. However, on most other parameters much less information is available (Table 1), which might have caused a considerable bias in the analysis.

Regional differences in biodiversity and in the sensitivity of species to climate change

In general, a south-north gradient in European Trichoptera species richness can be observed. This pattern is mainly a result of fluctuations in continental ice cover during the Pleistocene, which in turn caused several range extensions and regressions of Trichoptera species (Malicky, 2000; Pauls et al., 2006). While glaciers covered most of northern Europe, species retreated to southern Europe or to ice free parts of high mountain areas. This isolation of populations resulted in many new species and increased diversity in high mountain ranges and in the Mediterranean region. Several distinct areas of speciation have been detected in the Alps (Malicky, 2000), the Pyrenees (Décamps, 1967), the Apennin (Cianficconi et al., 1997) and in the Balkans (Marinković-Gospodnetić, 1977; Kumanski and Malicky, 1984). Most species with a restricted distribution tend to be specialised either in feeding habits or habitat requirements. Bonada et al. (2007) compared taxonomic richness and trait composition of river macroinvertebrate assemblages (including Trichoptera) in the Mediterranean Basin and in temperate Europe. They conclude that climate change could reduce the range size of taxa occurring in both southern and northern regions of Europe. Since assemblages in the Mediterranean region were characterised by taxa with higher dispersion and colonisation capabilities, they further conclude that species loss in the temperate region following climate change could be compensated by immigration of Mediterranean taxa. This leads to a higher vulnerability of taxa restricted to temperate and northern regions, as Mediterranean taxa might move northwards. For Trichoptera species, our data contradict the hypothesis by Bonada et al. (2007). Almost all species occurring in the northern European ecoregions are distributed in central and/or southern Europe too (Fig. 1). Apparently, mainly generalists and species with a high dispersal capacity recolonised northern Europe after the last ice age, while specialist species and those with limited dispersal capacities extended their range only slightly. As a consequence, most of the species occurring in northern Europe are likely to be capable of dealing with the expected climate change impacts, since they are generalists or able to rapidly colonise other areas. Our data do not suggest that many Trichoptera species will disappear from central and northern Europe following climate change, providing space for Mediterranean taxa, which could thus compensate their habitat loss in the Mediterranean by colonising central European streams, as hypothesised by Bonada et al. (2007). In contrast to our study, however, the analysis of Bonada et al. (2007) is based on a relatively low taxonomic resolution (mainly genus level) and on high spatial resolution (specific stream localities), which is likely the main reason for the differing conclusions. In southern Europe, however, strong impacts on specialist species can be expected. Given the restricted distribution range of several species, we expect a high fraction of Mediterranean Trichoptera taxa to be endangered by climate change as opposed to northern European taxa (Fig. 2). This result also contradicts studies dealing with other taxonomic groups. According to Verboom et al. (2007), who combined different climatic, economic and biodiversity models, biodiversity will decline most strongly in Scandinavia. Models addressing the impact of climate change on vascular plants in Europe do not reveal a distinct south-north gradient in sensitivity. Bakkenes et al. (2002) modelled distributional changes of European vascular plants between 1990 and 2050. According to their model, a species loss of >25% can be expected for 10% of the European areas, but there is no clear geographic focus. Comparable results were obtained by Svenning and Skov (2006) dealing with 36 forest herb species. For birds, the strongest decline is expected for northerly distributed and specialist species (Julliard et al., 2004). Although some studies describe regional effects of climatic variation on the composition of benthic invertebrate communities (Bradley and Ormerod, 2001; Burgmer et al., 2007), only Bonada et al. (2007) have yet addressed the expected large-scale changes in the distribution of European aquatic insects. The clear north-south gradient in the sensitivity of Trichoptera, revealed in our study, is mainly a result of their limited dispersal capacity, which led to a high speciation rate during the Pleistocene and afterwards to a slow colonisation of northern Europe. We expect similar patterns for other taxonomic groups with equally limited dispersal capacity. However, since different conclusions have been drawn for entire macroinvertebrate assemblages (Bonada et al., 2007), it will be interesting to conduct sensitivity analyses for a wide range of aquatic organism groups.

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