A trait-based approach to assess climate change sensitivity of freshwater invertebrates across Swedish ecoregions

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Abstract Freshwater habitats and organisms are among the most threatened on Earth, and freshwater ecosystems have been subject to large biodiversity losses. We developed a Climate Change Sensitivity (CCS) indicator based on trait information for a selection of stream- and lake-dwelling Ephemeroptera, Plecoptera and Trichoptera taxa. We calculated the CCS scores based on ten species traits identified as sensitive to global climate change. We then assessed climate change sensitivity between the six main ecoregions of Sweden as well as the three Swedish regions based on Illies. This was done using biological data from 1,382 stream and lake sites where we compared large-scale (ecoregional) patterns in climate change sensitivity with potential future exposure of these ecosystems to increased temperatures using ensemble-modelled future changes in air temperature. Current (1961~1990) measured temperature and ensemble-modelled future (2100) temperature showed an increase from the northernmost towards the southern ecoregions, whereas the predicted temperature change increased from south to north. The CCS indicator scores were highest in the two northernmost boreal ecoregions where we also can expect the largest global climate change-induced increase in temperature, indicating an unfortunate congruence of exposure and sensitivity to climate change. These results are of vital importance when planning and implementing management and conservation strategies in freshwater ecosystems, e.g., to mitigate increased temperatures using riparian buffer strips. We conclude that traits information on taxa specialization, e.g., in terms of feeding specialism or taxa having a preference for high altitudes as well as sensitivity to changes in temperature are important when assessing the risk from future global climate change to freshwater ecosystems [Current Zoology 60 (2): 221-232, 2014].

Keywords Climate change, Indicators, Traits, Freshwater, Macroinvertebrates, Ecoregions

On a global scale, biodiversity is decreasing much faster than the natural background rate (Heywood, 1995; Jenkins, 2003), and freshwater habitats and organisms are among the most threatened ecosystems (Revenga et al., 2005; Ricciardi and Rasmussen, 1999; Strayer and Dudgeon, 2010). Freshwater habitats cover less than 1% of the Earth's surface area but contain about 10% of all known species (Strayer and Dudgeon, 2010). There has been substantial global losses of freshwater biodiversity and it is estimated that between 10,000 and 20,000 freshwater species have either become extinct or are seriously threatened, a figure much higher than in all other ecosystems (Sala et al., 2000). Humans are now the dominant drivers of environmental change in the

global water cycle and in freshwater aquatic ecosystems, reflecting the fact that we have now reached the Anthropocene (Dudgeon, 2010; Meybeck, 2003; Steffen et al., 2007). Global climate change is also predicted to severely affect streams, rivers and lakes, especially in combination with environmental stressors such as land use changes (e.g., Meyer et al., 1999; Moss et al., 2009; Sala, Chapin et al., 2000).

Global climate change will have a number of effects on freshwater ecosystems through increases in CO_2 levels, increases in air and water temperatures as well as changes in precipitation and runoff regimes (Poff et al., 2002). Globally, surface temperature averages have increased by 0.78°C when comparing the average of

Received Dec. 24, 2013; accepted Mar. 18, 2014.

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1850–1900 with the 2003–2012 period, and according to IPCC (2013) "it is extremely likely that human influence has been the dominant cause of the observed warming since the mid-20th century". All future scenarios for year 2100 (IPCC, 2013) predict that the global average temperature will be 5 to 12 standard deviations above the mean Holocene temperature (Marcott et al., 2013). At high northern latitudes (north of 45° N), both summer extreme temperatures and decadal averages measured in the last 10 years were warmer than those reported since 1400 (Tingley and Huybers, 2013). This is in agreement with the notion that glacial systems at high latitudes are likely to be disproportionally affected by the global climate change (Perkins et al., 2010).

Freshwater ecosystems are already undergoing changes in temperature and hydrological regime with effects on biotic communities in lakes (e.g., Ruhland et al., 2008, Smol et al., 2005, Williamson et al., 2009), streams and rivers (e.g., Brown et al., 2007; Finn et al., 2010, Muhlfeld et al., 2011). Many studies have predicted future changes in community composition in lakes and streams in response to climate change, including fish (Britton et al., 2010; Buisson et al., 2008), phytoplankton (Elliott et al., 2005; Jeppesen et al., 2009) and benthic macroinvertebrates (Bonada et al., 2007; Rosset and Oertli, 2011). Benthic macroinvertebrates such as aquatic insects are affected by alterations in temperature and hydrological regime during their entire life cycle (e.g., Durance and Ormerod, 2007; Haidekker and Hering, 2008; Vannote and Sweeney, 1980) in that temperature affects growth, metabolism, reproduction, emergence and distribution. Human-induced stressor effects on macroinvertebrates have commonly been assessed using indicators based on species composition (e.g., Dahl et al., 2004; Hering et al., 2004; Sandin and Hering, 2004). These kinds of traditional species-based indicators have, however, rarely been used to assess potential changes in relation to global climate change.

Trait information of aquatic insects, on the other hand, has been used to assess human induced stress on freshwater ecosystems (e.g., Doledec and Statzner, 2008; Johnson et al., 1997; Statzner et al., 2001), as well as the potential effects of global climate change (Bonada et al., 2007; Conti et al., 2014; Hering et al., 2009), relative to environmental preferences and adaptations, organismal development, body size, locomotion, feedingand reproductive strategies (Menezes et al., 2010; Statzner et al., 2001). In this paper, we focus on three benthic macroinvertebrate insect orders (Plecoptera – stoneflies, Ephemeroptera – mayflies and Trichoptera – caddisflies) (hereafter EPT) for which extensive species trait information is available through www.freshwaterecology.info, a taxa and autoecology database for freshwater organisms (Schmidt-Kloiber and Hering, 2012). Earlier studies have identified trait characteristics as useful indicators of global climate change sensitivity in Trichoptera (Hering et al., 2009), Plecoptera (Tierno de Figueroa et al., 2010) and for all three insect orders combined (Conti et al., 2014) at the European scale.

In this study, we developed a new Climate Change Sensitivity (CCS) indicator score based on a selection of EPT taxa. The aim of the CCS indicator is to provide a measure of the potential vulnerability of Swedish freshwater ecosystems to climate change. We focus on changes between current and future mean annual temperatures (i.e., the degree to which the system is exposed to climatic variation) and the sensitivity of the ecosystems to such changes (Cardona et al., 2012). The indicator is based on trait information rather than the community composition based assessment metrics traditionally used in freshwater biomonitoring (see e.g., Dahl et al., 2004; Ofenböck et al., 2004; Sandin and Johnson, 2000b; Schartau et al., 2008). We chose this approach because: (1) differences in regional species pools exist among areas, making comparisons of numerical community descriptors difficult, and (2) the influence of local environmental conditions on biodiversity is more consistent across traits than species-based metrics (Charvet et al., 2000). Using a large-scale benthic macroinvertebrate dataset covering lakes and streams across Sweden (Willander et al., 2003), we calculated CCS indicator scores based on ten species traits identified as sensitive to global climate change (see below). The CCS scores were compared using a unique dataset covering the six main ecoregions of Sweden as well as the three large-scale Illies (1978) regions in Sweden. We expect the CCS indicator scores to increase from southern to northern Sweden, mainly based on the probable occurrence of a higher number of temperature sensitive species in the north. This information is of vital importance when planning and implementing management and conservation strategies in freshwater ecosystems, as it can be used, for instance to mitigate increased temperatures using riparian buffer strips. As our indicator is site based it has a strong potential to be implemented in conservation and monitoring programmes to assess potential vulnerability of freshwater ecosystems to global climate change.

1 Materials and Methods

1.1 Site selection

Data were obtained from the Swedish National Lakes and Streams Survey of 2000 (Willander et al., 2003). Here, 705 streams/river stations and 677 lake stations (total 1,382 stations; one in each stream/lake) were sampled for benthic macroinvertebrates. The running water stations were randomly selected from the Swedish Meteorological and Hydrological Institute's watercourse and catchment register and stratified by size (half of the stations in catchments with an area of 15 to 50 km² and half in a 50 to 250 km² catchment area). The lake stations were randomly selected from the Swedish Meteorological and Hydrological Institute's digitised lake register. The lakes were also stratified by size (0.04–0.1; 0.1-1; 1-10; 10-100; >100 km²; for further details on the choice of sampling stations, see Johnson et al. (2004), Sandin (2003), Sandin and Johnson (2004).

1.2 Field sampling and laboratory analysis

Sampling was stratified by season, starting in the northern part of the country in September and finishing in the southern part in December 2000. All samples were collected using standardised kick sampling (European Committee for Standardization, 1994) where five 1 m long and 0.25 m wide samples are collected using a 0.25*0.25 m hand net with a 500 µm wide mesh and pooled. A total area of 1.25 m² was sampled at each stream/lake sampling station. For further information on sampling, see Wilander, Johnson and Goedkoop (2003) and (Sandin, 2003). Biological data is available from the Swedish University of Agricultural Sciences, www.slu.se. All samples were sorted and identified according to quality control and assurance protocols including, for instance, intercalibration of the identification skills of the taxonomists (Wilander et al., 2003). Most of the 184 Ephemeroptera, Plecoptera and Trichoptera taxa in the dataset were identified to species or species group level (124), but some only to genus (40) or family level (20), based on an operational taxa list with predefined taxonomic identification levels for each taxonomic group (from hereon called 'taxa').

1.3 Ecoregions and temperature data

The ecoregional delineation is based on the eight main ecoregions of Sweden (Nordic Council of Ministers, 1984) with the following modifications: Arctic and Alpine ecoregions were merged into the 'Arctic-alpine' ecoregion (as the Arctic ecoregion covers a very small part of Sweden). The Northern boreal ecoregion was merged with the Northern-southern boreal ecoregion into the 'Northern boreal' ecoregion. We thus end up with six main ecoregions - the Arctic-alpine ecoregion (135 sampled sites), the Northern (184 sites), Middle (381 sites) and Southern (149 sites) boreal regions, the Boreonemoral ecoregion (459 sites) and the Nemoral ecoregion (74 sampled lake or stream sites) (Gustafsson and Ahlén, 1996), see also Sandin (2003), Sandin and Johnson (2000a) (Fig. 1). This European ecoregional delineation fits well within the framework based on European zoogeographic regions (Illies, 1978), with three European regions in Sweden (Illies, 1978): region 20 - Borealic uplands (includes the Arctic-alpine ecoregion - 135 sampled stream or lake sites), region 22 -Fennoscandian shield (includes the Northern, Middle and Southern boreal ecoregions - 714 sampled sites) and region 14 - Central plains (encompasses the Borenemoral and Nemoral ecoregions - 533 sampled sites). Observed as well as modelled annual mean air temperatures were extracted from the CliMond (Global climatologies for bioclimatic modelling) database version 1.1. (Kriticos et al., 2012) as air temperatures are often used as a proxy for water temperature for freshwater ecosystems (Livingstone and Lotter, 1998; Pedersen and Sand-Jensen, 2007; Stefan and Preudhomme, 1993). We used current annual mean air temperatures (°C) (based on the period 1961-1990 and centered on 1975) in ESRI grid format with a resolution of 10'. Future temperatures for the year 2100 were modelled under two different gas emission scenarios (GESs): A1B



Fig. 1 The 705 streams and 677 lakes sampled in six main ecoregions of Sweden

and A2A. For each scenario, two Global Circulation Models (GCMs) were used: CSIRO-MK3.0 (CSIRO, Australia) and MIROC-H (Centre for Climate Research, Japan). Each CliMond data layer of Sweden consisted of 2,835 grid cells with measured or modelled annual mean air temperature data. With the two scenarios and two different models, a forecasting approach was used to compute an ensamble-modelled annual mean air temperature in each of the 2,835 grid cells by calculating the unweighted averages of temperatures, thus giving equal probabilities to each of the four models as suggested by Araújo and New (2007).

1.4 Traits selection and the CCS indicator

Following the approaches of Hering et al. (2009), Tierno de Figueroa et al. (2010) and Conti et al. (2014), we selected a suite of ten traits related to the potential vulnerability of EPT taxa to climate change (hereafter 'sensitivity traits') (Table 1). Among the 184 EPT taxa in this study, 139 were classified as possessing at least one trait in a trait state defined as being sensitive to climate change and were therefore retained for the analyses. We considered traits related to the specialisation of species: i) habitat specialist, ii) substrate preference, iii) current velocity preference and iv) feeding mode. Additionally, traits related to hydrological preferences were used: v) low resistance to drought, as well as traits in connection to temperature: vi) adaptation to cold temperatures (cold stenotherms), vii) preference for upper stream zones, viii) preference for high altitudes and ix) short emergence period (potentially leading to a phenological mismatch). One additional trait not included in the analyses referred to above was included in the analyses: x) taxa with low dispersal capacity, i.e., species unable to track the suitable geographic location of their climate niche with a changing temperature and climate (Pearson and Dawson, 2003). The traits were obtained from Schmidt-Kloiber and Hering (2012) with specific trait information for Trichoptera (Graf et al., 2008), Ephemeroptera (Buffagni et al., 2009) and Plecoptera (Graf et al., 2009). Seven traits were fuzzy coded (10 point system) where 0 indicates no preference and 10 indicates 100% affinity for the trait category. The other three traits classify the species into those with/without the trait category present (see http://www.freshwaterecology.info/abbreviations.php) (Table 1).

A Climate Change Sensitivity (CCS) indicator is proposed based on the presence/absence of the 139 indicator taxa possessing at least one sensitivity trait (Table 1).

Table 1 The 10 ecological and	life history tra	aits used to compute the CCS indicator	
Trait	No. of taxa	Description	References
Preference for upper stream zones	23	Taxa confined to upper stream zonation (upper trout, spring, spring-brook) classified as a sum of 5 or more in these zones	Hering et al., 2009; Tierno de Figueroa et al., 2010; Conti et al., 2014
Preference for high altitudes	8	Taxa confined to high altitudes > 1000 m, classified as a sum of 5 or more (high altitudinal regions; alpine, montane, nival, subalpine, subnival)	Tierno de Figueroa et al., 2010; Conti et al., 2014
Low resistance to drought	15	Taxa classified as having no resistance strategy and/or no resistance form for droughts	Conti et al., 2014
Temperature range preference	15	Temperature range preference classified as cold stenotherms or temperature preference classified as cold or very cold <10 and <6 with a sum of 5 or more	Hering et al., 2009; Tierno de Figueroa et al., 2010; Conti et al., 2014
Habitat specialist	54	Habitat specialist, taxa coded at least 5 for one major habitat type	Conti et al., 2014
Specialised substratum preference	59	Taxa coded at least 5 for one of the substratum categories	Conti et al., 2014
Specialised current preference	6	Taxa occurring in streams; coded at least 5 in zones with high current	Tierno de Figueroa et al., 2010; Conti et al., 2014
Feeding type specialist	71	Taxa coded at least 5 for one of the feeding types grazers, active or passive filter feeders	Hering et al., 2009
Low dispersal capacity	14	Dispersal capacity classified as low	
Short emergence period	50	Emergence period of the taxa < 2 months	Hering et al., 2009

$$CCS = \sum_{t=1}^{T} \sum_{s=1}^{S} I_{t,s.} P_s$$

where

$$I_{t,s} = \begin{cases} 1, & \text{if trait t is present for species S} \\ 0, & \text{else} \end{cases}$$
$$P_{s} = \begin{cases} 1, & \text{if species S is present} \\ 0, & \text{else} \end{cases}$$

t = climate change sensitive trait; T = number of traits (here 10); s = each species or taxa; S = total number of taxa possessing at least one of the ten traits (here 139). CCS has a minimum value of zero and a theoretical

upper limit of
$$\sum_{t=1}^{T} \sum_{s=1}^{S} I_{t,s} P_s$$

which in this case is 319, i.e., if a sampled stream or lake theoretically contains all 139 taxa exhibiting all possible climate-sensitive traits (some taxa possess more than one of the sensitivity traits). A low CCS value indicates that a stream or lake is not sensitive to climate change, whereas high CCS values suggest that multiple taxa possessing one or several climate change sensitive traits are present.

1.5 Statistical analyses

A one-sample *t*-test was used to test for differences in temperature between the ensamble forecast (based on scenarios A1B and A2 using the models from CSIRO and MIROC-H) and the observed data for the period 1961–1990 for the whole of Sweden and for each of the six ecoregions and three Illies regions individually. In the test, the difference between ensamble-modelled and measured annual mean air temperature for each grid cell was evaluated. One-way ANOVA followed by comparisons using the Tukey-Kramer HSD test was used to test the difference in temperature (measured and modelled), individual traits and CCS indicator scores among the main ecoregions and the Illies regions. All statistical analyses were done using JMP 10.0 (SAS Institute Inc.). All GIS analyses, such as raster matrix calculations, were undertaken using ESRI ArcMap 10.0.

2 Results

2.1 CCS indicator

The Climate Change Sensitivity (CCS) indicator developed in this study included 81 (58.3%) Trichoptera, 30 (21.6%) Ephemeroptera and 28 (20.1%) Plecoptera taxa, each possessing at least at least one trait in a state indicating climate change. To assess the importance of the inclusion of individual traits in the CCS indicator scores, the relationship between the score including all ten traits was regressed against each of ten scores excluding one trait at a time. The adjusted R²-fit between the CCS including all traits and CCS with one trait removed at a time was always greater than 0.98. The most common trait states indicating climate change present were feeding type specialism (76.7%) for Ephemeroptera, short emergence period (50.0%) for Plecoptera and habitat specialism (61.7%) for Trichoptera (Table 2). Four of the ten traits used here were present in 1/3 of the 139 EPT taxa included in the study. Three of these were specialist traits (feeding specialism, substratum preference and habitat specialist), the fourth being taxa with a short emergence period. This was in contrast to traits related to changes in temperature, i.e., taxa preferring cold temperatures (cold stenotherms), taxa restricted to high altitudes and taxa restricted to upper stream zones; only 5.8%-16.5% of the taxa possessed one of these traits. In five instances did one of the three taxa groups not include any taxa with a certain trait indicator. These were specialised current preference and

Table 2	Number of taxa	possessing a trait	with a trait state indica	ting climate chan	ge included in the	CCS indicator score
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Trait	Е	Р	Т	
Preference for upper stream zones	2 (6.7%)	10 (35.7%)	11 (13.6%)	
Preference for high altitudes	3 (10.0%)	5 (17.9%)	0 (0.0%)	
Low resistance to drought	1 (3.3%)	0 (0%)	14 (17.3%)	
Temperature range preference	7 (23.3%)	7 (25%)	3 (3.7%)	
Habitat specialist	4 13.3%)	0 (0%)	50 (61.7%)	
Specialised substratum preference	8 (26.7%)	6 (21.4%)	45 (55.6%)	
Specialised current preference	0 (0%)	3 (10.7%)	6 (7.4%)	
Feeding type specialist	23 (76.7%)	6 (21.4%)	41 (50.6%)	
Low dispersal capacity	0 (0%)	11 (39.3%)	3 (3.7%)	
Short emergence period	10 (33.3%)	14 (50.0%)	26 (32.1%)	

E = Ephemeroptera (30 taxa), P = Plecoptera (28 taxa), T = Trichoptera (81 taxa). Figures in parenthesis are the percentage of taxa indicating climate change out of the 139 taxa in the database.

short emergence period (Ephemeroptera), low resistance to drought and habitat specialism (Plecoptera), and preference for high altitudes (Trichoptera).

2.2 Temperature

The current average mean air temperature across the 2,835 raster cells was 2.37°C, whereas the ensamble-forecasted annual mean air temperature was 8.52°C. The measured annual mean air temperature (for the period 1961-1990) differed among the six ecoregions, increasing from the north to south; the same was true for the three Illies regions (Fig. 2A; ANOVA; P <0.0001 in both cases). The ensemble-forecasted annual mean air temperature for the year 2100 also differed among the six ecoregions (Fig. 2A; ANOVA, P < 0.001in both cases), increasing from the Arctic-alpine ecoregion in the north to the Boreonemoral and Nemoral regions in the south, the same being true for the three Illies regions. Variation in measured and ensambleforecasted annual mean air temperature among the grid cells within a region showed a different picture; the range as well as the standard deviation decreased from north to south in the six ecoregions, whereas the large and longest Illies region, the Fennoscandian shield, had a larger range as well as variation in annual mean air temperature than the two other Illies regions (Table 3).

The difference between the ensamble-forecasted temperature for the year 2100 and the measured annual mean air temperature for the period 1961-1990 showed quite a different pattern – the largest modelled change in temperature is predicted to occur in the Arctic-alpine (7.20 °C \pm 0.05; mean \pm SE) and Northern boreal ecoregions (7.06 °C \pm 0.04) for which the modelled change is statistically significantly higher (Fig 2B; ANOVA, P <0.001) than for the Middle (6.91 °C \pm 0.03) and Southern boreal ecoregions (5.28 °C \pm 0.06; mean \pm SE). The Boreonemoral (4.35 °C \pm 0.04) and Nemoral (3.78 °C \pm 0.10) regions showed a smaller change between the ensamble-forecasted and measured annual mean air temperature. The same pattern emerged for the three Illies regions, with the largest difference occurring between the modelled year 2100 temperature and the measured 1961-1990 temperature in the Borealic uplands (7.20 °C \pm 0.05) compared to the Fennoscandian shield (6.71 °C \pm 0.02) and the Central plains (4.28 °C \pm 0.04), with a statistically significant difference among all three regions (ANOVA, P < 0.001).

2.3 Ecoregions and CCS indicator scores

The CCS scores differed significantly among the ecoregions (including both stream and lake data) (Fig. 3A, ANOVA, F_5 = 14.60, P < 0.0001). Thus, the three boreal



Fig. 2 A) Measured annual mean air temperature in the period 1961–1990 (centred on 1975) and ensembleforecasted (for the year 2100) annual mean air temperature for the 2,835 raster cells in Sweden for the six ecoregions, B) difference in mean air temperature between ensemble-forecasted (for the year 2100) and measured annual mean air temperature in the period 1961–1990 (centred on 1975) for the 2,835 raster cells in Sweden for the six ecoregions

Whiskers represent 1.5 * the interquartile range in all cases.

regions – Northern (15.83 ± 0.84; mean ± *SE*), Middle (16.71 ± 0.58) and Southern (17.03 ± 0.93) – had the highest mean CCS indicator scores, although these did not differ significantly from those of the Nemoral region (13.86 ± 1.32). The Boreonemoral (11.41 ± 0.53) and Arctic-alpine regions (10.53 ± 0.98) had significantly lower CCS indicator scores. Comparisons between the three Illies regions showed significant differences (ANOVA, F_2 = 34.46, P < 0.0001); the Fennoscandian shield (ecoregion 22) had a higher mean CCS indicator score (16.55 ± 0.43) than the Borealic uplands (ecoregion 20; 10.53 ± 0.98) and the Central plains (ecoregion 14; 11.75 ± 0.49).

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			Anr	iual mean	ı air temp	erature (19	961-1990)	En	semble-forecaste	ed mean air ten	iperature (210	(0(
Type	Region	Number of grid cells	Mean	Max	Min	Range	Std Dev (o)	Mean	Max	Min	Range	Std Dev (o)
Main ecoregion of Sweden	Arctic/alpine	352	-1.18	2.43	-4.57	7.00	1.44	6.02	8.23	3.19	5.04	1.00
Main ecoregion of Sweden	Northern boreal	515	0.00	2.79	-2.81	5.60	1.47	7.06	9.08	4.95	4.14	0.79
Main ecoregion of Sweden	Middle boreal	971	1.31	4.92	-1.73	6.65	1.50	8.22	10.88	6.03	4.85	0.84
Main ecoregion of Sweden	Southern boreal	269	4.25	6.04	1.85	4.19	0.98	9.53	10.68	8.08	2.60	0.54
Main ecoregion of Sweden	Boreonemoral	637	6.33	7.78	5.07	2.71	0.56	10.68	11.96	9.28	2.68	0.54
Main ecoregion of Sweden	Nemoral	91	7.53	8.10	6.75	1.35	0.29	11.31	11.89	10.56	1.33	0.27
Illies region	Borealic uplands	352	-1.18	2.43	-4.57	7.00	1.44	6.02	8.23	3.19	5.04	1.01
Illies region	Fennoscandian shield	1755	1.38	6.04	-2.81	8.85	1.96	8.08	10.88	4.95	5.93	1.12
Illies region	Central plains	728	6.48	8.10	3.03	3.03	0.97	10.76	11.96	9.28	2.68	0.55





Error bars represent standard errors in all cases; significantly different ecoregion CCS scores are not connected by the same letter.

A clear difference also appeared in comparisons between CCS indicator scores in the 705 stream sites and the 677 lake sites (P < 0.0001). In the streams (including data from all ecoregions), the CCS scores (20.31 \pm 0.37) were almost three times higher than in the lake sites (7.65 ± 0.38) . Since it appears that there are more sensitive EPT indicators in streams compared to lakes, we also tested for ecoregional differences in CCS scores including only the 705 stream sites sampled in the study. A statistically significant difference emerged among the ecoregions when comparing the streams (Fig. 3B, ANOVA, F_5 = 45.99, P < 0.0001) where the Northern $(27.90 \pm 1.21; \text{ mean} \pm SE)$, Middle (26.46 ± 0.81) , and Southern boreal (25.45 ± 1.25) regions had significantly higher CCS indicator scores than the Arctic-alpine ecoregion (18.94 \pm 1.54), the Nemoral ecoregion (15.54 \pm 1.54) and the Boreonemoral ecoregion (13.44 ± 0.67) . The same held true for the three Illies regions (ANOVA,

 F_2 = 113.08, P < 0.0001) where the Fennoscandian shield had higher CCS indicator scores (26.58 ± 0.59) than the Borealic uplands (18.94 ± 1.54) and the Central plains (13.77 ± 0.61).

3 Discussion

The measured annual mean air temperature (for the period 1961–1990) shows a clear pattern with increasing temperatures from the Arctic-alpine and Northern boreal regions in the north of the country to the Boreonemoral and Nemoral ecoregions in the south. This is in contrast with the ensemble-modelled future temperature for Sweden where we expect the largest increases in temperature in the northern parts of the country. Similar results were found in a Swedish study (Lind and Kjellström, 2008¹), albeit these authors found that temperature will undoubtedly increase across all of Sweden already in the near future (the 30-year mean for 2011–2040).

The Climate Change Sensitivity (CCS) indicator developed in this study included 139 EPT taxa. The fact that the insect order Plecoptera includes many sensitive taxa was already emphasised by Tierno de Figueroa et al. (2010) who classified 63% of the European Plecoptera taxa as being vulnerable to climate change. Regarding Trichoptera 84% of the species evaluated by Hering et al. (2009) met at least one of the five climate change sensitivity criteria used in their study. Also Conti et al. (2014) found that many EPT taxa show a potential sensitivity to climate change. In their study most changes of EPT taxa in relation to climate change was predicted to take place in central Europe and the Alps, whereas only Plecoptera showed patterns of change also in northern Europe. A substantial species turn-over in macroinvertebrate communities with increasing temperature was furthermore shown in a study of geothermal streams in Iceland. Although the local species pool of the geothermal streams contained both Plecoptera and Trichoptera taxa, these were absent in the warmest streams (> 18 °C) (Friberg et al., 2009; Woodward et al., 2010).

The Climate Change Sensitivity (CCS) indicator is based on trait information rather than traditional assessment metrics. As can be seen from the analyses oftaxa within the three insect orders and their potential climate change sensitivity, there are differences in sensitivity between as well as within the three orders (Conti et al., 2014). Using the ten trait classifications instead of scores for individual taxa allows comparison of global change sensitivity across regions with potential differences in their regional species pools (which would make direct comparisons of taxonomic communities difficult); at the same time the influence of local environmental conditions on biodiversity will be more consistent across traits than when species-based metrics are used. The CCS indicator developed here could after further testing across e.g., Europe also potentially be included in monitoring schemes to assess potential vulnerability and conservation values in relation to future global climate change either alone or through the incorporation into multi-metric indicators of freshwater ecosystems.

Our study showed that trait information related to specialism (feeding mode, substrate preference, habitat specialism) is more common among the EPT taxa than trait information related to changes in temperature (cold temperature preference, high altitude preference, upper stream zonation preference). The same pattern has been shown for Trichoptera taxa (Hering et al., 2009) where feeding type specialism was the most common climate change sensitivity trait, whereas $< \frac{1}{4}$ of the taxa had a strong preference for the spring zone or were cold stenothermic. This pattern is partly due to a knowledge gap in information of ecological preferences and biological traits of freshwater species. To better our understanding of how freshwater ecosystems will respond to changes in climate, it is of vital importance to develop and expand databases including species trait information. In our study we have focused on annual (mean) increases in temperature, but it is also vital to study the effects of extreme temperatures (and other environmental variables) that could change and thus potentially structure freshwater ecosystems. This, in turn, can provide insight into the adaptive capacity of systems; that is, how these systems could cope with increasing amounts of stress in the future. It also has to be acknowledged that warming influences the biotic interactions and ecosystem functioning of stream and lake ecosystems and not only species directly through their traits. Cascading effects of climate change induced in fish communities (Jeppesen et al., 2012) on the invertebrate assemblages (and likely also the CCS indicator)can be strong (Brucet et al., 2012; Meerhoff et al., 2007) and warrant further studies. Similarly, trophic relationships in streams, as well as ecosystem functioning, have been shown to be strongly temperature

¹ Lind P, Kjellström E, 2008. Temperature and precipitation changes in Sweden, a wide range of model-based projections for the 21st century. RMK No. 113.

dependent (Friberg et al., 2009; Woodward et al., 2010).

In studies like ours, classification of taxa into specialists, e.g., those restricted to a single substratum type, is used as a proxy for niche width, as detailed information necessary to more precisely define the niche of individual species is presently very scarce (Hering et al., 2009). For some of the less known trait parameters in our study, such as drought resistance (10.8% of the taxa defined as being non-resistant to drought) or low dispersal capacity (10.1% of the taxa defined as being bad dispersers), the amount of information available to allow classification of taxa into categories is limited. The knowledge base for climatic variables has to be extended in the future to improve our predictions of potential changes in taxonomic composition in relation to global climate change (Conti et al., 2014) as specialised species with poor colonisation abilities and low dispersal rates are prone to extinction under climate change and other large-scale environmental changes (Kotiaho et al., 2005; Travis, 2003).

A clear geographical trend emerged in the CCS indicator scores, where the three boreal regions had higher CCS values (i.e. being more vulnerable to climate change) than the Arctic-alpine and the Boreonemoral regions (the difference from the Nemoral ecoregion being insignificant). This pattern was further emphasised when analysing only data from the 705 stream sites (which had higher CCS indicator scores than the lake sites); the three boreal regions had significantly higher CCS indicator scores than the three other ecoregions. The same pattern was found when analysing climate change vulnerability for the three Illies regions; thus, the Fennoscandian shield (the merged boreal ecoregions) had higher CCS scores for both streams and lakes as well as for streams only compared with the other two Illies regions. Such a trend has not been revealed in any of the so far conducted European-wide studies of macroinvertebrates in relation to climate change. The earlier studies of Trichoptera show almost no difference in the percentage of taxa vulnerable to climate change between the three Illies regions (Conti et al., 2014; Hering et al., 2009). Studies on Plecoptera reveal that the Central plains (the southernmost Swedish Illies region) contain the highest number of vulnerable species (Conti et al., 2014; Tierno de Figueroa et al., 2010). The same is true for analyses of Ephemeroptera (Conti et al., 2014). The main difference between the three above-mentioned studies and ours is that our investigation is based on field observations of taxa at individual sites, whereas the other studies used large-scale

information across Europe (i.e. an ecoregional distribution). These studies show that the most vulnerable taxa are specialist species in south-western Europe (mainly in the Iberian Peninsula, Italy and Greece) and in the alpine areas of central Europe (the Pyrenees, the Alps and the Carpathians), aquatic insects in northern Europe exhibiting the lowest sensitivity. Using sampling data of individual sites within ecoregions and a trait-based indicator of potential vulnerability, we obtain a more precise picture of the climate change vulnerability within and among Swedish ecoregions than when employing ecoregional data. This divergence is probably based on the fact that – when using presence-absence of taxa for each ecoregion – the presence of a few very rare and sensitive species within a region suffices to give the impression that the region is generally vulnerable to climate change. A next step to further test and develop the CCS indicator would be to use our site-based approach with large-scale data to assess potential conservation values and vulnerability to global climate change across larger regions, such as Europe.

We conclude that the region(s) with the highest predicted increase in temperature (most notably the Northern and Middle boreal ecoregions) potentially have the highest sensitivity to climate change based on macroinvertebrate trait information. It is important to identify areas with sensitive biota and predicted significant changes in temperature/climate in order to develop efficient future adaptation strategies to global climate change. The combination of climate change and habitat fragmentation poses a serious threat to species and ecosystems (McCarty, 2001). The abundance of specialised habitat species may decline, whereas fast-moving habitat generalist species could colonise new ecosystems beyond the northern border or expand their actual distribution (Parmesan et al., 1999; Warren et al., 2001). Freshwater ecosystems are already under serious threat by a large number of human-induced stressors, and it is therefore vital to understand where and how global climate change will add to the multiple existing stress effects on these important ecosystems and to implement the new knowledge in future management and conservation strategies for freshwater ecosystems.

Acknowledgements We thank all the people involved in the Swedish National Stream and Lake Survey of 2000, especially Lars Eriksson who was responsible for macroinvertebrate identification. Leonard Sandin was funded by the Marie Curie Action of the European Commission (FP7-2010-PEOPLE-IEF) through the FRESHCLIM project (project nr 273215) as well as by an individual grant from the Aarhus University Forskningsfond (AUFF-2010-FLS-6-44). Erik Jeppesen and Jens-Christian Svenning were supported by the Aarhus University Research Foundation under the AU IDEAS program (via Center for Informatics Research on Complexity in Ecology, CIRCE) and Nikolai Friberg by the Ring of Fire project. Astrid Schmidt-Kloiber, Erik Jeppesen and Nikolai Friberg were partly funded through the EU FP7 projects REFRESH (contract number 244121) and MARS (contract number 603378). We thank the three reviewers who gave valuable comments on an earlier version of the paper and Anne Mette Poulsen for editorial comments.

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