

Cryptic biodiversity loss linked to global climate change

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Global climate change (GCC) significantly affects distributional patterns of organisms¹, and considerable impacts on biodiversity are predicted for the next decades. Inferred effects include large-scale range shifts towards higher altitudes and latitudes², facilitation of biological invasions³ and species extinctions^{1,3}. Alterations of biotic patterns caused by GCC have usually been predicted on the scale of taxonomically recognized morphospecies¹. However, the effects of climate change at the most fundamental level of biodiversity—*intraspecific genetic diversity*—remain elusive⁴. Here we show that the use of morphospecies-based assessments of GCC effects will result in underestimations of the true scale of biodiversity loss. Species distribution modelling and assessments of mitochondrial DNA variability in nine montane aquatic insect species in Europe indicate that future range contractions will be accompanied by severe losses of cryptic evolutionary lineages and genetic diversity within these lineages. These losses greatly exceed those at the scale of morphospecies. We also document that the extent of range reduction may be a useful proxy when predicting losses of genetic diversity. Our results demonstrate that intraspecific patterns of genetic diversity should be considered when estimating the effects of climate change on biodiversity.

Numerous studies document the effects of GCC on biodiversity both at the ecosystem and species level, but not at the level of intraspecific genetic diversity. This is surprising, given that the use of molecular techniques in biodiversity research increasingly results in the recognition of high levels of cryptic biodiversity below the morphospecies level⁵. Efforts to delimit evolutionarily significant units (ESUs) for biodiversity-related fields acknowledge the fact that the morphospecies concept seems increasingly insufficient for holistic biodiversity estimates⁶. However, a concise framework for estimating the effects of GCC on cryptic biodiversity and spatial genetic differentiation is still lacking. Here we introduce a widely applicable approach based on the use of range-wide phylogeographic mitochondrial DNA data and species distribution modelling (SDM), which allows estimation of climate-related future changes of genetic and cryptic biodiversity. We reason that species with strong genetic population structure will experience massive losses of cryptic diversity and ESUs under GCC, and that examining GCC effects solely at the level of morphospecies will underestimate the extent of climate-driven biodiversity loss.

To test our hypotheses, we used range-wide mitochondrial sequence data (mitochondrial cytochrome *c* oxidase subunit I)

from nine aquatic insect species of European mountain regions. We examined seven species of caddisfly (*Chaetopterygopsis maclachlani*, *Drusus discolor*, *Drusus romanicus*, *Hydropsyche tenuis*, *Rhyacophila aquitana*, *Rhyacophila carpathica* and *Rhyacophila pubescens*; Trichoptera), the mayfly *Ameletus inopinatus* (Ephemeroptera) and the stonefly *Arcynopteryx compacta* (Plecoptera; Supplementary Table S1). The selected species have alpine, Arctic–alpine or endemic distributions (Supplementary Table S1) and are restricted to cold, fast-running, oxygen-saturated streams with low organic matter input⁷. These habitats are limited to higher altitudes, leading to insular distribution patterns of the species in the European mountains. Strong genetic population differentiation and high proportions of regionally endemic haplotypes have been shown for all but one range-restricted species (Supplementary Table S1), indicating very limited potential for long-distance dispersal. The species were chosen for their thermal sensitivity, their dispersal limitation and the availability of unbiased locality data and range-wide phylogeographic data sets. We applied an ensemble forecasting of species distributions to project future ranges of our study species under the Intergovernmental Panel on Climate Change (IPCC) 2080 A2a ('business as usual') and the IPCC 2080 B2a ('reduced CO₂ emissions') emission scenarios⁸. Assuming only short-distance dispersal, primarily in the form of local altitudinal shifts in response to climate warming, we inferred genetic diversity losses by associating predicted range losses with present haplotype distributions at the basin scale (see Methods).

Projections of future range shifts (SDM) showed significant losses of climatically suitable areas for all species under both IPCC emission scenarios (Fig. 1 and Supplementary Fig. S1 and Table S3). Range contractions were most severe at the low-latitude edges of species ranges and in low mountain ranges (Fig. 1). These areas are well known for high species diversity and for the frequent occurrence of endemic intraspecific lineages^{9,10}. Three species with restricted distribution are directly threatened by GCC-mediated extinction, as their present ranges are projected to become completely unsuitable or strongly reduced depending on the respective emission scenario (Fig. 1 and Supplementary Fig. S1 and Table S3). More extensive suitable areas under GCC were projected for each of the remaining six morphospecies. At present, all of these species have relatively large distributions. Suitable areas will generally shift from the Central European highlands to higher elevations in the Alps. Extensive suitable areas were projected in the north for the two Arctic–alpine species (Fig. 1 and Supplementary Fig. S1).

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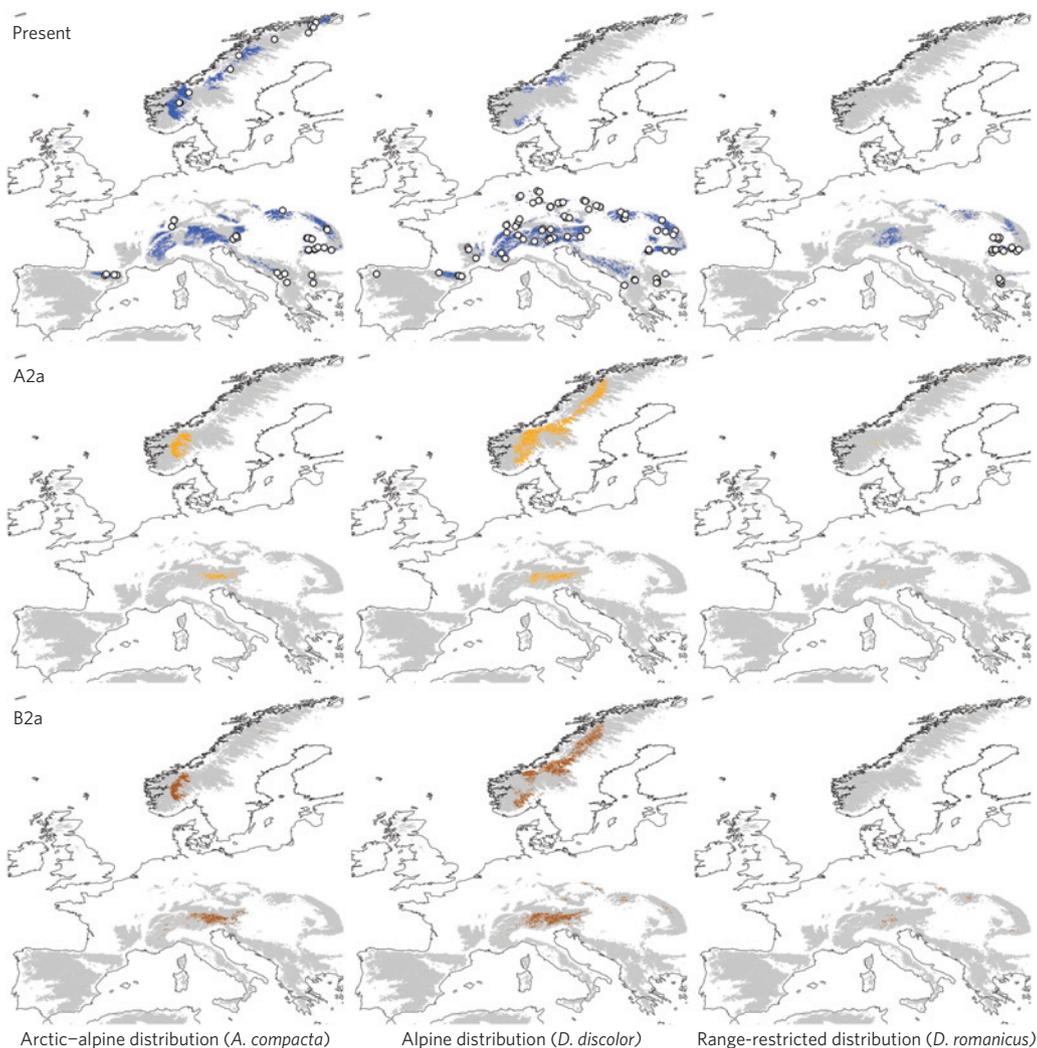


Figure 1 | Projections of climatically suitable regions for three montane aquatic insect species representing different distribution types in Europe. Distribution types are listed according to ref. 10. Top: present conditions; middle and bottom: IPCC 2080 emission scenarios A2a and B2a. Coloured shading indicates modelled present and future ranges; dots show sampling localities. Grey areas display elevations >500 m above sea level. Left: *A. compacta*; middle: *D. discolor*; right: *D. romanicus*. Analogous projections for the other species are shown in Supplementary Fig. S1. Projections of future range shifts (SDM) show significant losses of climatically suitable areas for all species under both emission scenarios (paired *t*-test on square-root-normalized absolute values of suitable area sizes of each species: present-A2a, $t = 8.5127$, $df = 8$, $P = 0.00002$; present-B2a, $t = 10.7075$, $df = 8$, $P = 0.00001$).

Five examined species comprise two or more ESUs based on 2% sequence divergence threshold (Fig. 2), and eight species comprise two or more ESUs based on the generalized mixed Yule-coalescent (GMYC) delineation (Supplementary Figs S2–S4 and Table S3). We found that substantially more ESUs face extinction by the loss of climatically suitable areas when compared with the morphospecies, regardless of the method used for ESU delineation (Figs 2 and 3 and Supplementary Figs S2–S4 and Table S2). Depending on the method of ESU delimitation, 52% and 59% of ESUs will be lost under the moderate CO₂ emission scenario (Fig. 3); 65 to 79% of ESUs will be lost under the more severe greenhouse-gas emission scenario. The results highlight the greater resolution achieved when using ESUs rather than morphospecies when predicting the impact of GCC on biodiversity. This is particularly relevant as detailed studies of intraspecific genetic variation often yield previously unrecognized, morphologically cryptic evolutionary lineages⁵. Losses of diversity under scenarios of GCC are even more severe when translated into haplotypes. A large number of haplotypes are geographically restricted to areas that will not be climatically suitable for them in the future. On average, 84% of haplotypes lose all of their areas

under the severe emission scenario, and 68% under the more moderate scenario (Figs 2 and 3 and Supplementary Table S3). These estimated losses of genetic diversity correlate with losses of suitable areas (Fig. 4). This indicates that the extent of GCC-induced range reduction may be a good predictor of changes in genetic diversity, at least for species with limited migration potential.

The highest levels of intraspecific genetic diversity losses measured as number of haplotypes and lost ESUs are projected in the Mediterranean region followed by the Central European highlands and the Carpathians (Supplementary Tables S4–S6). In many European species, genetic diversity is greatest in regions of their putative Pleistocene glacial refugia in southern Europe¹⁰. In general, ancestral refugial populations also show stronger genetic differentiation and exhibit the oldest splits⁹. Under our climate change projections, all but two populations in the classical southern refugia are projected to become extinct (two high-altitude Pyrenees populations of *A. compacta* are the exception; Supplementary Table S4 and S5). Thus, ancestral, highly diverse populations will be lost. Among our study species, deep ancestral splits are seen in *D. discolor*,

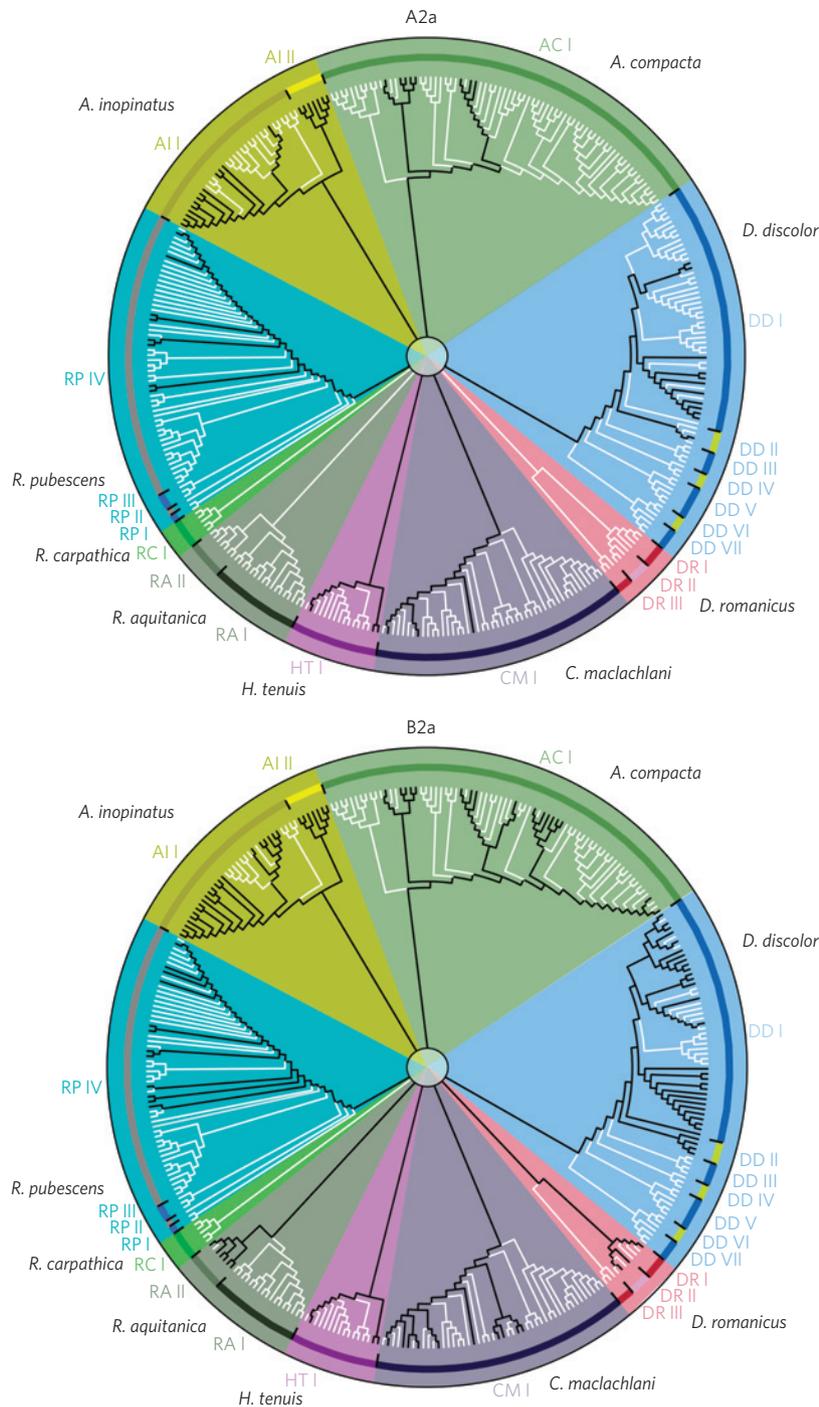


Figure 2 | Predicted loss of mitochondrial cytochrome c oxidase subunit I haplotypes for nine montane aquatic insect species in Europe under two IPCC 2080 CO₂ emission scenarios. Top: A2a 'business as usual' scenario; bottom: B2a 'reduced CO₂ emission' scenario. Shown is a combined UPGMA tree for all species. For clarity, species are separated by background colour. White branches show lost haplotypes (no climatically suitable areas projected). Highly diverged lineages (2% sequence divergence molecular operational taxonomic units) are marked on the outer circle. Molecular operational taxonomic units codes are given outside the circle and follow Supplementary Table S5.

D. romanicus and *R. pubescens*. The other species with Mediterranean populations (*A. compacta* and *H. tenuis*) show shallow splits resulting from postglacial recolonization of Central Europe from southern refugia and greatest diversity in the recolonized regions of the Carpathians and Central European highlands, respectively. This reflects the special situation of montane species in Europe with high genetic diversity in the Central European highlands^{9,11,12}. In general, our study supports the idea that climate change-induced biodiversity losses are projected to be

particularly severe in the Mediterranean region³ and many ancestral and genetically diverse southern lineages of temperate species are likely to become extinct.

GCC effects on genetic diversity may differently impact leading-edge, central and rear-edge populations^{2,13}. Our study supports this pattern, with marked decreases of intraspecific diversity mainly predicted for the genetically most diverse low-latitude and low-mountain populations. However, the coarse resolution of our modelling approach cannot discount future suitable habitat patches

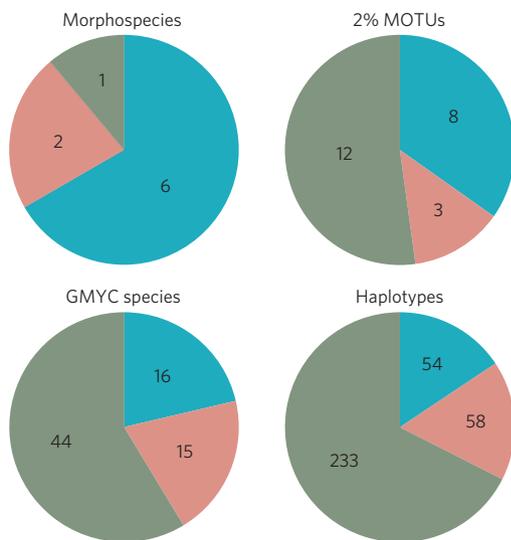


Figure 3 | Losses of morphospecies, ESUs and mitochondrial DNA haplotypes combined for nine montane aquatic insect species in Europe under two IPCC 2080 CO₂ emission scenarios. Absolute numbers of units that will persist under both future climate projections (blue), units that will be lost only under the 'business as usual' scenario (A2a; pink) and units lost under both scenarios (grey). MOTUs, molecular operational taxonomic units.

in small pockets of favourable microclimate conditions, for example in springs. It has been proposed¹³ that low-latitude rear-edge populations of numerous species survived past climate warming in very restricted climatic islands. We also consider future microrefugia possible for highland species; however, persisting populations will probably be highly vulnerable as a result of severely reduced effective population sizes. Although GCC will probably result in genetic impoverishment in rear-edge populations, shifting ranges may also enhance global intraspecific genetic diversity. This may result from local adaptation in leading-edge populations² or increased local intraspecific genetic diversity through hybridization of historically isolated lineages after a climate-driven secondary contact¹⁴.

Although our data indicate the usefulness of combining phylogeographic data sets based on mitochondrial DNA sequence

data and SDM, the drawn conclusions rely on several assumptions. We used neutral mitochondrial DNA haplotype variation as a surrogate for intraspecific genetic diversity. We specifically chose mitochondrial DNA as it is the most common marker for large-scale assessments of genetic population structure¹⁵ and it is widely used for the identification of cryptic evolutionary lineages¹⁶. Thus, the particular strength of the approach lies in the wide availability of such homologous data from varying organism groups of different geographic regions and ecological guilds. With decreases in sequencing costs, comparative homologous multi-locus data sets will become more readily available, allowing further improved estimates of genetic diversity losses⁴.

An important issue for SDM-based predictions of GCC effects on biodiversity is the difficulty of implementing dispersal and migration scenarios into projections of future distribution¹⁷. The discrepancy between the widespread use and importance of SDM in ecological studies on the one hand, and the rare implementation of sophisticated approaches for assessing dispersal on the other hand, is largely due to a limited understanding of dispersal rates and migration patterns for many taxa¹⁷. Dispersal of immature stages (eggs, larvae and pupae) of aquatic insects is often accidental or passive and usually restricted to within-stream movement, whereas dispersal among streams or catchments happens during the winged adult life stages¹⁸. Here we assumed that over the short timescales relevant to this study, cold-adapted insects will generally be limited to short-distance compensatory altitudinal shifts in response to climate warming. Our rationale for restricting dispersal to within basin movements is based on the general dispersal limitation of our study taxa. This assumption is supported by high rates of genetic differentiation found between populations (Supplementary Table S1). For instance, it was shown that *D. discolor* migrated altitudinally but not longitudinally during warm phases in the interglacial⁹. Thus, we considered gene flow among river basins rare—particularly in the timeframe of ~70 years relevant for this study—and used watersheds as proxies for dispersal barriers for larvae and adults. This approach seems suitable for other montane or Arctic–alpine aquatic taxa with restricted over-land dispersal, particularly in hololimnic organisms¹⁸. For other species that show greater long-distance dispersal propensities, however, the implementation of dynamic models that consider more complex dispersal scenarios¹⁷ will be of crucial importance when inferring GCC effects on genetic diversity.

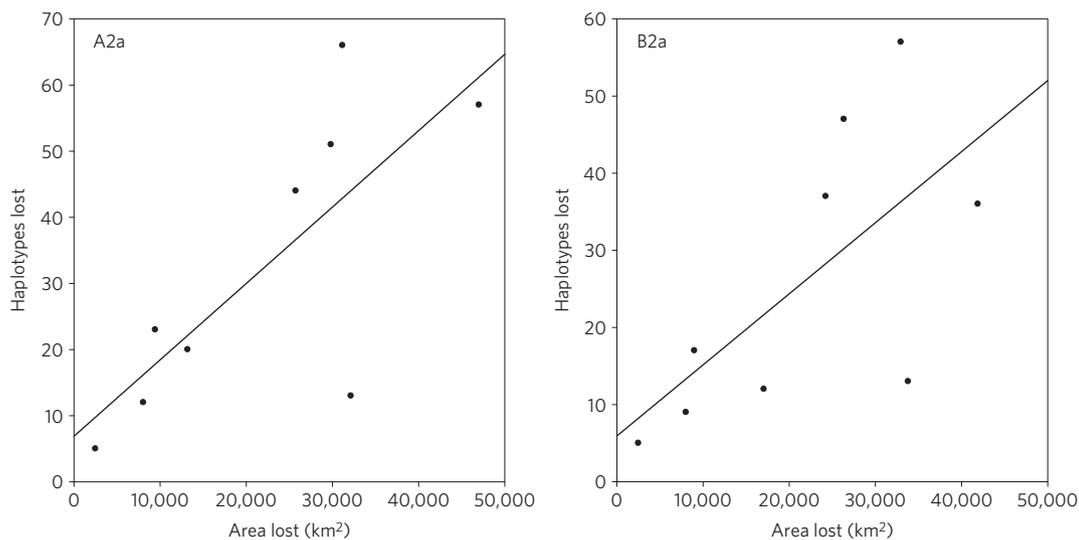


Figure 4 | Correlation between predicted losses of area and inferred losses of haplotypes. Left: A2a IPCC 2080 'business as usual' CO₂ emission scenario; $n = 9$, $R = 0.79$, $P = 0.012$; Right: B2a IPCC 2080 'reduced CO₂ emissions' scenario; $n = 9$, $R = 0.73$, $P = 0.025$. Pearson correlations were carried out on square-root-normalized absolute values of haplotype and area losses.

Genetic diversity has important ecological consequences for populations, communities and ecosystems¹⁹, because it provides the basis for phenotypic plasticity, local adaptation and adaptability to changing environmental conditions²⁰ including GCC²¹. For most species, including our study species, we have a limited understanding of physiological responses to varying environmental conditions²². There is some evidence for life-history plasticity in our study species: the Arctic–alpine stonefly *A. compacta* inhabits vastly different ecosystems in the Alps (springs) and the high-latitude regions (springs and lake shores)²³, and the mayfly *A. inopinatus* inhabits headwaters in Central Europe, larger rivers in the Tatra Mountains and small streams and lake shores in high-latitude regions¹². It is unknown whether these differences reflect local adaptation or true plasticity. It is also unclear how strongly climatic niches are conserved in aquatic insects. However, under an increasingly variable climate⁸, genetic diversity will become increasingly important for population and species survival. Moreover, the loss of cryptic evolutionary lineages reduces evolutionary potential and ends ongoing diversification processes that will impact future biodiversity.

Estimating losses in genetic diversity is one of the key challenges in biodiversity research when assessing the impact of GCC. Taking intraspecific genetic diversity and its geographic distribution into account provides improved insights into the effects of GCC on global and regional patterns of biodiversity. Our approach of applying SDM projections and assessments of spatial genetic structure is adaptable across taxa and makes use of well-developed tools and data sets in phylogeography¹⁵, DNA taxonomy²⁴ and DNA barcoding^{16,25}. Thus, the approach can be easily adapted to other study systems with reliable phylogeographic and faunistic data sets. Extensions of the approach to other systems and the incorporation of loci under climate-driven selection are the logical next steps that will provide more accurate predictions of GCC effects on genetic and cryptic diversity. Ultimately, only the fusion of SDM or dynamic modelling approaches, phylogeography and ecological genomics (by revealing climate-affected loci under selection), combined with deeper insights into species interactions, promises to unravel the mechanisms of how GCC affects species-level and intraspecific biodiversity. This knowledge may soon be of crucial importance to implement well-directed conservation strategies in a rapidly changing world.

Methods

Genetic data analysis and lineage delineation. We assessed neutral genetic variation using mitochondrial cytochrome *c* oxidase subunit I sequence data from 1,778 specimens of the nine species to project GCC-caused losses of genetic diversity and cryptic evolutionary lineages. Alignments for each species varied between 475 base pairs (bp) and 620 bp in length (Supplementary Table S1). UPGMA (unweighted pair group method with arithmetic mean) trees were constructed from haplotypes under the Jukes–Cantor model to visualize the mapped genetic diversity as haplotypes without phylogenetic inferences. We identified ESUs based on 2% sequence divergence (regularly applied in DNA barcoding of aquatic insects²⁵), and on a GMYC model of species delineation²⁶. The GMYC model assesses the highest likelihood of transition from intraspecific divergence to interspecific lineage formation using the predicted difference in branching rate on a tree under the two models of lineage evolution (neutral coalescent processes occurring within species and branching among species). The method recovers independently evolving lineages as putative species²⁶. Branch lengths were estimated with Bayesian relaxed lognormal clock analysis in BEAST v. 1.5 (ref. 27) using a coalescent prior according to ref. 26 (see Supplementary Information for details). Multiple GMYC thresholds were estimated separately for Trichoptera, Plecoptera and Ephemeroptera using the ‘SPLITS’ R package²⁸.

Species distribution modelling. We modelled the potential present range of the selected species on the basis of observation data and ten environmental variables at a resolution of 2.5 arc min (approximately 5 km²). Nine climatic variables were obtained from the public WorldClim database²⁹: mean diurnal range, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, annual precipitation, precipitation seasonality, precipitation of warmest quarter and precipitation of coldest quarter. In addition, we extrapolated a ‘slope’ layer from the 2.5 arc min ‘altitude’ layer of

WorldClim and used it for modelling as an important proxy for the occurrence of montane aquatic insects. SDMs were fitted using six algorithms as implemented in the BIOMOD (ref. 30) package version 1.1.5 in R. Potential future distributions of the species under 2080 climatic conditions were estimated using three climate models (CSIRO, HadCM3 and CCCMA) under two 2080 CO₂ emission scenarios⁸. We summarized the results of SDMs in consensus projections for each species and scenario with weighted averages based on area under the receiver operating characteristic curve (AUC) values of single-model outputs for each species and algorithm following ref. 31. See Supplementary Information for a detailed description of the modelling procedure.

Estimating the survival of haplotypes and ESUs. We evaluated haplotype distribution and potential haplotype losses based on haplotype/basin association. On the basis of collection localities, we assigned each haplotype to the basins where it was sampled. Haplotype fate was determined on the basis of the projected availability of climatically suitable areas in the associated basin. We assumed unlimited dispersal within a basin and no minimum area required for population persistence. Thus, we considered haplotype survival even if only a single grid cell with suitable climatic conditions was projected within a basin. This approach leads to a rather conservative estimate of haplotype losses. We assumed ESU survival if at least one haplotype per ESU was projected to survive under the above-outlined approach.

We used sixth Pfafstetter level drainage basins derived from vector streamlines and flow direction (Supplementary Fig. S5). Most of these basins (96%) extend below 400 m above sea level. The selected species rarely find suitable ecological conditions in water bodies at altitudes below 400 m above sea level. At these lower latitudes, O₂-saturation is likely to be the limiting factor for the study species. Many water bodies below this altitude are also strongly affected by human impact. This makes them unsuitable for the high habitat-quality demands of the selected species. Thus, larval dispersal between basins through low-altitude connections is very unlikely.

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Author contributions

M.B., C.N. and S.U.P. conceived the research. M.B., C.N. and S.U.P. conducted the research. S.D., C.H.M.E., P.H., S.L., J.S., K.T., M.B. and S.U.P. contributed new reagents/analytic tools. M.B. and S.D. analysed the data. M.B., C.N. and S.U.P. wrote the manuscript. C.N. and S.U.P. contributed equally to the study. All authors discussed the results and commented on the manuscript.

Additional information

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