Glacier retreat reorganises river habitats leaving refugia for Alpine invertebrate biodiversity poorly protected

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Abstract

Alpine river biodiversity around the world is under threat from glacier retreat driven by rapid warming, yet our ability to predict the future distributions of specialist cold-water species is currently limited. Here, we link future glacier projections, hydrological routing methods and species distribution models to quantify the changing influence of glaciers on population distributions of 15 alpine river invertebrate species across the entire European Alps, from 2020 to 2100. Glacial influence on rivers is projected to decrease steadily, with river networks expanding into higher elevations at a rate of 1% per decade. Species are projected to undergo upstream distribution shifts where glaciers persist but become functionally extinct where glaciers disappear completely. Several alpine catchments are predicted to offer climate refugia for cold-water specialists. However, present-day protected area networks provide relatively poor coverage of these future refugia, suggesting that alpine conservation strategies must change to accommodate the future effects of global warming.

Main text

Climate-driven modifications of ecosystems are expected to continue under twenty-first century global environmental change[1,2], further threatening biodiversity and ecosystem services. Understanding the spatial and temporal variability of future habitat conditions is therefore vital to identify locations where existing species' populations may persist or be at risk. Up to 80% of species are already undergoing range shifts[3], dispersing to higher latitudes or altitudes in an attempt to track the habitat conditions they require. Improved ecological monitoring and modelling tools are therefore needed to understand where and when species' distributions will shift in response to climate change, and to underpin the development of robust strategies for biodiversity conservation.

Alpine regions are warming at a faster rate than the global average[4], and high levels of endemism make alpine biodiversity particularly vulnerable to climate change as geographical barriers restrict opportunities for poleward range shifts[5]. Alpine species populations are therefore expected to shift to higher elevations under climate change. However, our understanding of how ecological communities will establish and persist at higher altitudes is limited, with particular uncertainties associated with rates of glacier change and landscape reorganisation as habitats expand into new proglacial (i.e., situated in front of a glacier) and post-glacial (i.e., where local glacier cover is lost) territory[6]. Many glaciers are losing mass at unprecedented rates and substantial further ice loss is expected throughout the twenty-first century[4] at the same time as species are shifting to higher elevations. Therefore, coupled models of future ice extent, glacial influence on downstream habitats, and species' ecological niches, are needed to infer where potential refugia for cold-adapted species may develop and persist.

Glacier mass loss alters the geomorphological and hydrological characteristics of downstream rivers, driving substantial modifications to freshwater biodiversity and ecosystem services[7]. Strong linkages are evident between alpine river biota and the upstream catchment area covered by glaciers, with cold-water specialists worldwide expected to be imperilled[8,9] (e.g., 11 to 38% of species loss predicted[10]). Conversely, temperature predictions for the Glacier National Park region of the US Rocky Mountains suggest that some cold-water specialists may persist even with complete deglaciation[11], whilst glacier loss will potentially benefit some species through the formation of new river systems[12,13] and amelioration of harsh habitat conditions[14,15]. However, understanding is derived largely from correlations of contemporary glacier cover with univariate diversity metrics (e.g., species richness, functional richness) using space-for-time substitution approaches, as few studies have sampled glacier-fed rivers repeatedly over time[16,17]. Advances in understanding of population-level responses to glacier retreat and associated river network reorganisation are needed to predict future alpine biodiversity and ensure that protected area policies provide maximum conservation potential.

Here, we present projections of future stream invertebrate distributions across all alpine zone (>2000 masl) sub-catchments of the European Alps containing glaciers under the 2020 baseline (total area = 34,218 km^2) at decadal intervals from 2020 to 2100 for 10 m × 10 m grid cells predicted to contain running water (referred to as 'river segments' throughout). All modelled species all have trans-Alps distributions. Projections were driven by a glacial influence model that determines the percentage of the upstream catchment under glacial ice cover for each river segment, with glacier extent from future glacier mass loss simulations informed by Global Glacier Evolution Model (GloGEM) projections[18] under an intermediate greenhouse gas emissions scenario (SSP2-4.5). Estimates of glacial influence are based on glacial ice cover in the upstream contributing area (i.e., the catchment area) of each river segment. Decreasing glacial influence is known to be linked tightly to amelioration of harsh habitat conditions, including increasing water temperatures, channel stability and organic matter availability[19].

Biodiversity projections were developed using multiple species distribution models (SDMs) integrating spatially-distributed invertebrate monitoring datasets with a set of key river environmental characteristics composed of glacial influence, hydrological and hydraulic drivers (contributing area, slope) and hydrochemical controls (pH). SDM predictions at decadal time slices were subsequently evaluated in relation to protected area coverage to assess the robustness of contemporary conservation efforts. The analysis focused on aquatic invertebrates because they are considered a model group for understanding the effects of environmental change owing to their high biodiversity and diverse environmental requirements[5,20]. Invertebrates are also key components of wider freshwater communities, performing vital functional roles in nutrient cycling and organic matter transfer from lower to higher trophic levels as prey items for fish, amphibians, birds and mammals.

Results

Changes in alpine river environments. Glacial influence on river ecosystems is projected to diminish progressively to the end of the twenty-first century in all river basins of the European Alps (Fig. 2) and across the majority of Alpine sub-catchments with glaciers under the 2020 baseline (Extended Data Fig. 1). The total surface area of these catchments containing running water is projected to increase from 65.9 km^2 in 2020 to 71.3 km^2 in 2100 (1% per decade) as glacier retreat creates new proglacial and post-glacial landscapes. These changes proceed at similar rates as estimated for salmon-accessible rivers in western North America under a comparable climate scenario (0-5.2% increase in river length per decade across coastal river basins)[12]. Furthermore, the proportion of the river network receiving flow from upstream areas with glacier cover declines steadily towards the end of the century. Projected declines in glacial influence are most pronounced in the Danube basin and least pronounced in the Rhône basin, reflecting the predominant control of elevation range and median elevation on future glacier evolution[21]. As glacier retreat progresses and the river network expands into territory previously under glacial ice (e.g., Fig. 1b-d), changes in contributing area, slope, and pH will occur (Extended Data Fig. 2), but these are negligible compared to declines in glacial influence. The direction of change for these parameters depends on the local geography of individual sub-catchments (Extended Data Fig. 3).

Alpine river invertebrate responses to glacier retreat. Central to our biodiversity modelling approach was the use of presence-background SDMs[22]. These were implemented within a rigorous statistical framework to account for spatial autocorrelation[23,24], collection bias[25] and heterogeneity in study design[26] inherent in the invertebrate monitoring datasets we assembled (total n = 656). Of 31 species represented in the datasets, there were sufficient data to model the distributions of 19 species (61%). Of these, SDM performance was considered acceptable for 15 species (48%; Supplementary Fig. 10-47) spanning the full range of glacial influence optima from 0% (the flatworm *Crenobia alpina*) to approaching 100% (e.g., the non-biting midge *Diamesa steinboecki*) (Extended Data Fig. 4). These modelled optima are strongly supported by local studies, including some from other mountain ranges[14,27].

Most species are predicted to suffer decreases in suitable habitat area across the European Alps by 2100, with consistent losses across all study basins for the non-biting midges *Diamesa latitarsis* grp., *D. steinboecki,* and *Diamesa bertrami*, the stonefly *Rhabdiopteryx alpina*, and the mayfly *Rhithrogena nivata* (Fig. 3; Extended Data Fig. 5). Conversely, populations of several species with low glacial influence optima will respond positively (e.g., *C. alpina, Rhithrogena loyolaea*). These model estimates support previous suggestions that there will be "winners" and "losers" in response to glacier retreat[9,28]. Most notably, at the sub-catchment level, suitable habitat area for *all* modelled species is predicted to increase in a subset of locations at the end of the century, especially in the northeastern part of the Rhône basin. As a consequence, some cold-adapted species could be expected to find refuge from widespread deglaciation in locations where glacier remnants persist[11] assuming they are able to disperse to these locations and establish viable populations. Inferences from population genetics suggest contemporary dispersal is possible across significant areas of mountainous terrain for some winged insects such as stoneflies (e.g. the endangered N. American glacial stonefly *Lednia tumana*[29]) but less likely for weak-flying species[30]. Other potential refuge areas could include rivers emanating from rock glaciers and icy seeps[31] but we acknowledge that datasets on these landforms are presently insufficient to incorporate into GLOGEM and our models. Species that find refuge in sub-catchments where small glacial ice masses are projected to persist to 2100 and beyond are still likely to be considered "losers" as a consequence of their vastly reduced and increasingly fragmented distributions. In contrast, species characteristic of rivers with low or zero glacial influence will experience overall increases in habitat area.

The binary classification of "winners" versus "losers" is complicated by non-linear responses of habitat suitability to glacial influence, with many species showing optima between 20 and 40% glacier cover (Fig. 3). These responses also play out differently over time in different river basins. For example, the stonefly *Dictyogenus alpinus* and the caddisfly *Drusus discolor* show positive responses over time in the Rhône basin compared to consistent declines elsewhere (Extended Data Fig. 5), whilst several species are predicted to become functionally extinct in the Danube basin (Extended Data Fig. 6). This diversity of responses illustrates clear regional and species-specific variation consistent with the substantial spatial heterogeneity underlying global insect population trends[32]. Importantly, this heterogeneity could provide new insights into potential refuge areas for alpine freshwater biodiversity, underpinning decisions on the modification of protected area networks.

Conservation of alpine biodiversity. Layering SDMs for individual populations enabled the number of species predicted to maintain or increase their suitable habitat area between 2020 and 2100 to be calculated for each sub-catchment. Existing protected areas overlayed on these data provide the basis for assessing the extent to which future refugia for alpine aquatic biodiversity are covered by present-day protected area networks. Sub-catchments predicted to serve as refugia for a greater number of species by 2100 are poorly represented in existing protected area networks relative to the wider landscape (Fig. 4). Protected areas cover only 12% of three sub-catchments predicted to serve as refugia for all 15 species, compared to a 25% coverage of protected areas across the whole study area (Fig. 4c). Sub-catchments identified as offering refugia to greater numbers of species retain higher levels of glacial influence in 2100 and have higher pH and larger catchment areas with steeper slopes (Fig. 4h). Though many future refuge areas that we identify technically represent *ex-situ* refugia[33] due to the expansion of river networks into new proglacial and post-glacial landscapes (e.g., Fig. 1b-d), conditions are predicted to change gradually through the twenty-first century, indicating the potential for alpine invertebrates to disperse upstream to colonise new habitat. These results contrast with a recent analysis of future climate refugia for four alpine bird species in the European Alps which found that *in-situ* refugia were relatively well represented by the current protected area system[34].

We predict elevational habitat shifts of up to 17.9 (±1.2 SD) m/decade (Fig. 5), findings which are supported by empirical evidence from studies in Glacier National Park, N. America, for a single species of stonefly[8]. These rates are generally lower than for alpine plants and birds, reported as up to 29.4 and 102 m per decade respectively[35,36]. However, our models suggest that as glaciers retreat, river habitat availability changes dynamically within and between sub-catchments and river basins (Fig. 3; Extended Data Fig. 5; Supplementary Fig. 48-62) rather than manifesting as simple linear decreases or increases. Two high glacial influence specialists (*R. alpina, D. steinboecki*) are predicted to undergo habitat suitability-weighted shifts to lower elevations in the Danube basin, but this is an artefact of glacial ice largely disappearing in the Eastern Alps by the end of the century (Fig. 2). Further analysis shows that these and several other species (the non-biting midges *Pseudokiefferiella parva*, *Eukiefferiella fuldensis*, *Orthocladius frigidus*, and the stonefly *D. alpinus*) are unlikely to persist in the Danube basin, with habitat suitability for these species remaining low (Extended Data Fig. 6). Thus, predicted downslope habitat shifts will not be realised as suitable habitat for these species largely disappears along with glacial ice.

The complex and shifting habitat mosaic indicated by our findings poses challenges for population viability because natural dispersal processes are often severely restricted for invertebrates in mountainous systems. This is due to high and steep relief between adjacent catchments and frequent inclement weather restricting overland movement successes, coupled with generally poor flying ability among most insect groups[5]. Conservationists may therefore need to consider augmented dispersal to improve the likelihood of successful relocation of cold-water specialists to potential refuge areas. Effective protection of future refugia for alpine species will require shared governance among nations with alpine territories to enable co-ordinated planning of conservation actions and monitoring of both source and refuge populations to determine conservation success[3]. Crucial to the conservation of aquatic species populations in refuge areas will be preventing increases in river catchment and habitat stressors that modify ecosystems in addition to climate-driven glacier retreat impacts, such as land-use change (e.g., pastoralism, ski-run development) and water withdrawals (e.g., hydropower expansion).

Discussion

By linking glacial, hydrological and species distribution models, our study locates potential refuge areas for aquatic alpine invertebrate species responding to glacier retreat at the scale of an entire mountain range for the first time. These advances in predictive capability can now be used to develop large-scale models in other mountain ranges where predominantly local-scale predictions are available for only a small number of species (e.g., Pyrenees[37]; North American Rockies[11]). A major benefit that our coupled modelling approach provides is identifying future refuge locations relative to current protected zones such as national parks or conservation areas. As many of the most effective areas for cold-water specialists fall outside of existing protected area networks, new concerns arise for biodiversity conservation because locations where glaciers persist into the late twenty-first century can be expected to be prioritised for human activities including hydropower dam construction and ski resort development[38]. As a consequence, our study provides one of the first detailed insights that substantial work will be needed to plan and manage emerging trade-offs balancing ecosystem services and biodiversity protection in rivers fed by rapidly retreating glaciers[7].

Our model performance results show that rigorous evaluation is necessary to account for spatial bias in biodiversity records[24,25], as many model variants performed no better than expected at random given the survey locations represented in the datasets (Supplementary Fig. 10-47). Furthermore, individual algorithms, including generalized linear models, generalized additive models and Maxent, showed better predictive performance than ensemble models for all but one species (*R. loyolaea*; Extended Data Fig. 7). SDMs are increasingly being used to model biodiversity responses to climate change but these findings add to growing evidence that SDM evaluations cannot rely on simplistic performance metrics and uncritical use of ensemble models[39,40]. By evaluating individual algorithms and incorporating null modelling to account for collection bias, our approach represents a robust framework for evaluating presence-background SDMs which is fit for the purposes of informing effective conservation management.

Further predictive improvements to our models could be made by incorporating density-dependent biotic interactions and dispersal processes that influence species persistence[41]. For example, whilst our models can reproduce species occupancy at sites with low glacial influence where predation and competition act to reduce abundance and exclude inferior competitors[42], these density-dependent effects are not modelled explicitly. There is a pressing need to quantify these effects across a greater number of alpine rivers and mountainous regions[20,37,43,44] to better understand the biotic mechanisms driving aquatic biodiversity responses to glacier retreat[28]. Additionally, despite our assembled datasets representing the best available alpine river biodiversity records, 12 of 31 species represented in the records were data deficient, and we were able to find acceptable models for only 15 of the remaining 19 species. More intensive monitoring of alpine river biodiversity is needed urgently so that robust species distribution modelling can be undertaken for a wide range of aquatic species, and used to support conservation decisions.

Overall, this study shows how changes in river environments in response to glacier retreat will vary considerably within diverse geographic zones such as the European Alps, and between alpine invertebrate species. This result emphasises the need to consider the geographical and taxonomic nuances of biodiversity change[32,45], as now exemplified for alpine invertebrates. From the development of integrated glaciology-hydrology-ecology modelling capabilities, the potential now exists for comparative predictions of aquatic plant, animal and microbial communities that are under increasing stress as glaciers retreat[12,15,46,47] in mountain systems worldwide. These prospects must be acted upon urgently to inform adaptation of freshwater conservation in the face of future climate-driven glacier change.

Methods

Contemporary topography and glacier ice. We mosaicked contemporary digital elevation models (DEMs) obtained from national airborne LiDAR campaigns that are typically at <10 m resolution, namely from SwissALTI (10 m), Digitales Geländemodell (DGM) Österreich (10 m), provincial surveys in N. Italy; Alto Adige/S. Tyrol (2.5 m), Trento (1 m), Valle d'Aosta (2 m) and Piemonte (5 m) and IGN France (25 m) and resampled them to a common 10 m resolution. We used glacier outlines from the Randolph Glacier Inventory version 6 referring to the year 2003[48]. More details of these datasets can be found in Supplementary Note 1.

Future glacier coverage. We made future glacier projections using the Global Glacier Evolution Model (GloGEM[18]). The model is discretized into 10 m elevation bands to facilitate large-scale application, but results for area and thickness changes in individual bands are extrapolated to a 25 x 25 m grid. GloGEM is forced with gridded monthly data on 2 m air temperature and total precipitation from the ERA5 re-analysis[49] for the past, and until 2100, with results of 13 Global Circulation Models (GCMs) from CMIP6[50]. GCMs were based on five different Shared Socio-economic Pathways (SSPs)[51] describing future greenhouse gas emissions. Our analysis used results of the intermediate scenario SSP2-4.5 which most closely corresponds to the current pledges of nations around the globe to limit atmospheric warming[52]. Whilst a full analysis of uncertainty due to glacier models, general circulation models, RCPs, and natural variability is beyond the scope of our study, for the European Alps, the overall uncertainty in glacier area change relative to the year 2003 accounts for +/-9% in 2050 and +/-7% in 2100[53].

Hydrological routing and glacial influence. We delineated flow paths using TauDEM[54] hydrological tools in ArcGIS 10.6.2 to fill minor topographical lows, obtaining a flow direction grid and a contributing area (CA) grid (i.e., the upstream area draining to each cell). We specifically used a D-Infinity algorithm that accommodates braided reaches as most appropriate for many alpine mountain rivers. The wetted channel network was determined as all segments with CA>5000 m^2, which our previous work has identified as representing European Alps headwaters well[55,56]. The spatially-distributed (i.e., of each and every grid cell) glacial influence (GI) was determined by differencing the CA result computed with and without glaciers included and reporting the result as a percentage for each river grid cell, which we refer to as a river segment. The complete workflow is detailed in Supplementary Note 1 together with an uncertainty analysis of grid resolution.

For projections of future hydrological routing and GI, we constructed future DEMs. First, glacier bed topography was obtained by subtracting contemporary ice thickness[57] from a surface DEM, both at 25 m resolution. Second, the glacier bed topography was mosaicked with the contemporary DEM mosaic to create a landscape-wide "ice-free" topography. Third, ice thickness for each future decade from GloGEM was then added to that landscape-wide bed topography to obtain a future (landscape and ice surface) DEM. Hydrological tools were run on each future DEM to project future river network distribution and properties. To enhance spatial and temporal predictions of biodiversity change, these analyses were undertaken at far greater spatial resolution than previous modelling studies for Pacific Salmon[12], both for proglacial rivers (10 m vs 30 m) and ice surfaces (25 m vs 90 m), and our approach further considers the importance of braided channel morphology as well as single-thread channels, which increases the likely accuracy of suitable habitat estimates.

Environmental data processing. To complement the GI and CA data derived from the hydrological routing analyses, we obtained additional spatial datasets representing hydraulic and hydrochemical influences on river environments. Because alpine river networks are expected to undergo considerable reorganisation as glacier retreat exposes new proglacial and post-glacial areas, we were limited to datasets representing the underlying landscape. For example, we could not use datasets tied to the existing river network, such as HydroATLAS[58]. To represent hillslope runoff and channel hydraulics, we obtained the dimensionless slope derived from the 25 m resolution Digital Elevation Model over Europe (EU-DEM[59]). To represent catchment influences on river hydrochemical conditions, we used the 250 m resolution soil water pH (0-5 cm depth) data from SoilGrids[60] as a proxy for the pH of streams draining these soils. Slope and pH datasets were disaggregated to 10 m resolution and stacked with glacial influence and CA data. All environmental layers were masked to ≥2000 masl elevation. For all analyses at the river basin level, we combined the Po and Adige river basins to ensure approximately equal river basin areas across the hydrographic regions considered. We considered the combination of the Po and Adige basins appropriate due to the close proximity of the basin outlets and their location to the south of the European Alps.

Biological data processing. We obtained alpine invertebrate community monitoring data from previous studies conducted by six separate research groups (total n = 656). Contemporary GI and CA were determined for each sampled location as described above. We retained only species level data, corrected taxonomy to currently accepted names using the Integrated Taxonomic Information System[61] and aggregated synonymous species. We did not filter the available samples by elevation and they were not exclusively within the alpine zone (>2000 masl). The minimum elevation of the samples was 1025 masl, and the 25th percentile of elevation was 2015 masl.

Several sources of heterogeneity affected the biological data. The taxonomic resolution at which organisms were enumerated in the assembled biological datasets varied from species to family and higher ranks. Three different sampling methods were used (Surber, Hess, kick-net), and sampling effort presumably varied widely in ways not reported in the data (e.g., observer variation). We therefore reduced the biological data to presence-only form, i.e., only presence records for each species were retained, without including absences. Presence-only records are the most widely available type of biodiversity data worldwide, and a large body of literature has developed focusing on the use of such records to model species distributions along environmental gradients[62].

Species distribution modelling. Previous research has shown that highly robust species distribution models (SDMs) can be developed using presence-only records if steps are taken to ensure potential biases are accounted for[24,25]. The resulting SDMs are commonly referred to as 'presence-background' models due to their inclusion of observed presence records and background samples, otherwise known as 'pseudo-absences', generated through random sampling of the environmental background. Among other standards common to all SDMs[63], developing robust presence-background SDMs relies on careful consideration of the number of background samples to draw, as well as model validation schemes that account for spatial structures in the data, including spatial autocorrelation[24] and collection bias[25]. Collection bias refers to the tendency for biodiversity data to be collected in certain locations within the landscape, such as those close to field stations, roads, and nature reserves. Presence-background SDMs affected by such biases are more likely to deviate significantly from the null model underlying background sample generation[25]. This can lead to inflation of model evaluation metrics, such as the area under the curve (AUC) of the receiver operating characteristic, and the violation of commonly applied assumptions about thresholds for considering SDM performance to be acceptable (e.g., AUC>0.7).

Through initial tests with three species representing the whole range of prevalence observed in the biological data, we selected the number of background points as 1000 from each major river basin as this provided a good balance between variance and CPU time (Supplementary Fig. 7-9). This background sample size was also close to a statistically representative sample of the background environment at α=0.05 and a margin of error of 5%, suggesting it was large enough to represent the environment within the regions of interest[62]. The background sample was drawn from raster data representing GI, CA, pH, and slope in 2020.

Prior to fitting SDMs for each species, presence and background points were organised into spatially separated folds with a spatial buffering strategy using the BlockCV package in R[24]. This involved first estimating the spatial autocorrelation range in candidate covariates using the *spatialAutoRange* function (median range = 10.2 km), and then generating spatially separated training and test folds by considering buffers of the resulting distance (10.2 km) around each observed presence point using the *buffering* function. The approach is a type of leave-one-out cross-validation in which each fold is generated by excluding both presences and background points within the buffer. Species were excluded from further modelling steps if the minimum number of presences in the folds was <10. This was an informed choice as previous research has shown that acceptable SDMs can be developed with as few as 10-14 presences[64,65]. Ultimately, the number of presences for the 19 species we modelled ranged from 28 to 157 (Supplementary Fig. 5), exceeding the lower threshold of 10-14 presences.

For each species, SDMs were fitted to each fold using the BIOMOD2 package in R[66]. Of the algorithms available in BIOMOD2, we selected eight algorithms: Artificial Neural Network; Flexible Discriminant Analysis; Generalized Linear Model; Generalized Boosting Model; Generalized Additive Model; Maxent (implemented as 'MAXENT.Phillips.2' in BIOMOD2); Random Forests; and Surface Range Envelop. Other algorithms implemented in BIOMOD2 produced errors under null modelling (see below) due to the generation of a small number of null data points with identical or nearidentical environments. We used the default settings in BIOMOD2 (see Supplementary Note 2 for more details). As well as retaining models from each individual algorithm, we calculated an ensemble average model and an AUC-weighted ensemble for each species. Models were primarily evaluated using the AUC and mean absolute error (MAE) on the out-of-sample presences. We also examined distributions of training bias and MAE on the in-sample presences (training MAE). We produced models using all four environmental variables as well as with all combinations of three variables, selecting the best performing model for each species (Extended Data Fig. 4, 7).

To ensure that we interpreted the performance of our models in light of potentially serious collection bias, we adopted a null model approach[25]. For each species, this involved repeated random resampling from all 656 biological data points. The sample size was fixed at the observed number of presences. For each random sample, we generated spatially separated training and test folds using the same approach as detailed above. We then randomly selected a single fold, fitted the null SDM using all eight BIOMOD2 algorithms plus the two ensemble models, and calculated the AUC. We repeated this procedure 1000 times and used a bootstrap hypothesis test to calculate the probability that the mean observed AUC was drawn from the same distribution as the null AUC.

Protected area analysis. We assessed the extent to which existing protected area networks in the European Alps coincided with areas predicted to serve as future refugia for alpine species. Shapefiles obtained from the European Environment Agency corresponding to the Natura 2000 network, the Emerald Network and nationally designated areas (Common Database on Designated Areas; CDDA) were aggregated into a single shapefile and cropped to represent only areas above the 2000 masl alpine limit. The aggregated and cropped protected areas shapefile was then overlaid with spatial data corresponding to the number of species for which mean suitability-weighted total habitat area was predicted to be maintained or increase between 2020 and 2100 in each sub-catchment; we considered these sub-catchments as potential refugia for the corresponding number of species. We then calculated the percentage aerial cover of each sub-catchment (areas >2000 masl) under at least one protected area designation. We reported this percentage at each level of the number of species predicted to find refuge in sub-catchments, which ranged from 0 to all 15 species. We also fitted a generalized linear model using a Poisson error distribution (log link) to explain the number of species finding refuge as a function of GI, CA, pH and slope (sub-catchment means). Independent variables were centred by their means and standardised to unit variance prior to model fitting.

Habitat elevation changes. Using the best performing model for each species (Extended Data Fig. 4, 7), we calculated the habitat elevation change from each model fold by first predicting decadal habitat suitability within every river segment. Then, for each decade and river basin, we extracted the elevation of every river segment from EU-DEM[59] and calculated the habitat suitability-weighted mean elevation. Finally, we fitted a linear model predicting the habitat suitability-weighted mean elevation as a function of decade to obtain an estimate of the mean decadal change. We repeated this procedure for each model fold to obtain a distribution of values, as summarised in Fig. 5.

Data Availability

Biological data are available in Supplementary Table 3. GloGEM data are available as supplementary material to the original paper[18].

Code Availability

Code is available in the supplementary material.

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Author Contributions Statement

M.A.W., J.L.C. and L.E.B. led the study and the writing of the manuscript. J.L.C. and M.H. performed the glacial and hydrological modelling. M.A.W. performed the species distribution modelling and all statistical tests. M.A.W., J.L.C., L.E.B. and W.J. designed the methodology. E.C., C.I., S.C-F, S.F., L.F., V.L., C.R. and L.E.B. collected field data and aquired funding for their collection. All authors contributed to review and editing.

Competing Interests Statement

The authors declare no competing interests.

Figure Legends

Fig. 1 | Data overview and example projected river network changes. a, Overview of study area and biological samples. **b**-**d**, Example of projected changes in river network structure and glacial influence on river habitat in Valais, Switzerland, 2020 (**b**), 2060 (**c**) and 2100 (**d**).

Fig. 2 |Glacial influence on alpine river systems. Projected changes in glacial influence for major river basins draining the European Alps. Left column shows total length of the stream network influenced and not influenced by glaciers. Right column shows distributions of glacial influence on stream networks in each basin and decade. In right column, white ticks show the distribution of glacial influence for biological samples at the time of collection.

Fig. 3 | Alpine river invertebrate population responses to glacier retreat. Maps for each species show the predicted change in suitable habitat area within river sub-catchments of the European Alps between 2020 and 2100. Sub-catchments with no glacial influence under the baseline condition are shown in grey. Inserts show the mean predicted habitat suitability (P_{occ}; lines) and 95% confidence intervals from cross-validation (shaded areas) as a function of glacial influence (GI; lower right of each map). Species plotted in ascending order of glacial influence optima. Silhouette images of adult life stages included for illustrative purposes only (note: analyses focused on larval stages for insects). These data are available for every decade (2020-2100) in Supplementary Fig. 48-62.

Fig. 4 | Locations of predicted refugia for alpine river invertebrates in 2100. a, Number of species predicted to maintain or increase their suitable habitat area between 2020 and 2100. **b**, Areas under conservation designation in the European Alps, including nationally protected areas from the Common Database on Designated Areas (CDDA). **c**, Percentage of catchment area under conservation designation as a function of the data shown in (a); black circles are individual sub-catchments; grey bars show means across all sub-catchments predicted to serve as refugia for a given number of species; horizontal line shows regional mean. **d-f**, Projected sub-catchment means of environmental variables in 2100: glacial influence (GI; **d**); contributing area (CA; **e**); pH (**f**); and slope (**g**). Sub-catchments with no glacial influence under the baseline condition (2020) are shown in grey. **h**, Coefficient estimates from a Poisson regression on the data shown in (a), with 95% confidence intervals (n=89 sub-catchments). *Slope is a dimensionless variable.

Fig. 5 | Predicted habitat elevation changes. Coloured bars show mean decadal change in suitability-weighted habitat elevation. Error bars show 95% confidence intervals from cross-validation. Species shown in ascending order of glacial influence optima from top left to bottom right. Sample sizes (n) denote the number of model folds.

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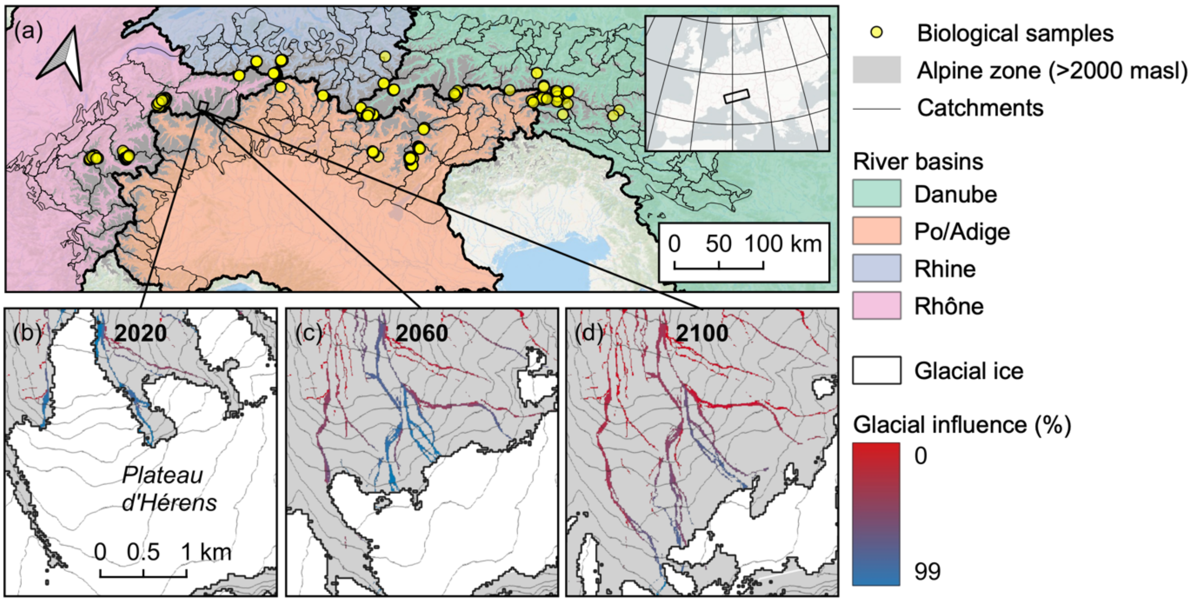

(a)
0 50 100 km
(b)
2020
Plateau d'Hérens
0 0.5 1 km
(c)
2060
(d)
2100
Biological samples
Alpine zone (>2000 masl)
Catchments
River basins
Danube
Po/Adige
Rhine
Rhône
Glacial ice
Glacial influence (%)
0
99

Figure 1

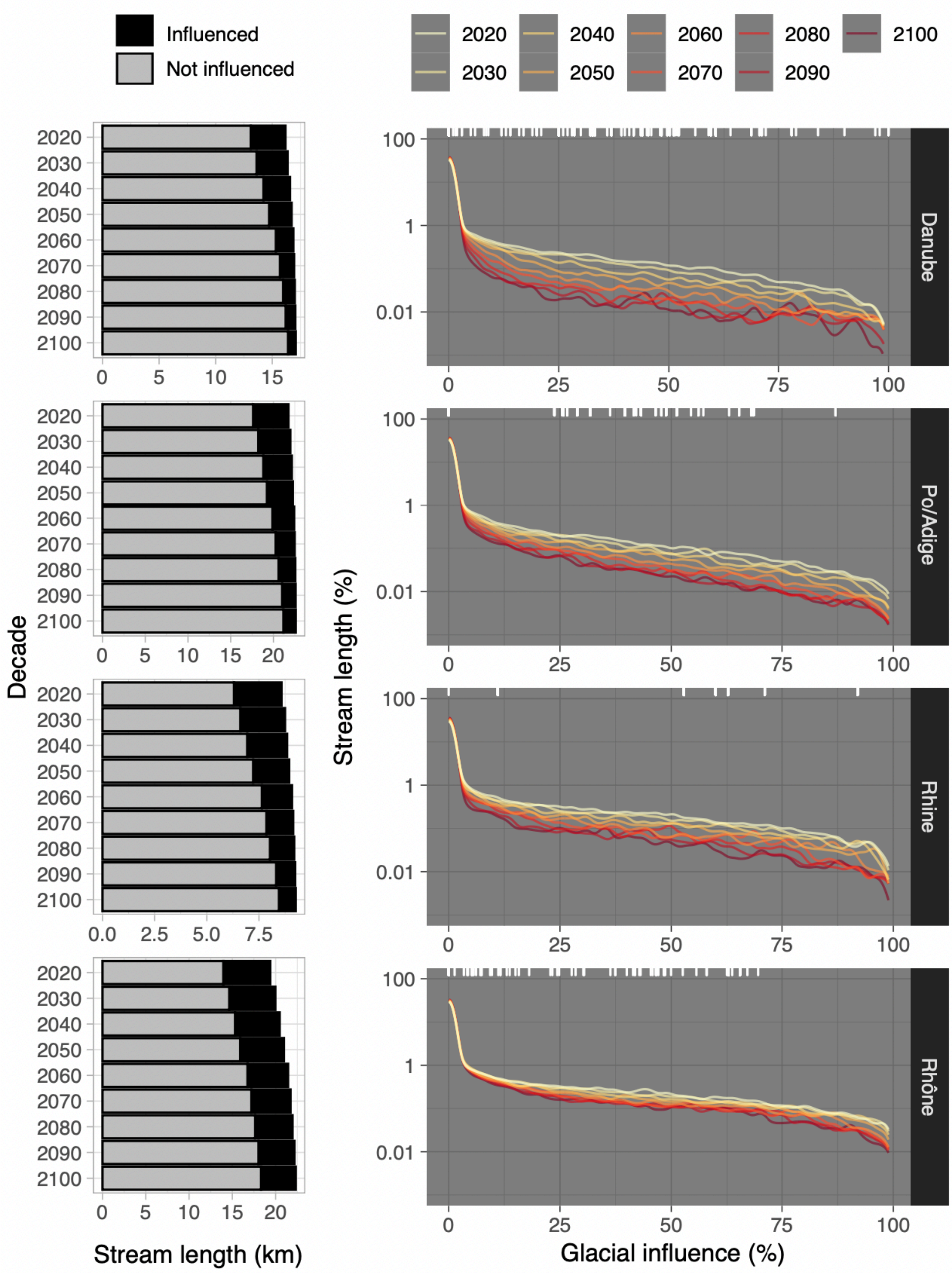

Influenced
Not influenced
2020
2030
2040
2050
2060
2070
2080
2090
2100
Decade
Stream length (km)
Stream length (%)
Glacial influence (%)
Danube
Po/Adige
Rhine
Rhône
100
1
0.01
0
25
50
75
100
0
5
10
15
20
0.0
2.5
5.0
7.5

Figure 2

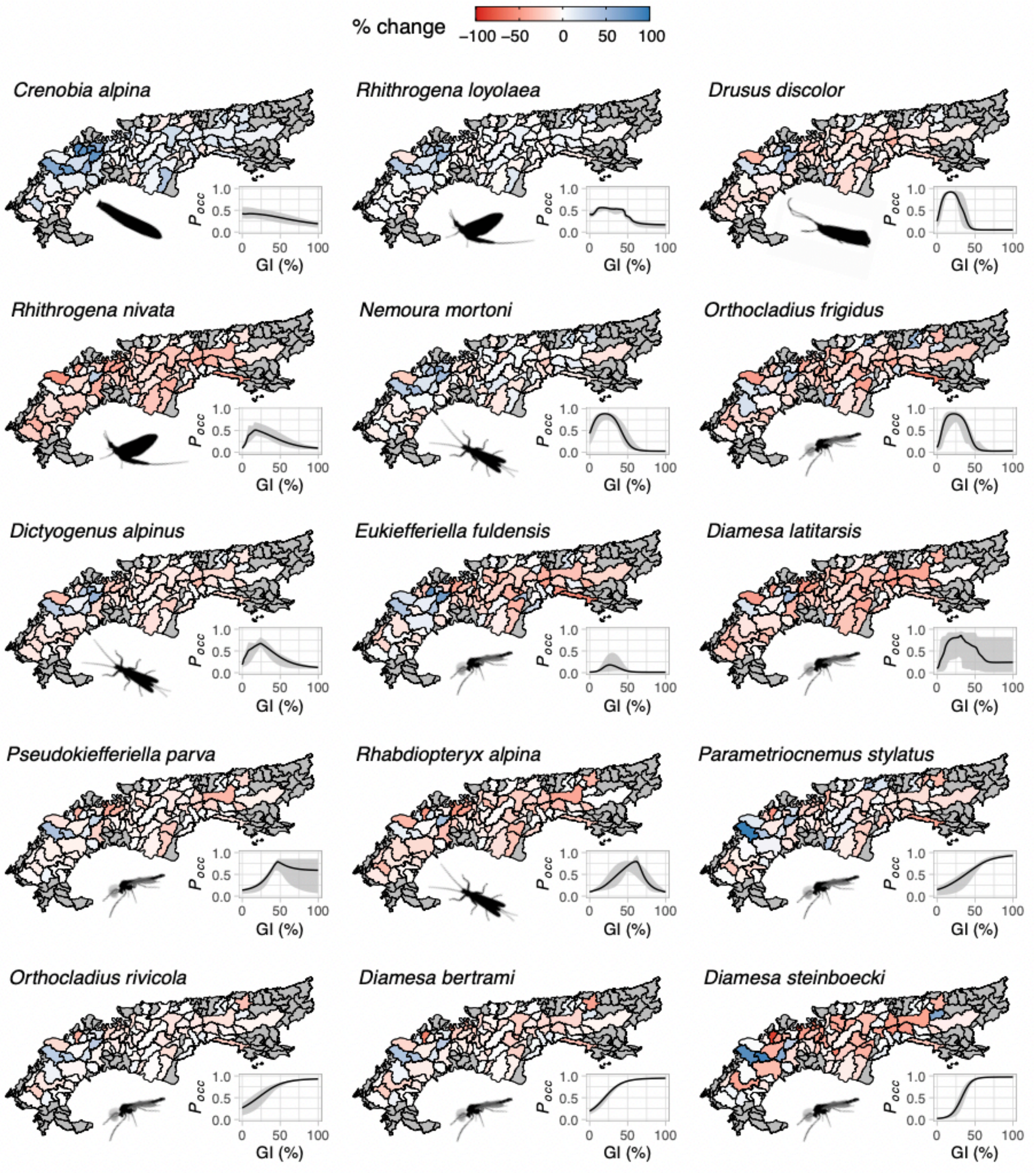

% change
−100
−50
0
50
100
Crenobia alpina
Rhithrogena loyolaea
Drusus discolor
Rhithrogena nivata
Nemoura mortoni
Orthocladius frigidus
Dictyogenus alpinus
Eukiefferiella fuldensis
Diamesa latitarsis
Pseudokiefferiella parva
Rhabdiopteryx alpina
Parametriocnemus stylatus
Orthocladius rivicola
Diamesa bertrami
Diamesa steinboecki
P_{occ}
1.0
0.5
0.0
0
50
100
GI (%)

Figure 3

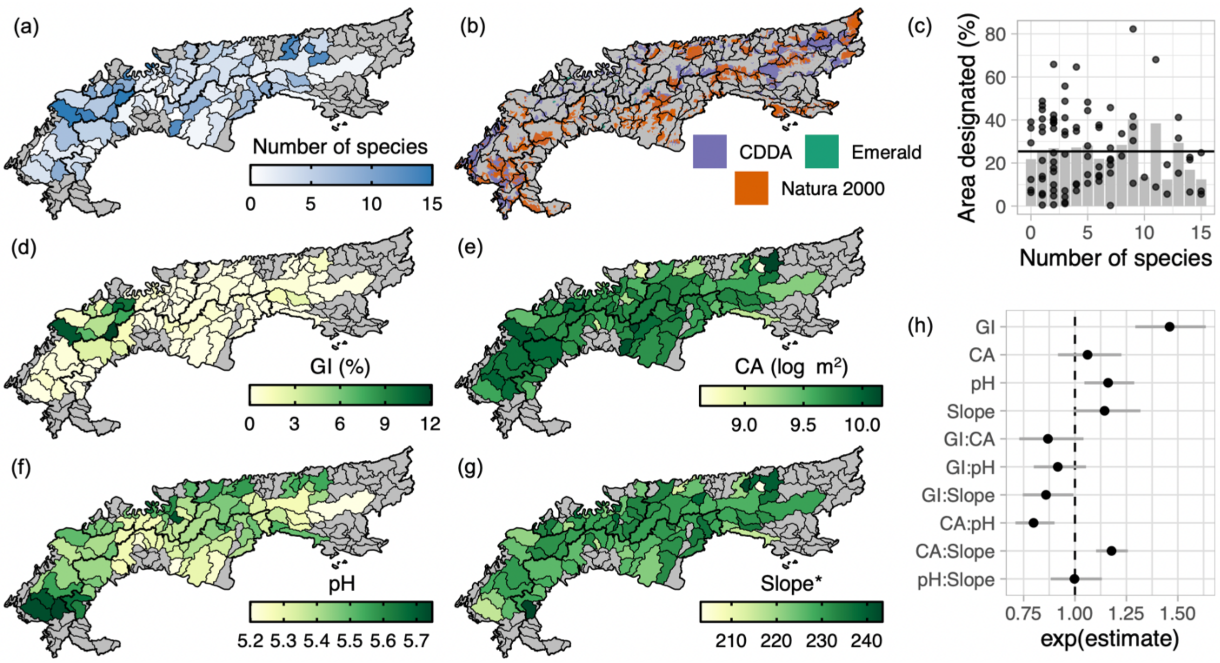

(a)
Number of species
0
5
10
15
(b)
CDDA
Emerald
Natura 2000
(c)
Area designated (%)
80
60
40
20
0
0
5
10
15
Number of species
(d)
GI (%)
0
3
6
9
12
(e)
CA (log m^2)
9.0
9.5
10.0
(f)
pH
5.2
5.3
5.4
5.5
5.6
5.7
(g)
Slope*
210
220
230
240
(h)
GI
CA
pH
Slope
GI:CA
GI:pH
GI:Slope
CA:pH
CA:Slope
pH:Slope
0.75
1.00
1.25
1.50
exp(estimate)

Figure 4

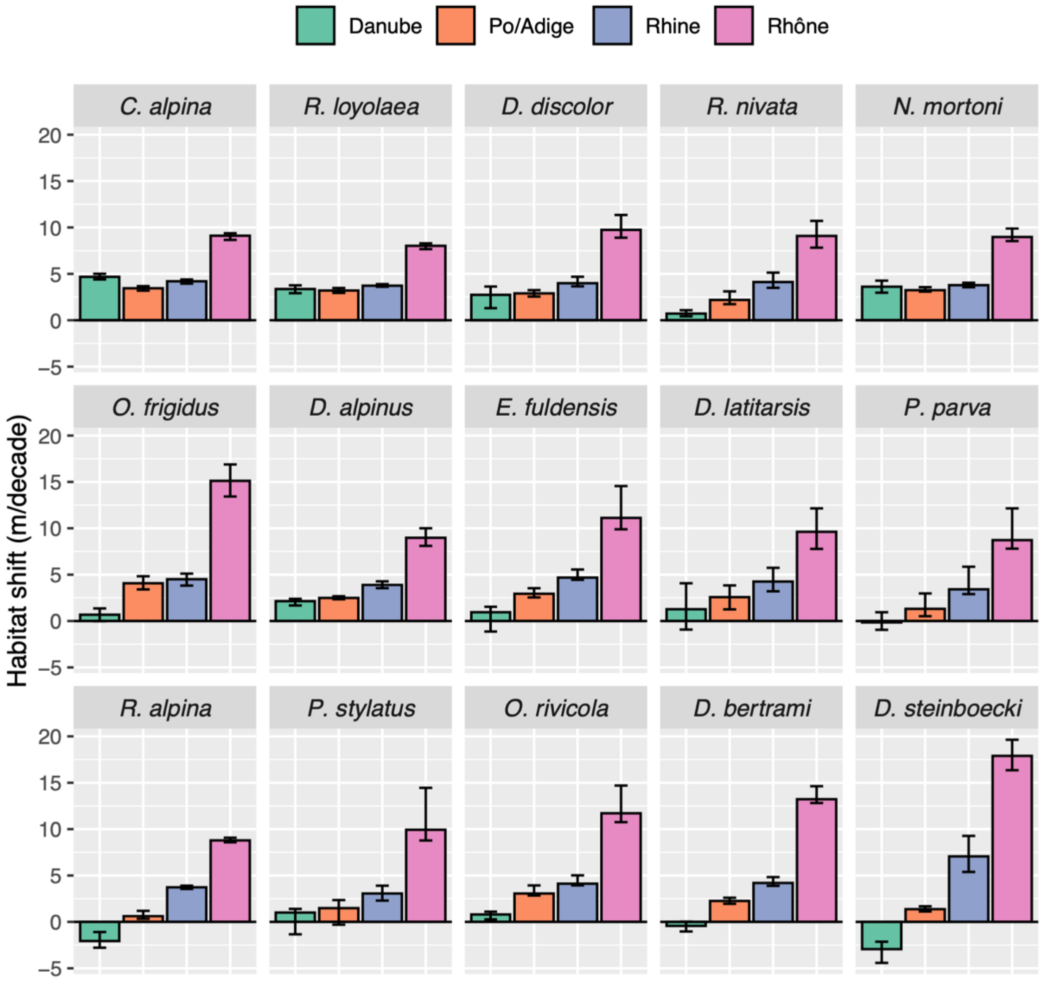
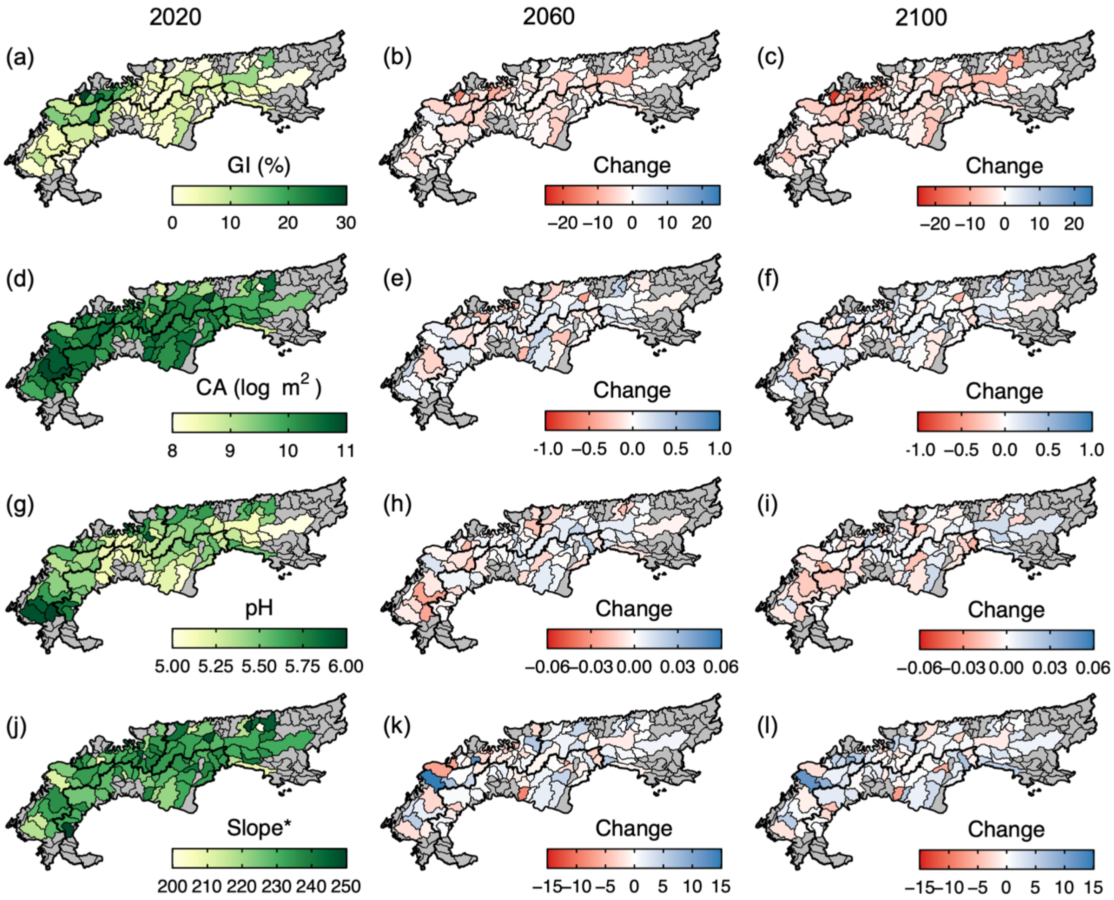
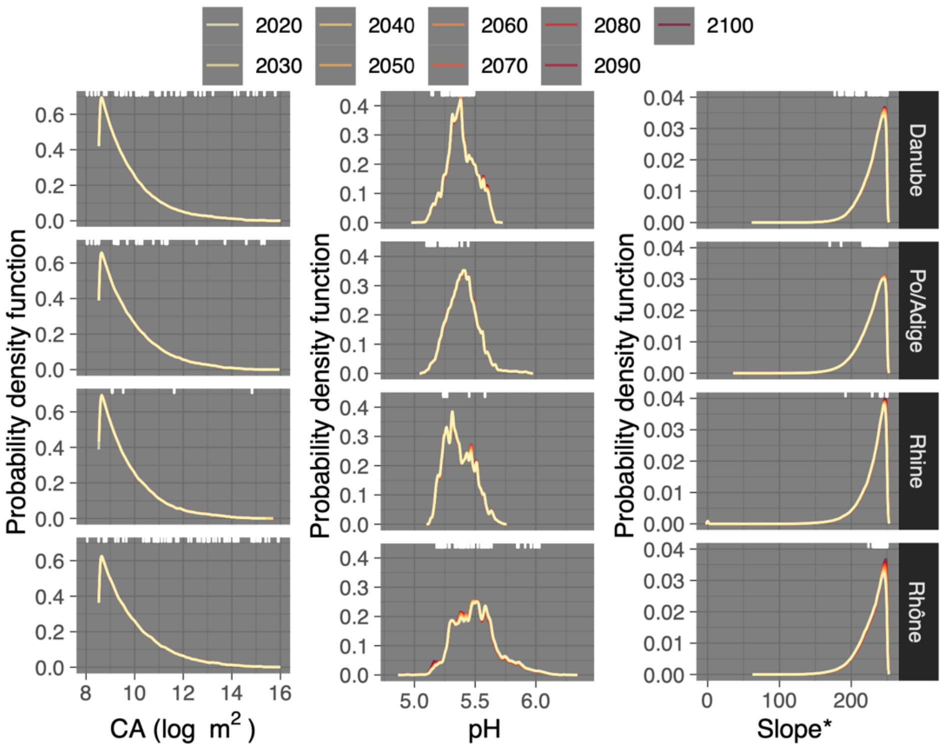

Danube
Po/Adige
Rhine
Rhône
Habitat shift (m/decade)
C. alpina
R. loyolaea
D. discolor
R. nivata
N. mortoni
O. frigidus
D. alpinus
E. fuldensis
D. latitarsis
P. parva
R. alpina
P. stylatus
O. rivicola
D. bertrami
D. steinboecki
20
15
10
5
0
−5

Figure 5



Extended Data Figure 1



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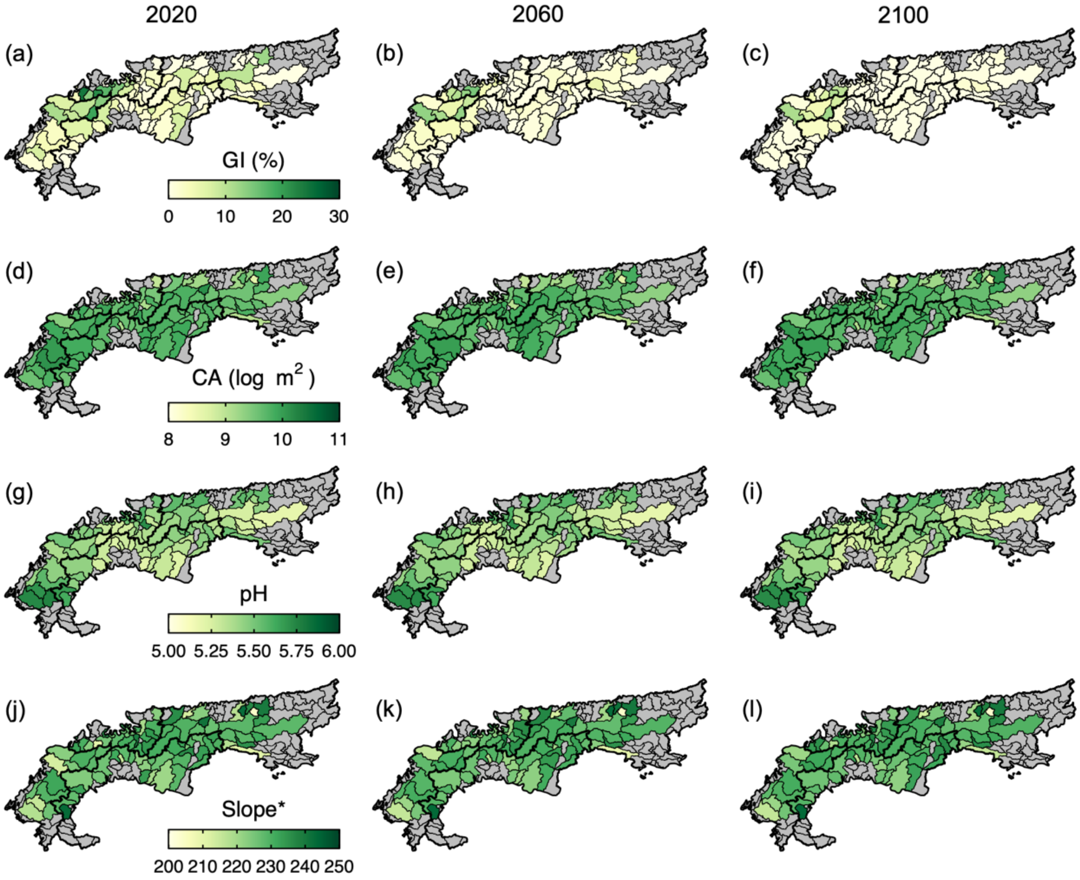

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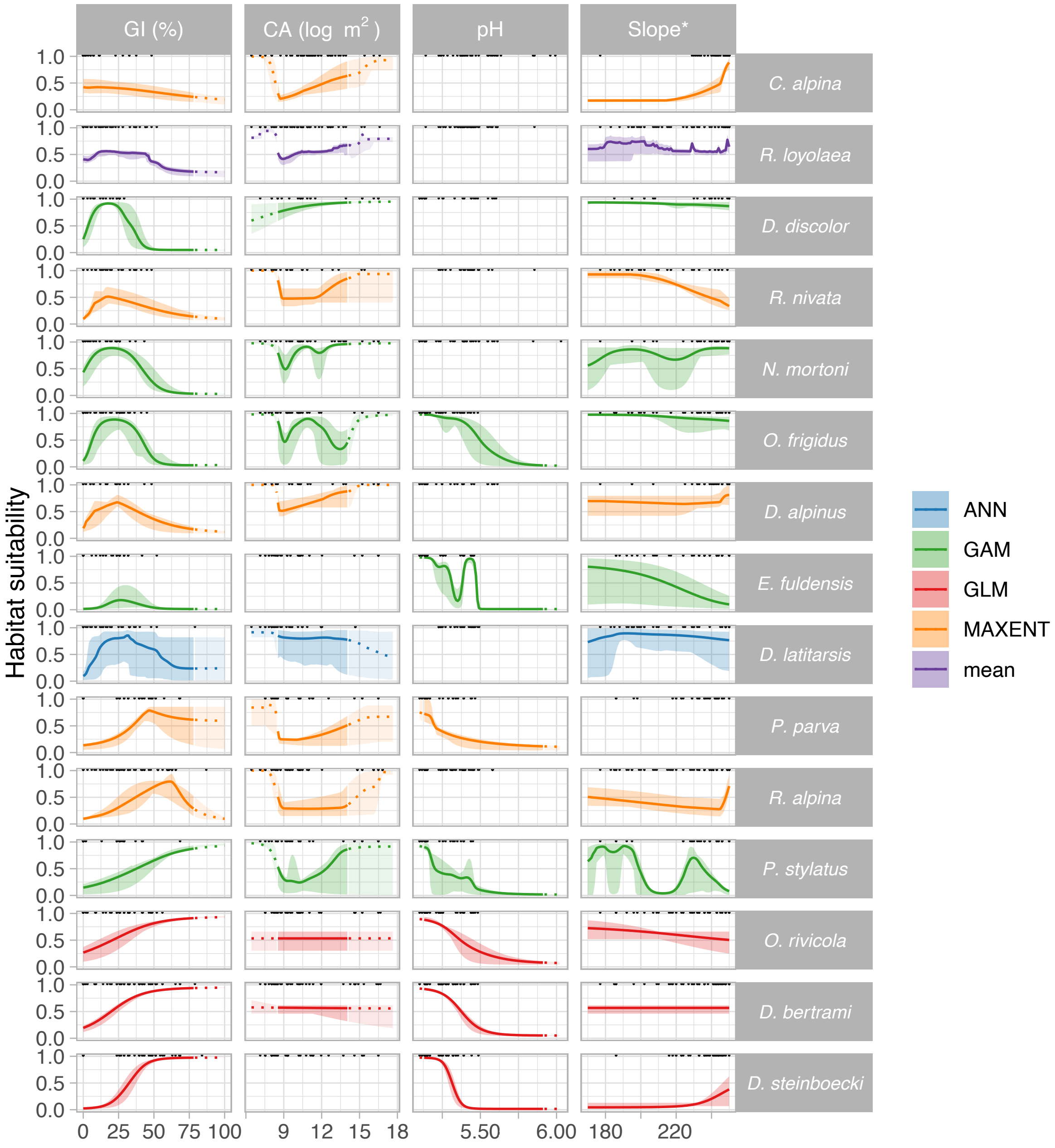
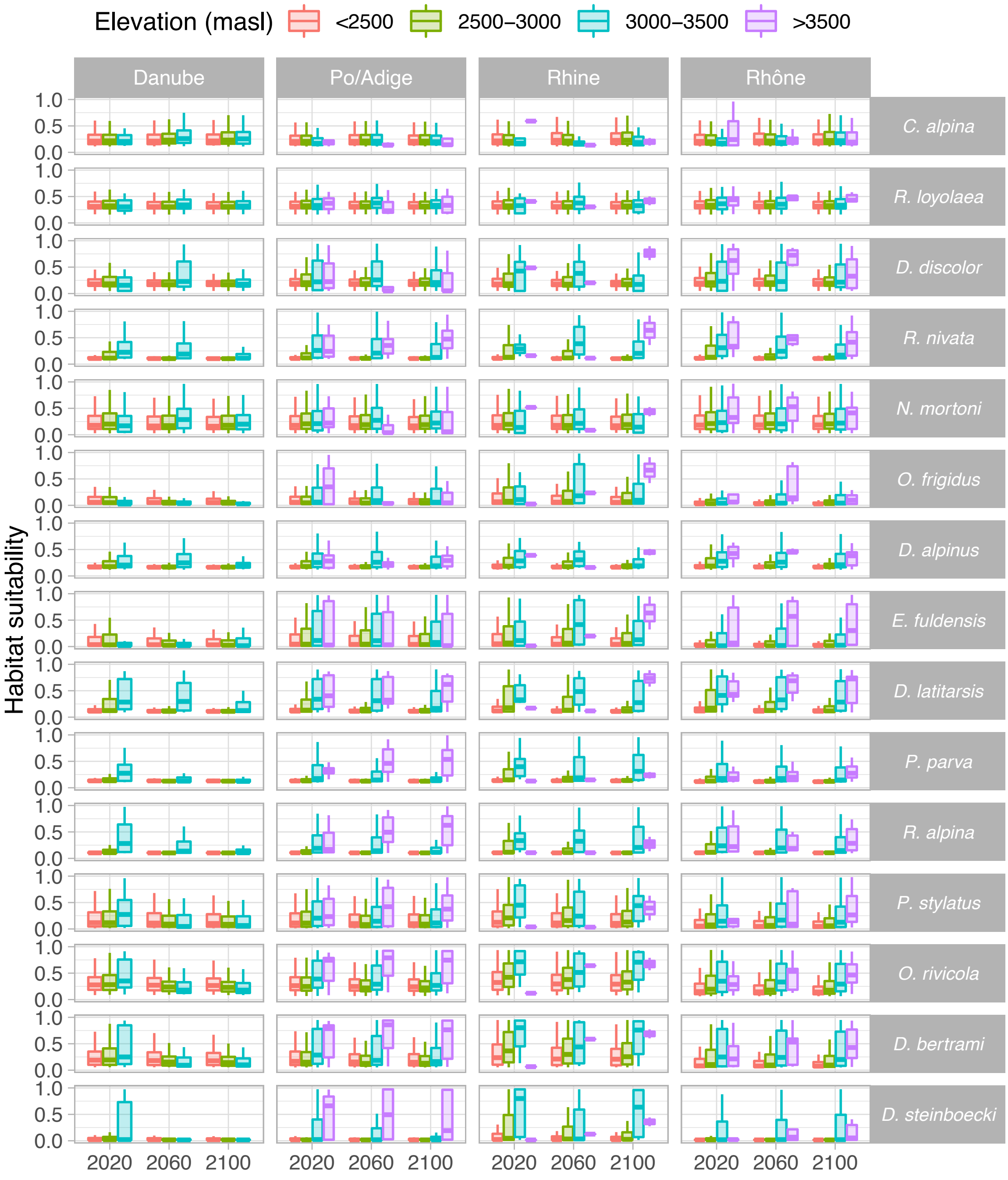


Extended Data Figure 4

Extended Data Figure 5



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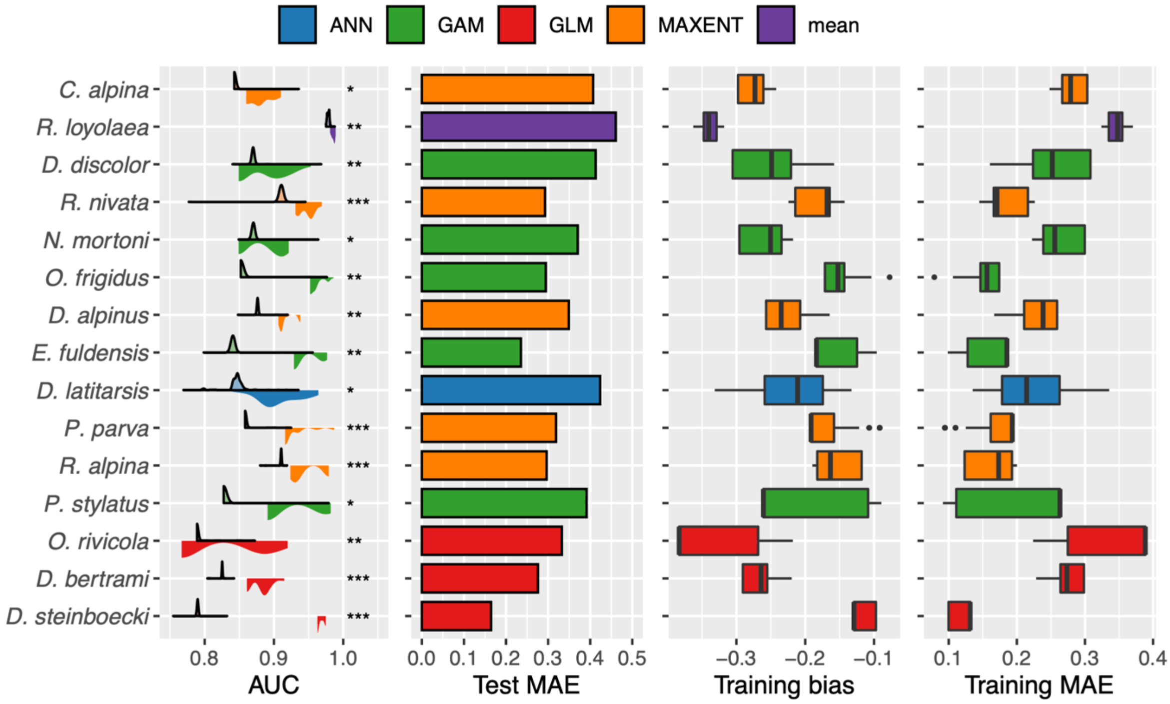

Extended Data Figure 7