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

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5

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20

21 **Abstract**

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

34 Climate-driven modifications of ecosystems are expected to continue under twenty-first century
35 global environmental change^{1,2}, further threatening biodiversity and ecosystem services.
36 Understanding the spatial and temporal variability of future habitat conditions is therefore vital to
37 identify locations where existing species' populations may persist or be at risk. Up to 80% of species
38 are already undergoing range shifts³, dispersing to higher latitudes or altitudes in an attempt to track
39 the habitat conditions they require. Improved ecological monitoring and modelling tools are
40 therefore needed to understand where and when species' distributions will shift in response to
41 climate change, and to underpin the development of robust strategies for biodiversity conservation.

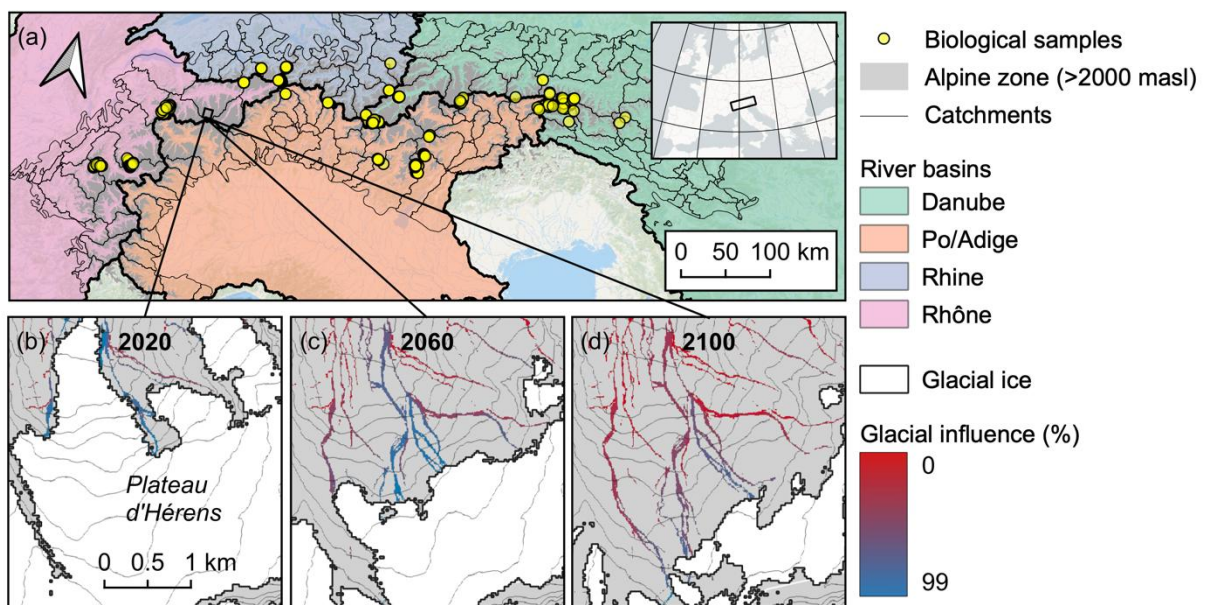
42 Alpine regions are warming at a faster rate than the global average⁴, and high levels of endemism
43 make alpine biodiversity particularly vulnerable to climate change as geographical barriers restrict
44 opportunities for poleward range shifts⁵. Alpine species populations are therefore expected to shift
45 to higher elevations under climate change. However, our understanding of how ecological
46 communities will establish and persist at higher altitudes is limited, with particular uncertainties
47 associated with rates of glacier change and landscape reorganisation as habitats expand into new
48 proglacial (i.e., situated in front of a glacier) and post-glacial (i.e., where local glacier cover is lost)
49 territory⁶. Many glaciers are losing mass at unprecedented rates and substantial further ice loss is
50 expected throughout the twenty-first century⁴ at the same time as species are shifting to higher
51 elevations. Therefore, coupled models of future ice extent, glacial influence on downstream
52 habitats, and species' ecological niches, are needed to infer where potential refugia for cold-adapted
53 species may develop and persist.

54 Glacier mass loss alters the geomorphological and hydrological characteristics of downstream rivers,
55 driving substantial modifications to freshwater biodiversity and ecosystem services⁷. Strong linkages
56 are evident between alpine river biota and the upstream catchment area covered by glaciers, with
57 cold-water specialists worldwide expected to be imperilled^{8,9} (e.g., 11 to 38% of species loss
58 predicted¹⁰). Conversely, temperature predictions for the Glacier National Park region of the US
59 Rocky Mountains suggest that some cold-water specialists may persist even with complete
60 deglaciation¹¹, whilst glacier loss will potentially benefit some species through the formation of new
61 river systems^{12,13} and/or amelioration of harsh habitat conditions^{14,15}. However, understanding is
62 derived largely from correlations of contemporary glacier cover with univariate diversity metrics
63 (e.g., species richness, functional richness) using space-for-time substitution approaches, as few
64 studies have sampled glacier-fed rivers repeatedly over time^{16,17}. Advances in understanding of
65 population-level responses to glacier retreat and associated river network reorganisation are needed
66 to predict future alpine biodiversity and ensure that protected area policies provide maximum
67 conservation potential.

68 Here, we present projections of future stream invertebrate distributions across all alpine zone
69 (>2000 masl) sub-catchments of the European Alps containing glaciers under the 2020 baseline (total
70 area = 34,218 km²) at decadal intervals from 2020 to 2100 for 10 m × 10 m grid cells predicted to
71 contain running water (referred to as "river segments" throughout). All modelled species all have
72 trans-Alps distributions. Projections were driven by a novel glacial influence model that determines
73 the percentage of the upstream catchment under glacial ice cover for each river segment, with
74 glacier extent from future glacier mass loss simulations informed by Global Glacier Evolution Model
75 (GloGEM) projections¹⁸ under an intermediate greenhouse gas emissions scenario (SSP2-4.5).
76 Estimates of glacial influence are based on glacial ice cover in the upstream contributing area (i.e.,
77 the catchment area) of each river segment. Decreasing glacial influence is known to be linked tightly
78 to amelioration of harsh habitat conditions, including increasing water temperatures, channel
79 stability and organic matter availability¹⁹.

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

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

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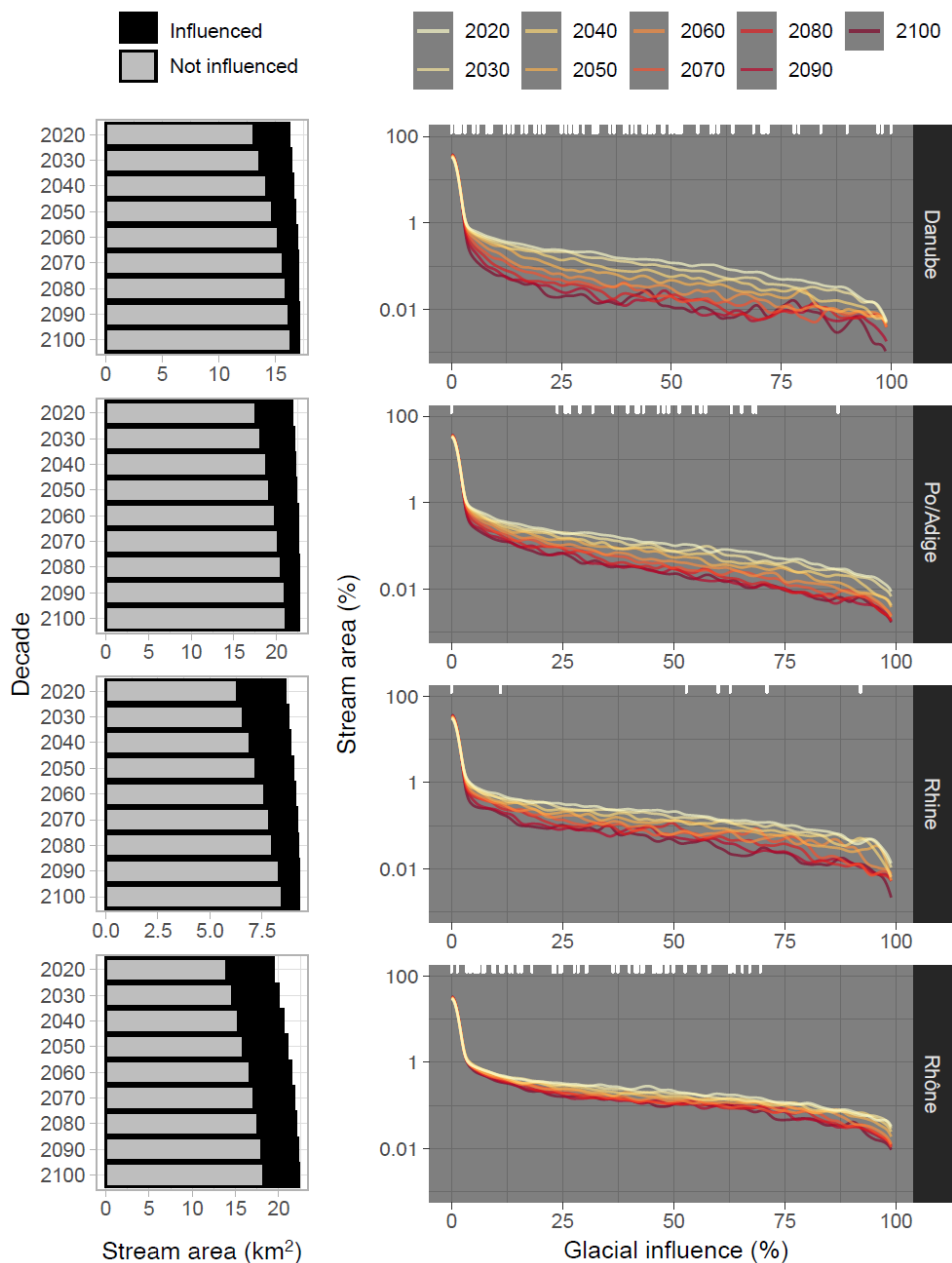
97 Results

98 **Changes in alpine river environments.** Glacial influence on river ecosystems is projected to diminish
 99 progressively to the end of the twenty-first century in all river basins of the European Alps (Fig. 2)
 100 and across the majority of Alpine sub-catchments with glaciers under the 2020 baseline (Extended
 101 Data Fig. 1). The total surface area of these catchments containing running water is projected to
 102 increase from 65.9 km² in 2020 to 71.3 km² in 2100 (1% per decade) as glacier retreat creates new
 103 proglacial and post-glacial landscapes. These changes proceed at similar rates as estimated for
 104 salmon-accessible rivers in western North America under a comparable climate scenario (0 to 5.2%
 105 increase in river length per decade across coastal river basins)¹². Furthermore, the proportion of the
 106 river network receiving flow from upstream areas with glacier cover declines steadily towards the
 107 end of the century. Projected declines in glacial influence are most pronounced in the Danube basin
 108 and least pronounced in the Rhône basin, reflecting the predominant control of elevation range and

109 median elevation on future glacier evolution²¹. As glacier retreat progresses and the river network
 110 expands into territory previously under glacial ice (e.g., Fig. 1b-d), changes in contributing area,
 111 slope, and pH (Extended Data Fig. 2) will occur, but these are negligible compared to declines in
 112 glacial influence. The direction of change for these parameters depends on the local geography of
 113 individual sub-catchments (Extended Data Fig. 3).

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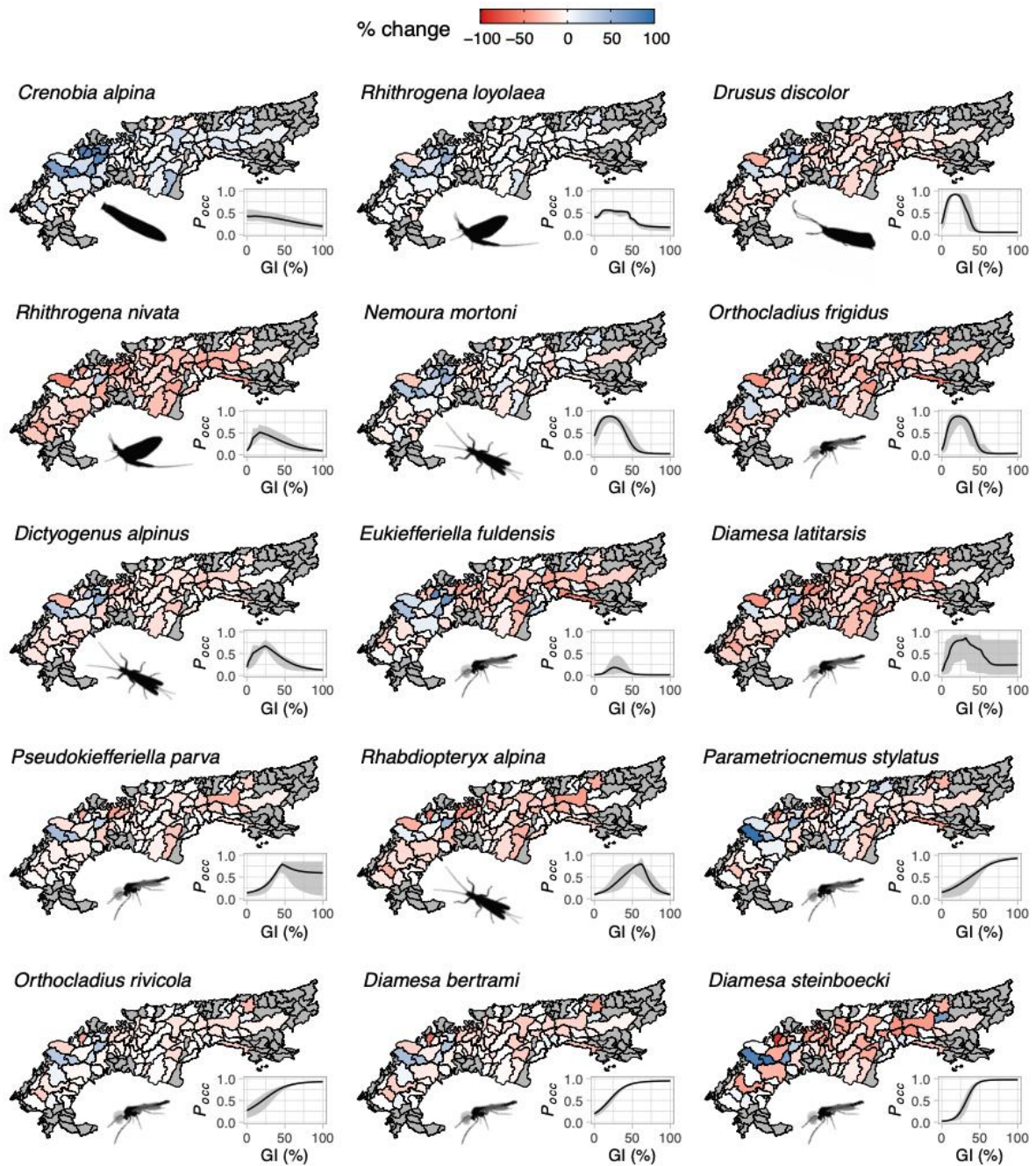
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117 **Fig. 2 | Glacial influence on alpine river systems.** Projected changes in glacial influence for major
 118 river basins draining the European Alps. Left column shows total area of the stream network
 119 influenced and not influenced by glaciers.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

123 **Alpine river invertebrate responses to glacier retreat.** Central to our biodiversity modelling
124 approach was the use of presence-background SDMs²². These were implemented within a rigorous
125 statistical framework to account for spatial autocorrelation^{23,24}, collection bias²⁵ and heterogeneity
126 in study design²⁶ inherent in the invertebrate monitoring datasets we assembled (total n = 656). Of
127 31 species represented in the datasets, there were sufficient data to model the distributions of 19
128 species (61%). Of these, SDM performance was considered acceptable for 15 species (48%;
129 Supplementary Information) spanning the full range of glacial influence optima from 0% (the
130 flatworm *Crenobia alpina*) to approaching 100% (e.g., the non-biting midge *Diamesa steinboeckii*)
131 (Extended Data Fig. 4). These modelled optima are strongly supported by local studies including
132 some from other mountain ranges^{14,27}.

133 Most species are predicted to suffer decreases in suitable habitat area across the European Alps by
134 2100, with consistent losses across all study basins for the non-biting midges *Diamesa latitarsis* grp.,
135 *D. steinboeckii*, and *Diamesa bertrami*, the stonefly *Rhabdiopteryx alpina*, and the mayfly
136 *Rhithrogena nivata* (Fig. 3; Extended Data Fig. 5). Conversely, populations of several species with low
137 glacial influence optima will respond positively (e.g., *C. alpina*, *Rhithrogena loyolaea*). These model
138 estimates support previous suggestions that there will be “winners” and “losers” in response to
139 glacier retreat^{9,28}. Most notably, at the sub-catchment level, suitable habitat area for *all* modelled
140 species is predicted to increase in a subset of locations at the end of the century, especially in the
141 northeastern part of the Rhône basin. As a consequence, some cold-adapted species could be
142 expected to find refuge from widespread deglaciation in locations where glacier remnants persist¹¹
143 assuming they are able to disperse to these locations and establish viable populations. Inferences
144 from population genetics suggests contemporary dispersal is possible across significant areas of
145 mountainous terrain for some winged insects such as stoneflies (e.g. the endangered N. American
146 glacial stonefly *Lednia tumana*²⁹) but less likely for weak-flying species³⁰. Other potential refuge
147 areas could include rivers emanating from rock glaciers and icy seeps³¹ but we acknowledge that
148 datasets on these landforms are presently insufficient to incorporate into GLOGEM and into our
149 models. Species that find refuge in sub-catchments where small glacial ice masses are projected to
150 persist to 2100 and beyond are still likely to be considered “losers” as a consequence of their vastly
151 reduced and increasingly fragmented distributions. In contrast, species characteristic of rivers with
152 low or zero glacial influence will experience overall increases in habitat area.

153 The binary classification of “winners” versus “losers” is complicated by non-linear responses of
154 habitat suitability to glacial influence, with many species showing optima between 20 and 40%
155 glacier cover (Fig. 3). These responses also play out differently over time in different river basins. For
156 example, the stonefly *Dictyogenus alpinus* and the caddisfly *Drusus discolor* show positive responses
157 over time in the Rhône basin compared to consistent declines elsewhere (Extended Data Fig. 5),
158 whilst several species are predicted to become functionally extinct in the Danube basin (Extended
159 Data Fig. 6). This diversity of responses illustrates clear regional and species-specific variation
160 consistent with the substantial spatial heterogeneity underlying global insect population trends³².
161 Importantly, this heterogeneity could provide new insights into potential refuge areas for alpine
162 freshwater biodiversity, underpinning decisions on the modification of protected area networks.



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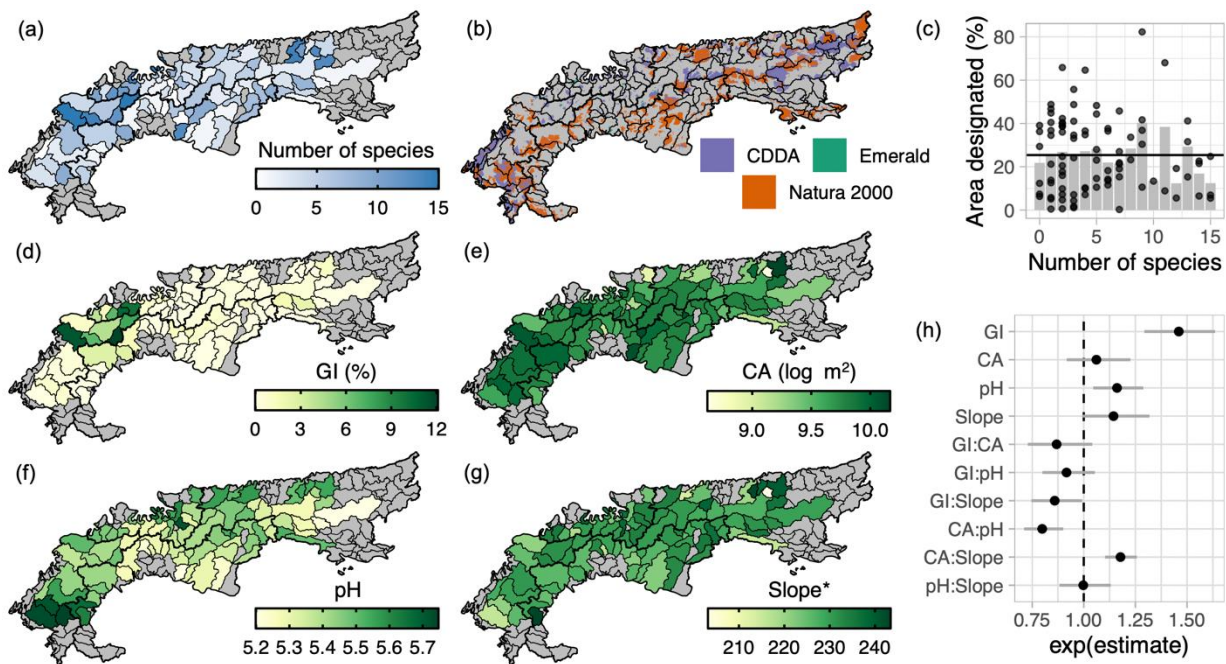
164 **Fig. 3 | Alpine river invertebrate population responses to glacier retreat.** Maps for each species
 165 show the predicted change in suitable habitat area within river sub-catchments of the European Alps
 166 between 2020 and 2100. Inserts show the predicted habitat suitability (P_{occ}) as a function of glacial
 167 influence (GI; lower right of each map). Sub-catchments with no glacial influence under the baseline
 168 condition are shown in grey. Species plotted in ascending order of glacial influence optima.
 169 Silhouette images of adult life stages included for illustrative purposes only (note: analyses focused
 170 on larval stages for insects). These data are available for every decade (2020-2100) in the
 171 Supplementary Information.

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175 **Conservation of alpine biodiversity.** Layering SDMs for individual populations enabled the number
 176 of species predicted to maintain or increase their suitable habitat area between 2020 and 2100 to be
 177 calculated for each sub-catchment. Existing protected areas overlaid on these data provide the
 178 basis for assessing the extent to which future refugia for alpine aquatic biodiversity are covered by
 179 present-day protected area networks. Sub-catchments predicted to serve as refugia for a greater
 180 number of species by 2100 are poorly represented in existing protected area networks relative to
 181 the wider landscape (Fig. 4). Protected areas cover only 12% of three sub-catchments predicted to
 182 serve as refugia for all 15 species, compared to a 25% coverage of protected areas across the whole
 183 study area (Fig. 4c). Sub-catchments identified as offering refugia to greater numbers of species
 184 retain higher levels of glacial influence in 2100 and have higher pH and larger catchment areas with
 185 steeper slopes (Fig. 4h). Though many future refuge areas that we identify technically represent *ex-*
 186 *situ* refugia³³ due to the expansion of river networks into new proglacial and post-glacial landscapes
 187 (e.g., Fig. 1b-d), conditions are predicted to change gradually through the twenty-first century,
 188 indicating the potential for alpine invertebrates to disperse upstream to colonise new habitat. These
 189 results contrast with a recent analysis of future climate refugia for four alpine bird species in the
 190 European Alps which found that *in-situ* refugia were relatively well represented by the current
 191 protected area system³⁴.



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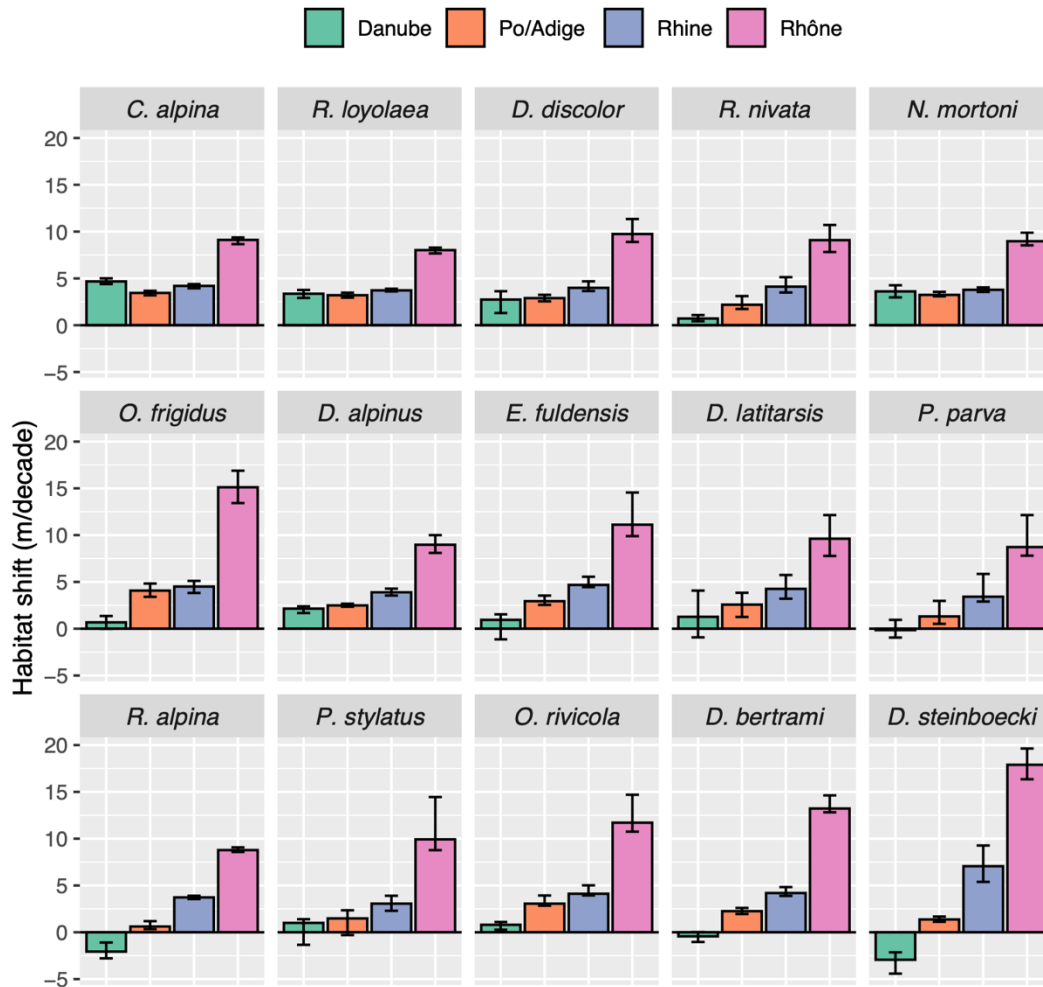
193 **Fig. 4 | Locations of predicted refugia for alpine river invertebrates in 2100.** **a**, Number of species
 194 predicted to maintain or increase their suitable habitat area between 2020 and 2100. **b**, Areas under
 195 conservation designation in the European Alps, including nationally protected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

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205 We predict elevational habitat shifts of up to 17.9 (± 1.2 SD) m/decade (Fig. 5), findings which are
206 supported by empirical evidence from studies in Glacier National Park, N. America, for a single
207 species of stonefly⁸. These rates are generally lower than for alpine plants and birds, reported as up
208 to 29.4 and 102 m per decade respectively^{35,36}. However, our models suggest that as glaciers retreat,
209 river habitat availability changes dynamically within and between sub-catchments and river basins
210 (Fig. 3; Extended Data Fig. 5; Supplementary Information) rather than manifesting as simple linear
211 decreases or increases. Two high glacial influence specialists (*R. alpina*, *D. steinboecki*) are predicted
212 to undergo habitat suitability-weighted shifts to lower elevations in the Danube basin, but this is an
213 artefact of glacial ice largely disappearing in the Eastern Alps by the end of the century (Fig. 2).
214 Further analysis shows that these and several other species (the non-biting midges *Pseudokiefferiella*
215 *parva*, *Eukiefferiella fuldensis*, *Orthocladius frigidus*, and the stonefly *D. alpinus*) are unlikely to
216 persist in the Danube basin, with habitat suitability for these species remaining low (Extended Data
217 Fig. 6). Thus, predicted downslope habitat shifts will not be realised as suitable habitat for these
218 species largely disappears along with glacial ice.

219 The complex and shifting habitat mosaic indicated by our findings poses challenges for population
220 viability because natural dispersal processes are often severely restricted for invertebrates in
221 mountainous systems. This is due to high and steep relief between adjacent catchments and
222 frequent inclement weather restricting overland movement successes, coupled with generally poor
223 flying ability among most insect groups⁵. Conservationists may therefore need to consider
224 augmented dispersal to improve the likelihood of successful relocation of cold-water specialists to
225 potential refuge areas. Successful protection of future refugia for alpine species will require shared
226 governance among nations with alpine territories to enable transboundary species translocations,
227 and with co-ordinated monitoring of both source and refuge populations to determine conservation
228 success³. Crucial to the conservation of aquatic species populations in refuge areas will be
229 preventing increases in river catchment and habitat stressors that modify ecosystems in addition to
230 climate-driven glacier retreat impacts, such as land-use change (e.g., pastoralism, ski-run
231 development) and water withdrawals (e.g., hydropower expansion).

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239 **Discussion**

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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.

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., Pyrenees³⁷; North American Rockies¹¹). 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 development³⁸. 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 glaciers⁷.

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

264 Further predictive improvements to our models could be made by incorporating density-dependent
265 biotic interactions and dispersal processes that influence species persistence⁴¹. For example, whilst
266 our models can reproduce species occupancy at sites with low glacial influence where predation and
267 competition act to reduce abundance and exclude inferior competitors⁴², these density-dependent
268 effects are not modelled explicitly. There is a pressing need to quantify these effects across a greater
269 number of alpine rivers and mountainous regions^{20,37,43,44} to better understand the biotic
270 mechanisms driving aquatic biodiversity responses to glacier retreat²⁸. Additionally, despite our
271 assembled datasets representing the best available alpine river biodiversity records, 12 of 31 species
272 represented in the records were data deficient, and we were able to find acceptable models for only
273 15 of the remaining 19 species. More intensive monitoring of alpine river biodiversity is needed
274 urgently so that robust species distribution modelling can be undertaken for a wide range of aquatic
275 species, and used to support conservation decisions.

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

285

286 **Methods**

287 **Contemporary topography and glacier ice.** We mosaicked contemporary digital elevation models
288 (DEMs) obtained from national airborne LiDAR campaigns that are typically at <10 m resolution,
289 namely from SwissALTI (10 m), Digitales Geländemodell (DGM) Österreich (10 m), provincial surveys
290 in N. Italy; Alto Adige/S. Tyrol (2.5 m), Trento (1 m), Valle d'Aosta (2 m) and Piemonte (5 m) and IGN
291 France (25 m) and resampled them to a common 10 m resolution. We used glacier outlines from the
292 Randolph Glacier Inventory version 6 referring to the year 2003⁴⁸. More details of these datasets can
293 be found in the Supplementary Information.

294 **Future glacier coverage.** We made future glacier projections using the Global Glacier Evolution
295 Model (GloGEM¹⁸). The model is discretized into 10 m elevation bands to facilitate large-scale
296 application, but results for area and thickness changes in individual bands are extrapolated to a 25 x

297 25 m grid. GloGEM is forced with gridded monthly data on 2 m air temperature and total
298 precipitation from the ERA5 re-analysis⁴⁹ for the past, and until 2100, with results of 13 Global
299 Circulation Models (GCMs) from CMIP6⁵⁰. GCMs were based on five different Shared Socio-economic
300 Pathways (SSPs)⁵¹ describing future greenhouse gas emissions. Our analysis used results of the
301 intermediate scenario SSP2-4.5 which most closely corresponds to the current pledges of nations
302 around the globe to limit atmospheric warming⁵². Whilst a full analysis of uncertainty due to glacier
303 models, general circulation models, RCPs, and natural variability is beyond the scope of our study,
304 for the European Alps, the overall uncertainty in glacier area change relative to the year 2003
305 accounts for +/-9% in 2050 and +/-7% in 2100⁵³.

306 **Hydrological routing and glacial influence.** We delineated flow paths using TauDEM⁵⁴ hydrological
307 tools in ArcGIS 10.6.2 to fill minor topographical lows, obtaining a flow direction grid and a
308 contributing area (CA) grid (i.e., the upstream area draining to each cell). We specifically used a D-
309 Infinity algorithm that accommodates braided reaches as most appropriate for many alpine
310 mountain rivers. The wetted channel network was determined as all segments with CA>5000 m²,
311 which our previous work has identified as representing European Alps headwaters well^{55,56}. The
312 spatially-distributed (i.e., of each and every grid cell) glacial influence (GI) was determined by
313 differencing the CA result computed with and without glaciers included and reporting the result as a
314 percentage for each river grid cell, which we refer to as a river segment. The complete workflow is
315 detailed in our Supplementary Information together with an uncertainty analysis of grid resolution.

316 For projections of future hydrological routing and GI, we constructed future DEMs. First, glacier bed
317 topography was obtained by subtracting contemporary ice thickness⁵⁷ from a surface DEM, both at
318 25 m resolution. Second, the glacier bed topography was mosaicked with the contemporary DEM
319 mosaic to create a landscape-wide “ice-free” topography. Third, ice thickness for each future decade
320 from GloGEM was then added to that landscape-wide bed topography to obtain a future (landscape
321 and ice surface) DEM. Hydrological tools were run on each future DEM to project future river
322 network distribution and properties. To enhance spatial and temporal predictions of biodiversity
323 change, these analyses were undertaken at far greater spatial resolution than previous modelling
324 studies for Pacific Salmon¹², both for proglacial rivers (10 m vs 30 m) and ice surfaces (25 m vs 90 m),
325 and our approach further considers the importance of braided channel morphology as well as single-
326 thread channels, which increases the likely accuracy of suitable habitat estimates.

327 **Environmental data processing.** To complement the GI and CA data derived from the hydrological
328 routing analyses, we obtained additional spatial datasets representing hydraulic and hydrochemical
329 influences on river environments. Because alpine river networks are expected to undergo
330 considerable reorganisation as glacier retreat exposes new proglacial and post-glacial areas, we
331 were limited to datasets representing the underlying landscape. For example, we could not use
332 datasets tied to the existing river network, such as HydroATLAS⁵⁸. To represent hillslope runoff and
333 channel hydraulics, we obtained the dimensionless slope derived from the 25 m resolution Digital
334 Elevation Model over Europe (EU-DEM⁵⁹). To represent catchment influences on river hydrochemical
335 conditions, we used the 250 m resolution soil water pH (0-5 cm depth) data from SoilGrids⁶⁰ as a
336 proxy for the pH of streams draining these soils. Slope and pH datasets were disaggregated to 10 m
337 resolution and stacked with glacial influence and CA data. All environmental layers were masked to
338 ≥2000 masl elevation. For all analyses at the river basin level, we combined the Po and Adige river
339 basins to ensure approximately equal river basin areas across the hydrographic regions considered.
340 We considered the combination of the Po and Adige basins appropriate due to the close proximity of
341 the basin outlets and their location to the south of the European Alps.

342 **Biological data processing.** We obtained alpine invertebrate community monitoring data from
343 previous studies conducted by six separate research groups (total n = 656). Contemporary GI and CA
344 were determined for each sampled location as described above. We retained only species level data,
345 corrected taxonomy to currently accepted names using the Integrated Taxonomic Information
346 System⁶¹ and aggregated synonymous species. We did not filter the available samples by elevation
347 and they were not exclusively within the alpine zone (>2000 masl). The minimum elevation of the
348 samples was 1025 masl, and the 25th percentile of elevation was 2015 masl.

349 Several sources of heterogeneity affected the biological data. The taxonomic resolution at which
350 organisms were enumerated in the assembled biological datasets varied from species to family and
351 higher ranks. Three different sampling methods were used (Surber, Hess, kick-net), and sampling
352 effort presumably varied widely in ways not reported in the data (e.g., observer variation). We
353 therefore reduced the biological data to presence-only form, i.e., only presence records for each
354 species were retained, without including absences. Presence-only records are the most widely
355 available type of biodiversity data worldwide, and a large body of literature has developed focusing
356 on the use of such records to model species distributions along environmental gradients⁶².

357 **Species distribution modelling.** Previous research has shown that highly robust species distribution
358 models (SDMs) can be developed using presence-only records if steps are taken to ensure potential
359 biases are accounted for^{24,25}. The resulting SDMs are commonly referred to as 'presence-
360 background' models due to their inclusion of observed presence records and background samples,
361 otherwise known as 'pseudo-absences', generated through random sampling of the environmental
362 background. Among other standards common to all SDMs⁶³, developing robust presence-background
363 SDMs relies on careful consideration of the number of background samples to draw, as well as
364 model validation schemes that account for spatial structures in the data, including spatial
365 autocorrelation²⁴ and collection bias²⁵. Collection bias refers to the tendency for biodiversity data to
366 be collected in certain locations within the landscape, such as those close to field stations, roads,
367 and nature reserves. Presence-background SDMs affected by such biases are more likely to deviate
368 significantly from the null model underlying background sample generation²⁵. This can lead to
369 inflation of model evaluation metrics, such as the area under the curve (AUC) of the receiver
370 operating characteristic, and the violation of commonly applied assumptions about thresholds for
371 considering SDM performance to be acceptable (e.g., AUC>0.7).

372 Through initial tests with three species representing the whole range of prevalence observed in the
373 biological data, we selected the number of background points as 1000 from each major river basin as
374 this provided a good balance between variance and CPU time (Supplementary Information). This
375 background sample size was also close to a statistically representative sample of the background
376 environment at $\alpha=0.05$ and a margin of error of 5%, suggesting it was large enough to represent the
377 environment within the regions of interest⁶². The background sample was drawn from raster data
378 representing GI, CA, pH, and slope in 2020.

379 Prior to fitting SDMs for each species, presence and background points were organised into spatially
380 separated folds with a spatial buffering strategy using the BlockCV package in R²⁴. This involved first
381 estimating the spatial autocorrelation range in candidate covariates using the *spatialAutoRange*
382 function (median range = 10.2 km), and then generating spatially separated training and test folds by
383 considering buffers of the resulting distance (10.2 km) around each observed presence point using
384 the *buffering* function. The approach is a type of leave-one-out cross-validation in which each fold is
385 generated by excluding both presences and background points within the buffer. Species were
386 excluded from further modelling steps if the minimum number of presences in the folds was <10.

387 This was an informed choice as previous research has shown that acceptable SDMs can be
388 developed with as few as 10-14 presences^{64,65}. Ultimately, the number of presences for the 19
389 species we modelled ranged from 28 to 157 (Supplementary Information), exceeding the lower
390 threshold of 10-14 presences.

391 For each species, SDMs were fitted to each fold using the BIOMOD2 package in R⁶⁶. Of the
392 algorithms available in BIOMOD2, we selected eight algorithms: Artificial Neural Network; Flexible
393 Discriminant Analysis; Generalized Linear Model; Generalized Boosting Model; Generalized Additive
394 Model; Maxent (implemented as 'MAXENT.Phillips.2' in BIOMOD2); Random Forests; and Surface
395 Range Envelop. Other algorithms implemented in BIOMOD2 produced errors under null modelling
396 (see below) due to the generation of a small number of null data points with identical or near-
397 identical environments. We used the default settings in BIOMOD2 (see Supplementary Information
398 for more details). As well as retaining models from each individual algorithm, we calculated an
399 ensemble average model and an AUC-weighted ensemble for each species. Models were primarily
400 evaluated using the AUC and mean absolute error (MAE) on the out-of-sample presences. We also
401 examined distributions of training bias and MAE on the in-sample presences (training MAE). We
402 produced models using all four environmental variables as well as with all combinations of three
403 variables, selecting the best performing model for each species (Extended Data Fig. 4, 7).

404 To ensure that we interpreted the performance of our models in light of potentially serious
405 collection bias, we adopted a null model approach²⁵. For each species, this involved repeated
406 random resampling from all 656 biological data points. The sample size was fixed at the observed
407 number of presences. For each random sample, we generated spatially separated training and test
408 folds using the same approach as detailed above. We then randomly selected a single fold, fitted the
409 null SDM using all eight BIOMOD2 algorithms plus the two ensemble models, and calculated the
410 AUC. We repeated this procedure 1000 times and calculated the probability that the mean observed
411 AUC was drawn from the same distribution as the null AUC.

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

427 **Habitat elevation changes.** Using the best performing model for each species (Extended Data Fig. 4,
428 7), we calculated the habitat elevation change from each model fold by first predicting decadal
429 habitat suitability within every river segment. Then, for each decade and river basin, we extracted
430 the elevation of every river segment from EU-DEM⁵⁹ and calculated the habitat suitability-weighted
431 mean elevation. Finally, we fitted a linear model predicting the habitat suitability-weighted mean

432 elevation as a function of decade to obtain an estimate of the mean decadal change. We repeated
433 this procedure for each model fold to obtain a distribution of values, as summarised in Fig. 5.

434

435 **Data and code availability statement**

436 Biological data and code are available in the supplementary material. GloGEM data are available as
437 supplementary material to the original paper¹⁸.

438

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462

463 **References**

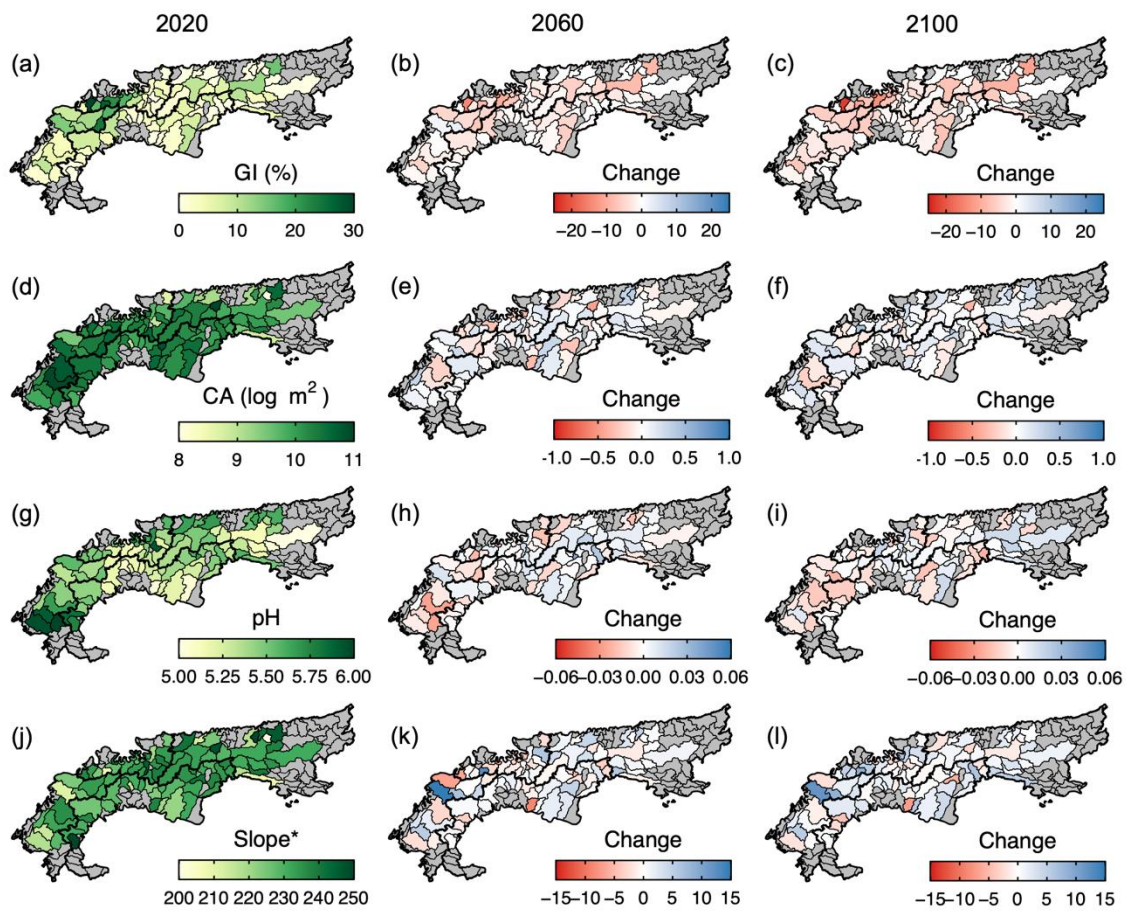
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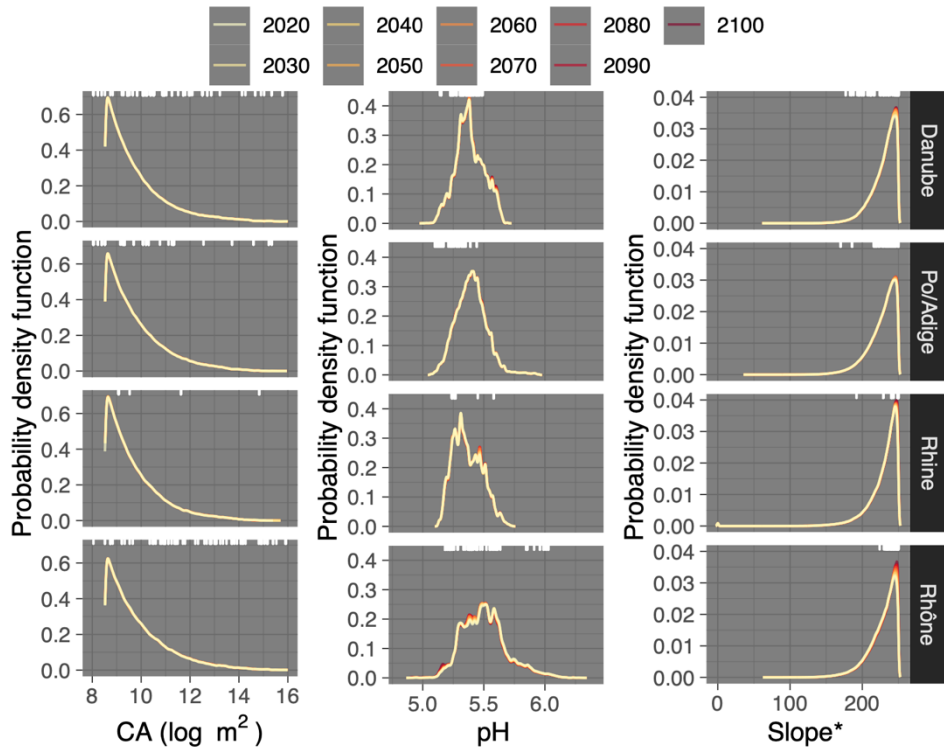
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- 613



615

616 **Extended Data Fig. 1 | Projected catchment level environmental changes in selected decades.** Left
 617 column shows baseline sub-catchment means of glacial influence (GI), contributing area (CA), pH and
 618 slope in 2020. Middle and left columns show changes in 2060 and 2100, respectively, as a
 619 percentage of 2020 sub-catchment means. Sub-catchments with no glacial influence under the
 620 baseline condition are shown in grey. *Slope is a dimensionless variable.

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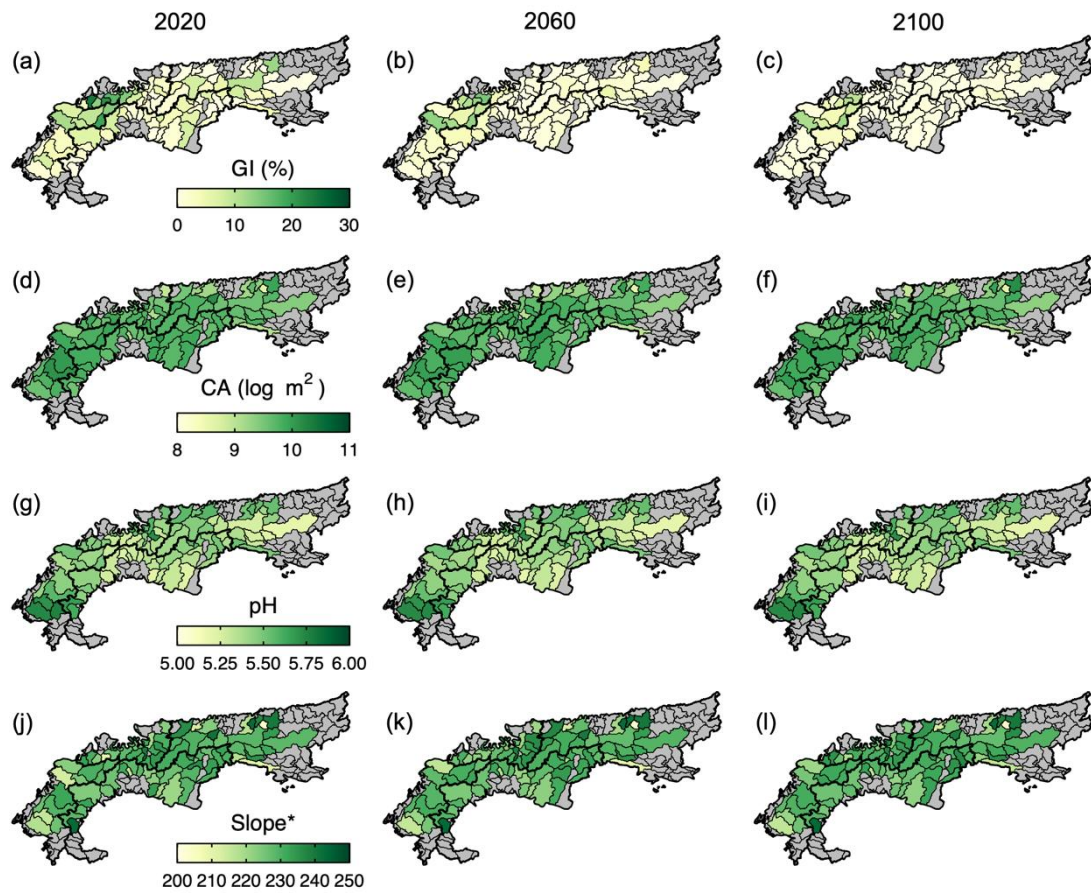
622

623 **Extended Data Fig. 2 | Distributions of environmental conditions at the river segment level.** Rows
 624 show probability densities for each major river basin. Columns show data for contributing area (CA),
 625 pH and slope respectively. White marks show the distribution of each variable for biological samples.

626

*Slope is a dimensionless variable.

627



628

629

Extended Data Fig. 3 | Projected catchment level environmental conditions in selected decades.

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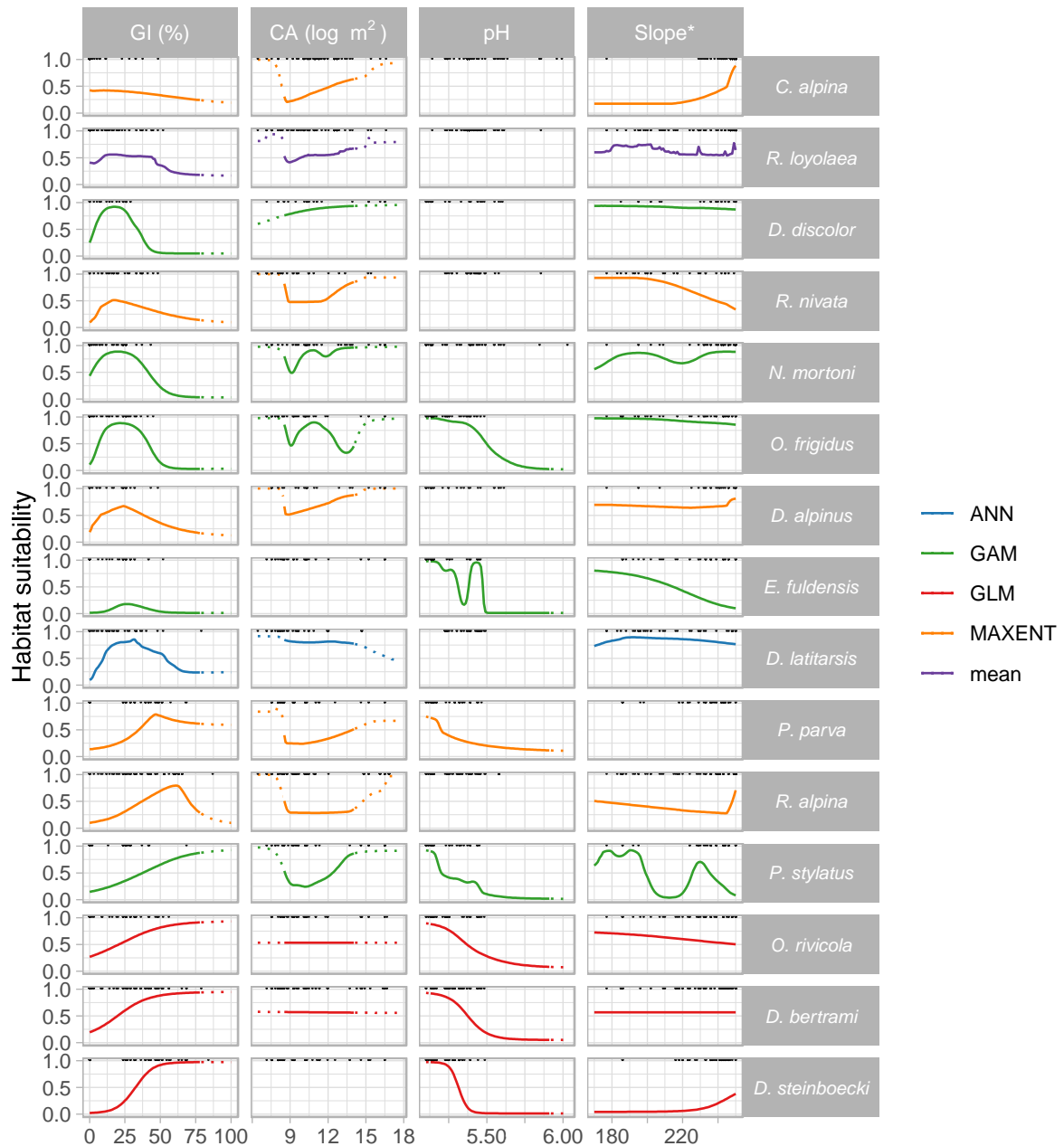
Rows show sub-catchment means of glacial influence (GI), contributing area (CA), pH and slope respectively. Columns show conditions in 2020, 2060 and 2100 respectively. Sub-catchments with no glacial influence under the baseline condition (2020) are shown in grey. *Slope is a dimensionless variable.

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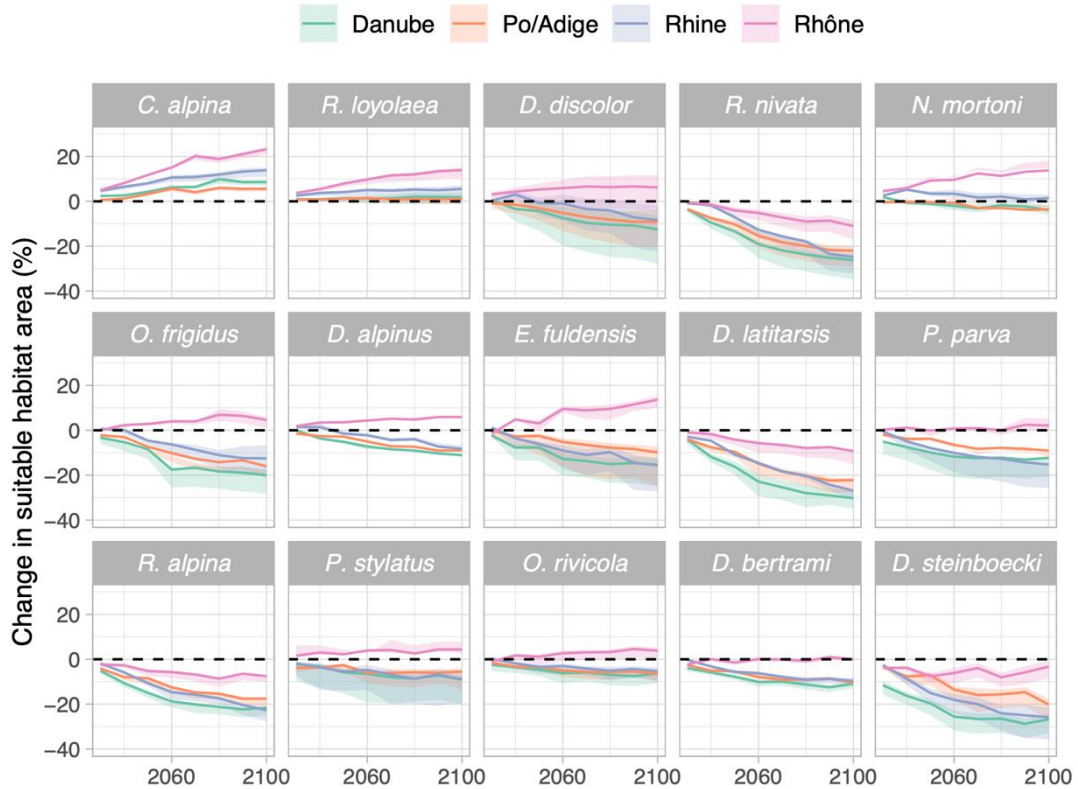
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635

636 **Extended Data Fig. 4 | Response curves for 15 alpine invertebrate species.** Rows show predictions
 637 from the best performing species distribution model for each species. Columns show response
 638 curves for each environmental variable, including glacial influence (GI), contributing area (CA), pH
 639 and slope. Curves for each variable were generated from models whilst holding all other variables at
 640 their mean values from the biological dataset. Colours correspond to the identity of the best
 641 performing model for each species, including Artificial Neural Network (ANN), Generalized Additive
 642 Model (GAM), Generalized Linear Model (GLM), Maximum Entropy (MAXENT) and an ensemble
 643 mean ('mean'). Solid lines and dashed lines respectively show curves within and outside of the 99%
 644 confidence limits of the background environmental data. Shaded areas show 95% confidence
 645 intervals from cross-validation. Black marks at the upper edge of each panel show the distribution of
 646 the corresponding variable where the species was recorded as present. *Slope is a dimensionless
 647 variable.



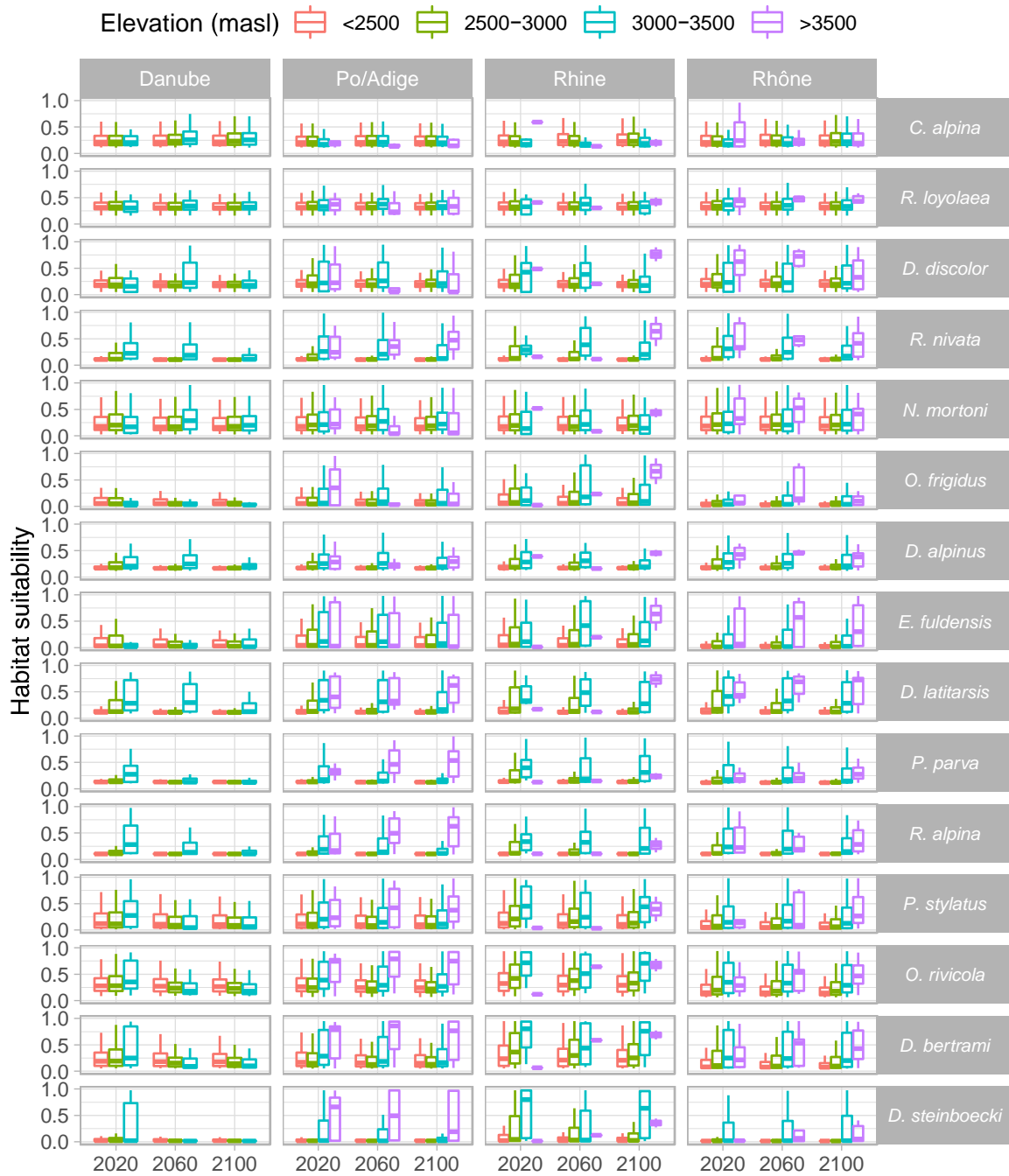
648

649 **Extended Data Fig. 5 | Predicted change in suitable habitat area for 15 alpine invertebrate species.**

650 Panels for each species show the change in suitability-weighted habitat area per decade relative to a

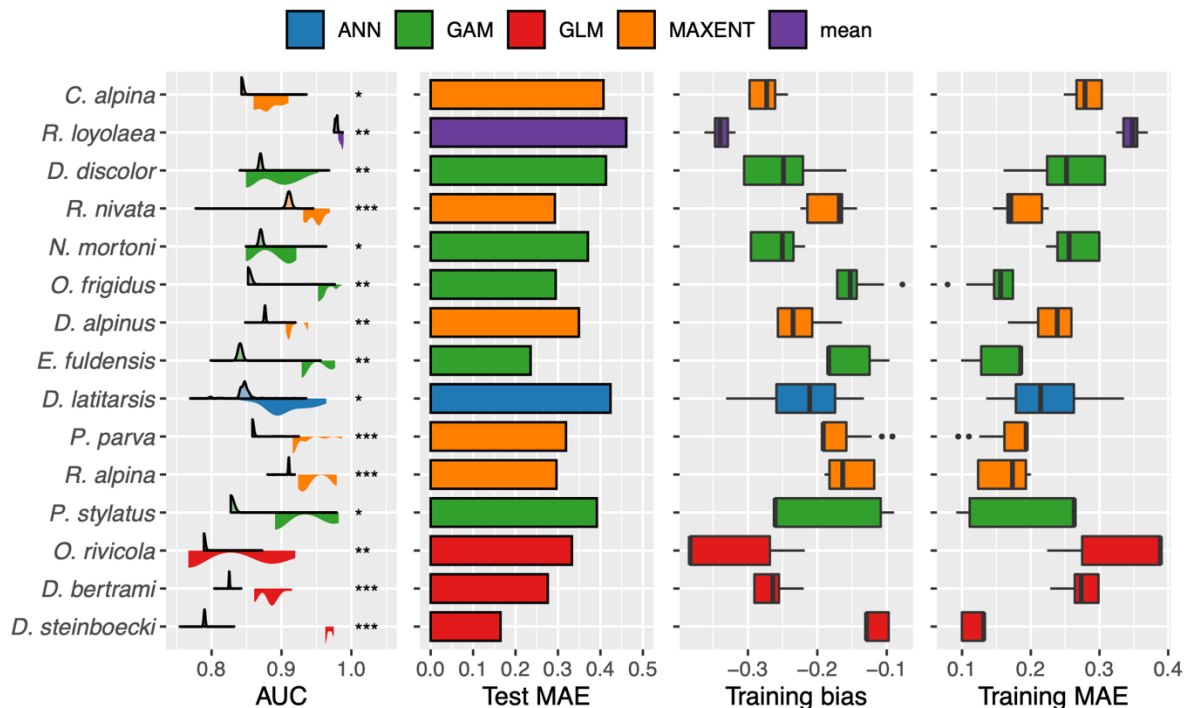
651 2020 baseline within major river basins. Lines denote the mean of model predictions and shaded

652 areas show 95% confidence intervals from cross-validation.



653

654 **Extended Data Fig. 6 | Predicted habitat elevation changes.** Distributions of habitat suitability by
 655 elevation band across selected decades by major river basin (columns) and species (rows). Boxplots
 656 show the median (centre line), interquartile range (box limits) and 1.5 x interquartile range
 657 (whiskers).



658

659 **Extended Data Fig. 7 | Species distribution model performance.** Performance metrics of the best
 660 performing model for each species, including area under the curve (AUC) of the receiver operating
 661 characteristic and mean absolute error (MAE) on the out-of-sample ('test') data and training data.
 662 Colours correspond to the identity of the best performing model for each species, including Artificial
 663 Neural Network (ANN), Generalized Additive Model (GAM), Generalized Linear Model (GLM),
 664 Maximum Entropy (MAXENT) and an ensemble mean ('mean'). The left panel shows the distribution
 665 of AUC values from the null model (upper, closed distribution) and from training folds (lower, open
 666 distribution). Asterisks denote the probability that the mean training AUC was drawn from the same
 667 distribution as the null model: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Species shown in ascending order of
 668 glacial influence optima. Boxplots show the median (centre line), interquartile range (box limits) and
 669 1.5 x interquartile range (whiskers).