

1 **The interaction of climate history and evolution impacts alpine biodiversity assembly**
2 **differently in freshwater and on land**

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31 **Abstract**

32 Quaternary climate fluctuations can affect biodiversity assembly through speciation in two
33 non-mutually-exclusive ways: a glacial species pump, where isolation in glacial refugia
34 accelerates allopatric speciation, and adaptive radiation during ice-free periods. Here we
35 detected biogeographic and genetic signatures associated with both mechanisms in the
36 generation of the European Alps biodiversity. Age distributions of endemic and widespread
37 species within aquatic and terrestrial taxa (amphipods, fishes, amphibians, butterflies and
38 flowering plants) revealed that endemic fish evolved only in lakes, are highly sympatric and
39 mainly of Holocene age, consistent with adaptive radiation. Endemic amphipods are ancient,
40 suggesting preglacial radiation with limited range expansion and local Pleistocene survival,
41 perhaps facilitated by a groundwater-dwelling lifestyle. Terrestrial endemics are mostly of
42 Pleistocene age, and are thus more consistent with the glacial species pump. The lack of
43 evidence for Holocene adaptive radiation in the terrestrial biome may be attributable to a
44 faster range expansion of these taxa after glacial retreats, though fewer stable environments
45 may also have contributed to differences between terrestrial areas and lakes. The high
46 proportion of young, endemic species make the Alps vulnerable to climate change, but the
47 mechanisms and consequences of species loss will likely differ between biomes because of
48 their distinct histories.

49 **Keywords:** Time for speciation, Allopatric speciation, Adaptive radiation, Pleistocene
50 refugia, Glacial species pump, European Alps

51 **1. Background**

52 Immigration, speciation and extinction are the three main processes underlying the assembly
53 of biodiversity in island-like habitats [1–4]. The relative contribution of these processes
54 depends on size, isolation and fragmentation of the region, ecosystem or habitat. For instance,
55 immigration rates decrease with increasing isolation, extinction rates decrease with increasing
56 area, and rates of in situ speciation increase with both area, isolation, and fragmentation
57 [1,2,5–7]. The occurrence and interaction of these processes over geological history leave
58 strong imprints in the contemporary structure of regional and local species assemblages,
59 including phylogenetic structure and relatedness. The species age distribution, and the nature
60 and degree of endemism are some of the resulting biodiversity features [8].

61 Some of the mechanisms that can lead to endemism are through cladogenetic speciation, i.e.,
62 when an ancestral species diverges into two or more derived species within an island,

63 archipelago or geographic region, or through anagenetic speciation, when a local or regional
64 population or set of populations diverges from its progenitors outside the island, archipelago
65 or region [3]. Recent cladogenetic and anagenetic speciation both result in neoendemic
66 species, which are young species with geographically restricted distributions. Moreover, if
67 cladogenetic and anagenetic speciation are the main processes behind regional biodiversity
68 assembly, a regional biota can be composed of many relatively young and closely related
69 species. Non-endemic species, in turn, are generally more widespread because they either
70 have immigrated to the focal region from the outside after range expansion or they have
71 arisen in the focal region and had time to spread beyond it. Such non-endemic species are
72 also expected to be older, according to the ‘age and area’ hypothesis [9], which predicts that
73 older species have had more time to disperse and hence become geographically more
74 widespread, whereas younger species often are still confined to smaller ranges. However, the
75 ‘age and area’ hypothesis assumes biome stability (including climatic stability) and does not
76 consider factors other than age that could in fact have strong effects on species range sizes.
77 For instance, population extirpation or local extinction [10], the presence and movement of
78 physical or climatic barriers in space and time [11], changes in habitat size through time,
79 variation between lineages in the ecological versatility and evolutionary adaptability of
80 species [12], variation in species dispersal ability [13,14] and ecological interactions [15] can
81 all be important predictors of species range size in addition to species age. The interaction of
82 these factors can explain, for instance, why some species, despite being so old, are
83 geographically narrowly confined in the present time (geographical relicts or paleoendemics)
84 [16].

85 Physically rugged mountain landscapes at lower and intermediate latitude, such as those of
86 the Alpine bioregion of Europe (hereafter the European Alps), are hotspots of biodiversity
87 and endemism [17–19]. In such environments, endemism and species radiations arise through
88 the interaction of dispersal limitation with steep ecological gradients and often archipelago-
89 like habitat structures [20–23]. In the European Alps, multiple terrestrial taxa have undergone
90 local radiations leading to the emergence of endemic clades in several groups such as
91 flowering plants [24–26] or butterflies [27,28]. Furthermore, some of the largest endemic
92 radiations in European freshwater habitats also took place in or around the Alps, especially
93 for amphipods [29–32] and fish [33,34]. Importantly, these radiations occurred in habitats
94 that are geographically isolated from similar habitats elsewhere, but surrounded by less
95 isolated habitats, containing diverse assemblages of widely distributed taxa. For example,

96 mountain-tops surrounded by lowlands, or permanently cold, deep lakes isolated from other
97 such lakes by the seasonally relatively warm, shallow flowing water of rivers.

98 The climatic and habitat instability driven by the Quaternary climate fluctuations [35] has
99 interacted evolutionary and ecological processes to shape biodiversity in the Alps [34,36–41].
100 This includes influences on speciation, extinction and immigration of lineages, and the
101 reshaping of species abundance, range distribution, richness and genetic diversity patterns
102 [42–44]. An important fraction of biodiversity in the Alps is due to recently colonizing
103 species that immigrated into the region from far away (such as central Asia), or expanded
104 their range from adjacent regions but have not yet speciated in the area. On the other hand,
105 endemic biodiversity may have emerged through two alternative, non-exclusive mechanisms
106 both driven by the succession of glacial–interglacial cycles: (1) the glacial species pump
107 [45,46], and (2) adaptive radiation during interglacial periods (hereafter adaptive radiation)
108 [47] (figure 1). The glacial species pump is a process in which allopatric speciation is
109 accelerated via the isolation of small populations in glacial refugia. It operates when the
110 expansion of glaciers makes large areas of a species’ range unavailable, but leaves isolated
111 pockets of suitable habitat (figure 1b; Hewitt 2000; Hewitt 2004; Holderegger and Thiel-
112 Egenter 2009; April et al. 2013). It can therefore be expected that glacial pump creates
113 assemblages composed of many species that originally emerged in allopatry (figure 1c) but
114 might have come into secondary contact more recently (figure 1e). The role of refugia in
115 promoting species persistence and in glacial vicariant speciation has been widely reported for
116 multiple extant European taxa, both animals and plants [36,37,e.g. 50–53].

117 After each glacial maximum, the retreat of glaciers opens up new, unoccupied habitat in both
118 terrestrial and aquatic ecosystems, which may lead early colonists to diversify *in situ* via
119 adaptive radiations [54] (figure 1b). Adaptive radiation takes place when an ancestor
120 diversifies ecologically and phenotypically, giving rise in a relatively short period of time, to
121 multiple species that are ecologically distinct [55]. Emblematic examples of adaptive
122 radiation during inter- or postglacial periods are associated the emergence of many lakes in
123 the Holarctic realm by the end of the last glacial period, providing opportunities for many
124 radiations of freshwater fish that occurred in parallel [33,34,47,56–59]. Such process would
125 be expected to generate sympatric or parapatric species by *in situ* cladogenetic speciation
126 [23]. In addition, postglacial expansion of populations also has the potential to bring together
127 lineages that had previously diverged in Pleistocene refugia [60]. Secondary contact of
128 lineages can also be important in adaptive radiation, either through causing ecological

129 character displacement in sympatry occurring in response to competition [55] (Schluter
130 2000, or through the occurrence of hybridization which may facilitate the onset of adaptive
131 radiations upon colonization of new environments [61,62]. This ‘hybrid swarm origin’
132 hypothesis of adaptive radiation posits that functional genetic variation, which becomes
133 enriched in hybrid zones, elevates the evolvability and response to natural selection in hybrid
134 populations [61,63].

135 Despite its large information content for investigating hypothesis regarding biodiversity
136 assembly and to understand biogeographic patterns in species distributions [64], few studies
137 have made use of the species age distribution (SAD) [41,65,66], and fewer had investigated
138 SAD from a multi-taxon perspective [8,67]. We conducted a comparative phylogenetic
139 analysis to quantify SADs and the extent and type of endemism in aquatic and terrestrial
140 ecosystems of the European Alps. Our work focuses on several taxonomic groups:
141 amphipods, fish, butterflies and amphibians with nearly complete taxon sampling, as well as
142 15 nearly completely sampled representative genera of perennial flowering angiosperms
143 plants (henceforth “plants”). We predicted that SADs support a scenario with dominance of
144 the glacial species pump for the origin of endemism in terrestrial groups, with species dating
145 to the Pleistocene; whereas SADs may indicate a prominent role of postglacial adaptive
146 radiation for groups that depend on open water habitats, i.e., fish. This is because high
147 altitude ranges in the terrestrial habitats became fragmented but not completely erased during
148 glacial maxima, whereas year-round open water bodies as habitat for fish were entirely absent
149 during glacial maxima, with a few exceptions at the edge of the southern Alps [68]. We also
150 predicted that SADs of both amphipods and amphibians will resemble fully terrestrial taxa
151 more than those of fish. Amphipods occupy both open and subterranean freshwater habitats,
152 and some of the subterranean habitats persisted during the glacial maxima [69], and most
153 amphibians require open water bodies only during spring and summer and are terrestrial for
154 the remainder of the year, while some lack an aquatic life stage altogether [70]. Therefore,
155 some amphibian species likely found Pleistocene refugia within the Alpine region during the
156 glacial maxima [71,72]. Regarding non-endemic species, we did not expect large differences
157 in age structure among taxa because non-endemics tend to be widespread, are probably
158 mostly older and diversified on a wider geographical scale drive by processes that may have
159 been decoupled from the climate dynamics of the Alps. Therefore, we predicted that non-
160 endemic species are older on average than endemics. Because dispersal ability, distance
161 between sink (new habitats that become available after glacial maxima) and sources of

162 colonization, historical stability and heterogeneity of habitat occupied vary between the
163 taxonomic groups, the magnitude of the difference in species ages between non-endemic and
164 endemic species will be taxon-dependent.

165 **2. Methods**

166 Our work focuses on the European Alps, following previous delimitations of European high
167 mountain systems [73] but including the peripheral lowland areas, where most of the
168 perialpine glacial lakes are located. To select the taxonomic groups to be included in this
169 work, we looked for lineages with reliable distribution data, robust dated phylogenetic trees
170 that include most of the diversity of the given lineage, and/or genetic data for most of the
171 recognized species, so that we could estimate and calibrate phylogenetic trees where none
172 existed. Then, we chose five major taxonomic groups to represent the terrestrial and aquatic
173 alpine and pre-alpine biomes of the region: nearly all known regional species of amphipods,
174 fishes, amphibians and butterflies, and 14 nearly completely sampled clades of flowering
175 plants (*Homogyne*, *Petasites*, *Tussilago*, *Campanula*, *Jasione*, *Phyoplexis*, *Knautia*,
176 *Androsace*, *Primula*, *Soldanella*, *Gentiana*, *Saxifraga*, *Carex* and *Festuca*). Only species
177 native to the European Alps were considered. To assemble species age distributions (stem
178 age, i.e., time since divergence from closest relative in million years, Ma), we combined
179 published time-trees and our own estimates (electronic Supplementary Methods).

180 (a) Endemism and speciation mode

181 Species were considered endemic if they naturally occur only in the alpine and/or perialpine
182 regions of the Alps. When a species was classified as endemic, we assigned its speciation
183 mode to anagenetic speciation (Alpine species diverged from its non-Alpine sister species,
184 but did not undergo *in situ* diversification) or cladogenetic speciation (Alpine species
185 emerged through *in situ* diversification, with either the non-endemic sister being native to the
186 region too, or the two or more sister species all being Alpine endemics), following Rosindell
187 and Phillimore (2011) (electronic supplementary material, tables S1). To apply these
188 definitions, we first identified the position of each of the endemic species within the
189 phylogeny (electronic supplementary material, file S2). Then, if the endemic species was
190 nested within a clade composed mainly of species that occur outside of the Alps, and its
191 direct sister species occurred only outside the Alps, we assumed anagenetic speciation. If the
192 species was nested within a group mostly of species native to the Alps, we assumed
193 cladogenetic speciation.

194 (b) Comparisons of species age distributions

195 We performed multiple permutation tests on the distribution of age estimates assembled from
196 all the species to identify differences in the age distributions among and within major clades.
197 Here, we asked 1) whether age distributions differed between endemic and non-endemic
198 species, overall and within each taxonomic group independently; 2) whether species age
199 distributions differed among taxonomic groups; 3) whether non-endemic species age
200 distributions differed among groups; and 4) whether endemic species age distributions
201 differed among groups. When a difference was significant, if a significant result was found,
202 we performed post-hoc pairwise permutations to identify which distribution and taxonomic
203 group (or groups) were distinct from one another, using Bonferroni correction for each group
204 of analyses. These analyses were performed using the function ‘oneway_test’ of the library
205 ‘coin’ [74] in R 4.0.2 1106 [75] with 10,000 resamples with a distribution approximated via
206 Monte Carlo resampling.

207 **3. Results**

208 A total of 617 species were included in our analyses: 39 amphipods, 124 fishes, 31
209 amphibians, 245 butterfly and 178 plant species (electronic supplementary material, table
210 S1). Approximately half of all fish and amphipod species were found to be endemic to the
211 European Alps (45.2 % and 49 %, respectively), whereas smaller fractions of 12 %, 13 % and
212 30 % of the butterflies, amphibians and plants, respectively, were found to be endemic (figure
213 2). Our analysis of speciation mode suggests that approximately half of the endemic
214 amphipods and plants, and one third of butterfly species emerged by cladogenesis (53 %, 52
215 % and 36 %, respectively). Cladogenesis was also inferred to be the mode of speciation for
216 the majority of the endemic amphibian and fish species (75 % and 98 %, respectively) (figure
217 2).

218 We found that 94 % of the extant species that now occupy the Alps, irrespective of endemism
219 status, emerged over the past 15 million years (from the Middle Miocene) (figure 2).
220 Endemics were overall younger than non-endemics (p-value < 0.0001), which was also true
221 for each taxonomic group when analysed individually (electronic supplementary material,
222 table S9). We found the species age distributions among non-endemic species to be similar
223 between taxonomic groups (figure 2), with most of the species ages spanning the Late
224 Pleistocene to Early Miocene (90 % fell between 0.3 and 20 Mya). The only exception was
225 the comparison of plants *vs.* amphibians, as we found non-endemic amphibians older than

226 non-endemic plants ($p < 0.0001$; electronic supplementary material S10). SADs of endemic
227 species were also similar among taxa (90 % fell between 0.25 and 8 Ma), except for fish,
228 which are younger than any other group (90 % fell between 0.6 and 114 Ky; $p < 0.0001$;
229 figure 2; electronic supplementary material S11).

230 We observed the following patterns in the SAD: i) endemics are younger than non-endemics
231 in all taxonomic groups, and ii) there is a high degree of similarity among taxa in the age
232 distributions when endemics and non-endemics are analysed separately. However, we found
233 on one hand that while most endemic fish species arose in the Holocene through
234 cladogenesis, very few endemic butterflies and no endemic species in the other groups arose
235 in the Holocene. On the other hand, only very few endemic fish (all from the southern
236 periphery of the Alps) date to the Pleistocene whereas most of the endemic butterflies and
237 many other endemic species date do.

238 **4. Discussion**

239 Inferring past evolutionary process from the structure of current biodiversity is one of the
240 goals of macroecology, macroevolution and biogeography. Species age distributions among
241 regional biota is one informative aspect of this structure [64]. We combined estimates of
242 species origination times with information on endemism and mode of speciation
243 (cladogenetic vs. anagenetic) to investigate the dominant mechanisms of biodiversity
244 assembly in different taxa and major biomes of the European Alps. We found that most of the
245 species diversity in fish, amphipods, amphibians, butterflies and plants is relatively young,
246 emerging at the beginning in the Middle Miocene, which coincided with the period of
247 maximum geological uplift in the region that culminated with the formation of the Alps [76].

248 Our multi-taxon comparative analysis had the advantage of directly comparing independently
249 evolving and ecologically distinct clades in the same region. It showed that speciation timing
250 was dramatically different between terrestrial taxa and those aquatic taxa that require
251 permanent open surface water (i.e., fish). While 80 % of the Alp's endemics in the terrestrial
252 groups originated between the Late Miocene and Late Pleistocene, most endemic fish species
253 arose only after the final retreat of the glaciers and re-establishment of permanent open water
254 bodies in the formerly glaciated areas. Combined with the observation that the vast majority
255 of endemic fish are products of cladogenetic speciation, this suggests that the assembly
256 process of the fish fauna of the Alps is dominated by an interaction between colonization
257 from outside the region and adaptive radiation during the last postglacial period, but similar

258 processes may have cyclically repeated themselves in previous interglacial periods,
259 alternating with extinction during glacial maxima. In contrast, for the terrestrial groups, our
260 results suggest that colonization from outside the region and the glacial species pump are the
261 dominant mechanisms, as anagenetic speciation was more important in these taxa, and
262 endemic richness assembled throughout the Pleistocene. Interestingly, we observed some
263 postglacial speciation in butterflies, coinciding with the major mode in fish, but being
264 dwarfed in butterflies by the much larger Pleistocene mode. We suggest that general, non-
265 exclusive mechanisms underlay these contrasting patterns: 1) Quaternary climate fluctuations
266 that accelerate allopatric speciation during cold stages but open up new ecological
267 opportunities for adaptive radiation during interglacial periods; 2) variation among groups in
268 their dispersal ability and associated rate of range expansion, and finally 3) the influence of
269 variation in seasonal and inter-annual habitat stability in either constraining or promoting
270 adaptive radiation. Below we discuss each of these mechanisms and how they may have
271 affected diversification in the different taxa studied here.

272 (a) The role of Quaternary climate fluctuations

273 We suggest our finding that most endemic fish are of postglacial origin, while endemics in
274 other groups arose in the Pleistocene or earlier, is explained by the different effects that the
275 Quaternary climate oscillations had on freshwater versus terrestrial habitat [68]. Permanent
276 open surface water habitats, as required by fishes, were absent in the glaciated parts of the
277 Alps during the Last Glacial Maximum (LGM), because all lakes and river valleys were
278 covered by thick glaciers. Therefore, the complete lack of endemic fish species older than
279 20,000 years on the northern and western flanks of the Alps is likely due to local extirpation
280 of all fish populations across the region during the LGM. With the progressive retreat of
281 glaciers, which achieved their modern configuration in the Late Holocene, fish would then
282 have returned to the region from areas located in downstream sections of the large rivers, that
283 were often far from the alpine region especially on the North face of the Alps [e.g. 77]. This
284 Holocene recolonization by older widespread species explains the large fraction of old,
285 widespread and non-endemic fish species in the northern and western Alpine region.

286 The first fish to colonize after the LGM were probably species adapted to cold water
287 conditions, such as salmonids and sculpins, that would have lived nearby in the rivers of the
288 Pleistocene tundra downstream of the Alpine glacier shield. Salmonids are indeed known for
289 their remarkable colonizing ability and rapid establishment in postglacial freshwater habitats

290 [78]. These fish would have encountered ecological opportunities in the emerging large and
291 deep lakes of the region and radiated into many distinct species as they adapted to the vacant
292 niches associated with distinct lacustrine zones. This process likely generated the young
293 endemic species, nowadays predominantly in three lineages, whitefish (*Coregonus* [79]), ,
294 chars (*Salvelinus* [80]) and sculpins (*Cottus* [34]), that have rapidly radiated in perialpine
295 lakes. The very few old, relic endemic fish species in the region that date to prior to the
296 Holocene, are the lake herring *Alosa agone*, and two trouts of the genus *Salmo* (*S. carpio* and
297 *S. sp.* ‘Blackspot’). These three species are endemic to lakes in Northern Italy and southern
298 Switzerland, a region where probably not all lakes were fully covered by ice sheets during the
299 LGM [68]. Therefore, these species likely originated during earlier interglacials, when
300 southern perialpine lakes would have become extensive, and then found refugia during the
301 LGM to persist to the present day [81]. That there are no young postglacial species among the
302 non-endemic fish is perhaps due to insufficient time and connectivity between lakes to allow
303 new species to arise in deep lakes elsewhere in Europe (e.g., in northern Germany and
304 Scandinavia) in the Holocene prior to expanding their range into the Alps or vice-versa. It is
305 important to mention that adaptive radiation of fish are far more frequent in deep lakes
306 [82,83], while riverine adaptive radiations are rare (but see [84–86]).

307 Unlike for fish, our analysis revealed that all endemic (and all nonendemic) amphipods, the
308 second fully aquatic taxon in our data, emerged during or before the Pleistocene. This could
309 be because amphipods can persist in smaller water bodies than fish, and many species in this
310 group are ice-associated, being able to survive under ice cover and in its immediate forefield
311 [87]. Both factors would have allowed some species to persist in the region throughout the
312 glaciations. Additionally, as suggested for other invertebrates [69], some species likely
313 survived in subterranean refugia, such as caves or groundwaters, habitats occupied by many
314 freshwater amphipod species today, notably species of *Niphargus*, the most species-rich
315 group in the region [29,32].

316 We found that endemic species in the terrestrial groups are much older than endemic fish
317 species. Pleistocene refugia are hypothesized for terrestrial taxa in many geographically
318 restricted areas on nunataks, i.e, mountain peaks that have never been glaciated [88], or
319 surrounding the Alps [41,89–92], such that extinctions during the glacial cycles did not wipe
320 out the terrestrial fauna entirely. It is very likely that terrestrial organisms, particularly
321 butterflies [41,93], plants [94–96] and amphibians [71,72] survived in glacial refugia in the
322 Alps and at its periphery. Therefore, differential impacts of Quaternary climate fluctuations

323 and the resulting glaciations on different habitats and taxa go a long way helping to explain
324 extant patterns of diversity and endemism in the region.

325 (b) Dispersal ability to explain postglacial radiation

326 Dispersal ability often negatively correlates with rapid niche evolution. The evolutionary
327 response to local environmental and ecological conditions tends to be faster in taxa with
328 limited dispersal, leading to faster niche shifts and higher rates of speciation and adaptive
329 radiation [97,98]. Therefore, the intriguingly few cases of postglacial speciation in fully
330 terrestrial species and amphibians could be related to the dispersal rates imposed by the
331 environments they occupy. Terrestrial taxa experience, in general, less dispersal limitation
332 than freshwater taxa. For example, many species have acquired adaptations for aerial
333 dispersal, such as active flying in butterflies [99,100] or passive airborne propagation in
334 many plants [101], allowing such taxa to disperse virtually in all directions. Conversely,
335 freshwater-bound taxa need to navigate the dendritic landscapes of rivers and lakes to
336 disperse, making it a lot more difficult to reach isolated habitat patches [102,103]. Given
337 these limitations to dispersal for many freshwater taxa, postglacial dispersal may have
338 happened at a much slower pace in fish than for most terrestrial taxa. Terrestrial species may,
339 hence, have expanded their ranges faster after glacial retreat, also likely facilitated by the
340 proximity of refugia to the Alps (including inner-alpine refugia), resulting in faster
341 recolonization of the newly open landscape through long-distance dispersal and range
342 expansion. Some recent studies have shown that many plant species rapidly and substantially
343 expanded their range during the recent postglacial period [104–106]. Faster filling of
344 emerging terrestrial habitats through range expansion left fewer opportunities/less time for
345 the first colonists to undergo ecological speciation and adaptive radiation in response to
346 ecological opportunity among terrestrial groups than among aquatic taxa. To test the relative
347 importance of dispersal limitation versus other aquatic/terrestrial differences, future work
348 could investigate mainly aquatic taxa with strong aerial dispersal abilities, such as Odonata
349 and other insects that spent most of their life cycle in freshwater and have short but highly
350 dispersive terrestrial adult phases.

351 (c) Seasonal and interannual environmental variation limiting ecological speciation

352 Habitat stability in the Postglacial Era may have been an additional factor explaining the
353 larger number of Holocene speciation events in fish, but not in terrestrial groups in our study.
354 Theory and models suggest that environmental fluctuations and stochasticity can reduce or

355 even inhibit ecological speciation in unstable habitats [107,108]. Rapid variation in
356 environmental conditions, both seasonal and interannual, make adaptation difficult and
357 ecological speciation nearly impossible.

358 Environmental conditions in terrestrial ecosystems are much more variable than aquatic
359 ecosystems [109,110], especially large and deep lakes, both in terms of seasonal and year-to-
360 year variation. For instance, whereas seasonal variations in solar irradiance, temperature and
361 snow cover make the high mountain terrestrial habitat extremely seasonal, with large year-to-
362 year variation in the onset and duration of seasons [111,112], they are nearly constant through
363 the year in the deeper parts of lakes [113,114]. The longer growing and reproductive season,
364 despite low productivity, and the much more stable environment in deep lakes may create
365 increased opportunities for ecological speciation and adaptive radiation compared to the
366 alpine terrestrial ecosystems.

367 In addition, despite their greater temporal stability, deep lakes also have much steeper
368 environmental gradients because pressure, light and temperature all change much faster with
369 depth in water than with elevation in the terrestrial realm. This unique property of water may
370 explain the high frequency of ecological speciation in deep lakes, with sister-species being
371 spatially very close to each other but occupying different water depths [58], as observed
372 among East African cichlids [115] and Alpine whitefish [116].

373 **5. Final considerations**

374 We suggest that the formation of the unique biota of the European Alps was driven by
375 interacting mechanisms: non-random Pleistocene survival, postglacial immigration, vicariant
376 speciation during glacial maxima and adaptive radiation in the Postglacial. These interacting
377 mechanisms left distinct imprints on the age structure of regional assemblages in different
378 biomes and associated taxon groups. Historical factors (Quaternary climate fluctuations and
379 Pleistocene refuge availability) impacted freshwater and terrestrial biomes in different ways,
380 and contemporary ecological factors such as environmental stochasticity and dispersal
381 limitations also vary between these biomes, shaping them very differently through ecological
382 and evolutionary processes. *In situ* speciation and adaptive radiation were prominent in fish,
383 but occurred mainly after the LGM, and only in deep lakes, likely due to the unavailability of
384 suitable freshwater habitat during the LGM and the stable conditions within habitats after the
385 LGM. Amphipods and all terrestrial clades have much older endemic species, perhaps
386 because their ecology (i.e., cold-resistant and groundwater-dwelling in amphipods) and the

387 availability of Pleistocene refugia within the region allowed many species to survive the
388 LGM. At the same time, none of the terrestrial groups generated many young postglacial
389 species, likely because higher Pleistocene survival and faster postglacial niche filling through
390 range expansion left fewer ecological opportunities and because larger seasonal variation in
391 the terrestrial environment places constraints on ecological speciation.

392 Knowing the history of biodiversity formation is crucial to establish effective strategies of
393 conservation [117]. For the Alps we show a high fraction of endemism in many groups, with
394 endemic species having survived in some taxa and ecosystems through repeated glacial
395 cycles, while those in others are due to prolific speciation after the retreat of the glaciers.
396 These results improve our understanding of how the Alpine hotspot of species diversity and
397 endemism emerged, and they reinforce that biodiversity in this region is fragile. Endemic
398 species are often range-restricted, show limited population size and are hence much more
399 vulnerable to climate change and other environmental changes than non-endemic species
400 [118], and because of that, they are of high concern for conservation. Even a comparatively
401 small and transient disturbance of an ecosystem can lead to the extinction of young species
402 that evolved in adaptation to specific ecological conditions as has already been observed in
403 the recent past for adaptive radiations of fish in Swiss lakes [116]. The sharp increase of
404 extinction rates driven by human activity in the Anthropocene threatens the biodiversity of
405 the European Alps, and especially that of endemic species [119]. Therefore, this region
406 deserves greater attention to conserve both the regional biodiversity, as well as the eco-
407 evolutionary processes that gave rise to it and that are required to continue operating if
408 biodiversity is to be maintained.

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737

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748 **Figure captions**

749

750 **Figure 1.** Evolutionary and ecological history of a hypothetical biodiversity assembly in an
751 alpine-like system. A) Biodiversity in a preglacial phase. B) Early glacial phase: glacial
752 periods erase freshwater habitats and fragment the terrestrial biome. Some populations
753 survive in refugia and C) can diverge into distinct species through allopatric speciation. D)
754 The retreat of glaciers opens up new, unoccupied habitats offering ecological opportunities
755 for colonizers. E) Some colonizers undergo adaptive radiation and niche space is filled up
756 again.

757

758 **Figure 2.** Species age distribution (SAD) of endemic and non-endemic species of, from top
759 to bottom, amphibians, amphipods, butterflies, fish and flowering plants. Pie charts show the
760 proportion of endemic and non-endemic species as well as the proportion of endemic species
761 that have emerged through cladogenetic or anagenetic speciation.



