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Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps

Yann Vitasse, Sylvain Ursenbacher, Geoffrey Klein, Thierry Bohnenstengel, Yannick Chittaro, Anne Delestrade, Christian Monnerat, Martine Rebetez, Christian Rixen, Nicolas Strebel, et al.

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3 **1 Phenological and elevational shifts of plants, animals and fungi**
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6 **2 under climate change in the European Alps**
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33

34 ABSTRACT

35 Mountain areas are biodiversity hotspots and provide a multitude of ecosystem services of

36 irreplaceable socio-economic value. In the European Alps, air temperature has increased at a

37 rate of about 0.36 °C decade⁻¹ since 1970, leading to glacier retreat and significant snowpack

38 reduction. Due to these rapid environmental changes, this mountainous region is undergoing

39 marked changes in spring phenology and elevational distribution of animals, plants and fungi.

40 Long-term monitoring in the European Alps offers an excellent natural laboratory to

41 synthesize climate-related changes in spring phenology and elevational distribution for a large

42 array of taxonomic groups. This review assesses the climatic changes that have occurred

43 across the European Alps during recent decades, spring phenological changes and upslope

44 shifts of plants, animals and fungi from evidence in published papers and previously

45 unpublished data. Our review provides evidence that spring phenology has been shifting

46 earlier during the past four decades and distribution ranges show an upwards trend for most of

47 the taxonomic groups for which there are sufficient data. The first observed activity of reptiles

48 and terrestrial insects (e.g. butterflies) in spring has shifted significantly earlier, at an average

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3 49 rate of -5.7 and -6.0 days decade $^{-1}$, respectively. By contrast, the first observed spring activity
4
5 50 of semi-aquatic insects (e.g. dragonflies and damselflies) and amphibians, as well as the
6
7 51 singing activity or laying dates of resident birds, show smaller non-significant trends ranging
8
9 52 from -1.0 to $+1.3$ days decade $^{-1}$. Leaf-out and flowering of woody and herbaceous plants
10
11 53 showed intermediate trends with mean values of -2.4 and -2.8 days decade $^{-1}$, respectively.
12
13 54 Regarding species distribution, plants, animals and fungi ($N = 2,133$ species) shifted the
14
15 55 elevation of maximum abundance (optimum elevation) upslope at a similar pace (on average
16
17 56 between $+18$ and $+25$ m decade $^{-1}$) but with substantial differences among taxa. For example,
18
19 57 the optimum elevation shifted upward by $+36.2$ m decade $^{-1}$ for terrestrial insects and $+32.7$ m
20
21 58 decade $^{-1}$ for woody plants, whereas it was estimated to range between -1.0 and $+11$ m decade $^{-1}$
22
23 59 for semi-aquatic insects, ferns, birds and wood-decaying fungi. The upper range limit
24
25 60 (leading edge) of most species also shifted upslope with a rate clearly higher for animals (from
26
27 61 $+47$ to $+91$ m decade $^{-1}$) than for plants (from $+17$ to $+40$ m decade $^{-1}$), except for semi-aquatic
28
29 62 insects (-4.7 m decade $^{-1}$). Although regional land-use changes could partly explain some
30
31 63 trends, the consistent upward shift found in almost all taxa all over the Alps is likely reflecting
32
33 64 the strong warming and the receding of snow cover that has taken place across the European
34
35 65 Alps over recent decades. However, with the possible exception of terrestrial insects, the
36
37 66 upward shift of organisms seems currently too slow to track the pace of isotherm shifts
38
39 67 induced by climate warming, estimated at about $+62$ to $+71$ m decade $^{-1}$ since 1970. In the light
40
41 68 of these results, species interactions are likely to change over multiple trophic levels through
42
43 69 phenological and spatial mismatches. This nascent research field deserves greater attention to
44
45 70 allow us to anticipate structural and functional changes better at the ecosystem level.
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56 72 *Key words:* biodiversity redistribution, climate change velocity, disequilibrium dynamics,
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58 73 global warming, migration, mountain ecosystems, phenological mismatches, upslope shift.
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54	96 I. INTRODUCTION
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56	97 Biodiversity loss and redistribution as well as extreme climatic events are probably the two
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58	98 most prominent environmental challenges with strong socio-economic consequences that
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2
3 99 humans have to face in the 21st century. Biodiversity loss, mainly caused by human alteration
4
5 100 of the landscape, has been occurring at an unprecedented rate since humans expanded across
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7 101 the globe (Butchart *et al.*, 2010). The distributions of many terrestrial organisms are currently
8
9 102 shifting in response to global warming and land-use changes in most parts of the world,
10
11 103 poleward and upslope to cooler latitudes and elevations, respectively, thus generating spatially
12
13 104 structured patterns in species redistribution (Chen *et al.*, 2011; Lenoir & Svenning, 2015;
14
15 105 Lenoir *et al.*, 2020). However, the rate of ongoing global warming is such that numerous plant
16
17 106 and animal species may not be able to adapt genetically, or to track their climatic niche
18
19 107 requirements closely, ultimately leading to local extinctions (reviewed in Jump & Penuelas,
20
21 108 2005; Aitken *et al.*, 2008; Corlett & Westcott, 2013; Cang, Wilson & Wiens, 2016; Jezkova &
22
23 109 Wiens, 2016), particularly in terrestrial ecosystems as opposed to marine ecosystems (Lenoir
24
25 110 *et al.*, 2020).

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30 111 Ongoing global warming is changing the geographic distribution of organisms on Earth
31
32 112 but their physiology and seasonal activities are also dramatically altered by climate change. In
33
34 113 fact, phenological changes, such as flowering or leaf senescence for plants, as well as mating,
35
36 114 breeding, spawning or hibernating for animals, are one of the most visible and sensitive
37
38 115 responses to ongoing global warming in natural ecosystems (Parmesan & Yohe, 2003; Cleland
39
40 116 *et al.*, 2007). For instance, in Europe, leaf-out of temperate trees has advanced by 8–15 days since
41
42 117 the 1950s (Fu *et al.*, 2019) and the migration dates of birds have advanced by about a week since
43
44 118 1959 in Canada and northern Europe (Lehikoinen *et al.*, 2019). In a temperate climate, spring
45
46 119 phenology reflects how the physiology and behaviour of organisms interacts with the
47
48 120 progressive return of favourable conditions for growth, i.e. mainly the increase in air
49
50 121 temperature and day length. Because animals are dependent on the development of plants, any
51
52 122 change in plant phenology may elicit a cascade of consequences in plant–animal interactions
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54 123 (Beard *et al.*, 2019; Visser & Gienapp, 2019; Kharouba & Wolkovich, 2020; Rehnus, Peláez
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3 124 & Bollmann, 2020). How the synchrony between animals and plant phenology will change
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5 125 under global warming is a challenging and timely question, but the consequences of such
6
7 126 synchrony are still poorly understood at the population, community and ecosystem levels due
8
9 127 to a lack of long-term ecosystem-based monitoring time series (but see Kharouba *et al.*, 2018;
10
11 128 Visser & Gienapp, 2019; Peláez *et al.*, 2020).

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13
14 129 The European Alps form an arc approximately 800 km in length from east to west and
15
16 130 around 200 km in width in western Europe with numerous peaks rising over 4,000 m. This
17
18 131 mountain system has been a prominent obstacle for plants and animals during the glacial and
19
20 132 post-glacial periods of the Pleistocene, thus being at the crossroads of several biogeographical
21
22 133 units (Taberlet *et al.*, 1998; Hewitt, 2000). The European Alps are a hotspot of biodiversity
23
24 134 offering myriad habitats and climates over very short distances (Körner, 2003; Zimmermann *et*
25
26 135 *al.*, 2013). About 13,000 vascular plant species (> 500 endemics) and about 30,000 animal
27
28 136 species inhabit the European Alps (Agrawala, 2007). Plants, animals and fungi living in this
29
30 137 region include generalist species found across all of Europe but also numerous specialist
31
32 138 species that have developed adaptations to harsh environments at high elevations, and are
33
34 139 found only in restricted areas such as mountain summits (i.e. sky islands). Angiosperm plant
35
36 140 species are found up to 4,507 m (*Saxifraga oppositifolia* L.) together with fungi and
37
38 141 arthropods (Körner, 2011), while bryophytes are found up to 4,559 m (Vaccari, 1914). In the
39
40 142 European Alps, as in all mountainous areas, the distance that an organism has to move in order
41
42 143 to cross isotherms is quite short compared to flatter regions, because of the sharp temperature
43
44 144 adiabatic gradient induced by elevational gradients (Rolland, 2003). This may, to a certain
45
46 145 extent, help species to track isotherm shifts better in mountainous regions (Brito-Morales *et*
47
48 146 *al.*, 2018). However, species living close to mountain summits will progressively be limited in
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50 147 habitat availability because moving upward generally means less land surface available, higher
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52 148 habitat fragmentation, and an inevitable increase in competition among co-existing species,
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3 149 eventually leading to local extinction events (Wiens, 2016; Giezendanner *et al.*, 2019). The
4
5 150 shift of species ranges in response to climate change is also increasingly hampered by human
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8 151 activities such as tourism, urbanization or agriculture, all of which alter species' habitat
9
10 152 suitability and distribution by fragmenting natural habitats (Elsen, Monahan & Merenlender,
11
12 153 2020). A warmer climate associated with changes in rain regime and snow cover will alter the
13
14 154 physiology and phenology of many species, which in turn will affect their fitness and biotic
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17 155 interactions. Numerous studies have shown tight relationships between snow conditions and
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19 156 population dynamics of alpine and arctic plants (e.g. Inouye, 2000, 2008; Körner, 2003; Wipf
20
21 157 & Rixen, 2010; Berteaux *et al.*, 2016) as well as population dynamics of animal species (e.g.
22
23 158 Korslund & Steen, 2006; Helle & Kojola, 2008; Robinson & Merrill, 2012). Hence, any
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26 159 changes in air temperature, precipitation and snow cover patterns in high mountain areas are
27
28 160 expected to elicit substantial modifications in plant–animal interactions. In the European Alps,
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30 161 the pace of climate warming is occurring at a faster rate than the average warming in the
31
32 162 northern hemisphere (Rebetez & Reinhard, 2008), generating faster velocities of isotherm
33
34 163 shifts. As a result, substantial shifts in spring phenology as well as numerous elevational range
35
36 164 shifts have already been observed for plants, animals and even fungi over recent decades (see
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38 165 studies in Tables 1 and 2). Long-term monitoring in the European Alps offers an excellent
39
40 166 natural laboratory to synthesize climate-related changes in spring phenology and elevational
41
42 167 distribution for a large array of taxonomic groups.

46
47 168 Here we aim at synthesizing the climatic changes that have occurred across the European
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49 169 Alps during recent decades and gathering the observed biotic responses in terms of both spring
50
51 170 phenological changes (the best documented season in terms of phenological observations) and
52
53 171 species range shifts, reported for flora, fauna and fungi. We provide a comprehensive
54
55 172 synthesis of these changes and discuss the consequences of such phenological and spatial
56
57 173 shifts on species interactions across different trophic levels. Moreover, we point out
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174 knowledge gaps that require more investigation in order to be able to predict future structural
175 and functional changes better at the ecosystem level under global warming.

176

177 **II. METHODS**

178 We searched the scientific literature for publications reporting either species elevational range
179 shifts or spring phenological trends over recent decades. For phenological changes, we
180 focused on the spring season because this is better documented in terms of phenological
181 observations compared to the autumn season (Gallinat, Primack & Wagner, 2015), allowing
182 for robust comparisons among taxa. We focused on any important phenological event such as
183 leaf emergence or flowering of plants, peaks of detectability for birds or observations of the
184 adult phase for amphibians and insects. For elevational range shifts, we focused on studies
185 reporting either shifts of the core distribution of a given species (hereafter ‘optimum’) or shifts
186 of the upper elevational limit (hereafter ‘leading edge’). We restricted our review to studies
187 relying on regular monitoring data covering at least 10 years across parts of the European Alps
188 (i.e. Austria, France, Germany, Italy, Lichtenstein, Slovenia and Switzerland) within the
189 period 1980–2020. For diachronic studies comparing historical and modern surveys, we used
190 only studies that conducted their modern survey(s) within the period 1980–2020 and where the
191 median year of the historical survey(s) was after 1950 [often called the ‘great acceleration’
192 period (Steffen *et al.*, 2015)] to avoid including decades with no or significantly lower
193 warming trends. Indeed, including studies using historical surveys prior to 1950 (e.g.
194 Holzinger *et al.*, 2008; Rumpf *et al.*, 2018) would inevitably underestimate the rate at which
195 biotic responses are taking place in response to ongoing climate change for recent decades.

196 We focused on the European Alps because this region is both a hotspot of biodiversity
197 and benefits from a long research history, allowing a long-term view and comprehensive
198 synthesis on climate change-related processes. We extended the study area to lowland regions

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3 199 in direct contact with the mountain range of the European Alps or to neighbouring mountain
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5 200 ranges (the Jura), provided that part of the European Alps was considered in the studied region
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7 201 and assumed to play a significant role in the results (e.g. Kuhn *et al.*, 2016).
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10 202 Raw data for phenological shift (per decade or per degree of warming) and migration
11
12 203 rate across elevations per unit time (per year or per decade) were extracted at the species level
13
14 204 from the publications reviewed herein, either from direct access *via* the journal webpage
15
16 205 (appendix or data depository), or indirectly by requesting species-level data from the study
17
18 206 authors. Depending on the study, different methods were used to generate species-level data
19
20 207 on phenological shift or elevational range shift per decade. For instance, some studies directly
21
22 208 reported the observed rates in phenological shift or elevational range shift per decade while
23
24 209 others reported the magnitude of the observed changes in phenology or elevational distribution
25
26 210 over a given time period. In the latter case we extracted information on the duration of the
27
28 211 time period covered by that study and computed the rates per decade. Phenological studies
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30 212 reporting the phenological change per degree of warming generally include a pre-season
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32 213 temperature window in their calculations, which is best correlated with the studied
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34 214 phenological event, i.e. a couple of weeks or months before the spring phenological event. For
35
36 215 more details, readers should refer to the publications listed in Table 1.
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42 216 All publications used for our synthesis are summarised in Tables 1 and 2, and the full
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44 217 data are provided as online supporting information in Tables S1 and S2, respectively. For
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46 218 more robust comparisons, taxonomic groups containing observations of phenological or range
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48 219 shifts for less than five species were discarded from our quantitative analyses, but are still
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50 220 included in the tables for completeness.
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54 221 In addition, we analysed two sources of previously unpublished data collected through a
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56 222 citizen science program in Switzerland: the *info fauna* database for both phenology and
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3 223 altitudinal migration of insects, reptiles and amphibians and the *PhenoForest* database for
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5 224 phenological trends of several tree species.
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8 225 From the Swiss central database of *info fauna*, we extracted all observations for
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10 226 amphibians, reptiles, lepidopterans, orthopterans, and odonates available between 1991 and
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12 227 2019. Although data collected before 1990 are available, we restricted our analyses to after
13
14 228 1990 because far fewer observers were active before 1990, which could influence trend
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16 229 analyses. Species with taxonomic uncertainty, with a limited number of observations per year
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18 230 (variable depending on taxonomic group, left to the experts' discretion), that are migrants or
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20 231 show other features that could impact the frequency of observations were also removed after
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22 232 careful examination by expert co-authors of this review. To avoid a distorting influence of
23
24 233 extreme values when assessing elevational range shifts from the raw data, we computed, for
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26 234 every year, the median (50%) and 95th percentile of the elevation as surrogates for the
27
28 235 optimum and leading edge, respectively, because these were less likely to be distorted than the
29
30 236 mean and maximum elevation values. Similarly, for spring phenology, we used the 5th
31
32 237 percentile of the distribution in the observations for a given species for every year. Linear
33
34 238 regressions were then conducted for all species of these parameters against years, and we
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36 239 report the slope values expressed per decade. In total, for *info fauna*, 273 animal species were
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38 240 included in our analyses, comprising 1,558,862 observations (average: 5,710
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40 241 observations/species; median: 2,807 observations/species; 5–95% quantile: 256–21,301) for
41
42 242 the altitude analysis and 1,560,265 observations (average: 5,715 observations/species; median:
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44 243 2,823 observations/species; 5–95% quantile: 196–20,380) for the phenology analysis. The *info*
45
46 244 *fauna* database gathers observations mainly from citizen volunteers and does not use a
47
48 245 systematic sampling design, rather representing haphazard sampling, which may introduce
49
50 246 statistical issues (Callaghan *et al.*, 2019). However, because we used only data from taxa with
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52 247 sufficient sample sizes and that were carefully checked by experts before they were entered
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3 248 into our database, we believe this data set should provide robust trends of how these species
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5 249 are currently migrating along elevational gradients. Additionally, the data from *info fauna* do
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8 250 not show identical trends among taxa; if a particular trend was due to observer bias, we would
9
10 251 expect to find similar patterns across various taxa, which was not the case.

12 252 The *PhenoForest* database consists of records of visual observations of the leaf-out
13
14 253 timing of eight species during the period 1998–2020 from volunteers in different sites in
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16
17 254 Switzerland (one observer per site, 16 permanent sites in total, 1–5 species per site). At each
18
19 255 site, 8–10 trees per species were identified and monitored every year by the same observer. To
20
21 256 estimate trends in the leaf-out dates over this study period, we applied a linear mixed-effect
22
23 257 model for each species with leaf-out dates as the response variable, year as the explanatory
24
25
26 258 variable and sites as a random intercept term, and extracted the estimated slope for each
27
28 259 species separately.

30 260 Following collection/calculation of all the species-level biotic responses in days per
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32
33 261 decade for shifts in spring phenology or meters per decade for elevational range shifts as
34
35 262 described above, we compared the estimated rates among taxonomic groups. We ran linear
36
37 263 mixed-effects models with species' phenological shift per year or species' elevational range
38
39 264 shift per decade as response variables, study/database as a random intercept term and
40
41
42 265 taxonomic group (with as many levels as taxonomic groups for which there were sufficient
43
44 266 data, i.e. groups containing at least five species) as the main fixed effect. Based on the model
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46 267 estimates of phenological shift per year or elevational range shift per decade for each
47
48
49 268 taxonomic group separately, we computed the associated 95% confidence intervals. *Post-hoc*
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51 269 Tukey tests were then applied to test for differences among the different taxonomic groups. In
52
53
54 270 the results, we report the mean shift of the phenology or migration of a given taxonomic group
55
56 271 across studies, using the estimated marginal mean value \pm CI from the mixed-effect model. We
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272 also report the mean \pm SE phenological and elevational shifts per study/database and
273 taxonomic group in Tables 1 and 2.

274 In order to visualize whether the rate of species migration lags behind the pace of
275 climate warming we computed the likely isotherm shifts that have occurred in the Alps since
276 1970. We used the annual warming trends shown in Fig. 1 for six stations across the Swiss
277 Alps of $0.36\text{ }^{\circ}\text{C decade}^{-1}$ (similar values are reported by the national offices of Meteorology
278 and Climatology, e.g. MeteoSwiss). To calculate the corresponding theoretical altitudinal
279 distance required to maintain the same air temperature, we applied an altitudinal lapse rate of
280 $0.51\text{--}0.58\text{ }^{\circ}\text{C }100\text{ m}^{-1}$, as typically evaluated for annual mean temperature across different
281 regions of the Alps [France, Germany, Austria, Italy and Switzerland (Rolland, 2003; Kirchner
282 *et al.*, 2013)]. The isotherm shift induced by climate warming was estimated in this way to
283 range between $+62$ and $+71\text{ m decade}^{-1}$ during the period 1970–2019.

284 All calculations and statistics were conducted using R 3.5.1 (R Core Team, 2017).

285

286 **III. SYNTHESIS**

287 **(1) Climate change in the European Alps**

288 *(a) Changes in air temperature, precipitation and snow cover*

289 *(i) Temperature*

290 Since the beginning of the 20th century, mean annual air temperature has increased by more
291 than 1.5°C across the European Alps (Böhm *et al.*, 2001; Begert, Schlegel & Kirchhofer,
292 2005; Rebetez & Reinhard, 2008), with this trend accelerating strongly during the second half
293 of the 20th century (Auer *et al.*, 2007; Acquafredda, Fratianni & Garzena, 2015) with an average
294 increase of about $0.36\text{ }^{\circ}\text{C decade}^{-1}$ between 1970 and 2019 (Klein *et al.*, 2016, Fig. 1). Air
295 temperature trends in the European Alps exceed the average trend observed over the Northern
296 Hemisphere by 1.6–2.5 times (Keiler, Knight & Harrison, 2010; Foster & Rahmstorf, 2011).

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3 297 The increase in air temperatures during the 20th century was most pronounced around the
4
5 298 altitude of the 0 °C isotherm (Serquet, Marty & Rebetez, 2013), in connection with the snow-
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7 299 albedo feedback of snow-covered surfaces and glaciers (Pepin & Lundquist, 2008; Scherrer *et*
8
9 300 *al.*, 2012). However, these trends hide strong seasonal disparities. During the 20th century in
10
11 301 Western Europe, air temperatures warmed more in winter compared to summer (Moberg *et al.*,
12
13 302 2006), but this ratio reversed by the end of the 20th and early 21st century (Klein *et al.*, 2018).
14
15 303 Hence, several studies have shown that summer and spring have warmed more than autumn
16
17 304 and winter since the 1970s (Rebetez & Reinhard, 2008; Klein *et al.*, 2018; Vitasse *et al.*,
18
19 305 2018a). Since the end of the 1980s, maximum air temperatures have been increasing more
20
21 306 than minimum temperatures in connection with the decrease in European air pollution and
22
23 307 particulate matter, especially in spring and at mid and high elevations (Rebetez & Reinhard,
24
25 308 2008; Vitasse *et al.*, 2018a).

309

310 *(ii) Precipitation and snow*

311 Annual precipitation has not changed across the European Alps over recent decades (Diolaiuti
312 *et al.*, 2012). Regionally, only a few increasing seasonal trends have been observed since the
313 beginning of the 20th century, mostly during autumn and winter (Schmidli & Frei, 2005;
314 Scherrer *et al.*, 2016). Winter precipitation sum has increased slightly, whereas trends towards
315 more intense but less frequent precipitation were observed in summer with no change in
316 overall precipitation sum (Moberg *et al.*, 2006; Appenzeller *et al.*, 2011; Fischer *et al.*, 2019).
317 Recently, European alpine countries have experienced several extreme drought events in
318 summer, associated with heat waves, which have led to forest dieback, vegetation damage and
319 insect outbreaks in the lowlands, particularly in 2003, 2012, 2015, 2016 and 2018 (Corona-
320 Lozada, Morin & Choler, 2019; Schuldt *et al.*, 2020). Intense hot drought events had also
321 occurred during the 20th century (e.g. in 1911, 1921, 1947, 1949, 1976) but air temperature

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3 322 was, on average, lower than today, so that the evapotranspiration in summertime was lower
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5 323 (Schär *et al.*, 2004) and consequently the vegetation was much less impacted by these events.
6
7 324 Because air temperature decreases steadily with elevation (and generally precipitation
8
9 325 increases), the climatic water balance of sites >1,200 m still remains positive in the central part
10
11 326 of the European Alps (Vitasse *et al.*, 2019). However, severe droughts are predicted to become
12
13 327 more frequent even at high elevations where organisms might be less adapted to cope with
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15 328 water limitation (Rosbakh *et al.*, 2017).

19 329 Snow cover has an important impact in plant and animal phenology in mountain
20
21 330 ecosystems. A significant reduction in the number of days with snow precipitation has been
22
23 331 reported at all elevations during the 20th century in the Alps, particularly since the 1980s and
24
25 332 in relation to warmer air temperatures (Laternser & Schneebeli, 2003; Pellicciotti, Bauder &
26
27 333 Parola, 2010; Valt & Cianfarra, 2010; Serquet *et al.*, 2011; Diolaiuti *et al.*, 2012; Marty &
28
29 334 Blanchet, 2012; Serquet *et al.*, 2013). A similar reduction has been observed across the
30
31 335 northern hemisphere since the 1970s (Hernández-Henríquez, Déry & Derksen, 2015),
32
33 336 especially in spring (Brown & Mote, 2009; Brown & Robinson, 2011), although this trend
34
35 337 varies widely at a global scale (Bormann *et al.*, 2018; Pulliainen *et al.*, 2020). Analyses of
36
37 338 snow water equivalent have shown a clear decrease in snow mass all over the European Alps
38
39 339 during the period 1973–2012, at all elevations and more pronounced in spring compared to
40
41 340 winter (Marty, Tilg & Jonas, 2017b). Mean snow depth has also been significantly reduced
42
43 341 during the same period in the European Alps at all elevations and for all seasons (Durand *et*
44
45 342 *al.*, 2009; Schöner, Auer & Böhm, 2009; Pellicciotti *et al.*, 2010; Marty & Blanchet, 2012;
46
47 343 Marty & Meister, 2012). Detailed analyses in the Swiss Alps have confirmed a general
48
49 344 decrease in all snow parameters at all elevations, with a faster reduction of snow cover at the
50
51 345 time of snowmelt compared to the time of snow onset (Klein *et al.*, 2016). Spring (March to
52
53 346 May) was the season with the highest air temperature increase over the last five decades, with
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3 347 a rate of $0.47\text{ }^{\circ}\text{C decade}^{-1}$ since 1970 in the Swiss Alps (Klein *et al.*, 2018, Fig. 1). This strong
4
5 348 warming has led to earlier snowmelt, for example $-5.2\text{ days decade}^{-1}$ across six locations in
6
7 349 the Swiss Alps ranging from 1,298 to 2,540 m between 1970 and 2019 (Fig. 1). In autumn
8
9 350 (September to November), the air temperature warming rate has been less than in spring,
10
11 351 although still sufficient to delay time of snow onset at an average rate of $+3.9\text{ days decade}^{-1}$
12
13 352 since 1970 for these six stations, leading to a significant increase in the snow-free period at an
14
15 353 average rate of $+9.1\text{ days decade}^{-1}$ in the Swiss Alps (Fig. 1). However, regional differences
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17 354 across the European Alps exist with on average stronger trends of snow depth reduction in the
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19 355 southern Alps over recent decades (Matiu *et al.*, 2021).
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26 357 *(b) Predicted climate change in the European Alps*

27
28 358 Air temperature will increase further in the coming decades if present emission rates of
29
30 359 greenhouse gases are not substantially reduced (IPCC, 2013). The difference between
31
32 360 predictions based on lower [representative concentration pathway (RCP) 2.6] or higher (RCP
33
34 361 8.5) greenhouse gas emission rates (IPCC, 2013) increases with time, particularly after 2050.
35
36 362 Déqué *et al.* (2007) predicted that air temperature in the European Alps would increase by
37
38 363 $0.30\text{ to }0.45\text{ }^{\circ}\text{C decade}^{-1}$ until 2100, with a higher expected increase in summer and autumn
39
40 364 and an increased frequency of summer heatwaves (Keiler *et al.*, 2010). Precipitations in
41
42 365 summer are expected to decrease over coming decades, although with a higher frequency of
43
44 366 extreme rainfall events (Rajczak & Schär, 2017; Hodnebrog *et al.*, 2019). Recent analyses
45
46 367 nevertheless showed that regional climate models (RCM, from the EURO-Coordinated
47
48 368 Regional Downscaling Experiment) could greatly underestimate the warming rate during the
49
50 369 growing season (Schwingshackl *et al.*, 2019; Boé *et al.*, 2020). This was due to models
51
52 370 omitting the plant physiological CO_2 response (Schwingshackl *et al.*, 2019) and
53
54 371 underestimating both the increase in shortwave radiation and changes in solar radiation
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3 372 connected with cloud cover and aerosols (Boé *et al.*, 2020). For the same reasons, regional
4
5 373 models also tended to underestimate the decrease in summer precipitation (Boé *et al.*, 2020) as
6
7
8 374 well as the increase in heavy rainfall events (Borodina, Fischer & Knutti, 2017).
9

10 375 A strong reduction of snow depth and snow cover is expected to continue at all
11
12 376 elevations across the European Alps during the 21st century (Jasper *et al.*, 2004; Rousselot *et*
13
14 377 *al.*, 2012; Schmucki *et al.*, 2015; Marty *et al.*, 2017a), particularly during the spring season
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16
17 378 (Magnusson *et al.*, 2010; Steger *et al.*, 2013). Permanent snow, glaciers and permafrost are
18
19 379 expected to decline strongly or disappear, with an overall melt of the snow cover in summer
20
21 380 (Magnusson *et al.*, 2010). At the end of the 21st century, continuous snow cover in winter may
22
23 381 only be present above 2,000 m, while mid-elevations (1,000–1,700 m) should experience
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25 382 random and/or discontinuous snow cover in about one in two winters (Schmucki *et al.*, 2017).
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28 383 These future expected changes in snow cover duration and thickness correspond to an average
29
30 384 upward elevation shift of 800 m of the snow cover by the end of the century, while snow cover
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33 385 seasons may be reduced by two or three months, depending on the scenario (Bavay,
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35 386 Grünewald & Lehning, 2013; Marty *et al.*, 2017a; Beniston *et al.*, 2018).
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37
38 387 Due to these rapid changes in air temperature and snowpack, the European Alps will
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40 388 undergo marked changes in the phenology and distribution of plants, animals and fungi, which
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42 389 are synthesized in the following sections.
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46 47 391 **(2) Phenological shifts**

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49 392 Our review reveals an advance in spring phenological events for most of the studied taxa, i.e.
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51 393 leaf-out and flowering for plants, singing activity, laying dates, arrival and hatching dates for
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53 394 birds, and the first yearly observation for insects, amphibians and reptiles although these were
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55 395 statistically significant only for reptiles and insects. There were also significant differences
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58 396 among these taxonomic groups (Fig. 2A). Reptiles and terrestrial flying insects such as
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3 397 Lepidoptera and Orthoptera showed the largest advance in their first yearly observation, with a
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5 398 significantly earlier -5.7 ± 3.8 days decade⁻¹ for reptiles (estimated marginal mean \pm CI; linear
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7 399 mixed-effects model) and -6.0 ± 1.0 days decade⁻¹ for terrestrial insects, whereas a non-
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9
10 400 significant trend towards a slight delay was found for the peak of singing activity, laying dates
11
12 401 or hatching dates of resident birds ($+1.3 \pm 4.5$ days decade⁻¹) and first yearly observation of
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14 402 amphibians ($+0.2 \pm 3.6$ days decade⁻¹; Fig. 2A). Insects with aquatic life stages (Odonata)
15
16 403 showed non-significant trends for an earlier first yearly observation of the adult stage ($-$
17
18 404 1.0 ± 2.2 days decade⁻¹, Fig. 2A). Plants also showed non-significant trends for an advance in
19
20 405 leaf-out or flowering of -2.8 ± 6.3 and -2.4 ± 2.7 days decade⁻¹ for herbaceous and woody
21
22 406 plants, respectively (Fig. 2A). A significant difference was found between semi-aquatic and
23
24 407 terrestrial insects (Table 1; Fig. 2A). Whereas resident birds showed a tendency for a slight
25
26 408 delay in their singing activity or laying dates ($+1.3 \pm 4.5$ days decade⁻¹), an advance was
27
28 409 detected for long- and short-distance migrant birds (-1.7 ± 3.1 and -3.2 ± 3.9 days decade⁻¹,
29
30 410 respectively; Fig. 2A), although these differences did not reach statistical significance. When
31
32 411 grouped by habitat type, a non-significant trend for a delay in singing activity or laying dates
33
34 412 was found for birds inhabiting forest or open land ($+0.5 \pm 6.9$ and $+0.6 \pm 5.9$, respectively),
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36 413 whereas a significantly different advance of about -7.5 ± 7.8 days decade⁻¹ was found for birds
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38 414 living in mixed habitats (Fig. S1).

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44 415 Regarding phenological sensitivity to air temperature, fewer studies were available for
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46 416 some taxa, potentially making it harder to detect statistically significant differences among
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48 417 taxa (Table 1, Fig. 2B). However, we also found significant advances in spring phenology per
49
50 418 degree of warming of -5.1 ± 3.9 days °C⁻¹ for woody plants and -4.9 ± 2.8 days °C⁻¹ for
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52 419 terrestrial insects, while non-significant trends for an advance were found in the other taxa.

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54 420 For plants, phenological events are largely mediated by temperature and have the
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56 421 potential to change considerably with climate warming. In alpine environments, the few long-
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3 422 term time series of phenological observations show the same consistent trends, for instance
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5 423 between the Rocky Mountains (USA), Greenland (Iler *et al.*, 2013) and the Tibetan plateau
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7 424 (Chen *et al.*, 2015). For the European Alps, we are not aware of any long-term studies of the
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9 425 phenology of alpine plants. However, indirect data for the beginning of vegetation growth
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11 426 detected by ultrasonic sensors (used to detect snow depth) are now available for about 20 years
12
13 427 across 30 alpine sites in the Swiss Alps (Vitasse *et al.*, 2017). These data reveal that vegetation
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15 428 onset in alpine plants occurred earlier at around -6.3 days $^{\circ}\text{C}^{-1}$, with no strong photoperiodic
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17 429 constraint, in agreement with findings from the Tibetan plateau (Chen *et al.*, 2015). At lower
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19 430 elevations in the Swiss Alps, long-term phenological observations are available from a citizen
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21 431 network. These data show a significant advance of leaf-out or flowering dates during the
22
23 432 period 1970–2012 by about -2.8 to -7.7 days $^{\circ}\text{C}^{-1}$ for various tree and shrub species and by
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25 433 about -3.7 to -7.4 days $^{\circ}\text{C}^{-1}$ for herbaceous species (Güsewell, 2014). It is known that spring
26
27 434 phenological plasticity to temperature varies strongly among tree species, which could alter
28
29 435 competition among species in response to global warming. For example, leaf-out of European
30
31 436 beech (*Fagus sylvatica*) is one of the least sensitive to air temperature change, with an advance
32
33 437 of less than -3 days $^{\circ}\text{C}^{-1}$, whereas ash (*Fraxinus excelsior*), sessile oak (*Quercus petraea*) and
34
35 438 larch (*Larix decidua*) are among the most sensitive at more than -6 days $^{\circ}\text{C}^{-1}$ (Migliavacca *et*
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37 439 *al.*, 2008; Vitasse *et al.*, 2013; Asse *et al.*, 2018; Bison *et al.*, 2019).

44 440 For animals, phenological changes are less documented and overall less pronounced for
45
46 441 large herbivores and birds that can migrate over long distances to track food availability and
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48 442 quality (i.e. tracking the ‘Green Wave’, e.g. Bischof *et al.*, 2012; Rehnus *et al.*, 2020). In the
49
50 443 lowland areas of the Swiss Alps (< 600 m), the date of highest singing activity of various birds
51
52 444 (mostly passerines), a proxy for the start of breeding, shifted earlier for the majority of species,
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54 445 and higher spring temperatures generally led to an earlier singing activity peak of around -1.1
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56 446 days decade $^{-1}$ for resident and short-distance migrant birds with slightly higher trends for
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3 447 trans-Saharan migrants (Strebel *et al.*, 2014; Table 1). Not surprisingly, insects seem to
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5 448 respond strongly to warming with the emergence date occurring earlier, for example by –21
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7 449 days decade⁻¹ for bark beetles (*Ips typographus*) over the period 1996–2005 in the south-
8
9 450 eastern Alps (Faccoli, 2009; Table 1). Similarly, butterflies seem to respond strongly to
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11 451 warming, with the purple emperor (*Apatura iris*) emerging earlier (–10.5 days decade⁻¹)
12
13 452 during the period 1982–2002 in northern Switzerland (Dell, Sparks & Dennis, 2005; Table 1).
14
15 453 Altermatt (2012) reported a temperature sensitivity of -4.9 ± 2.0 days °C⁻¹ for 28 butterfly
16
17 454 species studied in the Swiss lowlands over the period 1998–2010 (Table 1). Interestingly, our
18
19 455 review shows that within insects, species from Orthoptera and Lepidoptera have advanced
20
21 456 their spring phenology to a larger extent than species from Odonata (Fig. 2A). This might be
22
23 457 explained by their habitat use, because species of Odonata generally spend their larval stages
24
25 458 in ponds. The microclimate of ponds may buffer the effects of warming temperatures,
26
27 459 especially in spring due to the provision of water from the melting snowpack higher up,
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29 460 although more data will be necessary to allow robust comparisons of the phenological
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31 461 sensitivity of aquatic species to air temperature.
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40 463 (3) Elevational range shifts

41
42 464 Based on the current scientific literature focusing exclusively or partly on the European
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44 465 Alps, animals, fungi and plants have all shifted their optimum elevation upslope, reaching
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46 466 average rates of $+18.4 \pm 12.1$ ($N = 535$), $+18.8 \pm 26.8$ ($N = 118$) and $+24.8 \pm 13.6$ m decade⁻¹ ($N =$
47
48 467 1,480), respectively (mean \pm CI; Fig. 3A). All taxonomic groups, except semi-aquatic insects,
49
50 468 showed trends for a positive shift in optimum elevation (Fig. 3A), although this was
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52 469 statistically significant only for terrestrial insects ($+36.2 \pm 20.7$ m decade⁻¹), woody plants
53
54 470 ($+32.7 \pm 17.9$ m decade⁻¹) and herbaceous plants (23.1 ± 14.4 m decade⁻¹). The average upward
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56 471 shift obtained from *info fauna* data regarding the optimum elevation of butterflies ($+39.9$ m
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3 472 decade⁻¹, Table 2) agrees well with the trend reported in a recent study in Switzerland (+38 m
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5 473 between 2003 and 2010, or 48 m decade⁻¹) that systematically monitored butterfly
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7 474 communities (Roth, Plattner & Amrhein, 2014), suggesting that no major bias was introduced
8
9 475 by the haphazard sampling inherent in *info fauna* data. By contrast, ferns, birds and wood-
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11 476 decaying fungi showed small and non-significant changes in optimum elevation, ranging
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13
14 477 between +4 and +11 m decade⁻¹ (Fig. 3A).

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16
17 478 For the leading edge (upper elevational range limit), upward shifts were most
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19 479 pronounced for animals (on average +72.3±17.8 m decade⁻¹) than for plants (+28.2±21.8 m
20
21 480 decade⁻¹; Fig. 3B), with the exception of semi-aquatic insect species that showed a non-
22
23 481 significant trend for the leading edge to shift downward (−4.7±33.8 m decade⁻¹; Fig. 3B and
24
25 482 Table 2). Remarkably, only terrestrial insects (+90.5±14.0 m decade⁻¹) and reptiles (63.7±57.2
26
27 483 m decade⁻¹) showed an upward shift of their leading edge within the range or higher than the
28
29 484 pace of climate warming (Fig. 3B), estimated at ~62–71 m decade⁻¹ based on a warming rate
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31 485 of 0.36 °C decade⁻¹ (Fig. 1) and a temperature lapse rate of 0.51–0.58 m 100m⁻¹ (Rolland,
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33 486 2003; Kirchner *et al.*, 2013).

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40 488 *(a) Terrestrial plants and fungi*

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42 489 For plants, our review suggests that there may be substantial differences among the studied
43
44 490 taxonomic or functional groups, although these did not reach statistical significance, with
45
46 491 insignificant shifts in the optimal elevation of +12.0±26.9 and 4.2±33.7 m decade⁻¹ for ferns
47
48 492 and alpine plants and significant upward shifts of +23.1±14.4 and 32.7±17.9 m decade⁻¹ for
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50 493 herbaceous and woody species growing below the treeline (Fig. 3A). Notably, this general
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52 494 pattern among the taxonomic groups is the same for changes at the leading edge (Fig. 3B).
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54 495 Lenoir *et al.* (2008) showed for different mountain areas throughout France, including the
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56 496 western Alps, that the optimum elevation of 171 forest plants and trees moved upward in
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3 497 elevation at a mean rate of +29 m decade⁻¹ when comparing vegetation surveys conducted
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5 498 between 1905 and 1985 to surveys conducted between 1986 and 2005. However, when
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7 499 splitting the data between short-lived herbaceous species (e.g. grasses and sedges) and long-
8
9 500 lived woody species (trees and shrubs), Lenoir *et al.* (2008) found that only herbaceous plants
10
11 501 from the forest understorey have significantly shifted their elevational optimum upslope (mean
12
13 502 rate of +38 m decade⁻¹). Similarly, by revisiting historical relevés and species indicator values,
14
15 503 KÜchler *et al.* (2015) found an upward shift of forest plant species in the herbaceous layer of
16
17 504 Swiss forests at +10 m decade⁻¹ since the 1950s, while the elevational range of species from
18
19 505 the shrub and tree layers remained rather stable over the same time period. By contrast, our
20
21 506 quantitative review across the European Alps suggests that the optimum range of long-lived
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23 507 woody plants is shifting upward at a significant rate, at least at the same rate as non-alpine
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25 508 herbaceous plants (Fig. 3A). This discrepancy may stem from the fact that we did not
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27 509 constrain our review only to forest systems, unlike the above-mentioned studies which
28
29 510 specifically focused on range shifts of forest plants (Lenoir *et al.*, 2008; KÜchler *et al.*, 2015).
30
31 511 Thus, by including data from studies on forest systems with those reporting range shifts for
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33 512 woody plant encroachment beyond the treeline or following land abandonment below the
34
35 513 treeline, we have a greater opportunity to detect elevational range shifts for woody plants. By
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37 514 missing the upper part of the elevational gradient beyond the forest limit, studies restricted to
38
39 515 forest systems may have underestimated the true rate at which woody plant species are
40
41 516 responding to temperature increases or abandonment of land in the Alps. The dynamics of
42
43 517 recruitment of forest tree species at the upper elevational limits seems to be changing at a
44
45 518 relatively fast rate, with seedlings and saplings currently occurring well beyond the upper
46
47 519 elevational limit of adult trees (Vitasse *et al.*, 2012). Similarly, across several mountain areas
48
49 520 in western Europe, including the western Alps, Lenoir *et al.* (2009) reported differences in
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51 521 elevational distribution between seedlings and adult life stages of trees, suggesting an ongoing
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3 522 upward shift for woody plants but with quite high heterogeneity among species which could
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5 523 be due to species-specific variability in demographics and competitiveness (Scherrer *et al.*,
6
7 524 2020).

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10 525 The average rate at which alpine plant species shifted upslope appears to be lower than
11
12 526 for non-alpine plants or woody species below the treeline for both the optimum range and the
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14 527 upper elevational limits (Fig. 3), although note that these values did not differ statistically
15
16 528 significantly. This slower rate at which alpine plants may be shifting upslope could be due to
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18 529 lower dispersal ability, biotic interactions or possibly to the methods employed to assess such
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20 530 trends. For alpine plants, resurveys are often compared with historical surveys conducted
21
22 531 before 1950, i.e. during a period with lower warming rates than at present, but these studies
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24 532 were not included in our analysis, making this unlikely to explain the lower rate of upslope
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26 533 migration for alpine plants.

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30 534 While climate warming plays an undeniable role in the recent redistribution of plants in
31
32 535 mountain ecosystems (Steinbauer *et al.*, 2018), it might not be the only driver behind the
33
34 536 upslope shifts along elevational gradients: precipitation (Rapacciuolo *et al.*, 2014), land use
35
36 537 (Gehrig-Fasel, Guisan & Zimmermann, 2007; Guo, Lenoir & Bonebrake, 2018) or ongoing
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38 538 recolonization after the ‘Little Ice Age’ (Kammer, Schöb & Choler, 2007) might be additional
39
40 539 drivers, either accelerating or slowing down the rate of elevational range shifts. For example,
41
42 540 the treeline ecotone has been influenced by farming activities for several thousand years in the
43
44 541 Alps (Tinner & Theurillat, 2003), and a large part of this recent upward shift has been
45
46 542 attributed to substantial changes in land use, including: (i) land abandonment in the Swiss and
47
48 543 Austrian Alps (Gehrig-Fasel *et al.*, 2007; Gellrich *et al.*, 2007; Tasser *et al.*, 2007), which
49
50 544 seems to explain the large upward shift of *Abies alba* observed since the 1950s in the west
51
52 545 central Alps (Chauchard *et al.*, 2010), and (ii) a reduction of cattle grazing, especially in the
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54 546 Italian Alps (Piotti *et al.*, 2007). By excluding open habitats in their analyses, Bodin *et al.*

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2
3 547 (2013) showed that the upward shift they initially found for understorey forest plants became
4
5 548 insignificant, a result that may be related to forest microclimate dynamics potentially buffering
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7 549 the effects of warming for understorey plants compared with plant communities from more
8
9 550 open habitats (von Arx *et al.*, 2013; De Frenne *et al.*, 2019; Zellweger *et al.*, 2020). In some
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11 551 studies, a considerable part of the analysed herbaceous species may also shift downward
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13
14 552 (Lenoir *et al.*, 2010; Bodin *et al.*, 2013), potentially explained by more intensive management
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16
17 553 (disturbance) at lower elevations compared to forests at higher elevations (Lenoir *et al.*, 2010).

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19 554 Interestingly, fungi may also be shifting their elevation. Although data in the Alps
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21 555 originated from a single study, that study assessed the shift in optimum elevation of 118
22
23 556 species (Diez *et al.*, 2020). They found values ranging between +10.7 and +23.6 m decade⁻¹
24
25 557 for wood-decaying and soil-dwelling fungi with an intermediate value for ectomycorrhizal
26
27 558 fungi (+21.0 m decade⁻¹) (Table 2, Fig. 3A). A slower response of wood-decaying fungi
28
29 559 would be consistent with their dependence on wood resources and particularly dead wood,
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31 560 with the availability of woody plants likely delayed compared to the rate of climate change.
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36 37 562 (b) *Terrestrial animals*

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39 563 Except for birds, elevational range shifts of animal species in the Alps have been less
40
41 564 documented than for plants, with direct evidence available only for some groups. Our review
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43 565 reveals that terrestrial insects have moved significantly upslope in terms of both the optimum
44
45 566 and the leading edge (Fig. 3). In an analysis of four orders of insects, a significant upslope
46
47 567 movement is seen for each of the groups Lepidoptera, Coleoptera and to a lesser extent
48
49 568 Orthoptera in both measures of elevational range (Fig. 4). For semi-aquatic insects from the
50
51 569 group Odonata, neither range measure has changed significantly (Fig. 4). Insects, like most
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53 570 ectotherms, are very sensitive to changes in air temperature and consequently are likely to
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55 571 track climate warming closely. Accordingly, numerous upward range shifts have been
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3 572 documented for terrestrial insects, especially for pests which receive much more attention. For
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5 573 example, upward shifts in the elevational range of outbreaks of the European spruce bark
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7 574 beetle (*I. typographus*) were related to the increased frequency of drier summers in the Italian
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9 575 Alps (Marini *et al.*, 2012). The pine processionary moth (*Thaumetopoea pityocampa*) shifted
10
11 576 its distribution upward between 1975 and 2004 at average rates of +70 m decade⁻¹ and +29 m
12
13 577 decade⁻¹ on the southern and northern slopes of the Italian Alps, respectively, with this shift
14
15 578 related to the increase in minimum winter air temperature (Battisti *et al.*, 2005). As
16
17 579 ectotherms, insects do not regulate their body temperature, and thus climatic variation in
18
19 580 temperature will have a direct effect on their physiology. For example, warmer air
20
21 581 temperatures in summer generally reduce European bark beetle development time (i.e.
22
23 582 increased voltinism) (Jakoby, Lischke & Wermelinger, 2019), and therefore are likely to
24
25 583 increase infestation pressure (Marini *et al.*, 2012; Jakoby *et al.*, 2019). The reproductive cycle
26
27 584 of insects is expected to be faster under warmer air temperatures, potentially allowing an extra
28
29 585 generation per growing season at all elevations by the end of the century for European spruce
30
31 586 bark beetle (Jakoby *et al.*, 2019). Even though molluscs have a relatively low capacity to move
32
33 587 over large distances, an upward shift of the land snail *Arianta arbustorum* of about 164 m has
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35 588 been reported in a comparison of its distribution in 1916–1917 with its distribution in 2011–
36
37 589 2012 in the eastern Alps, and this upward shift was most pronounced (around 233 m) on
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39 590 south-facing slopes (Baur & Baur, 2013). Both habitat and microclimate are important factors
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41 591 for these organisms and the authors stressed that, on some mountain slopes, snails have
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43 592 already reached natural barriers (vertical rock walls with no soil), that prevent further upward
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45 593 shifts.

54 594 The mean elevation of reptiles has also changed considerably showing a non-significant
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56 595 shift in optimum elevation of +24.2±25.4 m decade⁻¹ (Fig. 3A) and a significant shift in their
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58 596 leading edge elevation of +63.7±22.3 m decade⁻¹; Fig. 3B). Nevertheless, more investigation
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3 597 should be conducted for this group as this result originates from a single network of citizen
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5 598 observations in the Alps. An increase in air temperature will allow reptiles to colonise higher
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8 599 elevations, although the extent to which this is possible may be limited by oxygen availability
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10 600 (Jacobsen, 2020).

11
12 601 Interestingly, we found no significant differences in the upwards shift of optimum
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14 602 elevation between plants, fungi and animals (Fig. 3A), whereas animals appear to be
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17 603 responding fastest in terms of the leading edge, especially for terrestrial insects (Fig. 3B). The
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19 604 distribution of mammals and birds is mainly driven by habitat and food availability, and a
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21 605 change in temperature may not affect their distribution directly if features of their habitat
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24 606 remain stable or depend more on the micro- than the macroclimate (Jähnig *et al.*, 2020) and on
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26 607 plant phenology (Peláez *et al.*, 2020). For instance, two studies conducted on European roe
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28 608 deer (*Capreolus capreolus*) identified a strong dependence on the quality of food resources,
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30 609 with individuals performing long-distance seasonal movements upward and downward to
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33 610 locate food resources within their home range and thus tracking plant phenology (Gaudry *et*
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35 611 *al.*, 2015; Peláez *et al.*, 2020). Another study revealed an upward shift of about $+37.5 \pm 10.3$ m
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37 612 decade⁻¹ of four mountain ungulate species in the Swiss Alps based on hunting records,
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39 613 attributing this upward shift to the lengthening of the snow-free period (Büntgen *et al.*, 2017,
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41
42 614 Table 2).

43
44 615 The effects of climate warming on animal distribution are likely to be complex, and will
45
46 616 include indirect effects. A good example is the Alpine chough (*Pyrrhocorax graculus*) that
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48 617 nests at high elevations in cavities and fissures on inaccessible rock faces and forages in open
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50
51 618 alpine meadows (Delestrade & Stoyanov, 1995). Climate and land use are affecting the
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53 619 distribution of plants and forests but obviously not the distribution of the cliffs it uses for
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56 620 nesting. While upward shifts in distribution of birds have been detected in some areas in the
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58 621 Alps such as the central Swiss Alps (Maggini *et al.*, 2011; Knaus, 2018), several other studies
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3 622 documented only marginal changes or no change in spite of significant air temperature
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5 623 increases during the study period (Archaux, 2004; Popy, Bordignon & Prodon, 2010).
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7 624 Consistently, our results revealed rather low and insignificant rates of optimum elevational
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9 625 range shift for birds in general, on average $+10.3 \pm 17.5$ m decade⁻¹, but Table 2 shows that
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11 626 there was much variation in the calculated values, with a trend for higher values in the Eastern
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13 627 and Southern Alps. This may be partly a result of human-induced land-use changes (Knaus,
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15 628 2018) as in these regions a strong upward shift of the treeline and reforestation of formerly cut
16
17 629 or unforested areas has taken place, moving up the habitat of specialized alpine birds such as
18
19 630 the rock ptarmigan (*Lagopus muta*) (Pernollet, Korner-Nievergelt & Jenni, 2015). Given their
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21 631 ecological role as consumers, it is likely that responses of bird communities to climate change
22
23 632 will lag behind that of some other taxonomic groups (Devictor *et al.*, 2012). It is possible that
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25 633 most specific elevational range shifts in mobile species like birds are related to site-specific
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27 634 factors associated with food availability, while for forest plants (Bertrand, Gegout &
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29 635 Bontemps, 2011) biotic interactions and population dynamics are likely to be more important
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31 636 (Scherrer *et al.*, 2020).
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40 638 (c) *Freshwater ecosystems*

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42 639 For freshwater ecosystems, only a few studies are available worldwide (Table 2), with several
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44 640 of these from the Alps. Comte & Grenouillet (2013) reported, across different mountain ranges
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46 641 in France including the western Alps, that the elevational range of stream fishes shifted
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48 642 upslope at a mean rate of about $+13.1 \pm 40.8$ m decade⁻¹ during the period 1986–2006 (Fig.
49
50 643 3A). For amphibians, dragonflies and damselflies, which depend directly on lakes, ponds,
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52 644 bogs, fens, streams and streamlets for their habitats, no significant upward shift was found in
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54 645 their optimum or leading edge elevation. The slower migration rates of semi-aquatic (e.g.
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56 646 dragonflies) and aquatic (e.g. fishes) animals compared to terrestrial animals or plants might
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3 647 be due to their strong dependence on freshwater habitats which are heavily fragmented by
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5 648 human activities (e.g. dams) and are also likely to exert strong microclimate buffering on
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7 649 warming rate, especially within mountain ranges where streams are fed by snow and glacier
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9 650 melt (McLaughlin *et al.*, 2017). In addition, most of these organisms are dependent on the
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11 651 vegetation that structures their habitat. Typically, dragonflies inhabiting subalpine and alpine
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13 652 zones live in bogs, fens and their associated small water bodies and runoff. The vegetation of
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15 653 these habitats is very specific and species requirements in terms of vegetation structure are not
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17 654 met in the pioneer water bodies of the upper level. The slower migration rate of these species
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19 655 could therefore partially be explained by their requirement for colonization by vegetation to
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21 656 occur first to offer new potential habitats for them. The formation of new bogs, fens or
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23 657 swamps may take several decades or even centuries.
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31 659 **(4) Plant–animal interactions mediated by species-specific phenological and spatial shifts**

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33 660 On the one hand, because plants are the first link of the food web, changes in plant phenology
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35 661 and composition will affect food quantity and quality for higher trophic levels, and may thus
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37 662 affect complex trophic interactions (Plard *et al.*, 2014; Thackeray *et al.*, 2016; Kharouba *et al.*,
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39 663 2018; Renner & Zohner, 2018; Kharouba & Wolkovich, 2020), animal performance (Sheridan
40
41 664 & Bickford, 2011) and species migration (Büntgen *et al.*, 2017; Peláez *et al.*, 2020; Rehnus *et*
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43 665 *al.*, 2020). Conversely, numerous seed plants are pollinated and dispersed by animals, and are
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45 666 affected by their interactions with herbivores, thus animal range shifts will be intimately
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47 667 involved with plant range shifts. Responses of herbivores to climatic changes are generally
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49 668 mediated through plant quality and quantity (Myserud *et al.*, 2001, 2008; Peláez *et al.*, 2020;
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51 669 Rehnus *et al.*, 2020). In temperate regions, vegetation quantity gradually increases in spring to
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53 670 reach a maximum in the middle of summer, while vegetation quality is generally highest
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55 671 shortly after the beginning of vegetation growth in spring. In mountain ecosystems, mobile
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3 672 organisms can track these changes by migrating upslope, following the ‘green wave’ induced
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5 673 by the progress of the season (Bischof *et al.*, 2012; Büntgen *et al.*, 2017; Herfindal *et al.*,
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7 674 2019). Migratory bird species have also been observed to follow this peak in nutrient
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9 675 availability during spring migration (Van der Graaf *et al.*, 2006). Our review found that birds
10
11 676 showed relatively small phenological and spatial changes in response to warming, perhaps
12
13 677 because birds are vagile and thus can adapt easily to changes in food availability. Similarly,
14
15 678 the parturition date of the European roe deer was shown to correlate better with spring plant
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17 679 phenology than with elevation in Switzerland (Peláez *et al.*, 2020). By contrast, species that
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19 680 are less mobile may become desynchronized in relation to their food resources as these move
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21 681 upwards in response to warming.
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26 682 An example of in which such desynchronization has had a positive biotic effect for trees
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28 683 is in the frequency of outbreaks of the larch budmoth (*Zeiraphera griseana*), which
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30 684 historically occurred over 12 centuries every 8–9 years but disappeared after 1982 in the
31
32 685 Engadine (eastern Swiss Alps). This was suggested to be due to a mismatch between the insect
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34 686 life cycle and larch budbreak (Esper *et al.*, 2007), which might have depended on climate
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36 687 warming (Johnson *et al.*, 2010). A recent outbreak did take place in 2017–2018, which was
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38 688 correlated with cold winter temperatures that reduced energy consumption during diapause in
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40 689 the moths, allowing them to emerge more in synchrony with the new foliage (Büntgen *et al.*,
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42 690 2020). Warmer winters may continue to decrease the fitness of this insect in the future and
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44 691 upward elevational shifts of outbreak epicentres are expected.
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49 692 On the contrary, many trees may experience more frequent severe defoliation due to pest
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51 693 outbreaks because warmer temperatures are expected to accelerate the life cycles of insects,
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53 694 potentially increasing the number of generations per season (Colombari *et al.*, 2012; Jakoby *et*
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55 695 *al.*, 2019). For example, the warmer and drier conditions that occurred in the late 1980s in the
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57 696 Italian prealps reduced the mortality of the web-spinning sawfly (*Cephalcia arvensis*) and
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3 697 accelerated its development, causing severe defoliation of Norway spruce (*Picea abies*)
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5 698 needles on which the larvae feed (Marchisio, Cescatti & Battisti, 1994). Similarly, pine shoot
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7 699 beetles (*Tomicus piniperda*) and other bark beetles are likely to weaken Scots pine (*Pinus*
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9 700 *sylvestris*) and Norway spruce in the inner valleys of the European Alps, where they already
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11 701 suffer from drought, under warmer climates that will permit additional insect generations
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13 702 during the growth season (Rigling & Cherubini, 1999; Rebetez & Dobbertin, 2004; Jakoby *et*
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15 703 *al.*, 2019; Schneider, Comte & Rebetez, 2021). Such differences in phenological sensitivity to
16
17 704 temperature are therefore expected to modify food-web interactions under climate change
18
19 705 (Vitasse *et al.*, 2011; Roberts *et al.*, 2015; Asse *et al.*, 2018). Phenological differences between
20
21 706 low- and high-elevation trees have reduced considerably over recent decades in the Swiss Alps
22
23 707 due to a stronger phenological advance at higher elevations (Vitasse, Signarbieux & Fu,
24
25 708 2018b), putting these plants at higher risk of frost exposure (Vitasse *et al.*, 2018a) and
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27 709 reducing the total period of availability of high-quality food for herbivores that follow the
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29 710 ‘green wave’ (Myerud *et al.*, 2008).

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31 711 In alpine environments, the life cycles of many plant and animal species are reliant on
32
33 712 the date of snowmelt and the rapid greening that follows. For example, variation in the
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35 713 snowpack accounts for a substantial part of variation in survival (about 16%) and reproduction
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37 714 (29%) of alpine marmots (*Marmota marmota*) (Tafani *et al.*, 2013). Snow cover phenology is
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39 715 the main driver of foraging habitat selection for the white-winged snowfinch (*Montifringilla*
40
41 716 *nivalis*) during the breeding season (Resano-Mayor *et al.*, 2019). Earlier snowmelt leads to
42
43 717 earlier vegetation onset which in turn increases the reproductive success of the rock ptarmigan
44
45 718 (*Lagopus muta*) (Novoa *et al.*, 2008), but decreases the litter size of alpine marmots (Tafani *et*
46
47 719 *al.*, 2013). Similarly, earlier vegetation onset due to warming can increase survival of ibex
48
49 720 (*Capra ibex*) through earlier access to food resources in spring (Pettorelli *et al.*, 2007), but a
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51 721 reduction of the snowpack in winter can also reduce the quality of the vegetation available in
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3 722 spring (Robinson & Merrill, 2012).
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5 723 The above examples of species interactions that are affected by phenological synchrony
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7 724 represent direct effects on a few specific taxonomic groups; indirect and more complex species
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9 725 interactions involving several trophic levels (network analyses) still await detailed
10
11 726 investigation. How the synchrony between winter climatic conditions, insect diapause, bird
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13 727 activity and spring vegetation is affected will determine the ability of many species to adapt to
14
15 728 climate change. This nascent research field should receive more attention to allow us to
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17 729 anticipate structural changes across multiple levels of ecosystems (Kharouba *et al.*, 2018;
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19 730 Visser & Gienapp, 2019).
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27 732 **(5) Research gaps and ecosystem-based monitoring**

28 733 Alpine ecosystems and the factors influencing species distributions have a long research
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30 734 history in the European Alps (Braun-Blanquet, 1954; Offner & Le Brun, 1956), for example
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32 735 with common garden experiments at different altitudes being performed in the Mont-Blanc
33
34 736 range in the late 19th century (Bonnier, 1888). We now have much data on elevational and
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36 737 phenological shifts for several taxa, and a better understanding of the factors influencing
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38 738 phenology and species distribution. This review provides evidence that recent climate change
39
40 739 may be affecting a wide range of taxonomic groups. However, our review also emphasizes
41
42 740 major gaps in our knowledge, especially regarding biotic responses to climate change, and in
43
44 741 particular, to a lack of long-term and ecosystem-based monitoring that could allow us to
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46 742 disentangle the direct and indirect effects of climate and land-use changes on different trophic
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48 743 levels (Yoccoz, Delestrade & Loison, 2010; Ims & Yoccoz, 2017).
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54 744 Long-term ecosystem research (LTER) programs exist in the Alps, but mostly with a
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56 745 focus on vegetation and soil, often in connection to ecosystem services and landscape patterns
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58 746 (Tappeiner, Borsdorf & Bahn, 2013; Lavorel *et al.*, 2017; Rogora *et al.*, 2018). They do not
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3 747 tend to integrate other ecosystem components such as herbivores, granivores and carnivores
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5 748 from groups as diverse as insects, birds and mammals. There is, however, evidence that
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7 749 changes in the abundance and distribution of species may be related to ecological interactions
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9
10 750 [e.g. the mismatch between larch leaf-out and budmoth emergence (Büntgen *et al.*, 2009;
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12 751 Johnson *et al.*, 2010)], or involve multiple trophic levels (Burgess *et al.*, 2018). The data
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14 752 available for different taxonomic groups often come from different time periods or places. The
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16
17 753 absence of a common design makes it difficult to build causal models integrating direct and
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19 754 indirect effects [e.g. Grace & Irvine, 2020; but see Thuiller *et al.* (2018) for a species
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21 755 distribution modelling approach to plant–herbivore interactions]. Our analysis identified a
22
23 756 large heterogeneity in species responses to climate change, making it difficult to understand
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25
26 757 and predict changes at the ecosystem level (Mouquet *et al.*, 2015). Although citizen science
27
28 758 has allowed the collection of a large amount of data from haphazard observations, there is a
29
30 759 clear need for more systematic monitoring. Joint analysis of these two sources of data would
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32
33 760 allow unbiased inferences (Dorazio, 2014). Developing integrated monitoring programs
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35 761 focusing on different trophic levels, and combining these with underlying conceptual models
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37 762 of the effects of climate and land-use changes on ecosystem structure and functioning should
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40 763 be a priority.

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45 765 **IV. CONCLUSIONS**

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47 766 (1) In the European Alps, spring phenology has advanced over recent decades for all taxa,
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49 767 except birds and amphibians, with these advances being statistically significant for
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51 768 ectothermic animals such as terrestrial insects and reptiles.

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54 769 (2) We found a trend for almost all studied taxa to shift their distribution range upslope, with
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56 770 significant changes in optimum elevation found for terrestrial insects, herbaceous and woody

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3 771 plants and in leading edge elevation for terrestrial insects, reptiles, birds and herbaceous
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5 772 plants.

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8 773 (3) We suggest that the trend for upward shift likely reflects the strong warming and the
9
10 774 receding of snow cover that has occurred across the European Alps over recent decades and
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12 775 reflects the tracking by these taxa of their climatic niche, although regional land-use changes
13
14 776 may also provide an explanation in some cases.

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17 777 (4) With the possible exception of some groups of terrestrial insects, such as butterflies, the
18
19 778 trend for an upward shift in plants, fungi and animals appears currently too slow to track
20
21 779 isotherm shifts induced by climate warming. Indeed, an upward shift of about 330 m would be
22
23 780 necessary to match the air temperature rise of close to 1.8°C that has occurred since 1970 in
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25 781 the European Alps region (i.e. 0.36 °C per decade). This roughly corresponds to a mean shift
26
27 782 of elevational range of about +62–71 m decade⁻¹, assuming an annual adiabatic lapse rate of
28
29 783 0.51–0.58 °C 100 m⁻¹ as measured across the Alps (Rolland, 2003; Kirchner *et al.*, 2013). The
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31 784 mean upward shift of most of the species groups observed over the last decades clearly lags
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33 785 behind this value (between –2 and +34 m decade⁻¹ for the optimum elevation and between –5
34
35 786 and +64 m decade⁻¹ for the upper elevational limit), except for terrestrial insects (+36.2 and
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37 787 +90.5 m decade⁻¹ for the optimum and upper elevational limits, respectively).

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40 788 (5) Species interactions mediated by phenological and spatial shifts are likely to be altered by
41
42 789 climate warming but very few studies currently focus on biotic interactions across multiple
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44 790 trophic levels. Integrating monitoring programs at ecosystem levels should be fostered to
45
46 791 allow better predictions of changes in plant and animal communities in response to climate
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48 792 change.

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51 793 (6) This review provides a valuable synthesis for future research focusing on the responses of
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53 794 organisms to climate warming in the European Alps.

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4
5 797 **AVAILABILITY**

6
7 798 We are grateful to all volunteers who provided observations for the following databases used
8
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12
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14
15 802 S.U. collected the data. Y.V. and J.L. synthesized the data. S.U. analysed the data from the *info*
16
17 803 *fauna* database and Y.V. from the *PhenoForest* database. M.R. wrote most of Section III.1
18
19 804 with contributions from G.K., who also created Fig. 1. Y.V. and J.L. wrote most of the text
20
21 805 with substantial inputs from all co-authors.

22
23 806 **Data availability:** all raw data at species-level resolution used in the quantitative analyses are
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25 807 provided in the online supporting information.

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29 809 **VI. REFERENCES**

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1356 VII. SUPPORTING INFORMATION

- 1357 Additional supporting information may be found online in the Supporting Information section
1358 at the end of the article.

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3 1359 **Fig. S1.** Mean phenological shift of the singing activity or laying dates per decade for birds
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5 1360 classified according to habitat.
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7 1361 **Table S1.** Spring phenological change per decade or/and per degree for each studied species.
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9 1362 **Table S2.** Elevational range shifts of the optimum distribution (i.e. elevation of maximum
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11 1363 abundance) or/and the leading edge (i.e. the upper range limit) for each studied species.
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3 1364 **Figure legends**
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8 1366 **Fig. 1.** Long-term time series of snow parameters (snowmelt timing and length of the snow
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10 1367 free period) and mean air temperature (spring temperature from March to May and annual
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12 1368 temperature) at six sites spread across the Swiss Alps during the period 1970–2019.
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14 1369 Data updated from Klein *et al.* (2016) representing yearly average anomalies over the period
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16 1370 1970–2019 across six sites in Switzerland located between 1,298 and 2,540 m (Arosa, Davos,
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18 1371 Grächen, Grimsel Hospiz, Scuol and Weissfluhjoch). Estimated trends from the Theil-Sen
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20 1372 estimator method across the six sites are reported with the associated standard errors (grey
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22 1373 shading) for each snow and temperature parameter. Significance of the slopes was tested using
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24 1374 Mann-Kendell tests, see Klein *et al.* (2016) for more details.
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31 1376 **Fig. 2.** Spring phenological change per decade (A) or per degree (B) for different plant and
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33 1377 animal groups studied in the European Alps region. Values correspond to the estimated
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35 1378 marginal mean of the mixed-effect model with study as a random factor; error bars are 95%
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37 1379 confidence intervals. The period of time varied among studies but was always more than 10
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39 1380 years within the period 1980–2020. Only groups with more than five species are shown (all
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41 1381 studies are reported in Table 1). Abbreviations: ldm, long-distance migrants; sdm, short-
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43 1382 distance migrants; res., resident; semi-aq., semi-aquatic. Different letters among groups
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45 1383 indicate significant differences (*post-hoc* Tukey tests at $\alpha = 0.05$).
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51 1385 **Fig. 3.** Empirical evidence for elevational range shifts of (A) the optimum distribution (i.e.
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53 1386 elevation of maximum abundance) and (B) the leading edge (i.e. the upper range limit)
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55 1387 reported for groups of taxa in the European Alps region. Values correspond to the estimate of
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57 1388 the mixed-effect model with study as a random factor; error bars are 95% confidence intervals.
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3 1389 The period of time investigated varied among studies but was always more than 10 years
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5 1390 within the period 1980–2020, or for diachronic studies comparing historical and modern
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8 1391 surveys, the modern survey was conducted within the period 1980–2020, and the median year
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10 1392 of the historical survey(s) was after 1950. Only groups with more than five species are shown
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12 1393 (all studies are reported in Table 2). Abbreviations: ecm, ectomycorrhizal; sapro., saprophytic;
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14 1394 semi-aq., semi-aquatic. Different letters among groups indicate significant differences (*post-*
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17 1395 *hoc* Tukey tests at $\alpha = 0.05$).

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22 1397 **Fig. 4.** Mean elevational shift per decade for four different orders of insects in terms of (A) the
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24 1398 optimum elevation (i.e. elevation of maximum abundance) and (B) the leading-edge elevation
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26 1399 (i.e. the upper range limit). Values correspond to the estimate of the mixed-effect model with
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28 1400 study as a random factor; error bars are 95% confidence intervals. The period of time
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30 1401 investigated varied among studies but was always higher than 10 years within the period
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33 1402 1980–2020. Different letters among groups indicate significant differences (*post-hoc* Tukey
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35 1403 tests at $\alpha = 0.05$).

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2 1404 Table 1. Documented spring phenological changes in animals and plants in the European Alps over the recent decades. Mean \pm standard errors
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5 1405 are reported where data are available for more than one species. For information on the *info fauna* and *PhenoForest* databases, see Section II.
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7 1406 The data set used for this table is provided as supporting online information in Table S1. Abbreviations: ldm, long-distance migrants; sdm, short-
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9 1407 distance migrants; res., resident.

Taxa	Study period	Area	Number of species	Phenological variable	Trends (days decade ⁻¹)	Temperature sensitivity (days °C ⁻¹)	References
PLANTS							
Woody plants	1970–2012	Alps and lowlands in Switzerland	14	Leaf-out or flowering	-3.4 \pm 0.3	-5.1 \pm 0.4	Güsewell (2014)
Herbaceous	1970–2012	Alps and lowlands in Switzerland	5	Flowering	-2.8 \pm 0.4	-5.6 \pm 0.6	Güsewell (2014)
Trees	1998–2020	Alps and lowlands in Switzerland	8	Leaf-out	-2.2 \pm 0.7	NA	<i>PhenoForest</i>
Woody plants	2005–2016	French Alps	6	Leaf-out	-0.5 \pm 2.3	NA	Bison <i>et al.</i> (2019)
ANIMALS							
Birds							
Birds (res.)	1995–2019	Lowland areas in Switzerland	8	Singing activity	+2.5 \pm 3.6	-2.1 \pm 0.8	Strebel <i>et al.</i> (2014)
Birds (sdm)	1995–2019	Lowland areas in Switzerland	12	Singing activity	-3.5 \pm 3.8	-1.0 \pm 0.5	Strebel <i>et al.</i> (2014)
Birds (ldm)	1995–2019	Lowland areas in Switzerland	14	Singing activity	-1.7 \pm 1.5	-1.0 \pm 0.5	Strebel <i>et al.</i> (2014)
<i>Passer italiae</i> (res.)	1982–2006	Northern Italy	1	Laying dates	-1.9	-1.7	Rubolini <i>et al.</i> (2007)
<i>Sturnus vulgaris</i> (sdm)	1982–2006	Northern Italy	1	Laying dates	-0.1	-0.2	Rubolini <i>et al.</i> (2007)
Birds (ldm)	1982–2006	Northern Italy	6	Arrival or laying dates	-1.8 \pm 0.8	-1.0 \pm 0.6	Rubolini <i>et al.</i> (2007)
<i>Ficedula hypoleuca</i> (ldm)	1960–1995	South Germany	1	Arrival dates	-0.7	0.06	Hölzinger (1997)
<i>Lagopus muta</i> (res.)	2000–2009	Northern French Alps	1	Median hatching date	-4.9	-4.2	Novoa <i>et al.</i> (2016)
Insects							
<i>Ips typographus</i>	1996–2005	Southeastern Alps	1	First observation	-21	NA	Faccoli (2009)
Lepidoptera, butterflies	1998–2010	Swiss lowlands	28	First observation	NA	-4.9 \pm 2.0	Altermatt (2012)
<i>Apatura iris</i>	1982–2002	Forest near Basel, Switzerland	1	First observation	-10.5	-6.4	Dell <i>et al.</i> (2005)
Lepidoptera, butterflies	1991–2019	Switzerland	138	First observation	-6.6 \pm 0.5	NA	<i>info fauna</i>
Odonata	1991–2019	Switzerland	40	First observation	-1.0 \pm 0.5	NA	<i>info fauna</i>
Orthoptera	1991–2019	Switzerland	64	First observation	-4.3 \pm 0.8	NA	<i>info fauna</i>
Amphibians							
Anura	1991–2019	Switzerland	10	First observation	-1.0 \pm 2.2	NA	<i>info fauna</i>
Urodela	1991–2019	Switzerland	5	First observation	+2.5 \pm 3.0	NA	<i>info fauna</i>

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<i>Reptiles</i>								
Squamata	1991–2019	Switzerland	14	First observation	-5.7±1.6	NA	<i>info fauna</i>	

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4 1409 Table 2. Elevational range shifts reported for diverse taxa in the European Alps region. Values are means \pm SE. In the ‘Limit’ column,
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6 1410 ‘optimum’ is the elevation of maximum abundance and ‘leading edge’ is the upper elevational limit of a given species. These two metrics are
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8 1411 calculated in different ways depending on the studies (see article references and Section II). For Dainese *et al.* (2017) only native species were
9
10 1412 included. For information on the *info fauna* database see Section II. The data set used for this table is provided as supporting online information
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12
13 1413 in Table S2. *N*, number of species. Abbreviations: ecm, ectomycorrhizal; sapro., saprophytic.

Taxa	Study period	Area	<i>N</i>	Mean shift (m decade ⁻¹)	Limit	References
PLANTS						
Alpine species	1956–2004 ¹	Central Italian Alps	93	+18.1 \pm 2.5	Leading edge	Parolo & Rossi (2008)
Alpine species	1989–2009	Northeast Italy	80	+26.1 \pm 10.0	Optimum	Dainese <i>et al.</i> (2017)
Forest plant species	1977–2005 ¹	Western French Alps, and other French mountains	97	+38.1 \pm 7.8	Leading edge	Kuhn <i>et al.</i> (2016)
Forest plant species	1977–2005 ¹	Western French Alps, and other French mountains	97	+25.7 \pm 4.6	Optimum	Kuhn <i>et al.</i> (2016)
Forest plant species	1985–1999	Southeast France and Corsica	175	+13.8 \pm 6.9	Optimum	Bodin <i>et al.</i> (2013)
Non-alpine plant species	1989–2009	Northeast Italy	1,128	+32.8 \pm 3.2	Optimum	Dainese <i>et al.</i> (2017)
BIRDS						
Various species	1982–2017	Italian Alps	29	+31.5 \pm 8.4	Optimum	Bani <i>et al.</i> (2019)
Various species	1982–2017	Italian Alps	29	+55.6 \pm 9.5	Leading edge	Bani <i>et al.</i> (2019)
Various species	1993–2016	Switzerland	71	+12.0 \pm 3.5	Optimum	Knaus (2018)
Various species	1993–2004 ¹	Italian Alps (Piedmont)	54	+7.2 \pm 9.4	Optimum	Popy <i>et al.</i> (2010)
Forest species	1978–2002	French northern Alps	24	-7.8 \pm 6.5	Optimum	Archaux (2004)
Forest species	1973–2001	French southern Alps	17	-6.3 \pm 6.3	Optimum	Archaux (2004)
<i>Lagopus muta</i>	1998–2011	Northern French Alps	1	-24.7	Optimum	Novoa <i>et al.</i> (2016)
<i>Lagopus muta helvetica</i>	1984–2012	Swiss Alps	1	+37.8	Optimum	Pernollet <i>et al.</i> (2015)
MAMMALS						
Ungulate species	1991–2013	Swiss Alps	4	+37.5 \pm 10.3	Optimum	Büntgen <i>et al.</i> (2017)
INSECTS						
<i>Lepidoptera</i>						

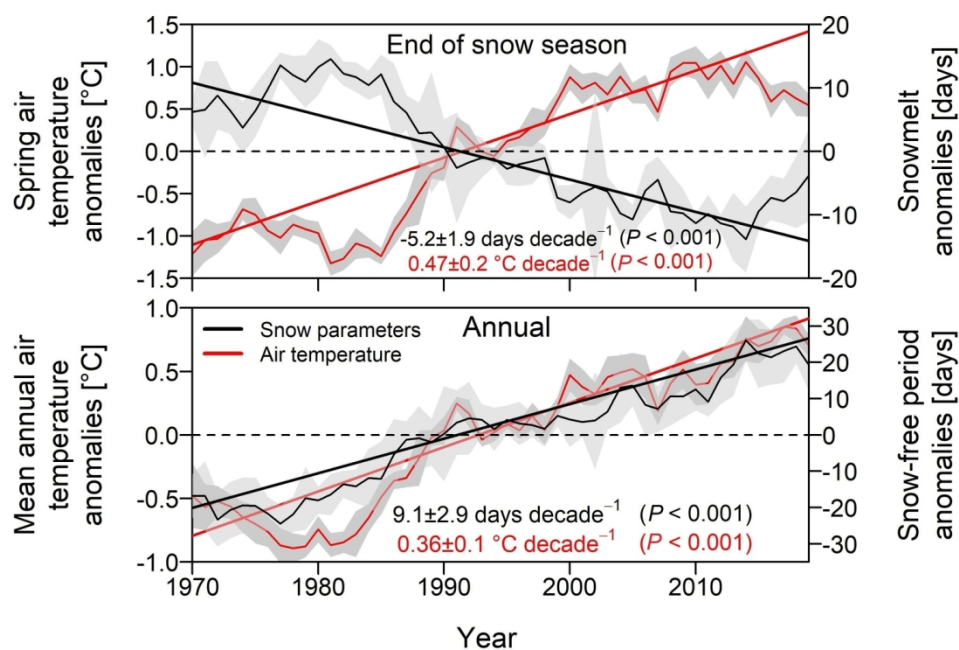
4	<i>Thaumetopoea</i>	1975–2004	Italian Alps	1	+49.8	Leading edge	Battisti <i>et al.</i> (2005)
5	<i>pityocampa</i>						
6	Various butterfly species	1991–2019	Switzerland	138	+39.9±6.5	Optimum	info fauna
7	Various butterfly species	1991–2019	Switzerland	138	+112.4±6.3	Leading edge	info fauna
8	Coleoptera						
9	Dung beetle species	1992–2007	South western Alps	30	+40.5±24.2	Optimum	Menéndez <i>et al.</i> (2014)
10	Dung beetle species	1992–2007	South western Alps	30	+80.6±39.8	Leading edge	Menéndez <i>et al.</i> (2014)
11	Odonata						
12	Various species	1991–2019	Switzerland	40	−2.6±5.9	Optimum	info fauna
13	Various species	1991–2019	Switzerland	40	−4.7±9.1	Leading edge	info fauna
14	Orthoptera						
15	Various species	1991–2019	Switzerland	64	+20.6±5.4	Optimum	info fauna
16	Various species	1991–2019	Switzerland	64	+46.9±6.9	Leading edge	info fauna
17	AMPHIBIANS						
18	Anura						
19	Various species	1991–2019	Switzerland	10	+13.9±4.8	Optimum	info fauna
20	Various species	1991–2019	Switzerland	10	+42.8±17.1	Leading edge	info fauna
21	Urodela						
22	Various species	1991–2019	Switzerland	7	+19.7±18.7	Optimum	info fauna
23	Various species	1991–2019	Switzerland	7	+53.5±16.7	Leading edge	info fauna
24	REPTILES						
25	Various species	1991–2019	Switzerland	14	+22.6±10.8	Optimum	info fauna
26	Various species	1991–2019	Switzerland	14	+63.7±12.7	Leading edge	info fauna
27	FISHES						
28	Stream fishes	1986–2006 ¹	Streams in France	32	+13.1±3.8	Optimum	Comte & Grenouillet (2013)
29	FUNGI						
30	ecm species	1960–2010	European Alps	56	+21.0±3.0	Optimum	Diez <i>et al.</i> (2020)
31	Litter/soil sapro. species	1960–2010	European Alps	29	+23.6±4.0	Optimum	Diez <i>et al.</i> (2020)
32	Wood sapro. species	1960–2010	European Alps	33	+10.7±2.6	Optimum	Diez <i>et al.</i> (2020)

¹Median years of the historical and modern survey.

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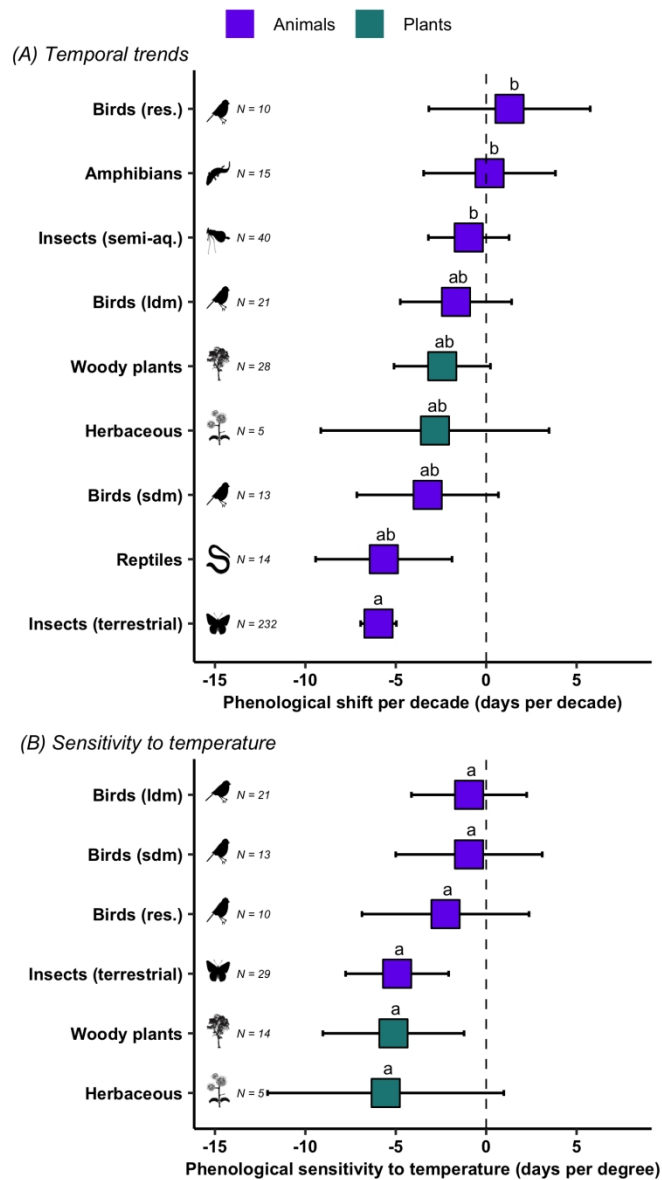
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Long-term time series of snow parameters (snowmelt timing and length of the snow free period) and mean air temperature (spring temperature from March to May and annual temperature) at six sites spread across the Swiss Alps during the period 1970–2019.

Data updated from Klein et al. (2016) representing yearly average anomalies over the period 1970–2019 across six sites in Switzerland located between 1,298 and 2,540 m (Arosa, Davos, Grächen, Grimsel Hospiz, Scuol and Weissfluhjoch). Estimated trends from the Theil-Sen estimator method across the six sites are reported with the associated standard errors (grey shading) for each snow and temperature parameter. Significance of the slopes was tested using Mann-Kendall tests, see Klein et al. (2016) for more details.

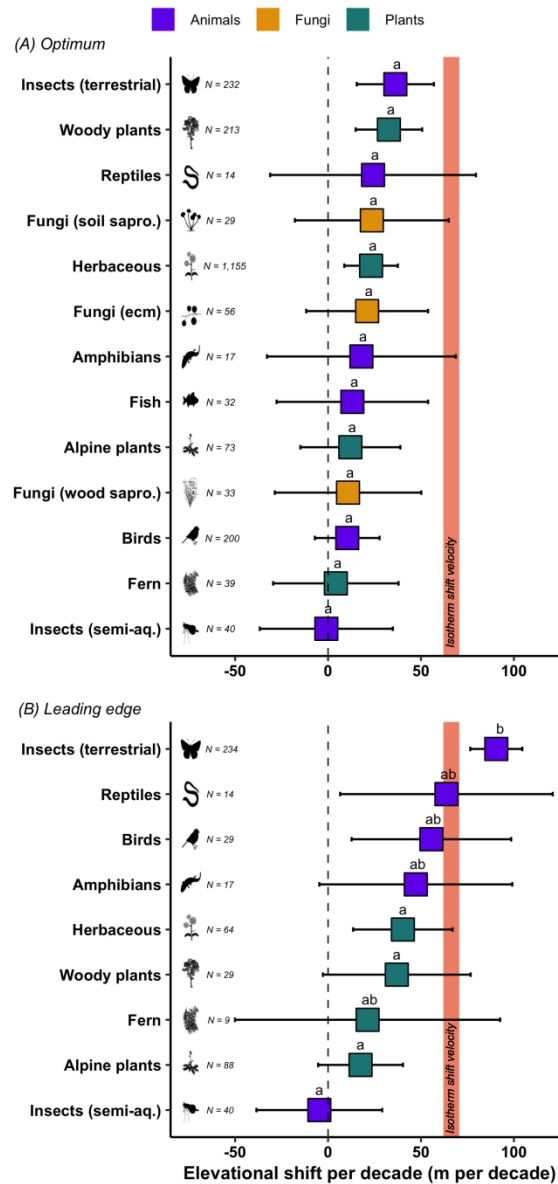
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45 Spring phenological change per decade (A) or per degree (B) for different plant and animal groups studied in
 46 the European Alps region. Values correspond to the estimated marginal mean of the mixed-effect model
 47 with study as a random factor; error bars are 95% confidence intervals. The period of time varied among
 48 studies but was always more than 10 years within the period 1980–2020. Only groups with more than five
 49 species are shown (all studies are reported in Table 1). Abbreviations: ldm, long-distance migrants; sdm,
 50 short-distance migrants; res., resident; semi-aq., semi-aquatic. Different letters among groups indicate
 51 significant differences (post-hoc Tukey tests at $\alpha = 0.05$).

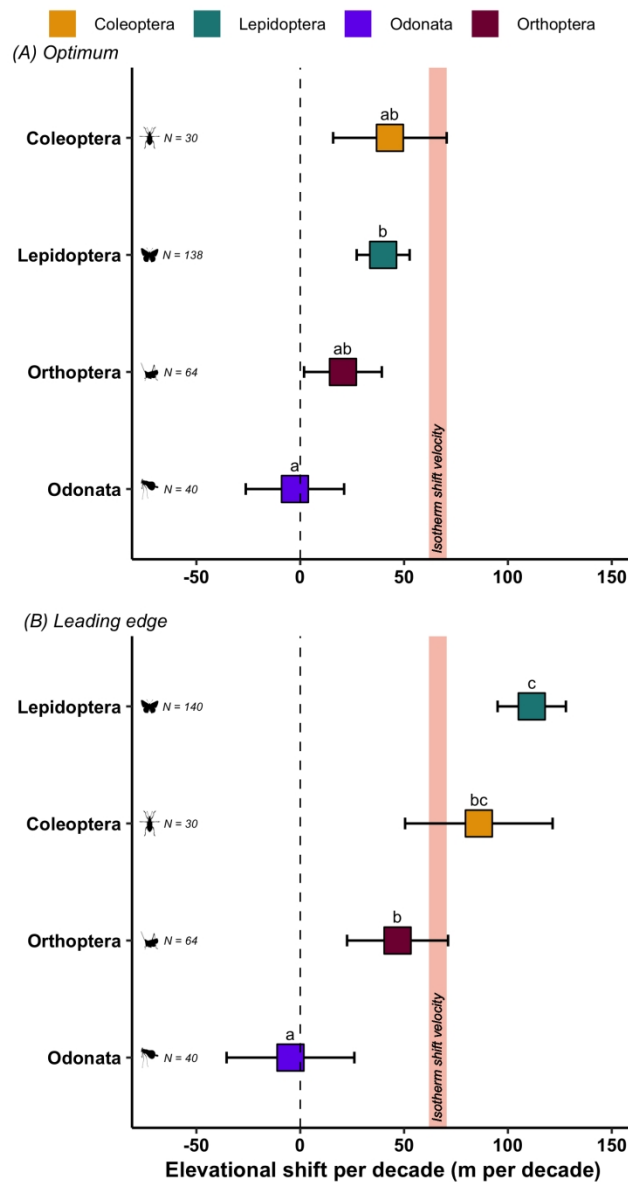
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Empirical evidence for elevational range shifts of (A) the optimum distribution (i.e. elevation of maximum abundance) and (B) the leading edge (i.e. the upper range limit) reported for groups of taxa in the European Alps region. Values correspond to the estimate of the mixed-effect model with study as a random factor; error bars are 95% confidence intervals. The period of time investigated varied among studies but was always more than 10 years within the period 1980–2020, or for diachronic studies comparing historical and modern surveys, the modern survey was conducted within the period 1980–2020, and the median year of the historical survey(s) was after 1950. Only groups with more than five species are shown (all studies are reported in Table 2). Abbreviations: ecm, ectomycorrhizal; sapro., saprophytic; semi-aq., semi-aquatic. Different letters among groups indicate significant differences (post-hoc Tukey tests at $\alpha = 0.05$).

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Mean elevational shift per decade for four different orders of insects in terms of (A) the optimum elevation (i.e. elevation of maximum abundance) and (B) the leading-edge elevation (i.e. the upper range limit). Values correspond to the estimate of the mixed-effect model with study as a random factor; error bars are 95% confidence intervals. The period of time investigated varied among studies but was always higher than 10 years within the period 1980–2020. Different letters among groups indicate significant differences (post-hoc Tukey tests at $\alpha = 0.05$).

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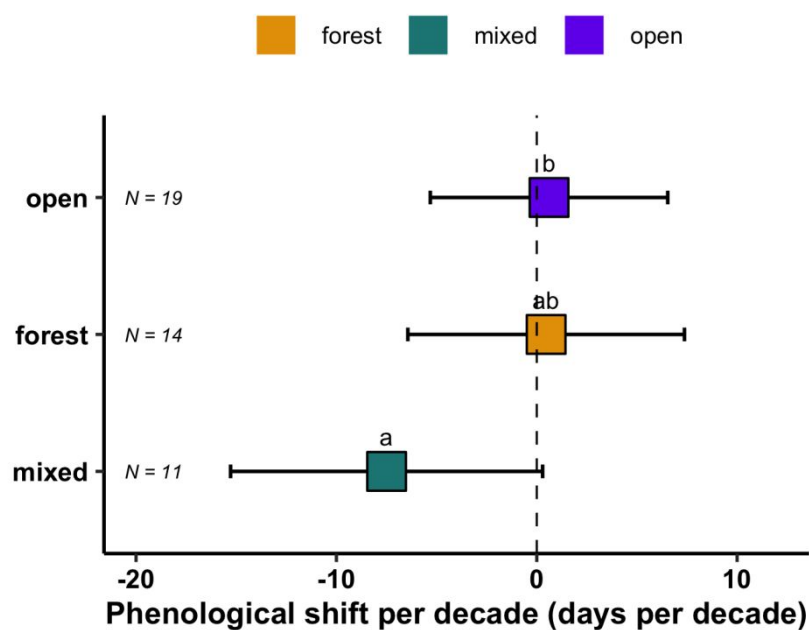


Fig. S1. Mean phenological shift of the singing activity or laying dates per decade for birds classified according to their habitat. Values correspond to the estimated marginal mean of the mixed-effect model with study as a random factor; error bars are 95% confidence intervals. The period of time investigated varied among studies but was always more than 10 years within the period 1980–2020. Different letters among groups indicate significant differences (*post-hoc* Tukey tests at $\alpha = 0.05$).