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

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ABSTRACT

Mountain areas are biodiversity hotspots and provide a multitude of ecosystem services of irreplaceable socio-economic value. In the European Alps, air temperature has increased at a rate of about 0.36°C decade^{-1} since 1970, leading to glacier retreat and significant snowpack reduction. Due to these rapid environmental changes, this mountainous region is undergoing marked changes in spring phenology and elevational distribution of animals, plants and fungi. Long-term monitoring in the European Alps offers an excellent natural laboratory to synthetize climate-related changes in spring phenology and elevational distribution for a large array of taxonomic groups. This review assesses the climatic changes that have occurred across the European Alps during recent decades, spring phenological changes and upslope shifts of plants, animals and fungi from evidence in published papers and previously unpublished data. Our review provides evidence that spring phenology has been shifting earlier during the past four decades and distribution ranges show an upwards trend for most of the taxonomic groups for which there are sufficient data. The first observed activity of reptiles and terrestrial insects (e.g. butterflies) in spring has shifted significantly earlier, at an average rate of −5.7 and −6.0 days decade^{-1}, respectively. By contrast, the first observed spring activity of semi-aquatic insects (e.g. dragonflies and damselflies) and amphibians, as well as the singing activity or laying dates of resident birds, show smaller non-significant trends ranging from −1.0 to +1.3 days decade^{-1}. Leaf-out and flowering of woody and herbaceous plants showed intermediate trends with mean values of −2.4 and −2.8 days decade^{-1}, respectively. Regarding species distribution, plants, animals

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and fungi ($N = 2133$ species) shifted the elevation of maximum abundance (optimum elevation) upslope at a similar pace (on average between +18 and +25 m decade^{-1}) but with substantial differences among taxa. For example, the optimum elevation shifted upward by +36.2 m decade^{-1} for terrestrial insects and +32.7 m decade^{-1} for woody plants, whereas it was estimated to range between −1.0 and +11 m decade^{-1} for semi-aquatic insects, ferns, birds and wood-decaying fungi. The upper range limit (leading edge) of most species also shifted upslope with a rate clearly higher for animals (from +47 to +91 m decade^{-1}) than for plants (from +17 to +40 m decade^{-1}), except for semi-aquatic insects (−4.7 m decade^{-1}). Although regional land-use changes could partly explain some trends, the consistent upward shift found in almost all taxa all over the Alps is likely reflecting the strong warming and the receding of snow cover that has taken place across the European Alps over recent decades. However, with the possible exception of terrestrial insects, the upward shift of organisms seems currently too slow to track the pace of isotherm shifts induced by climate warming, estimated at about +62 to +71 m decade^{-1} since 1970. In the light of these results, species interactions are likely to change over multiple trophic levels through phenological and spatial mismatches. This nascent research field deserves greater attention to allow us to anticipate structural and functional changes better at the ecosystem level.

Key words: biodiversity redistribution, climate change velocity, disequilibrium dynamics, global warming, migration, mountain ecosystems, phenological mismatches, upslope shift

CONTENTS

I. INTRODUCTION

Biodiversity loss and redistribution as well as extreme climatic events are probably the two most prominent environmental challenges with strong socio-economic consequences that humans have to face in the 21st century. Biodiversity loss, mainly caused by human alteration of the landscape, has been occurring at an unprecedented rate since humans expanded across the globe (Butchart *et al.*, 2010). The distributions of many terrestrial organisms are currently shifting in response to global warming and land-use changes in most parts of the world, poleward and upslope to cooler latitudes and elevations, respectively, thus generating spatially structured patterns in species redistribution (Chen *et al.*, 2011; Lenoir & Svenning, 2015; Lenoir *et al.*, 2020). However, the rate of ongoing global warming is such that numerous plant and animal species may not be able to adapt genetically, or to track their climatic niche requirements closely, ultimately leading to local extinctions (reviewed in Jump & Penuelas, 2005; Aitken *et al.*, 2008; Corlett & Westcott, 2013; Cang, Wilson & Wiens, 2016; Jezkova & Wiens, 2016), particularly in terrestrial ecosystems as opposed to marine ecosystems (Lenoir *et al.*, 2020).

Ongoing global warming is changing the geographic distribution of organisms on Earth but their physiology and seasonal activities are also dramatically altered by climate change. In fact, phenological changes, such as flowering or leaf senescence for plants, as well as mating, breeding, spawning or hibernating for animals, are one of the most visible and sensitive responses to ongoing global warming in natural ecosystems (Parmesan & Yohe, 2003; Cleland *et al.*, 2007). For instance, in Europe, leaf-out of temperate trees has advanced by 8–15 days since the 1950s (Fu *et al.*, 2019) and the migration dates of birds have advanced by about a week since 1959 in Canada and northern Europe (Lehikoinen *et al.*, 2019). In a temperate climate, spring phenology reflects how the physiology and behaviour of organisms interacts with the progressive return of favourable conditions for growth, i.e. mainly the increase in air temperature and day length. Because animals are dependent on the development of plants, any change in plant phenology may elicit a cascade of consequences in plant–animal interactions (Beard *et al.*, 2019; Visser & Gienapp, 2019; Kharouba & Wolkovich, 2020; Rehnus, Peláez & Bollmann, 2020). How the synchrony between animals and plant phenology will change under global warming is a challenging and timely question, but the consequences of such synchrony are still poorly understood at the population, community and ecosystem levels due to a lack of long-term ecosystem-based monitoring time series (but see Kharouba *et al.*, 2018; Visser & Gienapp, 2019; Peláez *et al.*, 2020).

The European Alps form an arc approximately 800 km in length from east to west and around 200 km in width in western Europe with numerous peaks rising over 4000 m. This mountain system has been a prominent obstacle for plants and animals during the glacial and post-glacial periods of the Pleistocene, thus being at the crossroads of several biogeographical units (Taberlet *et al.*, 1998; Hewitt, 2000). The European Alps are a hotspot of biodiversity offering myriad habitats and climates over very short distances (Körner, 2003; Zimmermann *et al.*, 2013). About 13000 vascular plant species (>500 endemics) and about 30000 animal species inhabit the European Alps (Agrawala, 2007). Plants, animals and fungi living in this region include generalist species found across all of Europe but also numerous specialist species that have developed adaptations to harsh environments at high elevations, and are found only in restricted areas such as mountain summits (i.e. sky islands). Angiosperm plant species are found up to 4507 m (*Saxifraga oppositifolia* L.) together with fungi and arthropods (Körner, 2011), while bryophytes are found up to 4559 m (Vaccari, 1914). In the European Alps, as in all mountainous areas, the distance that an organism has to move in order to cross isotherms is quite short compared to flatter regions, because of the sharp temperature adiabatic gradient induced by elevational gradients (Rolland, 2003). This may, to a certain extent, help species to track isotherm shifts better in mountainous regions (Brito-Morales *et al.*, 2018). However, species living close to mountain summits will progressively be limited in habitat availability because moving upward generally means less land surface available, higher habitat fragmentation, and an inevitable increase in competition among co-existing species, eventually leading to local extinction events (Wiens, 2016; Giezendanner *et al.*, 2019). The shift of species ranges in response to climate change is also increasingly hampered by human activities such as tourism, urbanization or agriculture, all of which alter species' habitat suitability and distribution by fragmenting natural habitats (Elsen, Monahan & Merenlender, 2020). A warmer climate associated with changes in rain regime and snow cover will alter the physiology and phenology of many species, which in turn will affect their fitness and biotic interactions. Numerous studies have shown tight relationships between snow conditions and population dynamics of alpine and arctic plants (e.g. Inouye, 2000, 2008; Körner, 2003; Wipf & Rixen, 2010; Berteaux *et al.*, 2016) as well as population dynamics of animal species (e.g. Korslund & Steen, 2006; Helle & Kojola, 2008; Robinson & Merrill, 2012). Hence, any changes in air temperature, precipitation and snow cover patterns in high mountain areas are expected to elicit substantial modifications in plant–animal interactions. In the European Alps, the pace of climate warming is occurring at a faster rate than the average warming in the northern hemisphere (Rebetez & Reinhard, 2008), generating faster velocities of isotherm shifts. As a result, substantial shifts in spring phenology as well as numerous elevational range shifts have already been observed for plants, animals and even fungi over recent decades (see studies in Tables 1 and 2). Long-term monitoring in the European Alps offers an excellent natural laboratory to synthetize climate-related changes in spring phenology and elevational distribution for a large array of taxonomic groups.

Here, we aim at synthetizing the climatic changes that have occurred across the European Alps during recent decades and gathering the observed biotic responses in terms of both spring phenological changes (the best documented season in terms of phenological observations) and species range shifts, reported for flora, fauna and fungi. We provide a comprehensive synthesis of these changes and discuss the consequences of such phenological and spatial shifts on species interactions across different trophic levels. Moreover, we point out knowledge gaps that require more investigation in order to be able to predict future structural and functional changes better at the ecosystem level under global warming.

II. METHODS

We searched the scientific literature for publications reporting either species elevational range shifts or spring phenological trends over recent decades. For phenological changes, we focused on the spring season because this is better documented in terms of phenological observations compared to the autumn season (Gallinat, Primack & Wagner, 2015), allowing for robust comparisons among taxa. We focused on any important phenological event such as leaf emergence or flowering of plants, peaks of detectability for birds or observations of the adult phase for amphibians and insects. For elevational range shifts, we focused on studies reporting either shifts of the core distribution of a given species (hereafter 'optimum') or shifts of the upper elevational limit (hereafter 'leading edge'). We restricted our review to studies relying on regular monitoring data covering at least 10 years across parts of the European Alps (i.e. Austria, France, Germany, Italy, Lichtenstein, Slovenia and Switzerland) within the period 1980–2020. For diachronic studies comparing historical and modern surveys, we used only studies that conducted their

Table 1. Documented spring phenological changes in animals and plants in the European Alps over the recent decades. Mean ± standard errors are reported where data are available for more than one species. For information on the *info fauna* and *PhenoForest* databases, see Section II. The data set used for this table is provided as supporting online information in Table S1

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 ± 0.3	−5.1 ± 0.4	Güsewell (2014)
Herbaceous	1970–2012	Alps and lowlands in Switzerland	5	Flowering	−2.8 ± 0.4	−5.6 ± 0.6	Güsewell (2014)
Trees	1998–2020	Alps and lowlands in Switzerland	8	Leaf-out	−2.2 ± 0.7	NA	*PhenoForest*
Woody plants	2005–2016	French Alps	6	Leaf-out	−0.5 ± 2.3	NA	Bison *et al.* (2019)
ANIMALS							
Birds							
Birds (res.)	1995–2019	Lowland areas in Switzerland	8	Singing activity	+2.5 ± 3.6	−2.1 ± 0.8	Strebel *et al.* (2014)
Birds (sdm)	1995–2019	Lowland areas in Switzerland	12	Singing activity	−3.5 ± 3.8	−1.0 ± 0.5	Strebel *et al.* (2014)
Birds (ldm)	1995–2019	Lowland areas in Switzerland	14	Singing activity	−1.7 ± 1.5	−1.0 ± 0.5	Strebel *et al.* (2014)
Passer italiae (res.)	1982–2006	Northern Italy	1	Laying dates	−1.9	−1.7	Rubolini *et al.* (2007)
Sturnus vulgaris (sdm)	1982–2006	Northern Italy	1	Laying dates	−0.1	−0.2	Rubolini *et al.* (2007)
Birds (ldm)	1982–2006	Northern Italy	6	Arrival or laying dates	−1.8 ± 0.8	−1.0 ± 0.6	Rubolini *et al.* (2007)
Ficedula hypoleuca (ldm)	1960–1995	South Germany	1	Arrival dates	−0.7	0.06	Hölzinger (1997)
Lagopus muta (res.)	2000–2009	Northern French Alps	1	Median hatching date	−4.9	−4.2	Novoa *et al.* (2016)
Insects							
Ips typographus	1996–2005	Southeastern Alps	1	First observation	−21	NA	Faccoli (2009)
Lepidoptera, butterflies	1998–2010	Swiss lowlands	28	First observation	NA	−4.9 ± 2.0	Altermatt (2012)
Apatura iris	1982–2002	Forest near Basel, Switzerland	1	First observation	−10.5	−6.4	Dell *et al.* (2005)
Lepidoptera, butterflies	1991–2019	Switzerland	138	First observation	−6.6 ± 0.5	NA	*info fauna*
Odonata	1991–2019	Switzerland	40	First observation	−1.0 ± 0.5	NA	*info fauna*
Orthoptera	1991–2019	Switzerland	64	First observation	−4.3 ± 0.8	NA	*info fauna*
Amphibians							
Anura	1991–2019	Switzerland	10	First observation	−1.0 ± 2.2	NA	*info fauna*
Urodela	1991–2019	Switzerland	5	First observation	+2.5 ± 3.0	NA	*info fauna*
Reptiles							
Squamata	1991–2019	Switzerland	14	First observation	−5.7 ± 1.6	NA	*info fauna*

ldm, long-distance migrants; sdm, short-distance migrants; res., resident.

modern survey(s) within the period 1980–2020 and where the median year of the historical survey(s) was after 1950 [often called the 'great acceleration' period (Steffen *et al.*, 2015)] to avoid including decades with no or significantly lower warming trends. Indeed, including studies using historical surveys prior to 1950 (e.g. Holzinger *et al.*, 2008; Rumpf *et al.*, 2018) would inevitably underestimate the rate at which biotic responses are taking place in response to ongoing climate change for recent decades.

We focused on the European Alps because this region is both a hotspot of biodiversity and benefits from a long research history, allowing a long-term view and comprehensive synthesis on climate change-related processes. We extended the study area to lowland regions in direct contact with the mountain range of the European Alps or to neighbouring mountain ranges (the Jura), provided that part of the European Alps was considered in the studied region and assumed to play a significant role in the results (e.g. Kuhn *et al.*, 2016).

Raw data for phenological shift (per decade or per degree of warming) and migration rate across elevations per unit time (per year or per decade) were extracted at the species level from the publications reviewed herein, either from direct access *via* the journal webpage (appendix or data depository), or indirectly by requesting species-level data from the study authors. Depending on the study, different methods were used to generate species-level data on phenological shift or elevational range shift per decade. For instance, some studies directly reported the observed rates in phenological shift or elevational range shift per decade while others reported the magnitude of the observed changes in phenology or elevational distribution over a given time period. In the latter case we extracted information on the duration of the time period covered by that study and computed the rates per decade. Phenological studies reporting the phenological change per degree of warming generally include a pre-season temperature window in their calculations, which is best correlated with the studied phenological event, i.e. a couple of weeks or months before the spring phenological event. For more details, readers should refer to the publications listed in Table 1.

All publications used for our synthesis are summarised in Tables 1 and 2, and the full data are provided as online supporting information in Tables S1 and S2, respectively. For more robust comparisons, taxonomic groups containing observations of phenological or range shifts for less than five species were discarded from our quantitative analyses, but are still included in the tables for completeness.

In addition, we analysed two sources of previously unpublished data collected through a citizen science program in Switzerland: the *info fauna* database for both phenology and altitudinal migration of insects, reptiles and amphibians and the *PhenoForest* database for phenological trends of several tree species.

From the Swiss central database of *info fauna*, we extracted all observations for amphibians, reptiles, lepidopterans, orthopterans and odonates available between 1991 and 2019. Although data collected before 1990 are available, we restricted our analyses to after 1990 because far fewer observers were active before 1990, which could influence trend analyses. Species with taxonomic uncertainty, with a limited number of observations per year (variable depending on taxonomic group, left to the experts' discretion), that are migrants or show other features that could impact the frequency of observations were also removed after careful examination by expert co-authors of this review. To avoid a distorting influence of extreme values when assessing elevational range shifts from the raw data, we computed, for every year, the median (50%) and 95th percentile of the elevation as surrogates for the optimum and leading edge, respectively, because these were less likely to be distorted than the mean and maximum elevation values. Similarly, for spring phenology, we used the 5th percentile of the distribution in the observations for a given species for every year. Linear regressions were then conducted for all species of these parameters against years, and we report the slope values expressed per decade. In total, for *info fauna*, 273 animal species were included in our analyses, comprising 1558862 observations (average: 5710 observations/species; median: 2807 observations/species; 5–95% quantile: 256–21301 observations/species) for the altitude analysis and 1560265 observations (average: 5715 observations/species; median: 2823 observations/species; 5–95% quantile: 196–20380 observations/species) for the phenology analysis. The *info fauna* database gathers observations mainly from citizen volunteers and does not use a systematic sampling design, rather representing haphazard sampling, which may introduce statistical issues (Callaghan *et al.*, 2019). However, because we used only data from taxa with sufficient sample sizes and that were carefully checked by experts before they were entered into our database, we believe this data set should provide robust trends of how these species are currently migrating along elevational gradients. Additionally, the data from *info fauna* do not show identical trends among taxa; if a particular trend was due to observer bias, we would expect to find similar patterns across various taxa, which was not the case.

The *PhenoForest* database consists of records of visual observations of the leaf-out timing of eight species during the period 1998–2020 from volunteers in different sites in Switzerland (one observer per site, 16 permanent sites in total, 1–5 species per site). At each site, 8–10 trees per species were identified and monitored every year by the same observer. To estimate trends in the leaf-out dates over this study period, we applied a linear mixed-effect model for each species with leaf-out dates as the response variable, year as the explanatory variable and sites as a random intercept term, and extracted the estimated slope for each species separately.

Following collection/calculation of all the species-level biotic responses in days per decade for shifts in spring phenology or meters per decade for elevational range shifts as described above, we compared the estimated rates among taxonomic groups. We ran linear mixed-effects models with species' phenological shift per decade or species' elevational range shift per decade as response variables, study/database

Table 2. Elevational range shifts reported for diverse taxa in the European Alps region. Values are means ± standard errors. In the 'Limit' column, 'Optimum' is the elevation of maximum abundance and 'Leading edge' is the upper elevational limit of a given species. These two metrics are calculated in different ways depending on the studies (see article references and Section II). For Dainese *et al.* (2017) only native species were included. For information on the *info fauna* database see Section II. The data set used for this table is provided as supporting online information in Table S2

Taxa	Study period	Area	*N*	Mean shift (m decade^{-1})	Limit	References
PLANTS						
Alpine species	1956–2004[a]	Central Italian Alps	93	+18.1 ± 2.5	Leading edge	Parolo & Rossi (2008)
Alpine species	1989–2009	Northeast Italy	80	+26.1 ± 10.0	Optimum	Dainese *et al.* (2017)
Forest plant species	1977–2005[a]	Western French Alps, and other French mountains	97	+38.1 ± 7.8	Leading edge	Kuhn *et al.* (2016)
Forest plant species	1977–2005[a]	Western French Alps, and other French mountains	97	+25.7 ± 4.6	Optimum	Kuhn *et al.* (2016)
Forest plant species	1985–1999	Southeast France and Corsica	175	+13.8 ± 6.9	Optimum	Bodin *et al.* (2013)
Non-alpine plant species	1989–2009	Northeast Italy	1128	+32.8 ± 3.2	Optimum	Dainese *et al.* (2017)
BIRDS						
Various species	1982–2017	Italian Alps	29	+31.5 ± 8.4	Optimum	Bani *et al.* (2019)
Various species	1982–2017	Italian Alps	29	+55.6 ± 9.5	Leading edge	Bani *et al.* (2019)
Various species	1993–2016	Switzerland	71	+12.0 ± 3.5	Optimum	Knaus (2018)
Various species	1993–2004[a]	Italian Alps (Piedmont)	54	+7.2 ± 9.4	Optimum	Popy *et al.* (2010)
Forest species	1978–2002	French northern Alps	24	−7.8 ± 6.5	Optimum	Archaux (2004)
Forest species	1973–2001	French southern Alps	17	−6.3 ± 6.3	Optimum	Archaux (2004)
Lagopus muta	1998–2011	Northern French Alps	1	−24.7	Optimum	Novoa *et al.* (2016)
Lagopus muta helvetica	1984–2012	Swiss Alps	1	+37.8	Optimum	Pernollet *et al.* (2015)
MAMMALS						
Ungulate species	1991–2013	Swiss Alps	4	+37.5 ± 10.3	Optimum	Büntgen *et al.* (2017)
INSECTS						
Lepidoptera						
Thaumetopoea pityocampa	1975–2004	Italian Alps	1	+49.8	Leading edge	Battisti *et al.* (2005)
Various butterfly species	1991–2019	Switzerland	138	+39.9 ± 6.5	Optimum	info fauna
Various butterfly species	1991–2019	Switzerland	138	+112.4 ± 6.3	Leading edge	info fauna
Coleoptera						
Dung beetle species	1992–2007	South western Alps	30	+40.5 ± 24.2	Optimum	Menéndez *et al.* (2014)
Dung beetle species	1992–2007	South western Alps	30	+80.6 ± 39.8	Leading edge	Menéndez *et al.* (2014)
Odonata						
Various species	1991–2019	Switzerland	40	−2.6 ± 5.9	Optimum	*info fauna*
Various species	1991–2019	Switzerland	40	−4.7 ± 9.1	Leading edge	*info fauna*
Orthoptera						
Various species	1991–2019	Switzerland	64	+20.6 ± 5.4	Optimum	*info fauna*
Various species	1991–2019	Switzerland	64	+46.9 ± 6.9	Leading edge	*info fauna*
AMPHIBIANS						
Anura						
Various species	1991–2019	Switzerland	10	+13.9 ± 4.8	Optimum	*info fauna*
Various species	1991–2019	Switzerland	10	+42.8 ± 17.1	Leading edge	*info fauna*
Urodela						
Various species	1991–2019	Switzerland	7	+19.7 ± 18.7	Optimum	*info fauna*

(Continues)

Table 2. *(Cont.)*

Taxa	Study period	Area	*N*	Mean shift (m decade^{-1})	Limit	References
Various species	1991–2019	Switzerland	7	+53.5 ± 16.7	Leading edge	*info fauna*
REPTILES						
Various species	1991–2019	Switzerland	14	+22.6 ± 10.8	Optimum	*info fauna*
Various species	1991–2019	Switzerland	14	+63.7 ± 12.7	Leading edge	*info fauna*
FISHES						
Stream fishes	1986–2006[a]	Streams in France	32	+13.1 ± 3.8	Optimum	Comte & Grenouillet (2013)
FUNGI						
Ecm species	1960–2010	European Alps	56	+21.0 ± 3.0	Optimum	Diez *et al.* (2020)
Litter/soil sapro. Species	1960–2010	European Alps	29	+23.6 ± 4.0	Optimum	Diez *et al.* (2020)
Wood sapro. Species	1960–2010	European Alps	33	+10.7 ± 2.6	Optimum	Diez *et al.* (2020)

N, number of species; ecm, ectomycorrhizal; sapro., saprophytic.
[a] Median years of the historical and modern survey.

as a random intercept term and taxonomic group (with as many levels as taxonomic groups for which there were sufficient data, i.e. groups containing at least five species) as the main fixed effect. Based on the model estimates of phenological shift per decade or elevational range shift per decade for each taxonomic group separately, we computed the associated 95% confidence intervals. *Post-hoc* Tukey tests were then applied to test for differences among the different taxonomic groups. In the results, we report the mean shift of the phenology or migration of a given taxonomic group across studies, using the estimated marginal mean value ± 95% confidence intervals from the mixed-effect model. We also report the mean ± standard errors of phenological and elevational shifts per study/database and taxonomic group in Tables 1 and 2.

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

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

III. SYNTHESIS

(1) Climate change in the European Alps

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

(i) Temperature. Since the beginning of the 20th century, mean annual air temperature has increased by more than 1.5°C across the European Alps (Böhm *et al.*, 2001; Begert, Schlegel & Kirchhofer, 2005; Rebetez & Reinhard, 2008), with this trend accelerating strongly during the second half of the 20th century (Auer *et al.*, 2007; Acquaotta, Fratianni & Garzena, 2015) with an average increase of about 0.36°C decade^{-1} between 1970 and 2019 (Klein *et al.*, 2016, Fig. 1). Air temperature trends in the European Alps exceed the average trend observed over the northern hemisphere by 1.6–2.5 times (Keiler, Knight & Harrison, 2010; Foster & Rahmstorf, 2011). The increase in air temperatures during the 20th century was most pronounced around the altitude of the 0°C isotherm (Serquet, Marty & Rebetez, 2013), in connection with the snow-albedo feedback of snow-covered surfaces and glaciers (Pepin & Lundquist, 2008; Scherrer *et al.*, 2012). However, these trends hide strong seasonal disparities. During the 20th century

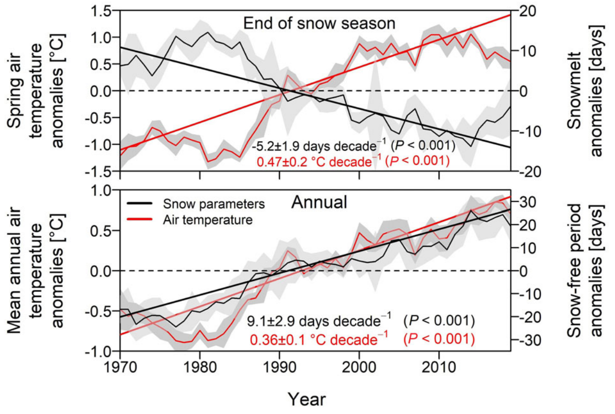

Fig 1. Long-term time series of snow parameters (snowmelt timing and length of the snow-free period) and mean air temperature (spring temperature from March to May and annual temperature) at six sites spread across the Swiss Alps during the period 1970–2019. Data updated from Klein *et al.* (2016) representing yearly average anomalies over the period 1970–2019 across six sites in Switzerland located between 1298 and 2540 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-Kendell tests, see Klein *et al.* (2016) for more details.

in Western Europe, air temperatures warmed more in winter compared to summer (Moberg *et al.*, 2006), but this ratio reversed by the end of the 20th and early 21st century (Klein *et al.*, 2018). Hence, several studies have shown that summer and spring have warmed more than autumn and winter since the 1970s (Rebetez & Reinhard, 2008; Klein *et al.*, 2018; Vitasse *et al.*, 2018*a*). Since the end of the 1980s, maximum air temperatures have been increasing more than minimum temperatures in connection with the decrease in European air pollution and particulate matter, especially in spring and at mid and high elevations (Rebetez & Reinhard, 2008; Vitasse *et al.*, 2018*a*).

(ii) Precipitation and snow. Annual precipitation has not changed across the European Alps over recent decades (Diolaiuti *et al.*, 2012). Regionally, only a few increasing seasonal trends have been observed since the beginning of the 20th century, mostly during autumn and winter (Schmidli & Frei, 2005; Scherrer *et al.*, 2016). Winter precipitation sum has increased slightly, whereas trends towards more intense but less frequent precipitation were observed in summer with no change in overall precipitation sum (Moberg *et al.*, 2006; Appenzeller *et al.*, 2011; Fischer *et al.*, 2019). Recently, European alpine countries have experienced several extreme drought events in summer, associated with heat waves, which have led to forest dieback, vegetation damage and insect outbreaks in the lowlands, particularly in 2003, 2012, 2015, 2016 and 2018 (Corona-Lozada, Morin & Choler, 2019; Schuldt *et al.*, 2020). Intense hot drought events had also occurred during the 20th century (e.g. in 1911, 1921, 1947, 1949, 1976) but air temperature was, on average, lower than today, so that the evapotranspiration in summertime was lower (Schär *et al.*, 2004) and consequently the vegetation was much less impacted by these events. Because air temperature decreases steadily with elevation (and generally precipitation increases), the climatic water balance of sites >1200 m still remains positive in the central part of the European Alps (Vitasse *et al.*, 2019). However, severe droughts are predicted to become more frequent even at high elevations where organisms might be less adapted to cope with water limitation (Rosbakh *et al.*, 2017).

Snow cover has an important impact in plant and animal phenology in mountain ecosystems. A significant reduction in the number of days with snow precipitation has been reported at all elevations during the 20th century in the Alps, particularly since the 1980s and in relation to warmer air temperatures (Laternser & Schneebeli, 2003; Pellicciotti, Bauder & Parola, 2010; Valt & Cianfarra, 2010; Serquet *et al.*, 2011; Diolaiuti *et al.*, 2012; Marty & Blanchet, 2012; Serquet *et al.*, 2013). A similar reduction has been observed across the northern hemisphere since the 1970s (Hernández-Henríquez, Déry & Derksen, 2015), especially in spring (Brown & Mote, 2009; Brown & Robinson, 2011), although this trend varies widely at a global scale (Bormann *et al.*, 2018; Pulliainen *et al.*, 2020). Analyses of snow water equivalent have shown a clear decrease in snow mass all over the European Alps during the period 1973–2012, at all elevations and more pronounced in spring compared to winter (Marty, Tilg & Jonas, 2017*b*). Mean snow depth has also been significantly reduced during the same period in the European Alps at all elevations and for all seasons (Durand *et al.*, 2009; Schöner, Auer & Böhm, 2009; Pellicciotti *et al.*, 2010; Marty & Blanchet, 2012; Marty & Meister, 2012). Detailed analyses in the Swiss Alps have confirmed a general decrease in all snow parameters at all elevations, with a faster reduction of snow cover at the time of snowmelt compared to the time of snow onset (Klein *et al.*, 2016). Spring (March to May) was the season with the highest air temperature increase over the last five decades, with a rate of 0.47°C decade^{-1} since 1970 in the Swiss Alps (Klein *et al.*, 2018, Fig. 1). This strong warming has led to earlier snowmelt, for example −5.2 days decade^{-1} across six locations in the Swiss Alps ranging from 1298 to 2540 m between 1970 and 2019 (Fig. 1). In autumn (September to November), the air temperature warming rate has been less than in spring, although still sufficient to delay time of snow onset at an average rate of +3.9 days decade^{-1} since 1970 for these six stations, leading to a significant increase in the snow-free period at an average rate of +9.1 days decade^{-1} in the Swiss Alps (Fig. 1). However, regional differences across the European Alps exist with on average stronger trends of snow depth reduction in the southern Alps over recent decades (Matiu *et al.*, 2021).

(*b*) *Predicted climate change in the European Alps*

Air temperature will increase further in the coming decades if present emission rates of greenhouse gases are not substantially reduced (IPCC, 2013). The difference between predictions based on lower [representative concentration pathway (RCP) 2.6] or higher (RCP 8.5) greenhouse gas emission rates (IPCC, 2013) increases with time, particularly after 2050. Déqué *et al.* (2007) predicted that air temperature in the European Alps would increase by 0.30 to 0.45°C decade^{-1} until 2100, with a higher expected increase in summer and autumn and an increased frequency of summer heatwaves (Keiler *et al.*, 2010). Precipitations in summer are expected to decrease over coming decades, although with a higher frequency of extreme rainfall events (Rajczak & Schär, 2017; Hodnebrog *et al.*, 2019). Recent analyses nevertheless showed that regional climate models (RCM, from the EURO-Coordinated Regional Downscaling Experiment) could greatly underestimate the warming rate during the growing season (Schwingshackl *et al.*, 2019; Boé *et al.*, 2020). This was due to models omitting the plant physiological CO_2 response (Schwingshackl *et al.*, 2019) and underestimating both the increase in shortwave radiation and changes in solar radiation connected with cloud cover and aerosols (Boé *et al.*, 2020). For the same reasons, regional models also tended to underestimate the decrease in summer precipitation (Boé *et al.*, 2020) as well as the increase in heavy rainfall events (Borodina, Fischer & Knutti, 2017).

A strong reduction of snow depth and snow cover is expected to continue at all elevations across the European Alps during the 21st century (Jasper *et al.*, 2004; Rousselot *et al.*, 2012; Schmucki *et al.*, 2015; Marty *et al.*, 2017*a*), particularly during the spring season (Magnusson *et al.*, 2010; Steger *et al.*, 2013). Permanent snow, glaciers and permafrost are expected to decline strongly or disappear, with an overall melt of the snow cover in summer (Magnusson *et al.*, 2010). At the end of the 21st century, continuous snow cover in winter may only be present above 2000 m, while mid-elevations (1000–1700 m) should experience random and/or discontinuous snow cover in about one in two winters (Schmucki *et al.*, 2017). These future expected changes in snow cover duration and thickness correspond to an average upward elevation shift of 800 m of the snow cover by the end of the century, while snow cover seasons may be reduced by 2 or 3 months, depending on the scenario (Bavay, Grünewald & Lehning, 2013; Marty *et al.*, 2017*a*; Beniston *et al.*, 2018).

Due to these rapid changes in air temperature and snowpack, the European Alps will undergo marked changes in the phenology and distribution of plants, animals and fungi, which are synthetized in the following sections.

(2) Phenological shifts

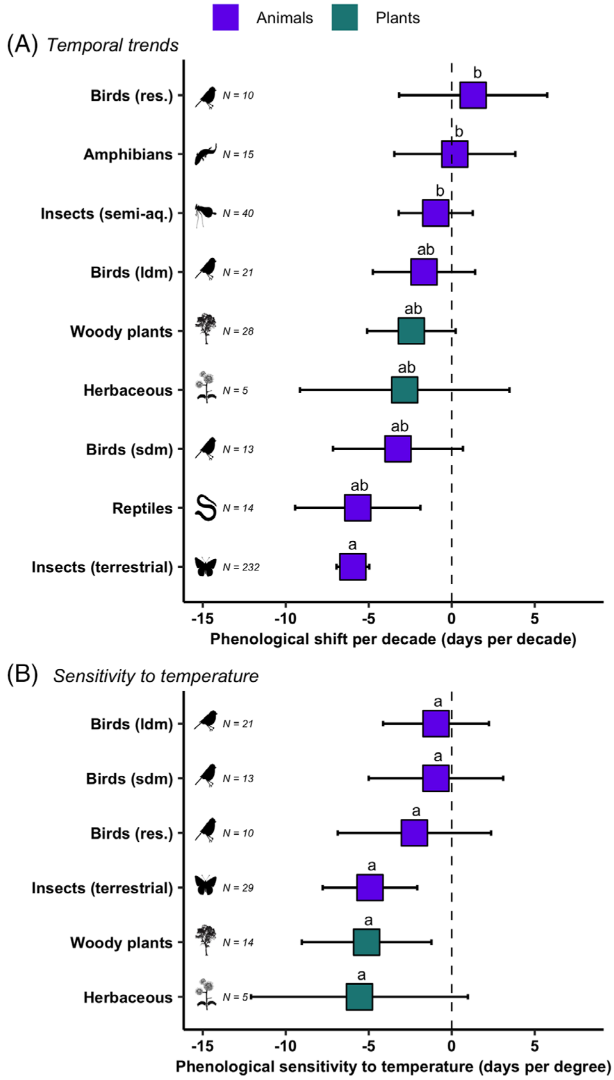

Fig 2. Spring phenological change per decade (A) or per degree (B) for different plant and animal groups studied in the European Alps region. Values correspond to the estimated marginal mean of the mixed-effect model with study as a random factor; error bars are 95% confidence intervals. The period of time varied among studies but was always more than 10 years within the period 1980–2020. Only groups with more than five species are shown (all studies are reported in Table 1). ldm, long-distance migrants; sdm, short-distance migrants; res., resident; semi-aq., semi-aquatic. Different letters among groups indicate significant differences (*post-hoc* Tukey tests at α = 0.05).

Our review reveals an advance in spring phenological events for most of the studied taxa, i.e. leaf-out and flowering for plants, singing activity, laying dates, arrival and hatching dates for birds, and the first yearly observation for insects, amphibians and reptiles although these were statistically significant only for reptiles and insects. There were also significant differences among these taxonomic groups (Fig. 2A). Reptiles and terrestrial flying insects such as Lepidoptera and Orthoptera showed the largest advance in their first yearly observation, with a significantly earlier −5.7 ± 3.8 days decade^{-1} for reptiles (estimated marginal mean ± CI; linear mixed-effects model) and −6.0 ± 1.0 days decade^{-1} for terrestrial insects, whereas a non-significant trend towards a slight delay was found for the peak of singing activity, laying dates or hatching dates of resident birds (+1.3 ± 4.5 days decade^{-1}) and first yearly observation of amphibians (+0.2 ± 3.6 days decade^{-1}; Fig. 2A). Insects with aquatic life stages (Odonata) showed non-significant trends for an earlier first yearly observation of the adult stage (-1.0 ± 2.2 days decade^{-1}, Fig. 2A). Plants also showed non-significant trends for an advance in leaf-out or flowering of -2.8 ± 6.3 and -2.4 ± 2.7 days decade^{-1} for herbaceous and woody plants, respectively (Fig. 2A). A significant difference was found between semi-aquatic and terrestrial insects (Table 1; Fig. 2A). Whereas resident birds showed a tendency for a slight delay in their singing activity or laying dates ($+1.3 \pm 4.5$ days decade^{-1}), an advance was detected for long- and short-distance migrant birds (-1.7 ± 3.1 and -3.2 ± 3.9 days decade^{-1}, respectively; Fig. 2A), although these differences did not reach statistical significance. When grouped by habitat type, a non-significant trend for a delay in singing activity or laying dates was found for birds inhabiting forest or open land ($+0.5 \pm 6.9$ and $+0.6 \pm 5.9$, respectively), whereas a significantly different advance of about -7.5 ± 7.8 days decade^{-1} was found for birds living in mixed habitats (Fig. S1).

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

For plants, phenological events are largely mediated by temperature and have the potential to change considerably with climate warming. In alpine environments, the few long-term time series of phenological observations show the same consistent trends, for instance between the Rocky Mountains (USA), Greenland (Iler *et al.*, 2013) and the Tibetan plateau (Chen *et al.*, 2015). For the European Alps, we are not aware of any long-term studies of the phenology of alpine plants. However, indirect data for the beginning of vegetation growth detected by ultrasonic sensors (used to detect snow depth) are now available for about 20 years across 30 alpine sites in the Swiss Alps (Vitasse *et al.*, 2017). These data reveal that vegetation onset in alpine plants occurred earlier at around -6.3 days °C^{-1}, with no strong photoperiodic constraint, in agreement with findings from the Tibetan plateau (Chen *et al.*, 2015). At lower elevations in the Swiss Alps, long-term phenological observations are available from a citizen network. These data show a significant advance of leaf-out or flowering dates during the period 1970–2012 by about -2.8 to -7.7 days °C^{-1} for various tree and shrub species and by about -3.7 to -7.4 days °C^{-1} for herbaceous species (Güsewell, 2014). It is known that spring phenological plasticity to temperature varies strongly among tree species, which could alter competition among species in response to global warming. For example, leaf-out of European beech (*Fagus sylvatica*) is one of the least sensitive to air temperature change, with an advance of less than -3 days °C^{-1}, whereas ash (*Fraxinus excelsior*), sessile oak (*Quercus petraea*) and larch (*Larix decidua*) are among the most sensitive at more than -6 days °C^{-1} (Migliavacca *et al.*, 2008; Vitasse *et al.*, 2013; Asse *et al.*, 2018; Bison *et al.*, 2019).

For animals, phenological changes are less documented and overall less pronounced for large herbivores and birds that can migrate over long distances to track food availability and quality (i.e. tracking the ‘green wave’, e.g. Bischof *et al.*, 2012; Rehnus *et al.*, 2020). In the lowland areas of the Swiss Alps (<600 m), the date of highest singing activity of various birds (mostly passerines), a proxy for the start of breeding, shifted earlier for the majority of species, and higher spring temperatures generally led to an earlier singing activity peak of around -1.1 days decade^{-1} for resident and short-distance migrant birds with slightly higher trends for trans-Saharan migrants (Strebel *et al.*, 2014; Table 1). Not surprisingly, insects seem to respond strongly to warming with the emergence date occurring earlier, for example by -21 days decade^{-1} for bark beetles (*Ips typographus*) over the period 1996–2005 in the south-eastern Alps (Faccoli, 2009; Table 1). Similarly, butterflies seem to respond strongly to warming, with the purple emperor (*Apatura iris*) emerging earlier (-10.5 days decade^{-1}) during the period 1982–2002 in northern Switzerland (Dell, Sparks & Dennis, 2005; Table 1). Altermatt (2012) reported a temperature sensitivity of -4.9 ± 2.0 days °C^{-1} for 28 butterfly species studied in the Swiss lowlands over the period 1998–2010 (Table 1). Interestingly, our review shows that within insects, species from Orthoptera and Lepidoptera have advanced their spring phenology to a larger extent than species from Odonata (Fig. 2A). This might be explained by their habitat use, because species of Odonata generally spend their larval stages in ponds. The microclimate of ponds may buffer the effects of warming temperatures, especially in spring due to the provision of water from the melting snowpack higher up, although more data will be necessary to allow robust comparisons of the phenological sensitivity of aquatic species to air temperature.

(3) Elevational range shifts

Based on the current scientific literature focusing exclusively or partly on the European Alps, animals, fungi and plants have all shifted their optimum elevation upslope, reaching 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} ($N = 1480$), respectively (mean ± CI; Fig. 3A). All taxonomic groups, except semi-aquatic insects, showed trends for a positive shift in optimum elevation (Fig. 3A), although this was statistically significant only for terrestrial insects ($+36.2 \pm 20.7$ m decade^{-1}), woody plants ($+32.7 \pm 17.9$ m decade^{-1}) and herbaceous plants ($+23.1 \pm 14.4$ m decade^{-1}). The average upward shift obtained from *info fauna* data regarding the optimum elevation of butterflies ($+39.9$ m decade^{-1}, Table 2) agrees well with the trend reported in a recent study in Switzerland (+38 m between 2003 and 2010, or +48 m decade^{-1}) that systematically monitored butterfly communities (Roth, Plattner & Amrhein, 2014), suggesting that no major bias was introduced by the haphazard sampling inherent in *info fauna*

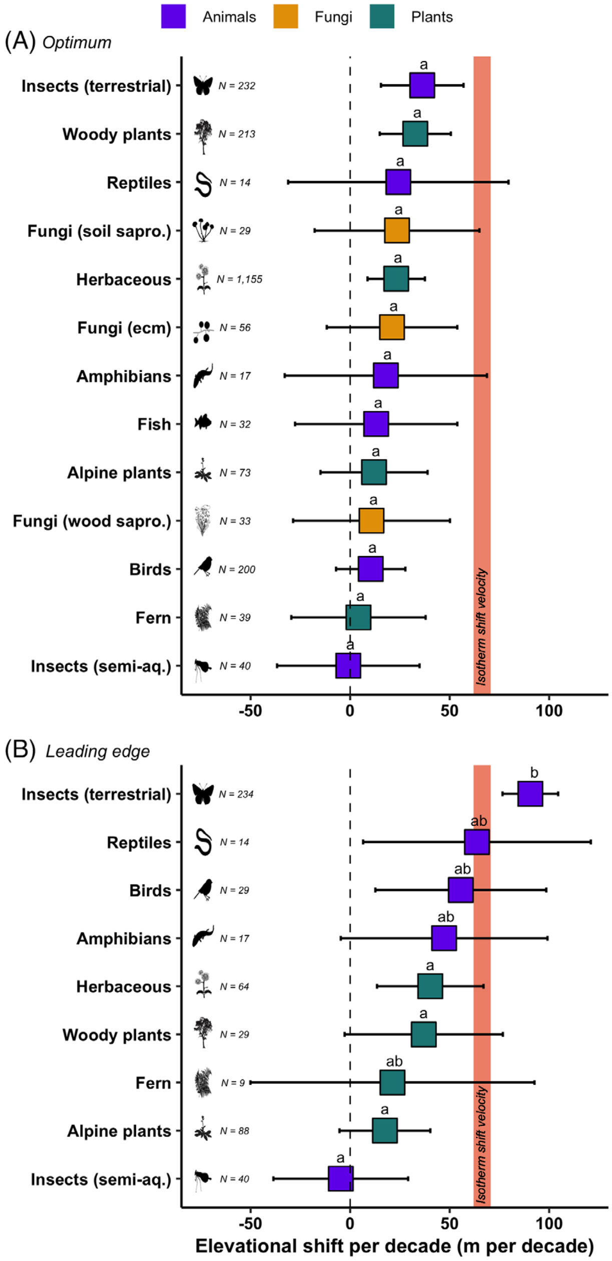

Fig 3. Empirical evidence for elevational range shifts of (A) the optimum distribution (i.e. elevation of maximum abundance) and (B) the leading edge (i.e. the upper range limit) reported for groups of taxa in the European Alps region. Values correspond to the estimate of the mixed-effect model with 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). ecm, ectomycorrhizal; sapro., saprophytic; semi-aq., semi-aquatic. Different letters among groups indicate significant differences (*post-hoc* Tukey tests at $\alpha = 0.05$).

data. By contrast, ferns, birds and wood-decaying fungi showed small and non-significant changes in optimum elevation, ranging between +4 and +11 m decade^{-1} (Fig. 3A).

For the leading edge (upper elevational range limit), upward shifts were most pronounced for animals (on average +72.3 ± 17.8 m decade^{-1}) than for plants (+28.2 ± 21.8 m decade^{-1}; Fig. 3B), with the exception of semi-aquatic insect species that showed a non-significant trend for the leading edge to shift downward (−4.7 ± 33.8 m decade^{-1}; Fig. 3B and Table 2). Remarkably, only terrestrial insects (+90.5 ± 14.0 m decade^{-1}) and reptiles (+63.7 ± 57.2 m decade^{-1}) showed an upward shift of their leading edge within the range or higher than the pace of climate warming (Fig. 3B), estimated at ~+62–71 m decade^{-1} based on a warming rate of 0.36°C decade^{-1} (Fig. 1) and a temperature lapse rate of +0.51–0.58 m 100 m^{-1} (Rolland, 2003; Kirchner *et al.*, 2013).

(*a*) *Terrestrial plants and fungi*

For plants, our review suggests that there may be substantial differences among the studied taxonomic or functional groups, although these did not reach statistical significance, with insignificant shifts in the optimal elevation of +12.0 ± 26.9 and +4.2 ± 33.7 m decade $^{-1}$ for ferns and alpine plants and significant upward shifts of +23.1 ± 14.4 and +32.7 ± 17.9 m decade^{-1} for herbaceous and woody species growing below the treeline (Fig. 3A). Notably, this general pattern among the taxonomic groups is the same for changes at the leading edge (Fig. 3B). Lenoir *et al.* (2008) showed for different mountain areas throughout France, including the western Alps, that the optimum elevation of 171 forest plants and trees moved upward in elevation at a mean rate of +29 m decade^{-1} when comparing vegetation surveys conducted between 1905 and 1985 to surveys conducted between 1986 and 2005. However, when splitting the data between short-lived herbaceous species (e.g. grasses and sedges) and long-lived woody species (trees and shrubs), Lenoir *et al.* (2008) found that only herbaceous plants from the forest understorey have significantly shifted their elevational optimum upslope (mean rate of +38 m decade^{-1}). Similarly, by revisiting historical relevés and species indicator values, Küchler *et al.* (2015) found an upward shift of forest plant species in the herbaceous layer of Swiss forests at +10 m decade^{-1} since the 1950s, while the elevational range of species from the shrub and tree layers remained rather stable over the same time period. By contrast, our quantitative review across the European Alps suggests that the optimum range of long-lived woody plants is shifting upward at a significant rate, at least at the same rate as non-alpine herbaceous plants (Fig. 3A). This discrepancy may stem from the fact that we did not constrain our review only to forest systems, unlike the above-mentioned studies which specifically focused on range shifts of forest plants (Lenoir *et al.*, 2008; Küchler *et al.*, 2015). Thus, by including data from studies on forest systems with those reporting range shifts for woody plant encroachment beyond the treeline or following land abandonment below the treeline, we have a greater opportunity to detect elevational range shifts for woody plants. By missing the upper part of the elevational gradient beyond the forest limit, studies restricted to forest systems may have underestimated the true rate at which woody plant species are responding to temperature increases or abandonment of land in the Alps. The dynamics of recruitment of forest tree species at the upper elevational limits seems to be changing at a relatively fast rate, with seedlings and saplings currently occurring well beyond the upper elevational limit of adult trees (Vitasse *et al.*, 2012). Similarly, across several mountain areas in western Europe, including the western Alps, Lenoir *et al.* (2009) reported differences in elevational distribution between seedlings and adult life stages of trees, suggesting an ongoing upward shift for woody plants but with quite high heterogeneity among species which could be due to species-specific variability in demographics and competitiveness (Scherrer *et al.*, 2020).

The average rate at which alpine plant species shifted upslope appears to be lower than for non-alpine plants or woody species below the treeline for both the optimum range and the upper elevational limits (Fig. 3), although note that these values did not differ statistically significantly. This slower rate at which alpine plants may be shifting upslope could be due to lower dispersal ability, biotic interactions or possibly to the methods employed to assess such trends. For alpine plants, resurveys are often compared with historical surveys conducted before 1950, i.e. during a period with lower warming rates than at present, but these studies were not included in our analysis, making this unlikely to explain the lower rate of upslope migration for alpine plants. While climate warming plays an undeniable role in the recent redistribution of plants in mountain ecosystems (Steinbauer *et al.*, 2018), it might not be the only driver behind the upslope shifts along elevational gradients: precipitation (Rapacciuolo *et al.*, 2014), land use (Gehrig-Fasel, Guisan & Zimmermann, 2007; Guo, Lenoir & Bonebrake, 2018) or ongoing recolonization after the 'Little Ice Age' (Kammer, Schöb & Choler, 2007) might be additional drivers, either accelerating or slowing down the rate of elevational range shifts. For example, the treeline ecotone has been influenced by farming activities for several thousand years in the Alps (Tinner & Theurillat, 2003), and a large part of this recent upward shift has been attributed to substantial changes in land use, including: (*i*) land abandonment in the Swiss and Austrian Alps (Gehrig-Fasel *et al.*, 2007; Gellrich *et al.*, 2007; Tasser *et al.*, 2007), which seems to explain the large upward shift of *Abies alba* observed since the 1950s in the west central Alps (Chauchard *et al.*, 2010), and (*ii*) a reduction of cattle grazing, especially in the Italian Alps (Piotti *et al.*, 2007). By excluding open habitats in their analyses, Bodin *et al.* (2013) showed that the upward shift they initially found for understorey forest plants became insignificant, a result that may be related to forest microclimate dynamics potentially buffering the effects of warming for understorey plants compared with plant communities from more open habitats (von Arx *et al.*, 2013; De Frenne *et al.*, 2019; Zellweger *et al.*, 2020). In some studies, a considerable part of the analysed herbaceous species may also shift downward (Lenoir *et al.*, 2010; Bodin *et al.*, 2013), potentially explained by more intensive management (disturbance) at lower elevations compared to forests at higher elevations (Lenoir *et al.*, 2010).

Interestingly, fungi may also be shifting their elevation. Although data in the Alps originated from a single study, that study assessed the shift in optimum elevation of 118 species (Diez *et al.*, 2020). They found values ranging between +10.7 and +23.6 m decade^{-1} for wood-decaying and soil-dwelling fungi with an intermediate value for ectomycorrhizal fungi (+21.0 m decade^{-1}) (Table 2, Fig. 3A). A slower response of wood-decaying fungi would be consistent with their dependence on wood resources and particularly dead wood, with the availability of woody plants likely delayed compared to the rate of climate change.

(*b*) *Terrestrial animals*

Except for birds, elevational range shifts of animal species in the Alps have been less documented than for plants, with direct evidence available only for some groups. Our review reveals that terrestrial insects have moved significantly upslope in terms of both the optimum and the leading edge (Fig. 3). In an analysis of four orders of insects, a significant upslope movement is seen for each of the groups Lepidoptera, Coleoptera and to a lesser extent Orthoptera in both measures of elevational range (Fig. 4). For semi-aquatic insects from the group Odonata, neither range measure has changed significantly (Fig. 4). Insects, like most ectotherms, are very sensitive to changes in air temperature and consequently are likely to track climate warming closely. Accordingly, numerous upward range shifts have been documented for terrestrial insects, especially for pests which receive much more attention. For example, upward shifts in the elevational range of outbreaks of the European spruce bark beetle (*I. typographus*) were related to the increased frequency of drier summers in the Italian Alps (Marini *et al.*, 2012). The pine processionary moth (*Thaumetopoea pityocampa*) shifted its distribution upward between 1975 and 2004 at average rates of +70 m decade^{-1} and +29 m decade^{-1} on the southern and northern slopes of the Italian Alps, respectively, with this shift related to the increase in minimum winter air temperature (Battisti *et al.*, 2005). As ectotherms, insects do not regulate their body temperature, and thus climatic variation in temperature will have a direct effect on their physiology. For example, warmer air temperatures in summer generally reduce European bark beetle development time (i.e. increased voltinism) (Jakoby, Lischke & Wermelinger, 2019), and therefore are likely to increase infestation pressure (Marini *et al.*, 2012; Jakoby *et al.*, 2019). The reproductive cycle of insects is expected to be faster under warmer air temperatures, potentially allowing an extra generation per growing season at all elevations by the end of the century for European spruce bark beetle (Jakoby *et al.*, 2019). Even though molluscs have a relatively low

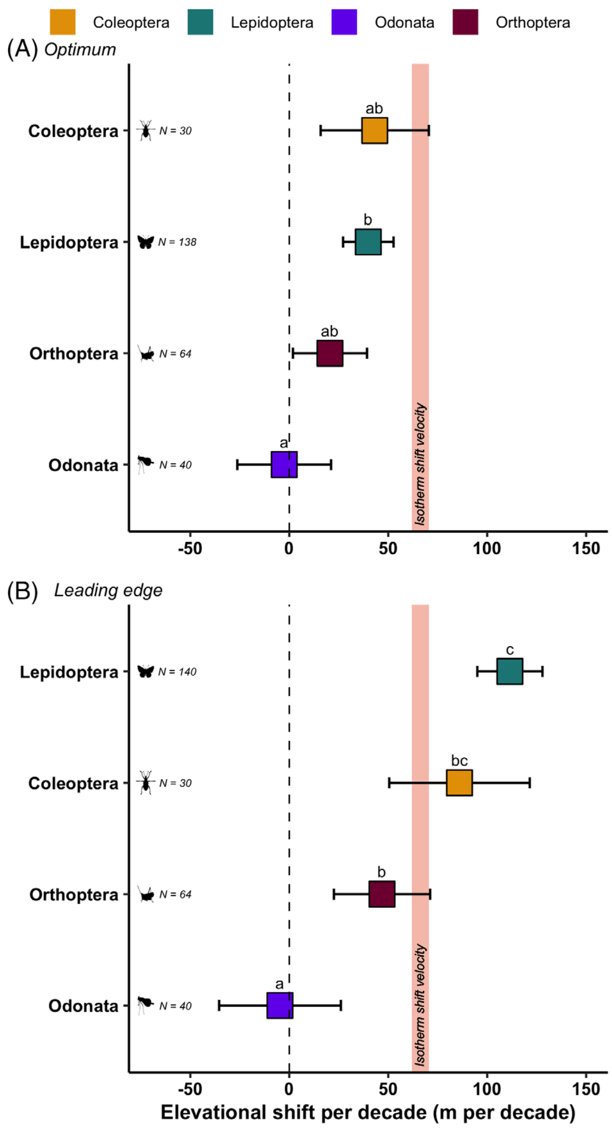

Fig 4. Mean elevational shift per decade for four different orders of insects in terms of (A) the optimum elevation (i.e. elevation of maximum abundance) and (B) the leading-edge elevation (i.e. the upper range limit). Values correspond to the estimate of the mixed-effect model with study as a random 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 $\alpha = 0.05$).

capacity to move over large distances, an upward shift of the land snail *Arianta arbustorum* of about 164 m has been reported in a comparison of its distribution in 1916–1917 with its distribution in 2011–2012 in the eastern Alps, and this upward shift was most pronounced (around 233 m) on south-facing slopes (Baur & Baur, 2013). Both habitat and microclimate are important factors for these organisms and the authors stressed that, on some mountain slopes, snails have already reached natural barriers (vertical rock walls with no soil), that prevent further upward shifts.

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

Interestingly, we found no significant differences in the upwards shift of optimum elevation between plants, fungi and animals (Fig. 3A), whereas animals appear to be responding fastest in terms of the leading edge, especially for terrestrial insects (Fig. 3B). The distribution of mammals and birds is mainly driven by habitat and food availability, and a change in temperature may not affect their distribution directly if features of their habitat remain stable or depend more on the micro- than the macroclimate (Jähnig *et al.*, 2020) and on plant phenology (Peláez *et al.*, 2020). For instance, two studies conducted on European roe deer (*Capreolus capreolus*) identified a strong dependence on the quality of food resources, with individuals performing long-distance seasonal movements upward and downward to locate food resources within their home range and thus tracking plant phenology (Gaudry *et al.*, 2015; Peláez *et al.*, 2020). Another study revealed an upward shift of about +37.5 ± 10.3 m decade^{-1} of four mountain ungulate species in the Swiss Alps based on hunting records, attributing this upward shift to the lengthening of the snow-free period (Büntgen *et al.*, 2017, Table 2).

The effects of climate warming on animal distribution are likely to be complex, and will include indirect effects. A good example is the Alpine chough (*Pyrrhocorax graculus*) that nests at high elevations in cavities and fissures on inaccessible rock faces and forages in open alpine meadows (Delestrade & Stoyanov, 1995). Climate and land use are affecting the distribution of plants and forests but obviously not the distribution of the cliffs it uses for nesting. While upward shifts in distribution of birds have been detected in some areas in the Alps such as the central Swiss Alps (Maggini *et al.*, 2011; Knaus, 2018), several other studies documented only marginal changes or no change in spite of significant air temperature increases during the study period (Archaux, 2004; Popy, Bordignon & Prodon, 2010). Consistently, our results revealed rather low and insignificant rates of optimum elevational range shift for birds in general, on average +10.3 ± 17.5 m decade^{-1}, but Table 2 shows that there was much variation in the calculated values, with a trend for higher values in the Eastern and Southern Alps. This may be partly a result of human-induced land-use changes (Knaus, 2018) as in these regions a strong upward shift of the treeline and reforestation of formerly cut or unforested areas has taken place, moving up the habitat of specialized alpine birds such as the rock ptarmigan (*Lagopus muta*)

(Pernollet, Korner-Nievergelt & Jenni, 2015). Given their ecological role as consumers, it is likely that responses of bird communities to climate change will lag behind that of some other taxonomic groups (Devictor *et al.*, 2012). It is possible that most specific elevational range shifts in mobile species like birds are related to site-specific factors associated with food availability, while for forest plants (Bertrand, Gegout & Bontemps, 2011) biotic interactions and population dynamics are likely to be more important (Scherrer *et al.*, 2020).

(*c*) *Freshwater ecosystems*

For freshwater ecosystems, only a few studies are available worldwide (Table 2), with several of these from the Alps. Comte & Grenouillet (2013) reported, across different mountain ranges in France including the western Alps, that the elevational range of stream fishes shifted upslope at a mean rate of about $+13.1 \pm 40.8$ m decade^{-1} during the period 1986–2006 (Fig. 3A). For amphibians, dragonflies and damselflies, which depend directly on lakes, ponds, bogs, fens, streams and streamlets for their habitats, no significant upward shift was found in their optimum or leading edge elevation. The slower migration rates of semi-aquatic (e.g. dragonflies) and aquatic (e.g. fishes) animals compared to terrestrial animals or plants might be due to their strong dependence on freshwater habitats which are heavily fragmented by human activities (e.g. dams) and are also likely to exert strong microclimate buffering on warming rate, especially within mountain ranges where streams are fed by snow and glacier melt (McLaughlin *et al.*, 2017). In addition, most of these organisms are dependent on the vegetation that structures their habitat. Typically, dragonflies inhabiting subalpine and alpine zones live in bogs, fens and their associated small water bodies and runoff. The vegetation of these habitats is very specific and species requirements in terms of vegetation structure are not met in the pioneer water bodies of the upper level. The slower migration rate of these species could therefore partially be explained by their requirement for colonization by vegetation to occur first to offer new potential habitats for them. The formation of new bogs, fens or swamps may take several decades or even centuries.

(4) Plant–animal interactions mediated by species-specific phenological and spatial shifts

On the one hand, because plants are the first link of the food web, changes in plant phenology and composition will affect food quantity and quality for higher trophic levels, and may thus affect complex trophic interactions (Plard *et al.*, 2014; Thackeray *et al.*, 2016; Kharouba *et al.*, 2018; Renner & Zohner, 2018; Kharouba & Wolkovich, 2020), animal performance (Sheridan & Bickford, 2011) and species migration (Büntgen *et al.*, 2017; Peláez *et al.*, 2020; Rehnus *et al.*, 2020). Conversely, numerous seed plants are pollinated and dispersed by animals, and are affected by their interactions with herbivores, thus animal range shifts will be intimately involved with plant range shifts. Responses of herbivores to climatic changes are generally mediated through plant quality and quantity (Mysterud *et al.*, 2001, 2008; Peláez *et al.*, 2020; Rehnus *et al.*, 2020). In temperate regions, vegetation quantity gradually increases in spring to reach a maximum in the middle of summer, while vegetation quality is generally highest shortly after the beginning of vegetation growth in spring. In mountain ecosystems, mobile organisms can track these changes by migrating upslope, following the 'green wave' induced by the progress of the season (Bischof *et al.*, 2012; Büntgen *et al.*, 2017; Herfindal *et al.*, 2019). Migratory bird species have also been observed to follow this peak in nutrient availability during spring migration (Van der Graaf *et al.*, 2006). Our review found that birds showed relatively small phenological and spatial changes in response to warming, perhaps because birds are vagile and thus can adapt easily to changes in food availability. Similarly, the parturition date of the European roe deer was shown to correlate better with spring plant phenology than with elevation in Switzerland (Peláez *et al.*, 2020). By contrast, species that are less mobile may become desynchronized in relation to their food resources as these move upwards in response to warming.

An example of in which such desynchronization has had a positive biotic effect for trees is in the frequency of outbreaks of the larch budmoth (*Zeiraphera griseana*), which historically occurred over 12 centuries every 8–9 years but disappeared after 1982 in the Engadine (eastern Swiss Alps). This was suggested to be due to a mismatch between the insect life cycle and larch budbreak (Esper *et al.*, 2007), which might have depended on climate warming (Johnson *et al.*, 2010). A recent outbreak did take place in 2017–2018, which was correlated with cold winter temperatures that reduced energy consumption during diapause in the moths, allowing them to emerge more in synchrony with the new foliage (Büntgen *et al.*, 2020). Warmer winters may continue to decrease the fitness of this insect in the future and upward elevational shifts of outbreak epicentres are expected.

On the contrary, many trees may experience more frequent severe defoliation due to pest outbreaks because warmer temperatures are expected to accelerate the life cycles of insects, potentially increasing the number of generations per season (Colombari *et al.*, 2012; Jakoby *et al.*, 2019). For example, the warmer and drier conditions that occurred in the late 1980s in the Italian prealps reduced the mortality of the web-spinning sawfly (*Cephalcia arvensis*) and accelerated its development, causing severe defoliation of Norway spruce (*Picea abies*) needles on which the larvae feed (Marchisio, Cescatti & Battisti, 1994). Similarly, pine shoot beetles (*Tomicus piniperda*) and other bark beetles are likely to weaken Scots pine (*Pinus sylvestris*) and Norway spruce in the inner valleys of the European Alps, where they already suffer from drought, under warmer climates that will permit additional insect generations during the growth season (Rigling & Cherubini, 1999; Rebetez & Dobbertin, 2004; Jakoby *et al.*, 2019; Schneider, Comte & Rebetez, 2021). Such differences in phenological sensitivity to temperature are therefore expected to modify food-web interactions under climate change (Vitasse *et al.*, 2011; Roberts *et al.*, 2015; Asse *et al.*, 2018). Phenological differences between low- and high-elevation trees have reduced considerably over recent decades in the Swiss Alps due to a stronger phenological advance at higher elevations (Vitasse, Signarbieux & Fu, 2018*b*), putting these plants at higher risk of frost exposure (Vitasse *et al.*, 2018*a*) and reducing the total period of availability of high-quality food for herbivores that follow the 'green wave' (Mysterud *et al.*, 2008).

In alpine environments, the life cycles of many plant and animal species are reliant on the date of snowmelt and the rapid greening that follows. For example, variation in the snowpack accounts for a substantial part of variation in survival (about 16%) and reproduction (29%) of alpine marmots (*Marmota marmota*) (Tafani *et al.*, 2013). Snow cover phenology is the main driver of foraging habitat selection for the white-winged snowfinch (*Montifringilla nivalis*) during the breeding season (Resano-Mayor *et al.*, 2019). Earlier snowmelt leads to earlier vegetation onset which in turn increases the reproductive success of the rock ptarmigan (*Lagopus muta*) (Novoa *et al.*, 2008), but decreases the litter size of alpine marmots (Tafani *et al.*, 2013). Similarly, earlier vegetation onset due to warming can increase survival of ibex (*Capra ibex*) through earlier access to food resources in spring (Pettorelli *et al.*, 2007), but a reduction of the snowpack in winter can also reduce the quality of the vegetation available in spring (Robinson & Merrill, 2012).

The above examples of species interactions that are affected by phenological synchrony represent direct effects on a few specific taxonomic groups; indirect and more complex species interactions involving several trophic levels (network analyses) still await detailed investigation. How the synchrony between winter climatic conditions, insect diapause, bird activity and spring vegetation is affected will determine the ability of many species to adapt to climate change. This nascent research field should receive more attention to allow us to anticipate structural changes across multiple levels of ecosystems (Kharouba *et al.*, 2018; Visser & Gienapp, 2019).

(5) Research gaps and ecosystem-based monitoring

Alpine ecosystems and the factors influencing species distributions have a long research history in the European Alps (Braun-Blanquet, 1954; Offner & Le Brun, 1956), for example with common garden experiments at different altitudes being performed in the Mont-Blanc range in the late 19th century (Bonnier, 1888). We now have much data on elevational and phenological shifts for several taxa, and a better understanding of the factors influencing phenology and species distribution. This review provides evidence that recent climate change may be affecting a wide range of taxonomic groups. However, our review also emphasizes major gaps in our knowledge, especially regarding biotic responses to climate change, and in particular, to a lack of long-term and ecosystem-based monitoring that could allow us to disentangle the direct and indirect effects of climate and land-use changes on different trophic levels (Yoccoz, Delestrade & Loison, 2010; Ims & Yoccoz, 2017).

Long-term ecosystem research (LTER) programs exist in the Alps, but mostly with a focus on vegetation and soil, often in connection to ecosystem services and landscape patterns (Tappeiner, Borsdorf & Bahn, 2013; Lavorel *et al.*, 2017; Rogora *et al.*, 2018). They do not tend to integrate other ecosystem components such as herbivores, granivores and carnivores from groups as diverse as insects, birds and mammals. There is, however, evidence that changes in the abundance and distribution of species may be related to ecological interactions [e.g. the mismatch between larch leaf-out and budmoth emergence (Büntgen *et al.*, 2009; Johnson *et al.*, 2010)], or involve multiple trophic levels (Burgess *et al.*, 2018). The data available for different taxonomic groups often come from different time periods or places. The absence of a common design makes it difficult to build causal models integrating direct and indirect effects [e.g. Grace & Irvine, 2020; but see Thuiller *et al.* (2018) for a species distribution modelling approach to plant–herbivore interactions]. Our analysis identified a large heterogeneity in species responses to climate change, making it difficult to understand and predict changes at the ecosystem level (Mouquet *et al.*, 2015). Although citizen science has allowed the collection of a large amount of data from haphazard observations, there is a clear need for more systematic monitoring. Joint analysis of these two sources of data would allow unbiased inferences (Dorazio, 2014). Developing integrated monitoring programs focusing on different trophic levels, and combining these with underlying conceptual models of the effects of climate and land-use changes on ecosystem structure and functioning should be a priority.

IV. CONCLUSIONS

(1) In the European Alps, spring phenology has advanced over recent decades for all taxa, except birds and amphibians, with these advances being statistically significant for ectothermic animals such as terrestrial insects and reptiles.
(2) We found a trend for almost all studied taxa to shift their distribution range upslope, with significant changes in optimum elevation found for terrestrial insects, herbaceous and woody plants and in leading edge elevation for terrestrial insects, reptiles, birds and herbaceous plants.
(3) We suggest that the trend for upward shift likely reflects the strong warming and the receding of snow cover that has occurred across the European Alps over recent decades and reflects the tracking by these taxa of their climatic niche, although regional land-use changes may also provide an explanation in some cases.
(4) With the possible exception of some groups of terrestrial insects, such as butterflies, the trend for an upward shift in plants, fungi and animals appears currently too slow to track isotherm shifts induced by climate

warming. Indeed, an upward shift of about 330 m would be necessary to match the air temperature rise of close to 1.8°C that has occurred since 1970 in the European Alps region (i.e. 0.36°C per decade). This roughly corresponds to a mean shift of elevational range of about +62–71 m decade^{-1}, assuming an annual adiabatic lapse rate of 0.51–0.58°C 100 m^{-1} as measured across the Alps (Rolland, 2003; Kirchner *et al.*, 2013). The mean upward shift of most of the species groups observed over the last decades clearly lags behind this value (between −2 and +34 m decade^{-1} for the optimum elevation and between −5 and +64 m decade^{-1} for the upper elevational limit), except for terrestrial insects (+36.2 and +90.5 m decade^{-1} for the optimum and upper elevational limits, respectively).

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

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

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Author contributions: Y.V. and M.R. conceptualized and planned the work. Y.V., J.L. and S.U. collected the data. Y.V. and J.L. synthetized the data. S.U. analysed the data from the *info fauna* database and Y.V. from the *PhenoForest* database. M.R. wrote most of Section III.1 with contributions from G.K., who also created Fig. 1. Y.V. and J.L. wrote most of the text with substantial inputs from all co-authors.

Data availability: all raw data at species-level resolution used in the quantitative analyses are provided in the online supporting information.

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VII. Supporting information

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

Figure S1. Mean phenological shift of the singing activity or laying dates per decade for birds classified according to habitat.

Table S1. Spring phenological change per decade or/and per degree for each studied species.

Table S2. Elevational range shifts of the optimum distribution (i.e. elevation of maximum abundance) or/and the leading edge (i.e. the upper range limit) for each studied species.

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