



Millipedes step up: species extend their upper elevational limit in the Alps in response to climate warming

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Abstract. 1. Climate warming is predicted to result in changes to phenology, behaviour and abundance as well as poleward shifts or upslope displacements of the distribution of species. However, climate-warming induced changes in distribution patterns have rarely been studied in ground-dwelling arthropods.

2. We investigated changes in the upper elevational limit and relative abundance of 11 millipede species by repeating historical surveys from 1917 to 1919 in five valleys in the Swiss National Park (Eastern Alps) in 2018–2019.

3. We found that the upper elevational limit for 10 out of 11 millipede species has risen, on average, by 161 m in 100 years, accompanying a 1.5 °C rise in mean annual temperature in the investigation area. The 10 millipede species differed in upslope expansion of their distribution with the shift ranging from 50 m to 363 m.

4. The relative abundances of species (percentage of individuals sampled for each of the 11 millipede species) were very similar in 1917–1919 and 2018–2019. Only three species showed a change in frequency >6% over 100 years: two species had reduced abundances by 13.7% and 12.5% in the recent survey, while one species increased in abundance by 12.2%.

5. We provide evidence showing that soil-dwelling millipede species with low dispersal ability have raised their upper distribution limit to higher elevation between the surveys done in 1917–1919 and 2018–2019. This upslope shift in distribution is most probably due to the significant increase in temperature recorded in the investigation area in past decades.

Key words. Alps, Diplopoda, global warming, ground-dwelling invertebrates, historical data, mountain species, Myriapoda, range shift, Swiss National Park.

Introduction

The climate has been warming since the beginning of the 20th century, and temperature increases have been attributed to increased greenhouse gas emissions (Occc, 2008; Xu *et al.*, 2018). Since recording began in 1864, the increase in the annual mean temperature in Switzerland is higher (1.8 °C) than the global average (0.85 °C) (Allgaier Leuch *et al.*, 2017). Alpine areas belong to those regions expected to experience above average warming with continued global climate change (Beniston, 2003; IPCC, 2013). Under human-induced climate

change, species may adapt to the new conditions (genetic evolution) and/or alter their phenology, behaviour and abundance, and shift their distributional ranges so as to follow favourable conditions (Menzel *et al.*, 2006; Parmesan, 2006; Moritz & Agudo, 2013; Lenoir & Svenning, 2015; Bishop *et al.*, 2019). Local and regional extinctions are expected for species that are unable to adapt or move (Maggini *et al.*, 2011).

There is increasing evidence for poleward warming-induced expansions of distribution boundaries for several insect groups, such as butterflies and moths (e.g. Mikkola, 1997; Hill *et al.*, 2002; Parmesan, 2006; Mason *et al.*, 2015; Forsman *et al.*, 2016), or dragonflies and damselflies (Hickling *et al.*, 2006; Mason *et al.*, 2015; Termaat *et al.*, 2019). Similarly, in mountain areas, the distribution ranges of plant and animal species are moving towards higher elevations in response to recent climate warming (Lenoir *et al.*, 2008; Chen *et al.*, 2011;

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Maggini *et al.*, 2011; Bässler *et al.*, 2013; Baur & Baur, 2013, Menéndez *et al.*, 2014, Marshall *et al.*, 2020). These shifts may include upwards expansions of the distributional range to include newly climatically suitable habitat, retraction at the lower limit due to loss of no longer suitable habitat in the lower parts of the range (Lenoir & Svenning, 2015) and shifts in the optimal elevation (Wilson *et al.*, 2007; Lenoir & Svenning, 2015). However, despite these trends being widespread and consistent across taxa, the response to climate warming seems to be species specific, and most studies on climate-driven range shifts report that some species are not moving, or are even moving in the opposite direction (Hickling *et al.*, 2006; Parmesan, 2006; Lenoir *et al.*, 2008; Chen *et al.*, 2011; Maggini *et al.*, 2011). Possible reasons for species-specific range shifts are intrinsic factors including dispersal ability, habitat specialisation and physiological limits, and extrinsic factors such as barriers to dispersal, microclimatic conditions, and local topography (Moritz & Agudo, 2013). Species' range shifts may lag behind climate to a different degree further increasing the variability in observed responses. The new species assemblage at more northern latitude (or southern in the southern hemisphere) or higher elevation may also depend on interactions among species, which have so far received little attention (Menéndez *et al.*, 2006; Urban *et al.*, 2012).

Shifts in the upper elevational limit have predominantly been examined in conspicuous groups such as plants (Chen *et al.*, 2009; Lenoir *et al.*, 2015) and animals with a high dispersal ability, such as birds and butterflies (Parmesan *et al.* 1999; Parmesan 2006; Lenoir *et al.*, 2015), an exception being a land snail with a low dispersal ability (Baur & Baur, 2013). Species with low dispersal ability are assumed to be most sensitive to climate change, because they may not move fast enough and/or their evolutionary response times may not be sufficient considering the current rate of temperature increase (Lenoir *et al.*, 2015; Meester *et al.*, 2018).

Millipedes, a remarkably diverse class of arthropods with more than 11 000 described species (Enghoff *et al.*, 2015), play a key role in ecosystem functioning. Most of the species are detritivores contributing to soil formation, nitrogen mineralisation and litter decomposition (Cárcamo *et al.*, 2000; Golovatch & Kime, 2009; David, 2015). The dispersal ability of millipedes is typically low and most species have a relatively small distribution range (Golovatch & Kime, 2009). David (2009) hypothesised that global warming may result in higher rates of population growth in some temperate millipede species, while cold-adapted species living on mountain summits may suffer from a reduction of their habitat. However, the existence of micro-refugia in topographically complex mountain areas may allow millipede species to survive in relatively small patches of shrinking habitat provided they are not too isolated (Moritz & Agudo, 2013; David, 2009). There is so far no published study on climate change effects on the elevational distribution of species of millipedes (Myriapoda, Diplopoda).

In the present work, we investigated for the first time the upper limit shift of millipede species in the past decades as a result of climate warming. Bigler (1929) investigated the millipede diversity in the Swiss National Park (SNP) and its surroundings in the Eastern Alps and presented detailed information on the

elevational distribution of the various species in the years 1917–1919. SNP is a strict nature reserve with no human disturbance or land-use change since 1914. Thus, changes in the distribution range of species in the SNP are not confounded by human activities. We resurveyed the same valleys and mountain slopes after 100 years to examine whether there are shifts in the upper elevational limit of the various millipede species and whether the relative abundance of the species changed during this period. In particular, we asked the following questions:

- 1 Did the 11 millipede species change their upper elevational limit in the SNP in the past 100 years?
- 2 Did the relative abundances of these millipede species change over a period of 100 years?

Materials and methods

Study area

The SNP was established in 1914 in the Eastern Alps, Switzerland (46° 39' N, 10° 12' E), as a strict nature reserve (category Ia; IUCN/WCMC, 1994). The park's main targets are ecosystem protection without any influence of humans or domestic animals and scientific research. There is no habitat and wildlife management, and public access is permitted only on marked paths in summer months. The SNP measures 170.3 km² and includes an elevational range from 1315 m to 3173 m a. s. l. (Baur & Scheurer, 2015). Forests cover 32% of the park area with the tree line around 2200 m a. s. l., alpine grasslands cover 20%, waters 1%, and rocks and scree slopes 47% (Baur & Scheurer, 2015). Carbonate rocks, especially dolomite and marl limestone, are the dominant bedrock (Trümpy *et al.*, 1997). Adjacent areas to the SNP are covered by forest, rocks and scree slopes and grassland, which is extensively managed by livestock farming (cattle, sheep).

The SNP and its surroundings are characterised by continental inner-alpine conditions. Mean annual temperature is 5.5 °C in Scuol, 3 km north from the SNP at 1303 m, and 0.7 °C in Buffalora, situated at the edge of SNP at 1968 m (mean 1981–2010; MeteoSwiss, 2020). The corresponding mean July temperatures are 15.2 °C and 10.7 °C. Mean annual precipitation slightly increases with elevation from 706 mm in Scuol at 1303 m to 793 mm in Buffalora at 1968 m (MeteoSwiss 2020). Mean annual temperature increased by 1.5 °C in the SNP between 1917 and 2019 (data from the Buffalora weather station; MeteoSwiss, 2020). In contrast, the amount of annual precipitation did not change over the period considered (MeteoSwiss, 2020).

Historical data

Bigler (1929) surveyed the millipede fauna in the then newly established SNP and its surroundings in the years 1917–1919. A wide part of the SNP was covered during the various sampling trips. Particular attention was paid to maintain a similar sampling effort along the vertical gradient in the valleys examined. Bigler (1929) used active capture and sieving of moss and soil to collect millipedes. He provided detailed information on the valleys,

in which sampling was performed, and gave the exact elevation of each record. Bigler (1929) also displayed elevational distributions for each species.

Recent data

We repeated Bigler's survey in 2018–2019. Following the historical description, we selected five transect lines in different valleys of the SNP and its surroundings [Val dal Botsch (hereafter valley B), Val Trupchun/Val Müschauns (valley M), Val Tavrü (valley T), Val Cluozza/Val Sassa (valley S), and Val Zeznina/Macun (valley Z; Fig. 1)] Three transect lines (B, M and S) were wholly located within the SNP. The lower part of the Val Tavrü-transect (T) was situated in the buffer zone of the Engiadina Val Müstair UNESCO biosphere reserve, and

the upper part did run along the border of the SNP. The lower part of the Val Zeznina/Macun-transect (Z) was in extensively managed grassland with some forest, while the upper part was in the SNP.

Beginning at 1800 m, we determined sampling sites along each transect line at an elevational interval of 100 m below 2000 m and at an elevational interval of 50 m above 2000 m. Transect lines mainly followed hiking paths and ended when the pass of the valley or a summit was reached (maximum elevation 2850 m). Transect lines covered most habitat types in the SNP, ranging from alpine forests in the lower part of the valleys to alpine meadows and rocky habitats at higher elevations. To minimise disturbance of wildlife, we followed the SNP guidelines for researchers and set the sampling sites less than 50 m from hiking trails. Altogether 91 sampling sites were distributed along the five transect lines.

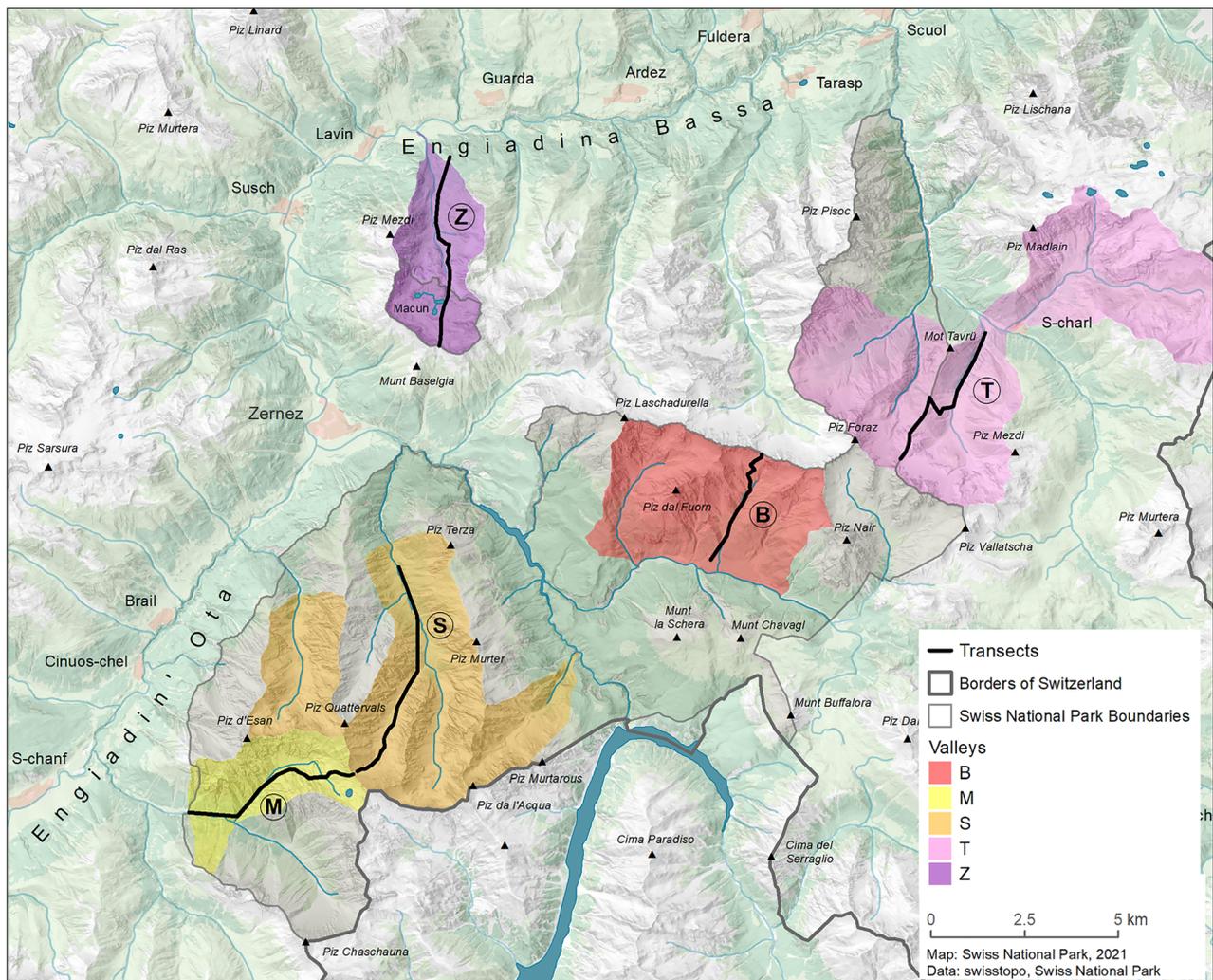


Fig 1. Map of the five valleys examined in the Swiss National Park and its surroundings, with the transect lines of the recent survey (black lines) and the valleys used for comparison with the historical data (coloured areas). Letters indicate the name of the transects: B – Val dal Botsch (red); M – Val Trupchun/Val Müschauns (yellow); T – Val Tavrü (pink); S – Val Cluozza/Val Sassa (orange), and Z – Val Zeznina/Macun (purple). Map provided by Tamara Estermann (GIS and ICT Department, Swiss National Park).

We applied three sampling techniques to collect millipedes. First, we visually searched for millipedes (hereafter active capture) on the ground, in leaf litter, and under bark, logs and stones at each sampling site for a total of 75 person minutes distributed over 2 days. Millipedes were captured with forceps and stored in 70% ethanol. Sampling was restricted to an area of approximately 30 m × 30 m or 15 m × 60 m along steep slopes. Second, we placed five shelters (cardboard sheets measuring 25 cm × 25 cm) fastened with some stones on the ground of each sampling site. Cardboard sheets substituted wooden boards, a frequently used method to capture millipedes (Hamazaki, 1996). We exposed cardboard sheets for 15–30 days, after which we carefully lifted them and captured the millipedes attached to or below the cardboards with forceps. As their effect is not cumulative (millipedes can move away from them at any time), the number of cardboards was not adjusted according to exposure time. Third, we placed 5–10 pitfall traps (plastic cups, 5.8 cm diameter) partially filled with propylene glycol in a row with an inter-trap distance of 3–5 m in each sampling site. Pitfall traps were exposed for 15–30 days, and number of traps was adjusted in advance to have 160 trap days per site.

Field work was conducted between July and September in 2018 (B, M and half T) and 2019 (Z, S and second half of T). We visited each sampling site twice (for active capture and installing and emptying the traps). Sites in the lower part of the valleys were sampled 1 month earlier than those in the upper part to compensate for the delayed summer at higher elevation.

The millipedes were identified by J. D. Gilgado by comparing external and gonopod morphology (modified copulatory eighth leg of the male), in some cases after dissection, with either the descriptions and drawings in Bigler (1929), the original descriptions of the species, or in the case of the genus *Glomeris* Latreille, 1802, with the keys and drawings in Hoess (2000). Nomenclature followed Kime & Enghoff (2011, 2017) for the orders Glomerida, Polydesmida and Julida, and the Fauna Europaea website (Enghoff, 2017) for the order Chordeumatida. The sampled millipedes are deposited at the collection of the Bündner Naturmuseum in Chur (Grisons, Switzerland).

Comparing historical and recent data

For the comparison of the two data sets, we only used records made at elevations of 1800 m and higher. In the historical data set, we considered records made in the same valleys as in the recent transect study (valleys M and Z). For comparisons with the other three recent transect lines, we also included historical data obtained in small valleys that were adjacent to the corresponding transect valley and had a similar orientation (Fig. 1). For valley B, we thus also considered historical data from Val Ftur and Val da Stabelchod, for valley S from Val Diavel, Val Tantermozza and Val da l'Aqua, and for valley T from Val Foraz, Val Sesvenna and Val Mingèr (Fig. 1).

We focussed on changes in the upper limit of the millipede distributions and developed the survey design accordingly. Shifts of the upper distribution limit have been studied more frequently than changes in the lower distribution limit (Lenoir & Svenning, 2015). Shifts in upper distribution limit are also more

reliable because direct impacts of human activities and land-use changes can mask climate change-related shifts in the lowlands (Van der Putten, 2012). Moreover, for most of the millipede species present in the SNP, their lower limit of distribution is far below the lowest elevation in the SNP (Pedroli-Christen, 1993), which makes an investigation of the lower limit of distribution impossible.

Bigler (1929) did not present absence data of millipede species at high elevations. Consequently, his highest record of a millipede species in a valley does not automatically present the upper elevational limit of the species in that valley. However, there is indirect evidence that the highest historical record of a species also represents the upper elevational limit of the species at that time in cases when Bigler presented records of other millipede species at even higher elevations in that valley. Two high-mountain millipede species [*Pterygophorosoma alticolum* (Verhoeff, 1894) and *Trimerophorella rhaetica* (Rothenbühler, 1901)] were already recorded on the summits in the historical survey. We omitted the two species from the historical–recent comparison of their upper elevational limit but used their elevational records as evidence that Bigler has searched for millipedes at these elevations. We considered the highest record of the other millipede species as the upper elevational limit at that time when at least one other species was recorded 50 m further up in the valley.

Bigler (1929) reported 23 millipede species in the study area (see above) in 1917–1919 (Supporting Information Appendix 1), but for two species (*Atractosoma meridionale* Fanzago, 1876 and *Glomeris transalpina* C. L. Koch, 1836) he presented no detailed sampling information. Of the 21 species with such information, we only considered data of 11 species for the comparison with recent data for the following reasons: six species [*Craspedosoma taurinorum* Silvestri, 1898, *Haasea flavescens* (Latzel, 1884), *Iulogona tirolensis* (Verhoeff, 1894), *Leptoiulus simplex* Verhoeff, 1894, *Ochogona caroli* (Rothenbühler, 1900) and *Orthochordeumella pallida* (Rothenbühler, 1899)] were not found in the same valley(s) we studied in the recent survey, two species were represented by a single record in the historical data [*Cylindroiulus zinalensis* (Faës, 1902) and *Ophiulus solitarius* Bigler, 1929], and two species (*P. alticolum* and *T. rhaetica*) are high-mountain species, which occurred already on the summits 100 years ago (see above; Supporting Information Appendix 1). One of these high-mountain species, *P. alticolum*, does not occur below 2000 m in Switzerland (Pedroli-Christen 1993), and Bigler (1929) did not find it below 2200 m in the study area. As our transects cover the lower part of its elevational range, we provide additional information about the shift of its lower limit.

The historical dataset provides precise information for 651 millipede individuals in the study area, while in the recent survey data from 4184 individuals were considered (Supporting Information Appendix 1). Considering the 11 selected species, the historical survey includes information on 520 individuals, and the recent survey on 1442.

Statistical analyses

We assigned the historical records of Bigler (1929) to the five valleys (B, M, T, S and Z) considering the criteria presented

above. As recent records we considered the data obtained along the transect lines in the corresponding valleys.

All statistical analyses were performed in the R environment (R Core Team, 2020). We used a rarefaction analysis to examine whether differences in sampling effort (number of individuals captured; see above) between the historical survey and the recent survey influenced species diversity (Supporting Information Appendix 2). We conducted individual-based rarefaction with down-weighting to the smallest number of individuals recorded in the historical survey in each valley. Rarefaction analysis was performed using the iNEXT package in R (Hsieh *et al.*, 2016). We calculated the Shannon-Wiener diversity index of both the historical and recent records for each valley and the Sørensen similarity between the historical and recent records using the vegan package in R. We used non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarities to examine potential changes in species composition over the period of 100 years (vegan package in R).

To analyse changes in abundance and upper elevational range we considered only data of the 11 selected species (see above) (Supporting Information Appendix 1). In this analysis, we considered species as study unit and the valleys in which they were recorded as replicates. For the comparisons of historical and recent records, we used two different approaches. In the first approach (hereafter called ‘all records’), we considered all records from the historical and recent surveys. Because the two surveys differed in number of individuals captured, we also used a sub-sampling procedure to evaluate whether the sampling effort affects the estimate of the upper elevational limit of a species in a valley (hereafter ‘sub-sampling’). For each species, the procedure randomly chose the same number of individuals as found in the historical survey from the recent dataset, recorded the elevation at which they were captured and determined the highest elevation at which an individual of the random subset was found. This procedure was repeated 100 times and the average of the upper limit was calculated for each species in each valley. For both approaches, we used a paired *t*-test to examine whether the millipede species showed an upslope expansion of their elevational distribution over 100 years (see Fig. 4 for number of valleys).

We used Spearman rank correlation to test whether the shift in mean upper limit is correlated with the relative abundance (expressed in %) of the millipede species in 1917/1919, the

relative abundance of the species in 2018/2019 and the change in relative abundance over 100 years.

Results

Historical and recent millipede records

Bigler (1929) found 23 millipede species in the investigation area (Supporting Information Appendix 1). We recorded 19 millipede species in our re-survey 100 years later (Supporting Information Appendix 1). In both the historical and recent surveys, the five valleys varied in species richness and Shannon-Wiener diversity index (Table 1). However, in both surveys, the highest species richness were recorded in the valleys B, T and S, and the lowest in the valleys M and Z (Table 1). Differences in sampling effort between the historical and recent survey did hardly affect species diversity (Supporting Information Appendix 2). The rarefaction analyses showed that both accumulation curves (historical and rarefied recent) mostly overlap. An exception was valley Z, in which the historical species accumulation curve did not reach a plateau, suggesting a higher species richness in the recent dataset due to a higher sampling effort.

Historical and recent frequency distributions of millipede species are similar, taking into account that Bigler (1929) did not report abundance data for two species (*A. meridionale* and *G. transalpina*; Fig. 2). In the historical survey, *Leptoiulus alemannicus* (Verhoeff, 1894) was the most frequent species, accounting for 30.0% of all individuals sampled, followed by *Glomeris helvetica* Verhoeff, 1894 (15.2%), *P. alticolum* (13.5%), *Ophiulus nigrofuscus* (Verhoeff, 1894) (9.4%) and *Pseudocraspedosoma grypischium* (Rothenbühler, 1900) (6.8%). In the recent survey, *P. alticolum* was the most frequent species, accounting for 42.1% of all individuals sampled, followed by *G. transalpina* (19.7%), *L. alemannicus* (8.8%), *Leptoiulus helveticus* (Verhoeff, 1894) (6.2%) and *O. nigrofuscus* (4.6%).

Similarity of species assemblages between the historical and recent survey was relatively high in the valleys B, M and Z, but low in the valleys T and S (Table 1). The length of the arrows obtained in the NMDS multivariate analysis supports this finding (Fig. 3). In the valleys B, M and Z, relatively small changes in millipede species composition were found between 1917/1919

Table 1. Diversity of millipede assemblages in the five valleys examined and similarity of species composition between the historical and recent record.

		Valley				
		B	M	T	S	Z
Species richness	1917/1919*	11	6	10	17	3
	2018/2019	13	10	14	12	11
Shannon-Wiener diversity index	1917/1919*	1.92	2.19	1.42	1.54	2.3
	2018/2019*	2.28	1.64	2.23	0.55	1.64
Sørensen similarity	1917/1919* vs. 2018/2019*	0.762	0.637	0.364	0.334	0.615

*Bigler (1929) reported that *Atractosoma meridionale* and *Glomeris transalpina* occurred almost everywhere but did not provide information on their numbers and sampling sites. Therefore, both species are not considered for the richness of the historical data, as well as for the Shannon-Wiener diversity index and Sørensen similarity in both datasets.

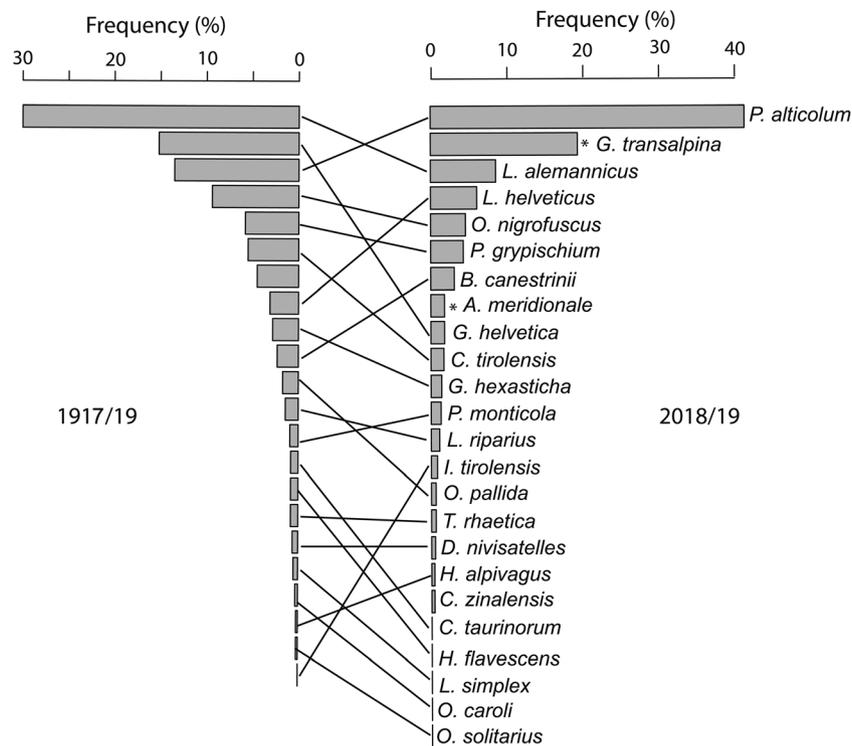


Fig 2. Comparison of frequency distributions of all millipede species sampled in the historical (1917/1919) and recent (2018/2019) survey in five valleys in the Swiss National Park. In the historical survey, two species (*Atractosoma meridionale* and *Glomeris transalpina*) are not depicted because frequency data are lacking (indicated by *).

and 2018/2019, indicated by the short arrows (Fig. 3). In the valleys T and S, larger changes in species composition were recorded over the 100 years (Fig. 3).

Changes in upper elevational limit over 100 years

Regarding all 11 millipede species with historical and recent records, the mean upper elevational limit has risen by 161 ± 42 m (mean \pm SE, paired *t*-test, $t = 3.843$, $n = 11$, one-sided $P = 0.0016$; Fig. 4a). Similarly, the random subsampling analysis revealed an average rise of the upper elevational limit of 153 ± 45 m ($t = 3.391$, $n = 10$, $P = 0.0039$; Fig. 4b, Supporting Information Appendix 3), indicating that the estimate of the upper elevational limit was not influenced by the different sampling efforts. Most interestingly, the various species showed different shifts in the upper distribution range (Fig. 4). Ten of the 11 species raised their mean upper elevational limit with an upslope expansion range of 50 m in *Hypsolulus alpivagus* (Verhoeff, 1897) to 363 m *Bergamosoma canestrinii* (Fedrizzi, 1877) (Fig. 4a). In one species (*Glomeris hexasticha* Brandt, 1833), a lower upper elevational limit (-100 m) was recorded in 2018/2019 than 100 years ago (Fig. 4a).

P. alticolum is the only species for which it was possible to examine a potential change in the lower elevational limit. The lower elevational limit of this species raised by 167 m over

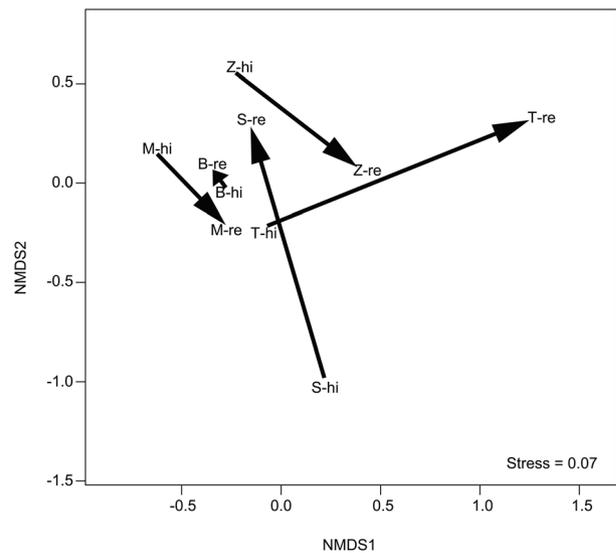


Fig 3. NMDS analysis of changes in millipede species composition in five valleys (B, M, T, S and Z) between 1917/1919 (historical survey) and 2018/2019 (recent survey). The longer the arrow the greater the change in species composition in the valley.

100 years in the three valleys examined (valley M: 200 m; valley T: 300 m, valley S: 0 m; Supporting Information Appendix 1).

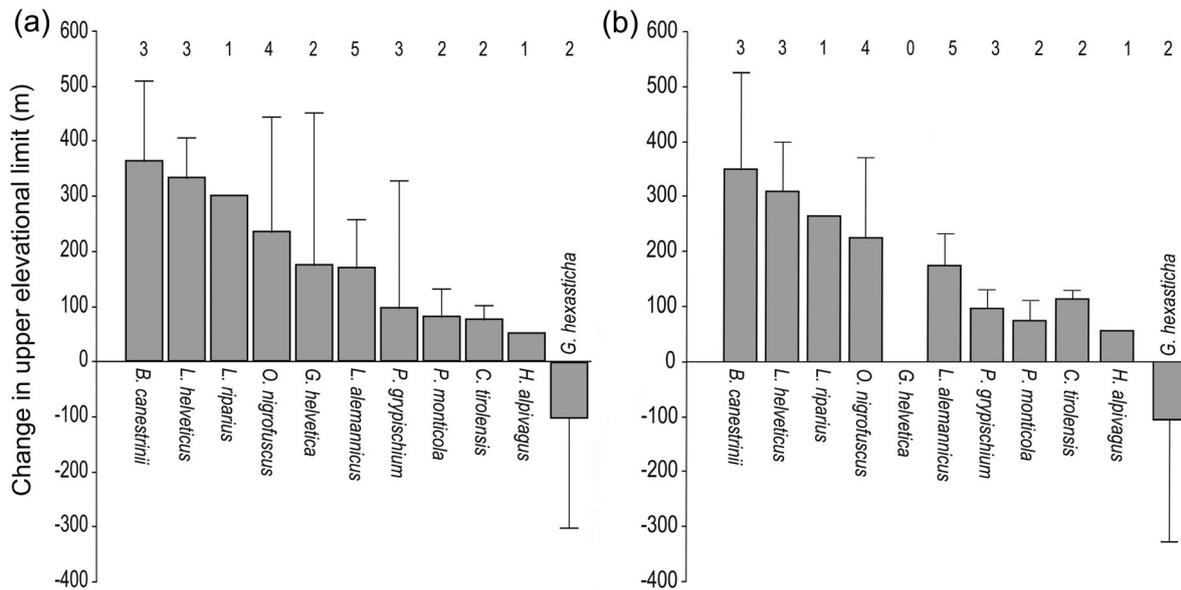


Fig 4. Change in upper elevational limit of 11 millipede species in different valleys in the Swiss National Park between 1917/1919 and 2018/2019. Mean values and s.e. are given. Figures on top of bars indicate the number of valleys in which the species was found. (a) “All records” approach, considering all historical and recent data are considered. (b) “sub-sampling” approach, considering a random selection of the same number of individuals as found in the historical survey from the recent dataset for each species. We determined the highest elevation at which an individual of the random subset was found. This procedure was repeated 100 times and the average of the upper limit was calculated for each species in each valley. This procedure was not applied to *Glomeris helvetica* because the number of individuals in the historical survey is larger than that in the recent survey.

The frequency distributions of the number of individuals sampled of the 11 millipede species in both the historical and recent surveys are very similar (Fig. 5). Only three species showed a change in frequency >6% over 100 years: *G. helvetica* and *L. alemannicus* had reduced abundances of 13.7% and 12.5%, respectively, while *L. helveticus* showed an increased abundance by 12.2%. No correlation was found between the shift in upper elevational limit and the change in species abundance over 100 years ($r_s = 0.481$, $n = 11$, $P = 0.137$). Similarly, there was no correlation between the shift in upper elevational limit and both species abundance in 1917–1919 and species abundance in 2018–2019 ($r_s = 0.172$, $n = 11$, $P = 0.614$ and $r_s = 0.472$, $n = 11$, $P = 0.146$).

Discussion

Historical and recent millipede records

We found an increase in the upper elevational limit in 10 of 11 millipede species compared with the data collected 100 years earlier by Bigler (1929). Interestingly, however, the relative abundances of the millipede species in the two surveys were similar, and the species composition did not change much over 100 years. Millipedes are poor dispersers (Hopkin & Read, 1992), and populations can survive in small habitat patches provided the abiotic conditions remain suitable (David, 2009). The five valleys examined differed slightly in

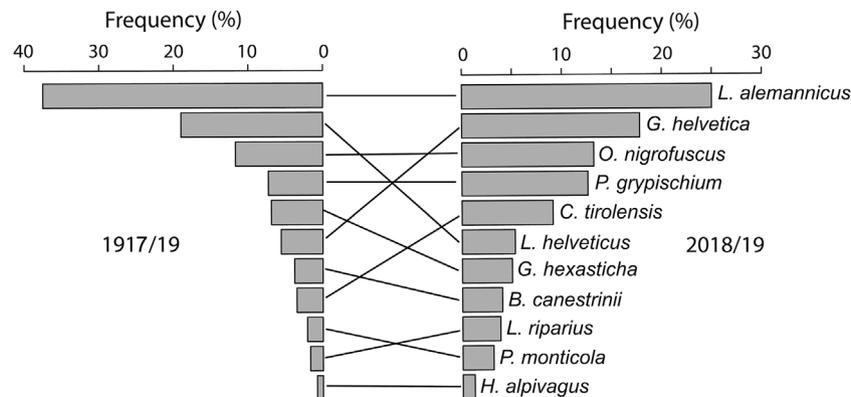


Fig 5. Comparison of frequency distributions of 11 millipede species sampled in five valleys in the Swiss National Park in 1917/1919 and 2018/2019.

change in millipede species assemblages (Fig. 3). This could – at least partly – be explained by a variable (not standardised) sampling effort in different valleys in the historical survey. We relied on the data reported by Bigler (1929). Any survey data depend on both the sampling effort and the population size of a species, which might fluctuate considerably among years. However, millipedes are relatively long-living arthropods, and some mountain species are known to live for at least 9 years, which may partly damp among-year variation in abundance (Minelli, 2015).

Despite an increased sampling effort in the recent survey, we could not find five species reported by Bigler (1929). The rarity of these species, a mismatch between the seasonal activity of a species and the sampling time as well as a possible misidentification of a species by Bigler (1929) may explain why we missed these species. *Craspedosoma taurinorum* was rare in the historical survey (only three individuals were recorded at one site in valley M). *Haasea flavescens* usually lives in very humid places in forests near rivers (Pedroli-Christen, 1993). This species was also rare in the historical survey (two individuals at one site in valley S). We sampled in a similar habitat close to the historical locality but could not find the species. Similarly, *Leptoiulus simplex* was rare in the historical survey (five individuals at two sites), although the species is quite common in other parts of the Alps (Pedroli-Christen 1993; Kime & Enghoff, 2017). *Ochogona caroli* might also be rare in the investigated valleys (six individuals found at two sites in the historical survey). This species is mainly active in autumn, in October and later (Pedroli-Christen, 1993). In the recent survey, sampling was performed between July and September, which could explain why we missed this species. Bigler (1929) found one individual of an unknown species at a site in valley T and used this male to describe the new species *O. solitarius* (Supporting Information Appendix 1). We sampled more than 150 individuals of the same order (Julida) in this valley, including 35 *Ophiulus* individuals but found no *O. solitarius*. Pedroli-Christen (1993) suggested that *O. solitarius* is not a valid species but a synonym of *O. nigrofuscus*, a species found in both surveys. A revision is needed to officially synonymise the species' name.

In the recent survey, we recorded *Dactylophorosoma nivisatelles*, a species not found in the historical survey of Bigler (1929). Most probably *D. nivisatelles* arrived in the SNP in the past decades. Pedroli-Christen (1993) provided the first records of *D. nivisatelles* in Switzerland, for a location at 10–15 km distance from the SNP. Thus, the species could have expanded its range in recent years.

Changes in upper elevational limit over 100 years

Mountains are important to study in the field of climate change research because even less mobile species might be able to respond readily to global warming due to the short distances along the local temperature gradients (Thuiller, 2007). This would result in different responses or faster responses when compared to the situation along latitudinal climate gradients. The 11 millipede species considered in the upper-limit comparison of the two surveys showed a mean upslope shift in the upper

elevational limit of 161 m over a period of 100 years. However, the magnitude of increase of the upper elevational limit varied among species. Our findings of a leading edge expansion and interspecific variation in upslope shift agree with most previous studies on elevational shifts in the distribution of plant and animal species (e.g. Chen *et al.*, 2011, Lenoir & Svenning, 2015).

Our study is the first one focusing exclusively on climate warming-related elevational shifts in millipede distribution. Hickling *et al.* (2006) examined changes in latitude and mean elevation of various animal groups, including millipedes, in 10 km × 10 km squares in Great Britain. Data sets with 25 years between were compared. When all squares were considered, Hickling *et al.* (2006) found that the mean elevation of the squares had increased by 24 m for six millipede species (9.6 m per decade). However, this pattern disappeared when only well-investigated squares were considered. It has been argued that the millipede results of Hickling *et al.* (2006) should be interpreted with caution because a considerable number of squares were poorly surveyed in the first period (David 2009). The shift reported for millipedes by Hickling *et al.* (2006) is much lower than the 16.1 m per decade found in our study, but the measures used to show a shift in distribution area are very different between the two studies.

The upslope shift recorded in millipedes is remarkably similar to that found for a land snail species partly on the same slopes in the SNP (165 m in 95 years, 17.4 m per decade; Baur & Baur, 2013). Both snails and millipedes are decomposers and poor dispersers. It is possible that other soil invertebrates have a similar magnitude in upslope shift of their distribution. The shift of 16.1 m per decade found for millipedes in our study is exceeding the median of 11 m per decade found for several groups of terrestrial organisms worldwide (Chen *et al.*, 2011). It is, however, lower than those found for several other organisms in the Alps, especially those recorded in plants [e.g. the 200 m for the mistletoe *Viscum album* in 85 years (23.5 m per decade, Dobbertin *et al.*, 2005), or the 23.9 m per decade for several plant species (Parolo & Rossi, 2008)].

In the Alps, the mean temperature decreases by 0.56 °C per 100 m of elevation (Rolland 2003). The increase of 1.5 °C in the mean annual temperature measured at the Buffalora weather station between 1917 and 2019 would correspond to an elevational upslope movement of 268 m. This is more than the average shift of the upper elevational range of 161 m recorded in our study. Only three of the 11 millipede species showed an upslope shift of 268 m or more. In the remaining species, the upslope expansion of their distribution was less pronounced. This suggests a time lag between the temperature increase and the response of some millipede species. Similar time lags in temperature-related upslope shift have been reported in plants, vertebrates and invertebrates (Chen *et al.*, 2011; Urban *et al.*, 2012; Lenoir & Svenning, 2015).

In many studies, it is difficult to disentangle effects of climate change from effects of changes in land use (e.g. Hickling *et al.*, 2006; Wilson *et al.*, 2007). The SNP is a strict nature reserve with no human disturbance or land-use change since 1914. Thus, the rise of the upper elevational limit recorded in millipedes cannot be explained by land-use changes or human activities but most probably by increase of the temperatures.

The species-specific response may be influenced by the dispersal capability and/or habitat preference of a species. In our study, six millipede species (*B. canestrinii*, *L. helveticus*, *Leptoiulus riparius* (Verhoeff, 1894), *G. helvetica*, *L. alemannicus* and *H. alpivagus*), including the three species with the largest upslope movement, show a strong preference for open habitats (Pedroli-Christen, 1993; Kime & Enghoff, 2011, 2017). Two of them (*L. riparius* and *G. helvetica*) are even thermophilous. It may be relatively easy for these species to expand their distribution upslope in alpine meadows and rocky habitats above the tree line (which is around 2200 m in the SNP). The remaining five species are more eurytopic (Pedroli-Christen, 1993; Kime & Enghoff, 2011, 2017). *Glomeris hexasticha*, the only species that showed a slight downward shift in its upper elevational limit, is the only millipede with a preference for forests among the species considered (Kime & Enghoff, 2011). While the species' habitat preference may play a role for their upslope shift, species traits have shown little explanatory power to predict species movements in a range of taxonomical groups (Angert *et al.*, 2011; Lenoir & Svenning; 2015).

Extrinsic factors may also influence the upper edge of the elevational range of a species. The complex topography of mountain areas provides a variety of local microclimates, which is known to affect the local biodiversity, and in turn may influence the species' response to climate change (Klanderud & Birks, 2003; Chen *et al.*, 2011; Suggitt *et al.*, 2011; Moritz & Agudo, 2013). For example, vertical rocky cliffs are functioning as barriers, preventing further upslope dispersal in the land snail *Arianta arbustorum* (Linnaeus, 1758) in the SNP (Baur & Baur, 2013). So far we do not know what landscape features may constitute dispersal barriers for millipedes. When a species expands its distribution area, a non-analogue community with a different species composition, richness, and abundance is being created. Within this new community novel interactions could influence the different species in a differential way (Le Roux & McGeoch, 2008; Urban *et al.*, 2012; Van der Putten, 2012). These new interactions can lead to a lag in the upslope shift of poor competitor species (Urban *et al.*, 2012; Bishop *et al.*, 2019).

The upward shift of high-mountain species living already now in the nival and alpine zone is limited by the elevation of the mountains they inhabit and the area of suitable habitat. Because these species cannot escape to higher elevations to survive, and their habitat is expected to be significantly reduced (David 2009), they may go extinct on mountains that are too low to maintain their required climatic conditions under projected climate change scenarios (Dullinger *et al.* 2012; Lenoir & Svenning, 2015). Thus, any further upslope shift of these 'summit species' could only be investigated by studying the retraction at the lower limit, or the shift in their optimum elevation. The upward shift in the lower elevational limit recorded in *P. alticolum* (167 m) suggests a potential range loss for high-mountain specialists, very similar in magnitude to the shift in the upper range limit for the other studied species. An upward shift in the lower limit implies a significant reduction in the total range of the species (Wilson *et al.*, 2005). A further temperature increase may drastically reduce the inhabitable area for *P. alticolum* in the SNP and probably in other mountain areas in the coming decades.

High-mountain species also pose a methodological problem, because the summits are often not accessible and suitable habitat might be rare or even lacking. Thus, any estimate of upper elevational limit in these species might be inaccurate due to a lack of sampling or reduced sampling effort at extremely high elevations. In additional sampling sites, we found *P. alticolum* and *T. rhaetica* at elevations of up to 2945 m in Spi da Baselgia, 95 m above the highest sampling point of transect Z. This means that both species may have occurred in non-accessible spots higher than the highest sampling sites in both surveys. We therefore omitted these two species from the analysis of the shift in upper elevational limit and the comparison of the species abundance. This step made the estimates of upper elevational limit more accurate for other species, because Bigler and we did not find these species in high-elevation sampling sites, in which *P. alticolum* and *T. rhaetica* were recorded. However, four widely distributed species (*B. canestrinii*, *L. helveticus*, *O. nigrofuscus* and *P. grypischium*) were found at the highest sampling sites of the recent survey. It is therefore possible that our estimate of the upward shift of these species is rather conservative. In addition to the 11 species examined, *Orthochordeumella pallida* is one of the recorded species for which historical data at the level of valleys are lacking, but for which its recent distribution is overall increasing and reaching higher elevations than in the historical survey (Supporting Information Appendix 1). This species is also expanding poleward in Europe (Davidson & Weddle 2021).

Changes in millipede relative abundances over 100 years

Climate warming does not only affect the distribution of species but also their phenology and abundance, which in turn may influence ecosystem functioning (Lenoir & Svenning, 2015; Bishop *et al.*, 2019). Climate warming is expected to accelerate population growth in millipedes, which may result in an increase of their overall abundance (David, 2009). However, side effects of the climate change such as changes in precipitation, plant composition and leaf litter quality may have the opposite effect (David, 2009). We do not know whether climate warming is affecting the absolute millipede abundance in the study area. However, our results revealed that the relative abundances of the 11 millipede species did hardly change over 100 years (Fig. 5). In general, common species remained common, while rare species remained rare, except for three species. *Glomeris helvetica* is one of the species that became more abundant. This species shows a preference for xeric and warm open habitats with little soil, such as alpine meadows and rocky sites (Kime & Enghoff, 2011). Due to the increasing temperature, more open areas are now available that were too cold for *G. helvetica* in the past. For *C. tirolensis*, we have no explanation for its increase in relative abundance. *Leptoiulus helveticus* was found at a lower relative abundance in the recent survey than 100 years ago. This species showed an upslope expansion of its range of more than 300 m. One would expect that a wider range would also result in a higher relative abundance. It is possible that *L. helveticus* may suffer from competition with high-mountain specialists such as *P. alticolum* in newly colonised sites at higher elevation.

Conclusions

Our study is to our knowledge the first that examined climate warming-related changes in upper elevational distribution limit and relative abundances of millipede species. We found upslope shifts of the upper distribution limit in 10 out of 11 species investigated. The magnitude of this elevational shift is similar to that of another soil invertebrate (a land snail) in the same area, but it is smaller than those of plants or vertebrates in the Alps. The change of the distribution areas of millipede species could impact the soil dynamics and nutrient recycling in alpine habitats in unexpected ways. Furthermore, specialist species could become threatened by habitat loss and competition with other species. As the temperature increase continues, a higher impact is expected in the future.

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Conflict of interest

The authors declare that there is no conflict of interest.

Data availability statement

Data available on request from the authors

Supporting information

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

Appendix 1. Elevational distribution of millipede species in 1917–1919 (historical survey) and 2018–2019 (recent survey).

Horizontal bars indicate in which elevational band individuals of a species were found.

Appendix 2. Accumulation curves of historical data and rarefacted recent data. Individual-based rarefaction with down-weighting to the smallest number of individuals recorded in each sampling site was performed using the iNEXT package in R. Letters indicate the name of the transects: B – Val dal Botsch; M – Val Trupchun/Val Müschauns; T – Val Tavrü; S – Val Cluozza/Val Sassa, and Z – Val Zeznina/Macun.

Appendix 3. Changes in upper elevational limit of 11 millipede species in different valleys in the Swiss National Park between 1917–1919 and 2018–2019. Mean values and s.e of two different approaches are presented. In the “all records” approach all historical and recent data are considered. In the “sub-sampling” approach, we randomly chose the same number of individuals as found in the historical survey from the recent dataset. Then, we recorded the elevation where they were captured and determined the highest elevation at which an individual of the random subset was found. This procedure was repeated 100 times and the average of the upper limit was calculated for each species in each valley. N indicates the number of valleys.

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