Research Square

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Pronounced pollinator elevational range shifts over 200 years in the European Alps

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Research Article

Keywords: altitudinal shifts, bees, bumblebees, citizen science, climate change, downslope, hoverflies, upslope

Posted Date: October 29th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11527388/v1

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Additional Declarations: The authors declare no competing interests.

Abstract

Pollinators in the European Alps are especially prone to the consequences of climate change. A common response to rising temperatures is to shift to higher elevations but the high complexity of mountain landscapes might buffer anticipated shifts on large spatial scales. An overarching assessment of elevational shifts of alpine pollinators throughout the Alps is lacking. We used a recently published curated dataset of bee and hoverfly records in Europe to calculate species elevation shifts of bumblebees, other wild bees and hoverflies in the European Alps since the 19th century. We found a large proportion of species shifting uphill with some species exceeding rates of 4–5 m per year, with high elevation species showing enhanced shift rates. We also found some species showing no response or shifting downslope. Our results indicate a high sensitivity of alpine pollinator species to rising temperatures and a high potential for spatial mismatches between interacting species.

Introduction

Climate change continues to alter environmental conditions for many species (Harvey et al. 2023). Temperatures are on the rise globally, resulting in longer vegetation periods and less snow during winter (Kotlarski et al. 2023) and weather extremes like heat waves are becoming more common (Harvey et al. 2023). Species are directly and indirectly affected by these changes. Rising temperatures increase metabolism rates, a lower snow cover during winter can have consequences on reproduction and heat waves and droughts reduce plant flowering and thus food availability (Harvey et al. 2023; Korten and Steffan-Dewenter 2026). At the same time, increased temperatures force some species to shift ranges or phenology or enable species to colonize new habitats (Halsch et al. 2021; Oliveira et al. 2026).

Mountains represent vulnerable environments in this manner, as climate change proceeds faster in mountain areas (Mountain Research Initiative EDW Working Group 2015). In the European Alps for example, temperature increase two times faster compared to the global mean (Kotlarski et al. 2023). While species there are particularly exposed to the consequences of climate change, mountains also offer the possibility to escape rising temperatures and extreme heat by shifting upslope (Meza-Joya et al. 2025; McCain and Garfinkel 2021). Upslope shifts have been detected as a common response in many species across the globe, e.g. insects like bumblebees, bees and butterflies (Maihoff et al. 2023; Marshall et al. 2020; Biella et al. 2024; Kerner et al. 2023; Bässler et al. 2013), plants (Zu et al. 2021; Zu et al. 2026) or birds (Couet et al. 2025; Luisier et al. 2026). However, often the rate of elevation shifts varies between different species, even within one taxonomic group (Lenoir et al. 2010).

Varying rates of elevation shifts introduce new problems to species and species communities. If for example a butterfly species proceeds to shift up faster than its larval food plants, then there is potential for mismatch, in extreme cases threatening extinction of one or both interaction partners (Kerner et al. 2023). In specialized pollination systems, interaction partners (i.e., pollinator and plant) highly depend on each other for reproduction and ultimately survival of the species (Garibaldi et al. 2015). Another example might be the introduction of new competitors, if a competitor using the same foraging niche

shifts upwards, while the other species does not (Barthell and Resasco 2025). In resource-poor environments such as high elevation habitats, newly arriving species from downslope might be life-threatening competition to species adapted to these environments (Barthell and Resasco 2025).

In the case of pollinators such threats might have consequences for entire ecosystems. To study them, knowledge about the rate of upslope shifts of pollinator species is needed. There have been some studies on elevational shifts of single species or shifts of communities in specific regions of the Alps (e.g., Kerner et al. 2023; Maihoff et al. 2023; Biella et al. 2017; Biella et al. 2024). However, to date it remains unknown if elevational shifts of pollinators occur at large spatial scales in the European Alps and across taxonomic groups. On large spatial scales, elevational shifts might be buffered by local topographic and microclimatic complexity (Álvarez et al. 2024). Many Orthoptera for example have been shown to not shift elevation at larger spatial scales (Zuna-Kratky et al. 2017), while still showing local uphill shifts in some regions around the world (Meza-Joya et al. 2023). We here used a validated dataset of bee and hoverfly records, two of the main pollinator groups in temperate mountain regions, to fill this gap and calculate species elevational shifts in the European Alps since the 19. Century.

Methods

We used a curated dataset of bee and hoverfly species records in Europe to compute elevational ranges (Sentil et al. 2026). This dataset includes records for over 2,000 bee species and almost 900 hoverfly species, collected from various sources like historic and recent collections and online databases and has been validated by taxonomic experts (Sentil et al. 2026).

All computations have been performed in R 4.5.2 (R Core Team 2025). We started by cutting records to the perimeter of the Alpine convention including a 50 km buffer to capture elevational shifts of species originally occurring in lower elevations of the Alps, increase data availability, especially for rare species, and to ensure that elevational ranges of species were completely covered. This left us with 183,163 records of 47 species of bumblebees, 482,117 records of 937 species of other wild bees and 52,309 records of 526 species of hoverflies. We then divided records into 6 time periods based on data availability and climate change speed: before 1900, 1900–1950, 1951–1980, 1981–2000, 2001–2010, after 2011. We calculated the presence of each species per time period and raster cell of a digital elevation model (Hengl et al. 2020, 30 × 30 m) to reduce the sampling bias towards densely populated urban areas or tourism hotspots in lower elevations, as records in the dataset are not randomly distributed across the Alps. We then calculated the trimmed mean of elevation with 95 % of the data, 2.5 % and 97.5 % quntiles of elevatio (for the pper and lower edge of elevation) and the elevational range as the difference between the upper and the lower edge for each species.

To calculate the elevational range shift per species group (bumblebees, other wild bees, hoverflies), we used linear mixed models with *glmmTMB* (version 1.1.14; McGillycuddy et al. 2025; Brooks et al. 2017) with the trimmed mean elevation for each species as a response, the time period as a fixed and the pollinator species as a random effect. We followed the same approach to model shifts of elevational

range, and upper and lower edge of the elevational range. For these models, we only used data points calculated from more than 20 records per species and only data from time periods in which at least 5 % of all species of a pollinator group have been recorded to nsure data quality and appropriate coverage of the community. To calculate elevational shifts per species, we used linear models for each species with the elevation as a response and the year of the record as a predictor. We only did this for species with at least 200 records in the dataset.

Results

We observed an average elevational shift of + 98.5 m upslope for bumblebees between 1817 and 2023 (Fig. 1, Table S1), + 56.3 m for other wild bees between 1805 and 2023 (Fig. 2, Table S2) and + 158.5 for hoverflies between 1981 and 2023 (Fig. 3, Table S3). For hoverflies, time periods before 1981 did not include enough species to meet our criteria. Elevational range of bumblebees increased by 434.5 m on average with the upper bound shifting uphill by 421.5 m on average and the lower bound only by 32.5 m, although showing an accelerated upslope shift of 196 m during the last time period (Table S1). Elevational range of other wild bees increased by 141.5 m on average with the upper bound shifting by + 223.6 m and the lower bound by – 78.0 m on average (Table S2). Elevational range of hoverflies increased only by 17.0 m, with the upper bound shifting 166.7 m upslope and the lower bound following with 128.0 m on average (Table S3).

The highest upward shift was recorded for *Bombus alpinus* and *B. quadricolor* with more than 4 m per year during the study period, which results in a range shift of almost + 574 m in the time period between their oldest and their most recent record in the dataset (Fig. 1). Some species shifted downslope, e.g., *B. lucorum* with a rate of more than 5 m per year, resulting in a shift of – 814 m between 1870 and 2022 (Fig. 1, Table S4). Other species showed neither a significant up-, nor downslope shift during the study period, e.g., *Bombus gerstaeckeri* (Fig. 1, Supplement 4). In total, 41% of bumblebee species shifted uphill, 24% shifted downhill and 35% showed no significant change (Fig. 1, Table S4).

We also found an upward shift in many other wild bee species, e.g., *Lasioglossum rufitarse* with a rate of almost 6 m per year (+ 771 m in total) and *L. laevigatum* with 5 m per year (763 m in total) (Fig. 2, Table S5). Some species shifted downhill, e.g., *Seladonia subaurata* with more than 6 m per year (– 965 m in total) and other species showed no significant shift (Fig. 2, Table S5). Overall, 26% of species shifted uphill, 21% downhill and 53% showed no change (Fig. 2, Table S5).

For hoverflies, an upward shift was only observed in one species, *Merodon cinereus* with more than 4 m per year (+ 849 m in total) and a downslope shift in three species, e.g., *Chrysotoxum cautum* (-9 m per year, -980 m in total) (Fig. 3, Table S6). Almost 90% of hoverfly species did not shift elevation.

Discussion

We found elevational shifts across many pollinator species in bumblebees, other wild bees and hoverflies. Especially species distributed in the Alps and at higher elevations showed upslope shifts, e.g.,

the bumblebee species *Bombus alpinus*, *B. mesomelas*, *B. pyrenaeus* or *B. mucidus*, other bee species like *Hylaeus alpinus* or the hoverfly *Merodon cinereus*. For some of these species, elevational shifts have been documented before, for example an upslope shift of the lower elevation limit of *B. alpinus* of 479 m (Biella et al. 2017), which is in the same range as the 574 m we found here. Species already living in high elevations might thus be especially threatened with extinction due to climate change as they travel up the mountain and will ultimately reach the top, where further upslope shift is not possible anymore and vegetation might be scarce (Freeman et al. 2026). However, species losses as a result of elevational shifts have not yet been recorded (Chen et al. 2025). The reason for that might be that often, there is still space left before reaching mountain tops. Also, we showed for bees that upslope shifts of mean elevation are on average driven by a shift of the upper boundary of the elevational range, while the lower boundary stays constant or shifts at a slower pace. Thus, warming temperatures often enable species to colonize new habitats towards mountain tops, while low elevation habitats are still suitable for them. However, species loss might occur in the future, once low elevation habitats start to get to warm and alpine high elevation specialists might be threatened already (Biella et al. 2017). A warning sign might be accelerated upslope shifts of the lower elevation edge for bumblebees during the most recent time period in our model. Upslope shifts might further be limited by decreasing resource availability. The high-elevation specialist *Bombus alpinus* for example might soon reach its upper limit as vegetated area decreases above 2500 m, where it now has its mean distribution (Table S7, Figure S1). The role of resource availability in modulating such elevational shifts needs further investigation.

Upslope shifts were not consistent across species, with some species even shifting downhill. Downslope shifts might represent an artefact in the data. Some species, e.g. *Seladonia subaurata*, that have been recently increasing their range or large and easily identifiable species like *Bombus pascuorum* are encountered in urban areas in low elevations (Hofmann et al. 2018). Here they are commonly recorded via citizen science platforms like iNaturalist (https://www.inaturalist.org) or Observation.org (https://observation.org/) (Sentil et al. 2026), shifting the mean towards lower elevations. Such a bias can be in the most recent time period (2011-2023) for bumblebees and bees in low elevation areas (Figure S2, Figure S3). Thus, downslope shifts in our study should be interpreted with caution. With this bias in mind, observed upslope shifts might underestimate actual upslope shifts in some taxa, making our community shift estimates rather conservative.

Downslope shifts might in some cases represent shifts of species into forested areas or areas with higher canopy cover to use them as shelter from heat extremes (Geres et al. 2025). This is a strategy that has been shown in other taxa, e.g., Alpine chamois (*Rupicapra rupicapra*) (Anderwald et al. 2024). It might especially apply to species, that use forests anyway, e.g., bee species like *Osmia parietina* that use resources present in forests for nesting (Westrich 2019). This might also be the reason that we found only limited evidence of elevation shifts of hoverfly species, which are usually considered forest-dwelling species and might be less prone to temperature increase and heat extremes (Le Berre et al. 2026; Geres et al. 2025). Other explanations for downslope shifts include lower competitive pressure in lower elevations due to upslope shifts of other species and tracking of other climatic niches, e.g. precipitation (Freeman et al. 2026).

Elevational shifts, regardless of the direction, might lead to mismatches, that could lead to systematic consequences and local species losses. Pollinators, which are mobile taxa, shift their elevational range faster than their foraging plants (Kerner et al. 2023; Bässler et al. 2013). This can be problematic especially in highly specialized pollination systems (Garibaldi et al. 2015). In the worst case this can lead to the extinction of plant or pollinator species, if plants are not getting pollinated effectively or pollinators are not able to collect enough food. There is also potential for other mismatches, e.g., between clepto-parasitic bumblebee species and their hosts. We found evidence of an upslope shift of *Bombus quadricolor* with a rate of over 4 m per year. This species parasitizes *B. lucorum* and *B. soroeensis* (Westrich 2019). For both of these species, we could not find an increase in elevation and for *B. lucorum* we even found a downslope shift. This might potentially lead to decreases in abundance and local extinction of parasitic species like *B. quadricolor* in the Alps (Bower et al. 2023).

Elevational range shifts might represent existential threats for many species. However, species shifting their elevational range might be in favor as they can escape rising temperatures (Halsch et al. 2021). Species like bumblebees are highly mobile and are capable of traveling several kilometers (Osborne et al. 2008). Thus, they can track their favored temperature niche. Less mobile species, like very small bees or hoverflies might not be able to (Greenleaf et al. 2007). Also, specialized species might not be able to establish in higher elevations, where their foraging plants are missing. For example, we did not detect an upslope shift of *Bombus gerstaeckeri*, which is specialized on *Aconitum* spp., a plant, that gros in medium elevations (Westrich 2019). *B. gerstaeckeri* might be suffering under increased temperatures but can simply not establish outside of the range of its food plant. Overall, more research is needed to study the consequences of elevational range shifts and the effects changing climate has on species living in mountainous regions. Climate change mitigation and the protection of highly vulnerable areas, especially high- and medium-elevation habitats are necessary to safeguard pollinator communities in the Alps.

Declarations

Acknowledgements and Data

Data used for this manuscript is openly available with this publication: https://doi.org/10.1038/s41597-026-06644-2. The digital elevation model can be downloaded at https://doi.org/10.5281/zenodo.4056634.

KF and CR acknowledge funding from the Interreg Alpine Space Program (ProjectID ASP0500335, AlpsLife).

The authors declare no conflicts of interest.

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Figures

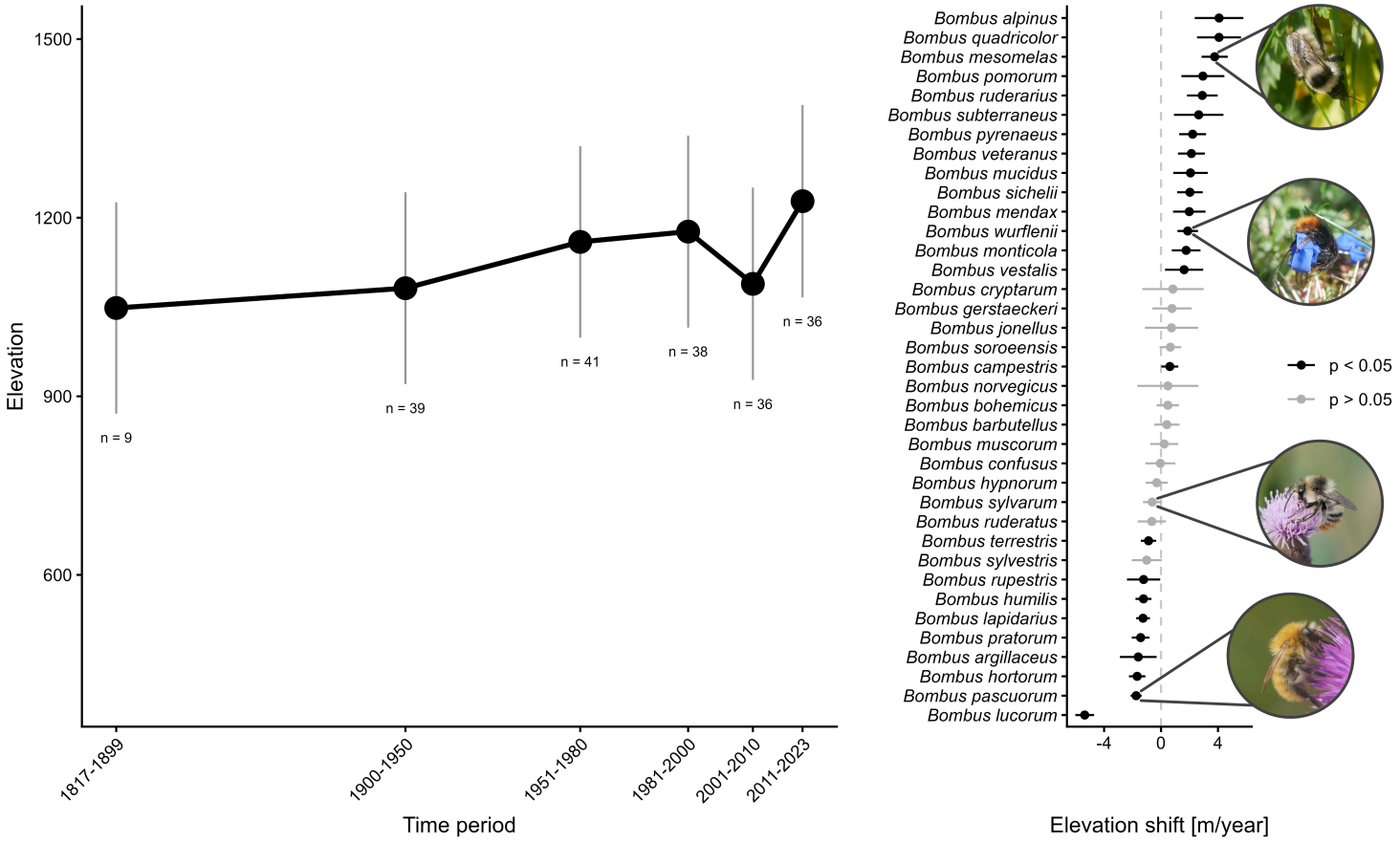


Figure 1

Elevational shifts of bumblebee species. The left panel shows elevation of the entire community sampled in each time period and an average upslope shift of 98.5 m over the study period. Points indicate the mean elevation and the error bars show the 95 % confidence interval. The number of species included in each year is indicated by the number below the error bars. In the right panel, elevational shifts

of all bumblebee species can be seen. Each point indicates the elevation shift per year over the study period and the error bars indicate the 95 % confidence interval. The color indicates the statistical significance of the shift. In the right panel, pictures of exemplary species are shown (© Kilian Frühholz).

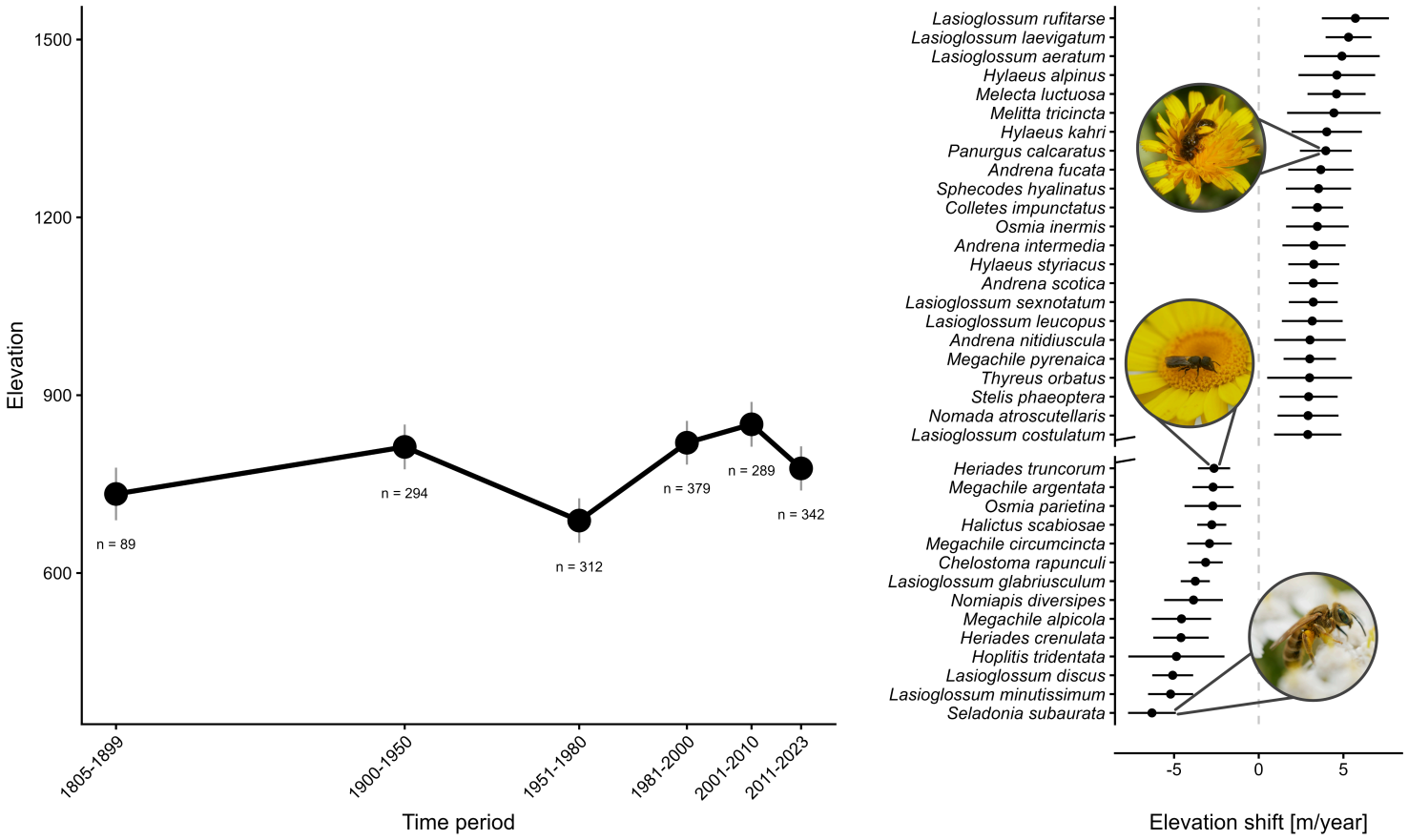


Figure 2

Elevational shifts of wild bee species excluding bumblebee species. The left panel shows elevation of the whole community sampled in each time period and an average upslope shift of 56.3 m over the study period. Points indicate the mean elevation and the error bars show the 95 % confidence interval. The number of species included in each year is shown by the number below the error bars. In the right panel, elevational shifts of the bee species can be seen. Each point indicates the elevation shift per year over the study period and the error bars indicate the 95 % confidence interval. To increase visibility only the upper and the lower end of the y axis are shown here. In the right panel, pictures of exemplary species are shown (© Kilian Frühholz).

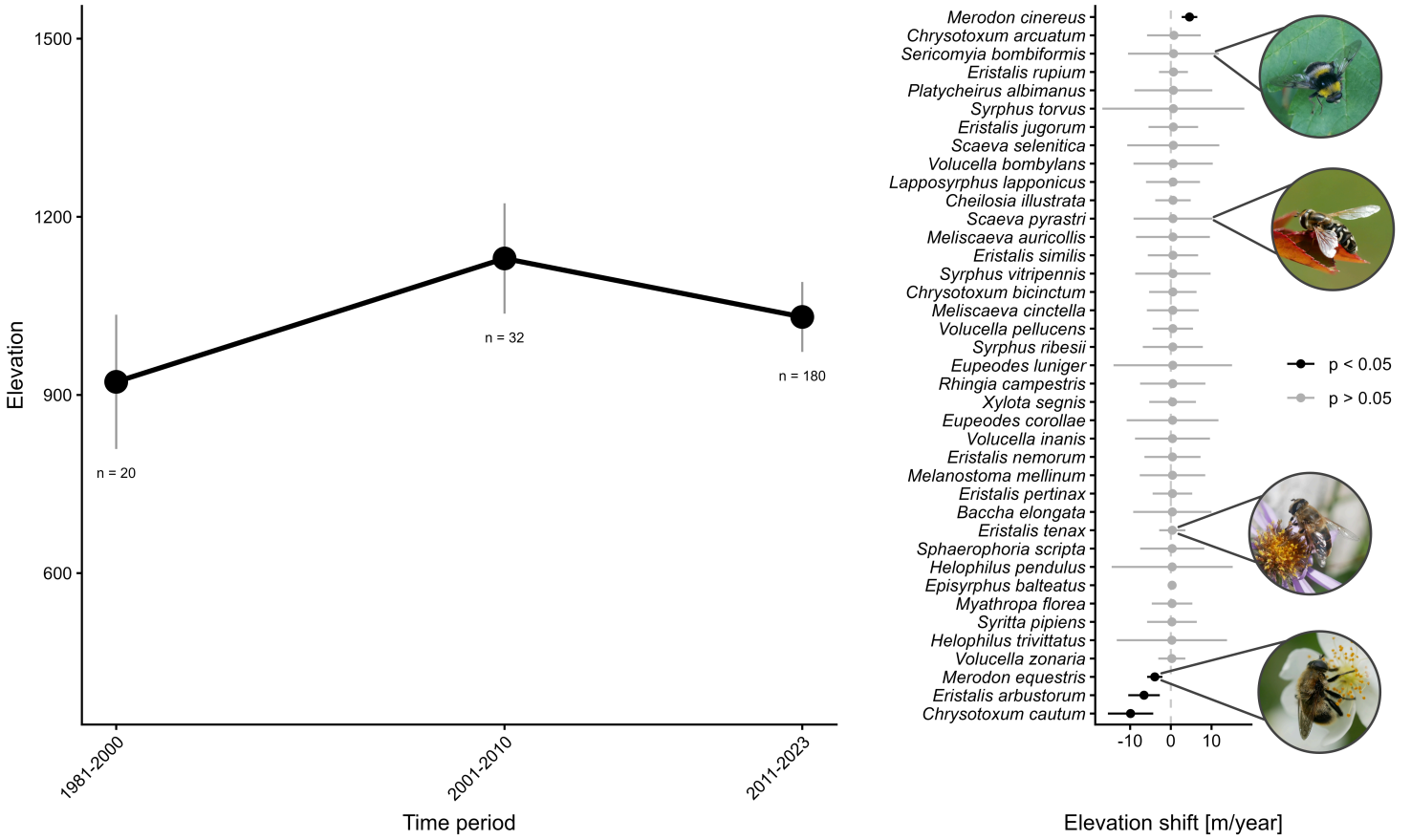


Figure 3

Elevational shifts of hoverfly species. The left panel shows elevation of the whole community sampled in each time period and an average upslope shift of 158.5 m between 1981 and 2023. Time periods before 1981 did not include sufficient data. Points indicate the mean elevation and the error bars show the 95 % confidence interval. The number of species included in each year is shown by the number below the error bars. In the right panel, elevational shifts of hoverfly species can be seen. Each point indicates the elevation shift per year over the study period and the error bars indicate the 95 % confidence interval. The color indicates the statistical significance of the shift. In the right panel, pictures of exemplary species are shown (© Kilian Frühholz).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- TableS7specieselevation.csv
- elevationshiftsupplementv1.docx