



Butterfly species respond differently to climate warming and land use change in the northern Alps



Jan Christian Habel^{a,*}, Werner Ulrich^b, Patrick Gros^c, Mike Teucher^d, Thomas Schmitt^{e,f}

^a Evolutionary Zoology, Department of Environment and Biodiversity, University of Salzburg, A-5020 Salzburg, Austria

^b Department of Ecology and Biogeography, Nicolaus Copernicus University Toruń, 87-100 Toruń, Poland

^c Haus der Natur, Museumsplatz 5, A-5020 Salzburg, Austria

^d Department of Geoecology, Institute of Geosciences and Geography, Faculty of Natural Sciences III, Martin Luther University Halle-Wittenberg, D-06099 Halle (Saale), Germany

^e Senckenberg German Entomological Institute, D-15374 Müncheberg, Germany

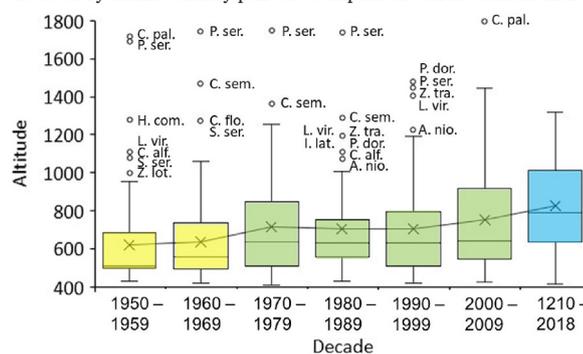
^f Entomology and Biogeography, Institute of Biochemistry and Biology, Faculty of Science, University Potsdam, D-14476 Potsdam, Germany

HIGHLIGHTS

- Lowland butterfly species have shifted their average occurrence and also lower and upper occurrence limits more than 300 m uphill.
- Mobile generalist species exhibited strongest and sedentary specialist species weakest shifts.
- Our results underline that the effects of climate warming and land use change have a strong and currently increasing impact on species.

GRAPHICAL ABSTRACT

Box and Whiskers plots of butterfly altitudinal distribution within seven study decades. Different colours of boxes indicate significant differences ($P < 0.01$) between median altitudes (vertical box lines, means are denoted by an 'x') assessed by Mann-Whitney pairwise comparisons. Abbreviations indicate outliers i.e. species.



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ABSTRACT

Climate change has a worldwide impact on biodiversity and ecosystem functions, in particular by causing shifts in species distributions and changes in species communities. Here, we analyse altitudinal range shifts of 30,604 lowland butterfly and burnet moth records from 119 species over the past seven decades across the federal state of Salzburg (northern Austria) spanning an altitudinal gradient of >2500 m. For each species, we compiled species-specific traits on their ecology, behaviour, and life-cycle. During the study period, the butterflies have shifted their average occurrence and also lower and upper occurrence limits >300 m uphill. This shift is particularly obvious for the last ten years. Habitat generalist and mobile species exhibited strongest and habitat specialist and sedentary species weakest shifts. Our results underline that the effects of climate change have a strong and currently increasing impact on the patterns of species distribution and local community composition. Hence, we confirm the observation that ubiquitous, mobile species with a broad ecological amplitude can cope better with environmental changes than specialist and sedentary species. Furthermore, the strong changes in land use in lowland areas might additionally enhanced this up-hill shift.

* Corresponding author.

E-mail address: Janchristian.habel@plus.ac.at (J.C. Habel).

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1. Introduction

Climate change is increasingly transforming ecosystems. It is shifting the distributions of species poleward and to higher elevations (Parmesan et al., 1999; Parmesan and Yohe, 2003), with the latter particularly demonstrated for the European Alps (Roth et al., 2014; Bonelli et al., 2021; Rödder et al., 2021; Neff et al., 2022; Kemer et al., 2023). In combination with the co-occurring land use changes particularly in lowland regions (e.g. the transition of grasslands into arable fields, transition of former agricultural land into settlements, industrial areas or skiing facilities, but also abandonment of mid- and high-altitude grasslands), species community structures are rapidly changing (Liu et al., 2018). In this context, these land use change can further increase or even counteract up-hill shifts, depending on the type of change in land use and the ecology of the affected species (Gehrig-Fasel et al., 2007; Cannone and Pignatti, 2014). As a result, interactions among species and the functioning of ecosystems can change, are highly disturbed or even decoupled (Alexander et al., 2018; Renner and Zohner, 2018).

Due to niche conservatism (Wiens and Graham, 2005), species often follow their species-specific climatic niches (Parmesan and Yohe, 2003), but these responses differ considerably depending on the species ecology, behaviour, physiology, life-history, and plasticity (Bellard et al., 2012; Sexton et al., 2017; Herrera et al., 2018; Couet et al., 2022). Species with a narrow ecological amplitude are expected to respond more sensitive to abiotic and biotic changes than species covering a broad ecological spectrum (Wiens and Graham, 2005) because the climatic needs are much quicker transgressed if being narrow causing either altitudinal shifts or extinction (Bellard et al., 2012). Therefore, species with an extended climatic niche occurring along a large altitudinal gradient (from lowlands to high mountain areas) most likely are little responsive to climate change, as such species can better cope with climatic changes (Filazzola et al., 2020). We assume that the abundance of such species is peaking at an intermediate point of the elevational range they occur, and then gradually get scarcer with increasing altitude (cf. Burner et al., 2019). Climate change for such species therefore should result in a filling towards the former upper distribution limit (Gehrig-Fasel et al., 2007) and shifting of the upper distribution limit into higher altitudes (Petitpierre et al., 2016).

In general, species restricted exclusively to mountain habitats are assumed to respond more sensitive to climate warming than lowland species (Theurillat and Guisan, 2001; Maharjan et al., 2023). Furthermore, as high mountain habitats are still less suffering from land use change than lowland areas (Bolliger et al., 2007), the evaluation of the combined impact of climate change and land use change can be best assessed by the analysis of species with a wide altitudinal distribution from the lowlands to high mountain areas, in particular by studying their altitudinal changes in the lowlands and at the upper edge of their distribution. However, range shifts also depend on the dispersal capacity of species (Dapporto and Dennis, 2013), and in highly mobile species groups like birds, upper limits seem to be more affected than lower ones (Campos-Cerqueira et al., 2017). Accordingly, dispersive species might better be able to adjust their occurrences to changing environmental conditions if there are suitable conditions available to disperse to.

The mobile group of butterflies and burnet moths (hereafter simply called butterflies) is a highly suitable model system to study responses on climate change (Settele et al., 2008). Butterflies are largely understood in their taxonomy and ecology (Dapporto et al., 2019; Wiemers et al., 2018, 2020; Middleton-Welling et al., 2020; Hofmann and Tremewan, 2020), and have been studied intensively for various regions across Central Europe (e.g. Ebert and Rennwald, 1991; Stettmer et al., 2022). For the federal state of Salzburg (northern Austria), butterflies have been monitored intensively over the past 100 years (cf. Habel et al., 2022). Occurrence data (i.e. presence-only data) have been compiled in a database stored at the Haus der Natur museum Salzburg. This data set represents a highly valuable basis to analyse responses of butterflies to climate change over time. In addition, the federal state of Salzburg provides a highly pronounced altitudinal gradient of >3000 m (i.e. 381–3657 m asl) and,

therefore, is particularly suitable for investigating altitudinal distribution shifts of biota.

Mountain butterflies occupy a very narrow climatic niche (Settele et al., 2008), and thus react in a particularly strong way to climate change (see Rödder et al., 2021). While we analysed distribution shifts of mountain butterflies for the same study area in a previous study (Rödder et al., 2021), we are here focusing exclusively on lowland butterflies species that in the majority of cases occupy a much broader climatic niche. In consequence, we assume that their ecological plasticity and range of recombination is significantly greater in the face of climate change if compared to typical mountain butterflies covering a very distinct and rather narrow climate niche. Furthermore, lowland species (at least in the selected study area) are further affected by land use change (Habel et al., 2021).

In this study, we investigate altitudinal range shifts of lowland butterflies occurring in the federal state of Salzburg and taking place over the last seven decades, a time window for which we have solid data spread over all altitudinal bands constantly. Therefore, we exclusively consider species that do not have a lower altitudinal distribution limit in our study region (Stettmer et al., 2022). These are species in most cases widely distributed in the Central European lowlands and hilly areas (Reinhardt et al., 2021). We have deliberately not included typical mountain butterfly species in this study, as we already know that these species respond highly sensitive to climatic changes (Rödder et al., 2021), as many other high mountain species do (Walther et al., 2005; Jurasinski and Kreyling, 2007). Furthermore, as they are missing from the low altitudes, they are not present in the areas of strongest land use change and therefore do not allow any conclusion on this aspect. In our analyses, we combine the occurrence data of the selected butterflies with species' specific traits on their ecology, biogeography and behaviour. Based on long-term monitoring data, we address the following questions:

1. Did lowland butterflies shift to higher elevations during the past decades?
2. Did the shape of species altitudinal distributions change?
3. Are these altitudinal shifts related to ecological traits?

2. Material and methods

2.1. Data set

The data on butterflies and burnet moths recorded in the federal state of Salzburg (northern Austria) used for this study are primarily based on the entomological collection of the "Haus der Natur", museum of natural sciences in Salzburg (<https://www.hausdernatur.at/en/>). The data were collected by different entomologists and kept in the form of collections and observation lists. Since no information on the abundance of the individual species was provided in most cases, the information is restricted to presence-only data, with respective location and date. These data were completed by further records of recent butterfly assessments, various literature sources, and from various mobile apps (e.g. [Observation.org](https://www.observations.org/)). Out of these data, we extracted all lowland species excluding all mountain species (i.e. species found exclusively above elevations of 600 m asl in the federal state of Salzburg). Due to the limited number of records, we only used records from 1950 onwards and divided this time frame into seven decades (1950–1959, 1960–1969 ... 2010–2018). All raw data used here are compiled in Appendix A.

The selected time period includes the onset of the Eastern Alpine temperature increase, as well as major changes in land use change (Tribusch et al., 2022). The federal state of Salzburg is characterised by a strong change in land use. Numerous near-natural habitats have been converted into intensively managed agricultural areas. Fields and meadows were intensified and for the most part merged into large agricultural fields. As a result, landscape homogenisation increased significantly. At the same time, alpine pasture farming at higher altitudes was often abandoned, resulting in the ongoing succession of open extensively used meadows (Tribusch et al., 2022).

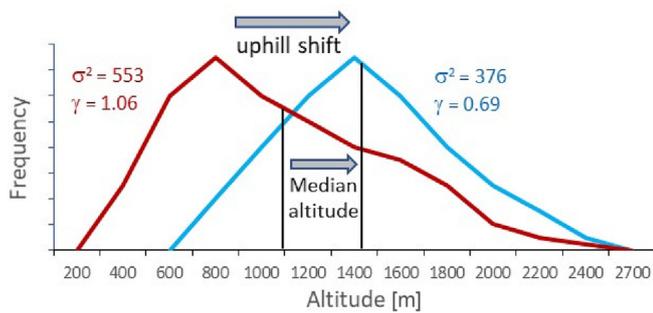


Fig. 1. Simulated altitudinal distribution data to show frequencies of occurrence along the altitudinal gradient before (brown) and after (blue) an uphill shift. This shift should increase mean and median altitude, might change the variance of the altitudinal distribution and might decrease the skewness of the distribution if maximum and/or minimum altitudes are constrained.

In total, we considered 30,604 records representing 119 species, out of which 94 occur in each study decade (Appendix B: Table B1). For each record, we assessed the median altitude from the associated longitudinal and latitudinal coordinates (Table A1). As the precision of these coordinates is limited to about 15 m, we used the average altitude of a square of 100 m² around the coordinates to estimate record's altitude.

2.2. Traits

Each species responds differently to environmental change, according to its habitat preference, ecological amplitude, and dispersal. Studies have shown that forest species react differently than open land species (Seibold et al., 2019), and that ecologically specialised (i.e. monophagous) species that are restricted to nitrogen-poor ecosystems react very sensitively to environmental changes (Habel et al., 2022). In addition, it has already been shown several times that sedentary species suffer particularly strongly from the fragmentation of habitats (Habel et al., 2016). Taking these interrelationships into account, for each species, we compiled information on the use of habitat type, nutrient requirements, phagy, and dispersal behaviour. We consider the following meaningful traits: oligotrophic vs. eutrophic habitats, woodland vs. grassland species, dispersive vs. sedentary species, and habitat generalist vs. specialist species (based

on phagy, habitat demands and dispersal). These traits were created based on various literature sources (Weidemann, 1988; Bink, 1992; Stettmer et al., 2022) and adapted according to local conditions. Table A2 provides all classifications, details on classifications and respective species' specific data.

2.3. Statistics

We divided the observed altitudinal range of occurrences (300–2700 m asl) into eight 300 m intervals and assessed species identities, numbers of records, and for each interval the number of occurring species for each interval. Numbers of records within each decade and altitudinal interval are shown in Figs. B1 and B2.

To answer our first and second starting question, we extracted within each interval for each species the median altitudinal occurrence, the respective standard deviation and skewness of altitudinal distribution and the three lowest and highest occurrences. From these data, we assessed species and trait specific temporal shifts in altitude using linear regression, one-way ANOVA with standard errors from randomised group membership, and non-parametric Kruskal-Wallis and Mann-Whitney pairwise comparisons. Altitudinal shifts affect the median species altitude, but might also affect the shapes of observed distributions of occurrence as assumed by our second starting question and shown by the simulated data in Fig. 1. If minimum and particularly maximum altitude are constrained in a species' specific manner, an initially positively skewed distribution should shift towards a more symmetrical distribution quantified by lower skewness (Fig. 1). An up-hill shift might be accompanied by an altered range in occurrence. Such a range contraction or expansion should be visible by a change in the variance and the respective coefficient of variation (CV). To assess temporal changes in medium altitude, skewness and CV, we calculated Pearson correlations between medium altitude, skewness and CV, we calculated Pearson correlations between decade on the one hand and median altitude (r_A), skewness (r_S), and CV (r_{CV}) on the other for all 94 species occurring in all seven study decades. Under the assumption of up-hill shift, we expected a prevalence of positive time–median correlations. Under the assumption of constraints on altitudinal distributions (our second starting question) we also expected a trend towards more symmetric distributions evident by predominantly negative time–skewness correlations. Additionally, we calculated time–CV correlations to assess range expansion or contraction. Errors always denote standard errors. To answer our third questions, we compared the altitudinal distributions between species characterised by the above mentioned traits.

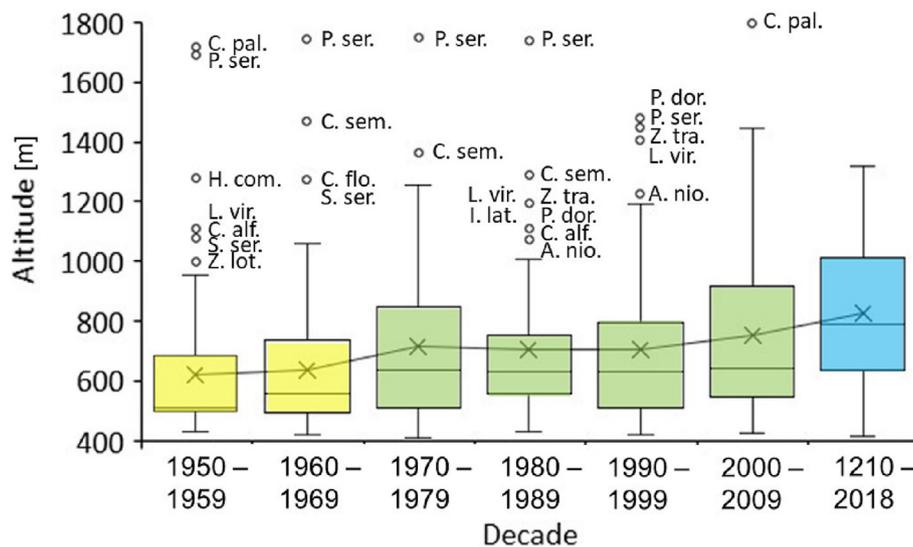


Fig. 2. Box and Whiskers plots of butterfly altitudinal distribution within seven study decades. Significant differences ($P < 0.01$, assessed by Mann-Whitney pairwise comparisons) between median altitudes per decade (vertical box lines, arithmetic means are denoted by an 'x') are indicated by different bar colours. Same bar colours indicate no significant difference. Abbreviations: A. nio.: *Fabriciana niobe*, C. flo.: *Carcharodus floccifera*, C. pal.: *Colias palaeno*, C. alf.: *Colias alfacariensis*, C. sem.: *Cyaniris semiargus*, H. com.: *Hesperia comma*, I. lat.: *Issoria lathonia*, L. vir.: *Lycaena virgaureae*, P. dor.: *Polyommatus dorylas*, P. ser.: *Pyrgus serratalae*, S. ser.: *Spialia sertorius*, Z. lot.: *Zygaena loti*, Z. tra.: *Zygaena transalpina*.

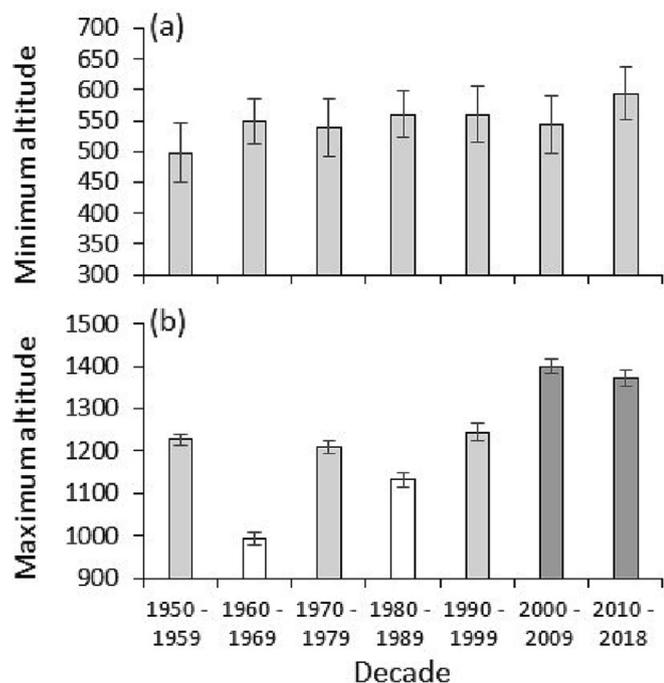


Fig. 3. Average minimum (a) and maximum (b) recorded altitudes (in m) of 119 butterfly species during seven 10-year time windows (1950–1959 ... 2010–2018). Error bars denote parametric standard errors. Different bar colours in each panel indicate significant differences (Mann-Whitney pairwise comparisons, $P < 0.01$). The white bars in (b) mark decades possibly biased by under-sampling or imprecise GPS localisation at highest altitudes.

We note that the decades 1960–1969 and 1980–1989 have comparably low record numbers at highest altitudes (Fig. B1). In theory, this might lower the probability of recording the highest occupied altitudes and affect the calculation of the average maximum altitude of all species. However, the observed maximum altitudes of some species (Fig. 2), the overall altitudinal distribution (Fig. 2), as well as total record numbers and observed species richness from these two decades did not deviate from the other decades (Table B1). The observed deviation of average maximum latitude in these two decades might stem either from unfavourable weather conditions or imprecise GPS localisation. Due to lack of respective high resolution climate and location data we were unable to test for these causes. The possible biases for the two decades regard only Fig. 3b and do not affect any of the results of the present study.

3. Results

Medium altitude of species records increased significantly (one-way ANOVA: $P < 0.00001$) from 510 m asl in the first to 819 m in the last study decade (Fig. 2). This increase is equivalent to an altitudinal shift of 4.5 m per annum. Pairwise comparisons identified significant ($P < 0.01$) increases from the second to the third as well as the sixth to the seventh decade (Fig. 2). Median altitude in the first and second decade was 533 m (upper and lower quartile: 502, 695 m), 636 m (531, 828 m) during the third to sixth decade, and 819 m (639, 1044 m) in the last decade (Fig. 2). Arithmetic mean altitude increased from 630 m (± 21 SE) in the first two, 720 m (± 21) in the next four decades towards 861 m (± 27) in the last study decade (Fig. 2). Boxplots identified a number of species being high altitudinal outliers in several decades. This mainly concerns the species *Cyaniris semiargus* and *Pyrgus serratalae*, being outliers in at least three of the decades (Fig. 2).

We found a significant (one-way ANOVA: $P < 0.0001$) positive trend for a temporal up-hill shift with respect to the lower occurrence boundaries (Fig. 3). In the first study decade (1950–1959), the average mean minimal lower occurrence of the butterflies of our study region was 497 m asl (± 14 SE), but 594 m (± 20) in the last decade (2010–2018), indicating an annual altitudinal increase of 1.4 m. Importantly, in the first study decade, only three of the 111 recorded lowland species (i.e. *Hesperia comma*, *Polyommatus damon*, *Spialia sertorius*) were only found above 600 m (i.e. 2.7%), while this number increased to 22 species (21.4% of 103 recorded species) in the last study decade. Highest recorded altitudes also increased from an average of 1226 m (± 48) in the first decade to 1372 m (± 44) in the last decade (Fig. 3), indicating an up-hill shift of 2.1 m per year. The up-hill shift was strongest since 2000 (Fig. 3).

Analysing the species individually, 88 of the 94 species occurring in all study decades (i.e. 93.6%) had significant positive altitude–decade correlations, hence indicating a temporal increase in altitude (Fig. 4). In turn, skewness–decade correlations were negative for 76 species (80.8%), in line with a more symmetrical altitudinal distribution in more recent times (Fig. 4). Additionally, CV–decade correlations were negative for 68 species (72.3%), confirming a temporal trend towards altitudinal range contraction (Fig. 4).

The trait specific approach revealed similar temporal altitudinal trends (Tables 1, B2, Fig. B3). Irrespective of trait, lowest average altitudes were observed in the first two decades; the highest average altitude in the last decade (Table 1, Fig. B3). Sedentary species are the only exception showing no significant positive altitude–decade correlation but increased average altitudinal distributions in the 1970s and 1980s (Table 1, Fig. B3). The strongest altitudinal shifts during the study period exhibited the species depending on eutrophic environments (291 m, i.e. an annual shift of 4.3 m) and dispersive species (285 m, 4.2 m/a). The smallest shift occurred in sedentary (154 m, 2.3 m/a) and habitat specialist species (173 m, 2.5 m/a) (Table B2).

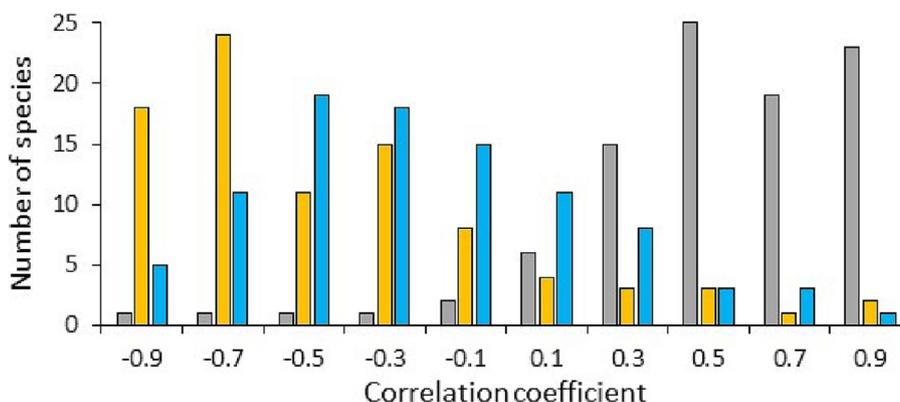


Fig. 4. Distribution of correlation coefficients of all 94 species recorded in each of the seven study decades between the decade–median altitude (r_A , grey), decade–skewness (r_S , yellow), and decade–CV correlations (r_{CV} , blue). Median, skewness, and CV of each species were calculated from all records within a focal decade.

Table 1

Summary table of trait specific temporal trends of butterfly altitudinal distributions. N: number of records. r_A : Pearson correlation between study year and recorded altitude calculated over all records N. KW: Kruskal–Wallis test values for differences in altitude between decades. Bold number denotes significant values at $P < 0.001$. Columns contain mean (\pm one standard error) altitudes per decade calculated over all records.

Trait	Eutrophic	Oligotrophic	Woodland	Grassland	Generalists	Specialists	Dispersive	Sedentary
N	7040	10,917	6299	14,957	21,770	8834	14,501	5794
r_A	0.06	0.08	0.10	0.06	0.09	0.03	0.09	-0.01
KW	204	342	465	464	902	167	594	138.5
1950–1959	786 \pm 29	803 \pm 13	687 \pm 20	768 \pm 11	724 \pm 11	816 \pm 15	847 \pm 14	690 \pm 17
1960–1969	797 \pm 41	792 \pm 15	591 \pm 15	784 \pm 13	708 \pm 14	809 \pm 17	721 \pm 17	738 \pm 2
1970–1979	905 \pm 23	865 \pm 13	679 \pm 14	849 \pm 11	809 \pm 10	856 \pm 14	831 \pm 13	754 \pm 16
1980–1989	793 \pm 15	842 \pm 11	670 \pm 13	824 \pm 9	764 \pm 8	822 \pm 13	775 \pm 10	758 \pm 14
1990–1999	852 \pm 15	801 \pm 9	644 \pm 8	761 \pm 7	759 \pm 7	784 \pm 11	782 \pm 9	669 \pm 11
2000–2009	841 \pm 10	838 \pm 7	674 \pm 7	786 \pm 6	763 \pm 5	814 \pm 8	795 \pm 6	693 \pm 8
2010–2018	924 \pm 10	935 \pm 8	791 \pm 7	901 \pm 7	878 \pm 5	885 \pm 8	914 \pm 7	745 \pm 8

4. Discussion

The results of this study indicate a significant shift of the mean altitude level for most lowland butterfly species, by >300 m within seven decades (Fig. 2). This trend of shifting distributions to higher elevations has accelerated especially during the past ten years. Numerous studies indicated that species respond to climate change by shifting their distribution ranges, for plants (Sittaro et al., 2017) and animals (Chen et al., 2011). It has been shown, that many species migrate northwards (Parmesan et al., 1999; Ott, 2001; Kwon et al., 2014; Dew et al., 2019; Funderup Nielsen et al., 2019) and colonise the higher altitudes of mountain massifs (McCain and Garfinkel, 2021; Rödder et al., 2021). These shifts are mainly driven by rising temperatures. However, also other climatic factors such as precipitation i.e. humidity may play a central role (McCain and Garfinkel, 2021), especially against the background of successful larval development of arthropods, such as butterflies. This may also lead to a west-east shift across Central Europe, i.e. the extinction of continental and boreo-montaneous species from the Western Palaearctic region (Habel and Assmann, 2010). It can be assumed that with these species-specific range shifts, numerous interactions are disrupted or completely decoupled due to temporal and spatial mismatches (Schweiger et al., 2012), and because species (e.g. plants and animals) migrate at different speeds (Sales et al., 2021).

Our data confirm that this trend has been particularly accelerating during the past ten years. This might be related to the effects of recent weather extremes (in particular hot summers recorded for the Alps and other high mountain systems, Gobiet and Kotlarski, 2020), which support species expansions and thus drive responses to climate warming (Crozier, 2004). Studies have shown that, especially in recent years, the effects of climate change are becoming more pronounced and therefore the responses of species are becoming more measurable (Rödder et al., 2021). While the effect of climate change on the loss of biodiversity has so far been estimated to be rather small (Maxwell et al., 2016), these effects will probably become much more pronounced in the future, and is currently already affecting shifts in species community composition (see Jaureguiberry et al., 2022). In addition, systems, including nature with ecosystems and species, may still have been able to buffer the changes and were still within the possible variability of an organism, but in the meantime this threshold is now being exceeded for many species, and thus the species are starting to respond to the environmental changes.

Looking at the trends obtained in our study more in detail, it is noticeable that the upper and lower distribution limits are shifting in parallel (with the upper limit expanding quicker than the lower limit retracting, Fig. 3, Table B1). In this context, climate warming obviously represents the main driver for the colonisation of new habitats at higher altitudes. Hereby, a clear distinction must be made between the possible effects of climate change and habitat destruction (Pimm, 2008), i.e. the two major aspects of global change. Against the background of our results, a shift of the distribution areas to the higher altitudes could also be due to the loss of populations in the lower altitudes due to the strong destruction of habitats there, especially of nitrogen-limited ecosystems (in our study area, see Habel et al., 2021, but also in other parts of Austria, Hülber et al., 2017). The present results show that especially mobile generalists shift to the

higher altitudes, while sedentary specialist species react less strongly. This clearly shows that climate change plays a key role here, and that the land use effect has a subordinate effect on the shift of distribution areas in this case. Our findings also support the relevance of considering species ecology and behaviour in such analyses, as each species responds differently to changing environmental factors. Previous studies also show that the response to climate change is trait-specific (Couet et al., 2022).

It is hardly possible to give any general forecast on the persistence of species diversity in times of global change. However, mobile species with broad ecological amplitudes react stronger to climate change in our study region than sedentary specialists do. These findings underline how the ability to respond to climate change strongly depends on additional factors, such as landscape configuration (Wilson et al., 2009; Fourcade et al., 2017), and that it is strictly species specific. As generally accepted, strong geographical isolation of habitats and local populations and the strong barrier effect of an intensively used landscape matrix result in numerous species that exist in isolation and that move only to a limited extent through the landscape (see Öckinger et al., 2010, 2012). This situation has a particularly negative impact on sedentary specialist species (Thomas, 2016). It is precisely for these species that hardly any habitats are still available in the landscape, in our study region in particular in the lowlands. If this is compounded by a high degree of site-restriction, it could quickly lead to a situation in which such species can hardly react to changes in climate. This underlines that most European landscapes are not fit for climate change due to landscape degradation. Consequently, the double-crisis of climate and land use change might in combination be responsible for the loss of a major proportion of biodiversity in the near future.

Our present results and the above discussion show clear trends, that indicate potential effects mainly driven by climate change. However, these trends must be critically reflected. The fact that insect abundances strongly fluctuate among generations (see Hausmann et al., 2022) underpins the high value and relevance of long-term observations (as used here). However, the access to the higher altitudes of the Alps has improved considerably over time, especially by the construction of roads and the mobility of people due to the increasing use of cars. Thus, observations from higher altitudes might have increased, in particular due to increased spatial accessibility. Thus, at least part of the upward shift in occurrence might be due to increased sampling intensity at higher elevations. However, as all species show a very clear and uniform trend, it can be assumed that the area-spreading effects of climate change play a central role here.

CRedit authorship contribution statement

JCH and TS designed the study, PG provided the data set, WU and MT conducted the analyses, all contributed while writing and the interpretation of the results.

Data availability

All data are online available as supplementary material.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.164268>.

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