



Effects of climate- and land-use change on the cold-adapted Poplar Admiral butterfly

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Abstract

Climate change leads to shifts in the distribution of species and may affect the life-cycle of species. In consequence, interactions between species such as butterflies and their food-plants may become decoupled and populations can lose their original habitats. Furthermore, various processes can also be strongly influenced in the course of a life cycle. In Central Europe, such dynamics are currently affecting particularly cold-adapted species. A noteworthy example is the cold-adapted Poplar Admiral butterfly, *Limenitis populi*. Its larvae feed on the aspen tree *Populus tremula*. This butterfly species vanished from major parts of its Western Palearctic distribution over the past decades and there exist today in small and isolated relict populations, mainly in higher elevations. In this study, we conducted Species Distribution Models for *L. populi* and its larval food plant *P. tremula*. We modelled the past, current and future distribution of both species over the Western Palearctic region, with a special emphasis on the European Alps. We considered climate- and land-use change. Our models show that both species change their distributions into higher altitudes and towards Fennoscandia. Climatic parameters such as elevation and precipitation particularly affected the distribution changes. Records collected over the past decades show that *L. populi* shifted significantly along the altitudinal gradient of the Alps, while *P. tremula* showed no significant shift into higher elevations. It can be assumed that the distribution of *L. populi* strongly relies on the distribution of its food plant and elevation. The climatic changes could have a strong impact on the entire life-cycle of this species, and have a particular effect on the larval and overwintering stages. With this study we would like to emphasize the relevance to consider the entire life-cycle when interpreting effects from climate change on organisms.

Keywords *Limenitis populi* · *Populus tremula* · Distribution · Range shifts · Species Distribution Model · Climate change · Land-use change · Weather · Life-cycle · Larval stage

Introduction

Climate change has a major impact on biodiversity and ecosystem functioning (Wudu et al. 2023). Studies have shown that plant and animal species respond to climate change by spatial and temporal shifts (Rubenstein et al. 2023). Species have migrated northwards (Sunde et al. 2023) and into higher elevations (Dieker et al. 2011; Rödder et al. 2021;

Habel et al. 2023) to follow their species' specific climatic optimum. In addition to such spatial range changes, species also respond to climatic modifications by phenological shifts (Vitali et al. 2023; Löckinger et al. 2024). Numerous species appear earlier during spring, and also extend their flight time into the autumn season (Habel et al. 2024). These spatial and temporal changes can lead to the decoupling of interacting species (e.g. insect-host-plants, hosts-parasites), with severe consequences for its successful development and thus long-term persistence of species (Schweiger et al. 2012; Renner et al. 2018).

Responses of species to climatic change depend on their ecological and behavioural characteristics (Kerner et al. 2023; Löckinger et al. 2024). Mobile species, such as butterflies may rapidly colonise new areas under favourable conditions, while less mobile species such as plants react rather slowly (Kerner et al. 2023). Thermophilic species such as

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some Mediterranean species are currently benefiting from global warming and thus expand their distribution ranges northwards (Cuvelier and Vervaeke 2023). Cold-adapted species suffer most from climate change and are therefore vanishing from major parts of the Western Palearctic region (Habel et al. 2011; Essens et al. 2017; Corradini et al. 2021).

The Poplar Admiral, *Limenitis populi*, is such a cold-adapted butterfly species, which occurs across the entire Holarctic region (Daru 2025). Climate change might have caused the vanishing of this butterfly species over major parts of the Western Palearctic (Lafranchis 2000; Weiss and Manil 2011; Corradini et al. 2021). Today, this butterfly centres over major parts of Eastern Asia and occurs in small relict populations across the Western Palearctic (Kudrna et al. 2015). These relict populations across Central Europe are mainly restricted to higher elevations such as the European Alps and various European Middle Mountains (Kudrna et al. 2015; Corradini et al. 2021). Its larvae feed almost exclusively on the tree species *Populus tremula*. Part of the life cycle of this butterfly species (as with other Nymphalid butterflies) is the creation of a hibernaculum from a leaf in which the young caterpillar hibernates (Herrmann 2007). This life-stage could be particularly affected by climate change.

In this study, we will analyse potential effects of climate and land-use change on the distribution of *L. populi* and its main larval food plant *P. tremula* across the Western Palearctic, with special focus on the European Alps. For these two species we will analyse potential altitudinal shifts from the past until today. We will run Species Distribution Models to project the current and future distribution of *L. populi* across the Alps and for the entire Western Palearctic. Based on the results obtained, we attempt to answer the following questions:

- (i) Are there changes in the distribution of *L. populi* and *P. tremula* across the Western Palearctic and across the European Alps?
- (ii) Which variables shape the distribution of *L. populi* and *P. tremula*?
- (iii) Does the historical and current occurrence data confirm range shifts obtained from Species Distribution Models?
- (iv) How could climatic changes affect the entire life-cycle, particularly the larval stage, of *L. populi*?

Materials and methods

Study species

The Poplar Admiral butterfly *Limenitis populi* is one of the largest butterfly of Europe and has a Holarctic distribution (Kudrna et al. 2015). *Limenitis populi* relies on the tree species *Populus tremula*, its main larval food plant in Central Europe (Stettmer et al. 2022). Adults are difficult to observe as they spend most of the time at the canopy, but females lay their eggs also at leaflets located at the lower parts of the tree (Corradini et al. 2021; JCH, PG pers. obs.). The detection of this species might be easier by searching for species' specific feeding traces of the caterpillars on leaves of *P. tremula* during summer or by searching for hibernacula during autumn and winter (JCH, PG, Peter Huemer pers. obs.) (Fig. 1). The species is on the wing in one generation in Central Europe (late May-early July), with a flight peak beginning June (Settele et al. 2025). The flight time is locally restricted to 2–3 weeks only (Betz 1966; Tolman and Lewington 1987) which makes species detection even more difficult. It can be assumed that this butterfly species has a strong dispersal; flight distances of 4.8 km have already been proven for individuals in Fennoscandia (Gorbach et al. 2010). The species shows a typical protandry (Gorbach et al. 2010). Larvae are feeding on leaflets of the food plant during summer. In the third larval stage, the caterpillar creates a small shelter from a part of a leaf (hibernaculum), in which the caterpillar overwinters (Herrmann 2007). In spring, the caterpillar rehydrates from hibernation desiccation and subsequently feeds on the buds and leaflets of the food plant until pupation (Weidemann 1987). In most populations of the Western Palearctic region, the perceptible population density of this butterfly species is comparatively low (Weidemann 1987), and recent studies indicate a significant shift of this butterfly into higher elevations (Gorbach et al. 2010; Kantonen 2013a, b; Corradini et al. 2021).

Occurrence data and environmental variables

To project the current and potential future distribution of *L. populi* and of *P. tremula* across the Western Palearctic, we included all suitable records of both taxa from the Global Biodiversity Information Facility database (GBIF; <https://www.gbif.org/>) from 2010 onwards. Our polygon extent was: -26.7 66.09, -30.2 28, -13.14 26.91, 6.24 34.9, 10.56 33.64, 31.28 34.56, 41.18 41.22, 40.26 43.46, 48.58 41.88, 50.74 47.2, 60 55.44, 59.14 65, 67.46 68.81, 63.64 70.4, 23.2 71, -26.7 66.09. We chose this period because of the large number of observations available and because strong changes in the distribution of species due to climate change have already been documented for this period (Habel et al.

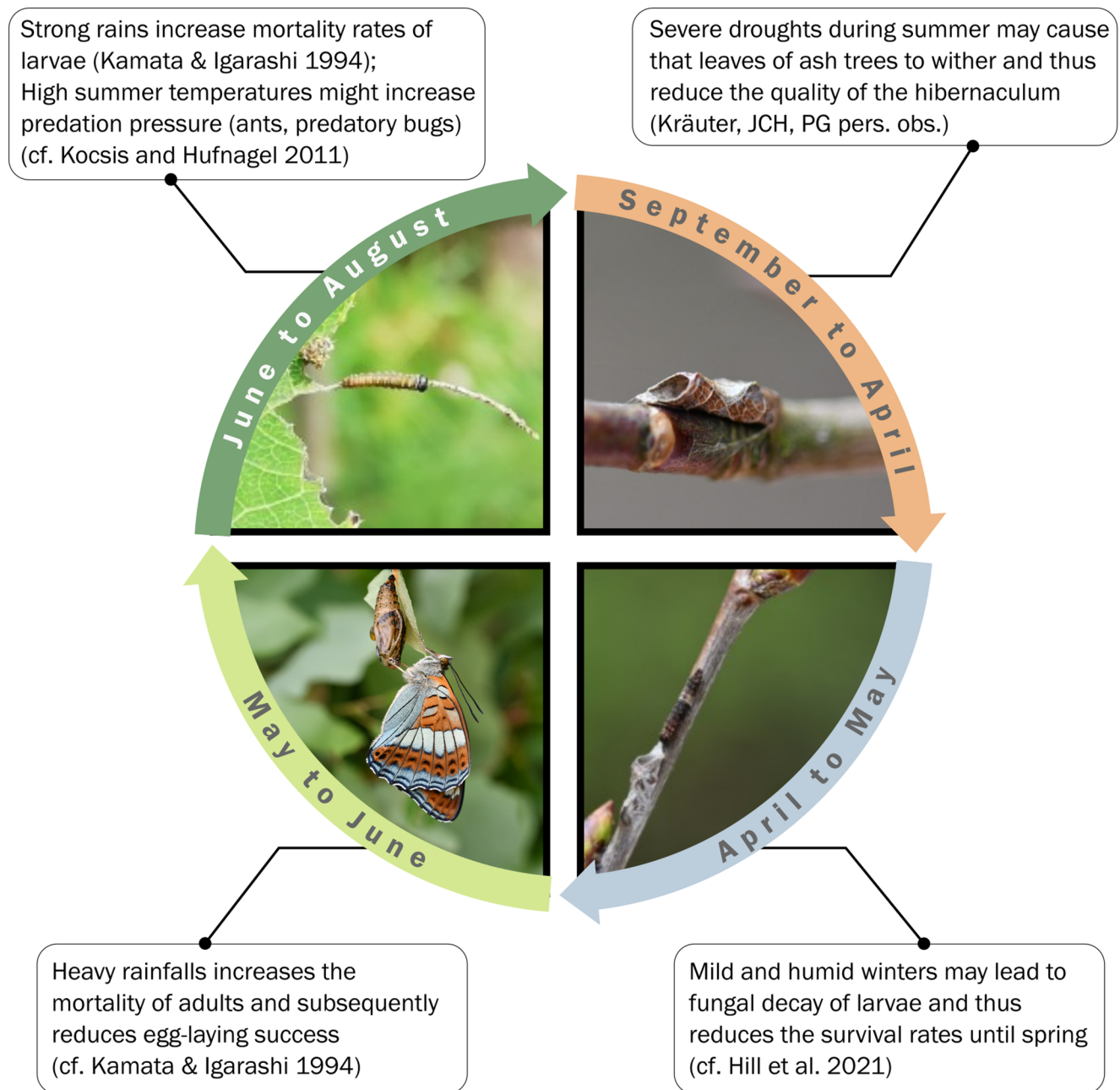


Fig. 1 Life-cycle of *Limenitis populi*, with developmental stages and potential impact from climate change and local weather conditions (photographs: upper left W. Kräuter, others JC Habel)

2023). In total, we downloaded 6,810 occurrence points of *L. populi* (considering all stages of development) and 77,782 occurrence points of *P. tremula* (see Fig. 2b and d). Data were accessed on 23rd October 2024 (GBIF occurrence download: <https://doi.org/10.15468/dl.2knyvc>, <https://doi.org/10.15468/dl.7sam25>).

A second model with higher resolution was fitted for the European Alps to assess potential distribution changes following the altitudinal gradient. Our polygon extent was: 4.86 48.52, 4.86 43, 17.23 43, 17.23 48.52, 4.86 48.52.

For this model, we combined data from GBIF (Data were accessed on 28th February 2025; GBIF occurrence download: <https://doi.org/10.15468/dl.n3v9rh>, <https://doi.org/10.15468/dl.rt65js>) and data from the Haus der Natur museum (Salzburg, Austria) (supplementary Tables 1, 2). Hereby we also only considered data from 2010 onwards. The final dataset was composed from a total of 887 occurrence points for *L. populi* and 12,732 for *P. tremula*. We removed all records without coordinates and duplicates from our data set (cf. Cobos et al. 2018). In addition, spatial filtering was

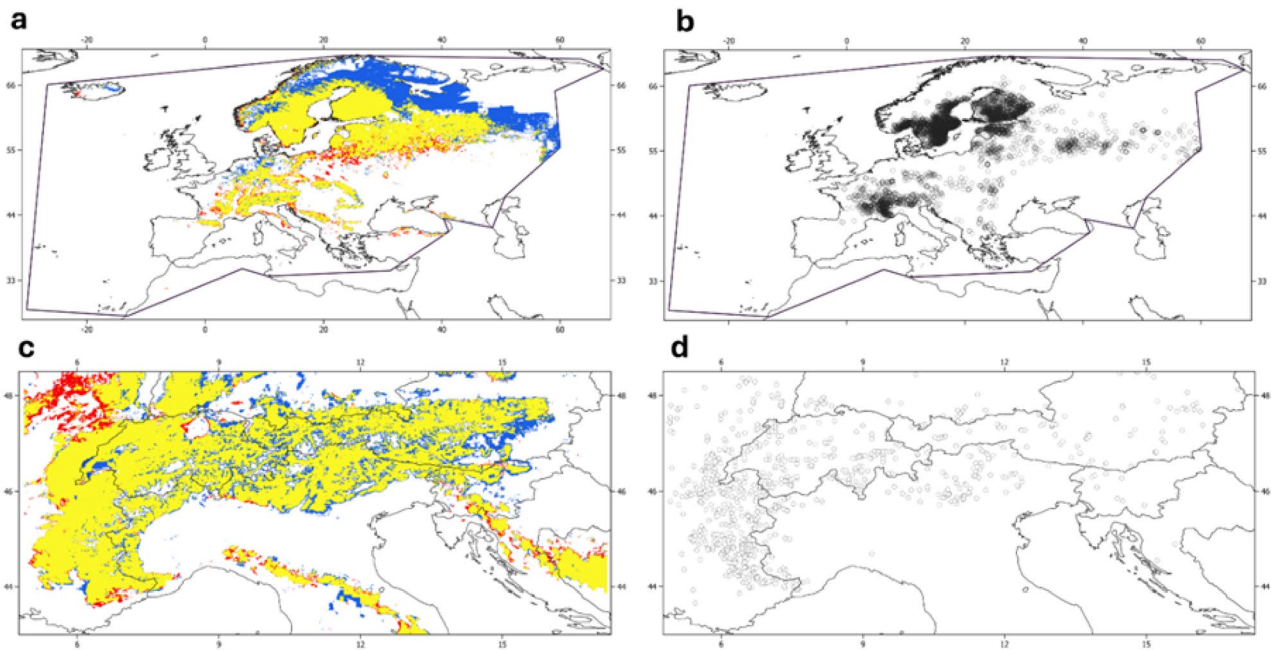


Fig. 2 Distribution shift and occurrence points of *Limenitis populi* across the Western Palearctic (**a**, **b**) and in the European Alps (**c**, **d**) respectively. Regions in red indicate areas of range contraction, in yellow

low suitable continuous habitats where the species can persist, and in blue areas of range expansion. In (**a**) and (**b**) the black line shows the polygon considered in this study

applied to reduce data redundancy and mitigate the effect of environmental variable covariance in the model. This ensured that each grid contained only one distribution data point at final resolution. Finally, the occurrence points of each species were plotted and checked by eye to identify spurious outliers.

To build the models of current species distribution for both, *L. populi* and *P. tremula*, we downloaded the 19 bio-clim variables as well as snow cover days (scd), potential net primary productivity (npp) and growing degree days (gdd) from CHELSA under the shared socioeconomic pathways 370 (ssp. 370) (Karger et al. 2023; <https://chelsa-climate.org/>; access date June 28 2024) for the time period 1981–2010. Data from this time period was considered to reflect current conditions more accurately than the alternative, which ranges from 2010 to 2040 and is based on extrapolations.

Current land use and land cover variables (year 2015) were downloaded from Land-Use Harmonization² (LUH2; Hurtt et al. 2020; <https://luh.umd.edu/data.shtml>) and GCAM-Demeter (<https://data.pnnl.gov/group/nodes/dataset/13192>) (access date November 11th 2024). These were selected considering the ecology of the species (see supplementary information 1a). We also downloaded the elevation from Earth Explorer - USGS (GTOPO30; <https://earthexplorer.usgs.gov/>) (access date June 27th 2024) at a resolution of 30 arc seconds and we extracted from it slope, aspect and the terrain ruggedness index (TRI) using the R

package *terra* (Hijmans et al. 2025). As these variables generally show a high collinearity among each other, we made pairwise Pearson correlations for sub-selection. Variables were excluded when correlation coefficients exceeded 0.75 (Rissler et al. 2006), selecting only the biologically most relevant ones (see supplementary information 1 b-f; Torres and Jayat 2010).

For future conditions, data for the selected variables were obtained from CHELSA for the year 2041–2070 under the shared socioeconomic pathways 370 (ssp. 370) (Karger et al. 2023) (access date June 28th 2024). For land use and land cover the data were downloaded from LUH² (Hurtt et al. 2020; <https://luh.umd.edu/data.shtml>) and GCAM-Demeter (<https://data.pnnl.gov/group/nodes/dataset/13192>), respectively, for 2055 (access date November 11th 2024).

Species distribution modelling

To quantify the geographic sampling bias in our dataset, we used the R package *sambias* (Zizka et al. 2020) for each species. The algorithm quantifies the impact of streets, cities, water bodies, and airports on sampling rates across a given area, by modelling sampling rate as predicted by distance from the features (Zizka et al. 2020). Features were obtained from Natural Earth Data© (2009–2025; <https://www.naturalearthdata.com>; accessed January 15th 2025). The resulting bias map was implemented to generate 10.000

background points using the R package *flexsdm* (Velazco et al. 2022). *flexsdm* was also used to extract environmental data values at background points. To mitigate environmental and spatial biases within occurrence data, we performed environmental filtering (number of bins=25; Varela et al. 2014; Castellanos et al. 2019; Shipley et al. 2022). Species distribution models for *L. populi* and *P. tremula* were estimated using the *megaSDM* v 2.0.0 package (Shipley et al. 2022), which served as a frontend to the original *MaxENT* software with a replicate number of 4. To test the accuracy of the models, we computed the area under the receiver operating characteristic curve (AUC). The model was considered to have a high discrimination power if AUC values are higher than 0.8 (maximum 1; Fielding and Bell 1997). To model future distributions, a dispersal rate of 4.8 km/year was used following Gorbach et al. (2010). Binary presence/absence maps were obtained by *MaxENT*, using the “Maximum.test.sensitivity.plus.specificity” option (see Liu et al. 2005). Maps of distribution shifts were created using the *createTimeMaps* function (Shipley et al. 2022) considering the same dispersal rate. These maps were based on the binary distribution maps that were generated for all time steps and display the regions vacated and migrated to during each time period (Shipley et al. 2022). Finally, the models were illustrated with *QGIS* (QGIS Development Team 2022).

Altitudinal shifts

Analysis of altitudinal data was done for two time periods: past shifts were inferred from historical museum specimens and observed data, predictions of future elevation shifts were gained from the SDMs. We restricted the investigation of historical data to the area of the Land Salzburg (Salzburg, Austria) for the sake of comparable climatic conditions with other studies on the European Alps (Corradini et al. 2021). We used records of *L. populi* (1917 to 1995) and *P. tremula* (1892 to 2023) from the Haus der Natur (Salzburg, Austria; supplementary Tables 1 and 2), to identify potential shifts in mean elevation of records over time. We used original elevation data as written on the collectors' labels, if available. Missing elevation data were inferred based on the locality using the R-package *elevatr* v. 0.99.0 (Hollister 2023), which accessed Terrain Tiles on 2025-04-03 from <https://registry.opendata.aws/terrain-tiles>. Two separate ordinary least squares models were fit to infer a shift in mean record elevation in dependence of time for *L. populi* and *P. tremula*. Record numbers of *P. tremula* strongly increased after 2008 so that the model had to be restricted to the time after 2008.

Potential future elevational shifts of occurrences of *L. populi* and *P. tremula* were assessed based on the binary SDMs of the respective species (see supplementary

information 4). We extracted elevation values from GTOPO30 at all pixels where the binary SDMs predicted the respective species to occur. We then randomly subsampled the elevation values to include 2500 values per species and time step and applied a GLM with a Gamma-distribution, which fit the right-skewed, positive continuous data well. Uncertainty intervals (profile-likelihood) and p-values (two-tailed) were computed using a Wald t-distribution approximation as implemented in the R package *parameters* (Lüdecke et al. 2020).

Results

Species distribution models

Our occurrence dataset after environmental filtering (Varela et al. 2014) contained 5,918 data points for *L. populi* and 48,127 for *P. tremula* for the Western Palearctic. The occurrence dataset for the European Alps was 873 data points for *L. populi* and 11,984 for *P. tremula*. Results of sampling bias estimation can be found in the supplementary information 2.

In the Western Palearctic, the variables with the highest contribution to the models for *P. tremula* were precipitation and temperature variables bio18 (42,5% - Precipitation of Warmest Quarter) and bio7 (27,8% - Temperature Annual Range) respectively and the land cover variable “Needleleaf evergreen tree – boreal” (9%). The current potential distribution of *P. tremula* (51,5%) and the land cover variable “Needleleaf evergreen tree – boreal” (21,7%) showed the highest contribution in shaping *L. populi* distribution. In the European Alps the variable that most affected the distribution of *L. populi* and its food plant was the elevation (46,9% and 45,2%, respectively).

The potential future distribution of *P. tremula* (see Fig. 3) and *L. populi* (supplementary information 3) showed that both species will persist in parts of Central Europe and expand towards Fennoscandia (see maps of distribution shift for *L. populi* Fig. 2a, and *P. tremula* in Fig. 3e; the binary maps are available in the supplementary information 4). In the European Alps region both species showed a tendency to persist in their current distribution with expansions in some area (see Fig. 2c for *L. populi* and Fig. 3f for *P. tremula*). Areas of range contraction are mainly in the lowland regions in the case of *L. populi* (see Fig. 2), and at the most western and southern margin of the distribution range of *P. tremula* (see Fig. 3).

Altitudinal shift

The analysis of the altitudes in the Land of Salzburg (Salzburg, Austria) at which historical and recent specimens of *P.*

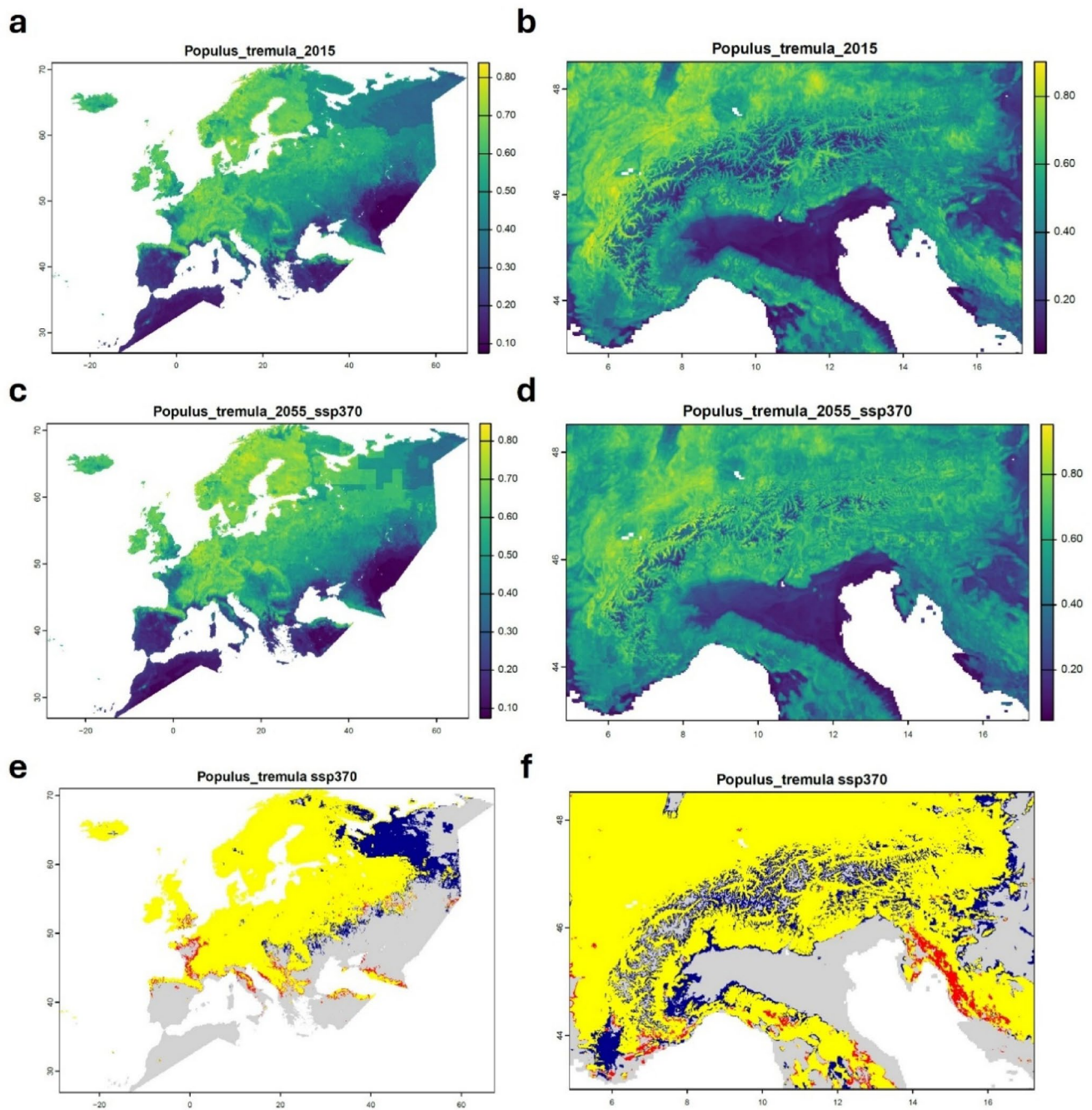


Fig. 3 Current (a, b; 1981–2010) and future (c, d; 2041–2070) suitable habitats of *Populus tremula* in the Western Palearctic and European Alps region as well as maps of distribution shift for the same regions

(e, f). Regions in red indicate areas of contraction, in yellow suitable habitats where the species can persist, and in blue areas of expansions

tremula and *L. populi* were recorded revealed a significant mean increase of 3.04 m (se=1.09 m) per year (62 observations; $p<0.001$; adj. $r^2 = 0.105$; Fig. 4). No significant shift in elevation was observed for *P. tremula* after 2008 (Fig. 4b). The GLM based on the binary SDMs predicted a shift of the mean elevation of occurrence of *P. tremula* by 62.22 m (95% CI: 31.50–92.72 m) per 40 years (1.56 m per year; $p<0.001$) and of *L. populi* by 57.41 m (95% CI: 22.49–92.39 m) per 40 years (1.44 m per year; $p<0.001$) (Fig. 5).

Discussion

Our predictions suggested an altitudinal shift for *L. populi* from past to present, as well as in the future. Our model outcomes show that *L. populi* persist in some areas of Central Europe, and strongly expand towards the north-east, and also colonize areas in higher altitudes (e.g. the European Alps) (Fig. 2a and c). These trends go in line with results obtained in previous studies on *L. populi*. Corradini and colleagues (2021) showed that populations vanished from the lowlands of France and today still occur in the higher elevations of the French Alps. The authors projected a total shift of 322 m within 58 years (5.55 m per year). According to our modelling outcomes, we found an altitudinal shift of 3.04 m per year.

Such altitudinal range shifts as responses to climate change can be frequently observed for cold-adapted species. In a study on the boreo-montane Violet Copper butterfly *Lycaena helle*, the authors state a wide distribution across the Central European lowlands during the early postglacial period, reconstructed on the basis of molecular data and species distribution models (Habel et al. 2010). In the case of *L. helle*, a major proportion of the populations from lowland regions might have disappeared in the course of postglacial warming, so that today only small relict populations can be found in the higher altitudes of the Pyrenees, Alps and Carpathians, as well as in some European middle mountains (Habel et al. 2011). Based on models and taking into account future climatic changes, most populations of this butterfly species might disappear from most European middle mountains and parts of the European Alps in the near future (Martin et al. 2014). *L. populi* shows a very similar trend, with shifts into higher altitudes and latitudes (see also Settele et al. 2008). These responses go in line with predicted distribution shifts for other cold-adapted i.e. boreo-montane and continental butterfly species, such as *Boloria eunomia* and *Boloria selene* (Maresova et al. 2019). It is not yet clear how species use the temperature range of within a region to potentially buffer against climate change. In extremely warm summers, for example, higher areas could be colonised ad hoc, or particularly shady slopes (e.g. change from the south to the north side of a slope). Even if

Fig. 4 Occurrences of *Limnitis populi* (a) and *Populus tremula* (b) at respective altitudes in the European Alps. The regression line illustrates the statistically significant increase in elevation of about 3 m per year

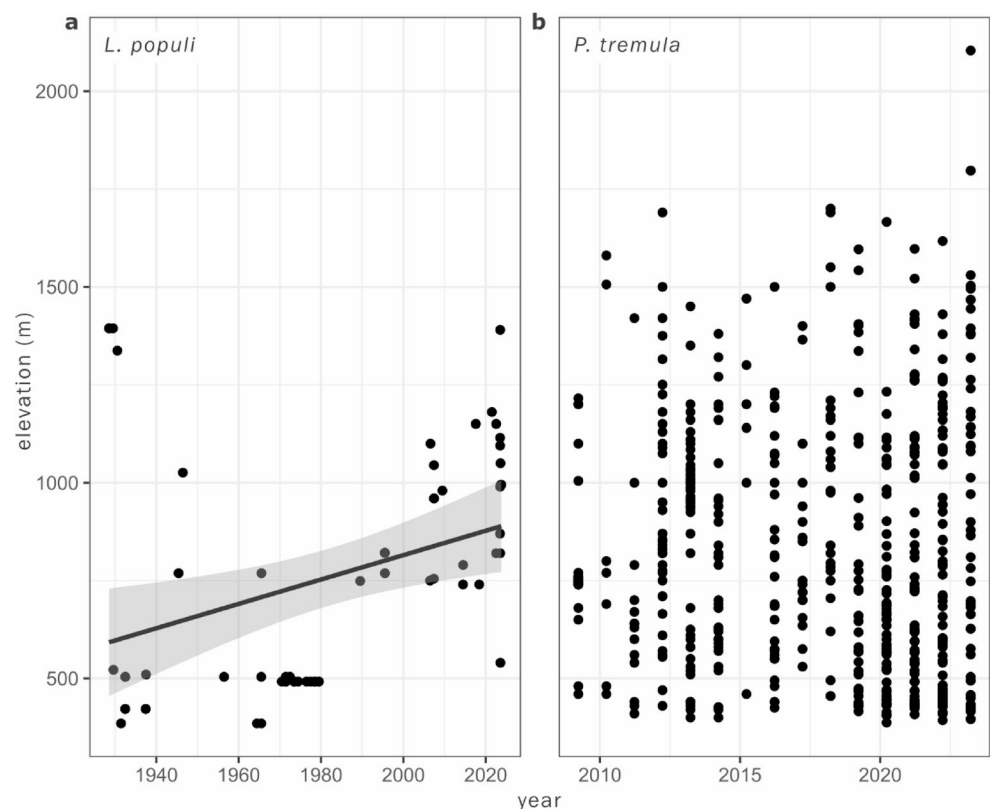
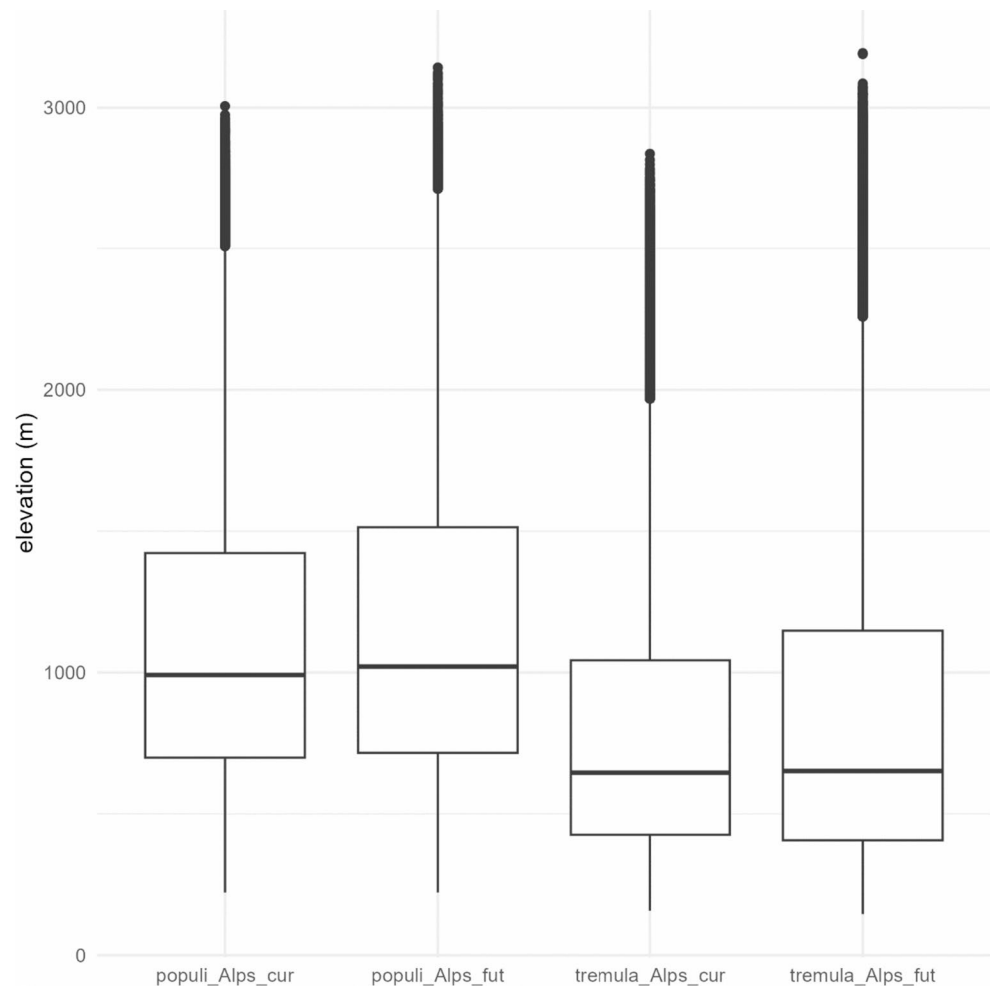


Fig. 5 Current and potentially future occurrence of *Limenitis populi* and *Populus tremula* in the European Alps, calculated based on binary SDMs



the climatic conditions in Iceland and Spain are not suitable for *L. populi*, the presence of its food plant to which the species is strongly linked generates an over-predictions of the SDMs.

Our models show that the distribution of *L. populi* across Western Europe mainly depend from the occurrence of *P. tremula* and needle-leaf evergreen forest (two non-climatic variables). However, the distribution of *P. tremula* is strongly affected and predicted from precipitation (42.5%) and temperature (27.8%) (two climatic variables) and the occurrence of needle-leaf evergreen boreal forests (the third variable, 9%). Thus, in our study system, climate might have an indirect effect on the predicted distribution of *L. populi* according to our models. Since *L. populi* is dependent on this tree species as main larval food plant, its distribution follows the occurrence of this plant species. Adequate habitats have largely disappeared at lower altitudes due to climate change but also due to the intensification of land use, including forestry, the species is now shifting to potential habitats at higher altitudes (P.G., J.C.H., pers. obs.). The targeted removal of *P. tremula* also plays a central role here, as these trees are of no or only little value in forestry (Hardenbol

et al. 2020; Kivinen et al. 2020), and the linear and abrupt boundaries between forest and open land, and the resulting lack of ecotones, which in the past were often a habitat for *P. tremula* stands (Hardenbol et al. 2020). The combination of climatic change and the removal of *P. tremula* may have led to the fact that most observations of *L. populi* in the European Alps are at an altitude of around 1000 m (J.C.H., P.G., pers. obs.). Different responses to climate change can lead to a spatial mismatch between the larval food plant and the butterfly, as has already been shown for various butterflies and plant species (see Schweiger et al. 2012; Kerner et al. 2023).

Climate change as well as local weather events might impact the life-cycle of *L. populi* and could have a particularly strong impact on the larval stages of this species (also see Stuhldreher et al. 2014; Klockmann and Fischer 2019) (see Fig. 1). It can be observed that in particularly hot summers the activity of potential predators (e.g. ants, predatory bugs) is very high, with negative effects on the survival rates of butterfly larvae in the L1/L2-stage (Kocsis and Hufnagel 2011). During summer and autumn, regionally occurring droughts can lead to premature dropping and/or withering

of larval food plant foliage. In addition, the increasing number of heavy rainfall events in the wake of climate change is increasingly washing down young caterpillars from the leaves (as identified for other lepidopterans, see Kamata and Igarashi 1994). There are also climatic changes at the time of egg laying, which are increasingly characterized by heavy rainfall events. A species with a single generation and a comparatively short flight time might suffer under such changed climatic conditions. This could have negative effects on the construction of the hibernaculum (shelter to overwinter) and thus significantly reduce the survival rates over larvae during winter (P.G., J.C.H., pers. observ.). In addition, changes of winter climate (towards warm and humid conditions) might accelerate mortality rates of larvae due to metabolism and/or fungal decay, as well as increased activity of predators during this dormant phase (see also Hill et al. 2021). Although all these factors may affect the species life-cycle, we do not know and understand which ones have a greater impact on population dynamics.

With this study we analysed and discussed effects of climate- and land-use change as well as local weather events on the two species *P. tremula* and *L. populi* butterfly. Our models show that climate change (via the larval food plant) has an effect on the butterfly species. Both factors, land-use change and climate change have a joint effect on the larval food plant and the butterfly. With this study we would like to emphasize that climate change might have a particular impact on the larval stage of this, and many other organisms. To date, very little is known and researched about these effects on the different stages, and further very detailed studies are needed incorporating the entire life-cycle.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-025-00716-1>.

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Author contributions JCH, PG, JE and VT developed the idea, VT and JE conducted the models, all contributed while writing this manuscript and interpreting the results.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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