

Temperatures during the development season are increasingly favourable for polyvoltine pest species in Switzerland

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ABSTRACT

With global warming, the mean temperature during the insect development season has been increasing in Switzerland over the last decades, and this trend is predicted to continue. As a result, the annual number of generations could increase for polyvoltine insect species. Some pest species, such as the box tree moth (*Cydalima perspectalis*), the grapevine moth (*Lobesia botrana*), the codling moth (*Cydia pomonella*), and the Comstock mealybug (*Pseudococcus comstocki*), are therefore likely to produce more generations in the future, leading to more damage to forests, vineyards and crops. These species all have a base development temperature (t_b) of around 10 °C. In this study, we examined the extent to which changes in daily mean temperature (Tmean) averaged over the development season (April through September) could potentially increase the voltinism of these species in various regions of Switzerland. We analysed long-term daily Tmean data from the period 1980–2021 at 67 meteorological stations covering an elevation range from 203 to 2283 m a.s.l. We then used two climate scenarios (RCP2.6 and RCP8.5) to analyse daily Tmean during the period 2022–2099. We computed growing degree days (GDDs) above $t_b = 10$ °C and looked at the trends across elevation. Our results show that daily Tmean averaged across the development season increased more than the daily Tmean averaged over the entire year over the last 40 years. There was an average increase of 60 GDDs per decade during this period, with larger increases occurring at lower elevations. Our results indicate that by the end of the 21st century there could be more GDDs on the Swiss Plateau than currently occur at lower elevations on the southern side of the Alps and that the number of GDDs currently occurring on the Swiss Plateau could be found at middle elevations (800–1400 m a.s.l.). Future temperature conditions can thus be expected to favour additional generations of pests annually at lower elevations and to allow them to complete a full single cycle per year at higher elevations.

1. Introduction

Climate change is expected to have a major influence on the outbreaks of pest species during the next decades. Insect pests are therefore a major issue for the adaptation of both crops and forests to future climatic conditions (Deutsch et al., 2018; Netherer and Schopf, 2010). As insects are ectothermic organisms, their demography is strongly sensitive to ambient temperature during period of development from egg to adult. In a temperate climate, it is likely that thermophile pest species will benefit from the higher temperatures during the development period occurring as part of global warming (Schneider et al., 2022). In particular, some polyvoltine species (i.e. species which are able to produce more than one generation per year) may be able to produce more generations annually than in the past (Altermatt, 2010). A warmer

development season can also favour new exotic thermophile species (Yan et al., 2017). These trends could lead to more damage to forests and crops in the future (Bjorkman and Niemela, 2015). It is thus crucial to study how temperature conditions during the development season are changing and to understand their potential impacts on the population dynamics of polyvoltine insects.

An increase in voltinism has already been observed for some butterfly species across Europe, especially since the 1980s (Altermatt, 2010). Concerning pest species, some cases have been detected in Central Europe. For example, the spruce bark beetle (*Ips typographus*) has been able to produce three generations, instead of two, on the Swiss Plateau since 2003 (Jakoby et al., 2016). Likewise, a second generation has recently been observed for the marmorated stink bug (*Halyomorpha halys*; Stoeckli et al., 2020). In a temperate climate, the increase in

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voltinism is associated with both a warmer and a longer development season. Warmer springs induce an earlier start of the first generation and of other phenological events (Forrest, 2016). At the same time, the mean temperature during the development season (T_{mean}) plays a key role in the voltinism of many pest species, with the warmer conditions allowing them to complete additional cycles.

In Central Europe, the mean temperature during the development season can be characterized by the mean temperature from April through September (Potopová et al., 2016). The life cycle of polyvoltine species depends on the amount of heat accumulated annually, mostly during this period. Voltinism can be modelled using growing degree days (GDDs), which involves determining a base development temperature (t_b) threshold, i.e. the lowest temperature at which a species can complete a generation. The number of GDDs tends to increase as the development season becomes warmer under climate change, which could allow polyvoltine species to complete more generations during the year. In this study, we identified four major polyvoltine pest species spread across Switzerland for which specific GDD requirements are known.

a) Box tree moth

Native of East Asia, the box tree moth was first observed in Switzerland in 2007 (Leuthardt et al., 2013). This pest is now widespread in Swiss gardens and forests (Kenis et al., 2013). Based on European populations, Nacambo et al. (2014) set the t_b for this species at 9.5 °C, with 540 GDDs necessary to complete a generation. Studying populations in Japan, Maruyama and Shinkaji (1987) set the t_b at 10.5 °C, with 615 GDDs necessary to complete a generation. Two generations per year have been observed in northwestern Switzerland (Nacambo et al., 2014).

b) Grapevine moth

The grapevine moth originates from Southeastern Europe and is now widespread in European vineyards, including in Switzerland (Castex et al., 2020). This pest generally produces two generations per year in Northern Europe, and up to five generations per year in Spain (Gutierrez et al., 2017). Gutierrez et al. (2017) set the t_b of this species at 10 °C, while Briere and Pracros (1998) estimate it at between 8 °C and 12 °C. The number of GDDs per generation has been estimated at 458 GDDs for $t_b = 10$ °C (Touzeau, 1981).

c) Codling moth

The codling moth attacks apple orchards throughout most of the world. In California, its t_b was set at 10 °C by Pitcairn et al. (1992), with the number of GDDs per generation ranging from 595 (first generation) to 685 (third generation). Pickel et al. (1986) set the t_b at 11.1 °C, with 575 GDDs per generation. In Switzerland, the codling moth produces two generations per year at lower elevations (Stoeckli et al., 2012).

d) Comstock mealybug

The Comstock mealybug originates from Eastern Asia and was first observed in the South of France and in Italy in 2004. In Switzerland, this species has been reported since 2016 in the Rhone Valley, where it causes damage to fruit crops (Terrettaz et al., 2020). Its t_b has been estimated at around 10 °C, with 840 GDDs needed to complete a generation in Korea (Jeon et al., 2003). In Southern Europe, the Comstock mealybug produces two to three generations per year.

The aim of this study was to determine the extent to which changes in the daily mean temperature (T_{mean}) during the development season could impact the voltinism of pest species across a wide elevation range in Switzerland. We first analysed trends in daily T_{mean} averaged over the development season (April through September) and over the entire

year. We then computed GDDs above $t_b = 10$ °C and analysed trends across elevation. An increase in the number of GDDs would mean a greater potential for additional generations per year of the four species in Switzerland.

2. Materials and methods

2.1. Meteorological stations

We selected all meteorological stations managed by MeteoSwiss that are located below the treeline, i.e. around 2400 m a.s.l. in Switzerland (Gehrig-Fasel, Guisan and Zimmermann, 2007). Each station has collected daily minimum (T_{min}) and maximum (T_{max}) temperature data since 1980 or longer. We chose to start our analysis in 1980 to include a sufficient number of stations. We included data series with up to 10% missing values. Missing values were not gap-filled. This selection resulted in 67 stations covering elevations between 203 and 2283 m a.s.l. and located in all climatic regions of Switzerland (Fig. 1; see Table S1 in the Supplementary Material for a summary of their elevation distribution and Table S2 for a complete list of the stations).

We then selected the same 67 stations in the CH2018 dataset provided by the National Centre for Climate Services (NCCS) to model trends for the future decades (Crocchi-Maspoli et al., 2018). This dataset is based on the EURO-CORDEX climate projections and provides data at the local scale. The data were produced using a downscaling method (quantile mapping). Daily T_{min} and T_{max} data are available until 2099. As the dataset is calibrated based on the period 1981–2010, it is likely that the modelled data do not exactly match the observed data for recent years. We selected two climatic scenarios corresponding to two different Representative Concentration Pathways (RCPs), namely RCP2.6 and RCP8.5 (IPCC, 2013). RCP2.6 corresponds to the lowest greenhouse gas emissions scenario considered by the IPCC, with a peak around 2020 followed by a substantial reduction thereafter. RCP8.5 corresponds to the highest greenhouse gas emissions scenario considered by the IPCC, with a continuous rise throughout the 21st century. The EURO-CORDEX climate models we used have a spatial resolution of 12 km before downscaling. The simulations we used are DMI-HIRHAM_ECEARTH_EUR11_RCP26 (for RCP2.6) and CLMCOM-CCLM4_ECEARTH_EUR11_RCP85 (for RCP8.5). They were both extracted from the CH2018 dataset and provide daily T_{min} and T_{max} for each of the 67 stations.

2.2. Analysis and threshold definition

We first analysed trends over time in daily T_{mean} averaged over the development period (start of April to end of September) and over the entire year. Daily T_{mean} was computed as the mean of daily T_{min} and T_{max} . We determined linear trends for past and future periods (1980–2021 and 2022–2099). We also used 11-year moving averages to better visualize the trends. We then computed growing degree days (GDDs) using a threshold that is relevant for the development of the four target pest species described in the introduction. GDD is defined as daily T_{mean} minus t_b (in °C), where $\text{GDD} = 0$ when $T_{\text{mean}} \leq t_b$. GDD values are summed over the year to calculate annual GDDs (Tschurr et al., 2020). We chose $t_b = 10$ °C based on the literature, as it approximatively corresponds to the t_b of all four species. We started each count on the first day of the year. As elevation is a crucial factor determining temperature in the Swiss context (Hufty, 2001; Joly et al., 2012), we grouped our stations into six elevation classes (<500, 500–800, 800–1100, 1100–1400, 1400–1700, and >1700 m). We added a seventh class for the stations located <500 m on the southern side of the Alps, as bioclimatic conditions are known to be specific in this region, with higher temperatures (Zubler et al., 2014; Tschurr et al., 2020). We calculated the number of GDDs over three periods, i.e. the last 40 years (1980–2021), the middle 30 years of the 21st century (2035–2064) and the final 30 years of the 21st century (2070–2099).



Fig. 1. Locations, codes and elevations of the 67 MeteoSwiss meteorological stations used in this study.

All data analyses, including linear regression models and 11-year moving averages, were performed using R version 3.0.2 (R Core Team, 2019).

3. Results

3.1. Trends in daily Tmean averaged over the development season and over the entire year

Daily Tmean averaged over the development season (DS Tmean)

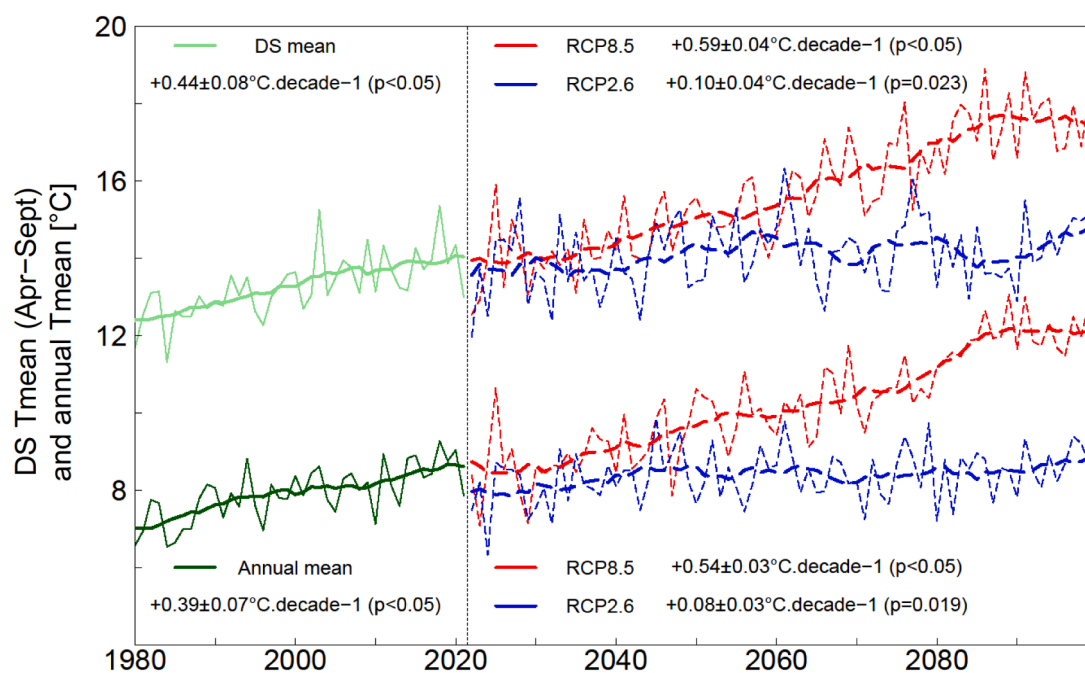


Fig. 2. Trends in daily mean temperature (Tmean) averaged over development season (DS, start of April to end of September) and over the entire year, averaged across the 67 meteorological stations during the periods 1980–2021 (thin solid lines) and 2022–2099 (dashed lines). Eleven-year moving averages are shown as thick solid lines, and slopes (\pm SE) of the linear regressions are displayed.

increased significantly during the period 1980–2021 ($0.44\text{ }^{\circ}\text{C decade}^{-1}$, $p < 0.05$; Fig. 2), slightly more than daily Tmean averaged over the entire year (annual Tmean; $0.39\text{ }^{\circ}\text{C decade}^{-1}$, $p < 0.05$; Fig. 2). Both future scenarios showed a significant increase in DS Tmean and annual Tmean for the period 2022–2099. Trends differed substantially between the two scenarios, with $0.59\text{ }^{\circ}\text{C decade}^{-1}$ (DS Tmean) and $0.54\text{ }^{\circ}\text{C decade}^{-1}$ (annual Tmean) for scenario RCP8.5 compared with $0.10\text{ }^{\circ}\text{C decade}^{-1}$ (DS Tmean) and $0.08\text{ }^{\circ}\text{C decade}^{-1}$ (annual Tmean) for scenario RCP2.6. The transition between the historical data and the projections suggests that temperatures are underestimated in scenario RCP2.6, at least for the current period.

3.2. Trends in growing degree days

Overall, the number of GDDs (with $t_b = 10\text{ }^{\circ}\text{C}$) increased significantly over the period 1980–2021, at a rate of $60.34\text{ GDDs decade}^{-1}$ ($p < 0.05$; Fig. 3). Under both future scenarios, there was a significant increase for the period 2022–2099, by 14.53 (RCP2.6) to 105.20 (RCP8.5) GDDs decade^{-1} . The largest increase was observed in the lower elevation classes, with a clear maximum on the southern side of the Alps ($107.17\text{ GDDs decade}^{-1}$; Fig. 4 and Table 1). Trends were quite similar in the two elevation classes below 800 m a.s.l. on the northern side of the Alps (70.66 to $77.36\text{ GDDs decade}^{-1}$) and in the three classes between 800 and 1700 m a.s.l. (46.33 to $49.80\text{ GDDs decade}^{-1}$). The smallest increase was found above 1700 m a.s.l. ($20.42\text{ GDDs decade}^{-1}$). The transition between historical data and projections clearly indicates that the number of GDDs is underestimated in scenario RCP2.6, at least for the 2020s.

3.3. Mean number of growing degree days per year

During the period 1980–2021, the largest annual number of GDDs with $t_b = 10\text{ }^{\circ}\text{C}$ was observed below 500 m a.s.l. on the southern side of the Alps, with $1627\text{ GDDs per year}$ on average (Table 2, Fig. 5). Under scenario RCP8.5, this value was exceeded by the end of the 21st century at stations up to 800 m a.s.l. on the northern side of the Alps. Similarly, by the end of the 21st century under scenario RCP8.5, the number of GDDs at stations between 800 and 1400 m a.s.l. exceeded the values

during the period 1980–2021 below 800 m a.s.l. on the northern side of the Alps. Under scenario RCP2.6 there was only a slight increase in the mean values at all elevations during the next decades compared with 1980–2021, and values were stable between the middle and the end of the 21st century.

At lower elevations, a particularly large number of GDDs were observed at stations near large lakes during the period 1980–2021 (Table S2). On the southern side of the Alps, this concerned Lugano (1729.82 GDDs) and Locarno (1732.28 GDDs , highest values across all stations). On the northern side of the Alps, stations located around lake Geneva (Genève, Pully, Nyon) and around lake Neuchâtel (Neuchâtel) also recorded a large number of GDDs in comparison with other stations at similar elevations.

4. Discussion

Our results show that DS Tmean increased slightly more than annual Tmean during the period 1980–2021 in Switzerland (Fig. 2). Previous studies have indicated that daily Tmean has been increasing more in summer and spring than in autumn and winter since the mid-1970s in Central Europe (Matiu et al., 2016; Rebetez and Reinhard, 2008). Thus, we had expected a larger difference between the development season and the whole year. Our analysis based on climatic scenarios indicates that DS Tmean will increase slightly more than annual Tmean in the future.

The number of GDDs ($t_b = 10\text{ }^{\circ}\text{C}$) increased significantly over time across all elevations, but at a substantially higher rate at lower elevations (Table 1). This can be explained by the fact that the part of the year in which daily Tmean is $>10\text{ }^{\circ}\text{C}$ is shorter at higher elevations. The expected increase in the number of GDDs is consistent with the findings of Tschurr et al. (2020), who projected an increase in the number of GDDs ($t_b = 5\text{ }^{\circ}\text{C}$) in Switzerland, especially at lower elevations.

Our results based on RCP8.5 suggest that by the end of the 21st century the development season on the Swiss Plateau could be similar, in terms of GDDs, to what is currently observed on the southern side of the Alps (Table 2). This could favour the spread of invasive species from warmer regions into the northern side of the Alps (Vittoz et al., 2013). At the same time, the development season at middle elevations (800 – 1400

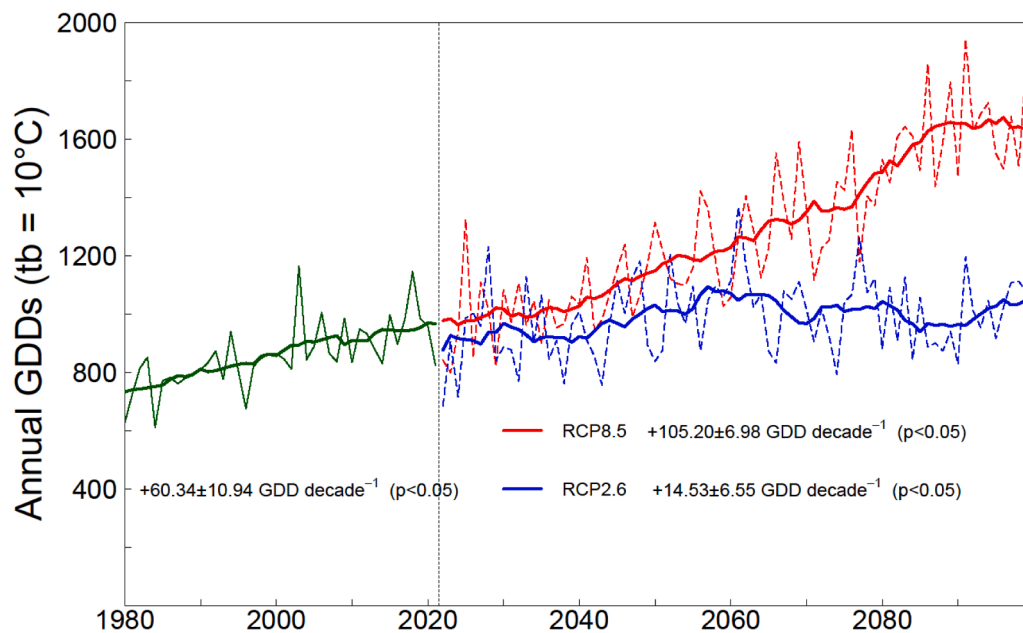


Fig. 3. Trend in the annual number of growing degree days (GDDs, for base development temperature [t_b] = $10\text{ }^{\circ}\text{C}$) per year, averaged across 67 meteorological stations during the periods 1980–2021 (thin solid lines) and 2022–2099 (dashed lines). Eleven-year moving averages are shown as thick solid lines, and slopes (\pm SE) of the linear regressions are displayed.

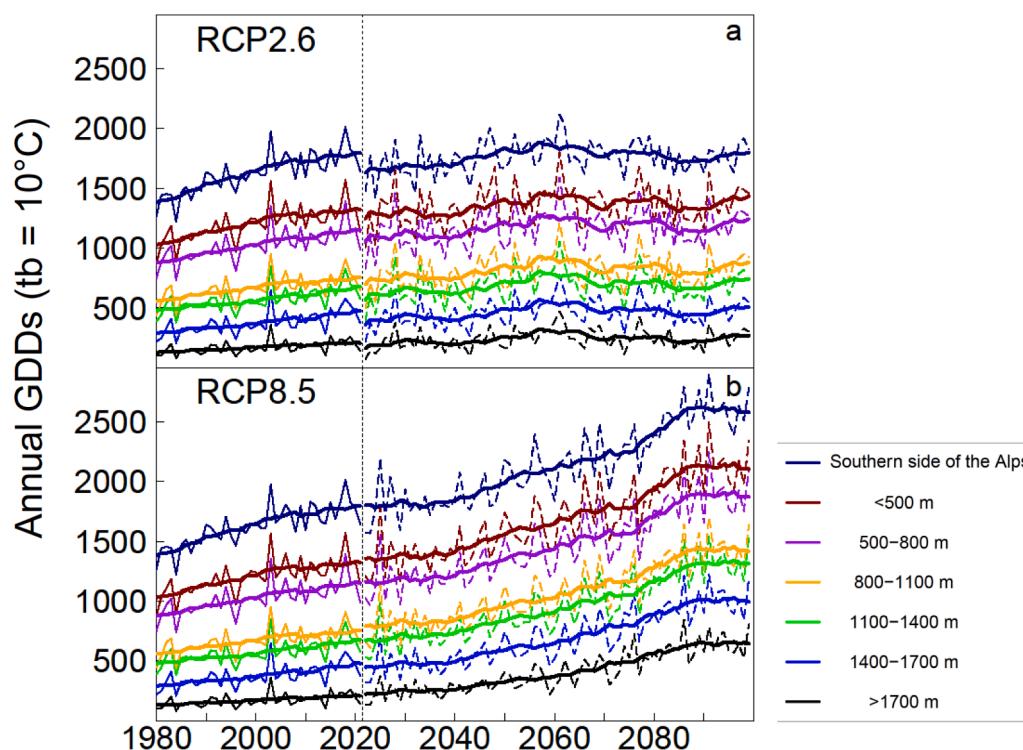


Fig. 4. Trend in the annual number of growing degree days (GDDs, for base development temperature [tb] = 10 °C) per year for meteorological stations in different elevation classes during the periods 1980–2021 (thin solid lines) and 2022–2099 (dashed lines). Eleven-year moving averages are shown as thick solid lines. Results based on (a) climatic scenario RCP2.6 and (b) RCP8.5.

Table 1

Change in the annual number of growing degree days (GDDs, for base development temperature [tb] = 10 °C) per decade during the periods 1980–2021 and 2022–2099 (under scenarios RCP2.6 and RCP8.5) for various elevation classes. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Change in GDDs (tb = 10 °C) per decade			
Elevation class (m a.s.l.)	1980–2021	2020–2099	
		RCP8.5	RCP2.6
<500, southern side of the Alps	+107.17***	+128.1***	+14.55*
<500	+77.36***	+120.6***	+16.65*
500–800	+70.66***	+114.1***	+16.73*
800–1100	+49.80***	+99.97***	+15.35*
1100–1400	+49.16***	+99.66***	+13.65*
1400–1700	+46.33***	+87.01***	+12.00*
>1700	+20.42**	+65.95***	+8.07*
All stations	+60.34***	+105.20***	+14.53*

m a.s.l.) could become similar to what is currently observed on the Swiss Plateau. Some pest species could complete a single generation at higher elevations where this is currently not possible. At lower elevations, the trends observed (above +100 GDDs per decade) suggest that the four pest species mentioned in the introduction are likely to produce at least one more generation per year by the end of the century. Their GDDs requirements range from 450 (grapevine moth) to 840 (comestock mealybug) GDDs per generation, while GDDs are expected to increase by approximately 1000 by the end of the century at lower elevations (Fig. 5b).

The results we obtain with RCP2.6 clearly suggest that this scenario underestimates the temperatures for the present period. This can be explained by the fact that the scenarios were fitted using data over the period 1981–2010, and because this scenario relies on a strong reduction of greenhouse gas emissions, which has not been occurring yet. Our results suggest that this scenario looks increasingly more unrealistic, and that it should be corrected or abandoned in the future.

Finally, our results highlight contrasts between the northern and southern sides of the Alps, and the role of the large lakes on the Swiss

Table 2

Mean number of growing degree days (GDDs, for base development temperature [tb] = 10 °C) per year, calculated for the past four decades (1980–2021) and projected for two future periods (2035–2064 and 2070–2099) based on climatic scenarios RCP8.5 and RCP2.6. Minimum and maximum values amongst the meteorological stations are indicated in brackets.

Elevation class (m a.s.l.)	1980–2021	2035–2064		2070–2099	
		RCP8.5	RCP2.6	RCP8.5	RCP2.6
<500, southern side of the Alps	1627 (1484–1732)	1974 (1799–2088)	1792 (1647–1881)	2459 (2107–2595)	1770 (1621–1859)
<500	1204 (1102–1389)	1532 (1402–1753)	1387 (1237–1526)	1985 (1826–2240)	1375 (1260–1522)
500–800	1025 (889–1236)	1327 (1134–1568)	1192 (1021–1409)	1757 (1538–2047)	1190 (1036–1384)
800–1100	667 (573–732)	936 (811–1037)	837 (701–930)	1322 (1192–1435)	828 (711–919)
1100–1400	570 (419–684)	818 (675–960)	708 (545–822)	1205 (1040–1385)	697 (538–810)
1400–1700	376 (283–568)	570 (420–863)	478 (340–753)	917 (727–1286)	472 (353–730)
>1700	171 (96–290)	313 (194–461)	252 (143–413)	581 (412–774)	242 (134–388)

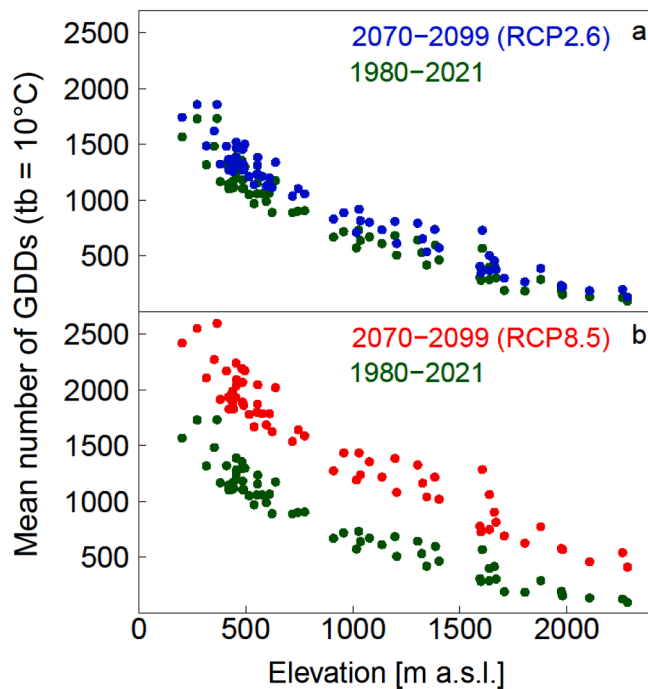


Fig. 5. Mean number of growing degree days (GDDs, for base development temperature $[t_b] = 10\text{ }^{\circ}\text{C}$) per station as a function of altitude, calculated for the past four decades (1980–2021) and projected for the end of 21st Century (2070–2099). Results based on (a) climatic scenario RCP2.6 and (b) RCP8.5.

Plateau. The use of standard meteorological stations does not allow exploration of other microclimatic contrasts, as temperatures are measured in open sites in a standardized way (WMO, 2018). For example, differences between urban and forest climates can affect species such as the box tree moth, as they exist in both ecosystem types.

4.1. Limitations of the study

While this study was mainly based on daily mean temperatures during the development season, other climatic factors have an impact on pest populations in temperate climates, especially minimum temperatures during winter (Schneider et al., 2021). During the development season, climatic factors such as precipitation could be considered, even though their impact on pest development is more difficult to assess in temperate climates (Schneider et al., 2022).

Finally, the population dynamics of pest species are complex to model. While Tmean during the development season has a major impact on voltinism, the population size of a species is also driven by various non-climatic factors, such as predators, parasitoids, and pest control activities by humans.

5. Conclusions

Our analyses show that mean Tmean averaged over the development season has been increasing slightly more than Tmean averaged over the entire year over the last 40 years in Switzerland. In this context, the number of GDDs ($t_b = 10\text{ }^{\circ}\text{C}$) has also been increasing, especially at lower elevations. The maximum increase has occurred at lower elevations on the southern side of the Alps.

By the end of the 21st century, according to scenario RCP8.5 (high greenhouse gas emissions), the number of GDDs on the northern side of the Alps, up to 800 m a.s.l., could exceed what is currently observed on the southern side of the Alps. At the same time, the number of GDDs between 800 and 1400 m a.s.l. are expected to exceed what is currently observed on the Swiss Plateau below 800 m a.s.l..

Under scenario RCP2.6 (strong reduction of greenhouse gas emissions during the next decades), the number of GDDs is predicted to increase much less, with a maximum reached already by the middle of the 21st century.

These results suggest that polyvoltine species such as the box tree moth, the grapevine moth, the codling moth and the Comstock mealybug are likely to produce additional generations during the next decades, and to reach higher elevations. The likelihood of the occurrence of additional generations largely depends on the climatic scenario, i.e. on the greenhouse gas emissions during the next decades.

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.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2023.109503](https://doi.org/10.1016/j.agrformet.2023.109503).

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