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Editors' Choice

The impacts of climate and the extreme drought in 2018 on population growth in Swedish moth species

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Abstract

1. Insects are pivotal to ecosystem diversity and functionality, yet they face increasing threats from anthropogenic climate change impacts. A growing body of studies reports the effects of changing temperature and precipitation patterns, but relatively few studies focus on the consequences for insect populations because of extreme weather events.
2. Here, we examine population growth responses to temperature, precipitation and the extreme summer drought in Sweden in 2018. For this purpose, we used longitudinal data for 54 moth species collected between 2005 and 2023 using light traps at three sites in southeastern Sweden.
3. We found a positive relationship between temperature and population growth rates across all study sites, while precipitation showed a positive relationship at two sites and no effect at the third. The results indicated a negative time-lag effect on population growth, at two of the sites, of precipitation the previous year, while there were no significant effects of temperature the previous year. Despite the extreme drought in 2018, moth populations remained resilient, with no dramatic decline in population growth between 2018 and 2019.
4. Our results contrast earlier studies reporting severe declines in population growth in response to extreme drought events. The discrepancy may reflect a combination of region-specific effects of extreme weather events and that selected species in this study predominantly consist of range-expanding and migratory species, better able to withstand adverse conditions due to a higher climatic tolerance and being habitat and food plant generalists.
5. Our findings underscore the importance of an increased knowledge of site-specific responses and effects of extreme weather events such as droughts when outlining conservation efforts.

KEYWORDS
climate change, drought impact, Lepidoptera, long-term study, population dynamics, precipitation

INTRODUCTION

Insects play a crucial role in diverse ecosystems, yet their populations are increasingly vulnerable to the escalating impacts of anthropogenic climate change (Eggleton, 2020). Changing temperature and precipitation patterns can contribute to temporal and spatial abundance fluctuations and impact the distribution of insect populations both directly, via effects of abiotic conditions on reproduction, growth and survival, and indirectly, through effects mediated via interactions with host plants, competitors, predators or parasites (Harvey et al., 2020). Understanding these impacts is complicated by life stage-specific responses (Kingsolver et al., 2011) and potential carry-over effects between generations (Post & Forchhammer, 2002).

The increasing frequency and intensity of extreme weather events, particularly droughts, poses additional threats to insect populations (Halsch et al., 2021). Moths are especially vulnerable to drought conditions through multiple mechanisms; direct physiological stress impacting reproductive performance and the viability of both adults and larvae, reduced host plant quality and disrupted phenological synchrony with food plants (Palmer et al., 2017). However, responses to drought may vary geographically due to local adaptations and habitat differences. Species in historically drier regions may show greater resilience, while populations in typically moister areas might be more sensitive to drought events (Suggitt et al., 2018; Uhl et al., 2022).

The unprecedented heatwave and drought of 2018 across Europe (Buras et al., 2020) offered a unique opportunity to investigate these effects. While severe butterfly population declines were observed following this drought (Johansson et al., 2020; Karimi, 2023), knowledge gaps persist regarding moths' responses. This distinction is important because moths, which comprise over 90% of Lepidoptera species, may respond differently due to their nocturnal activity patterns and distinct life history strategies (Anderson et al., 2023). As key ecosystem components involved in pollination and trophic interactions, moths also serve as valuable indicators of environmental change (Hill et al., 2021).

Southeast Sweden provides an ideal setting for investigating drought impacts on moths across varying local conditions. The region experiences a rain-shadow effect from the Scandinavian mountains, creating naturally drier conditions than surrounding areas. Within this region, our three study sites represent a gradient of maritime influence and habitat types: two coastal mainland locations with different degrees of agricultural intensity, and one island site with more diverse natural vegetation. These habitat differences may buffer or amplify drought effects through varying microclimate conditions and resource availability (Suggitt et al., 2018). In 2018, Sweden experienced its most severe drought since meteorological record-keeping began in 1860, with record high temperatures and low precipitation (Sjökvist et al., 2019). While we previously documented a general positive relationship between moth population growth and temperature in this region (Betzholtz et al., 2023a), site-specific responses to extreme events remain unexplored. Yet, understanding such local variations is crucial for predicting population responses to future climate extremes and developing targeted conservation strategies.

In this study, we analyse a long-term dataset (2005–2023) of 54 moth species across three sites in southeastern Sweden to investigate: (1) the effects of precipitation, temperature and year on population growth, (2) whether these responses vary across sites with different habitat characteristics and (3) the impact of the extreme 2018 summer drought on population growth. Additionally, we test for time-lag effects to assess how previous year conditions influence population dynamics. This multi-site approach allows us to evaluate whether local habitat differences modify species' responses to extreme climate events.

MATERIALS AND METHODS

Light trap design and operation

The dataset employed for this study originates from three light-trap sites located in Nedra Ålebäck (56.605853 N/16.686114 E) and Össby (56.270783 N/16.490312 E) in the province of Öland, and on the island of Utlängan (56.022731 N/15.797629 E) in the province of Blekinge (Betzholtz et al., 2023b) (Figure 1a). The traps at Nedra Ålebäck and Össby are located 800 and 400 m, respectively, from the eastern coastline of the Baltic Sea, surrounded by a landscape dominated by meadows and farmlands. Utlängan is an island with an area of 215 ha located 7 km southeast of the mainland. It is characterized by wooded and meadow habitats interspersed with semi-natural grasslands. The trap is positioned 200 m from the island's eastern coastline. At each site, we used a Ryrholm-type light-trap (Leinonen et al., 1998), equipped with a 125 W mercury vapour lamp. Each trap was constructed with a collecting chamber (45 × 45 × 60 cm) containing multiple egg-carton layers to provide shelter for captured moths. A chloroform-based killing agent was placed in large glass containers in the collection chamber, covering the evaporation taking place between emptying occasions. The lamps were automatically switched on at dawn and off at dusk using twilight sensors, and the traps included a rain-shield and funnel system to maximize catch efficiency while protecting specimens from precipitation.

The traps were operated every night, continuously between 1 May and 31 October each year from 2005 to 2023, and were emptied every second to third week. At each emptying occasion the specimens were carefully transferred to labelled containers for transport to the laboratory, killing agent was refilled and the egg cartoons were replaced. In this way, specimen quality remained suitable for reliable identification of 54 analysed moth taxa (Table S1), predominantly comprising range-expanding and migratory species, but also including species occurring locally in the study region. In the laboratory, one of the authors (PEB) identified all specimens to ensure consistency in taxonomic determination. By maintaining identical trap designs, consistent collection intervals and standardized protocols across all sites throughout the study period, we established a robust framework for comparing moth abundances and population trends among sites and across years. While our sampling design does not allow analysis of how nightly weather conditions affect activity patterns, it is instead well-suited for investigating broader climatic impacts on population dynamics.

The general climate in the study region is characterized by rather cold winters and warm, dry summers. According to SMHI, the daily mean temperature is −1 to 2°C during mid-winter and 16 to 17°C during summer. During the heatwave in the summer of 2018 the temperature was 3.5°C above average. The study region is one of the

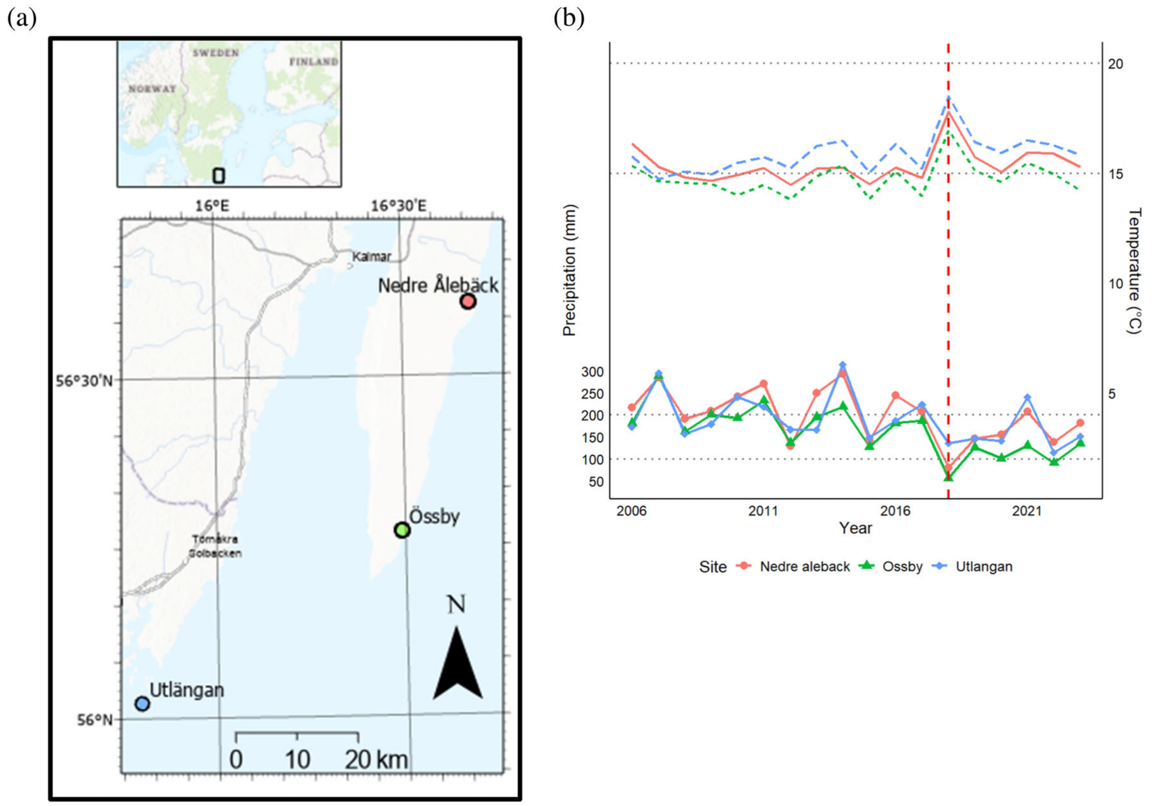

FIGURE 1 Spatial and temporal precipitation and population dynamics of the studied moth assemblages. (a) The three light-trap sites in southeast Sweden: Nedra Ålebäck, Össby and Utlängan. (b) Temporal annual precipitation and temperature trends at the three study sites from 2005 to 2023. The primary Y-axis (left) shows the total precipitation from May to August in millimetres (mm), while the secondary Y-axis (right) represents the average temperature in degree Celsius (°C). The lines represent the temporal trends for each site, with different shapes used to distinguish between them. A vertical dashed red line marks the year 2018, which is identified as a significant drought year. Horizontal dotted lines at 100 and 200 mm indicate reference points for precipitation, and lines at 15 and 20°C serve as reference points for temperature.

driest in Sweden, with a yearly mean precipitation of 450 mm (Persson, 2015). During the extreme summer drought in 2018, the total precipitation was 42 mm, compared to the 30-year average (1991–2020) of 180 mm for the summer months (May–August). This represents a 77% reduction from the long-term mean, making it the driest summer since records began in 1860 (Sjökvist et al., 2019).

Data analysis and statistics

We investigated the impact of current and previous year using total summer precipitation and average temperature from May to August on population growth in moths in each of our study sites. We gathered meteorological data from three strategically located stations within a 10-km radius of each light-trap site: Segerstad, Norra Möckleby and Ungskär (proximate to Össby, Nedra Ålebäck and Utlängan, respectively) (Andersson et al., 2021). When data was missing due to a malfunction of the meteorological station, we used data from the nearest functioning station.

To quantify species and site-specific population growth, we calculated the population growth rate (r) using the formula: $r = \log_e(\mathrm{Nt} + 1/\mathrm{Nt})$, where Nt + 1 is the population size in the current year, and Nt is the population size in the previous year (Sibly & Hone, 2002). Before calculating, we added 1 to each population size to avoid issues with zero values (Krebs, 2014). With this calculation, a positive value indicates population growth, a negative value indicates population decline and a value of zero indicates a stable population. Population growth was only calculated if a species existed in at least one of two consecutive years.

We used statistical modelling to explore climate's impact on population growth. Data analyses were conducted in R version 4.3.3 (R Core Team, 2023), including the lme4 package (1.1–35.5) (Bates et al., 2014). First, we used linear mixed-effects models (GLMM) to investigate the relationship between moth population growth rates and climatic variables at each study site. The models were fitted using the lmer function from the lme4 package. The response variable was the population growth rate. To avoid problems associated with statistical overfitting, data for the different study sites were analysed in separate models. The fixed effects included current year precipitation, current year temperature, previous year precipitation, previous year temperature, the number of individuals in the previous year and year to account for potential temporal trends (year treated as a continuous variable). Current-year weather variables were used to assess direct effects on viability of late larval stages and adult moths, while

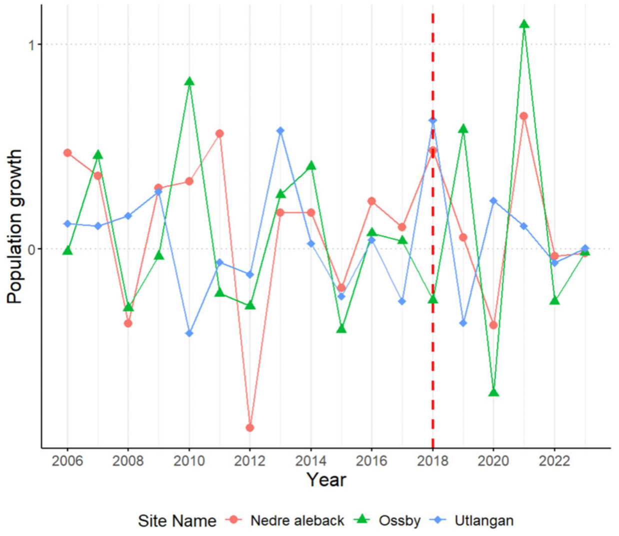

FIGURE 2 Averaged temporal trends in 54 moth species population growth rates at the three study sites (Utlängan, Nedra Ålebäck and Össby) from 2005 to 2023. The Y-axis represents the average population growth rate for each site. Positive values on the Y-axis indicate population growth (i.e., an increase in population size compared to the previous year), while negative values indicate a population decline. A value of 0 signifies no change in the population size of the prior year. Each line connects a site's annual average growth rates, with distinct point shapes differentiating the sites. The vertical dashed red line marks the year 2018, which was a significant drought year.

previous-year variables were included to capture potential impacts on viability and reproductive output of adult moths, as well as viability of eggs and larval stages, and carry-over effects. To account for species-specific responses to the predictors, we included random intercepts and slopes for the year within each species. To ensure that our models were not affected by multicollinearity among predictor variables, we performed a correlation analysis and calculated the variance inflation factor (VIF) for all predictors. The correlation analysis revealed that none of the predictor pairs had a correlation coefficient exceeding 0.5, indicating no strong linear relationships. Additionally, VIF values for all predictors were below the conventional threshold of 5, with the highest VIF observed being 1.96 for the variable year, which is well within the acceptable range (O'brien, 2007).

Secondly, to specifically evaluate the effect of the extreme drought in 2018, we constructed a GLMM to determine whether population growth rates during and after the drought years (2018 and 2019, respectively) differed significantly from those observed in other years throughout the study period. This analysis combined data from all three sites, in contrast to the site-specific analyses conducted earlier. In two separate GLMMs, we set the year variable to use 2018 and 2019 as reference categories, allowing for direct comparisons against all other years, as we expected the 2018 drought to result in significantly lower population growth in 2019. This approach was essential for detecting the drought's immediate or lagged effects on population growth. Year was treated as a categorical variable, with 2018 and 2019 each set as the reference year in separate models. In each model, year was included as a fixed effect to evaluate annual differences in population growth rates, with random intercepts for both site and species.

RESULTS

We analysed the population growth rates of 54 moth species at the three different sites. The average population growth rate was 0.08, with a minimum observed growth rate of −4.34 and a maximum of 3.93. The study regions experienced a range of climatic conditions during the study period. The average temperature varied from 13.8°C to 17.0°C, while precipitation ranged from 56.6 to 288.7 mm (Figure 1b).

Climatic factors had varying impacts on the population growth rates of moth assemblages at the three study sites (Figures 2, 3, S1, and S2, Table 1). In Utlängan, temperature in the current year emerged as a significant positive predictor of population growth (Estimate = 0.159, $p = 0.011$), while individual abundance from the previous year showed a strong negative association (Estimate = −0.004, $p < 0.001$). Although precipitation in the current year did not significantly affect population growth (Estimate = −0.001, $p = 0.409$), precipitation from the previous year was just outside the conventional level of statistical significance (Estimate = −0.122, $p = 0.051$) and had a negative slope, suggesting a potential adverse effect. At Nedra Ålebäck, both precipitation (Estimate = 0.004, $p < 0.001$) and temperature (Estimate = 0.355, $p < 0.001$) during the current year were significant positive predictors of population growth. The number of individuals from the previous year was negatively associated with population growth (Estimate = −0.001, $p = 0.009$), while the previous year's precipitation and temperature showed no significant effects. At Össby, precipitation during the current year significantly and positively impacted population growth (Estimate = 0.005, $p = 0.002$), and the temperature was also a significant positive predictor (Estimate = 0.205, $p = 0.010$). Like at Utlängan, precipitation from the previous year was nearly significant with a negative slope (Estimate = −0.003, $p = 0.052$), indicating a possible adverse impact. The number of individuals from the previous year was negatively associated with population growth (Estimate = −0.002, $p = 0.001$), while the previous year's temperature showed no significant effect.

During the extreme drought in 2018, the two study sites on Öland experienced their lowest summer precipitation levels during the study period, while the site in Blekinge was not affected to the same degree (Figure 1b). When using 2018 as the reference year, the population growth rate in 2018 was significantly higher than in other years (Table 2). Specifically, 2018 showed significantly higher growth than 2008, 2012, 2015, 2017, 2020, 2022 and 2023. For instance, population growth in 2018 was significantly higher than in 2020 (Est = −0.622, SE = 0.143, $z = 4.359$, $p < 0.001$) and in 2022 (Est = −0.477, SE = 0.141, $z = 3.373$, $p < 0.001$). Additionally, there was an almost significant difference between 2018 and the post-

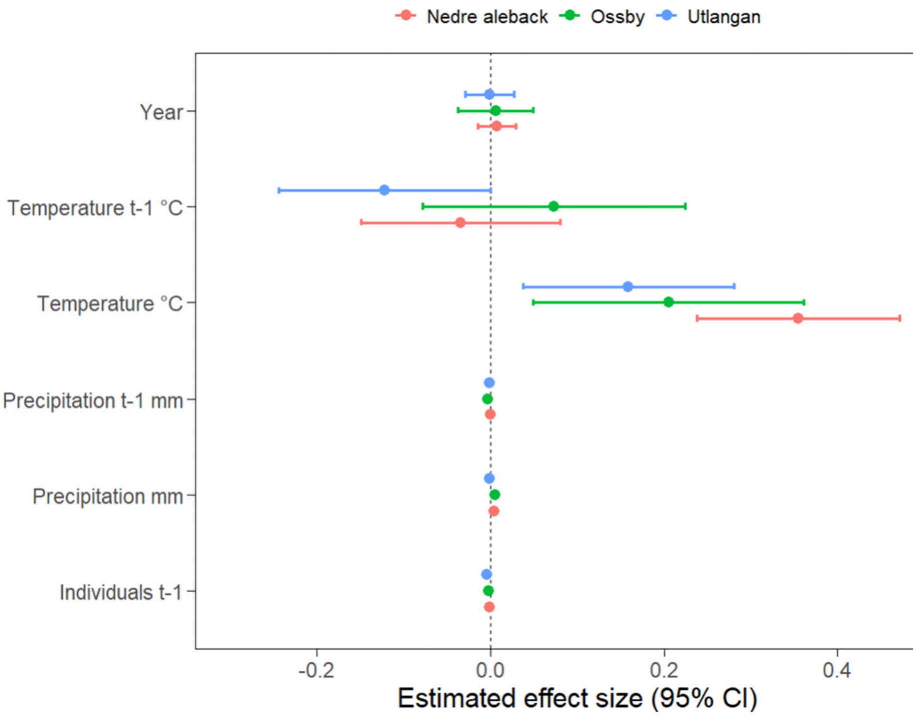

FIGURE 3 Estimated effect sizes (with 95% confidence intervals) of the predictors' temperature and precipitation and year and number of individuals in the previous year on the population growth rate of 54 moth species at the three study sites: Utlängan, Nedra Ålebäck and Össby. Positive effect sizes indicate a positive relationship between the predictor and the growth rate, while negative effect sizes indicate a negative relationship. The dotted vertical line is at $X = 0$.

drought year 2019, with a lower growth rate in 2019 (Est $= -0.282$, SE $= 0.144$, $z = -1.953$, $p = 0.051$). Conversely, when using 2019 as the reference year, the population growth rate in 2019 was not significantly different from several other years, except for a few cases where growth was lower, such as in 2012 (Est $= -0.518$, SE $= 0.161$, $z = -3.215$, $p = 0.001$), 2015 (Est $= -0.336$, SE $= 0.145$, $z = -2.321$, $p = 0.02$) and 2020 (Est $= -0.340$, SE $= 0.138$, $z = -2.464$, $p = 0.014$). Population growth in 2021, however, was significantly higher than in 2019 (Est $= 0.539$, SE $= 0.138$, $z = 3.90$, $p < 0.001$).

DISCUSSION

Our findings reveal a complex interplay between climate variables and moth population dynamics across southeastern Sweden. The consistently positive relationship between temperature and population growth rates across all study sites aligns with previous observations in the region (Betzholtz et al., 2023a) and underscores temperature's pivotal role in driving moth population dynamics (Halsch et al., 2021; Harvey et al., 2023). This temperature sensitivity likely reflects moths' ectothermic nature and ability to capitalize on warmer conditions for increased metabolic activity, reproductive output and survival (Hahn & Denlinger, 2011). That there were no significant signatures on population growth of temperature the preceding year at any of the three sites suggests that time-lag effects of between year temperature fluctuations were negligible. Regarding precipitation, we found site-specific responses, with a positive effect of precipitation on population growth at Nedra Ålebäck and Össby, contrasting with no effect at Utlängan. These site-specific differences are consistent with studies by Baguette and Mennechez (2004) and Forister et al. (2010), who report that the impact of precipitation on insect populations can vary significantly depending on local environmental conditions. Unlike for temperature, the results indicated a negative time-lag effect on population growth of precipitation the previous year at two of the sites. Such delayed effects of precipitation have been noted in other studies as well, where they can contribute to fluctuations in population dynamics through indirect mechanisms (Pelini et al., 2010). Although our traps were operated continuously, short-term weather events can influence moth flight activity and thus the number of individuals captured on any given night. Periods of rainfall, wind or lower temperatures may reduce flight activity, potentially introducing additional variability into our measures of population growth (Conrad et al., 2002; Muirhead-Thomson, 1991; Yela & Holyoak, 1997). Taken together, these findings indicate that local environmental conditions and habitat characteristics may modulate the importance of temperature and precipitation for population growth of moths (Suggitt et al., 2018).

While the positive effects of temperature that we observed may hold in relatively cool northern European regions such as southeastern Sweden, this pattern does not necessarily generalize to warmer areas. In regions with relatively cool climate, a moderate warming may still

TABLE 1 Results from linear mixed-effects models (LMMs) including fixed effects for the current year's precipitation and temperature, the previous year's precipitation and temperature, the number of individuals of the prior year (individuals) and year.

Site	Variable	Estimate	Std. error	*t*-value	*p*-value
Utlangan	(Intercept)	2.102	27.858	0.075	0.940
Utlangan	Precipitation (mm)	−0.001	0.001	−0.827	0.409
Utlangan	Temperature (°C)	0.159	0.062	2.570	0.011*
Utlangan	Precipitation $t-1$ (mm)	−0.001	0.001	−0.787	0.432
Utlangan	Temperature $t-1$ (°C)	−0.122	0.062	−1.954	0.051.
Utlangan	Individuals $t-1$	−0.004	0.001	−5.977	<0.001***
Utlangan	Year	−0.001	0.014	−0.078	0.938
Nedre aleback	(Intercept)	−20.003	22.721	−0.880	0.379
Nedre aleback	Precipitation (mm)	0.004	0.001	4.646	<0.001***
Nedre aleback	Temperature (°C)	0.355	0.060	5.956	<0.001***
Nedre aleback	Precipitation $t-1$ (mm)	0	0.001	−0.229	0.819
Nedre aleback	Temperature $t-1$ (°C)	−0.034	0.059	−0.583	0.560
Nedre aleback	Individuals $t-1$	−0.001	0	−2.616	0.009**
Nedre aleback	Year	0.007	0.011	0.640	0.523
Ossby	(Intercept)	−16.081	45.264	−0.355	0.723
Ossby	Precipitation (mm)	0.005	0.002	3.174	0.002**
Ossby	Temperature (°C)	0.205	0.080	2.576	0.010*
Ossby	Precipitation $t-1$ (mm)	−0.003	0.002	−1.947	0.052
Ossby	Temperature $t-1$ (°C)	0.073	0.077	0.948	0.344
Ossby	Individuals $t-1$	−0.002	0.001	−3.452	0.001***
Ossby	Year	0.006	0.022	0.265	0.791

Note: Each row presents each predictor's estimated effect size, standard error, *t*-value and *p*-value. Significant effects are denoted with asterisks: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. The models include random intercepts and random slopes for year within species to account for species-specific trends.

enhance metabolic rates and prolong activity seasons. However, this apparent benefit may not persist under sustained or more intense warming. Evidence from other European regions, including Germany and Italy, suggests that excessively high summer temperatures can have detrimental effects on moth populations once species-specific thermal thresholds are surpassed (Habel et al., 2024; Uhl et al., 2022). Moreover, declines in other insect groups at higher latitudes underscore that warming is not universally advantageous. Bumblebees, for instance, have experienced significant range contractions and population declines under climate change, even in cooler northern regions, as warming conditions exceed their historical climatic niches (Kerr et al., 2015; Soroye et al., 2020). These patterns highlight that initial positive responses to moderate warming may eventually give way to negative impacts if temperatures continue to rise beyond physiological tolerances. Conservation strategies should acknowledge these varying responses, focusing on short-term gains from mild warming and the long-term challenges posed by the overall warming, including increasingly frequent and severe heatwaves.

Despite the extreme drought in 2018, moth populations remained resilient, with no dramatic decline in population growth between 2018 and 2019. This unexpected resilience in moth populations contrasts sharply with previous studies documenting severe negative impacts from droughts on insect and butterfly populations (Harris et al., 2019; Johansson et al., 2022; van Bergen et al., 2020; Wilson & Fox, 2021). This resilience is particularly noteworthy when compared to other insect groups that experienced significant declines due to climate-driven mismatches with their food resources (Harvey et al., 2023; Leybourne et al., 2021; Weiss et al., 2024). While Orthoptera and Coleoptera often show sharp declines during droughts, especially among specialized or less mobile species (Joern & Laws, 2013; Leather, 2021), our analysis found no strong deviations in moth population growth rates during 2018 or 2019. This may be attributed to the temperate climate of Scandinavia, which potentially confers a degree of protection not seen in Mediterranean or tropical ecosystems where drought effects are more pronounced (Schoonhoven et al., 2005; Sintayehu, 2018). Additionally, the nocturnal activity patterns of moths might shield them from some of the more immediate and intense effects of daytime heat and desiccation during droughts (Scoble, 1988). Another explanation for the discrepancy may be our study's predominance of range-expanding and migratory species, which likely possess broader physiological tolerances and adaptive capacities (Parmesan, 2006). Their generalist nature might allow those species to exploit a variety of host plants and microhabitats even under unfavourable conditions (Ashe-Jepson et al., 2023; Franzén & Nilsson, 2012; Hunter et al., 2014; Jonason et al., 2014; Kindvall, 1995). A high mobility in these taxa may also weaken the link

TABLE 2 Comparison of population growth rate in the drought year 2018 (a) and the post-drought year 2019 (b) to all other years using GLMM analysis to indicate estimated coefficients, *z*-values and *p*-values.

	A				B			
Year	**Est**	**SE**	***z*-value**	***p*-value**	**Est**	**SE**	***z*-value**	***p*-value**
Intercept	0.354	0.105	3.356	0.001.	0.071	0.099	0.724	0.469
2006	−0.132	0.201	−0.657	0.511	0.150	0.198	0.760	0.448
2007	−0.063	0.175	−0.358	0.720	0.219	0.171	1.282	0.200
2008	−0.475	0.177	−2.680	0.007	−0.193	0.173	−1.112	0.266
2009	−0.147	0.176	−0.833	0.405	0.135	0.172	0.786	0.432
2010	−0.130	0.168	−0.778	0.437	0.152	0.164	0.927	0.354
2011	−0.243	0.164	−1.486	0.137	0.039	0.160	0.242	0.809
2012	−0.800	0.165	−4.842	<0.001	−0.518	0.161	−3.215	0.001
2013	−0.020	0.164	−0.122	0.903	0.262	0.160	1.642	0.101
2014	−0.160	0.151	−1.054	0.292	0.122	0.147	0.833	0.405
2015	−0.618	0.149	−4.139	<0.001	−0.336	0.145	−2.321	0.020
2016	−0.234	0.155	−1.512	0.131	0.048	0.150	0.320	0.749
2017	−0.396	0.152	−2.599	0.009	−0.114	0.148	−0.770	0.441
2018					0.282	0.144	1.953	0.051
2019	−0.282	0.144	−1.953	0.051				
2020	−0.622	0.143	−4.359	<0.001	−0.340	0.138	−2.464	0.014
2021	0.257	0.143	1.800	0.072	0.539	0.138	3.904	<0.001
2022	−0.477	0.141	−3.373	0.001	−0.194	0.136	−1.425	0.154
2023	−0.367	0.142	−2.590	0.010	−0.084	0.137	−0.618	0.537

between the local climate in the previous year and subsequent population growth. If a substantial portion of the individuals captured in a given year did not develop locally but instead migrated from regions with different weather conditions, the resilience we detected may partly stem from the demographic buffering provided by regular immigration from source areas less affected by local stressors. This dynamic underscores the importance of considering spatial population processes and species mobility when interpreting temporal patterns in population growth, and will be crucial for predicting their responses to environmental variability and extreme weather events (Ashe-Jepson et al., 2023; Hu et al., 2021; Lavergne et al., 2010). Therefore, it would be interesting to examine if responses in population growth would be the same when including all occurring moth species in a region, and not a dataset dominated by range-expanding and migratory species, because this understanding is crucial when developing conservation strategies tailored to different insect taxa's specific needs and vulnerabilities.

CONCLUSIONS

Our study reveals a complex interplay between temperature and precipitation on population dynamics in southeastern Sweden, with pronounced site-specific responses. We also found an unexpected resilience in moth populations from the extreme summer drought of 2018. Together, these findings suggest that abundance fluctuations in moth communities are shaped by local habitat characteristics and regional climate patterns. Our findings highlight the potential for specific areas to serve as climatic refugia, emphasizing the critical need for spatially explicit conservation strategies (Hannah & Midgley, 2023). The observed resilience may be underpinned by rapid evolutionary adaptation (Martin et al., 2023), phenotypic plasticity (Charmantier et al., 2008) or a combination of broader dietary ranges, higher mobility and greater adaptability among range-expanding moth species (Hill et al., 2021). As climate change intensifies, location-dependent responses will be crucial in predicting future biodiversity patterns and informing adaptive management strategies.

AUTHOR CONTRIBUTIONS

Per-Eric Betzholtz: Conceptualization; investigation; methodology; data curation; writing – review and editing; writing – original draft. **Anders Forsman:** Writing – review and editing; methodology. **Markus Franzén:** Data curation; software; methodology; writing – original draft; writing – review and editing; formal analysis.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

We have submitted our data, code and metadata documentation to Dryad: http://datadryad.org/stash/share/ZUV-PxRjDcPcDqRAxmxQ7JZm1_bJcCyGi9vwaBJbJ_8.

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SUPPORTING INFORMATION

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

Table S1. Species included in the study ($n = 54$) ordered alphabetically.

Figure S1. Raw data plot between precipitation (mm) and population growth rate for 54 moth species.

Figure S2. Temporal trends in population growth of 54 moth species at each study site.

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