nature climate change

Article

https://doi.org/10.1038/s41558-025-02248-7

Extreme weather events have strong but different impacts on plant and insect phenology

Received: 15 January 2024

Accepted: 13 January 2025

Published online: 21 February 2025

Check for updates

Daijiang Li [1,2], Michael Belitz [3], Lindsay Campbell [4,5] & Robert Guralnick [3]

The ability to explain and predict phenology across space, time and taxa has largely relied on annual average and seasonal climatic variables, ignoring the potential role of extreme weather events (EWEs) in regulating phenology. Yet, EWEs, which are predicted to increase in their severity and frequency with climate change, are also probably strong proximal phenology cues. Here we leveraged expansive community science resources to determine how EWEs affect plant flowering and insect flight beginning, termination and duration for 581 angiosperm species and 172 Lepidoptera across the contiguous United States. Our results provide evidence that plant and insect phenology is highly responsive to EWEs after accounting for seasonal and annual average climatic variables. The impact of EWEs on phenology varies depending on climatic context, and plant and insect responsiveness, while often similar, can be in the opposite directions. This suggests that EWEs may be key drivers of multitrophic phenological mismatches.

Global climate change is happening in the form of gradual shifts in average climatic conditions as well as increasing frequency and magnitude of extreme weather events (EWEs). While EWE definitions vary[1], narrower delimitations focus on climatological events where the value of a weather or climate variable exceeds a threshold in the upper or lower range of observed values over a given time period[2,3]. Examples of EWEs include heat waves, cold snaps, heavy rainfall and droughts[4–8]. Despite both forms of climate change dramatically affecting biological systems and exerting a heavy toll on society, most research focuses on impacts of gradual shifts in average climatic conditions[5]. Our understanding of EWEs on species and ecosystems is less well studied, especially at broader extents and across taxonomic groups[9–11].

Phenology—the timing of recurring seasonal activities of animals and plants—is maybe the most amenable process for tracking species and ecosystem response to climate change[12,13] as phenology often shows high sensitivity to environmental conditions[13,14]. Phenological shifts of species can have large consequences on the population dynamics of interacting species, biodiversity and ecosystem functioning[15,16]. As a result, a significant body of research has focused on phenological sensitivity in the face of climate change and its consequences across trophic levels[17]. Most change-oriented studies have focused on annual, seasonal or heat accumulation (for example, annual average temperature and growing degree day) metrics for understanding phenological sensitivity and change[13,18,19]. However, the major physiological challenges climate change poses are directly related to proximal stressors such as EWEs and how organisms make allocation and timing decisions in the face of those stressors[20]. For example, if larval stages of insects are too responsive to early spring heat waves, they may be more susceptible to mortality when temperatures return to normal or during cold snaps[21]. Further, if insects and plants have differential responses to extreme events, these could exacerbate cases of phenological mismatch where herbivores or pollinators mistime the availability of

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA. [2]Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA. [3]Florida Museum of Natural History, University of Florida, Gainesville, FL, USA. [4]Florida Medical Entomology Laboratory, University of Florida, Vero Beach, FL, USA. [5]Department of Entomology and Nematology, University of Florida, Gainesville, FL, USA. e-mail: daijianglee@gmail.com

https://doi.org/10.1038/s41558-025-02248-7

key resources, which has been shown to have direct demographic consequences in higher trophic levels[22]. In temperate regions, both insects and plants generally exhibit similar directional responses to annual climate variables, although the magnitude of these effects often varies across species and trophic levels[23]. Phenological responses of insects and plants to EWEs could also align, but this aspect remains underexplored.

Recent work supports the importance of phenological sensitivity of species to EWEs. For example, Patterson et al.[24] found that EWEs induced earlier larvae hatching of the endangered Karner blue butterfly, causing phenological mismatch between the butterfly and its lupine host plant, leading to local extinction of the butterfly. Others[25] found that the number of extremely hot and cold days had larger impacts on moth and butterfly flight periods than average climatic variables using natural history collections of over a hundred species. Another study[9] found that severe drought and heavy rainfall affected the flower phenology of ten plant species at the same magnitude as one decade of gradual increase of average temperature in Europe. Also, Zhang et al.[26] found that the flowering times of 12 plants were affected by EWEs, with extreme precipitation being more effective in altering flowering dates than just seasonal temperature. Such studies, however, are still rare, remain narrow in terms of taxonomic and spatial scales, and rarely investigate compounding EWEs. The result is a critical knowledge gap about ecological impacts of EWEs across organisms, populations and ecosystems under current and future climate change[1].

Here we used community science data from iNaturalist to examine the importance of EWEs as acute and proximal stressors that determine how hundreds of Angiosperm plants ('plants' hereafter) and Lepidoptera ('insects' hereafter) species respond phenologically across the contiguous United States between 2016 and 2022 (Fig. 1). In particular, we focus on timing of plant flowering and adult insect flight, because plants interact with adult moths and butterflies, in part, for pollination, and thus our study can inform on the potential for mismatches. We use these data resources to test the following key predictions. (1) EWEs are important drivers of phenology given their roles as proximal phenological cues, especially impacting offset and duration; and that plant flowering and insect flight timing have similar responses to these events given both have been sculpted by environmental forces in the same regions over long time periods. (2) EWEs have strong interactions with average or seasonal climatic variables and with other EWEs; and that these interactions affect plants and insects similarly.

Importance of EWEs on phenology

When linking predictors to phenology of plants and insects in linear mixed models (LMMs), including EWEs (daily temperature >2 s.d. from the mean daily value and absolute value of daily rainfall anomaly index >2 calculated over a 22 year time period) with average or seasonal climatic variables largely improved model performance when compared with models that included average or seasonal variables alone (Table 1). These results show that the effects of EWEs strongly impact phenological responses of both plants and insects. As expected, average temperature had the strongest effects on the onset (beginning), offset (ending) and duration of plant flowering and insect flight period (Fig. 2 and Supplementary Table 1). EWEs, however, had comparable effect sizes on phenology to other commonly studied climatic variables such as precipitation, temperature seasonality and precipitation seasonality (Fig. 2 and Supplementary Table 1).

The response of plants and insects to some annual average climate variables were different (for example, offset dates in response to average temperature; Fig. 2 and Supplementary Fig. 1). More often, plants and insects showed consistent responses to EWEs (Fig. 2, Supplementary Fig. 2 and Supplementary Table 1). Specifically, an increasing number of extreme warm days advanced onset, delayed offset and extended duration for both plants and insects (Fig. 2 and Supplementary Fig. 2). An increasing number of extreme cold days advanced

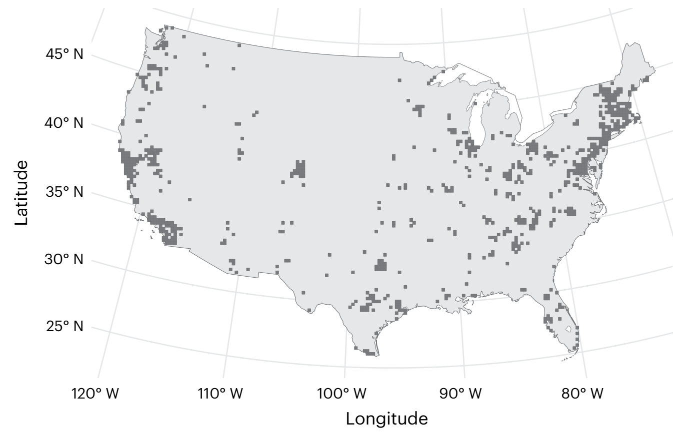


Fig. 1 | Map of grid cells (25 × 25 km²) with both plant and Lepidoptera data used in the final analyses. The final dataset included 581 plant species and 172 Lepidoptera species.

the onset and extended the flight period for insects[25] while having no impact on flowering phenology of plants after accounting for other variables (Supplementary Fig. 1). Interestingly, an increasing number of extreme wet and extreme dry days both delayed onset and offset and extended duration for plants and insects, with the responses of insects being generally stronger than in plants (Supplementary Fig. 2 and Supplementary Table 1).

Interactive effects of EWEs on phenology

There is strong evidence that extreme weather interacts with climatic variables to affect the phenology of plants and insects (Table 1). The Akaike information criterion (AIC) of the model further dropped significantly (>170) for onset, offset and duration when including interactions between extreme weather and annual average climatic variables in the models described above (Table 1). Furthermore, some interactions between extreme weather and climatic variables vary between plants and insects (see below for examples; Supplementary Table 2).

For onset, significant interactions were documented between extreme cold and average temperature, between extreme wet and total precipitation, between extreme dry and total precipitation, between extreme warm and extreme dry (that is, hot and dry) and between extreme warm and average temperature (Fig. 3 and Supplementary Table 2). The first four interactions were substantially different between plants and insects, with the interaction between extreme warm and average temperature being consistent between plants and insects (Fig. 3a). As noted above, extreme cold caused earlier flight onset for insects, but climate context matters, and the impact is especially strong in warm areas (Fig. 3b). However, extreme cold did not have a large effect on plant flowering onset (Fig. 3b and Supplementary Fig. 2). The impact of extreme wet delaying insect flight onset was stronger in dry areas (Fig. 3c). Extreme dry weather further delayed insect flight onset in dry areas but slightly advanced insect flight onset in wet areas; this interaction was not significant for plants (Fig. 3d). Extreme warm weather advanced onset in general for both plants and insects, but this impact was stronger for plants when combined with extreme dry conditions and weaker for insects (Fig. 3e). Early- and late-season species may show differential responses to EWEs. When only early species were included, significant three-way interactions between EWEs, climatic variables and taxon still exist, although some interactive effects changed (Extended Data Fig. 1). For example, extreme cold now delayed insect onset in warm areas (Extended Data Fig. 1b); the interactive effects between extreme wet and precipitation as well as between extreme warm and extreme dry were no longer different between plants and insects (Extended Data Fig. 1c,e). Overall, models with only early species also provided strong

Table 1 | Models that included extreme weather events were selected as the top model over those with only annual climate variables

Phenology	Model	AIC	BIC	ΔAIC	ΔBIC	Model weight
Onset	Climatic variables×Taxon	156,321	156,468	849	702	0
	Climatic variables×Taxon+Extreme weather×Taxon	155,974	156,183	502	417	0
	Climatic variables×Extreme weather×Taxon	155,472	155,766	0	0	1
Offset	Climatic variables×Taxon	154,185	154,332	725	617	0
	Climatic variables×Taxon+Extreme weather×Taxon	153,771	153,980	311	265	0
	Climatic variables×Extreme weather×Taxon	153,460	153,715	0	0	1
Duration	Climatic variables×Taxon	18,830	18,977	333	209	0
	Climatic variables×Taxon+Extreme weather×Taxon	18,669	18,878	172	110	0
	Climatic variables×Extreme weather×Taxon	18,497	18,768	0	0	1

Models with interactions (×) between average climatic variables and extreme weather events had the lowest AIC and BIC for all phenophases. Climatic variables include annual average temperature, annual total precipitation, temperature seasonality and precipitation seasonality. Extreme weather events include extreme warm, extreme cold, extreme wet and extreme dry. Taxon includes plant and insect.

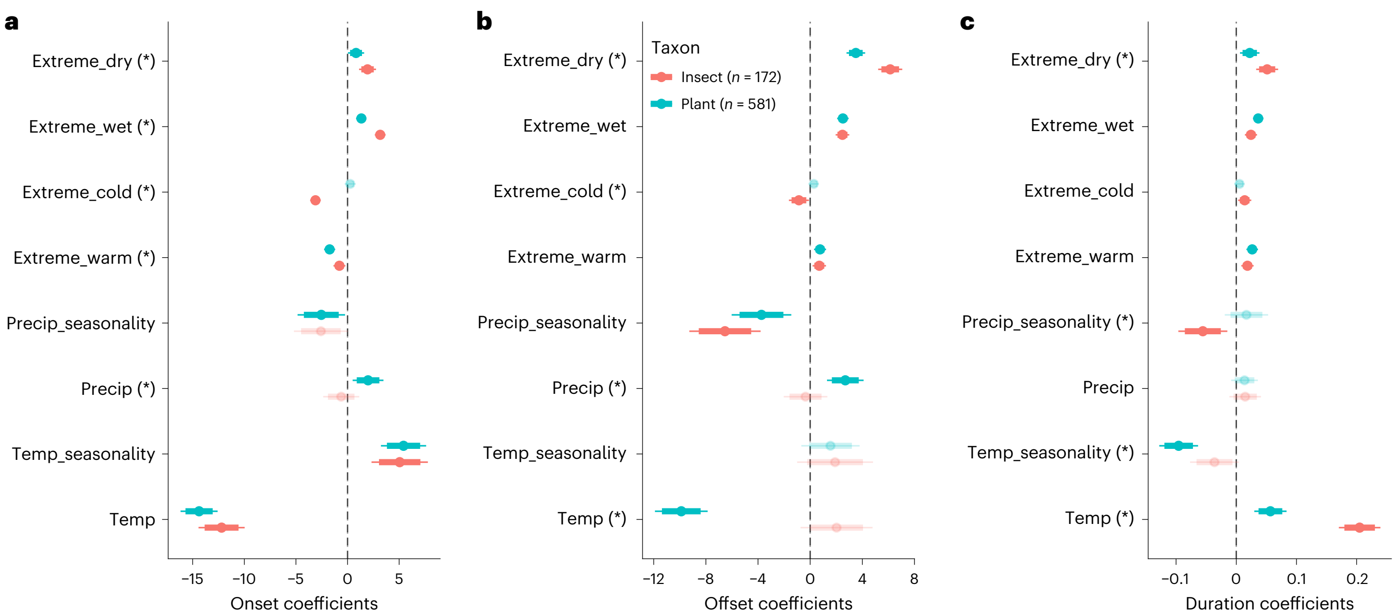


Fig. 2 | Estimated impacts of annual climatic variables and EWEs on phenology for plants and insects. a–**c**, The points represent estimated coefficients while the horizontal lines represent their confidence intervals (CI; 95% as thin lines and 85% as thick lines) of the onset (**a**), offset (**b**) and duration (**c**) of phenology for models with annual climatic variables interacting with taxon (plant and insect) and extreme weather events interacting with taxon. Asterisks indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects (that is, strong interaction between environmental variable and taxon). The lighter, transparent colours indicate that the 95% CI of a parameter includes zero (the dashed vertical line). The 85% CI is reported as it is consistent with how terms are selected under the AIC-based model selection criteria. Precip, precipitation; temp, temperature.

evidence that EWEs interacted with climatic variables and other EWEs, affecting onset of plants and insects.

For offset, two interactions had significant coefficient estimates and these interactions were consistent between plants and insects (Fig. 4a,d,e and Supplementary Table 2). Extreme warm in general delayed offset but the effect was stronger with more extreme wet days (Fig. 4d). Extreme wet also delayed offset and the effect was stronger in dry areas (Fig. 4e). The interactive effects of extreme cold and average temperature, as well as extreme warm and extreme dry, were different between plants and insects (Fig. 4b,c). Focusing on only late flowering or flying species for offset, most patterns were unchanged although some interactions were no longer significant (Extended Data Fig. 2). For example, extreme warm and extreme dry still have different interactive effects on plants and insects for this submodel (Extended Data Fig. 1c). Again, models with only late species also suggested that EWEs interacted with other variables, impacting offset of plants and insects.

For duration, extreme weather in general extended duration and again interacted with climatic variables for both plants and insects (Fig. 5 and Supplementary Table 2). Extreme warm extended duration for both plants and insects in similar ways, especially in warm areas (Fig. 5b). Extreme cold extended insect flight duration in warm areas and shortened it in cold areas (Fig. 5c); this interaction was not significant for plants. Extreme wet interacted with precipitation for plants but not insects (Fig. 5d), extending plant flowering duration in general, and this effect was stronger in dry areas. Extreme dry extended plant flowering duration in dry areas but shortened the duration slightly in wet areas (Fig. 5e); this interaction, however, was not significant for insects. When limiting to a subset of plant species that have known pollination relationships with Lepidoptera, model results were largely similar with results based on all species (Fig. 3 versus Extended Data Fig. 3; Fig. 4 versus Extended Data Fig. 4; and Fig. 5 versus Extended Data Fig. 5), providing compelling evidence to support the hypothesis

https://doi.org/10.1038/s41558-025-02248-7

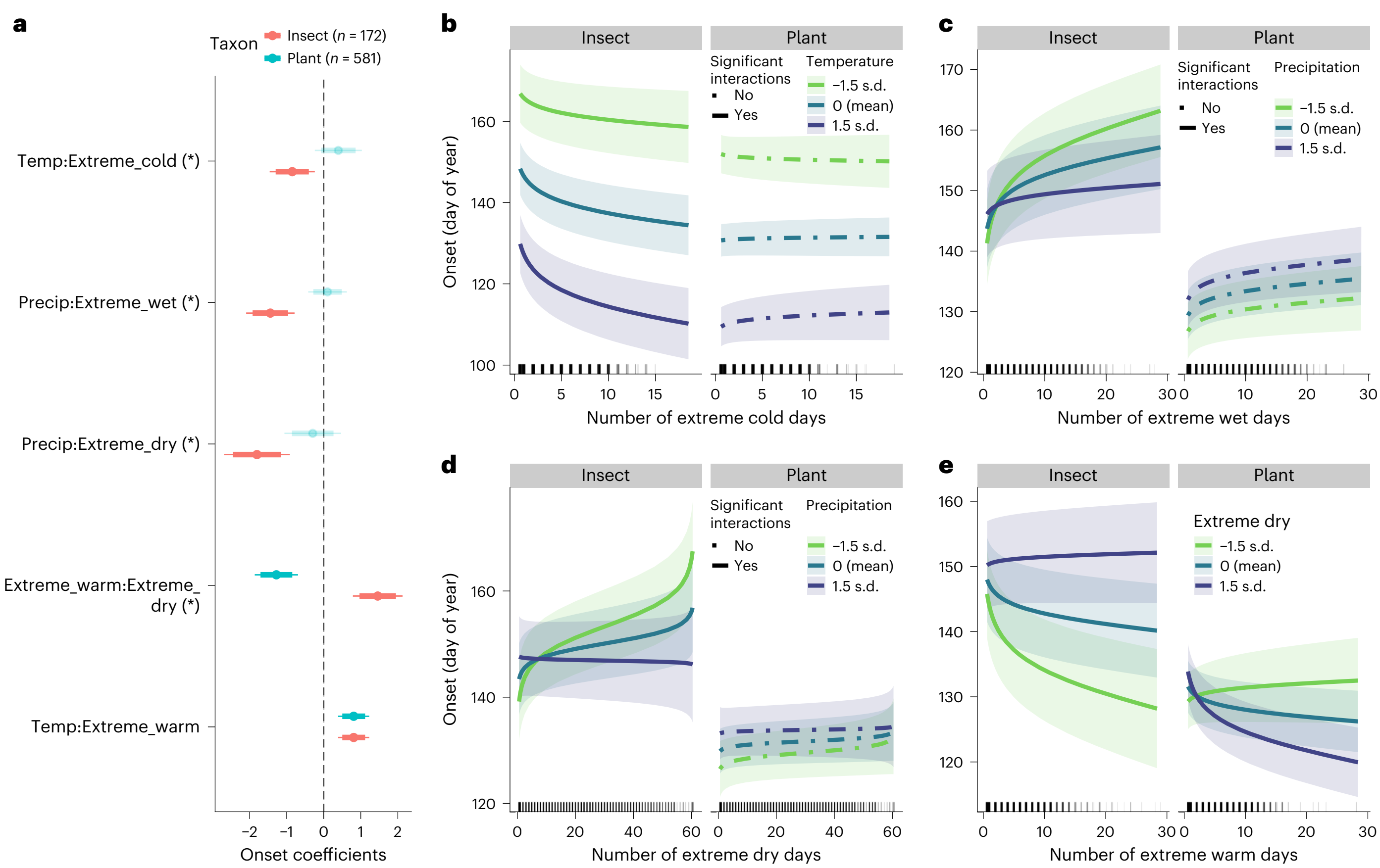


Fig. 3 | EWEs interacted with annual climatic variables and other EWEs to affect the onset (day of year) of plant flowering and flying period of insects. **a**, Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) CIs of all the significant interactions between extreme weather events and other variables. Asterisks indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter, transparent colours indicate that the 95% CI of the parameter includes zero (the dashed vertical line). **b**–**e**, All interactions among extreme weather events (extreme cold days (**b**), wet days (**c**), dry days (**d**) and warm days (**e**)), climatic variables and taxon that were significantly different between plants and insects. Dashed lines in **b**–**e** indicate that the interaction was not significant for plants. The bands around each fitted line represent the 95% CI. The *x* axes represent the number of extreme weather days in the 60 day time period before onset (jittered rugs).

that EWEs interact with climatic variables and other EWEs in affecting plant and insect phenology.

Discussion

Current macrophenological studies rarely consider EWEs and their impact on phenology. Here we have simultaneously examined impacts of multiple types of EWEs on both plant and insect phenology in the same region and time period. Our results provide overwhelming evidence that EWEs and the climate context in which they occur are crucial to understanding realized phenological response in both plants and insects.

The overall importance of extreme weather events

Our work clearly demonstrates that EWEs alone have a strong impact for plant and insect onset, offset and duration and that including these predictors leads to improved model fits. Unsurprisingly, extreme warm drove earlier onset, later offset and longer durations for both plants and insects, although plants had slightly stronger responsiveness. For onset, extreme warming may initiate and speed development, resulting in earlier onset in both groups[27,28]. Experimental and empirical observations have also shown extended flowering duration under warming generally[19,29] and this may extend to extreme warm conditions. Although extreme heat can cause faster metabolic rates in individuals[30] and shorter flowering duration, if not fatal, it also can help increase photosynthesis and thus energy to allocate towards reproductive events affording longer duration[31]. For insects, extreme warmth may temporarily limit flight activity and energy expenditures, resulting in maintaining activity longer when conditions improve and leading to later offsets and extended durations. Limited insect flight activity under extreme warm may also lead to extended plant flowering duration to assure eventual pollination when pollinators are scarce[32]. Warming, including extreme warmth, may extend the potential window for plants to grow and flower, leading to prolonged flowering duration.

To our surprise, extreme cold was not an important driver of plant flowering phenology. We anticipated that extreme cold would delay onset timing and potentially offset for plants. Lack of sensitivity may reflect other factors not considered here, including photoperiod or heat accumulation, but could also be an indicator of belowground overwintering providing protection from extreme cold for multiple plant species examined here[33]. In stark contrast, extreme cold was always important for insects, leading to much earlier onsets, marginally earlier offsets and overall longer durations. Earlier onset was unexpected; however, extreme temperatures before onset have shown sometimes paradoxical outcomes. Recent work showed that sepsid flies exposed to non-lethal extreme cold accelerated development once temperatures warmed[34,35], which could result in earlier flight onset in the natural environment, while warmer winter temperatures actually led to later onset for three out of five butterfly species in the United Kingdom[36], which was attributed to chilling requirements needed to terminate diapause. For offsets, extreme cold in late summer or early autumn may

https://doi.org/10.1038/s41558-025-02248-7

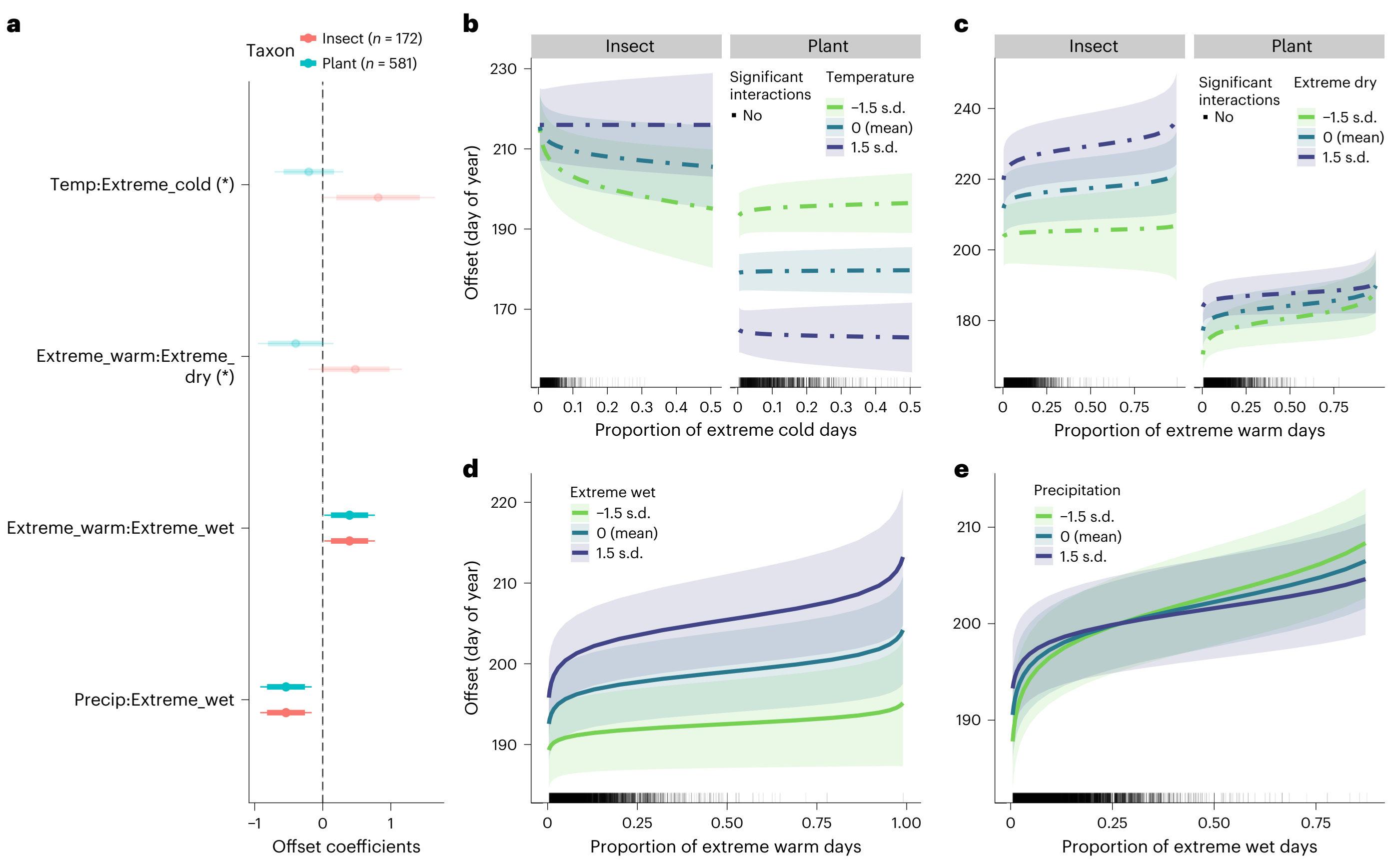


Fig. 4 | EWEs interacted with annual climatic variables and other EWEs to affect the offset (day of year) of plant flowering and flying period of insects. **a**, Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) CIs of all the significant interactions between extreme weather events and other variables. Asterisks indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter, transparent colours indicate that the 95% CI of a parameter includes zero (the dashed vertical line). **b**–**e**, All interactions among extreme weather events (extreme cold days (**b**) and warm and dry days (**c**), warm and wet days (**d**) and wet days (**e**)) climatic variables, and taxon that were significantly different between plants and insects. Dashed lines in **b** and **c** indicate that the interaction was not significant. In **d** and **e**, plants and insects share the same interaction pattern. The bands around each fitted line represent the 95% CI. The *x* axes represent the proportion of extreme weather days between onset dates and offset dates (rugs).

impact physiological function contributing to early winter dormancy of insects, which is initiated by reduced temperatures and photoperiod for many species[37]. Overall, these results contrast with our recent work demonstrating that extreme cold drives later offsets for Lepidoptera, especially for multivoltine species, in the eastern United States[25]. Here we have expanded our extent to the entire continental United States, which may contribute to this outcome and, as we demonstrate below, climate context in which EWEs occur is important to understanding phenological response.

The impact of extreme wet and dry is stronger than extreme warm and cold, and both extreme wet and dry lead to later onset and offset for insects and plants. However, insects show more phenological sensitivity than plants, probably driven by key requirements of larval insects to complete their life cycles and challenges, especially in water-stressed regions[38]. Offset is more impacted than onset for both groups and later offsets drive longer flowering and flight durations. Extreme dry conditions, in particular, are an especially strong driver of later insect offset. These results are counter to work by Forister et al.[39] who examined flight dynamics of lowland and higher elevation butterflies during a millennial-scale drought and found earlier onset and offset dynamics. However, similar to our results, previous studies found that both drought[9,40–42] and increased spring precipitation[43] delayed plant flowering phenology, which may be due to redistribution of energy to reproduction when under stress so that offspring can germinate when environmental conditions improve. For offset, extreme wet or dry conditions may act to limit insect foraging and pollination, ultimately leading to both delayed insect flight and plant flowering termination[9].

The importance of conditional effects on EWEs

A key finding from this work is that the context under which EWEs occur is a critical component to understanding how EWEs will impact realized phenological response across different geographic areas. In particular, our results show strong context-specific responses, demonstrating how EWEs interact with average or seasonal climate conditions or with other EWEs to impact plant and insect phenology. The direction and magnitude of response to an EWE can differ completely between plants and insects, depending on context. Here we focus on three key contextual results rather than decomposing all results individually.

The first result is that plant and insect onset dramatically differ in how they respond to extreme warm and dry conditions. We find strong interactions for both groups but in different directions. Extreme warm and dry conditions together lead to marginally later onset in Lepidoptera but earlier onset in plants. Extreme dry conditions in already arid conditions strongly delays adult flight onset in insects but not for plant flowering onset. For plants, this result is similar to what Crimmins et al.[44] found in an arid environment and probably reflects a survival strategy of plants to ensure complete reproductive phases under dry conditions. By contrast, it may be highly adaptive for insects to delay larval and pupal stages, and thus adult flight onset, because of their vulnerability to extreme precipitation events in dry conditions during those life stages[45].

https://doi.org/10.1038/s41558-025-02248-7

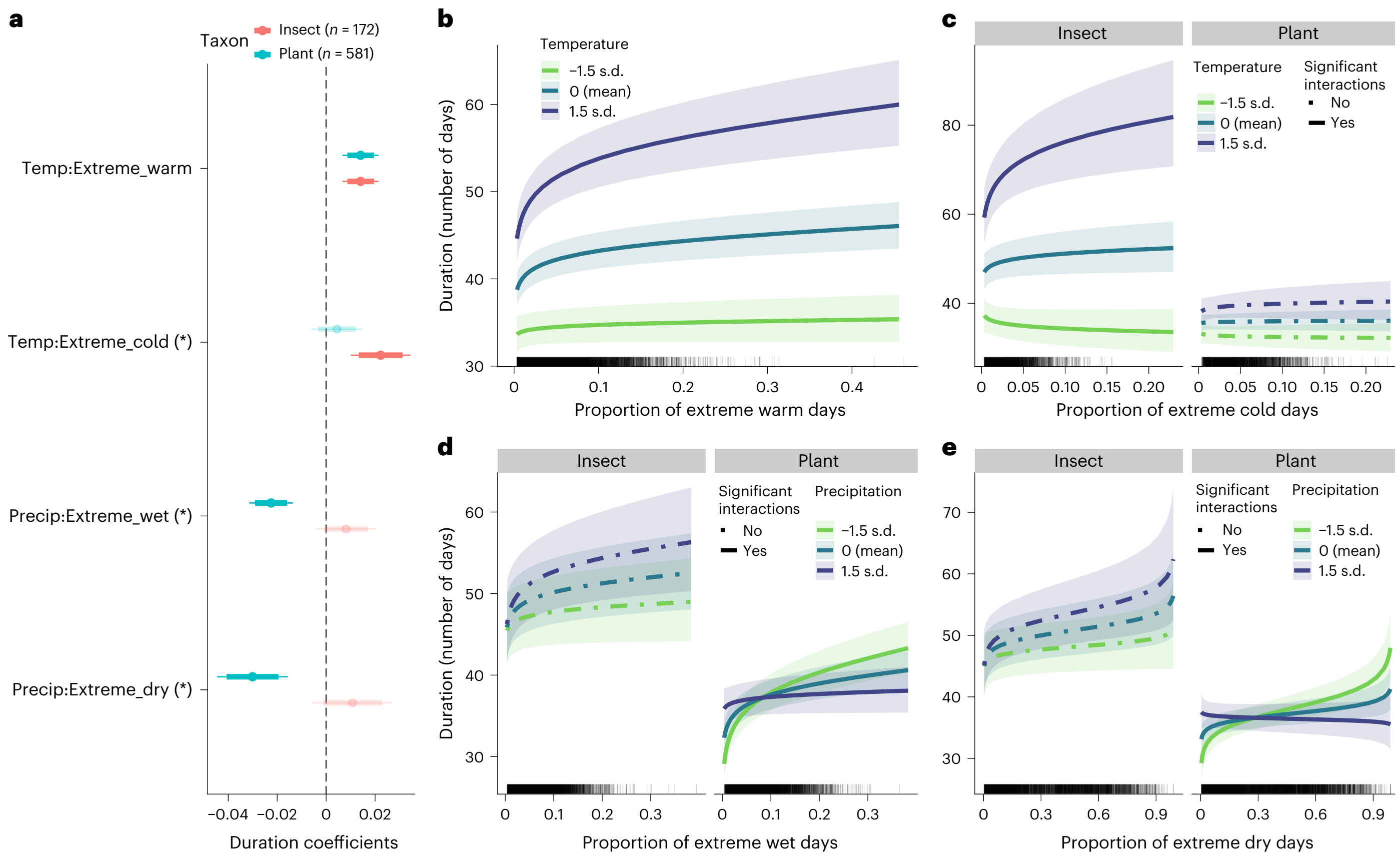


Fig. 5 | EWEs interacted with annual climatic variables and other EWEs to affect the duration (log number of days) of plant flowering and flying period of insects. a, Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) CIs of all the significant interactions between extreme weather events and other variables. Asterisks indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter, transparent colours (transparency) indicate that the 95% CI of a parameter includes zero (the dashed vertical line). **b**–**e**, All interactions with extreme weather events retained in the final model. Dashed lines in **c**–**e** indicate that the interaction was not significant. The bands around each fitted line represent the 95% CI. The *x* axes represent the proportion of extreme weather days from 60 days before onset dates to offset dates (rugs).

The second key result is that, in contrast to onset results, we find more consistent and somewhat weaker plant and insect offset responses to EWEs. Offset is later with more extreme warm or wet events and extreme wet delays offset the greatest under arid conditions. We have argued above that EWEs may force both plants and insects to delay timetables for interactions such as pollination[32]; finding that EWEs typically delay offset supports that expectation.

Finally, we found that extreme events almost always lengthen the duration of phenological events, and their impacts on phenological responsiveness are strongest in warm and dry regions. For plants, but not insects, the impact of extreme precipitation is much stronger in drier regions. These results are directly related to differential onset dynamics where onsets in dry conditions are later for insects but not for plants, while dry conditions shift offset later in both insects and plants. Thus mechanisms for duration lengthening are inherent in the processes operating on both onset and offset dynamics and differential responses have the potential to impact phenological matching.

Limitations

While we explicitly focused on adult flight timing in Lepidoptera and flowering in Angiosperms, we did not include events that occur during insect and plant development. In insects, larval development often occurs in late winter and early spring when animals are most vulnerable to extreme weather conditions[45] and we may miss early season impacts. Second, we opted to not further complicate models by including species traits, which can be important for mediating response[25]. We did subset analyses to examine responsiveness for earlier and later season species, separately for onset and offset. Our taxon selection for the full models focused on species for which data were available, rather than selecting species with known interactions. Nevertheless, the same results hold when limiting to plant species known to be pollinated by Lepidoptera. Third, we did not investigate changes in overlap between plants and insects within assemblages because of data constraints. Results presented here were based on community-level responses of plants and insects to climatic variables which may not apply to individual plant–insect pairs. Finally, our study area spans the contiguous United States, which is not representative of all climate regimes or species, particularly polar or tropical regions.

Conclusion

Forecasting how plant and animal phenology responds under global change has proved challenging[13,46], in part, because many models focus primarily on heat and water accumulation or average measures as predictors while ignoring variables such as EWEs. Here we show that plant and insect phenology is highly responsive to EWEs and that their responses differ in magnitude and context. Our framework and results provide useful context for further examination of EWE drivers of key phenological events across trophic levels. This in turn helps with better predicting likelihood of trophic mismatches and consequences to ecosystem services and developing effective mitigation and resilience plans in the face of climate change.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-025-02248-7.

References

1. Van de Pol, M., Jenouvrier, S., Cornelissen, J. H. & Visser, M. E. Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Phil. Trans. R. Soc. B* **372**, 20160134 (2017).
2. Ummenhofer, C. C. & Meehl, G. A. Extreme weather and climate events with ecological relevance: a review. *Phil. Trans. R. Soc. B* **372**, 20160135 (2017).
3. IPCC. *Special Report on Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation* (eds Field, C. B. et al.) (Cambridge Univ. Press, 2012).
4. Seneviratne, S. I. et al. in *Climate Change 2021: The Physical Science Basis* (eds Masson-Delmotte, V. et al.) Ch. 11 (Cambridge Univ. Press, 2021).
5. IPCC. *Climate Change 2023: Synthesis Report* (eds Core Writing team, Lee, H. & and Romero, J.) (IPCC, 2023).
6. Fischer, E., Sippel, S. & Knutti, R. Increasing probability of record-shattering climate extremes. *Nat. Clim. Change* **11**, 689–695 (2021).
7. Harris, R. M. et al. Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Change* **8**, 579–587 (2018).
8. Suarez-Gutierrez, L., Müller, W. A. & Marotzke, J. Extreme heat and drought typical of an end-of-century climate could occur over Europe soon and repeatedly. *Commun. Earth Environ.* **4**, 415 (2023).
9. Jentsch, A., Kreyling, J., Boettcher-Treschkow, J. & Beierkuhnlein, C. Beyond gradual warming: extreme weather events alter flower phenology of european grassland and heath species. *Glob. Change Biol.* **15**, 837–849 (2009).
10. Sabater, S. et al. Extreme weather events threaten biodiversity and functions of river ecosystems: evidence from a meta-analysis. *Biol. Rev.* **98**, 450–461 (2023).
11. Parmesan, C., Root, T. L. & Willig, M. R. Impacts of extreme weather and climate on terrestrial biota. *Bull. Am. Meteorol. Soc.* **81**, 443–450 (2000).
12. Davis, C. C., Willis, C. G., Primack, R. B. & Miller-Rushing, A. J. The importance of phylogeny to the study of phenological response to global climate change. *Phil. Trans. R. Soc. B* **365**, 3201–3213 (2010).
13. Piao, S. et al. Plant phenology and global climate change: current progresses and challenges. *Glob. Change Biol.* **25**, 1922–1940 (2019).
14. Chmura, H. E. et al. The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecol. Monogr.* **89**, e01337 (2019).
15. Iler, A. M., CaraDonna, P. J., Forrest, J. R. & Post, E. Demographic consequences of phenological shifts in response to climate change. *Annu. Rev. Ecol. Evol. Syst.* **52**, 221–245 (2021).
16. Visser, M. E. & Gienapp, P. Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**, 879–885 (2019).
17. Gallinat, A. S. et al. Macrophenology: insights into the broad-scale patterns, drivers, and consequences of phenology. *Am. J. Bot.* **108**, 2112–2126 (2021).
18. Fu, Y. H. et al. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107 (2015).
19. Li, D. et al. Climate, urbanization, and species traits interactively drive flowering duration. *Glob. Change Biol.* **27**, 892–903 (2021).
20. Grossman, J. J. Phenological physiology: seasonal patterns of plant stress tolerance in a changing climate. *New Phytol.* **237**, 1508–1524 (2023).
21. Filazzola, A., Matter, S. F. & MacIvor, J. S. The direct and indirect effects of extreme climate events on insects. *Sci. Total Environ.* **769**, 145161 (2021).
22. Youngflesh, C. et al. Demographic consequences of phenological asynchrony for North American songbirds. *Proc. Natl Acad. Sci. USA* **120**, e2221961120 (2023).
23. Renner, S. S. & Zohner, C. M. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **49**, 165–182 (2018).
24. Patterson, T. A., Grundel, R., Dzurisin, J. D., Knutson, R. L. & Hellmann, J. J. Evidence of an extreme weather-induced phenological mismatch and a local extirpation of the endangered Karner blue butterfly. *Conserv. Sci. Pract.* **2**, e147 (2020).
25. Guralnick, R., Campbell, L. & Belitz, M. Weather anomalies more important than climate means in driving insect phenology. *Commun. Biol.* **6**, 490 (2023).
26. Zhang, J. et al. Rapid shifts of peak flowering phenology in 12 species under the effects of extreme climate events in Macao. *Sci. Rep.* **8**, 13950 (2018).
27. Ma, C.-S., Ma, G. & Pincebourde, S. Survive a warming climate: insect responses to extreme high temperatures. *Annu. Rev. Entomol.* **66**, 163–184 (2021).
28. Crabbe, R. A. et al. Extreme warm temperatures alter forest phenology and productivity in Europe. *Sci. Total Environ.* **563**, 486–495 (2016).
29. Zhou, Z. et al. Lengthened flowering season under climate warming: evidence from manipulative experiments. *Agric. For. Meteorol.* **312**, 108713 (2022).
30. Dusenge, M. E., Duarte, A. G. & Way, D. A. Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytol.* **221**, 32–49 (2019).
31. Hatfield, J. L. & Prueger, J. H. Temperature extremes: effect on plant growth and development. *Weather Clim. Extrem.* **10**, 4–10 (2015).
32. Motten, A. F. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecol. Monogr.* **56**, 21–42 (1986).
33. Neufeld, H. S. & Young, D. R. in *The Herbaceous Layer in Forests Of Eastern North America* (ed. Gilliam, F.) 38–90 (Oxford Academic, 2003).
34. Buckley, L. B. Temperature-sensitive development shapes insect phenological responses to climate change. *Curr. Opin. Insect Sci.* **52**, 100897 (2022).
35. Khelifa, R., Blanckenhorn, W. U., Roy, J., Rohner, P. T. & Mahdjoub, H. Usefulness and limitations of thermal performance curves in predicting ectotherm development under climatic variability. *J. Anim. Ecol.* **88**, 1901–1912 (2019).
36. Stålhandske, S., Gotthard, K. & Leimar, O. Winter chilling speeds spring development of temperate butterflies. *J. Anim. Ecol.* **86**, 718–729 (2017).
37. Denlinger, D. L. *Insect Diapause* (Cambridge Univ. Press, 2022).
38. Chen, C., Harvey, J. A., Biere, A. & Gols, R. Rain downpours affect survival and development of insect herbivores: the specter of climate change? *Ecology* **100**, e02819 (2019).
39. Forister, M. L. et al. Impacts of a millennium drought on butterfly faunal dynamics. *Clim. Change Responses* **5**, 3 (2018).
40. Currier, C. M. & Sala, O. E. Precipitation versus temperature as phenology controls in drylands. *Ecology* **103**, e3793 (2022).

41. Nagy, L., Kreyling, J., Gellesch, E., Beierkuhnlein, C. & Jentsch, A. Recurring weather extremes alter the flowering phenology of two common temperate shrubs. *Int. J. Biometeor.* **57**, 579–588 (2013).
42. Lailvaux, S. P., Breuker, C. J. & Van Damme, R. Water stress affects development time but not takeoff performance in the butterfly *Pararge aegeria*. *Physiol. Biochem. Zool.* **90**, 54–62 (2017).
43. Song, Z. et al. Surprising roles of climate in regulating flowering phenology in a subtropical ecosystem. *Ecography* **44**, 1379–1390 (2021).
44. Crimmins, T. M., Crimmins, M. A. & Bertelsen, C. D. Spring and summer patterns in flowering onset, duration, and constancy across a water-limited gradient. *Am. J. Bot.* **100**, 1137–1147 (2013).
45. McDermott Long, O. et al. Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *J. Anim. Ecol.* **86**, 108–116 (2017).
46. Ibáñez, I. et al. Forecasting phenology under global warming. *Phil. Trans. R. Soc. B* **365**, 3247–3260 (2010).

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

© The Author(s), under exclusive licence to Springer Nature Limited 2025

Methods

Phenological data

We accessed the iNaturalist research-grade observations for flowering plants and Lepidoptera archived at the Global Biodiversity Information Facility (GBIF) on 20 November 2023[47]. Research-grade records are those for which at least two-thirds of iNaturalist users agree with each other's identifications[48]. For this study, we only used observations that were collected between 2016 and 2022 within the contiguous United States because this time period and extent provided the broadest coverage of phenological observations for both plants and insects and our methods require relatively dense data for estimating phenophases. Furthermore, long-term daily weather data needed to calculate extreme weather is available for this time period and area (see section on 'Climate and weather data'). We filtered records to only Angiosperm and Lepidoptera found in the contiguous United States. The use of community science resources, now commonplace for phenological studies[19,49], provides the means to scale up the number and types of species that can be examined while also allowing fine spatial grain, facilitating the detection of local-scale impacts of EWEs across broad geographic extents.

Rather than further scoring plant phenology ourselves, we opted to only use records that had existing plant flowering observations. For plants, we kept 2,539,475 research-grade observations that were annotated as 'flowering' or 'flower budding' or 'flowering|flower budding'. To verify that plant flowering annotations are accurate, we hand-scored a random subset of these (6,000 records) and found that iNaturalist annotations are accurate (>96%, unpublished data), with more omission errors than commission. Since we here use presence-only phenology estimation methods, the low commission rate gave us confidence in using these annotations directly. We further added the 205,993 manually scored flowering records from 52 species generated by Li et al.[19] to the plant dataset. The top ten families included in this Article were Asteraceae, Liliaceae, Fabaceae, Ranunculaceae, Asparagaceae, Plantaginaceae, Apocynaceae, Boraginaceae, Ericaceae and Rosaceae. For insects, we focused on adult Lepidoptera (butterflies and moths) from the following eight families: Papilionidae, Nymphalidae, Pieridae, Lycaenidae, Hesperiidae, Riodinidae, Saturniidae and Sphingidae. These well-sampled groups are also well known, making them particularly useful for this effort. For both plants and Lepidoptera, we further removed records whose coordinates had uncertainty >30 km. Species with <100 total observations were also removed. Since our insect phenophase of interest was the adult flight period, we removed species from the Lepidoptera dataset that have showy and common larval forms (for example, Monarch butterflies), and filtered all records labelled as caterpillars, eggs or pupae. We have estimated an error rate <0.25% for larval forms included mistakenly in the remaining dataset. In addition, we have removed migratory species as local climate influence on their phenology may be minimal. In the final raw dataset, we have 1,104,939 flowering records from 1,867 plant species and 1,639,773 Lepidoptera records from 519 species.

Phenometric estimates

To estimate the onset (that is, beginning), offset (that is, ending) and duration of plant flowering and Lepidoptera flight phenology in different locations, we first divided the contiguous United States into 25 × 25 km^2 equal area grid cells (Fig. 1). This spatial resolution provided a balance between data availability of phenological records and capturing local to regional scale phenology and weather phenomena. For the observations of each species within each grid cell, we then conducted extensive quality control following the same workflow and best practices described in refs. 19,50. In particular, we accounted for sampling biases unique to iNaturalist data resulting from an annual spring City Nature Challenge programme. During this time period the number of observations in some grid cells are significantly higher than normal, which can cause biases in the estimations of phenometrics. To mitigate this bias, for each species–year–grid cell combination, we randomly thinned days with greater than average number of observations per day to their corresponding daily average number of observations[19]. For each species–year–grid cell combination, we also removed observations whose dates were beyond 3.5 s.d. (that is, extremely early or late) of all records within that combination. We only kept species–year–grid cell combinations with at least five observations from three unique days after the initial quality control. We also removed plant species with flowering time across calendar years because of challenges to estimating their phenometrics despite availability of statistical methods that can be used for such species (for example, circular analysis)[51–53]. Similarly, we have removed year-round flight Lepidoptera species. Species with less than five year–grid cell combinations were also excluded. Given an aim is to compare phenological responses of flowering plants and Lepidoptera to EWEs, we only kept grid cells that have at least one species from both taxonomic groups. After these filtering steps, 208,787 flowering records from 1,068 plant species and 764,280 records from 462 Lepidoptera species remained to be used for phenometric estimates.

For the remaining species–year–grid cell combinations, we estimated the onset and offset of plant flowering and Lepidoptera flight phenology (as day of year) using the R package phenesse v.0.1.2 (ref. 54), which provides relatively robust estimates of phenometrics even with low sampling intensity. We used quantile estimates of 5 and 95 percentiles as proxies for the onset and offset of phenometrics[19,54]. Durations were calculated as the number of days between the estimated onset and offset dates. For each species, we conducted quality control by removing potential outliers whose pheno-estimates were >3.5 times away from the median estimates of the phenometrics compared with the median absolute deviation. We further removed species–year–grid cell combinations with estimated duration <5 days as such estimates were probably caused by the lack of data. Filtered cases were rare, for example, <1% of all species–year–cell combinations. The final dataset included 7,565 and 9,444 unique species–year–grid cell combinations with estimated onset, offset and duration for plant flowering (581 species from 766 grid cells) and Lepidoptera flight phenology (172 species from 766 grid cells), respectively. The number of distinct observation days for each estimate was kept to be included in the downstream statistical models to account for sampling effort[50]. Our phenology estimates span 7 years (2016 to 2022).

Climate and weather data

We obtained daily weather and annual climate data from Daymet[55,56], with coverage across North America from 1980 to present at 1 × 1 km^2 spatial resolution. Annual climate summaries were used to obtain overall climatic conditions, while daily weather data were used to determine whether a specific range of dates had extreme temperature or precipitation weather events (Extended Data Fig. 6). Temperature seasonality was calculated as the standard deviation of monthly average temperature times 100. Precipitation seasonality was calculated as the coefficient of variation of monthly total precipitation.

For each year–grid cell combination, we extracted the annual average temperature, total precipitation and their seasonalities for that year, as well as those from the previous 4 years. We then calculated the average values of each climatic variable across these 5 years and used this value as the annual average climatic conditions for that year–grid cell combination to account for potential lagged effects of climate on phenology.

For daily weather data, we focused on temperature and precipitation. To determine if an individual day had extreme weather, we used a 7 day window approach centred on that day (for example, 3 days before and 3 days after) to reduce the potential effects of stochasticity of daily weather. Specifically, we compared the daily maximum and minimum temperature and total precipitation of the 7 day window with values for the same 7 day window centred on the same calendar day from 1980 to 2022. We considered extremely warm or cold days as the days

https://doi.org/10.1038/s41558-025-02248-7

when the maximum or minimum temperature of its corresponding 7 day window was above or below 2 s.d. of the maximum or minimum temperatures for the base periods, respectively. To determine whether a day was extremely dry or wet, we calculated the modified rainfall anomaly index (mRAI)[57] because a standard deviation approach was not appropriate given asymmetrical distribution of daily precipitation (for example, values <2 s.d. from the mean would produce negative values). We calculated the mRAI for individual days using the corresponding 7 day window using the following equation:

$$\mathrm{mRAI}_i = \pm \mathrm{SF} \times \frac{P_i - \bar{P}}{\bar{E} - \bar{P}}$$

where P_i is the total precipitation of the 7 day window centred on the target day, $\bar{P}$ is the median total precipitation of the 7 day window centred on the same calendar day from 1980 to 2022, $\bar{E}$ is the mean of the 10% most extreme precipitation sums for the base periods (10% percentile for extreme dry and 90% percentile for extreme wet) and ±SF is the scaling factor with a value of 2 if $P_i \geq \bar{P}$ and a value of −2 if $P_i \leq \bar{P}$. If mRAI_i is <−2 or >2, we consider that day as extremely dry or wet, respectively.

For the onset of plant flowering and flight phenology of Lepidoptera, we calculated the number of days with extreme weather (hot, cold, dry and wet) 60 days before the day of onset[25]. For offset, we calculated the number of days with extreme weather between the period from the estimated onset date to the estimated offset date. For duration, we summed the total number of extreme days for onset and offset. Because species with longer durations could have more extreme weather days by chance, we converted the number of extreme weather days to proportions by dividing the number of extreme days by the total number of days considered (for example, 60 days + total duration). Proportional data were then logit-transformed before model fitting[58].

Our overall goal was to investigate whether and how extreme weather events affect the phenology of plants and insects after considering annual average and seasonal climatic variables, which serve as a means to establish a general climate context (overall warm/cool and wet/dry). Given this goal, we did not investigate all potential phenological drivers, such as human population density[59], day length[60] or seasonal growing degree days[61]. Others[25] showed that seasonal growing degree day and extreme events are only very weakly correlated.

Statistical analysis

To investigate whether EWEs affect the timing of both plant flowering and Lepidoptera flight periods even after considering the effects of average and seasonal temperature and precipitation, we fit two nested LMMs for onset, offset and duration separately using the R packages lme4 (v.1.1-31)[62] and lmerTest (v.3.1-3)[63]. We specified the nested LMM models with this general form of $y \sim x1 * \text{taxon} + \ldots + x4 * \text{taxon} + (1 \mid \text{species}) + (1 \mid \text{id\_cells}) + (1 \mid \text{year}) + (0 + x1 \mid \text{species}) + \ldots + (0 + x4 \mid \text{species})$. The nested LMM model included the estimated phenometric values (for example, estimated onset day of year, offset day of year or log-transformed number of days for durations) as the response variable (y) with annual average temperature ($x1$), annual total precipitation ($x2$), temperature seasonality ($x3$) and precipitation seasonality ($x4$) all interacting with taxon (plants or Lepidoptera) as fixed effects; random effects included species names (species), grid cell identities (id_cells) and year for intercepts and the environmental variables used for fixed terms for slopes of species. The second LMM model had the same design as the nested model plus the four EWEs (as logit-transformed proportion of days) and interactions between the four EWEs and taxon as additional fixed effects. Both LMMs were fitted with maximum likelihood instead of restricted maximum likelihood to allow meaningful model comparisons. All predictors were scaled to have mean 0 and standard deviation 1 before model fitting (here and below) to ensure comparable effect sizes across covariates. We then compared models with and without EWEs via a likelihood ratio test. We used AIC and Bayesian information criterion (BIC) scores to determine whether EWEs also played important roles in affecting plant flowering and Lepidoptera flight phenology after accounting for average or seasonal climate. The interactions between EWEs and taxon informed whether the effects of EWEs on phenology were different between plants and insects.

To investigate whether EWEs interact with average climate variables to affect phenology and whether such interactions are consistent across taxonomic groups, we fitted LMMs with three-way interactions between EWEs, average climatic variables and taxon (that is, $x * \text{EWEs} * \text{taxon}$ in the R formula) in addition to the terms included in the models described above. Significant three-way interactions would suggest that plants and Lepidoptera have different interactions between extreme weather and average climatic variables. Rather than investigating all possible combinations between EWEs and average climatic variables, we built the full model to include only interactions that we believed to be potentially important and ecologically meaningful. Specifically, these included three groups of interactions. First, we added interactions between extreme warm or cold and annual average temperature to investigate whether the effects of extreme warm or cold on phenology varies across regions with different annual average temperature. Second, we added interactions between extreme wet or dry and annual total precipitation to investigate whether the effects of extreme wet or dry on phenology varies across regions with different annual precipitation. Third, we added interactions between extreme warm and extreme wet or dry, given that such interactions are becoming more frequent and are likely to impact the phenology of both plants and Lepidoptera. Starting with the full model described here, we then conducted stepwise model selections for onset, offset and duration to derive a final model for each phenophase using the step function provided by the R package lmerTest[63]. For each final model, environmental variables (both average climatic variables and EWEs) that were retained were also included as random slope terms for species so that the estimated coefficients of fixed terms were the conditional average responses of phenology to each environmental variable across all species.

All models described above included the number of distinct observation days as a fixed term to account for impacts of sampling effort on the estimated phenometrics suggested by Belitz et al.[50]. We tested multicollinearity among covariates for all models by calculating variance-inflation factors (VIF) using the vif function provided by the R package car (v.3.1-2)[64]. Terms in the final models with data from both plants and insects all have VIF values <5, indicating that multicollinearity among predictors was not a problem here. For the final models, we also checked for potential spatial autocorrelation in the residuals and did not find strong evidence that it was present (Supplementary Fig. 3). Given the large number of species and grid cells, we were not able to fit phylogenetic generalized linear mixed models (PGLMMs) to account for possible phylogenetic autocorrelation[65] in the final models, as such models were computationally demanding[66]. Instead of running PGLMMs with both plant and insect data together, we used a subset approach and ran PGLMMs[66] on the onset, offset and duration of flowering plant and Lepidoptera separately and were able to obtain results for offset and duration of insect flight as well as the duration of plant flowering. Other models were not able to finish on a server with 64 CPU cores and 128 gigabyte memory after 2 days, after which they were automatically terminated. The results from these three models suggested that PGLMM gave qualitatively similar results with the LMMs (Supplementary Tables 3, 4 and 5), providing confidence that our results presented here were robust. Flowering plant phylogeny was derived using the R package rtrees (v.1.0.3)[67]; insect phylogeny was derived using similar methods described in ref. 68. All analyses were conducted with R v.4.3.1 (ref. 69).

The models described above used phenological records of plant and insect species from different seasons. These models are appropriate to look for general patterns across space and species. However, it is possible that the conclusions based on the models with all species may not apply to early or late species as they can have different responses to EWEs. In addition, species included in the above models were largely determined by their data availability; not all species have known pollination relationships with Lepidoptera. To ensure the robustness of the above models, we have conducted two additional sets of analyses. First, we classified species into 'early' and 'late' categories and refitted the final models above using only 'early' species for onset and using only 'late' species for offset. We determined a species to be 'early' if its median estimated onset date was before the end of April; we determined a species to be 'late' if its median estimated offset date was after the end of August; the remaining species are 'middle' species. We did not compare all phenophases of early/late plants and insects because the impacts of the offset of early plants on insects may be complemented by 'middle' plants and vice versa. Similarly, the impacts of the onset of late plants on insects may be complemented by 'middle' plants and vice versa. The results based on 'early' species (271 plant species and 39 insect species) for onset and the results based on 'late' species (99 plant species and 52 insect species) for offset are all qualitatively similar to the models with all species together (Extended Data Figs. 1 and 2). Second, we compiled a list of plant species/genera that are known to be pollinated by Lepidoptera by conducting an extensive literature search. We then only used this subset of 317 plant species and 159 Lepidoptera species after removing Lepidoptera that have reduced or non-functional adult mouth parts to refit the final models above. Note that the plant species not included in the list can also be pollinated by Lepidoptera; we just could not find existing evidence in the literature. These models with a subset of plant species that are known to be pollinated by Lepidoptera also provided qualitatively similar results with models using all species (Extended Data Figs. 3–5). These additional analyses suggested that our models with all species together were robust.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data used in this article are publicly available. GBIF data are available at ref. 47. Climate and weather data were downloaded from https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=2130 and https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=2129.

Code availability

Code scripts used in this article are available via Zenodo at https://doi.org/10.5281/zenodo.14291652 (ref. 70).

References

47. iNaturalist research-grade observations GBIF occurrence download. *GBIF* https://doi.org/10.15468/DL.XHHHJJ (2018).
48. Campbell, C. et al. Identifying the identifiers: how iNaturalist facilitates collaborative, research-relevant data generation and why it matters for biodiversity science. *BioScience* **73**, 533–541 (2023).
49. Barve, V. V. et al. Methods for broad-scale plant phenology assessments using citizen scientists' photographs. *Appl. Plant Sci.* **8**, e11315 (2020).
50. Belitz, M. W., Larsen, E. A., Shirey, V., Li, D. & Guralnick, R. P. Phenological research based on natural history collections: practical guidelines and a lepidopteran case study. *Funct. Ecol.* **37**, 234–247 (2023).
51. Fisher, N. I. *Statistical Analysis of Circular Data* (Cambridge Univ. Press, 1995).
52. Davis, C. C. et al. New directions in tropical phenology. *Trends Ecol. Evol.* **37**, 683–693 (2022).
53. Daru, B. H., Kling, M. M., Meineke, E. K. & Wyk van, A. E. Temperature controls phenology in continuously flowering *Protea* species of subtropical Africa. *Appl. Plant Sci.* **7**, e01232 (2019).
54. Belitz, M. W., Larsen, E. A., Ries, L. & Guralnick, R. P. The accuracy of phenology estimators for use with sparsely sampled presence-only observations. *Methods Ecol. Evol.* **11**, 1273–1285 (2020).
55. Thornton, M. et al. *Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 4 R1* (ORNL DAAC, 2022).
56. Thornton, M. et al. *Daymet: Annual Climate Summaries on a 1-km Grid for North America, Version 4 R1* (ORNL DAAC, 2022).
57. Hänsel, S., Schucknecht, A. & Matschullat, J. The modified rainfall anomaly index (mRAI)—is this an alternative to the standardised precipitation index (SPI) in evaluating future extreme precipitation characteristics? *Theor. Appl.Climatol.* **123**, 827–844 (2016).
58. Warton, D. I. & Hui, F. K. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**, 3–10 (2011).
59. Li, D., Stucky, B. J., Deck, J., Baiser, B. & Guralnick, R. P. The effect of urbanization on plant phenology depends on regional temperature. *Nat. Ecol. Evol.* **3**, 1661–1667 (2019).
60. Way, D. A. & Montgomery, R. A. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant Cell Environ.* **38**, 1725–1736 (2015).
61. Cayton, H. L., Haddad, N. M., Gross, K., Diamond, S. E. & Ries, L. Do growing degree days predict phenology across butterfly species? *Ecology* **96**, 1473–1479 (2015).
62. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
63. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26 (2017).
64. Fox, J. & Weisberg, S. *An R Companion to Applied Regression* (Sage, 2019).
65. Ives, A. R. & Helmus, M. R. Generalized linear mixed models for phylogenetic analyses of community structure. *Ecol. Monogr.* **81**, 511–525 (2011).
66. Li, D., Dinnage, R., Nell, L. A., Helmus, M. R. & Ives, A. R. Phyr: an R package for phylogenetic species-distribution modelling in ecological communities. *Methods Ecol. Evol.* **11**, 1455–1463 (2020).
67. Li, D. Rtrees: an R package to assemble phylogenetic trees from megatrees. *Ecography* **2023**, e06643 (2023).
68. Belitz, M. W. et al. Climate drivers of adult insect activity are conditioned by life history traits. *Ecol. Lett.* **24**, 2687–2699 (2021).
69. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2023).
70. Li, D. Data for 'Extreme weather events have strong but different impacts on plant and insect phenology'. *Zenodo* https://doi.org/10.5281/zenodo.14291652 (2024).

Acknowledgements

This study would not have been possible without the observational data contributed by thousands of observers to iNaturalist. This study was supported by NSF-DBI award no. 2223508 to D.L., NSF-DBI award no. 2223512 to R.G. and USDA National Institute of Food and Agriculture, Hatch project 1021482 to L.C.

Author contributions

All authors conceived the study. D.L. compiled the data with help from M.B. D.L. conducted data analysis with help from all other co-authors. D.L., R.G. and L.C. wrote the first draft of the paper with help from M.B. All authors contributed substantially to the final paper.

Competing interests
The authors declare no competing interests.

Additional information
Extended data is available for this paper at https://doi.org/10.1038/s41558-025-02248-7.

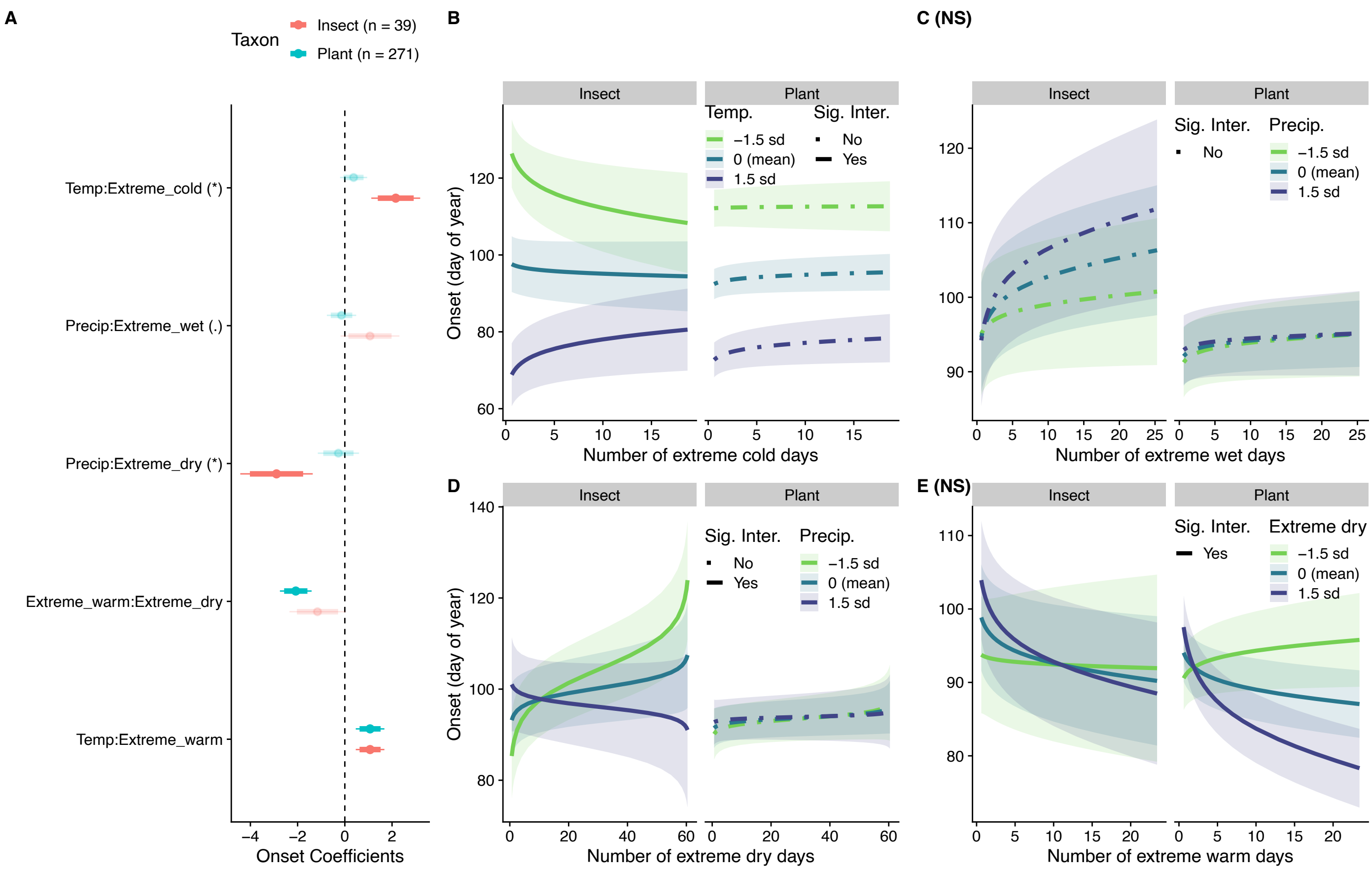
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41558-025-02248-7.

Correspondence and requests for materials should be addressed to Daijiang Li.

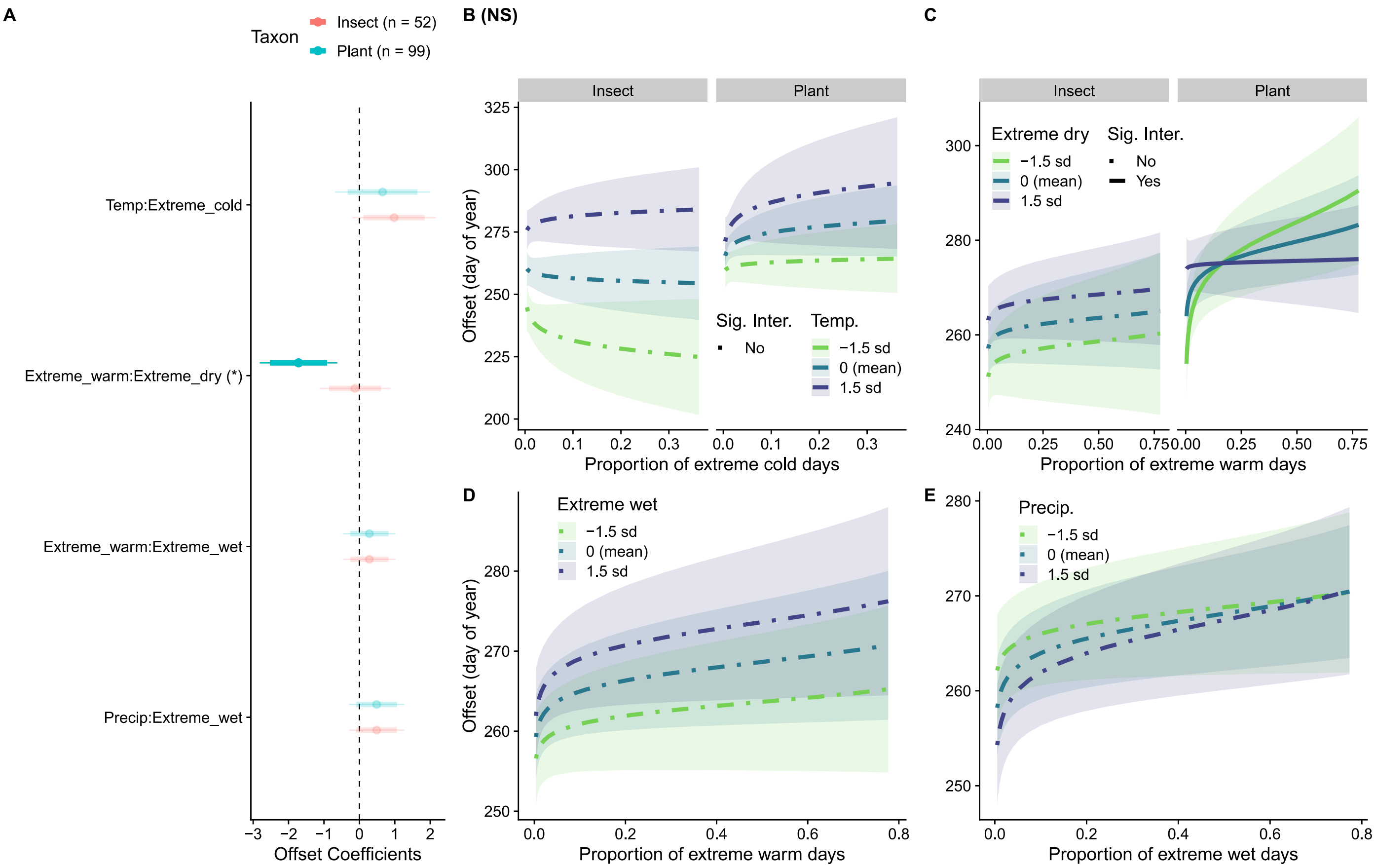
Peer review information *Nature Climate Change* thanks Yanjun Du, Pau Colom and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

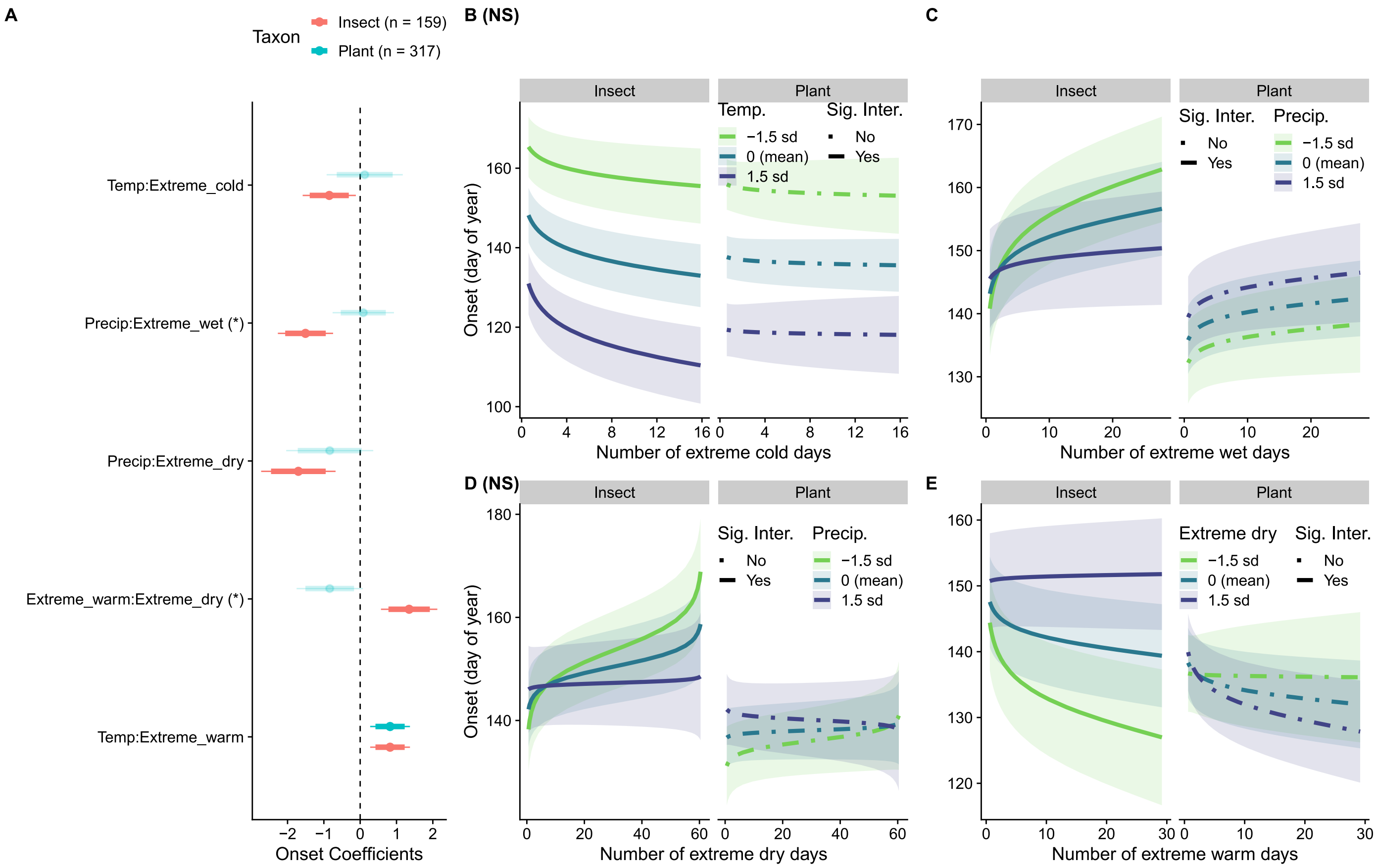
 https://doi.org/10.1038/s41558-025-02248-7



Extended Data Fig. 1 | Extreme weather events interacted with annual climatic variables and other extreme weather events to affect the onset (day of year) of plant flowering and flying period of insects for early species (onset before May). (a) Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) confidence intervals (CI) of all the significant interactions between extreme weather events and other variables. The (*) after the environmental variables on the y-axis indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter colors (transparency) indicate that a parameter's 95% confidence interval includes zero (the dashed vertical line). (**b**-**e**) Tested 3-way interactions among extreme weather events, climatic variables, and taxon. In panels **b** and **d**, the interaction was significantly different between plants and insects. In panels **c** and **e**, NS indicated that the interaction was not significantly different between plants and insects. Dashed lines in panels **b**-**e** indicate that the interaction was not significant for plants or insects. The effect of the interaction between average temperature and extreme warm was not plotted here as it was consistent between plants and insects. X-axes represented the number of extreme weather days in the 60-day time period before onset.

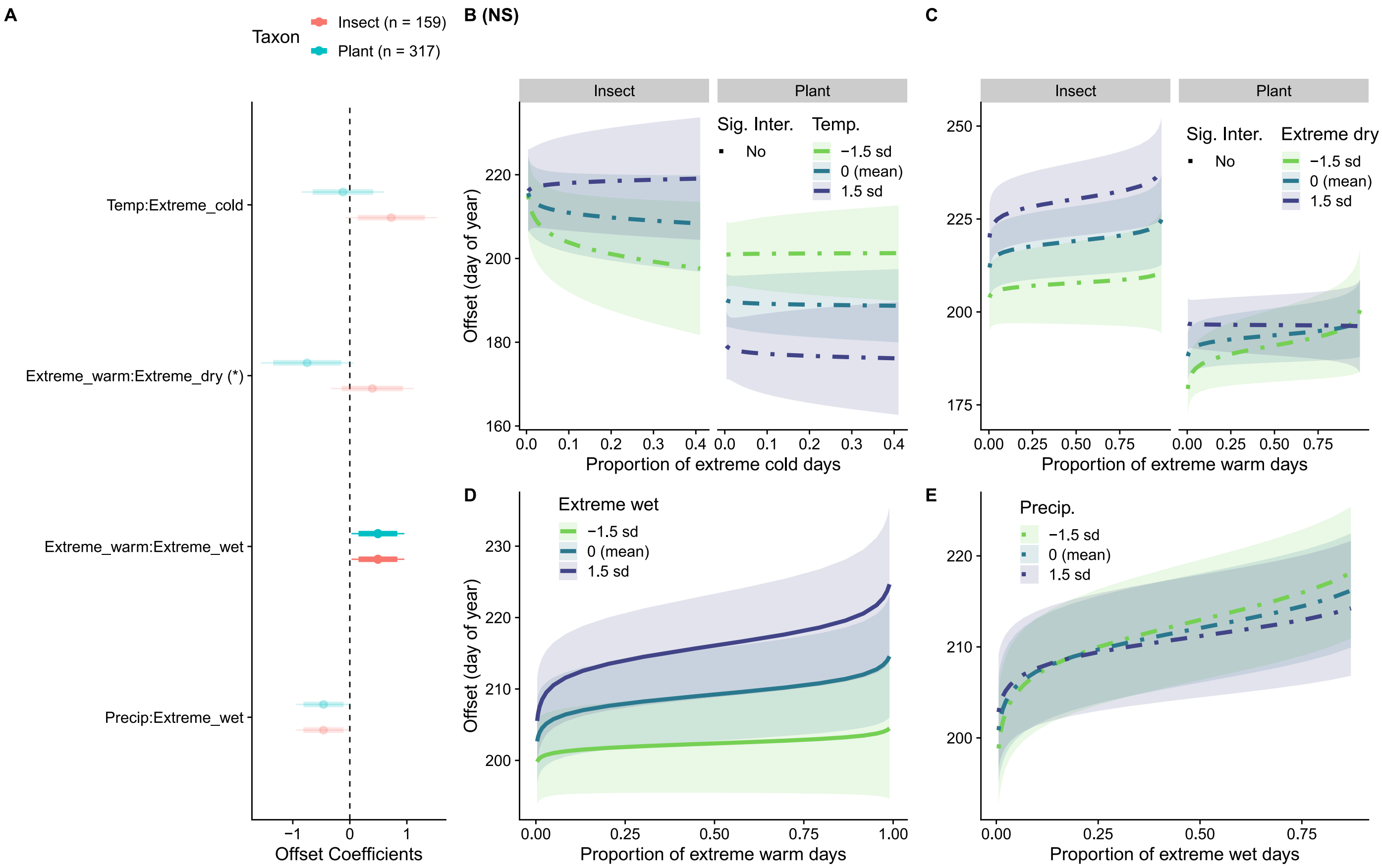


Extended Data Fig. 2 | Extreme weather events interacted with annual climatic variables and other extreme weather events to affect the offset (day of year) of plant flowering and flying period of insects for late species (offset after the end of August). (**a**) Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) confidence intervals (CI) of all the significant interactions between extreme weather events and other variables. The (*) after the environmental variables indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter colors (transparency) indicate that a parameter's 95% confidence interval includes zero (the dashed vertical line). (**b**–**e**) Tested 3-way interactions among extreme weather events, climatic variables, and taxon. In panel B, NS indicated that the interaction was not significantly different between plants and insects. Panel D and E had one plot for both plants and insects, indicating they share the same interaction patterns. Dashed lines in panels B-E indicate that the interaction was not significant for plants or insects. X-axes represented the proportion of extreme weather days between onset dates and offset dates.

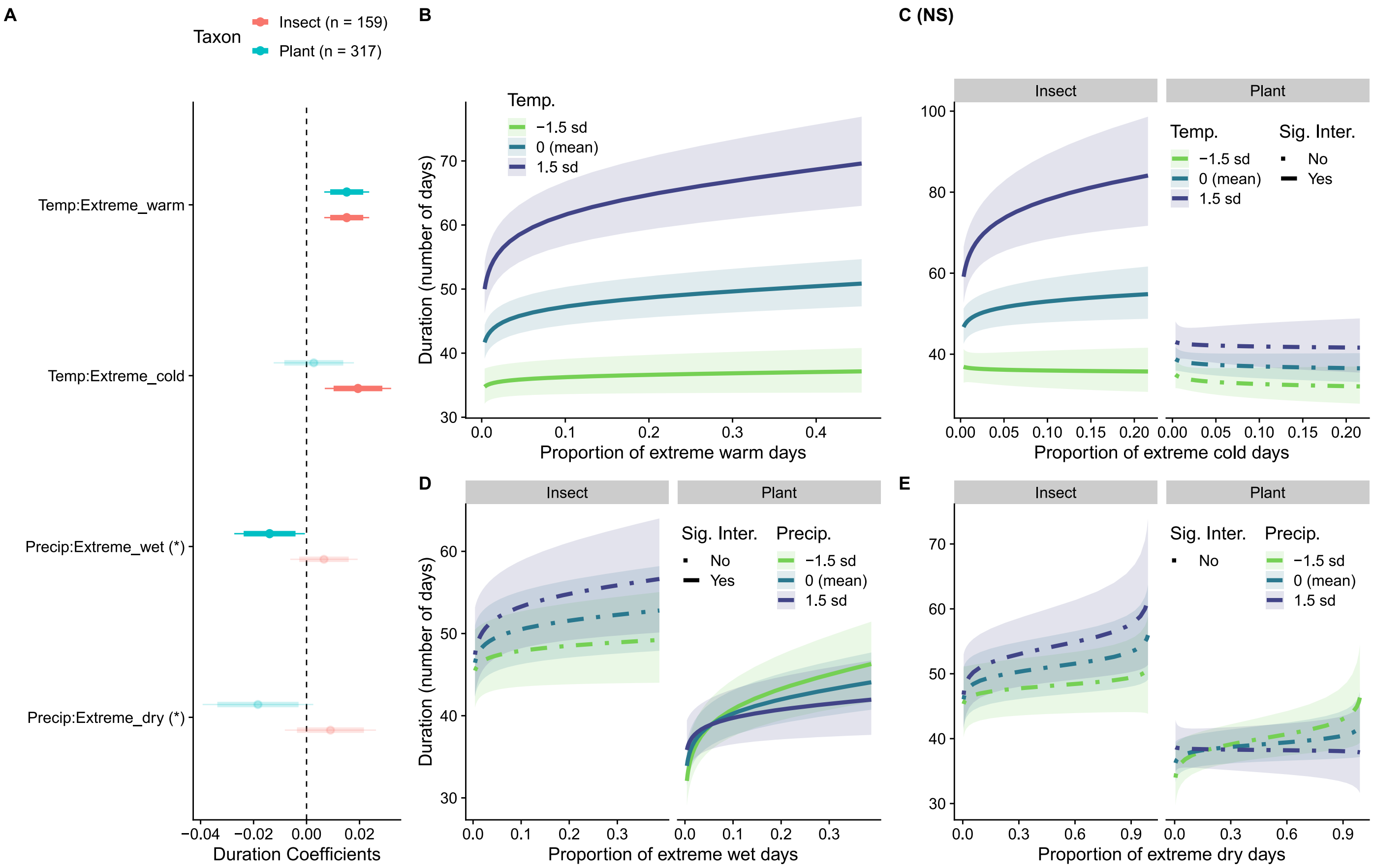


Extended Data Fig. 3 | Extreme weather events interacted with annual climatic variables and other extreme weather events to affect the onset (day of year) of flowering of plant species that are known to be pollinated by Lepidoptera and the flying period of Lepidoptera. Despite only using a subset of the plant species, the main result that EWEs interacted with climatic variables and other EWEs in affecting phenology still holds. (**a**) Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) confidence intervals (CI) of all the significant interactions between extreme weather events and other variables. The (*) after the environmental variables on the y-axis indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter colors (transparency) indicate that a parameter's 95% confidence interval includes zero (the dashed vertical line). (**b-e**) Tested 3-way interactions among extreme weather events, climatic variables, and taxon. NS in the parentheses indicated that interaction was not significantly different between plants and insects. Dashed lines in panels B-E indicate that the interaction was not significant for plants or insects. The effect of the interaction between average temperature and extreme warm was not plotted here as it was consistent between plants and insects. The X-axes represent the number of extreme weather days in the 60-day time period before onset.

https://doi.org/10.1038/s41558-025-02248-7

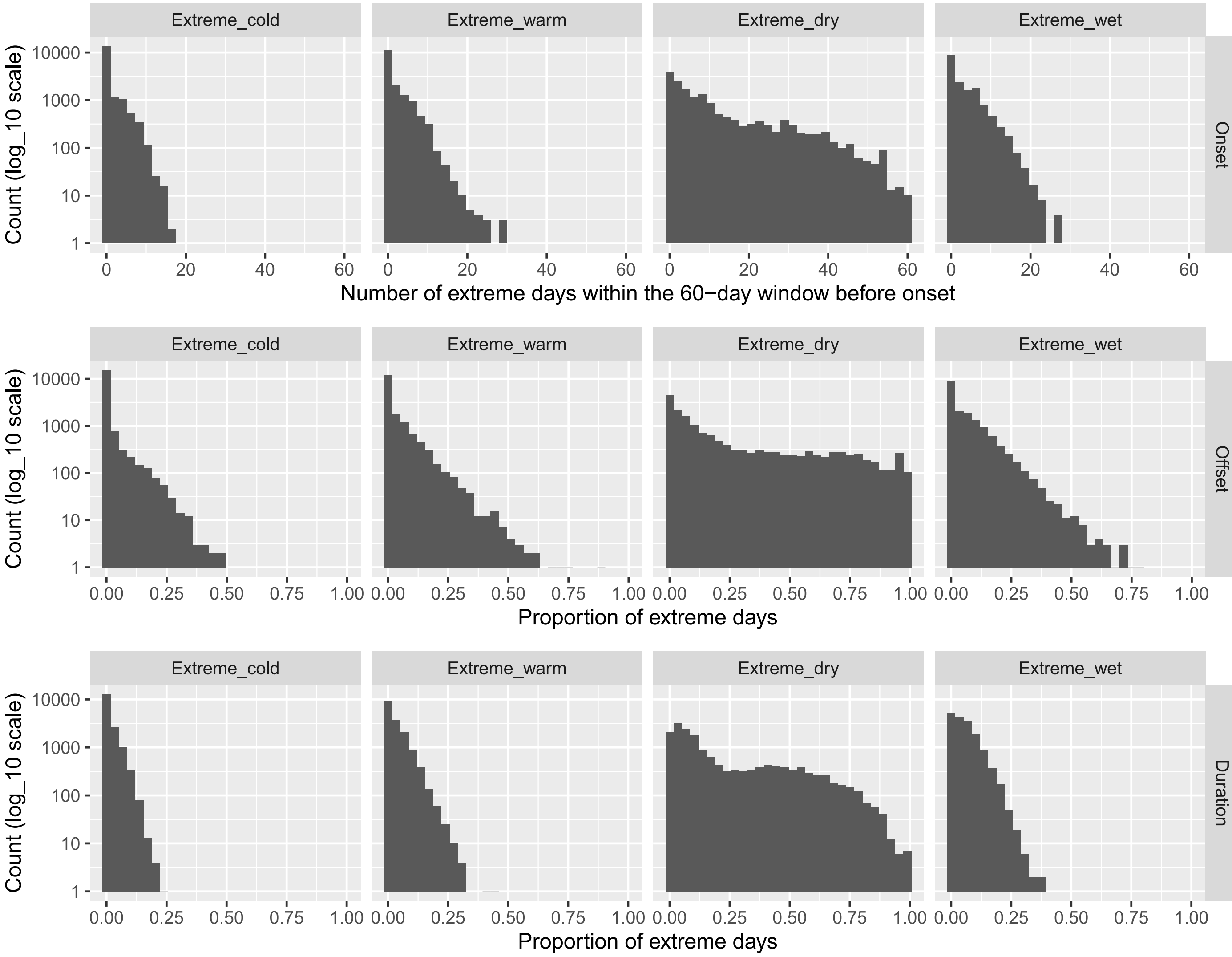


Extended Data Fig. 4 | Extreme weather events interacted with annual climatic variables and other extreme weather events to affect the offset (day of year) of flowering of plant species that are known to be pollinated by Lepidoptera and the flying period of Lepidoptera. Despite only using a subset of the plant species, the main result that EWEs interacted with climatic variables and other EWEs in affecting phenology still holds. (**a**) Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) confidence intervals (CI) of all the significant interactions between extreme weather events and other variables. The (*) after the environmental variables indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter colors (transparency) indicate that a parameter's 95% confidence interval includes zero (the dashed vertical line). (**b-e**) Tested 3-way interactions among extreme weather events, climatic variables, and taxon. NS in panel B indicated that the interaction between plants and insects was not significantly different. Panel D and E had one plot for both plants and insects, indicating they share the same interaction patterns. Dashed lines in panels B-E indicate that the interaction was not significant for plants or insects. The X-axes represent the proportion of extreme weather days between onset dates and offset dates.



Extended Data Fig. 5 | Extreme weather events interacted with annual climatic variables and other extreme weather events to affect the duration (number of days) of flowering of plant species that are known to be pollinated by Lepidoptera and the flying period of Lepidoptera. (**a**) Estimated coefficients (central points) and their 95% (thin lines) and 85% (thick lines) confidence intervals (CI) of all the significant interactions between extreme weather events and other variables. The (*) after the environmental variables indicate that the focal environmental variable had significantly different effects on the phenology of plants and insects. The lighter colors (transparency) indicate that a parameter's 95% confidence interval includes zero (the dashed vertical line). (**b-e**) All interactions with extreme weather events retained in the final model. Panel B had one plot for plants and insects, indicating that they share the same interaction pattern. NS in panel C indicated that the interaction between plants and insects was not significantly different. Dashed lines in panels C-E indicate that the interaction was not significant. The X-axes represent the proportion of extreme weather days from 60 days before onset dates to offset dates.

https://doi.org/10.1038/s41558-025-02248-7



Extended Data Fig. 6 | Extreme weather events data. Histograms of extreme weather events data used for final analyses.

nature portfolio

Corresponding author(s): Daijiang Li

Last updated by author(s): Dec 5, 2024

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We downloaded the whole GBIF dataset manually and no software was used.
Data analysis	We used R v4.3.1 to analyze the data, using R packages lme4 (version 1.1-31), lmerTest (version 3.1-3), and phyr (version 1.1.2). All code scripts used were archived as a public GitHub repository https://github.com/daijiang/pheno_extreme_weather.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All data used in this study are publicly available. GBIF data were archived at https://www.gbif.org/occurrence/download/0000778-231120084113126. Climate and weather data were downloaded from https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=2130 and https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=2129.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We conducted a large-scale study of the influences of extreme weather events (EWEs) on the phenology of both plant flowering and insect (Lepidoptera) flight for hundreds of species using >8 million in situ observations across the United States provided by the community science program iNaturalist.
Research sample	Raw data were generated by thousands of community scientists who contributed their observations to iNaturalist. We downloaded the research grade dataset that iNaturalist deposited to GBIF every week on November 20, 2023.
Sampling strategy	We carefully explored the raw data and conducted extensive quality control before using them to estimate phenometrics. After then, we carefully validated the estimated phenometrics for both plants and moths before conducting statistical analyses.
Data collection	Raw phenological data were generated by thousands of community scientists who contributed their observations to iNaturalist. Climate and weather data were downloaded from Daymet, which provides data across continental North America and Hawaii from 1980 to present at 1 km by 1 km spatial resolution.
Timing and spatial scale	We used quality controlled phenological observations within the contiguous United States from 2016 to 2022.
Data exclusions	For the research grade records, we removed those with coordinates uncertainty > 30 km. Species with < 100 total observations were also removed. Since our insect phenophase of interest was the adult flight period, we removed species from the Lepidoptera dataset that have showy and common larval forms, e.g., Monarch butterflies, and filtered out all records labeled as caterpillars, eggs, or pupae.
Reproducibility	No experiments were conducted.
Randomization	We used observatory data, no randomization involved.
Blinding	The observatory data were generated by many community scientists. No blinding involved.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☐	☒	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	No laboratory animals used in this study.
Wild animals	We used observatory records of Lepidoptera (butterfly and moth) across the United States provided by thousands of community scientists who contributed their observations to iNaturalist. Data contributors normally just took pictures of the moths without interrupting them.
Reporting on sex	No sex-based analysis used.
Field-collected samples	No field collected samples used (we only used images and observations).
Ethics oversight	No ethical approval required for this study.

Note that full information on the approval of the study protocol must also be provided in the manuscript.