





Ecological performance determines phenological responses of butterflies in Northern Austria

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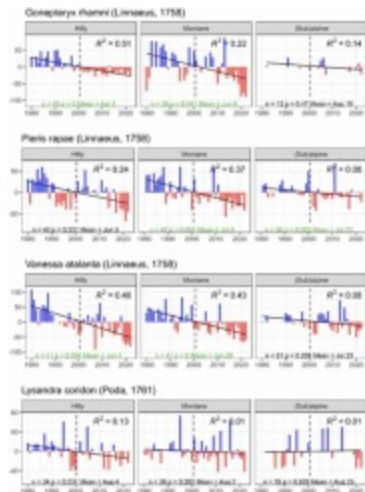
Highlights

- Butterflies and Zygaenid moths across Northern Austria were studied over a period of four decades using extensive museum data.
- Comparing the time windows 1980—2000 and 2001—2022, we found species-specific responses to climate change differing between spring and autumn.
- Species hibernating as imago or pupae, as well as migratory habitat ubiquists showed particularly strong phenological responses.
- Ecological specialists suffered most from climate change as these are least able to adapt to new thermal conditions and altered seasonality.

Abstract

Climate change influences the composition of species and the phenology of insect. Species tend to appear earlier in spring and to be active later in autumn. However, species respond differently to climatic changes according to their ecological and behavioural performance. However, it has not yet been clarified which ecological characteristics determine which responses. In this study, we analysed potential phenological shifts of butterflies and burnet moths across Northern Austria over a period of four decades. To investigate this, we used extensive museum data and compared the time windows 1980 to 2000 and 2001 to 2022. We found species' specific responses to climate change differing for spring and autumn. Species hibernating as imago or pupa as well as migratory habitat ubiquists showed particularly strong phenological responses. These species may become active immediately when weather conditions become suitable. The later occurrence of species during autumn is largely controlled by day length. Therefore, altering temperature regimes did not detectably influence autumn activity. Our study highlights that ecological specialists suffer most from climate change as these are least able to adapt to new thermal conditions and altered seasonality.

Graphical Abstract



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Deviation of first observations per year from the mean first observation of all years in days (ΔD_i^s) illustrated for some typical butterfly species showing phenological shifts (*Gonepteryx rhamni*, *Pieris rapae*, *Vanessa atalanta*, *Lysandra coridon*); deviations earlier than mean in red, later in blue. The results of non-parametric testing for identically distributed deviations between the periods 1980–2000 and 2001–2022 are summarised at the bottom of the

panels (n = testing sample size, significant results in green, i.e. $p < 0.05$). The vertical dashed line depicts the separation of the time windows, R^2 of linear regression lines is given in the top right corner.



Keywords

Climate change; Butterflies; Burnet moths; Times series; Alps; Seasons; Vegetation period; Traits; Life cycle; Larval ecology; Behaviour; Phenology

1. Introduction

Current climate change has been linked to altered ecological systems and changes in insect community functioning (Forrest, 2016, Lamprecht et al., 2018). Species' distributions are shifting northwards and into higher altitudes in mountain regions (Bonelli et al., 2021, Rödder et al., 2021, Neff et al., 2022, Kerner et al., 2023). Increasing temperatures also caused changes in species behaviour and life history (Forrest, 2016, Vitali et al., 2023). In general, insects rapidly adapt to prolonged vegetation periods and occur today up to 2 to 3 weeks earlier in spring than four decades ago (Habel et al., 2024, Vitali et al., 2023). In addition, insects are also observed later in autumn (Habel et al., 2024). The extent to which these phenological shifts affect ecosystem functioning is so far only marginally understood (Iler et al., 2021, Fu et al., 2022).

Adaptations to changing climatic conditions appear to be species specific (Kerner et al., 2023). Numerous case studies and model projections have shown how single species react, or might react, to altered temperatures and precipitation regimes (cf. Díez et al., 2012, Milenovic et al., 2023). For example, cryophilic species and those adapted to continental climate regimes, i.e. that cannot tolerate the current 'Atlantification' of the European climate, might suffer most (Habel et al., 2011), while others already change their life histories over major parts of Central European lowlands as adaptive response. Particularly the latter species are expected to prolong annual activity, decrease developmental times and increase their number of generations (Régner et al., 2023). In addition, currently observed warmer and wetter winters as well as heat waves in summer might increase mortality of insects (McCauley et al., 2018, Iler et al., 2021).

These species-specific reactions to changing climate have their counterpart at the community level. Shifts in spatial and altitudinal distributions in combination with altered phenology should cause changes in species' composition. Indeed, a number of analyses on insect communities have shown profound climate driven changes in the composition of e.g. butterflies (Bonelli et al., 2021, Habel et al., 2024, Stefanescu et al., 2003), longhorn beetles (Vitali et al., 2023) and dragonflies (Cancellario et al., 2022). Whether these changes have caused a net loss of diversity still remains controversial (Festa et al., 2023).

A better understanding of how species respond to climate change and which species suffer the most needs comparative and trait-based analyses including information on species' morphology, behaviour, and ecology (see Kellermann and Heerwaarden, 2019). In this respect, lepidopterans, particularly butterflies, have become a standard indicator taxon. Most butterflies require species-specific abiotic and biotic conditions for successful development, and are known to respond highly sensitive to environmental changes such as climatic and land-use changes (Bink, 1992, Settele et al., 2008). Recent work has shown that particularly mobile and habitat generalist butterflies have largely stable populations, with thermophilic species even benefiting from climate warming, while sedentary specialist species suffer most under climate change (Habel et al., 2024).

However, only few studies so far have focused on how species' performance determine phenological responses in the wake of climate change. First studies about North American butterflies showed that in particular polyphagous, multivoltine, and herb-feeding butterflies prolong their flight periods due to climate change (Zografou et al., 2021). In contrast, other studies indicate that herb-feeding butterflies in Europe are least affected by climate change (Altermatt, 2010). In addition, Diamond et al., (2011) showed that butterflies with monophagous larvae and species hibernating in advanced developmental stages (e.g. pupae) respond strongest to increasing temperatures. These partly contrasting results might be due to the selection and analyses of specific species, and the respective study region. It therefore is of high relevance to conduct a study that incorporates a large study area, and the complete set of butterfly species occurring across the respective region, to derive general trends and responses.

In the here presented study, we analyse phenological responses of butterflies and burnet moths to climate change depending on their species' specific performance. Therefore, we use long-term observation data collected across the northern Austrian Alps, covering an altitudinal range from 380 to more than 3000 m a.s.l. This region is facing severe effects of climate change, with an increase of annual average air temperature in the Alpine areas of Salzburg as high as 1.8 °C (2011 to 2020 vs. 1951 to 1990) (www.zamg.ac.at ↗). Based on

these data, Rödder et al. (2021) and Habel et al. (2022, 2023) already revealed changes in the diversity of butterfly and burnet moths due to land-use and climate change. These changes were most pronounced for mobile species and habitat generalists, which gained dominance in recent butterfly communities. Thus, we expect to see these traits also to be linked to altered phenologies. As increasing winter temperatures selectively affect species hibernating at different life stages (Fric et al., 2020, Teder, 2020, Larsen et al., 2024), we expected species hibernating as adults or as pupae to respond strongest to increasing temperatures in spring, as individuals in an advanced developmental stage might respond immediately to suitable temperatures.

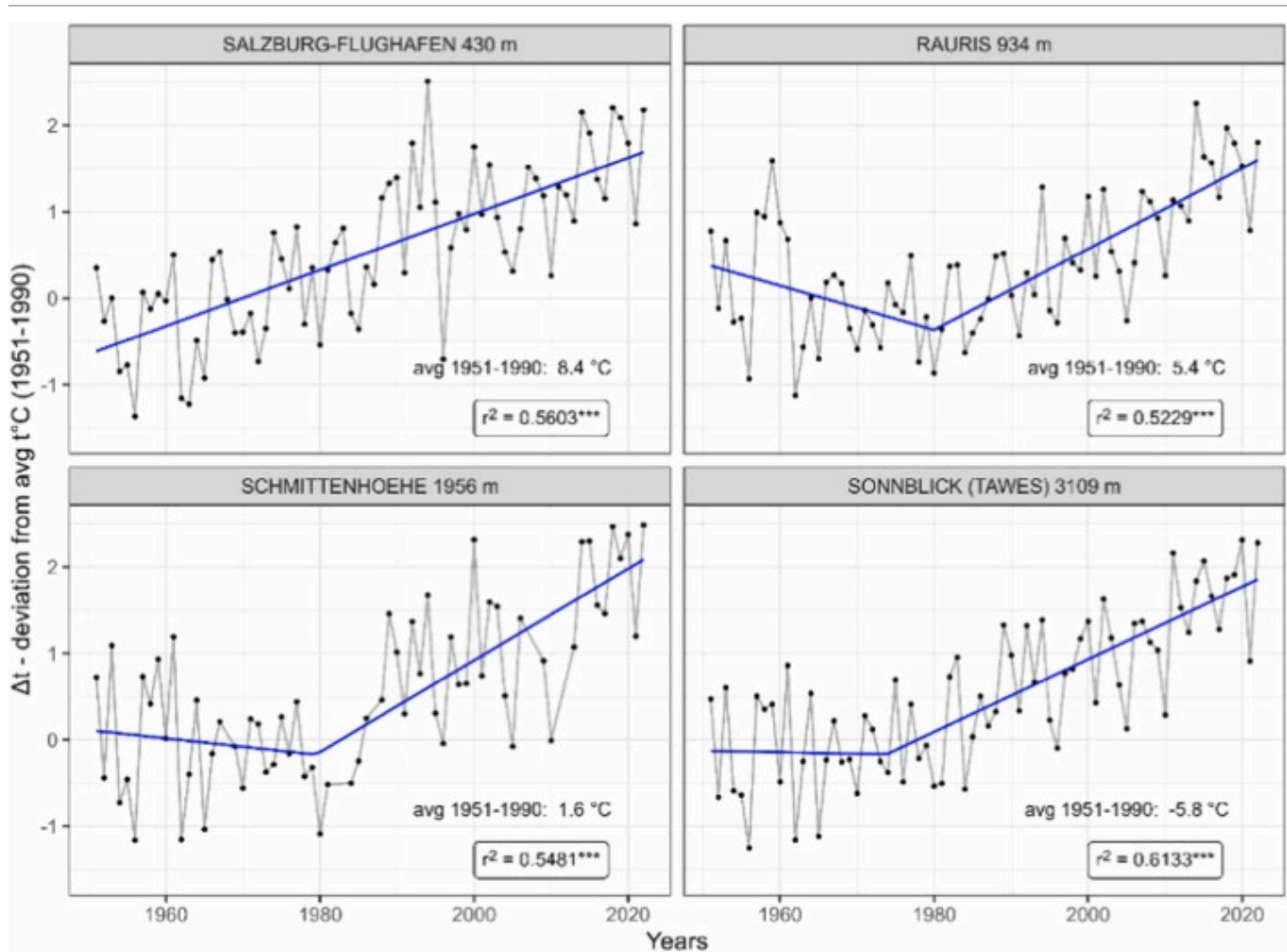
Here, we study annual phenologies and investigate whether and how ecological, behavioural, and life cycle traits of butterflies and burnet moths correlate with phenological shifts during the last decades. For this, we use climate data and museum records for the region of Northern Austria covering a period of four decades (two time windows 1980 to 2000 and 2001 to 2022). In addition, we compiled extensive trait data from literature for all species analysed. Based on these data, we address the following three research questions:

1. Which species appear earlier and/or later in the year?
2. Which traits are associated with phenological shifts?
3. Are these phenological shifts linked to altered climate regimes?

2. Material and methods

2.1. Climate data

Climate data covering the years 1960–2022 were compiled from four weather-stations located in the federal state of Salzburg (northern Austria), namely Salzburg Flughafen (430 m a.s.l.), Rauris (934 m a.s.l.), Schmittenhöhe (1956 m a.s.l.) and Sonnblick (3109 m a.s.l.) (Fig. 1). These data contain monthly records of average temperature t , precipitation r , sunshine s and ice days i (temperature all day < 0 °C). Data were provided by GeoSphere Austria, Bundesanstalt für Geologie, Geophysik, Klimatologie und Meteorologie (data hub hosted by Zentralanstalt für Meteorologie und Geodynamik ZAMG and Geologische Bundesanstalt GBA; [https://data.hub.geosphere.at/dataset/klima-v1-1m ↗](https://data.hub.geosphere.at/dataset/klima-v1-1m)). All raw data used for subsequent calculations are given in the Appendix S1.



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Fig. 1. Deviation of average yearly air temperature Δt for four weather stations 1951–2022. The straight lines refer to linear segmented regression with multiple potential breakpoints (Muggeo, 2008). Coefficients of determination R^2 (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and average air temperature 1951–1990 are provided.

We first looked at the climate data to assess when and to what extent climatic conditions started to change in our study area to deduce when we can expect butterflies to adjust their phenology. We identified changes in temperature trends at about 1980, with higher estimated trends in the last decades for higher elevations (Fig. S1). In consequence, we only considered butterfly data since the year 1980 in our subsequent analyses. We tested for identically distributed climatic trends among seasons and stations (see Burchett et al., 2017) and found strongest increases in temperature during spring and summer with modelled temperature increases of up to 0.8 °C per decade at higher altitudes (Fig. S1). Including additional weather parameters pointed to altitude specific changes in climate (Fig. S2, S3). Consequently, we performed our analyses separately for three different elevation levels:

hilly areas 380–800 m a.s.l., montane areas 801–1500 m a.s.l., (sub)alpine areas >1500 m a.s.l.

2.2. Butterfly data

We used the data of Habel et al. (2023a) on Lepidoptera (butterflies and burnet moths) recorded in the federal state of Salzburg (northern Austria), which were provided by the entomological collection of the “Haus der Natur” museum of natural sciences in Salzburg ([https://www.hausdernatur.at/en/ ↗](https://www.hausdernatur.at/en/)). These data were collected by different professional and citizen entomologists, and kept as collections, observation lists and field books. The raw data are provided as a figshare data set by Ulrich et al. (2023). For this study, we exclusively used those species for which detailed trait information exist, and which can also be determined without higher risks of errors. Therefore, for Zygaenidae, we only included burnet moth species, i.e. the subfamily Zygaeninae, while forester moths, i.e. subfamily Procridinae, were excluded as they are difficult to identify to species level and thus records might be incomplete and incorrect. For each of the three altitudinal bands (as defined above), we organised the data into annual time series at a daily basis and used only those species' time series containing at least 50 records in total. We did not consider sightings from December to February to avoid recordings of individuals during hibernation. In total, the reduced data contained 49,133 single records of imagines of 122 species of butterflies and Zygaenid moths, covering the time period 1980 to 2022 and the altitudinal range 381—3029 m a.s.l. For each record, exact date (day, year) and location (GPS-coordinates) were available (see Ulrich et al., 2023).

2.3. Traits

We compiled detailed information on the ecology and behaviour for all butterfly and burnet moth species (hereinafter referred to as butterflies). We took the following parameters into account: Habitat preference of imagines (ubiquist, (sub)alpine grassland sensu lato, forest, lower altitude grassland and shrubs, wetland), generalist vs. specialist (based on food plant specialisation and habitat demand), dispersal behaviour (sedentary, mobile, highly mobile, migratory), nutrient richness of imaginal habitats (eu-, meso-, oligotrophic), and phagy of larvae (mono-, oligo-, polyphagous). Additionally, we used information about the hibernation of species (hibernation as imagines, pupae, larvae, and/or eggs) and further details about hibernation and larval ecology: Hibernation in 1) stratum, 2) as single larva or in groups, 3) as larvae in webs, 4) creation of a webs during the first larval stage (L1), or creation of leaf bags, 5) type and location of egg oviposition, 6) type of larval food plant, and 7) type of pupae. All trait data were taken from literature (Weidemann, 1986,

Weidemann, 1988, Bink, 1992, Bräu et al., 2013, Stettmer et al., 2022) and adjusted to local conditions of our study area by PG. The classification of traits and species-specific classifications are listed in [Appendix S2](#).

2.4. Statistics

2.4.1. Testing method

Multivariate comparisons of phenological data across species traits were done using non-parametric F-approximations of Wilks' Lambda test statistics (hereafter npmv test, implemented in the R-package npmv, [Liu et al., 2011](#), [Burchett et al., 2017](#)). This test is a non-parametric, highly robust version of MANOVA with a rank-based variation on Wilks' Lambda, which does not require multivariate normality. It is designed for small, multivariate samples, and relies on the F-approximation by [Rao \(1951\)](#). The test is performed under the null hypothesis of identical multivariate distributions.

2.4.2. Butterfly data

To answer our first starting question, we calculated for each species and altitudinal band the difference of the first three and last three observations in spring and last three observations in autumn in year t (D_t^s and D_t^a , respectively) from the mean first and last observation of all years ($\overline{D^s}$ and $\overline{D^a}$), i.e. the deviation $\Delta D_t^s = D_t^s - \overline{D^s}$ and $\Delta D_t^a = D_t^a - \overline{D^a}$ in days. To ensure that these estimations are not biased, we compared our results taking either the first two sightings per year or the first three: For all combinations of species \times altitudinal band, 96.9% of the comparisons resulted in the same decision of “significant” vs. “not significant” for first sightings and 98.8% for last sightings. To identify all species appearing significantly earlier in spring and later in autumn, we compared the deviation in spring and autumn, ΔD_t^s and ΔD_t^a , in the two time windows t_1 (1980–2000) and t_2 (2001–2022) according to our climate analysis results, using non-parametric testing with a univariate response, with a resulting p-value for each species \times altitudinal band combination.

To answer the second question about which ecological traits might influence butterfly phenology, we performed several steps for producing a high quality, interpretable model. First, we analysed associations of phenology shifts with traits. To identify relevant traits that explain differences in phenology shifts, we calculated the difference in mean first (and last) sighting in both time windows (unstandardised effect size), $\overline{\Delta D_{t_2}^s} - \overline{\Delta D_{t_1}^s}$ and $\overline{\Delta D_{t_2}^a} - \overline{\Delta D_{t_1}^a}$. This yields a shift in days per species, which, in turn, can be used to test for identical multivariate distributions of the first and last shifts among traits. We used npmv to identify traits that did not vary significantly ($p > 0.05$) among the two time windows.

Consequently, these traits were not considered for models to explain first or last butterfly sightings.

We built three models: a simple linear regression model without random effect (LM_first and LM_last), a LMM with all potential predictors as stated above (LMM_first_0 and LMM_last_0) and a LMM with reduced predictors (LMM_first_1 and LMM_last_1), using backwards elimination of random and fixed terms with the Satterthwaite approximation of degrees of freedom and F-tests ($\alpha = 0.05$; [Satterthwaite, 1946](#), [Bates et al., 2015](#), [Kuznetsova et al., 2017](#)). An overview of all models is provided in [Appendix S3](#). Aiming at a model fully explaining the phenology of butterflies via traits and meteorological data seems overly ambitious. Moreover, unaccounted variance can reduce the power of tests on the predictors and increase the risk of Type I errors ([Barr, 2013](#)). Therefore, species' identity was included in the models as a random effect to account for species-specific effects not explained by the provided traits, including random slopes with all meteorological variables (third starting question), allowing for different reactions to climate change for each species. D_t^s and D_t^a values per species \times year \times altitudinal band served as dependent variables in the LMM models ($N = 4497$). As baseline fixed predicting variables, we chose the significant traits identified by npmv tests (autumn activity, dispersal, generalist, generations per year, habitat as imago, habitat as larva, hibernation stage, hibernation strata, larval nutrient, and pupal type), elevation, the number of annual records n , and the weather variables Δt , Δs , and Δr in winter and spring for first sightings, as well as summer and autumn for last sightings.

All models were cross-validated, to quantify potential overfitting. The models were built on data until 2009 and tested on data after 2010. Reported model quality criteria include conditional R^2 ([Nakagawa et al., 2017](#)), the mean absolute error (MAE) on training and test data and the Akaike information criterion (AIC). For the final models, we reported the coefficients as unstandardised effect sizes, standard error, the estimated degrees of freedom with Satterthwaite's method ([Satterthwaite, 1946](#)), Wald t-statistics, p-value and partial η^2 based on the F-values of ANOVA type II ([Friedman, 1982](#), [Ben-Shachar et al., 2020](#)).

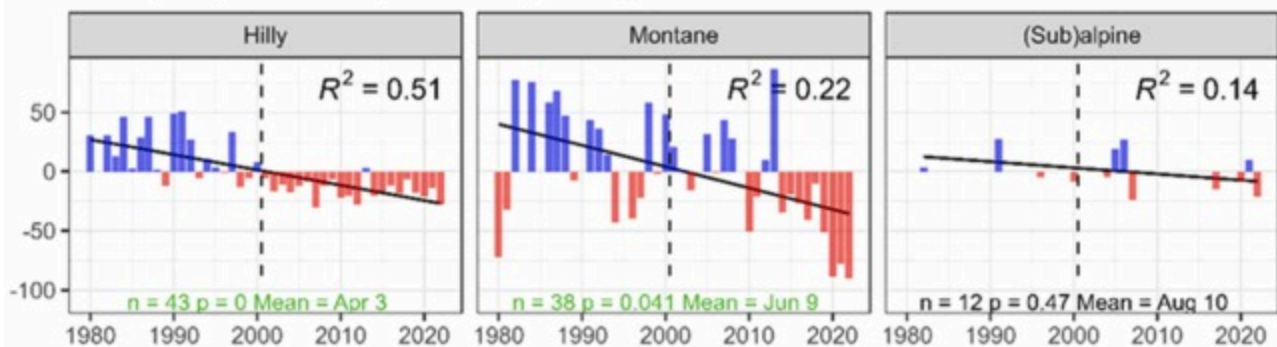
3. Results

3.1. Phenological shifts

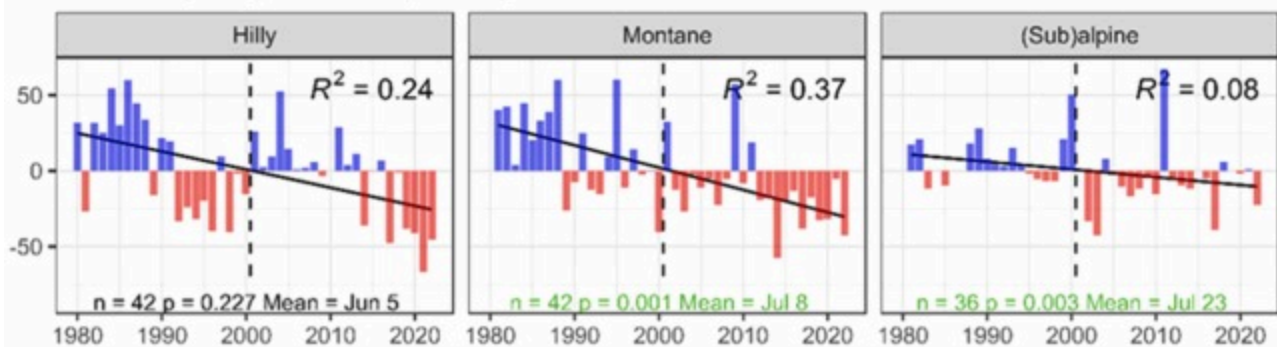
A total of 52 out of 122 species appeared significantly earlier in spring, 33 % in hilly, 54 % in montane and 13 % in (sub)alpine areas, with a mean prior appearance trend of 1.1 days per year. Only 9 species showed significantly later appearance, 6 in hilly and 2 in montane areas,

with a mean later appearance trend of 1.1 days per year. Shifts in (sub)alpine areas were not detectable for late sightings. When comparing the two time windows, the first observations on average appear 10.5 days earlier in the second time window. Last sightings in autumn have shifted on average to earlier dates, but only by about 4.7 days. This trend does not apply to all species and across all altitudes equally. Strongest phenological shifts in spring occurred in the hilly and the montane region and were particularly observed for *Nymphalis antiopa*, *Polygonia c-album*, *Gonepteryx rhamni*, *Vanessa atalanta*, *Parnassius apollo*, *Aglais urticae*, *Callophrys rubi*, *Plebejus argus*, *Pieris rapae*, *Thymelicus lineola*, and *Aglais io* (sorted by descending phenological response). We found no significant differences in the responses between butterflies and burnet moths. Examples of the yearly phenological shifts are shown for four common butterfly species in [Fig. 2](#). A complete overview of first and last observations for all butterflies is given in the electronic [appendices S4 and S5](#).

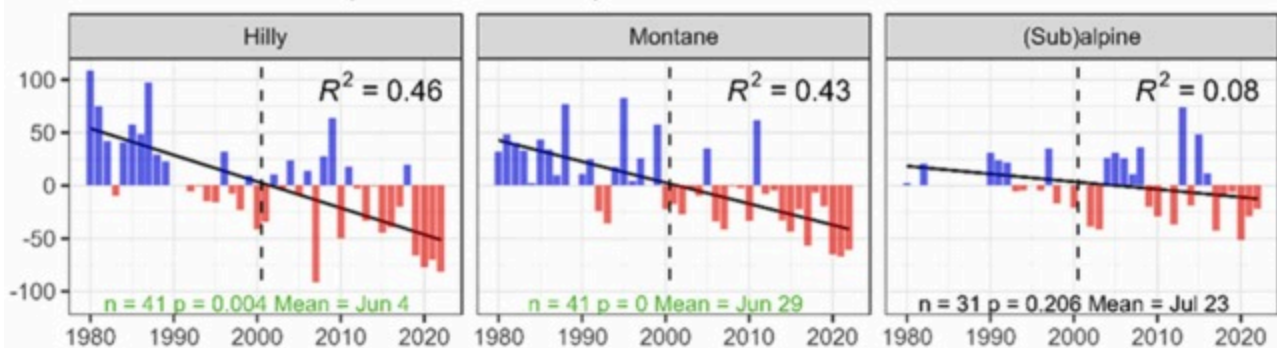
Gonepteryx rhamni (Linnaeus, 1758)



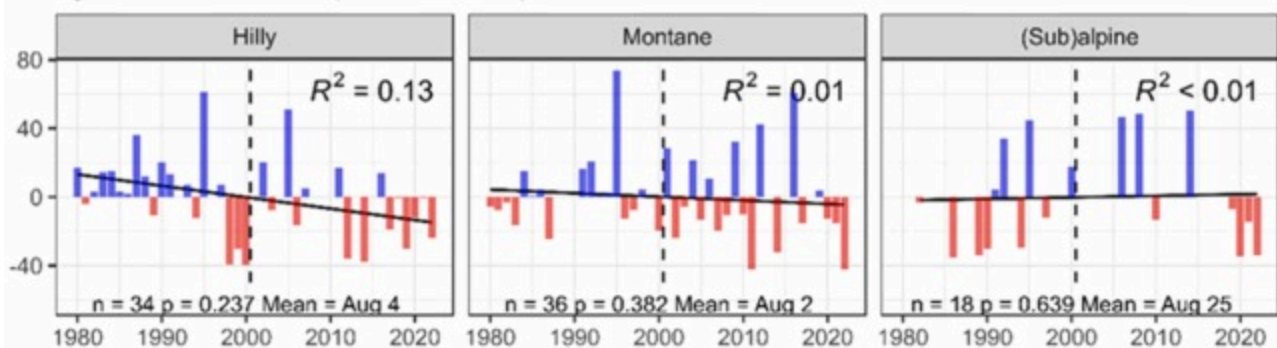
Pieris rapae (Linnaeus, 1758)



Vanessa atalanta (Linnaeus, 1758)



Lysandra coridon (Poda, 1761)



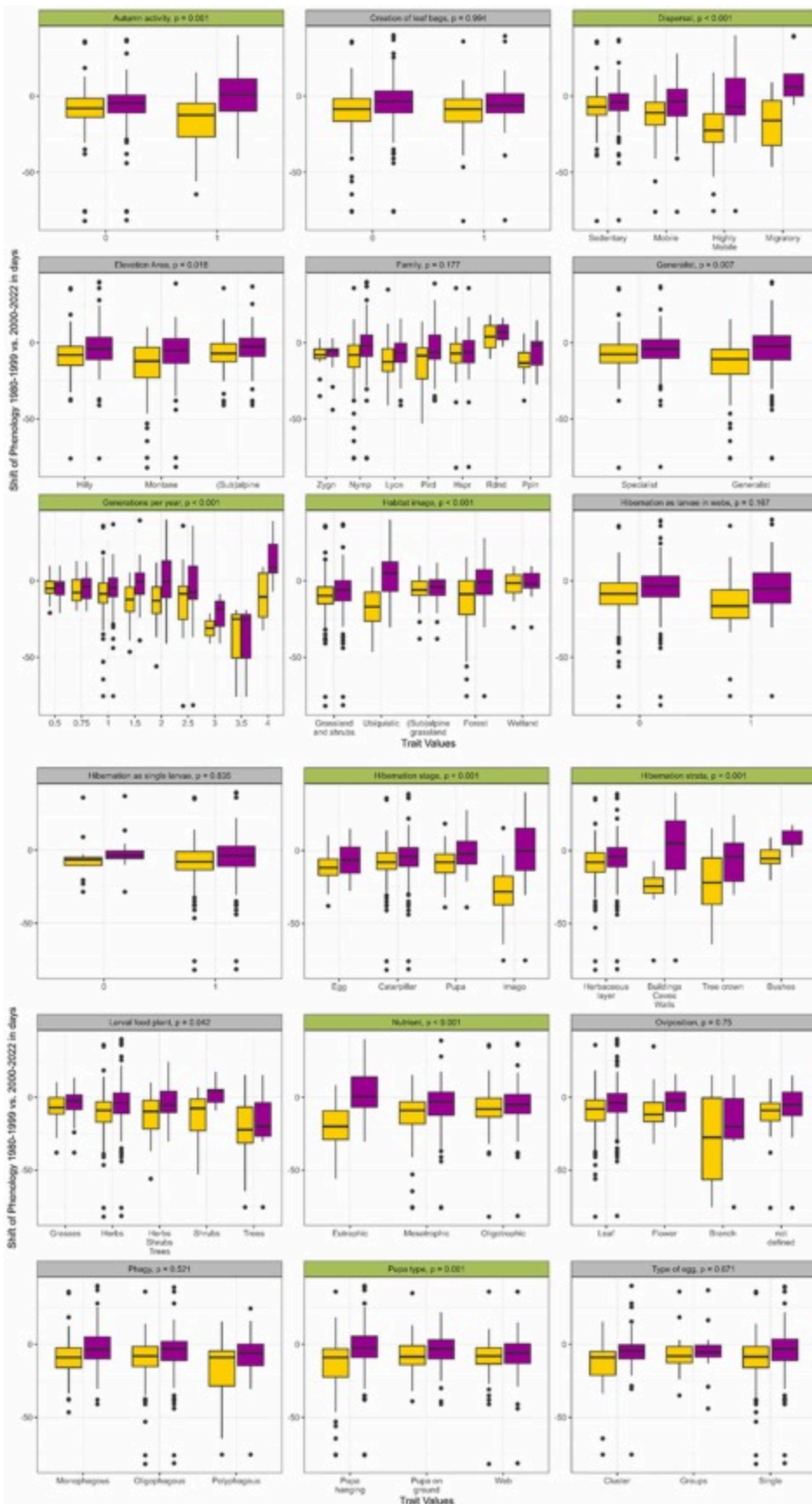
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Fig. 2. Deviation of first observations per year from the mean first observation of all years in days (ΔD_t^s) illustrated for four typical butterfly species showing phenological shifts (*Gonepteryx rhamni*, *Pieris rapae*, *Vanessa atalanta*, *Lysandra coridon*); deviations earlier than mean in red, later in blue. The results of non-parametric testing for identically distributed deviations between the periods 1980 to 2000 and 2001 to 2022 are summarised at the bottom of the panels (n = testing sample size, significant results in green, i.e. $p < 0.05$). The vertical dashed line depicts the separation of the time windows, R^2 of linear regression lines is given in the top right corner.

3.2. Modelled phenology

Hibernation type, oviposition, and phagy did not have a significant influence on phenology shift. The strongest effects had elevation, dispersal, hibernation stage, deviation of temperature and sun hours in spring (Fig. 3). Partial η^2 effect sizes indicated the strongest effects for elevation, dispersal, hibernation stage, as well as deviation of temperature and sun hours in spring. The coefficient for highly mobile butterflies indicates a less pronounced shift to earlier sightings than for other dispersal categories. For the last sightings, the effect sizes of elevation and climate deviations are comparatively small. Most interestingly, predictor elimination only left a random intercept but no random slopes, which accounts for the interaction of species with climate change (Table 1, Table 2, Table 3). When calculating the joint effects of hibernation stage + dispersal + random effect, we obtain an average effect of +29.5, +11.1, +9.6 and -0.2 days of earlier sighting in spring for migratory, highly mobile, mobile, and sedentary species, respectively, corresponding to the expected shifts from comparing the two time windows.



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Fig. 3. Phenology changes of first sightings (yellow, $\overline{\Delta D}_{t_2}^s - \overline{\Delta D}_{t_1}^s$) and last sightings (purple, $\overline{\Delta D}_{t_2}^a - \overline{\Delta D}_{t_1}^a$) between the time windows t_1 (1980–2000) and t_2 (2001–2022) in days depending on different traits. Box plots showing medians, upper and lower quartiles, whiskers (= 1.5 times interquartile range), and outliers. Testing for identical distributions between categories was performed by using npmv tests from Burchett (2017). Considering that altogether 18 different traits and 2 outcomes are tested, we worked with a Bonferroni correction and considered the adjusted significance level of $0.05/36=0.00139$. The panel title is highlighted in green if the obtained p-value is below the adjusted significance level.

Table 1. Overview of all models (linear *LM* and linear mixed *LMM*). Dependent variables: first and last sighting per year × species × altitudinal band combination; resulting output R^2 , mean absolute error (MAE) and Akaike Information Criterion (AIC).

Model	Predictors	R^2 (fixed + random)			
		MAE train	MAE test	AIC	
LM_first	$\Delta t_{\text{Winter}} + \Delta t_{\text{Spring}} + \Delta r_{\text{Winter}} + \Delta r_{\text{Spring}} + \Delta s_{\text{Winter}} + \Delta s_{\text{Spring}} + \text{Elevation} + n + \text{Nutrient} + \text{Habitat}_{\text{imago}} + \text{Habitat}_{\text{larvae}} + \text{Generalist} + \text{Dispersal} + \text{Hibernation}_{\text{stage}} + \text{Hibernation}_{\text{strata}} + \text{Generations}_{\text{per_year}} + \text{Pupa}_{\text{type}} + \text{Autumn}_{\text{activity}}$	0.50	18.5	19.7	41671
LMM_first_0	$(\Delta t_{\text{Spring}} \text{Taxonomy}) + (\Delta s_{\text{Spring}} \text{Taxonomy}) + (\Delta r_{\text{Spring}} \text{Taxonomy}) + (\Delta t_{\text{Winter}} \text{Taxonomy}) + (\Delta s_{\text{Winter}} \text{Taxonomy}) + (\Delta r_{\text{Winter}} \text{Taxonomy}) + \Delta t_{\text{Winter}} + \Delta t_{\text{Spring}} + \Delta r_{\text{Winter}} + \Delta r_{\text{Spring}} + \Delta s_{\text{Winter}} + \Delta s_{\text{Spring}} + \text{Elevation} + n + \text{Nutrient} + \text{Habitat}_{\text{imago}} + \text{Habitat}_{\text{larvae}} + \text{Generalist} + \text{Dispersal} + \text{Hibernation}_{\text{stage}} + \text{Hibernation}_{\text{strata}} + \text{Generations}_{\text{per_year}} + \text{Pupa}_{\text{type}} + \text{Autumn}_{\text{activity}}$	0.62 (0.49 + 0.13)	15.4	20.6	40749
LMM_first_1	$(\Delta t_{\text{Spring}} \text{Taxonomy}) + (\Delta s_{\text{Spring}} \text{Taxonomy}) + \Delta t_{\text{Winter}} + \Delta t_{\text{Spring}} + \Delta r_{\text{Winter}} + \Delta s_{\text{Spring}} + \text{Elevation} + n + \text{Dispersal} + \text{Hibernation}_{\text{stage}}$	0.62 (0.48 + 0.13)	15.4	17.2	40793
LM_last	$\Delta t_{\text{Summer}} + \Delta t_{\text{Autumn}} + \Delta r_{\text{Summer}} + \Delta r_{\text{Autumn}} + \Delta s_{\text{Summer}} + \Delta s_{\text{Autumn}} + \text{Elevation} + n + \text{Nutrient} + \text{Habitat}_{\text{imago}} + \text{Habitat}_{\text{larvae}} + \text{Generalist} + \text{Dispersal}$	0.34	18.8	20.3	41938

Model	Predictors	R ² (fixed + random)	MAE train	MAE test	AIC
	+ Hibernation_stage + Hibernation_strata + Generations_per_year + Pupa_type + Autumn_activity				
LMM_last_0	($\Delta t_{\text{Summer}} _{\text{Taxonomy}}$) + ($\Delta t_{\text{Autumn}} _{\text{Taxonomy}}$) + ($\Delta r_{\text{Summer}} _{\text{Taxonomy}}$) + ($\Delta r_{\text{Autumn}} _{\text{Taxonomy}}$) + ($\Delta s_{\text{Summer}} _{\text{Taxonomy}}$) + ($\Delta s_{\text{Autumn}} _{\text{Taxonomy}}$) + Δt_{Summer} + Δt_{Autumn} + Δr_{Summer} + Δr_{Autumn} + Δs_{Summer} + Δs_{Autumn} + Elevation + n + Nutrient + Habitat_imago + Habitat_larvae + Generalist + Dispersal + Hibernation_stage + Hibernation_strata + Generations_per_year + Pupa_type + Autumn_activity	0.51 (0.30 + 0.21)	15.3	19.0	40883
LMM_last_1	(1 Taxonomy) + Δt_{Summer} + Δt_{Autumn} + Δr_{Summer} + Δr_{Autumn} + Δs_{Summer} + Elevation + n + Habitat_larvae + Dispersal + Hibernation_stage	0.50 (0.27 + 0.23)	15.5	17.3	40918

Table 2. Linear mixed model *LMM_first_1* with estimates of the coefficients, standard error, estimates of degrees of freedom (df), t-statistic, p-value and partial η^2 , N = 4497.

Predictor		Estimate	Std.Error	df	t-value	Pr(> t)	
(Intercept)		192.39	13.22	105.69	14.55	<0.001	-
Elevation		0.03	<0.001	4048.18	33.64	<0.001	0.22
Dispersal	Mobile	-20.84	13.45	104.91	-1.55	0.124	0.15
	Highly mobile	-9.39	15.21	104.17	-0.62	0.548	
	Sedentary	-30.28	13.30	104.89	-2.28	0.025	
Hibernation stage	Egg	12.14	3.79	112.24	3.20	<0.001	0.39
	Imago	-44.84	8.38	102.66	-5.35	<0.001	
	Pupa	-27.70	4.27	112.75	-6.48	<0.001	
Δt	Winter	1.07	0.21	4358.00	5.01	<0.001	0.01
Δt	Spring	-5.17	0.37	737.82	-14.08	<0.001	0.21

Predictor		Estimate	Std.Error	df	t-value	Pr(> t)	η^2
Δr	Winter	0.08	0.02	4353.69	4.42	<0.001	<0.01
Δs	Spring	-0.11	0.01	402.04	-8.35	<0.001	0.15
N		-0.85	0.04	4391.14	-22.33	<0.001	0.10

Table 3. Linear mixed model *LMM_last_1* with estimates of the coefficients, standard error, estimates of the degrees of freedom (df), t-statistic, p-value and partial η^2 , N = 4497.

Predictor		Estimate	Std. Error	df	t-value	Pr(> t)	η^2
(Intercept)		179.35	6.62	108.14	27.08	<0.001	-
Elevation		0.01	<0.001	4335.34	16.47	<0.001	0.06
Habitat_larvae	Grasses	2.43	6.98	104.38	0.35	0.728	0.11
	Herbs	-1.30	6.67	104.47	-0.20	0.846	
	Shrubs	15.99	11.01	106.10	1.45	0.149	
	Trees	-20.60	9.54	106.67	-2.16	0.033	
Dispersal	Migratory	45.42	15.04	101.11	3.02	<0.001	0.26
	Mobile	14.87	3.32	105.08	4.48	<0.001	
	Highly mobile	35.63	8.93	101.35	3.99	<0.001	
Hibernation_stage	Egg	8.53	4.30	106.09	1.98	0.050	0.25
	Imago	-23.94	10.00	101.39	-2.39	0.018	
	Pupa	-25.53	4.90	106.25	-5.21	<0.001	
Δt	Summer	-3.55	0.35	4415.84	-10.09	<0.001	0.03
Δt	Autumn	2.47	0.35	4411.78	6.97	<0.001	0.01
Δr	Summer	-0.05	0.01	4413.19	-4.36	<0.001	<0.01
Δr	Autumn	-0.09	0.01	4414.15	-6.21	<0.001	0.01
Δs	Summer	-0.04	0.01	4413.52	-4.09	<0.001	<0.01
N		0.77	0.04	4460.58	20.37	<0.001	0.07

4. Discussion

The ecological and behavioural performance of a species strongly determines the response to climate change. Hence, our trait analyses showed that responses particularly depend on the developmental stage, in which butterflies hibernate, with species hibernating as adults or pupae exhibiting the strongest phenological shifts. As individuals of such imaginal overwintering species as *Polygonia c-album*, *Gonepteryx rhamni*, *Vanessa atalanta*, *Aglais urticae*, and *Aglais io* become active during the first days of the year offering mild and sunny weather, they immediately respond to the conditions during early spring (cf. [Ebert and Rennwald 1991](#)) and hence clearly adapt their phenologies to the ongoing climatic changes. Phenology shifts also exist for migratory species; some of them do not travel back to the Mediterranean region any longer, but overwinter successfully in Central Europe, such as *Vanessa atalanta* ([Kühn, 2019](#)). Consequently, adults of this particular species are flying even during warm winter days. Furthermore, species overwintering as pupae also showed substantial phenological shifts. Higher spring temperatures drive the earlier eclosion of the butterflies from the chrysalis, and they therefore are observed now considerably earlier in the year than in the past, with prominent examples like *Callophrys rubi*, *Plebejus argus*, and *Pieris rapae*. Furthermore, the type of pupae might also impact potential phenological responses during early spring. Species with pupae freely hanging in the vegetation and hence being more exposed to environmental temperatures are responding stronger to climate change than species that pupate in the litter or in a cone (hereby sheltering them more from environmental conditions).

Generalist species at large showed stronger phenological shifts than specialists. The majority of these generalist species show strong dispersal behaviour, cover large distribution ranges, and are bi- or multivoltine ([Bartonova et al., 2014](#)). Thus, as a rule of thumb, generalists have higher ecological plasticity, and hence exhibit a higher level of adaptability to environmental changes. Moreover, most generalist species hibernate in a more advanced developmental stage (such as pupae or even imagines) ([Börschig et al., 2013](#)). These mentioned factors are pre-conditions for earlier occurrence in spring, as also shown by our analyses. In line with this, generalist butterflies also show stronger latitudinal shifts in their distributions in reaction to global warming than specialist butterflies ([Fox et al., 2007](#), [Habel et al., 2024](#)).

In line with [Habel et al. \(2024\)](#), who were more generally analysing data from our study region for butterflies and moths with more species of the latter included, we found no generally prolonged autumn flight periods in butterflies here, but nonetheless significant shifts to later activity for some of their species, such as *Aglais io*, *Vanessa atalanta*, *Colias*

croceus, *Araschnia levana*, *Pieris rapae*, *Aglais urticae*, *Polygonia c-album*, *Limenitis camilla*, and *Pyrgus malvae* (sorted by descending phenological response).

Later flight activities in the lower altitudes also might be explained by specific performance of species. The last sightings' linear mixed model (*LMM_last_1*, [Table 3](#)) revealed that particularly species with high dispersal capacity (i.e. migratory and mobile species) and species with their larvae feeding on shrubs appear consistently later in autumn. This also applies to species that overwinter as adults (e.g. *Aglais io*, *Vanessa atalanta*, *Aglais urticae*, *Polygonia c-album*) and species that, in the wake of mild winters, shift from migratory to non-migratory behaviour, such as *Vanessa atalanta*. All these species nowadays are observed until late in autumn. In addition, some few species also develop additional generations in response to prolonged vegetation periods, such as *Pieris rapae* and *Parage aegeria*. However, non-stop development is rare in butterflies, as the development of the pupae and the start of hibernation (but also summer-diapause) for most species is triggered by day-length ([Schiesari and O'Connor, 2013](#)), and thus might only rarely be driven by changes in autumn climatic conditions.

Ecological performance of species hence has major influence on phenological responses. However, the responses in spring and autumn, often being significant for the hilly and montane altitudinal level, were not observed at higher altitudes above 1500 m a.s.l. This finding goes in line with other studies underlining that phenological shifts still mainly occur at lower elevations ([Habel et al., 2024](#)). This might be due to much longer vegetation periods at lower elevations, which offer longer time periods to respond to changing environmental conditions. At higher elevations where the vegetation period is restricted to a narrow time window, most species, in contrast, eclose mostly simultaneously and thus the imagines largely overlap temporally in their flight periods, not allowing the separation between typical spring and summer species or generations ([Stettmer et al., 2022](#)). This time window apparently is still not shifting, most likely due to the influence of the length of snow cover, which at high elevations is more triggered by precipitation than by temperature, and possible shifts from biannual to annual cycles ([Habel et al., 2024](#)).

Climatic conditions have already changed considerably in our study area, hence these changes most likely are the main driver for the observed phenological shifts. However, the different seasons are affected in different ways by climate change what can lead to varying reactions of species. For example, the considered climatic data revealed a significant increase in temperature and sunshine hours in spring, well going in line with our analyses. This underlines that spring climate changes might well explain the respective phenological shifts at the beginning of the butterfly flight season. On the other hand, phenological effects

in autumn are much less pronounced than in spring, because temperatures in autumn increased considerably less than in spring; in addition, rainfall is tending to increase, sunshine to decrease. Hence, the observed autumn changes are less suitable for longer butterfly occurrence than spring changes are for earlier appearance. Furthermore, while higher temperatures in autumn were modelled to cause shifts to later activity, higher temperatures in summer and more rain in both seasons are influencing autumn generations to appear earlier in the year. In consequence, multivoltine species could potentially develop additional generations in the now warmer autumn months, but they still might not have sufficient time for doing so. Another reason for earlier last records might be that last generations are shifting to earlier dates because all preceding generations have appeared earlier in reaction to warmer spring and summer temperatures.

Our study hence provides clear trends and shows significant correlations between the ecological characteristics of species and their respective responses to climatic changes. However, we also have to point out several potential shortcomings when interpreting our obtained results. The different sample sizes available for each species per time period is challenging. It has to be argued that extended flight activity during spring and autumn is more likely to be observed for years represented by larger sample sizes. However, this bias should be mostly consistent over the entire study period. We considered this challenge by using modified versions of first and last sightings as explained in material and methods section, with always obtaining rather similar results, hence supporting the validity of our results. Furthermore, the sample size n per species \times year \times altitudinal band was included as predictor in the LMMs to allow some of the variance to be explained by the varying number of individuals recorded.

Author contribution

All authors developed the idea, PG, TS and JCH compiled the data, ML, WU, and WT performed statistical analyses, all authors contributed while interpreting the results and writing the manuscript.

Declaration of Competing Interest

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

Appendix A. Supplementary material

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Data Availability

Data will be made available on request.

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