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Population ecology

Species with more volatile population dynamics are differentially impacted by weather

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Climatic variation has been invoked as an explanation of population dynamics for a variety of taxa. Much work investigating the link between climatic forcings and population fluctuation uses single-taxon case studies. Here, we conduct comparative analyses of a multi-decadal dataset describing population dynamics of 50 co-occurring butterfly species at 10 sites in Northern California. Specifically, we explore the potential commonality of response to weather among species that encompass a gradient of population dynamics via a hierarchical Bayesian modelling framework. Results of this analysis demonstrate that certain weather conditions impact volatile, or irruptive, species differently as compared with relatively stable species. Notably, precipitation-related variables, including indices of the El Niño Southern Oscillation, have a more pronounced impact on the most volatile species. We hypothesize that these variables influence vegetation resource availability, and thus indirectly influence population dynamics of volatile taxa. As one of the first studies to show a common influence of weather among taxa with similar population dynamics, the results presented here suggest new lines of research in the field of biotic–abiotic interactions.

1. Introduction

The mechanisms that determine population dynamics have enjoyed a great deal of attention from ecologists, primarily in the form of a lengthy debate about the relative roles of density-dependent and density-independent processes in determining observed dynamics (e.g. [1–4]). This dialogue has resulted in widespread appreciation for the importance of both classes of processes. For example, the importance of climatic variation as a density-independent driver of population dynamics is now an amply supported tenet of population ecology, particularly for short-lived invertebrates with high vital rates (e.g. [5–15]). The link between weather and population dynamics has received renewed interest in recent decades because of the pressing need to predict organismal responses to climate change [12].

Much work documenting the influence of weather on population dynamics does go through examination of single-taxon-by-weather interactions (e.g. [2,4,5]). Inferences made from these analyses, while informative, are necessarily limited to the taxon under examination. Comparative analyses describing common responses to weather across taxa are relatively rare and have typically sought to identify similar responses to climatic variation among taxa grouped by shared morphology or life-history traits [6,8,11]. Here we take an unusual approach and index species in terms of population dynamics to search for common responses to weather across a spectrum of population volatility.
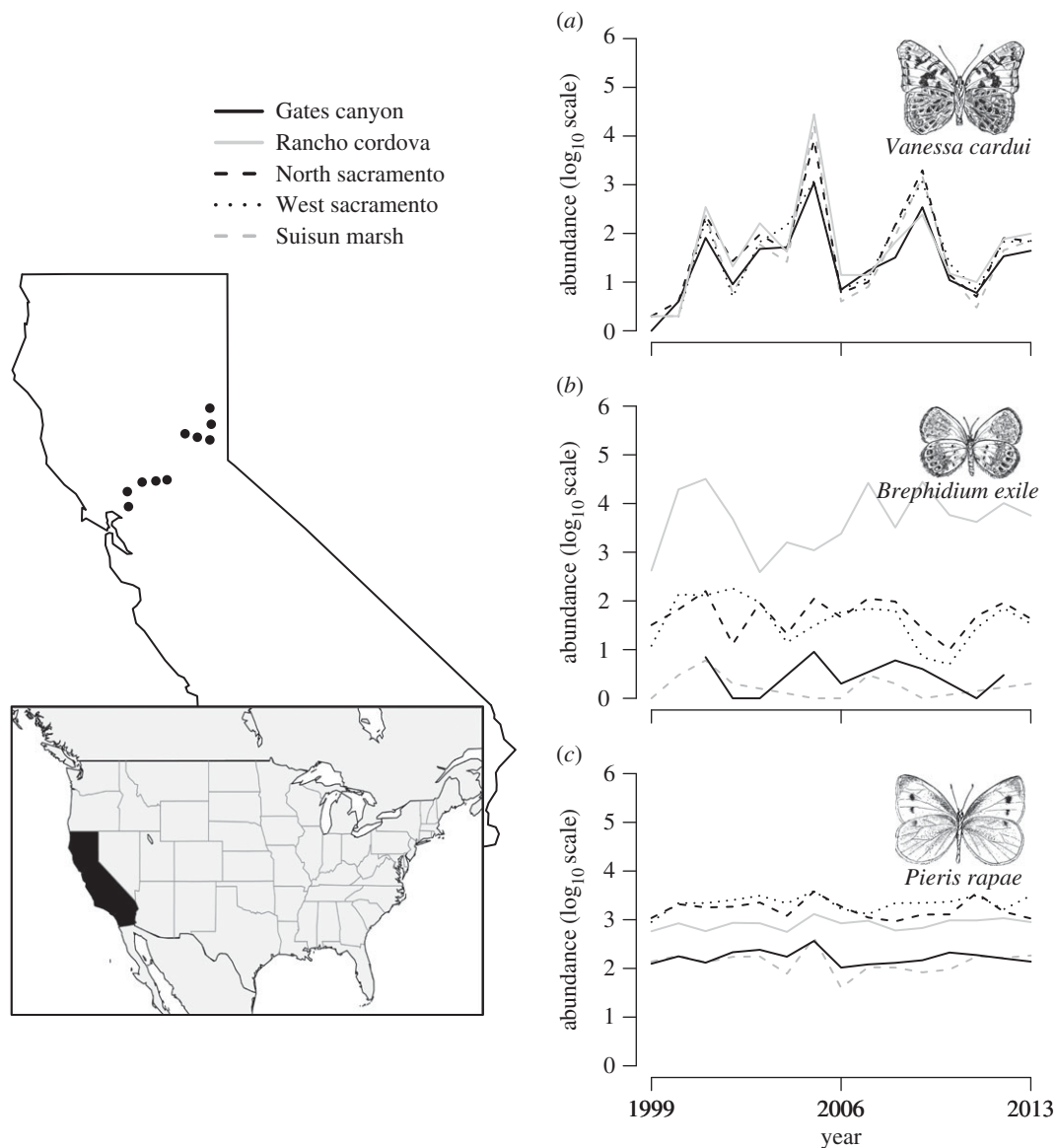
Figure 1. Map of study locations in Northern California, USA. Fifty butterfly species occurring at these locations were ranked by average population volatility. Inset are interannual time series showing the variation in population dynamics encompassed by these species. (*a*) *Vanessa cardui* was ranked the most volatile species; (*b*) *Brephidium exile*, the tenth most volatile and (*c*) *Pieris rapae*, the 49th most volatile. Time series constructed using count data from the five low-elevation sites. Illustrations: M.F.

Specifically, we use data describing population dynamics of 50 co-occurring butterfly species to ask: do species exhibiting similar population dynamics also exhibit a commonality of response to certain weather variables? An affirmative answer to this question can be predicted based on the oft-documented limitation of herbivorous insects by vegetation resource availability [2,4,7,10,13]. Weather may influence vegetation in terms of quality (i.e. new growth, flowering), phenology and quantity [2,4,5]. Consequently, weather may indirectly limit population size for herbivorous insects. Furthermore, the high vital rates of many insects allow them to quickly respond to weather-induced changes in vegetation, in effect 'tracking' vegetation resources; in some cases this may lead to 'overshooting' carrying capacity and subsequent rapid decline [7,10,13]. Thus, we reason, relatively volatile insect species might show a commonality of response to those weather conditions that particularly influence vegetation resources (e.g. heavy rainfall or drought). On the other hand, comparatively stable insect species should be less influenced by weather, because of

either intrinsic causes (e.g. low vital rates) that preclude 'tracking' resource change, or because their population sizes are primarily limited by some other factor besides resource availability (e.g. natural enemies). An alternative, or null, expectation is widespread species-specific responses to weather, resulting in few detectable patterns across taxa.

Our analyses use a multi-decadal, single observer dataset collected at 10 locations in Northern California comprised abundances and presence/absence data for butterflies. These data have previously been used to explore species-specific responses to weather at a single site [9] and document widespread declines across taxa [14]. We used these data to rank species in terms of volatility, from those with relatively stable populations to those exhibiting high interannual variation in density (study locations and example population histories in figure 1). Here we present analyses comparing the relative influence of weather across this spectrum of volatility to illuminate potential common responses to weather among volatile species.

2. Material and methods

The butterfly population data spans more than three decades (observations begin in 1972–1988, depending on the site; electronic supplementary material, table S1) and were collected by A.M.S. at 10 locations (figure 1), including multiple habitat types and encompassing an altitudinal gradient. Sites were visited every two weeks and detections (henceforth 'day positives') of butterfly species compiled for all sites and all years. Additionally, since 1999, counts of individuals have been collected at the low-elevation sites. The count data were used to calculate the coefficient of variation (CV) in abundance for each species resident at more than one site, and for which at least 100 individuals were observed over the course of the study (50 species). CV was then used as an index to rank species by relative population volatility (henceforth 'rank volatility'). Although species likely differ in detectability, any such differences do not appear to affect our analyses, as rank volatility was not correlated with overall abundance (e.g. very rare or abundant species are not outliers in term of volatility; see electronic supplementary material). Nonparametric analyses (Kruskal–Wallis tests and Spearman's rho) were used to investigate relationships between rank volatility and life-history traits. Traits examined included many of those commonly used to group butterflies including geographical range, wingspan, voltinism, overwintering life-history stage and host breadth. All life-history information was regionally specific.

The impact of climate on each species was examined via hierarchical Bayesian analysis in order to model the transect-wide influence of model variables through the utilization of site-specific weather data [9,15]. The model fit a binomial response consisting of the proportion of day positives to visits for a given year, thus accounting for variation in sampling effort among years. A separate model was constructed for each species. Model terms included site-specific, seasonal mean maximum and mean minimum temperatures and precipitation, year (to examine interannual population change) and annual indices of the El Niño Southern Oscillation (ENSO) [16]. For these sites and species, day positives are an effective index of abundance [17]. Day positives rather than counts were used for these analyses as the latter are useful for quantifying variation, but are limited to the years since 1999.

Analyses produced posterior probability distributions (PPDs) for species-specific regression coefficients describing the impacts of weather variables. Means from PPDs were used as point estimates of abiotic effects (means are appropriate given symmetrical PPDs). PPDs were also used to test for differential impacts of weather across rank volatility. To accomplish this, we calculated the correlation between PPD samples output by every iteration of the PPD sampling algorithm and rank volatility (Pearson's r). Correlation coefficients generated were tabulated, and the resulting frequency distributions examined, to assess the differential impact of weather across the spectrum of rank volatility while retaining uncertainty associated with PPD estimates.

To account for potential phylogenetic non-independence of species-specific results, we calculated phylogenetic independent contrasts [18] and used contrast-corrected data to repeat all analyses. Corrected data described non-normal distributions; consequently, Spearman's rank correlation was used to examine the relationship between those data and rank volatility.

3. Results

Our analysis successfully provided insight into the relationship between climatic variation and population dynamics for each species examined (electronic supplementary material, table S2). Species-specific parameter estimates varied widely,

however, several trends in the impact of model variables were noted. First, for most species, increased winter and spring precipitation negatively impacted day positives, while increased summer precipitation had the opposite effect. Second, almost every species examined appeared to be in decline.

Iterative correlation of rank volatility with samples representing PPDs for each model variable showed that certain variables differentially impacted more volatile species (figure 2; electronic supplementary material, table S3). Climate conditions with a high certainty of differentially and negatively impacting volatile species included: warmer mean minimum temperatures in the spring and autumn, warmer mean maximum temperatures in the winter, and heavier winter precipitation. Conditions that differentially and positively impacted volatile species included: warmer summer mean minimum temperatures, wetter springs and summers, and more marked ENSO events.

Rank-based correlation was used to repeat analyses using data corrected for phylogenetic autocorrelation. Analyses using corrected data showed similar directionality and relative correlation strength as uncorrected data examined using either rank-based or parametric correlation (electronic supplementary material, tables S3 and S4). Life-history variables were not significantly correlated with rank volatility.

4. Discussion

Our analysis demonstrated, with high certainty, differential impacts across rank volatility for 9 of the 14 weather variables examined (figure 2). With somewhat less certainty, rank volatility was associated with four of the remaining weather variables. Given that population trajectories of volatile species are by definition quite variable, we might expect statistical power to be inflated for these species. Thus, it is possible that heightened responsiveness to weather is simply more readily detected for volatile species relative to stable species. However, the commonality of response among volatile species to weather our analyses demonstrate would not be expected based solely on scaling volatility and statistical power.

Precipitation variables, in particular, showed dissimilar responses between volatile and stable species. For example, of variables considered, ENSO indices showed the greatest differential positive impact on volatile species. In Northern California, the ENSO causes unusual precipitation patterns [19]. Seasonal and local precipitation variables also differentially impacted volatile species during every season (less so for autumn compared with other seasons). Precipitation impacts host and nectar plant abundance, and may be a primary driver of vegetation resource availability, particularly in the water-limited Californian climate. In previous analyses of long-term data of butterfly populations subject to differing climate regimes, precipitation was also identified as a salient factor affecting butterfly abundance [9,11]. While correlative, our analyses add to existing work suggesting the possibility of ubiquitous indirect population limitation in insects through impacts of precipitation on host plants [4,5,7,10].

Understanding the effect of temperature variation on butterfly population dynamics is more challenging. Temperature may impact insects in numerous ways, both directly via physiological or behavioural changes, and indirectly through influencing interspecific interactions [20,21]. While temperature patterns in our results were less apparent, for many taxa we saw a change in sign between effects of maximum

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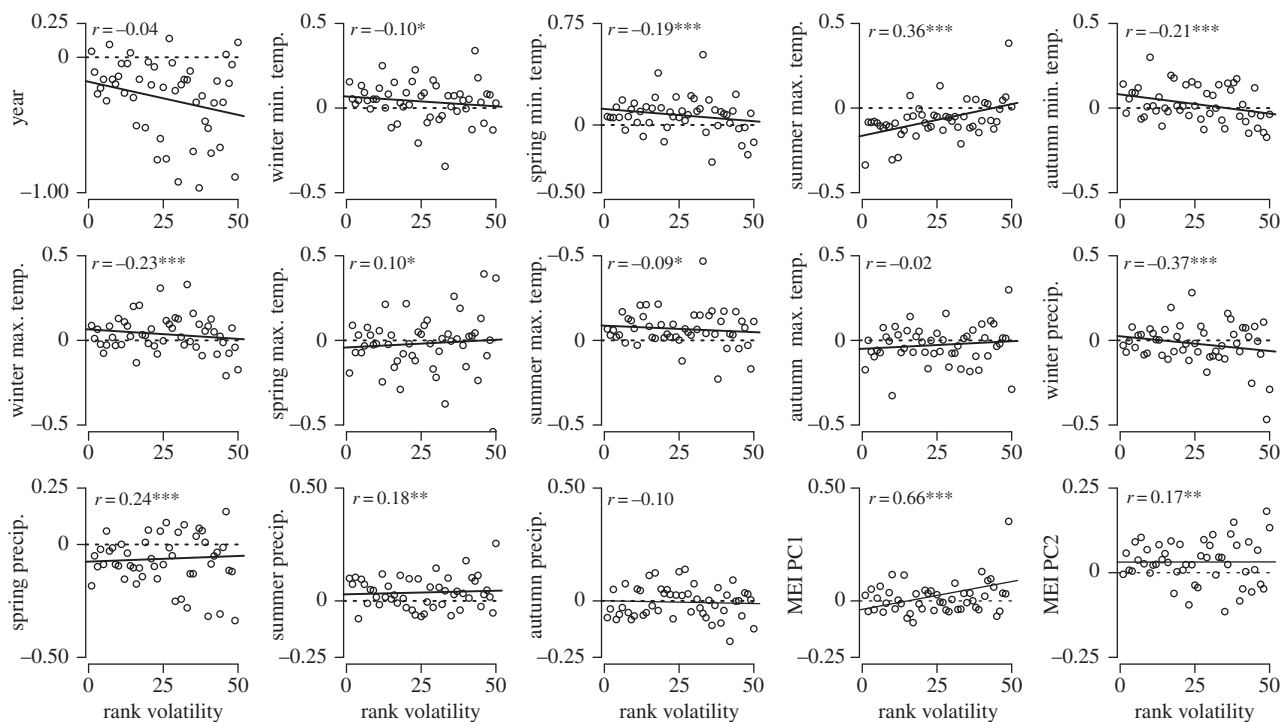
*certainty of non-zero correlation >85%, **>95% and ***>99%

Figure 2. Rank volatility is plotted against species-specific point estimates (open circles) of regression coefficients describing the impact of model variables. Correlation coefficients describe the differential impact of each variable across the spectrum of volatility. This illustrates which weather variables influence volatile species differently than stable species. The variables 'MEI PC1' and 'MEI PC2' are composite variables that act as indices of the El Niño Southern Oscillation. Trendlines (solid) and zero lines (dotted, showing where coefficients are equal to zero) are plotted for visualization.

and minimum temperatures in at least one season. For instance, *Poanes melane* was positively impacted by warmer minimum spring temperatures, but negatively impacted by warmer maximum spring temperatures. Given that maximum and minimum temperatures are changing at differing rates [22,23], this pattern demonstrates the importance of considering both variables in explorations of how climate change may impact organisms, as opposed to basing predictions solely on average temperatures.

In conclusion, our analyses used unparalleled data on western North American butterflies to show that species differing in terms of population dynamics may also predictably differ in their relationships with weather. Our results suggest a perspective that should be added to the usual search for common responses to weather among taxa grouped by natural history or life-history attributes. Future studies at larger

geographical scales and of additional taxonomic groups could adopt this perspective to determine the generality of common responses to weather among volatile taxa.

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