Unexpected phenological responses of butterflies to the interaction of urbanization and geographic temperature

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Abstract. Urbanization and global climate change can profoundly alter biological systems, yet scientists often analyze their effects separately. We test how the timing of life cycle events (phenology) is jointly influenced by these two components of global change. To do so, we use a long-term phenological data set of 20 common butterfly species from 83 sites across the state of Ohio, USA, with sites that range from rural undeveloped areas to moderately sized cities. These sites span a latitudinal gradient in mean temperature of several °C, mimicking the range of projected global climate warming effects through the end of the century. Although shifts toward earlier phenology are typical of species' responses to either global climate change or urbanization, we found that their interaction delayed several Ohio butterfly species' first appearance and peak abundance phenology. Exploitative species exhibited smaller delays in first appearance and peak abundance phenology in areas that were urbanized and geographically warm. Our results show that phenological responses to urbanization are contingent upon geographic variation in temperature, and that the impacts of urbanization and global climate change should be considered simultaneously when developing forecasts of biological responses to environmental change.

Key words: *anthropogenic change; citizen science; global climate change; impervious surface; Lepidoptera; nonadditive effects; phenology; physiology; temperature; trait-based modeling.*

Introduction

Shifts toward earlier phenology, the timing of life cycle events and a key indicator of biological responses to environmental change (IPCC 2007), have been found with urbanization (White et al. 2002, Neil and Wu 2006) and are among the most common responses to global climate change (Roy and Sparks 2000, Forister and Shapiro 2003, Stefanescu et al. 2003, Parmesan 2007). Urbanization and global climate change are occurring simultaneously, yet there are no studies that explicitly consider their combined influence and only a handful of studies that have investigated the impacts of global climate change in the context of other types of land-use change (Warren et al. 2001, Hof et al. 2011, Altermatt 2012). Because the combined effects of urbanization and global climate change may generate relatively extreme environments compared with either source of change on

its own, it is unclear how phenology will be altered when both factors interact.

Phenological change is strongly associated with temperature-driven effects on organismal physiology (reviewed in Helmuth et al. 2005), providing a mechanistic link between shifts toward earlier phenology and the increases in temperature associated with global climate change and urbanization. On average, global climate change is expected to contribute 3–4°C of warming by the end of the century (IPCC 2013). In parallel, urbanization—particularly urban heat island effects, characterized by warmer urban temperatures compared with surrounding rural environments—can contribute 1–3°C of localized warming in air temperature, and 5–9°C of warming in surface temperature (Imhoff et al. 2010; see Appendix A). Warming is generally associated with shifts toward earlier phenology, which can be advantageous, for example by allowing better access to limited resources and by affording more annual generations (Tobin et al. 2008). Indeed, meta-analyses of phenotypic selection in the wild have revealed strong directional selection for earlier phenol-

ogy across diverse taxa (Kingsolver et al. 2012). Yet, the relationship between earlier phenology and warming is not necessarily monotonic. When temperatures become stressfully high, phenology can instead become delayed (Ibáñez et al. 2010, Nufio et al. 2010).

Here we test whether such conditions could be generated from the interaction between geographic temperature (a proxy for global climate change; Blois et al. 2013) and urbanization. Phenological advancement or delay in this scenario depends on the relative positions of current environmental temperature, the magnitude of temperature increase, and species' phenological thermal optima. Among ectothermic species, there is considerable variation in thermal optima for many performance traits, including those that underlie phenology (Angilletta 2009). In general, ectothermic species, particularly those at higher latitudes, tend to occupy environments below their thermal optimum (Deutsch et al. 2008). If we consider a species with a relatively low phenological thermal optimum, as environmental temperatures increase under the separate impacts of global climate change or regional urbanization, we would expect to see phenological advancement as environmental temperatures approach the species' thermal optimum. However, as environmental temperatures increase further, such as under the combined impacts of global climate change and regional urbanization, we would expect to see phenological delay when environmental temperatures exceed the species' thermal optimum (Fig. 1a). In this way, the combined effects of global climate change and urbanization may produce nonlinear phenological responses. In contrast, if we consider a species with a relatively high phenological thermal optimum, we would expect to see continuous advancement of phenology as environmental temperatures approach, but do not exceed, the species' thermal optimum (Fig. 1b).

We explore the phenological responses of 20 butterfly species to urbanization and geographic temperature across Ohio, USA. The data set contains long-term (13-year), volunteer-based weekly butterfly observations from 83 unique transect sites, and importantly, expands the geographic extent of North American butterfly phenology estimated with regular-interval, fixed-transect methods. From the butterfly monitoring data set, we compute and analyze the first appearance, peak abundance, last appearance, and flight breadth of 20 species as functions of urbanization and geographic temperature. We then ask: (1) How do the combined effects of urbanization and geographic temperature influence butterfly phenology? (2) Are responses consistent with models of temperature-driven effects on butterfly phenology, or are butterflies responding to other aspects of environmental change? (3) Can species-level traits be used to resolve interspecific variation in phenological responses?

METHODS

Butterfly and environmental data collection

We analyzed the phenology of 20 common butterfly species monitored by the Ohio Lepidopterists (monitoring protocols *available online*)[8] across 83 transects in Ohio (Northeastern USA; central latitude and longitude: 40°21.7′ N, 82°44.5′ W), spanning the years 1996–2008. The abundance of all adult butterfly species within a 5-m range of each transect was recorded approximately weekly from 1 April to 31 October. We did not consider species with emergences prior to 1 April to ensure appropriate detection of date of first appearance. Because butterflies are monitored throughout the growing season, we were able to characterize changes in multiple phenophases throughout the adult flight period. Specifically, we quantified site- and species-specific dates of first appearance, last appearance, and peak abundance in addition to flight period breadth (the number of days between first and last appearance), based on the distributions of butterfly abundance as a function of ordinal date. We used generalized additive models (GAM) with a burn-in interval corresponding with the 5th and 95th percentiles to estimate butterfly phenology for each species at a given site within a given year (Appendix A; see Hodgson et al. 2011).

To quantify urbanization, we used percentage impervious surface (Landsat imagery) from the 2001 and 2006 National Land Cover Database, NLCD (Fry et al. 2011) at a 30-m grid cell resolution. Surveys performed up to and including 2001 were assigned values from the 2001 NLCD; surveys performed after 2001 were assigned values from the 2006 NLCD. Values range from 0% to 100%, indicating the degree to which the area is covered by impervious features (Appendix B: Fig. B1). Impervious surface is strongly correlated with surface and air temperatures, both globally ($r^2 = 0.7–0.9$; Imhoff et al. 2010) and in Ohio ($r^2 = 0.8$, Hinkel 2007). Because many butterflies can forage and disperse over several hundred meters (Stevens et al. 2010), we used the average impervious surface of the 1 km radius around each survey site.

Data on geographic variation in temperature were quantified as air temperatures from a network of weather stations (interpolated to the locations of butterfly transects; for methodological details, see Zipkin et al. 2012). We present results using the average daily maximum temperature for the length of the monitoring season, calculated separately for each combination of the 83 sites and 13 years (25.9° ± 1.4°C, mean ± SD). Importantly, we obtained qualitatively similar results for models of butterfly phenology using alternative indices of temperature (Appendix A). Because urban meteorological stations are erected in

[8] http://www.ohiolepidopterists.org/bflymonitoring/
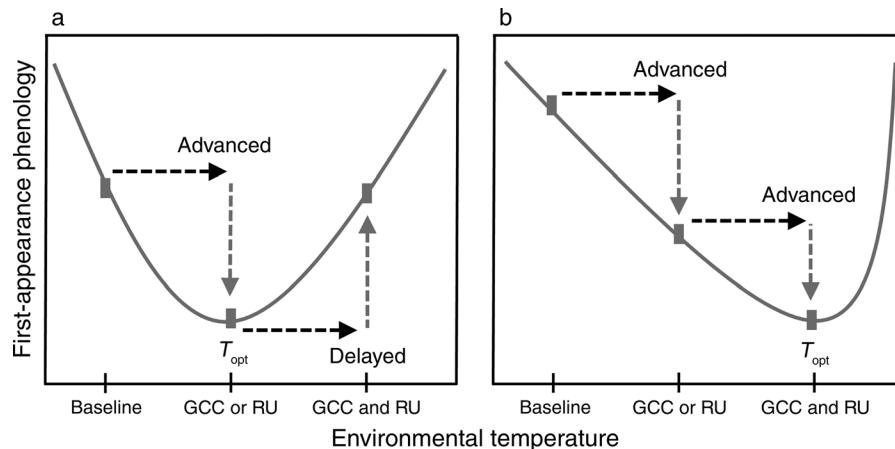
FIG. 1. Conceptual figure for phenological delay or advancement under baseline conditions, global climate change (GCC), and/ or regional urbanization (RU). First-appearance phenology is shown as a function of environmental temperature for butterfly species with (a) a low thermal optimum (T_{opt}) exhibiting phenological delay under the combined effects of GCC and RU, and (b) a high thermal optimum (T_{opt}) exhibiting phenological advancement under the combined effects of GCC and RU.

locally cool areas such as parks and urban edges in compliance with siting standards (Peterson 2003), they generally avoid capturing urban heat island effects; remaining urban heat island effects are often statistically removed from weather station temperature data (Hausfather et al. 2013). Consequently, the percentage of impervious surface in our study region is uncorrelated with geographic temperature (based on the site-level mean daily maximum temperature during the monitoring season: $r = 0.047$, 95% CI = 0.017–0.074).

We examined the ability of species-level traits to resolve interspecific variation in butterfly phenological responses to urbanization and geographic temperature (e.g., Stefanescu et al. 2005, Altermatt 2010, Diamond et al. 2011). Butterfly trait data were obtained from field guides; for trait details, see Appendix A and Appendix B: Table B1. Because phenological responses of the species used in our analyses are not independent, owing to their shared evolutionary history, we incorporated phylogenetic structure (Hawkins and DeVries 2009) into our analyses.

Statistical analyses

For each of the 20 butterfly species, we developed hierarchical multivariate generalized linear mixed models of phenology (with inverse-Wishart priors) at each of the four phenophases: first appearance, peak abundance, last appearance, and flight breadth (MCMCglmm in R; Hadfield 2010). Although we examine phenological changes for the four phenophases, we largely focus on first appearance, because first appearance approximates emergence from overwintering (a biologically relevant phenological event), peak abundance can be difficult to estimate for species with multiple annual generations of which there are several in our data set, and the GAM burn-in intervals and inclusion of abundance covariates

in phenological models (which we will describe) serve to mitigate biases in estimating first appearance (Moussus et al. 2010). Urbanization (percentage impervious surface, (ln + 1)-transformed), geographic temperature (maximum temperature, °C), their interaction, and butterfly abundance (median abundance, ln-transformed) were included as continuous covariates. We included butterfly abundance as a covariate to mitigate the potential impacts of sampling bias on phenological change. Individual butterflies in larger populations are more likely to be detected, which can give the impression of earlier first-appearance phenology when compared with smaller populations (van Strien et al. 2008). Site and year were included as random factors.

We then examined the potential for species' traits to explain interspecific variation in phenological responses to urbanization and geographic temperature. We used principal components analysis (PCA) on the coefficients for urbanization, geographic temperature, and their interaction from the individual species' first-appearance models to reduce the dimensionality of our trait-based model response variable to a single metric that summarizes the functional form of a butterfly species' phenological response. PCA was based on the correlation matrix (rather than the covariance), owing to differences in scale among the urbanization and geographic temperature coefficients. PCA values of greater magnitude in the positive direction indicate delayed phenology in areas that are both urbanized and geographically warm, and PCA values of greater magnitude in the negative direction indicate advanced phenology. We considered the following species-level traits as predictors: larval host plant species diversity (number of larval host plant genera yielded similar results; we focus on number of species for interpretability), dominant larval host plant type, migrant status,
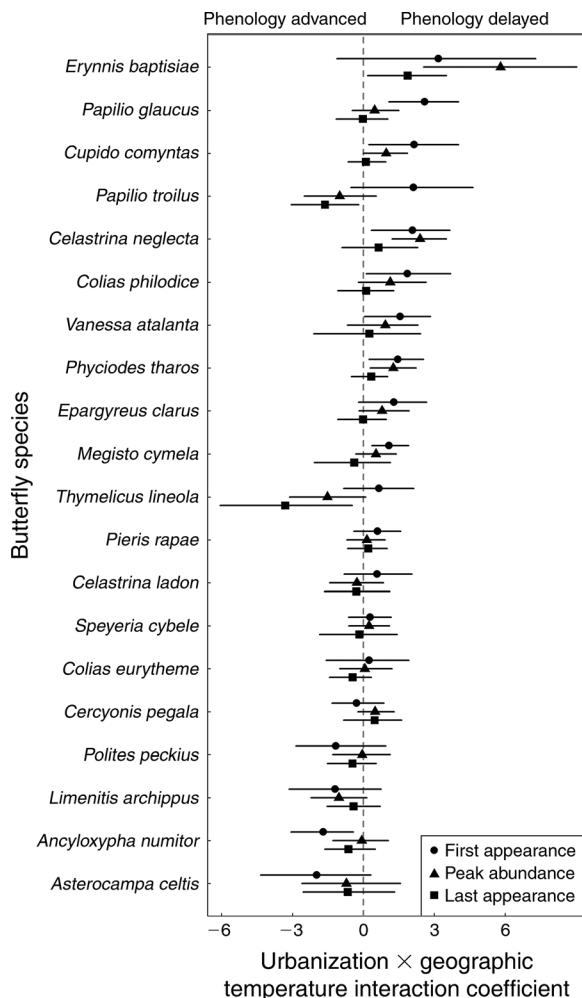
FIG. 2. The influence of urbanization and geographic temperature on butterfly phenophases for 20 species. Posterior mean and 95% credible interval are shown for the urbanization and geographic temperature interaction coefficient for first appearance (circles), peak abundance (triangles), and last appearance (squares). Species are plotted by descending order of the magnitude and direction of the interaction coefficient for first appearance. The vertical dashed line at zero indicates no interaction effect between urbanization and geographic temperature. Positive coefficients indicate interaction effects between urbanization and geographic temperature such that phenology is delayed when both factors increase; negative coefficients indicate interaction effects between urbanization and geographic temperature such that phenology is advanced when both factors increase.

native status, overwintering stage, voltinism, and population size.

We used a generalized least squares modeling framework in which we accounted for the nonindependence arising from species' shared evolutionary history by scaling the model covariance by the degree of phylogenetic signal, i.e., the maximum likelihood branch transformation (Pagel's λ; Pagel 1999), given the data and the model (Appendix A; Appendix B: Table B6

presents phylogenetic signal of the individual traits). Further, to propagate the uncertainty from the within-species models through to the between-species trait-based models, we weighted the error variance of the trait-based model by the variances of the urbanization and geographic temperature coefficients of the individual species models (Appendix A). We then performed model selection on an initial pool of models comprising, in addition to an intercept-only model, all combinations of these listed traits, and the two-way interaction between the two continuous covariates. The Bayesian information criterion (BIC) was used to identify the best-fitting models, and models with ΔBIC < 7 were considered part of the best-fitting model subset. All analyses were performed in R (version 3.0.1; R Development Core Team 2013).

RESULTS AND DISCUSSION

Combined effects of urbanization and geographic temperature on butterfly phenology

Eight of 20 species exhibited significant shifts in first-appearance phenology in response to the combined effects of urbanization and geographic temperature across the state of Ohio, USA. Of these, seven exhibited unexpected shifts toward delayed phenology in urbanized areas that were geographically warm (Figs. 2 and 3). Three of these seven and one additional species also showed delays in peak abundance. Together these results mean that a total of eight out of 20 species showed some type of early-phase phenological delay based on the combined impacts of geographic temperature and urbanization. Given that shifts toward earlier emergence and peak abundance phenology are common for ectothermic species responding either to urbanization or to global climate change (Forrest and Miller-Rushing 2010), the surprisingly high frequency of phenological delay in the early phenophases of Ohio butterflies under the combined impacts of urbanization and geographic temperature (a frequently used proxy for temporal changes in climate; Blois et al. 2013) indicates that these two factors can indeed have important nonadditive phenological consequences.

For the species with significant phenological responses to the combined effects of urbanization and geographic temperature, the earlier phenophases (first appearance and peak abundance) were generally more strongly affected compared with the later phenophase (Figs. 2 and 3; Appendix B: Tables B2 and B3, Fig. B2). The one exception was the nonnative European skipper, *Thymelicus lineola*, which despite exhibiting no phenological change in first appearance and peak abundance, exhibited a significant phenological advancement of last appearance, and a significantly compressed flight period. Three additional species, *Papilio troilus*, *Papilio glaucus*, and *Cupido comyntas*, exhibited significant compression of the flight period, largely through delays in the early phenophases, although compression of the flight period
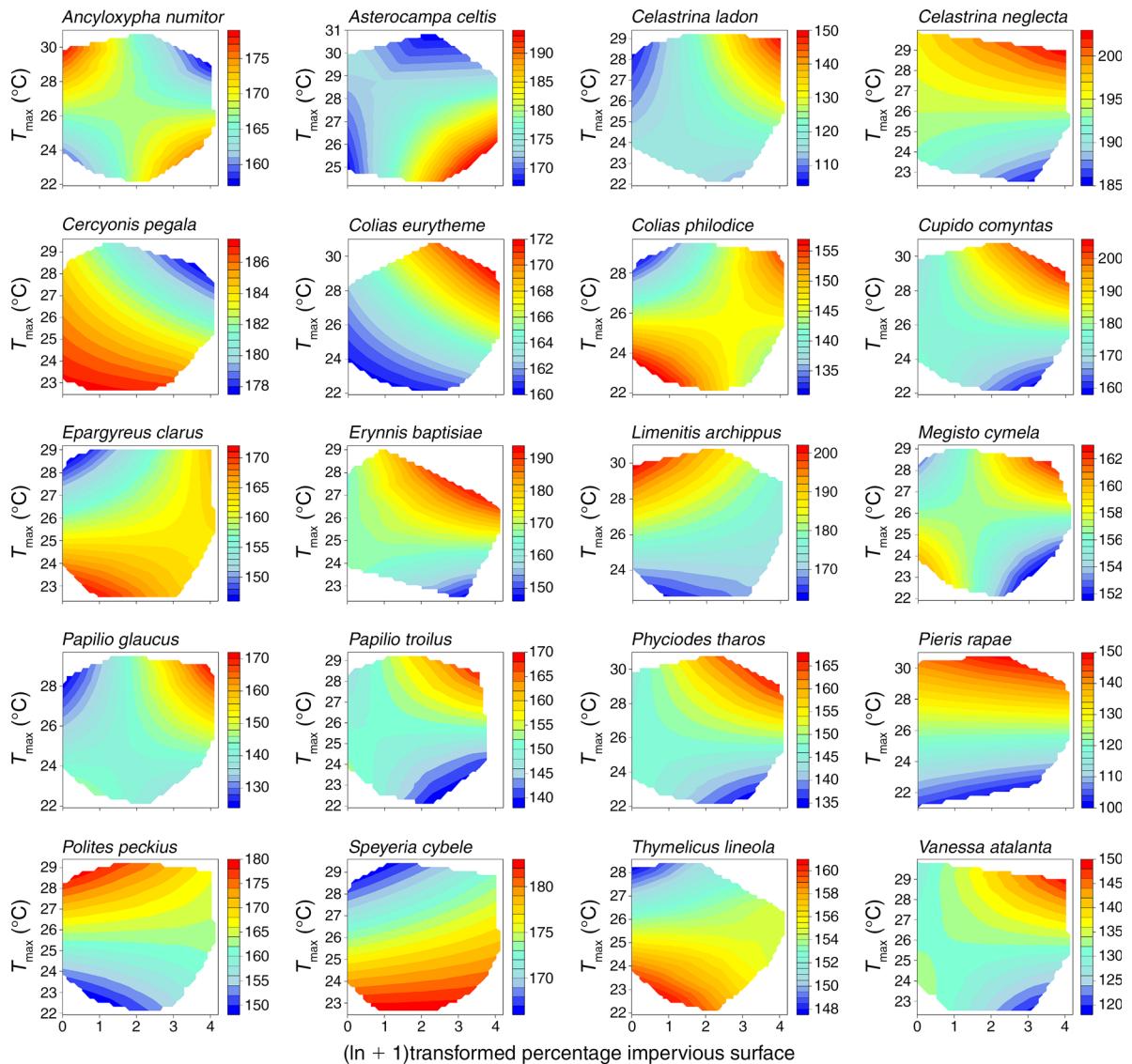
Fig. 3. First-appearance phenological responses to urbanization and geographic temperature by 20 butterfly species. Model response surfaces are presented for the ordinal date of first appearance as a function of (natural log + 1)-transformed percentage impervious surface and of maximum temperature, T_{max}. Earlier ordinal dates of first appearance are in cooler colors (blue), later dates are in warmer colors (red); values in the keys are day of the year, with 1 January being day 1. The effects of abundance are not present in these response surfaces; see Appendix B: Table B2 for model results that account for abundance. Panels are presented in alphabetical order by Latin binomial (by genus, then species).

for *P. troilus* also reflected late phenophase advancement (Appendix B: Tables B4 and B5, Figs. B3 and B4).

Mechanisms underlying phenological responses to urbanization and geographic temperature

The variation among butterfly species in their phenological responses to urbanization and geographic temperature suggests that the mechanisms underlying these responses are likely to vary in kind and in relative strength across the butterfly community. In many systems, phenological change is linked with temperature-driven effects on organismal physiology (reviewed

in Helmuth et al. 2005). For example, modeling work on the monarch (*Danaus plexippus*) showed that delayed phenology in Ohio was associated with both the coolest and hottest growing season in Texas, i.e., the origin of the monarch generation arriving in Ohio (Zipkin et al. 2012). In our study, the shape of the phenological response surfaces also strongly suggests that temperature has an important impact on many species. Specifically, the seven species with significant first-appearance phenological delays in areas that were both urbanized and geographically warm tended to also exhibit phenological delays in areas that were both

rural and geographically cool (Fig. 3). This pattern is consistent with the model presented in Fig. 1a in which early-phase phenology is delayed when environmental temperature either fails to reach a species' thermal optimum (i.e., in rural, geographically cool areas) or exceeds a species' thermal optimum (i.e., in urbanized, geographically warm areas).

We note, however, that although each of these seven species exhibited delayed phenology under the combined effects of urbanization and geographic temperature, there was substantial variation among species in how strongly each factor impacted phenology. That is, although each of these species had significant positive urbanization × geographic temperature interaction coefficients (indicating phenological delay), the main-effect coefficients for urbanization and geographic temperature varied from weakly trending to strongly significant (although all were negative, indicating phenological advancement). Part of this variation may stem from difficulty in interpreting main effects in cases of significant interactions, although it might also reflect biological variation in species' responses to different sources of environmental change.

Interestingly, no species exhibited phenological responses consistent with the model presented in Fig. 1b in which early-phase phenology continues to advance as butterflies experience environmental temperatures that approach their thermal optimum. This result could suggest that the butterflies in our study group possess relatively low thermal optima such that the scenario in Fig. 1b is not realized. However, a more likely interpretation is that some butterfly species in our study system are responding to aspects of the environment other than the direct impacts of temperature change on phenology.

Although our study suggests an important link between regional urban warming, larger-scale climatic warming, and butterfly phenological change, our findings have several caveats. First, given that adult butterflies can be excellent behavioral thermoregulators via microsite selection (Hardy and Dennis 2007) and body orientation (Kingsolver 1983), it is likely that the observed phenological shifts of adult butterflies represent cumulative effects of temperature throughout butterfly ontogeny. For example, urban and geographic warming may extend the previous year's growing season such that butterfly emergence is delayed in the next year. Further, winter warming may stress less mobile immature overwintering stages (most butterflies in our study system overwinter as larvae and pupae), causing butterflies to be metabolically active when they should be dormant (Williams et al. 2012, Roland and Matter 2013), and potentially contributing to stress-induced phenological delays.

Second, we are currently limited in the components of urbanization and climate change that we are able to quantify. For example, alterations to the mean and variance of temperature in the specific urban environ-ments where butterfly counts were obtained are largely unknown. Further, although our hypothetical models of butterfly phenological change are based on increasing mean temperature, urbanization is often associated with decreased temperature variance (Oke 1997), as are lower-latitude geographic locations, whereas temperature variance is generally expected to increase with global climate change (IPCC 2013). How such alterations to mean temperature and the contrasting alterations to temperature variance interact to impact organismal performance and phenology among different geographic locations under regional urbanization and global climate change is an important open question.

Apart from direct impacts of temperature on butterfly physiology, the indirect effects of temperature on butterfly host plant phenology or quality (van Asch and Visser 2007), butterfly dispersal from rural sources to urban sinks (Altermatt 2012), and alterations of the food web to which butterflies belong (i.e., host plants or predators), in addition to the non-temperature impacts of urbanization involving changes to habitat structure and composition (Grimm et al. 2008), might also influence butterfly responses. Importantly, our study can identify species with which to examine these indirect and non-temperature effects in greater detail. Species that do not fit our model of temperature-driven impacts on phenology, such as *Ancyloxypha numitor* (which exhibits delayed phenology with either geographic temperature or urbanization, but advanced phenology under their combined effects), or *Speyeria cybele* (which exhibits advanced phenology with geographic temperature, but is phenologically insensitive to urbanization), are excellent candidates.

Resolving interspecific variation in phenological responses using species' traits

Our trait-based models explained a considerable amount of the variance in butterfly responses to geographic temperature and urbanization (among the best-fitting models, r^2 values ranged from 0.7 to 0.92). Overwintering stage was common among the variables in the best-fitting models, with a high relative importance value of 0.79. Species that overwinter in more advanced developmental stages (i.e., pupae) tended to experience greater phenological delays in areas that were urbanized and geographically warm; however, none of the individual coefficients for overwintering stage was significant (Fig. 4; Appendix B: Table B7). We suggest that although this result lends further support to the increasing importance of overwintering stage in understanding ectotherm phenological and demographic responses to environmental change (e.g., Diamond et al. 2011, Breed et al. 2012), more comparative and experimental work is needed in this area. The dominant larval host plant type was also found among the best-fitting models, with species that feed on forbs exhibiting significantly stronger phenological delays than species that feed on grasses; whether this result reflects variation
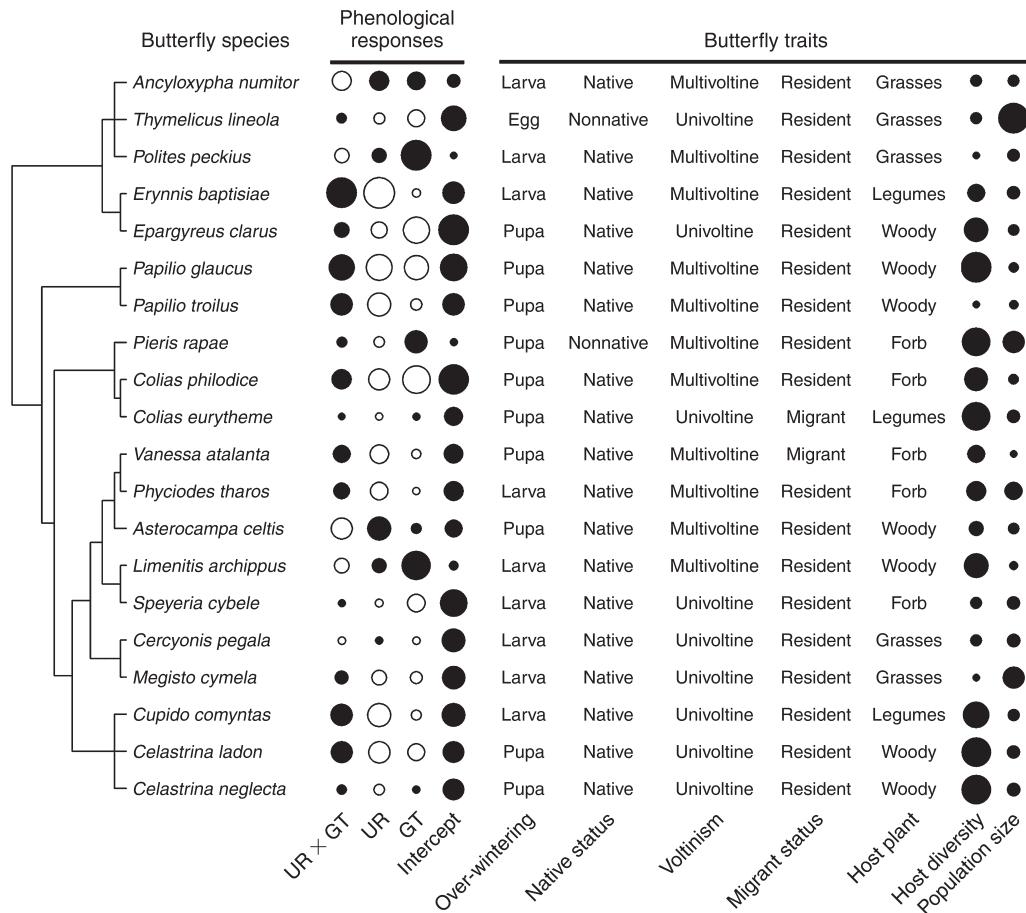
FIG. 4.   Butterfly phylogenetic associations, phenological responses, and species' traits for 20 species. Phenological responses are presented as the coefficients from models of first appearance: coefficients shown include the urbanization × geographic temperature interaction, the main effect of urbanization, the main effect of geographic temperature, and the intercept (for actual values, see Appendix B: Tables B2–5 and 7). The circle size indicates the relative magnitude of the coefficient, and the circle shading indicates whether the coefficient is positive (solid circle) or negative (open circle). Butterfly traits are indicated by text corresponding with the appropriate factor level for categorical traits, and increasing circle size for larger values of continuous traits. Note that trait-based models used PC1 of the urbanization, geographic temperature, and urbanization × geographic temperature coefficients as the response variable; PC1 proportion of variance explained is 0.856; eigenvector loadings are: −0.605 for urbanization, −0.516 for geographic temperature, and 0.607 for urbanization × geographic temperature.

in butterfly physiology or alterations to urban plant composition remains to be tested (Shapiro 2002). More generally, our trait-based approach has generated testable hypotheses for future experiments.

Compared with native butterflies, the two nonnative butterfly species had earlier overall ordinal dates of first appearance (compare the "intercept" coefficients for native and nonnative species in Fig. 4), and exhibited milder delays or even phenological advancement in areas that were both urbanized and geographically warm. Although it is difficult in this case to disentangle the effects of native status from date of first appearance per se, when we examined the phenological patterns within the native butterflies only, we found that species that emerge earlier in the year, when environmental temperatures are cooler, exhibited milder phenological delays compared to butterflies that emerge later when temper-

atures are warmer ($r = 0.783$, $P < 0.001$, df = 16; i.e., there is a positive correlation between species' baseline ordinal date of first appearance and PC1 from the geographic temperature and urbanization model coefficients). Because seasonal differences in temperature are linked with phenological responses, this finding further supports the role of temperature in shaping butterfly phenology.

Butterfly species considered more exploitative also exhibited milder phenological delays or even advancement of first-appearance phenology (Fig. 4). We classified exploitative species as those with one or more of the following traits: large population size, greater larval host plant species diversity, nonnative, multivoltine, and seasonal migrants (each of these traits had high relative importance values > 0.7 in the model selection approach; the interaction of host plant diversity and

population size was a significant predictor of butterfly phenology, and the latter three traits exhibited noticeable trends; see Appendix B: Table B7). Exploitative species that shift their phenology earlier in response to environmental changes in climate and land use may have greater ability to take advantage of limited resources and potentially increase the number of generations annually, leading to higher fitness via higher population growth rate and perhaps greater potential for adaptation (Tobin et al. 2008). Indeed, we might expect butterfly communities to shift toward those dominated by exploitative species under the combined effects of urbanization and global climate change. In the UK, generalist butterflies have been shown to be more resilient to climatic and habitat changes (Warren et al. 2001).

The major finding of our study was the surprisingly high occurrence (nearly half of the 20 butterfly species that we examined) of nonadditive impacts of urbanization and geographic temperature on phenology. These effects appear to be particularly severe for less exploitative butterfly species. Uncovering the mechanisms of these unexpected delays in early-phase phenology under the combined effects of urbanization and geographic warming, and the degree to which these unexpected responses may be found across different trophic levels, are key priorities for future work. More generally, our study demonstrates the importance of considering multiple sources of environmental change when assessing and forecasting impacts on biological systems.

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SUPPLEMENTAL MATERIAL

Appendix A

Details on modeling butterfly phenology and environmental change (*Ecological Archives* E095-228-A1).

Appendix B

Survey map and phenological model summaries (*Ecological Archives* E095-228-A2).