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Disentangling the paradox of insect phenology: are temporal trends reflecting the response to warming?

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Abstract The strength and direction of phenological responses to changes in climate have been shown to vary significantly both among species and among populations of a species, with the overall patterns not fully resolved. Here, we studied the temporal and spatial variability associated with the response of several insect species to recent global warming. We use hierarchical models within a model comparison framework to analyze phenological data gathered over 40 years by the Japan Meteorological Agency on the emergence dates of 14 insect species at sites across Japan. Contrary to what has been predicted with global warming, temporal trends of annual emergence showed a later emergence day for some species and sites over time, even though temperatures are warming. However, when emergence data were analyzed as a function of temperature and precipitation, the overall response pointed out an earlier emergence day with warmer conditions. The apparent contradiction between the response to temperature and trends over time indicates that other factors, such as declining populations, may be affecting the date phenological events are being recorded. Overall, the responses by insects were weaker than those found for plants in previous work over the same time period in these ecosystems, suggesting the potential for ecological mismatches with deleterious effects for both suites of species. And although temperature may be the major driver of species phenology, we should be cautious when analyzing phenological datasets as many other factors may also be contributing to the variability in phenology.

Keywords Hierarchical Bayes · Insect emergence · Japan · Phenology · Temperature

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Introduction

Because many organisms respond to changes in climate, phenology has become an increasingly important component of study in ecosystems around the world (Menzel et al. 2006; Parmesan 2006; Rosenzweig et al. 2008). As the mean global temperature continues to rise, the phenologies of many plants and animals are changing (Amano et al. 2010; Root et al. 2003; Thackeray et al. 2010). However, the degree to which different species populations are affected by temperature is highly variable. Certain species show little or no response to increasing temperatures (Parmesan and Yohe 2003; Visser 2008), apparently using

other abiotic or biotic cues to trigger flowering, leaf out, migration, emergence, reproduction or other phenological events. Other species exhibit a strong negative relationship with temperature, advancing their phenologies significantly in response to warmer temperatures (Menzel et al. 2006; Rosenzweig et al. 2008).

In the case of insect phenology (e.g., emergence dates), much of our understanding comes from agricultural systems for which some of the longest-term datasets exist (Parmesan 2006; Zhang et al. 2009). In these insect systems and others, warmer temperatures in recent years have led to shifts in emergence dates and distribution ranges for a variety of species (Altermatt 2010a; Diamond et al. 2011; Doi et al. 2008; Hickling et al. 2006; Hodgson et al. 2010; Stefanescu et al. 2011; Thomas et al. 2001). Shifts in phenology may have beneficial or detrimental impacts on insect populations. For example, shifting phenology in response to climate may allow species to stay within suitable ranges of abiotic conditions, while inability to shift could subject species to unfavorable conditions. Such shifts in phenology may also have cascading negative effects on other species in the community, if ecological mismatches arise, for example, between plants and their insect pollinators (Hegland et al. 2009; Memmott et al. 2007), between herbivorous insects and their plant food sources (Altermatt 2010b; Dixon 2003; Fabina et al. 2010; Forkner et al. 2008), or between insects and their predators (Both et al. 2009, 2010). During the summer, species may face phenological challenges that differ from those of the spring or fall, particularly with respect to water requirements and the increasing possibilities of drought risk. This may affect insects directly (Leeper and Taylor 1998; Robinet and Roques 2010; Rouault et al. 2006; Zhang et al. 2009), or indirectly via the plants they consume (Huberty and Denno 2004; Itioka and Yamauti 2004; Mody et al. 2009).

Insect phenology can be highly variable and show contradictory trends within and among species, seasons, and localities (Hodgson et al. 2010; Primack et al. 2009). The challenge is to understand how and why this variability occurs under given conditions and be able to determine the factors affecting phenology so we can still forecast future trends under the predicted climate. Although spring phenological responses have been shown to vary spatially (Primack et al. 2009), the precise patterns of variation are unknown and spatial patterns of summer events are unexplored. Using long-term observational records of Japan's diverse insect assemblage allows us to quantify spatial and temporal differences in species' phenology. In the current study, we aimed to answer the following questions. How has the timing of insect emergence, as measured by date of first observance or date a species was first heard, changed over time? How is insect phenology affected by climate

(temperature and precipitation)? Are these responses comparable to those of plants in the same region?

Materials and methods

Data gathered by the Japanese government were used to address our questions with particular reference to environmental change. During this period, Japan has undergone significant warming due to global warming and the urban heat island effect (Awa and Kobayas 2010; IPCC 2007; Primack et al. 2009). Nearly all sites showed significant warming trends over the time span covered by the data (Online Resource 1). Fourteen insect species that emerge over the course of the spring and summer are included in the analysis presented here. Each of these species is readily recognized by its song or physical appearance, and was seen or heard at more than five stations over up to 44 years.

Phenology and weather data

The Japan Meteorological Agency (JMA) is a government department within the Ministry of Land, Infrastructure, Transport and Tourism that takes daily climate measurements and monitors a variety of plant and animal phenologies with the aim of predicting phenophases—a distinct stage in an organism's life cycle—of culturally important species at 102 local meteorological observatories (Japan Meteorological Agency 2010). By using data collected throughout Japan, a country spanning boreal to subtropical climates, our study will contribute to the understanding of the effects of climate change on insects in a large variety of ecosystems and habitats. In addition, the long time-span of the study, 1961–2004, allows for temporal analysis of the highly variable phenology of these species. The taxonomic, spatial and temporal scope of these datasets helps to make the patterns found within them applicable to other parts of the world.

There has been limited use of these datasets in earlier studies. For example, Koike et al. (2006) and Doi et al. (2008) included observations of *Pieris rapae* (small white butterfly) made by the JMA in their cross-trophic level analyses and documented that the date of the first appearance of this butterfly has advanced to a lesser degree than the flowering of trees in the area, and in some cases was even delayed. Koike et al. (2006) also found a difference in how strongly butterfly phenology changed compared to laying dates of a tropical migratory bird species, *Sturnia philippensis* (red-cheeked starling). Although this butterfly is not a major food source of the starling, it can be regarded as among a similar group of insects within the bird's diet. Doi (2008) examined the emergence dates of the *Orthetrum albistylum speciosum,* (common skimmer) finding

that they are now emerging later in the spring than in the past, perhaps due to longer voltine periods at certain latitudes. These insect species are included in the 14 species analyzed here.

Models for insect phenology

Temporal trends

We first established whether dates of insect emergence have been shifting over time using multi-level regression models for each species in which phenology date [first appearance (FAP) or first singing (FSI)] was regressed against year:

$$\text{Date}_{\text{site,year}} = \alpha_{\text{site}} + \beta_{\text{site}} \cdot \text{year} + \varepsilon_{\text{site,year}}$$

Site-specific intercepts, α_{site}, and slopes, β_{site}, were modeled hierarchically, such that parameters describing the relationship over time at each site were drawn from overall distributions for each species. For the intercepts, $\alpha_{\text{site}} \sim \text{Normal}(\alpha_0, \sigma^2)$, where α_0 is the overall intercept for a species and is given a noninformative prior $\alpha_0 \sim \text{Normal}(0, 1{,}000)$. The variance among sites is estimated as σ^2 and given a noninformative prior distribution $\sigma^2 \sim \text{Uniform}(0, 10{,}000)$. Slopes, β_{site}, were similarly modeled hierarchically with $\beta_{\text{site}} \sim \text{Normal}(\beta_0, \sigma^2)$, and β_0 represents the overall trend over time for the species. This hierarchical model structure allowed for the possibility of site-specific trends over time due to unmeasured factors (β_{site}), while estimating an overall trend over time for each species (β_0). Finally, error terms, $\varepsilon_{\text{site, year}}$, were estimated from a normal distribution $\varepsilon_{\text{site,year}} \sim \text{Normal}(0, \sigma_\varepsilon^2)$ where, $1/\sigma_\varepsilon^2 \sim \text{Gamma}(0.01, 0.01)$.

Response to temperature

We then developed five models that reflected different hypotheses about what influences insect phenology and how it may vary geographically across Japan for each species (Table 2). These models tested the relative importance of temperature and precipitation (Model A), whether there was a significant latitudinal effect in addition to the latitudinal variation in temperature (Model B), whether climate effects were site-specific (Model C), and whether the site level responses were regionally patchy (spatially autocorrelated in addition to any latitudinal gradient, Model E). In addition to these models, we tested a model reflecting that relationships with climate may actually change across the latitudinal gradient by including interactions between climate and latitude (Model D). Details can be found in Table 2. The general structure of the model (Model A) was:

$$\text{Date}_{\text{site,year}} = \lambda_{\text{site}} + \eta_{\text{site}} \cdot \text{temperature}_{\text{site, year}} + \theta_{\text{site}} \cdot \text{precipitation}_{\text{site,year}} + \omega_{\text{site,year}}$$

The random effects term, $\omega_{\text{site,year}}$, follows a normal distribution, $\omega_{\text{site,year}} \sim \text{Normal}(0, \sigma_\omega^2)$, where $1/\sigma_\omega^2 \sim \text{Gamma}(0.01, 0.01)$. The site-associated parameters, λ, η, θ, were estimated from normal distributions with parameter values calculated at the species level, $\lambda_{\text{site}} \sim \text{Normal}(\lambda_0, \sigma_\lambda^2)$, $\eta_{\text{site}} \sim \text{Normal}(\eta_0, \sigma_\eta^2)$, and $\theta_{\text{site}} \sim \text{Normal}(\theta_0, \sigma_\theta^2)$. These species level parameters where then estimated from non-informative prior distributions, $\lambda_0 \ \eta_0 \ \theta_0 \sim \text{Normal}(0, 10000)$, and $\sigma_\lambda^2, \sigma_\eta^2, \sigma_\theta^2 \sim \text{Uniform}(0, 10{,}000)$.

Because the range of event dates varied considerably species to species (Table 1), temperature for each site and year was calculated as the sum of daily mean temperatures for the 90 days preceding the earliest mean site for each species. Thus, the window over which temperature was summed remained the same for each species across all sites. This method provides easier comparisons along the latitudinal range and avoids the circularity of using each year's or each site's phenological dates to define the period of time of the explanatory variables. Precipitation was calculated similarly using daily precipitation data.

All the models were fit in a hierarchical Bayesian framework that allowed site-specific responses to be nested within an overall species level response (Gelman and Hill 2007), as described above for the temporal trend models. Species were modeled independently, however. This hierarchical approach has proven to be a useful way to allow site-to-site variability in responses while estimating overall species responses that incorporate variation within and among sites (Ibáñez et al. 2010). In addition, this hierarchical structure allows sites with relatively few observations to be informed by more thoroughly sampled sites. We used non-informative prior distributions for all parameters to allow the data to control parameter estimates.

Models were fit using OpenBUGS (Thomas et al. 2006) called from R using the BRugs package (R Core Development Team 2008). Model convergence was assessed visually and using the Gelman-Rubin statistic (Brooks and Gelman 1998) after an initial burn-in period of 10,000 iterations. Posterior means for each estimated parameter were estimated from 10,000 additional iterations. Because the hierarchical analysis yielded parameters describing the effects of climate at each site and an overall species-level parameter for each climate variable, we report two measures of climatic effects for each species. Firstly, we counted the number of sites at which the site-level regression coefficients were either significantly negative or positive (η_{site} and θ_{site}, using 0.90 as the credible interval as the significance threshold). Secondly, we used the overall species level parameters (η_0 and θ_0) to directly calculate the probability that each species had a positive or negative response overall to each climatic variable. This probability was calculated as the portion of the species-level regression coefficient's posterior distribution that is greater than or

Table 1 The species included in this analysis with scientific and common names

Scientific name	Common name	No. of sites	Mean emergence date	Adult habitat	Juvenile habitat
Orthetrum albistylum	Skimmer (dragonfly)	67	29 May	Fields	Water (pond)
Sympetrum frequens	Darter (dragonfly)	38	5 September	Fields	Water (pond)
Gampsocleis buergeri	Japanese katydid	25	24 July	Fields	Fields
Gryllus yemma	Emma field cricket	38	16 August	Fields	Fields
Isoptera sp.	Termite	7	11 May	Wood or soil	Wood or soil
Tanna japonensis	Evening cicada	74	16 July	Forest	Underground
Graptopsaltria nigrofuscata	Large brown cicada	74	20 July	Forest	Underground
Oncotympana maculaticollis	Robust cicada	31	30 July	Forest	Underground
Meimuna opalifera	Last-summer cicada	51	5 August	Forest	Underground
Platypleura kaempferi	Kempfer cicada	52	7 July	Forest	Underground
Cryptotympana facialis	Facialis cicada	14	4 July	Fields	Underground
Papilio machaon	Swallowtail butterfly	70	29 April	Fields	Fields
Pieris rapae crucivora	Small white butterfly	87	2 April	Shaded areas	Shaded areas
Polistes jadwigae	Paper wasp	12	17 April	Fields	Underground

Mean first emergence date is the mean value of first emergence dates across all stations and years. Range of emergence dates is the mean emergence date at the station with the earliest mean to the mean emergence date at the station with the latest mean. Adult and juvenile habitat describes a general location of a species in these different life stages (Hirashima and Morimoto 2008; Ishida et al. 1988; Oka 2006; Sugimura et al. 1999; Takamizawa 2005)

less than zero (in whichever direction it is trending). Finally, to evaluate the relative support for the different models tested (Table 2), we calculated the deviance information criteria (DIC) for each model, where the lowest value suggests the model with greatest support from the data (Spiegelhalter et al. 2002).

Results

Temporal trends

Of the 14 species analyzed for changes in phenology over time, 3 exhibited a trend towards earlier emergence and 10 species exhibited later emergence since 1961 at a majority of stations at which they were observed (Table 3). The extent to which the phenology of each species has changed was variable with species such as *Graptopsaltria nigrofuscata* (large brown cicada) emerging significantly earlier at 56 of the 74 stations at which it was heard (β_{site} parameters were negative), with a probability from the hierarchical model of >0.99 of earlier emergence when analyzed across stations (β_0 negative). This species emerged 0.91 days earlier each decade (β_0*10). However, most species emerged later over time. *O. albistylum* (Pr > 0.99) exhibited the most dramatic shift in emergence with a 4.19-day delay per decade. *Papilio machaon* (swallowtail butterfly; Pr > 0.99), *P. rapae* (Pr > 0.99) and *Sympetrum frequens* (darter; Pr > 0.99) are also among the species displaying a significant shift towards later emergence across

stations and are emerging 1.24, 0.90, and 2.32 days later per decade, respectively.

Changes in phenology with temperature and precipitation

Based on Deviance Information Criterion (DIC), model C provided the best fit for 12 of the 14 species (Table 2). This model took into account temperature and precipitation as well as site-specific effects of temperature and precipitation. Because this model garnered the greatest support, we report results based on the posterior parameter distributions from this model.

Model selection supports the hypothesis that phenological responses to temperature and precipitation are site-specific. Models incorporating interactions between climate and latitude did not generally improve DIC values, suggesting that the underlying effects of climate on phenology do not systematically change across the latitudinal gradient for reasons other than the change in temperature. Also, models with spatial random effects did not gain as much support as simpler models, suggesting that spatial autocorrelation is not strong and that the site-specific climatic parameters are taking into account any spatial variation (e.g., locations nearby would have similar responses to temperature).

Twelve of the 14 species of insects analyzed show an earlier phenology during warmer years (Table 3b; Fig. 1). For 11 of these species, including all 6 cicada species, this has occurred at the majority of stations. The estimated

Table 2 Comparison of models of insect phenology showing DIC values

Species	Hypothesis	Single overall species-level responses to climate	Phenology changes across latitude in addition to site to site	Climatic effects are site-specific	Climatic effects change with latitude (Interactions)	Geographically patchy
	Model name	A	B	C	D	E
	Model event date ~	$\lambda_{site} + \eta \cdot temp + \theta \cdot precip + \omega$	$\lambda_{site} + \eta \cdot temp + \theta \cdot precip + \gamma \cdot latitude + \omega$	$\lambda_{site} + \eta_{site} \cdot temp + \theta_{site} \cdot precip + \omega$	$\lambda_{site} + \eta \cdot temp + \theta \cdot precip + \gamma \cdot latitude + \phi \cdot temp \times latitude + \kappa \cdot precip \times latitude + \omega$	$\lambda_{site} + \eta \cdot temp + \theta \cdot precip + spatial\ random\ effects$
	Event / No. sites					
Orthetrum albistylum	FAP / 67	13,940	13,930	**11,810**	13,920	13,930
Sympetrum frequens	FAP / 38	9,000	9,000	8,997	**8,989**	9,000
Gampsocleis buergeri	FSI / 25	5,221	5,221	**5,216**	5,224	5,221
Gryllus yemma	FSI / 38	10,980	10,980	**10,960**	10,970	10,980
Isoptera sp.	FAP / 7	**1,890**	1,897	1,900	1,899	1,894
Tanna japonensis	FSI / 74	14,590	14,590	**14,480**	14,590	14,590
Graptopsaltria nigrofuscata	FSI / 74	20,910	20,910	**20,770**	20,880	20,910
Oncotympana maculaticollis	FSI / 31	8,458	8,458	**8,447**	8,460	8,458
Meimuna opalifera	FSI / 51	13,030	13,030	**12,990**	13,000	13,030
Platypleura kaempferi	FSI / 52	13,010	13,010	**12,960**	13,010	13,010
Cryptotympana facialis	FSI / 14	2,340	2,341	**2,319**	2,344	2,340
Papilio machaon	FAP / 70	15,760	15,750	**14,920**	15,720	15,750
Pieris rapae crucivora	FAP / 87	18,920	18,920	**14,160**	18,920	NA
Polistes jadwigae	FAP / 12	2,162	2,163	**2,153**	2,171	2,163
		1	0	12	1	0

Values in *bold* indicate the best fitting model for each insect.

Regression parameters, λ, η, θ, γ, ϕ, and κ, were also modeled hierarchically where subscripted by "site". Model E suffered from poor MCMC convergence for *P. rapae*, and is therefore marked with an *NA* in the table

FSI first singing *FAP* first appearance *temp* temperature *precip* precipitation

Table 3 Results of analysis showing the species analyzed, the phenological event and the number of stations at which a species was seen or heard (*n*)

a) Time

Species	Event	*n*	Earlier	Pr (earlier)	Later	Pr (later)	Days/dec
Orthetrum albistylum	FAP	67	6 (1)	0.00	61 (49)	**>0.99**	4.19
Sympetrum frequens	FAP	38	9 (3)	0.00	29 (14)	**>0.99**	2.32
Gampsocleis buergeri	FSI	25	6 (2)	0.10	19 (6)	**0.90**	0.70
Gryllus yemma	FSI	38	8 (1)	0.01	30 (10)	**0.99**	0.61
Isoptera sp.	FAP	7	0 (0)	0.09	7 (2)	**0.91**	1.13
Tanna japonensis	FSI	74	31 (18)	0.74	27 (14)	0.26	−0.22
Graptopsaltria nigrofuscata	FSI	74	56 (37)	**>0.99**	18 (9)	0.00	−0.91
Oncotympana maculaticollis	FSI	31	15 (8)	0.33	16 (9)	0.67	0.20
Meimuna opalifera	FSI	51	27 (16)	0.82	24 (14)	0.18	−0.33
Platypleura kaempferi	FSI	52	22 (4)	0.16	30 (11)	0.84	0.20
Cryptotympana facialis	FSI	14	12 (10)	**0.92**	2 (2)	0.08	−1.43
Papilio machaon	FAP	70	10 (0)	0.00	60 (35)	**>0.99**	1.24
Pieris rapae crucivora	FAP	87	27 (6)	0.00	59 (30)	**>0.99**	0.90
Polistes jadwigae	FAP	12	0 (0)	0.01	12 (6)	**0.99**	1.71

b) Temperature

Species	Event	*n*	Earlier	Pr	Later	Pr	Days/deg
Orthetrum albistylum	FAP	67	35 (11)	0.30	32 (12)	0.70	0.29
Sympetrum frequens	FAP	38	0 (0)	0.00	38 (32)	**>0.99**	2.05
Gampsocleis buergeri	FSI	25	25 (22)	**>0.99**	0 (0)	0.00	−3.40
Gryllus yemma	FSI	38	37 (31)	**>0.99**	1 (0)	0.00	−1.23
Isoptera sp.	FAP	7	7 (7)	**>0.99**	0 (0)	0.00	−4.63
Tanna japonensis	FSI	74	71 (51)	**>0.99**	3 (2)	0.00	−3.15
Graptopsaltria nigrofuscata	FSI	74	73 (73)	**>0.99**	1 (0)	0.00	−3.71
Oncotympana maculaticollis	FSI	31	31 (30)	**>0.99**	0 (0)	0.00	−3.28
Meimuna opalifera	FSI	51	50 (48)	**>0.99**	1 (0)	0.00	−3.99
Platypleura kaempferi	FSI	52	52 (51)	**>0.99**	0 (0)	0.00	−3.13
Cryptotympana facialis	FSI	14	14 (14)	**>0.99**	0 (0)	0.00	−4.65
Papilio machaon	FAP	70	70 (60)	**>0.99**	0 (0)	0.00	−1.93
Pieris rapae crucivora	FAP	87	74 (37)	**>0.99**	13 (2)	0.00	−1.07
Polistes jadwigae	FAP	12	12 (10)	**0.99**	0 (0)	0.02	−1.24

c) Precipitation

Species	Event	*n*	Earlier	Pr	Later	Pr	Days/cm
Orthetrum albistylum	FAP	67	66 (19)	**>0.99**	1 (0)	0.00	−1.53
Sympetrum frequens	FAP	38	8 (0)	0.44	30 (0)	0.56	0.04
Gampsocleis buergeri	FSI	25	0 (0)	0.00	25 (0)	**>0.99**	0.56
Gryllus yemma	FSI	38	0 (0)	0.00	38 (0)	**>0.99**	0.39
Isoptera sp.	FAP	7	7 (2)	0.83	0 (0)	0.18	−0.38
Tanna japonensis	FSI	74	65 (27)	0.79	9 (2)	0.21	−0.09
Graptopsaltria nigrofuscata	FSI	74	4 (0)	0.09	70 (0)	**0.92**	0.12
Oncotympana maculaticollis	FSI	31	10 (0)	0.33	21 (0)	0.68	0.08
Meimuna opalifera	FSI	51	37 (0)	0.85	14 (0)	0.15	−0.09
Platypleura kaempferi	FSI	52	43 (0)	0.72	9 (0)	0.28	−0.07
Cryptotympana facialis	FSI	14	2 (0)	0.01	12 (1)	**0.99**	0.75
Papilio machaon	FAP	70	23 (0)	0.38	47 (1)	0.62	0.10

Table 3 continued

c) Precipitation

Species	Event	*n*	Earlier	Pr	Later	Pr	Days/cm
Pieris rapae crucivora	FAP	87	17 (0)	0.20	70 (3)	**0.80**	0.19
Polistes jadwigae	FAP	12	8 (4)	0.60	4 (2)	0.40	−0.35

Earlier and later values shown outside the parentheses represent the number of sites at which a species is trending towards earlier or later phenology with (*a*) time, (*b*) increased temperature, and (*c*) increased precipitation. Values within the parentheses are the number of sites at which there was at least a 0.90 probability that the relationship was earlier (negative) or later (positive), estimated from the posterior distributions of regression coefficients, β_{site} in Model C in Table 2. *Pr* (earlier) and *Pr* (later) are the probabilities that the overall species level parameter is less than (earlier) or greater than (later) zero, and bold indicates values at or above the 0.90 credible interval. *Days/dec* is the number of days of shift in phenological event towards earlier (negative) or later (positive) per decade. *Days/deg* gives the expected change in emergence per degree increase in temperature. *Days/cm* is the change in emergence date per cm of precipitation

FAP first appearance, *FSI* first singing

changes in emergence dates are 1.07–4.65 days earlier per 1°C increase over the preceding 90-day period (Fig. 2). The two dragonfly species, *O. albistylum* and *S. frequens,* were the only species that emerge later with increased temperature, though only *S. frequens* did so significantly; these are species that rely on aquatic ecosystems to lay their eggs and grow their larvae.

Precipitation was a poorer predictor of insect phenology than temperature (Table 3c; Fig. 1). Only one species, *O. albistylum* (a species associated with aquatic ecosystems)*,* emerges earlier with increased precipitation (1.53 days earlier per cm of precipitation), with a significant response at 19 of 67 stations. Four species, *Gampsocleis buergeri* (Japanese katydid), *Gryllus yemma* (emma field cricket)*, G. nigrofuscata* and *Cryptotympana facialis* (facialis cicada) emerge later with increased precipitation, emerging 0.56, 0.39, 0.12 and 0.75 days later, respectively, per cm increase.

Discussion

Temporal trends and spatial patterns

Although many species show a strong relationship between earlier phenology and increasing temperature, an interesting discrepancy has emerged in the literature that describes species that arrive or are active later over time, even in regions that are warming (Doi 2008; Ibáñez et al. 2010; Parmesan 2007). Our results reflect that discrepancy; despite the warming trends in climate the majority of insect species in our study are emerging later now than they did in 1961, but they are responding with earlier phenologies to warmer years. The shift in insect phenology observed in Japan is occurring across different taxonomic orders and also varies within orders suggesting it is caused by factors beyond those of life-history traits. The six cicada species, for example, have similar life-history traits yet differ in

how their emergence dates have shifted over time. Had we only studied the temporal trends in insect phenology, we could have been misled as to what the true effects of global warming are in the life cycle of these species.

Such discrepancy may be explained by factors other than temperature that may affect the time phenological events are recorded. For example, late recording dates may be an indicator of population declines, possibly caused by land-use changes and habitat loss in and around the areas of the urban and suburban observation stations (Fujihara et al. 2005; Nonomura et al. 2009). Over the years, these areas have been developed and the habitats have changed from rice paddy fields, wetlands, and grasslands to neighborhoods and city centers. This can create the effect of observing the first insect later, due to a reduced population size and a compression of the dates during which a species is observed (Miller-Rushing et al. 2008; Tryjanowski and Sparks 2001).

Temperature

With the majority of insect species exhibiting a significant phenological response to temperature, it is clear that air temperature in the months preceding emergence is an important factor in determining emergence dates. The occurrence of advancement of phenology with increased temperature is well documented for a variety of species (Menzel et al. 2006; Parmesan and Yohe 2003; Root et al. 2003) and, in general, biological activity in the temperate zone increases under warmer temperatures. This earlier emergence occurs when time is not included as a variable in the models, so it is in fact a relationship with temperature and not due to interactions between time and temperature. The positive relationships between species' responses to temperature and their trends over time (Online Resource 2) suggest that earlier emergence in warmer years has affected species' trends over time, but the predominance of positive trends, i.e., later phenology, over time
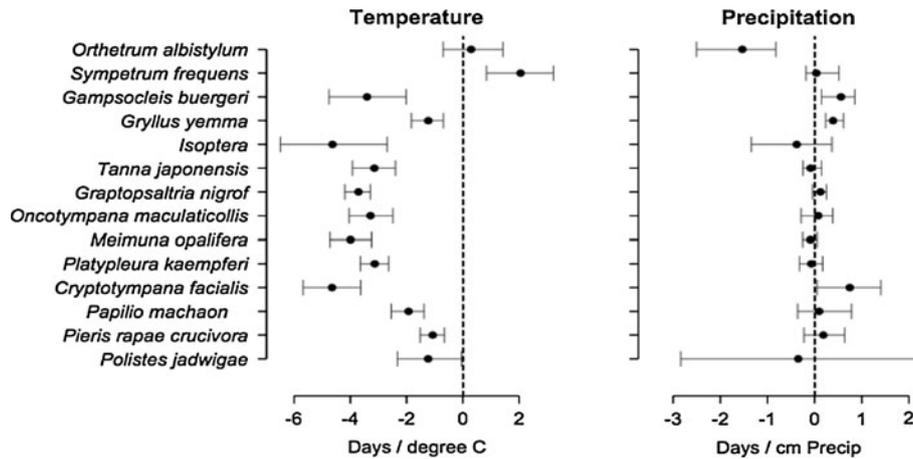
Fig. 1 Regression coefficients describing relationships between phenological event and each variable. These results are based on model C, incorporating temperature (η parameters) and precipitation (θ parameters) with site-specific effects. Intervals show 90% credible intervals; those not overlapping with the *dashed zero line* can be considered significant. For example, a majority of species have significantly negative relationships with temperature, a few have nonsignificant relationships, and one species, *S. frequens*, shows later phenology (FAP) with increased temperature

Fig. 2 Raw phenology data for all 14 species in response to temperature. *Circles* represent emergence date (FSI or FAP) as a function of temperature 90 days prior to mean emergence. All sites are included for each species. *Black lines* indicate predictions for mean emergence (*middle solid line*) and 95% predictive interval (*outer dotted lines*) derived from model C (in Table 2). All species showed significant overall relationships with temperature with the exception of *O. albistylum* [as seen in Table 3b, column Pr (later)]
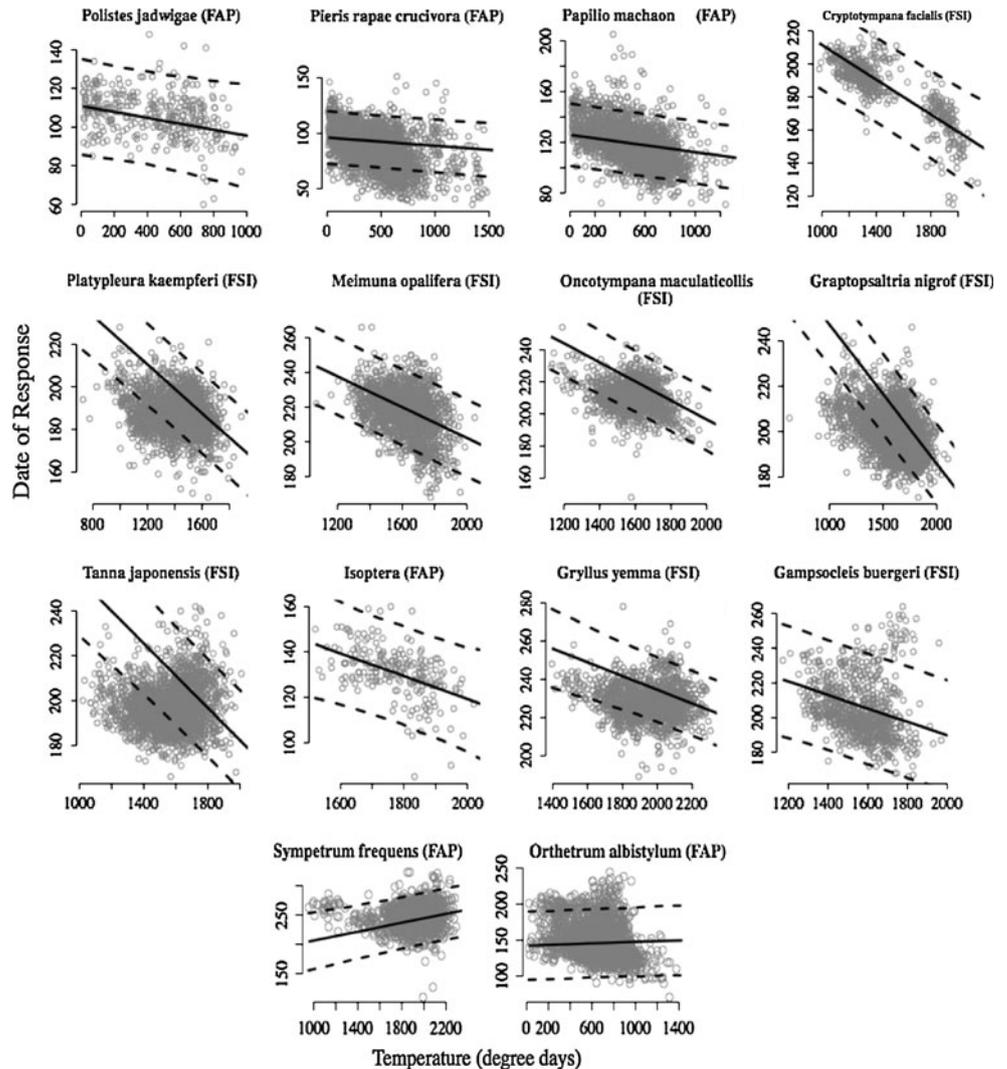
suggests an overriding influence of other factors such as population declines.

As a group, cicadas were among the most responsive to temperature, likely due to the thermal requirements of cicadas during their nymphal stage (Moriyama and Numata 2008). Moriyama and Numata (2008) found that both *G. nigrofuscata* and *C. facialis,* species occupying slightly different latitudinal ranges of Japan, had accumulated temperature requirements necessary for growth and development into the adult stage. It is probable that the other species of cicada analyzed here have similar requirements, accounting for their strong response to temperature.

The two species with later emergence with warming temperatures were dragonflies—*O. albistylum* (not significant) and *S. frequens* (significant). Temperature can affect voltinism in insects, with various consequences (Altermatt 2010a; Tobin et al. 2008). An additional generation can lead to considerable increases in population size, and has the potential to create an outbreak (Altermatt 2010a). It is possible that warmer years may lengthen the bivoltine cycle of *O. albistylum*, leaving only relatively few of the smallest nymphs to overwinter. This could have the effect of delaying the emergence time of the overwintering generation, and reducing the number of dragonflies that emerge in the first generation of the following year (Doi 2008). Population structure can therefore change from year to year, depending on climate and the number of generations a species is able to produce. It is also possible that populations of these species are declining due to habitat loss at a rate greater than the other 12 species in this analysis (Kadoya et al. 2009), or simply that as species which depend on an aquatic environment for larval development, it would be water temperature not air temperature that is the pertinent variable.

Precipitation

Although precipitation was not as important a predictor for insect phenology as temperature, several species displayed trends towards later and one towards earlier phenology with higher precipitation. *G. yemma* and *G. buergeri*, the only species in the order Orthoptera in this dataset, exhibited trends toward later emergence with increased precipitation at all stations at which they were heard. It is possible that the exposed nature of these species' juvenile stage in grasslands and fields makes them susceptible to harm due to an abundance of rain. *O. albistylum*, the only species exhibiting earlier emergence with higher precipitation, may be dependent upon rain or high humidity to complete stages of its life cycle. Droughts and extreme precipitation events can also influence when a newly-emerged insect is first heard or seen. To avoid desiccation or heavy rainfall insects may not fly or sing; however, this does not mean that they have not emerged.

Although the monthly climatic patterns analyzed in this study may determine the broad window when phenological activity is possible in a given year, daily and weekly temperature and precipitation events may actually trigger the exact timing. Ultimately, a greater understanding of extreme events is needed along with models that can estimate the effects of weather events on phenology (Jentsch et al. 2009).

Conclusions

The implications of these changes in insect phenology will depend on the relative magnitudes and directions of responses across trophic levels. Primack et al. (2009) and Ibáñez et al. (2010) showed that a suite of plant species at these same stations have shifted toward earlier spring phenology with increased temperature. The advancement of plant phenology from 0.35 to 7.70 days per 1°C, and the observed insect responses in this study, ranging from 2.03 days later to 4.81 days earlier, raise the possibility of significant ecological mismatches if trophic levels continue to diverge in their responses to increasing temperatures. Clearly, when tightly interacting species are identified, divergent responses may disrupt plant reproduction and insect development, leading to potential collapse of population numbers (Parmesan 2007). However, even shifts in generalist species may have important implications for both plant and insect dynamics. Shifting generalist herbivores relative to plant species may create new suites of interacting species with unknown evolutionary and ecological consequences. Plants may have to adapt to new pollinators and herbivores, while insect growth and development will require utilizing novel resources and plant chemistries. Indices of vegetation growth such as Normalized Difference Vegetation Index (NDVI) can be used to assess the level of "greenness" in a region and may be a practical metric for available insect food resources when relationships are more diffuse and with generalist species. Inclusion of both climatic and vegetation drivers will help distinguish the mechanisms driving insect phenology. By incorporating experiments and remote sensing with ongoing monitoring, there would be greater ability to anticipate mismatches between interacting species and quantify the impact of vegetation phenology, land use change and climate change on insect phenology.

This analysis has pointed out the disparity between temporal trends in insect phenology and their actual response to warming temperatures. Field studies and further investigations are needed to determine the suite of factors affecting when phenological events and/or their documentation take place. For example, mean or peak emergence dates, not just first appearance or singing,

would more accurately reflect overall changes in phenology (Miller-Rushing et al. 2008). Also, including site-specific effects, such as level of urbanization, human population size and other non-climate variables that might affect local population dynamics, could help to improve our understanding of the effects of global warming on insect phenology.

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