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Spatial and interspecific variability in phenological responses to warming temperatures

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ABSTRACT

A comprehensive understanding of species phenological responses to global warming will require observations that are both long-term and spatially extensive. Here we present an analysis of the spring phenological response to climate variation of twelve taxa: six plants, three birds, a frog, and two insects. Phenology was monitored using standardized protocols at 176 meteorological stations in Japan and South Korea from 1953 to 2005, and in some cases even longer. We developed a hierarchical Bayesian model to examine the complex interactions of temperature, site effects, and latitude on phenology. Results show species-specific variation in the magnitude and even in the direction of their responses to increasing temperature, which also differ from site-to-site. At most sites the differences in phenology among species are forecast to become greater with warmer temperatures. Our results challenge the assertion that trends in one geographic region can be extrapolated to others, and emphasize the idiosyncratic nature of the species response to global warming. Field studies are needed to determine how these patterns of variation in species response to climate change affect species interactions and the ability to persist in a changing climate.

1. Introduction

Phenological dynamics have been recognized as key attributes of plants and animals that are being affected by a warming climate (Parmesan and Yohe, 2003; Root et al., 2003; Cleland et al., 2007; Parmesan, 2007). As a result of rising temperatures, many plant species are leafing out and flowering earlier in the spring, many animals are active earlier, and many migratory birds are arriving earlier at points along their spring migration routes (e.g., Both et al., 2006; Inouye et al., 2000; Fitter and Fitter, 2002; Cotton, 2003; Miller-Rushing and Primack, 2008). However, the changes vary considerably among species; some species are changing dramatically while other are not changing at all (Fitter and Fitter, 2002; Lehikoinen et al., 2006; Sherry et al., 2007; Miller-Rushing and Primack, 2008). Knowing a particular species' response to global warming in the context of its surrounding environment will be crucial for the assessment of the effects of climate change on its populations, the communities to which it belongs, and biodiversity in general.

Given data constraints, most phenological studies focus on one or a few species in one or a few sites. More comprehensive studies may include a community of species at one site or examine a single species over a wider geographical area (e.g., Sparks and Carey, 1995; Dunn and Winkler, 1999; Fitter and Fitter, 2002; Doi, 2007; Miller-Rushing and Primack, 2008). However, groups of species may vary in their responses to climatic variation across a wide geographical range due to genetic and environmental variation (Davis and Shaw, 2001; Etterson and Shaw, 2001). Many species of plants, in particular, require a period of cold (vernalization) before they become fully competent to respond to warming conditions in the spring (Michaels and Amasino, 2000). In colder regions, increased temperatures will generally promote earlier leafing out, whereas in warmer regions, increased temperatures may delay leafing out because plants may not experience sufficient cold to overcome their winter chilling requirements (Zhang et al., 2007). In animals as well, species vary in which cues they use to time reproductive activity and other life history stages, and the

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relative importance of those cues also varies. For example, some migratory bird species and populations use day-length to regulate the timing of migration while others use temperature or a combination of day-length and temperature (Lyon et al., 2008; Morin et al., 2009).

Previous studies of single species have found geographical variation in species responses to climate change (e.g., Dunn and Winkler, 1999; Matsumoto et al., 2003; Doi and Takahashi, 2008), as has a study of numerous species across Europe (Menzel et al., 2006). However, the generality of this finding across taxonomic groups and locations is unclear, particularly in light of a recent meta-analysis of data on 203 species from across the northern hemisphere that found only weak latitudinal variation in the advancement of spring events (Parmesan, 2007). Discerning geographic variation in phenological change across a range of taxonomic groups is difficult because researchers must gather phenological data for several species in a consistent manner across a broad geographical range. Yet this information is critical for predicting species and community responses to future climate change and for planning actions to protect threatened elements of biodiversity.

In this paper, we report on the phenological observations collected for 12 plant and animal taxa by the meteorological agencies of Japan (102 sites since 1953) and Korea (74 sites with some since 1921) (Fig. 1a). Given the large spatial and temporal scale of the data, our goal is to use the information contained in these observations to understand the spatial and interspecific variability of species phenological response to global warming. The main questions we aim to answer are: is a species' phenological response to increasing temperatures consistent over a large geographic range? Or is it site-specific? Are species at a particular site having a similar phenological response to global warming? Or are the trends idiosyncratic for each species? Answering these questions will help us to better understand and predict the complex effects of climate change on natural populations, communities and biodiversity.

2. Materials and methods

2.1. Phenology and climate data

Since 1953 the Weather Service of Japan has been gathering data on over 120 phenological events at the grounds of 102 of their weather stations (data available from Japan Meteorological Agency, http://www.jmbsc.or.jp/english/index-e.html). The Weather Service of Korea has been gathering similar data on 20 phenological events at 74 weather stations with some observations dating from 1921 (data available from Korea Meteorological Administration, http://web.kma.go.kr/edu/unv/agricultural/seasonob/1173374_1389.html). Data for certain individual phenological events and sites have been previously analyzed, as reviewed by Kai et al. (1996) and Chen (2003) with more recent articles by Matsumoto et al. (2003), Ho et al. (2006), Doi (2007, 2008), Doi and Katano (2008), Doi and Takahashi (2008), and Doi et al. (2008). These weather stations are located across the latitudinal range of Japan, from northern Hokkaido (latitude 45°24.9′ N) to the southern islands (latitude 24°20.2′ N), with a corresponding gradient in annual temperatures from subtropical to boreal (Fig. 1a). Korea has a higher density of weather stations in a more continental area than Japan. Climate analyses have shown that this region has warmed in recent years (see also Section 3 and Fig. 1b), and models forecast that local temperatures will continue to rise in the future due to both global warming and increasing urbanization in the region (IPCC, 2007).

From this data set, we selected species from different trophic levels for which records of spring phenological observations were most complete across stations. Five species have records from both countries and seven species for Japan only (Table 1). We included first flowering of the widely planted Japanese apricot tree (*Prunus mume*), first appearance of the common white butterfly (*Pieris rapae*), first arrival of the migratory barn swallow (*Hirundo rustica*), first singing of the skylark (*Alauda arvensis*) and first appearance of black-spotted pond frogs (*Rana nigromaculata* and *Rana porosa*, closely related species that are mostly allopatric and are difficult to distinguish using morphological characters (Moriya, 1954; Sumida et al., 1998)). For Japan only, we also included first flowering of dandelion (native *Taraxacum* spp.), native *Camellia* shrub (*Camellia japonica*), and native *Wisteria* vine (*Wisteria floribunda*), first singing of non-migratory Japanese bush warbler (*Cettia diphone*), leaf bud burst of the widely planted, but non-native maiden hair tree (*Ginkgo biloba*) and the native mulberry tree (*Morus bombycis*), and first appearance of paper wasp (*Polistes jadwigae*). The observations were made by agency employees according to carefully defined sampling protocols that have remained constant for the duration of the study period. The protocols directed that a single individual plant for each species was observed close to each weather station for activity, and animal species were monitored at specific sites in the vicinity of each weather station where they were known to occur. The sampling methods of sites in Japan and South Korea are nearly identical. Given the magnitude (176 sites and over five decades of sampling) of the data set we are confident our analysis provided us with a reliable estimate of each species' response to warming temperatures.

2.2. A model for plant and animal phenology

From the data available to us (i.e., monthly mean temperature), we compared the predictive potential of several combinations of temperature during winter and early spring months in our analysis. For the final analysis we used a single fixed period of temperature records, mean winter temperature (November–March), which predicted our data best and provided one consistent parameter across all species, sites and years. This measure of winter temperature indicates both the severity of the winter and time and rate of warming in the spring, all of which are important for the spring phenology of many plants and animals (Sparks and Carey, 1995; Chuine, 2000). We recognize that certain animal species may be more sensitive to weather during more specific periods. For example, birds and amphibians may be sensitive to temperatures just before and during the egg-laying period (Dunn and Winkler, 1999; Hartel, 2008).

However, this approach of using a single index of mean winter temperature for all sites and species allowed us to avoid a statistically circular argument where the response variable (phenology) would be defining the explanatory variable (temperature). As data becomes available, we are planning further analyses that will involve using daily weather records to develop models for each species.

After trying several phenological models, we found that a two-parameter negative exponential model provided the best overall fit to the data across species (see Table 2 for alternative models we tested). We then modeled phenology at site s in year t as having a negative exponential response to temperature and a linear relationship with latitude:

$$\text{Phenology}_{st} = \alpha_s \cdot e^{(-\beta_s * temperature_{st})} + \gamma * latitude_s + \varepsilon_{st}$$

In the model the error terms were distributed as $\varepsilon \sim Normal(0, \sigma_\varepsilon^2)$. We fitted a different curve at each location (parameters α_s and β_s were estimated for each location). This approach allowed us to model the unique response to temperature at each site given by the particular characteristics of the location (climatic variables other than temperature, soils, etc.). α_s and β_s were estimated from $\alpha_s \sim Normal(a, \sigma_a^2)$ and $\beta_s \sim Normal(b, \sigma_b^2)$, respectively. Parameter

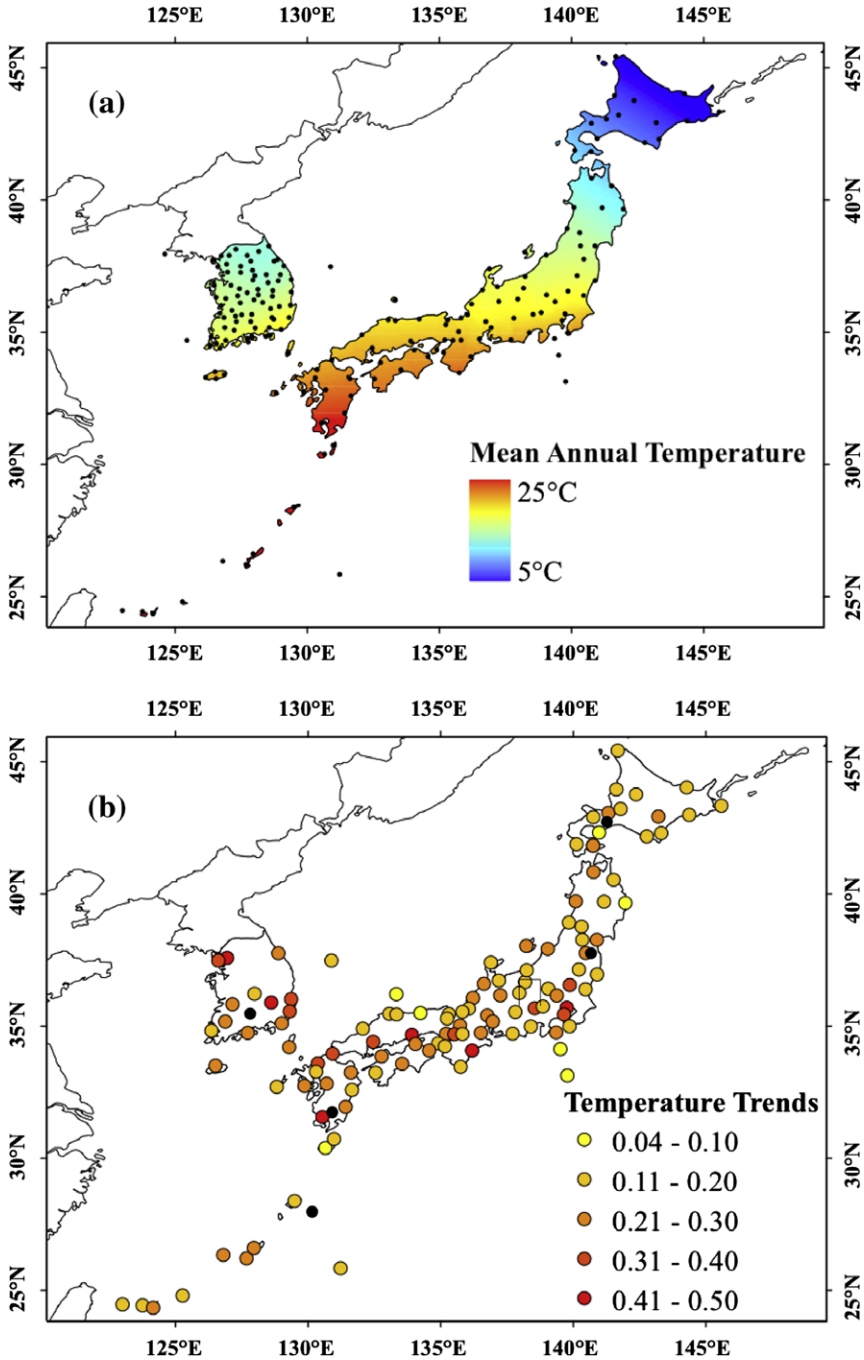

Fig. 1. Map of Japan and South Korea showing (a) the locations of the meteorological sites (dots) and mean annual temperature and (b) warming trends for November through March (°C/decade) for those stations for which we have a complete temperature record (1953–2005). Black circles indicate the six representative locations shown in the results.

γ, was considered to be the overall response to latitude, in this case a proxy for day-length or migratory distance, variables that also have the potential to determine when a phenological event takes place, $\gamma/Normal(0, 1000)$.

Parameters $\sigma^2_\varepsilon, \gamma, a, \sigma^2_a, b$, and σ^2_b, were then estimated at the species level, which allowed us to make comparisons on the overall response to increasing temperature among species. Their prior distributions were as follows:

$$\tau_\varepsilon = 1/\sigma^2_\varepsilon, \quad \tau_\varepsilon \sim Gamma(0.01, 0.01)$$
$$a \sim Gamma(2, 0.02) \quad \text{and} \quad b \sim Gamma(0.2, 0.2)$$
$$\sigma_a \sim Uniform(0, 100) \quad \text{and} \quad \sigma_b \sim Uniform(0, 10)$$

This selection of prior parameter values reflects the wide variability in the parameters ranges we observed in the data and maintains them within those realistic ranges; it also reduces the running time of the model.

To deal with the uncertainty in the temperature data, where the records were only approximations of the true conditions that affected the individuals, we followed a hierarchical Bayesian approach (Clark et al., 2003). The temperature values, *temperature*, included in the model were treated as latent variables that needed to be estimated. We took advantage of the Bayesian structure of the model and estimated temperature as a function of those records (*wmt*: winter mean temperature) within the range of vari-

Table 1
Species analyzed and the time series analyses of temperature and phenology data *vs*. year. Numbers of slope coefficients (by location) that were above or below zero are provided with the number of slopes that were statistically significant (*P*-values < 0.05) in parenthesis. Site data cover different periods of time and number of years for each species; for each species, we used only locations that had at least 5 years of data. FAP: first appearance, FBO: first leaf bud opening, FFT: first flowering time, FSI: first singing. N: number of observations, S: number of sites, Y: first and last year recorded (records are not complete at all locations).

Species	Temperature		Phenology	
	+ Increasing	– Decreasing	+ Later	– Earlier
Alauda arvensis bird FSI N: 4489 S: 131 Y: 1923–2005	125 (76)	6 (2)	89 (52)	42 (16)
Camellia japonica shrub FFT N: 3466 S: 81 Y: 1953–2005	80 (56)	1 (0)	32 (15)	49 (33)
Cettia diphone bird FSI N: 3845 S: 86 Y:1953–2005	86 (64)	0 (0)	51 (20)	35 (8)
Ginkgo biloba tree FBO N: 3040 S: 78 Y: 1953–2005	74 (62)	4 (3)	14 (3)	64 (30)
Hirundo rustica bird FAP N: 6558 S: 154 Y: 1923–2005	146 (114)	8 (2)	86 (33)	68 (19)
Morus bombycis tree FBO N: 1595 S: 36 Y: 1953–2005	36 (26)	0 (0)	13 (2)	23 (11)
Pieris rapae butterfly FAP N: 6848 S: 160 Y: 1923–2005	153 (150)	1 (0)	133 (60)	27 (7)
Polistes jadwigae wasp FAP N: 382 S: 12 Y: 1953–2005	12 (12)	0 (0)	10 (2)	2 (0)
Prunus mume tree FFT N: 6111 S: 150 Y: 1921–2005	142 (139)	8 (3)	39 (6)	111 (91)
Rana nigromaculata frog FAP N: 3893 S: 121 Y: 1923–2005	108 (54)	14 (0)	90 (50)	31 (11)
Taraxacum spp. forb FFT N: 3233 S: 71 Y: 1953–2005	70 (53)	1 (1)	26 (7)	45 (22)
Wisteria floribunda vine FFT N: 3358 S: 75 Y: 1953–2005	75 (56)	0 (0)	18 (1)	57 (27)

Table 2
Selection of some of the sub-models tested. We tested several combinations of these models, with and without random effects for site and/or year, fitting one curve/line per country or per site, and combining or separating the effects of temperature and latitude. For this study, we selected the negative exponential model G, which had the lowest DIC (see Section 2).

	Sub-model
A – Linear model for each country including site and year random effects	$\text{Phenology}_{st} = \eta_c + \gamma_1 * temperature_{st} + \gamma_2 * latitude_s + \mu_s + \lambda_t + \varepsilon_{st}$
B – Linear mixed model for each site and year random effects	$\text{Phenology}_{st} = \eta_s + (\gamma_1 + \mu_s) * temperature_{st} + \gamma_2 * latitude_s + \lambda_t + \varepsilon_{st}$
C – Inversed saturation for each country, with site and year random effects	$\text{Phenology}_{st} = g_c * \frac{temperature_{st}+\theta_c}{temperature_{st}} + \gamma * latitude_s + \mu_s + \lambda_t + \varepsilon_{st}$
D – Inversed saturation for each site and year random effects	$\text{Phenology}_{st} = g_s * \frac{temperature_{st}+\theta_s}{temperature_{st}} + \gamma * latitude_s + \lambda_t + \varepsilon_{st}$
E – Negative exponential for each country, with site and year random effects	$\text{Phenology}_{st} = a_c e^{-b_c temp_{st}} + \gamma * latitude_s + \mu_s + \lambda_t + \varepsilon_{st}$
F – Negative exponential for each country, spatially explicit and year random effects	$\text{Phenology}_{st} = a_c e^{-b_c temp_{st}} + w_s + \lambda_t + \varepsilon_{st} w_s\|_{k,k\neq s} \sim Normal(\rho\sum_k w_j \| \tau_w^{-1})$ spatial term
G – Negative exponential for each site	$\text{Phenology}_{st} = \alpha_s e^{-\beta_s temp_{st}} + \gamma * latitude_s + \varepsilon_{st}$
H – Negative exponential, temperature–latitude interaction	$\text{Phenology}_{st} = \alpha_s e^{-\beta_s temp_{st} latitude_s} + \varepsilon_{st}$

Subindices: *s* indicates site, *t* time or year, *c* country (Japan or South Korea).
η: intercept.
γ: fixed effects.
μ: site random effects.
λ: year random effects.
w: spatially explicit random effects.
g and θ: parameters of the inversed saturation model.
a, *b*, α, and β: parameters of the negative exponential model.

ability ($\sigma temp_s^2$: variance winter temperature) observed at each site, then $temperature_{st} \sim Normal(wmt_{st}, \sigma temp_s^2)$.

Posterior densities of the parameters were obtained by Gibbs sampling (Geman and Geman, 1984) using WinBUGS 1.4 (Spiegelhalter et al., 2002). Simulations were run for 50,000 iterations. Convergence was assessed from multiple chains with different initial conditions and Gelman and Rubin's R, as modified by Brooks and Gelman (1998), where convergence is assumed when *R* is close to 1. Convergence required from 1000 to 10,000 iterations. Preconvergence 'burn-in' iterations were discarded. Model selection was based on DIC (Deviance Information Criterion) (Spiegelhalter et al., 2006). The effective number of parameters was approximated by subtracting the deviance of the posterior means of the parameters from the posterior mean of the deviance. Adding this value to the posterior mean deviance gave a deviance information criterion for comparing models, where the best predictor of the data was the model with lowest DIC. By using DIC we were able to compare non-nested models.

Our negative exponential model gave a better fit than a linear model, because species tended to have the greatest phenological response to change in temperature under cool conditions. Small increases in temperature at cold locations had a large effect on

phenology, while similar changes in warm locations had less or no effect on phenology (see Fig. 2). We tested elevation as an additional explanatory variable but it did not improve our predictions, probably due to the high correlation between temperature and elevation. As a preliminary analysis of spatial and temporal autocorrelation we ran models with location and year random effects (Table 2 models A–F). We also tested a spatially explicit model (Table 2 model F), in which the error term, *w*, reflected the latitudinal pattern. However, these models performed no better than our simpler negative exponential model (Table 2 model G).

3. Results

3.1. Changes in temperature over time

Winter temperatures (November–March) have risen by an average of 1.2 °C over the region from 1953 to 2005 (Fig. 1b, Table 1). There was no obvious correlation of greater temperature increases with higher latitudes (temperature increase *vs.* latitude $R^2 = 0.01$, not shown). However, temperature increases were significantly correlated with the size of the human population in the city of the weather station ($p < 0.001$; $R^2 = 0.40$), reflecting the local impact of the urban heat island effect. Temperatures increased by an annual average of 0.017 °C (±0.007 SD) in cities with populations less than 250,000 and 0.027 °C (±0.008 SD) in the cities with more than 250,000 people.

3.2. Changes in phenology over time

Across all sites, the phenology of each species has changed in a unique manner over that time interval. *Prunus*, *Taraxacum* and *Wisteria* are flowering earlier at 111 of 150 sites, 45 of 71 sites and 57 of 75 sites, respectively, as indicated by a negative slope of phenology *vs.* year (Table 1). *Ginkgo* and *Morus* are also leafing out earlier at 64 of 78 sites and 23 of 36 sites, respectively. However, the first observations of *Rana*, *Pieris*, *Alauda*, *Polistes*, and *Cettia* are occurring later over time at the majority of sites (90 of 121 sites, 133 of 160 sites, 89 of 131 sites, and 10 of 12 sites, and 51 of 86 sites, respectively), contrary to studies showing earlier spring phenology with warming conditions (Parmesan, 2007). *Camellia* and *Hirundo* have variable changes among sites. In particular, *Hirundo* is arriving earlier over time in 51 of 81 sites of Japan, and arriving later in 56 of 73 sites of South Korea. This variation among species and sites reflects the complexity of species' responses to changes in climate.

3.3. Species' responses to temperature and latitude

Our results show that each of the species has responded to temperature changes at a different rate, as shown by different slopes of

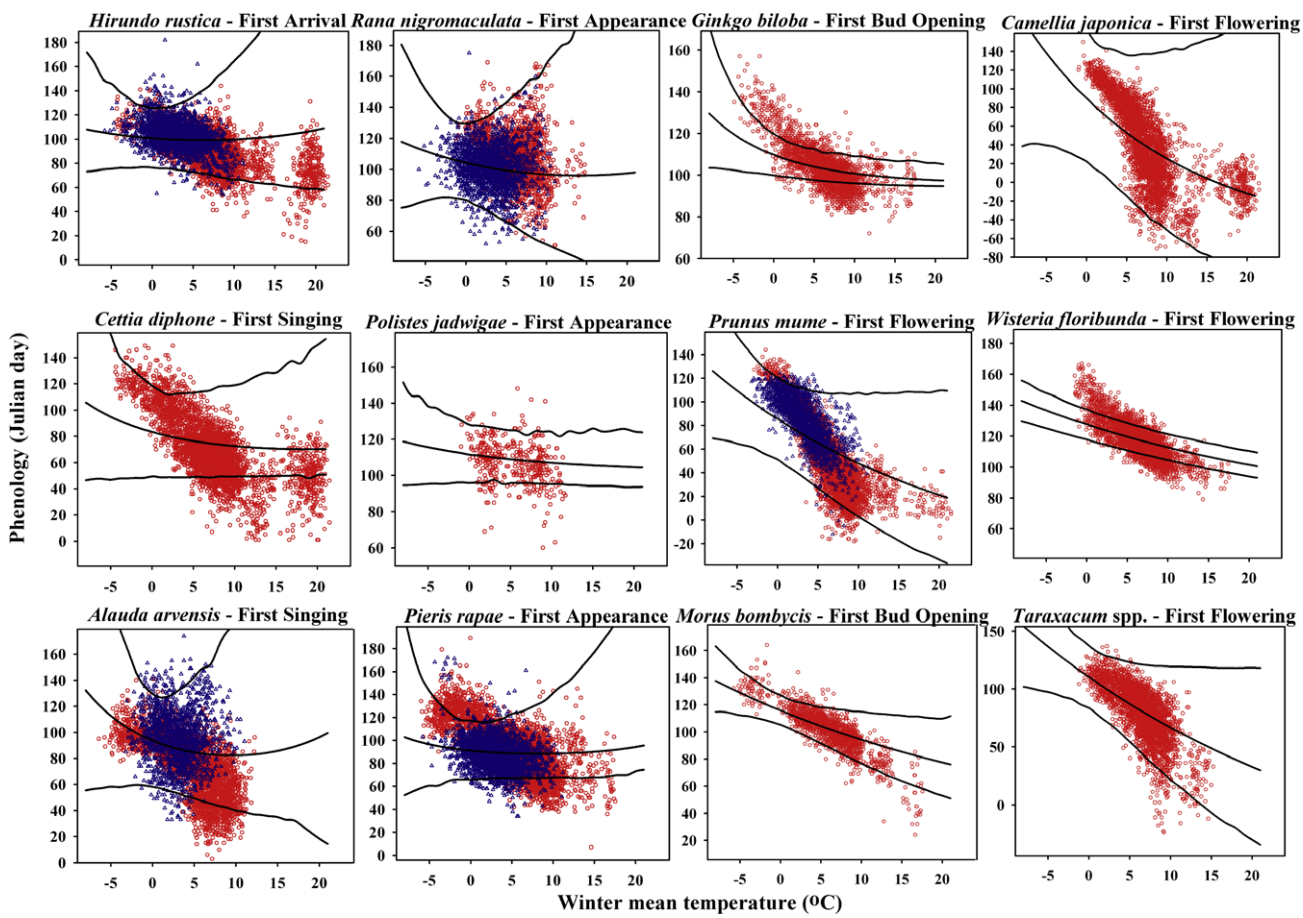

Fig. 2. Phenological events for 12 species plotted against mean winter temperature (November–March) for all stations and years for which data are available from Japan (red) and South Korea (blue). The sample size for each graph is shown in Table 1. To illustrate the overall species response to temperature we have added lines to represent the posterior estimates (mean and 95% predictive interval) of the species response to temperature at an average latitude of 36°N (this corresponds to an average winter temperature of 3.4 °C). Curves generated for different latitudes, higher and lower, would differ from those shown, due to local site effects, and would have covered those points at much colder and warmer temperatures. The predictive interval tends to be narrower at temperature values typical of that latitude, and the width of the intervals represents the variability of the phenological response at each given temperature.

the exponential curves (Table 3, Fig. 2). In particular, for three plant species, *Prunus*, *Taraxacum* and *Camellia,* flowering times occurred much earlier for each degree increase in temperature (>4.0 days earlier/°C) (Table 3). For *Hirundo* and *Rana*, two animal species, temperature seems to have had a negligible effect on changes in spring activity (slope < 1.0 day earlier/°C). The other seven species shifted their timing of activity at intermediate rates (Table 3, Fig. 2). Note that the lines in Fig. 2 represent the posterior estimates (mean and 95% predictive interval) of the species responses to temperature at an average latitude of 36°N; these estimates are not calibrated for latitudes with warmer and colder temperatures. Consequently, these overall lines do not fit the entire data set. The particular curves from more northern and southern latitudes would fit the data for colder and warmer temperatures.

In addition, our results show that phenological responses to temperature vary among locations for each species (Fig. 3). This likely occurred because the response to temperature at each location interacted with other factors characteristic of the site (e.g., precipitation, snow cover, soil type, wind, and population genetics). In summary, the hierarchical structure of the model allowed us to evaluate the overall species response to warming conditions (Fig. 2) while still incorporating site-specific patterns (Fig. 3).

The response to latitude also varied among species (Table 3). In our analysis we found both positive and negative γ parameters (estimates of the effect of latitude on phenology). Positive γ values indicate that for a given temperature, phenology occurs later at higher latitudes. Negative γ values indicate the opposite trend, with phenology occurring earlier at higher latitudes for a given temperature. Importantly, though, the model uses both latitude and temperature to predict phenology.

To evaluate the fit of our models we also assess observed data *vs*. predicted phenology for each of the species (Fig. 4). Not surprisingly, plant species responses are much better explained by temperature than are the responses of birds, butterflies, wasps, and frogs.

3.4. Trends and future projections

From the results shown above, we closely examined a subset of five locations in Japan and one in South Korea. These sample locations represent the latitudinal and temperature ranges found in the data, and were also selected for their relatively complete representation of species. Within each location the species differed in their predicted phenological responses to future warming temperatures, and these discrepancies also shifted from one location to another (Fig. 3). For example, when comparing forecasts for a 3 °C increase under a moderate climate change scenario by the year 2100 (IPCC, 2007), the phenological response clearly varied among species and sites. *Camellia* predictions ranged from flowering 6 days earlier at Yamagata to flowering 21 days earlier in Toyama (Fig. 4). *Rana* was predicted to appear anywhere from 12 days earlier (Yamagata) to 5 days later (Kumamoto). In contrast, forecasted changes in phenology for certain other species appear relatively constant among locations.

4. Discussion

Although the phenological data showed a high degree of variability, or "noise," and we had only a coarse estimate of winter temperatures (mean monthly winter temperatures), the large temporal and spatial extent of the records allowed us to evaluate each species' phenological response to warming. In particular, our results illustrate that species' responses to climate change are more variable than the predictions provided by many phenological studies, and that generalizations made for one species at one location may not translate to similar trends somewhere else. Due to the site-specific conditions created by not only temperature but also by many other variables characteristic of the site, species might be able to track the changing climate in some locations but not in others. The assessment of such differences will be critical for conservation efforts. Knowing which sites may constitute adequate

Table 3
Posterior mean estimates (SD) for the parameters included in the model. The slope of the negative exponential (the derivate at temperature equal zero, $-ab$) provides an estimate of the magnitude of each species response to increasing temperatures.

Species	a	b	$-ab$	γ	σ^2_ε	σ^2_a	σ^2_b
Alauda arvensis	85.74 (5.96)	0.024 (0.004)	−2.09	0.19 (0.15)	77.01 (5.72)	291 (42.07)	0.002 (0.0004)
Camellia japonica	219.4 (10.6)	0.038 (0.004)	−8.36	−3.60 (0.29)	55.31 (8.69)	1247 (232)	0.0007 (0.0001)
Cettia diphone	131.4 (6.02)	0.019 (0.002)	−2.54	−1.12 (0.12)	100.5 (5.58)	476.7 (95.66)	0.0001 (0.00003)
Ginkgo biloba	60.44 (7.02)	0.027 (0.004)	−1.67	1.46 (0.18)	9.48 (1.64)	97.93 (5.9)	0.00001 (0.00002)
Hirundo rustica	39.93 (6.19)	0.020 (0.007)	−0.80	1.71 (0.17)	62.86 (4.48)	127.5 (33.98)	0.002 (0.0006)
Morus bombycis	15.3 (2.57)	0.09 (0.027)	−1.36	2.57 (0.04)	44.46 (2.36)	72.37 (23.54)	0.015 (0.006)
Pieris rapae	44.51 (5.1)	0.036 (0.004)	−1.58	1.43 (0.12)	92.12 (3.31)	119.2 (15.87)	0.0008 (0.0002)
Polistes jadwigae	9.98 (5.63)	0.19 (0.11)	−2.04	2.95 (0.06)	101.9 (10.2)	300.6 (233.8)	0.028 (0.076)
Prunus mume	177.5 (2.4)	0.025 (0.001)	−4.57	−2.41 (0.05)	5.02 (1.48)	337.3 (43.1)	0.0002 (0.00002)
Rana nigromaculata	60.17 (21.8)	0.007 (0.004)	−0.43	1.27 (0.59)	106.8 (7.15)	89.69 (17.84)	0.002 (0.005)
Taraxacum spp.	242.8 (2.67)	0.02 (0.001)	−4.85	−3.76 (0.05)	20.6 (4.98)	200.6 (42.15)	0.0001 (0.00002)
Wisteria floribunda	61.92 (3.04)	0.027 (0.001)	−1.7	1.82 (0.07)	6.81 (1.92)	25.47 (4.82)	0.00002 (0.000002)

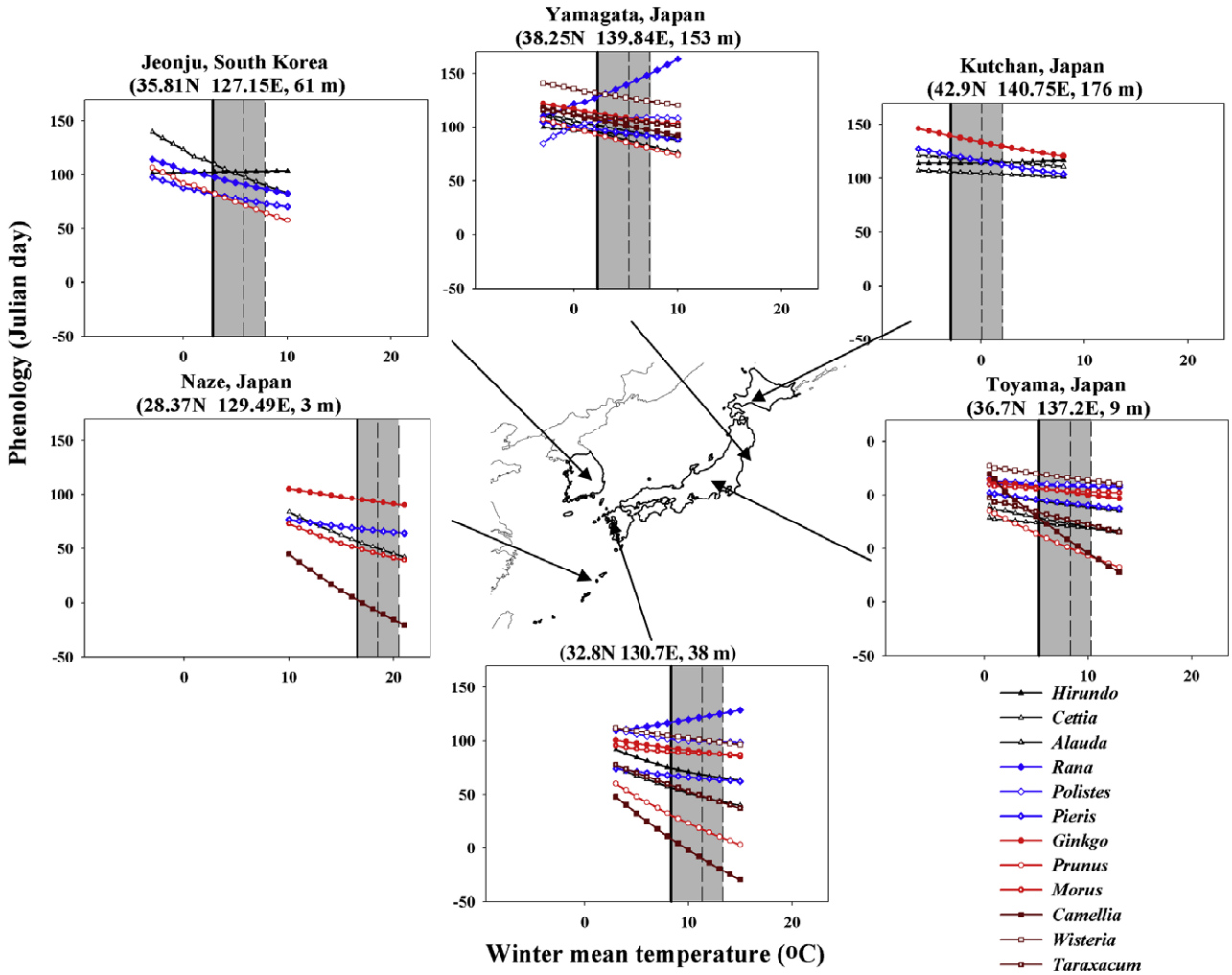

Fig. 3. Mean posterior estimates of the species phenological responses to temperature at six representative locations. Vertical lines indicate the mean winter temperature at each location (solid lines) and the forecasted increases in temperature of 3 and 5 °C (dashed lines). The shaded areas represent the changes in phenology under those climate scenarios. Predictive intervals are not shown for clarity.

refugia for endangered species, and which ones may not, will be key for the preservation of certain species.

Previous analyses of subsets of these data estimated the overall response of particular species to global warming (Matsumoto et al., 2003; Doi, 2007, 2008; Doi et al., 2008). Our work extends these previous studies by considering both geographical variation within one species and differences among species. Further, the hierarchical Bayesian model we developed allowed us to predict the overall phenological responses of species to future warming temperatures, while still identifying the specific trends at each location. Our forecasts are strengthened by the latitudinal gradient present in the observational data (from 45.41°N to 24.33°N), which provided a greater amount of variation in temperature and phenology than was present at any single site (the maximum inter-annual variability in one site was 12 °C, while the temperature range from the coldest to the warmest locations was nearly 24 °C). Therefore, we used southern (i.e., warmer) locations to inform how the same species in more northern locations will respond to novel warming temperatures. Our analysis partitioned the variability observed in the data into site-to-site differences (parameters σ_a and σ_b), and the overall variability related to the species response to temperature and latitude (parameter σ_ϵ). Such differentiation allowed us to better assess the overall effects of warming on the phenologies of the studied species (parameters a and b), and to estimate the site-specific phenological responses (parameters α_s and β_s).

In this study, five species show earlier activity over the last five decades, whereas seven species either show inconsistent phenological changes or show primarily later timing of activity. Here, the variation among species' and populations' phenological changes is likely due to a combination of factors, including changes in temperature and other climatic variables (Sherry et al., 2007), population sizes (Tryjanowski and Sparks, 2001; Miller-Rushing et al., 2008a,b), genetic differences, phenotypic plasticity, and land use. In particular, delays in the timing of spring activity can be caused by declining population sizes, which can shorten the duration of the event but not affect the mean value (Tryjanowski and Sparks, 2001; Miller-Rushing et al., 2008a,b); or could just be due to the fact that densities are lower and the probability of observing the event when it really first happens is lower. Such declines are occurring for many animal species in Japan (Higuchi, 1996; Lane and Fujioka, 1998). Nevertheless, we found that there are dramatic differences among species in their phenological responses to changes in temperature (Table 3, Fig. 2), responses that should be minimally affected by changes in population size. Our empirical observations and analyses provide strong evidence that as temperatures continue to warm in coming decades, the timing of important life history stages of various species will diverge not only at one site but also among sites (Figs. 2 and 3). Variation in changes in other weather variables, such as snow cover, precipitation, and wind, will likely add to the variation among species' phenologies.

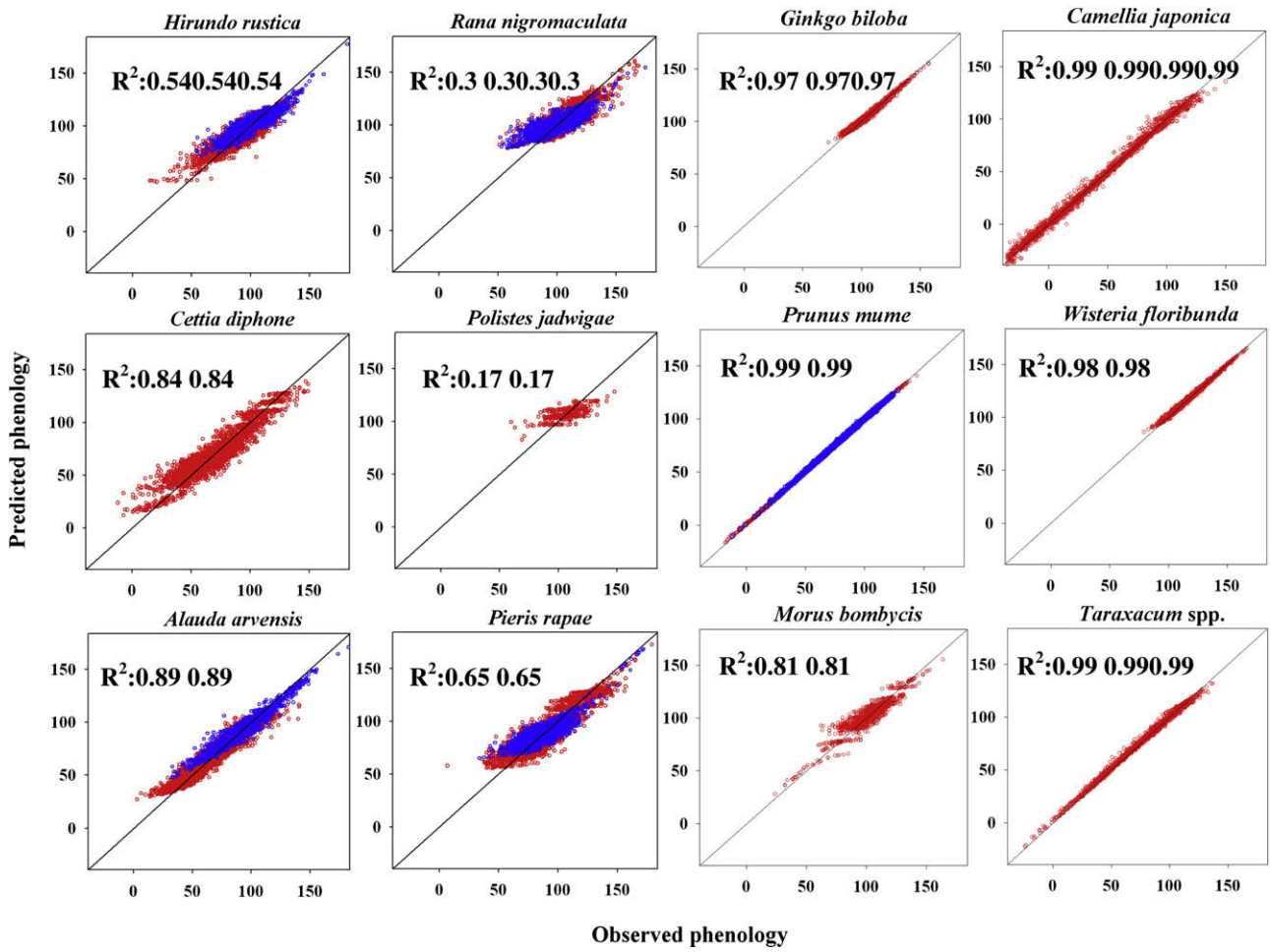

Fig. 4. Observed *vs.* predicted phenology for the 12 studied species, and R^2 values. The line represents the 1:1 relationship and red dots are for Japan data and predictions and blue dots for South Korean data and predictions.

Large numbers of ecological relationships are based on phenological events that occur at similar times, and a limited number of phenological imbalances or mismatches among species have already been documented (reviewed in Harrington et al., 1999; Stenseth and Mysterud, 2002; Visser and Both, 2005; Parmesan, 2006). Here we have shown that species are responding very differently to warming temperatures across trophic levels (i.e., plants and animals) and over broad geographical areas, suggesting that mismatches may already be a common occurrence and may become even more widespread in coming decades. Although there are no significant direct interactions among the species we examined, our results show that the phenologies of co-occurring organisms are shifting non-uniformly. As the phenologies of different species shift at different rates, relationships among species will change, altering biological communities. Some interactions will be lost and new interactions will occur. Certain species will probably decline and be eliminated while other species will increase in abundance. Rare species, species already declining for other reasons, and species of specialized habitats or with specialist relationships, may be most vulnerable to local extinction as the climate changes.

More field studies are urgently needed to determine the extent to which phenological shifts are occurring over large spatial scales. Our results clearly demonstrate that it is difficult to generalize from one site to another because of differences that exist between the phenological responses of individual species and sites. In addition, the relationship of phenology and temperature may not be linear, as has been commonly assumed. This nonlinearity might in part explain why the same species in different localities can show different responses to a warming climate (e.g., Sparks et al., 2005; Menzel et al., 2006). However, with large data sets that span broad geographic areas and temperature gradients, scientists can improve predictions of how phenological responses and ecological relationships will change in the future.

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