# Influences of species, latitudes and methodologies on estimates of phenological response to global warming

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#### Abstract

New analyses are presented addressing the global impacts of recent climate change on phenology of plant and animal species. A meta-analysis spanning 203 species was conducted on published datasets from the northern hemisphere. Phenological response was examined with respect to two factors: distribution of species across latitudes and taxonomic affiliation or functional grouping of target species. Amphibians had a significantly stronger shift toward earlier breeding than all other taxonomic/functional groups, advancing more than twice as fast as trees, birds and butterflies. In turn, butterfly emergence or migratory arrival showed three times stronger advancement than the first flowering of herbs, perhaps portending increasing asynchrony in insect-plant interactions. Response was significantly stronger at higher latitudes where warming has been stronger, but latitude explained <4% of the variation. Despite expectation, latitude was not yet an important predictor of climate change impacts on phenology. The only two previously published estimates of the magnitude of global response are quite different: 2.3 and 5.1 days decade $^{-1}$  advancement. The scientific community has assumed this difference to be real and has attempted to explain it in terms of biologically relevant phenomena: specifically, differences in distribution of data across latitudes, taxa or time periods. Here, these and other possibilities are explored. All analyses indicate that the difference in estimated response is primarily due to differences between the studies in criteria for incorporating data. It is a clear and automatic consequence of the exclusion by one study of data on 'stable' (nonresponsive) species. Once this is accounted for, the two studies support each other, generating similar conclusions despite analyzing substantially nonoverlapping datasets. Analyses here on a new expanded dataset estimate an overall spring advancement across the northern hemisphere of  $2.8 \, \text{days} \, \text{decade}^{-1}$ . This is the first quantitative analysis showing that data-sampling methodologies significantly impact global (synthetic) estimates of magnitude of global warming response.

*Keywords:* animal, climate change, global warming, insect–plant interactions, latitude, meta-analysis, phenology, plant, temperature, trophic interactions

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# Introduction

Increasing levels of greenhouse gases began to have a major impact on global climate only a few decades ago, yet there are already hundreds of studies documenting responses of wild species to that relatively small level of global warming (reviewed by IPCC, 2001a, b; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006). However, these responses are far from uniform. There are only a few species, which differ from

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the majority in direction of response, such as breeding later in spite of warming temperatures, but the strength of response in the expected direction varies by an order of magnitude across species. For example, multispecies studies have documented large differences in responses within given communities on a farm in the USA (among birds, butterflies, herbs and trees), in Britain (birds and butterflies) and across the whole of Europe (butterflies, trees and shrubs) (Bradley *et al.*, 1999; Menzel & Fabian, 1999; Parmesan *et al.*, 1999; Sparks, 1999; Menzel, 2000; Roy & Sparks, 2000). Further, many species (from 20% to 70% of species at a given location) have shown no response at all, exhibiting stable phenological patterns across years despite living in environments experiencing warming trends (Parmesan & Yohe, 2003).

Estimates of phenological response have the potential to be substantially influenced by the choice of study design and statistical methodology. However, because phenological data have been gathered and compiled in a diversity of ways over a diversity of time periods, their analysis is not straightforward, and there are as yet, no generally agreed methods. Several authors have identified particular problem areas and suggested refinements to deal with them. Sagarin (2001) pointed out a subtle source of bias present in virtually all analyses of temporal trends in phenology. He showed that analyses, which did not adjust event dates through time to account for long-term change in the calendar date of the vernal equinox had a bias toward stronger estimates of spring advancement. For example, the estimate of advancement of first bloom of Rudbeckia hirta (blackeyed Susan) from 1935 to 2000 was 5% stronger than the actual advancement. For all biological datasets analyzed, this resulted in a small but persistent overestimate of the magnitude of response to warming (Sagarin, 2001).

Sampling methodology, both within and across studies, could also have a large impact on estimates of response. One concern which has cropped up in several studies is that increases either in numbers of observers (particularly for databases derived mostly from amateur records) or real increase in population abundances could cause apparent expansions of ranges (Thomas & Lennon, 1999) or apparent earlier migrant arrival (Tryjanowski, 2001). Thus, what appears to be a change over time could, in reality, be due solely to statistical artifact stemming from a change in the absolute probability of sighting an individual at a particular place or time, with no real change in the species' range or phenology.

A suggested methodological refinement is use of Bayesian techniques for estimating response through time. For example, Bayseian methods can take into account changes in sampling density over time, by incorporating variability of sampling intensity into error terms across space and time for the desired estimate (Wikle, 2003). Dose & Menzel (2004) showed that Bayesian techniques for estimating changes in flowering time provided a means of asking quantitatively whether the rates of change were themselves changing. This technique enabled them to show a recent and significant increase in rate of phenological advance, thereby supporting previous, more qualitative claims that responses have become stronger in more recent (warmer) decades.

More general discussions of how differing methodologies might affect estimates of climate change impacts include concerns about effects of publication bias, differences across studies in time periods analyzed, nonrandom sampling within a species and nonrandom selection of species (Ahmad *et al.*, 2001; Parmesan & Yohe, 2003; Badeck *et al.*, 2004; Parmesan, 2004, 2005; Parmesan *et al.*, 2005). However, to date, no study has explicitly explored the impact of these effects on quantitative estimates of species' responses.

There are, as yet, only two quantitative, globally comprehensive datasets on phenological responses to recent climate warming: Root *et al.* (2003) and Parmesan & Yohe (2003) hereafter abbreviated as Retal and P&Y. Quantitative comparisons across broad taxonomic and functional groups have been limited to a single study (Root *et al.*, 2003). Because the criteria for data selection differed strongly between Retal and P&Y, the two resulting datasets were largely nonoverlapping. Therefore, a comparison between these studies has the potential to reveal the effects of differing data-selection techniques on overall conclusions.

Since the publication of Retal and P&Y, new data have been accumulating at an increasing rate (Parmesan, 2006), so these questions should ideally be tackled using all the accumulated information. However, before this can be achieved in a definitive manner, it would behoove the entire community to reach agreement on sampling and statistical methodology. Such agreement is still missing, in spite of the discussions referenced above showing that differences across studies in methodology have the potential to profoundly influence results. Before devoting efforts to new analyses of an ever-expanding database, priority should be given to developing consensus on how to best compile and interpret data across disparate studies to derive general conclusions. This paper attempts to inform such a future consensus by presenting new analyses of the existing datasets and by discussing the influence of the different approaches on the nature of the conclusions.

Specifically, I investigate the underlying causes of a more than two-fold difference in estimates of the mean magnitude of advance in timing of spring events between the two studies:  $2.3 \text{ days decade}^{-1}$  advance found by P&Y, and  $5.1 \text{ days decade}^{-1}$  advance found by Retal. Badeck *et al.* (2004) suggested that the difference between these two studies could be due to data being from different latitudes, different taxa, or different time periods. However, they did not investigate these possibilities analytically.

The two synthetic papers were both confined to data published in peer-reviewed literature, but differed in their criteria for data inclusion. This largely reflected differing aims of the two studies. Retal were focused on estimating the pervasiveness of a positive correlation between temperature trends and phenological trends for species *that were changing* through time. P&Y focused on estimating *total response* to climate change by analyzing the overall strength and consistency of response across all species, whether or not they showed phenological change. Further, P&Y attempted to control for publication bias by taking data only from multispecies studies (which included stable as well as responding species), while Retal used data from both single species and multispecies studies.

Here, I compare the two datasets to explicitly explore possible drivers of the difference in estimated strength of phenological responses between P&Y and Retal. A series of comparisons and analyses of the two datasets attempts to ascertain whether the differences in estimated responses represent biologically important phenomena or simply departures of methodology. A related question is: 'do the available data accurately reflect trends in natural systems, or are they biased?' One obvious source of bias would stem from positive (significant) results being more likely to be published than negative (nonsignificant) results. What are the effects of positive publishing bias on apparent strengths and patterns of overall global responses of wild species?

Further, I conduct new analyses across a substantially larger dataset than has previously been analyzed to explore effects on phenological advance of latitude and taxonomic/functional group affiliation. Because mean annual temperature rise has been much stronger at higher latitudes, there has been an expectation among biologists that magnitude of response in wild species would also be stronger at higher latitudes (IPCC, 2001a, b; Root *et al.*, 2003; Arctic Climate Impact Assessment, 2004; Badeck *et al.*, 2004).

Specifically, I address the following questions: What is the mean rate of response of wild species? Are some taxonomic groups more sensitive than others? Are species responding differently in geographic regions subject to different rates or patterns of climate change? In particular, is the magnitude of response stronger at higher latitudes, as expected from larger temperature increases toward the North Pole?

# Materials and methods

Full lists of species and published studies included in this study are given in P&Y and in Appendix 3 of supplemental materials in Retal which is available from *Nature's* website.

#### Responses across taxonomic groups and with latitude

Patterns of association between strength of response and taxonomic grouping or latitude were conducted for a new combined dataset compiled from studies conducted in the Northern hemisphere. The single southern hemisphere species, the little penguin, *Eudyptula minor*, from Retal was eliminated from analyses. Where necessary, corrections were made for data errors in the Retal dataset as posted on *Nature*'s website (see 'Modifications of datasets'). All statistical analyses were conducted with STATVIEW statistical software. Earlier timing was indicated with negative values, later timing with positive values. Analysis of effect of latitude on response (change in days decade<sup>-1</sup>) was by linear regression. Analysis of differences among taxonomic groups was by one-way ANOVA followed by Fisher's least significant difference (LSD) tests for multiple comparisons. Significance of effects was set at  $\alpha = 0.05$  throughout.

# Study designs: the two approaches

There were distinctly different methodologies for inclusion of species and studies between P&Y and Retal. Criteria for inclusion by Retal were: (1) Time series had to have at least 10 years of data from recent decades (1951–2001). (2) Study had to include an analysis of the association between temperature trends and phenological trends. (3) An observed change was only included if it showed more than 1 day decade<sup>-1</sup> of change, regardless of whether the change was significant.

Criteria for inclusion by P&Y were: (1) time series had to contain 20 years or more of data, starting from the past decade and working backward. (2) Single-species studies were excluded. Data were restricted to studies of suites of multiple species in the same area, with both responding and nonresponding species reported. This was done to minimize expected positive publishing bias from single-species studies, since a study of one species that fails to show effects of climate change is unlikely to be published. (3) An analysis of temperature trends over time had to have been published for the study region, but not necessarily in the same paper as the biological analysis (although most did coincide).

Both syntheses allowed minor deviations from their stated criteria: Retal included a few multispecies studies where only the mean response was known, hence nonresponding species likely contributed to the estimate of magnitude of response. P&Y included one amphibian study (six species) with only 17 years of data, because of rarity of nonbird vertebrate studies and because this UK study nicely complemented North American studies of 10 other amphibian species.

Despite this partial relaxing of the different criteria, there were only 59 species in common between the two synthetic studies, out of a total of 172 distinct species in P&Y and 87 distinct species in Retal. Retal included many single-species, single-location studies not included in P&Y. P&Y included some multispecies studies that had long biological time series and data on mean temperature change, but were excluded by Retal because they had not conducted an explicit statistical analysis of the strength of association between temperature trends and biological trends.

#### Modifications of datasets

The P&Y dataset was used without modification. Base analyses were conducted on the Retal dataset from Appendix 3, supplemental material posted on Nature's website without modification. The same set of analyses conducted on the unmodified (base) dataset was repeated with modified datasets: with and without the composite (mean) values from studies where species were not separated, and with and without replication of individual species in different studies. Finally, a combined dataset was compiled in which each datapoint represented one unique species (no replicate estimates for the same species and no means for multiple species were included), and in which some errors in original datasets were corrected. Details of the modifications are given below.

One reason for using only a single datapoint per species is that responses of conspecific populations are not likely to be independent, for two reasons. First, there may be migration that homogenizes responses across geographical regions; second, conspecific populations may respond similarly because of biological similarity. At the next taxonomic level up, responses of closely related species are also not independent, but for only one of these reasons, biological similarity derived from common ancestry. This can cause bias in any attempt to derive an overall mean biological response. For example, an overall mean derived from a dataset that overrepresented amphibians, which are responding particularly strongly to climate warming (see 'Results'), would overestimate the overall mean response. Ideally, to get an overall mean response, all the different taxonomic groups that exist should be represented in the dataset in the proportions in which they occur in nature. At present, the data do not exist to even approximate this. It is, however, possible to calculate an overall mean response for the data that do exist and then to examine them for differences among taxa or functional groups, as was first done by Retal.

There are very few species for which there is sufficient information across the species' range for detailed analysis of within-species variation of phenological trends. The rare exceptions include trees and shrubs in the European phenological gardens (Menzel & Fabian, 1999; Menzel, 2000), the tree swallow, *Tachycineta bicolor* (Dunn & Winkler, 1999) and the pied flycatcher, *Ficedula hypoleuca* (Both *et al.*, 2004). Therefore, most

analyses have been conducted at the species level or above. This reality of data limitation was reflected in the guidelines laid down by IPCC (2001b) for use of the species as the smallest unit.

Reduction of the Retal dataset to a single point per species was carried out because the inclusion of the same species more than once occurred in two ways. First, the same species was sometimes explicitly reported in different studies. Examples are apple trees (*Malus domesticus*) in Estonia (Ahas, 1999) and in Germany (Menzel *et al.*, 2001), and the pied flycatcher (*F. hypoleuca*) in Wales (Slater, 1999), the Netherlands (Both & Visser, 2001) and in Finnish Lapland (Jarvinen, 1989). By this means eight species contributed 21 points to the Retal data. The modification used here was to randomly choose one datapoint per species.

The second means by which a species was represented more than once was that some studies that only reported a mean value for many species included species that were in common with studies that reported each species separately. Thus, the same species may show up in two different datapoints. For example, Myneni et al. (1997) reported a mean change in 'green up' of all plants in northern latitudes estimated from satellite data, and Schwartz (1998) reported a change in 'green up' of plants in eastern North America estimated from a phenological model based on observed climate data. The studies overlap - the Schwartz study encompasses a subset of the Myneni et al. geographic area and so are not independent. Thirteen datapoints in Retal each represented mean values across a suite of species. Not all studies listed the species used to obtain these means. For studies that did list species, there was considerable overlap with studies that listed individual values for each species. A further modification of the dataset was created without this subset of composite, mean values, as well as without replicate values for individual species (eliminated by the first modification).

In compiling the combined dataset, only datapoints representing individual species were included (means across multiple species were excluded). Where there were multiple studies of the same species, one study was chosen at random for inclusion so that there was only one datapoint per species. In addition, the combined dataset corrected some errors present in the original Retal dataset. In particular, from the Beebee (1995) amphibian study, Retal mistakenly used values from the correlation coefficients  $(r \times 10)$  rather than from the slope of the regression line to estimate change through time. Finally, the Retal dataset only provided data for one out of the four amphibian species presented in Blaustein et al. (2001). The combined dataset here added in data for the three additional species of amphibian reported in that study.

#### Results

#### Differences across latitudes

A significant trend (P < 0.01) toward stronger advancement at higher latitudes was found in the combined dataset (N = 203, Fig. 1), but this association explains <4% of the variation in response across species ( $R^2 = 0.035$ ). To test whether a few extreme species might have been responsible for the significant association, the analysis was repeated eliminating four of the most extreme shifts toward earlier spring phenology (three amphibians and one bird at  $52^\circ$ - $54^\circ$ N latitude). A significant trend (P < 0.01) remained.

#### Differences among taxonomic/functional groups

For the combined dataset, there were significant differences across taxonomic groups in strength of response (N = 203, one-way ANOVA, F = 4.4, df = 8, 194, P < 0.0001). *Post-hoc* multiple comparisons for fish, flies and mammals were not made due to small sample sizes (n < 3 for each group). Amphibians showed a two to four times stronger spring advancement when compared with any or all other taxonomic groups (P < 0.001 for all comparisons of amphibians with other groups). The only other significant differences were that butterflies and birds showed a significantly stronger advancement than herbs (P < 0.01). (Table 1, Fig. 2).



**Fig. 1** Response in terms of days of change per decade for individual species by latitude in the combined dataset, N = 203. Data were analyzed both with and without the four most extreme species in terms of response (shaded circles). Line drawn is from linear regression.

Table 1	Comparisons across taxonomic groups in strength of
response	using the combined datasets with mean change in
timing st	and ardized to days decade <sup>-1</sup> , $N_{\text{total}} = 203$

Spring advancement in days decade <sup>-1</sup>		
Mean $\pm$ SE	( <i>n</i> )	
$-2.8 \pm 0.35$	(203)	
$-7.6\pm3.09^{a}$	(16)	
$-3.7\pm0.70^{\rm b}$	(41)	
$-3.7\pm0.78^{\rm b}$	(35)	
$-1.1\pm0.16^{\rm c}$	(85)	
$-1.1 \pm 0.68^{ m b,c}$	(6)	
$-3.3\pm0.87^{\mathrm{b,c}}$	(16)	
$-1.3 \pm 0.20^{*}$	(2)	
-5.0*	(1)	
-9.6*	(1)	

Each datapoint here represents a single species. A negative sign indicates advancement of spring events. Analysis was by one-way ANOVA, with *post-hoc* pairwise comparisons by Fisher's LSD. Significant differences between taxonomic groups are indicated by different letters (for each significant comparison, calculated probabilities came out to <0.01). \*Groups with less than three species not included in the pairwise comparisons analyses.

# *Differences across studies – effects of sampling methodology*

The three potential sources of sampling difference outlined in Badeck *et al.* (2004) are considered first (Table 2). Inspection reveals no substantial differences between the two datasets in mean latitude or taxonomic profiles. In contrast, mean time period of observation in Retal is about half that of P&Y, with medians showing even larger difference. Half the studies in Retal recorded changes only during the strong warming trend of the 1980s and 1990s, whereas half the studies in P&Y extended further back than the 1950s, into much cooler decades.

A pivotal difference between the two studies that has not been considered in prior discussions is whether or not the analyses included apparently 'stable' species. In P&Y, these represented 33% of all species (Fig. 3b). The remainder of the analyses here estimate the impact of this methodological divergence.

There are two ways in which the stable category was missing from the Retal dataset. The first way is very straightforward. Species reported as showing no change or  $<1 \text{ day decade}^{-1}$  change were explicitly eliminated by Retal before analysis. This procedure directly excluded from their analysis a large number of 'zeros' and very small changes. Changes of  $>1 \text{ day decade}^{-1}$  were included, regardless of whether the trend was significant over time (Fig. 3a).



**Fig. 2** Changes in timing of spring events in days decade<sup>-1</sup> for individual species grouped by taxonomy or functional type for the combined dataset. Each bar represents a separate, independent species. Negative values indicate advancement (earlier phenology through time) while positive values indicate delay (later phenology through time).

Study	Data profile	Latitude of data*	Taxonomic representation: <i>n</i>	Length of time series (years)
Parmesan & Yohe (2003)	172 individual species	Range: 42.5–59°	Birds: 21	Range: 17–99
		Mean: 49.8°	Butterflies: 35	Mean: 46.2
		Median: 52	Amphibians: 12	Median: 46
			Fish: 2	
			Trees: 12	
			Herbs&grass: 85	
			Shrub: 5	
Root et al. (2003)	87 individual species	Range: 31.9–71.2°	Birds: 24	Range: 10–54
	13 replicates of species	Mean: 51.7°	Butterflies: 30	Mean: 28.9
	13 composite means	Median: 52.5°	Fly: 1	Median: 23.5
			Moth: 1	
			Amphibians: 7	
			Fish: 2	
			Zooplankton: 1	
			Mammal: 1	
			Trees: 15	
			Herbs&grass: 3	
			Shrub: 2	

 Table 2
 Comparison of datasets between the two meta-analyses of global phenological changes

\*Latitudes are all northern hemisphere. Single southern-hemisphere data point in Root et al. (2003) excluded from latitude statistics.

The second way in which stable species were not represented is more subtle. It comes from the inclusion by Retal of single-species, single-location studies that do not report on other species at the same location. Onehundred percent of these studies show significant change, while in multispecies studies, on average only 67% of species are reported as changing phenologically (Parmesan & Yohe, 2003). The complete absence of single-species studies that report lack of response results from one type of publication bias: positive results from single species are much more likely to be published than neutral results (i.e. significant change over time is more likely to be published than no change). If we assume that the proportion of responding species is the same in habitats where multi- and singlespecies studies have been based, we can use the multispecies phenological studies reported by P&Y to deduce that the published single-species studies mask the ex-



**Fig. 3** Histograms of phenological trends across species from unaltered datasets from (a) Root *et al.* (2003) and (b) Parmesan & Yohe (2003). Arrows show estimated mean responses from (a) analyzing data from Root *et al.* (2003) as posted on *Nature's* website, without modification and (b) analyzing data from Parmesan & Yohe (2003) without modification. Zero line is indicated by dashed line.

istence of an additional 33% of unreported species living in the same habitats that would have shown little or no change.

In order to compare the two studies (P&Y and Retal) quantitatively, three analyses were conducted. First, a baseline analysis used the original unmodified Retal datset provided in Appendix 3 of the supplemental material for Retal posted on *Nature's* website. The resulting estimate of mean advancement, before any manipulation of the data, was 4.6 days decade<sup>-1</sup>. This is inexplicably lower than the 5.1 days decade<sup>-1</sup> reported by Retal. However, the 4.6 days decade<sup>-1</sup> estimate is still significantly higher than P&Y's estimate of 2.3 days decade<sup>-1</sup> (Table 3, *t*-test, df = 283, P < 0.001).

Second, the Retal dataset was modified to allow for unrecorded or unreported stable species by retrospectively adding 56 dummy 'zero' values to the analysis (33% of the total) corresponding to 56 'phantom' stable species excluded by Retal by the mechanisms listed above. The new analysis gives an estimate of mean advance in spring timing of 3.1 days decade<sup>-1</sup>, which is not significantly different from P&Y's estimate of 2.3 days decade<sup>-1</sup> (Table 3, *t*-test, df = 339, P = 0.11).

Third, stable species were deleted from the P&Y dataset (those with <1 day decade<sup>-1</sup> change). This drives the P&Y estimate up to 3.4 days decade<sup>-1</sup>, which is not significantly different from the unmodified Retal estimate of 4.6 days decade<sup>-1</sup> (Table 3, *t*-test, df = 226, P = 0.06).

#### Discussion

#### Latitudinal effects

Boreal regions have warmed by as much as 4 °C over the 20th century while much of the tropics has shown little change (IPCC, 2001a). Therefore, there is a clear expectation of stronger phenological response at higher latitudes. P&Y did not analyze their data for latitudinal trends. Retal did so and found an effect of latitude in the

Statistic	Unaltered datasets		Adding dummy stable species (zeros) to Root <i>et al.</i> (2003)		Deleting stable species (<1 day decade <sup>-1</sup> change) from Parmesan & Yohe (2003)	
	Parmesan & Yohe (2003)	Root <i>et al.</i> (2003)	Parmesan & Yohe (2003)	Root <i>et al</i> . (2003)	Parmesan & Yohe (2003)	Root <i>et al</i> . (2003)
Mean*	-2.3	-4.6	-2.3	-3.1	-3.4	-4.6
$\pm$ SE	-0.36	0.43	0.36	0.33	0.51	0.43
Median	-1.4	-3.4	-1.4	-2.1	-2.1	-3.4
Mode	0.0	-2.4	0.0	0.0	-1.5	-2.4
n	172	113	172	169	115	113
P (mean difference)	< 0.001		ns		ns	

Table 3 Results of reanalyses of datasets from Parmesan & Yohe (2003) and Root *et al.* (2003) to look for effects of study design on estimates of response

\*Mean is mean change in timing of event, standardized to days decade $^{-1}$ .

expected direction, with mean advance reported for species between 32° and 49.9° latitude of -4.2 days s decade<sup>-1</sup> and mean advance between 50° and 72° latitude of  $-5.5 \text{ day} \text{ decade}^{-1}$  (Kruskal–Wallis rank test for two means P < 0.0001). However, Retal's data, if plotted, show no visible trend with latitude and their result does not appear in reanalysis of their original published (unmodified) dataset, either when analyzed with an equivalent rank test (Mann–Whitney *U*-test for two means, N = 112, P = 0.36), or when analyzed by linear regression (slope of regression line =-0.008, P = 0.91).

New analysis of the combined datasets does show a significant increase in strength of spring advancement as one goes northward in the northern hemisphere, but this trend explains <4% of the overall variance in phenological change (Fig. 1, P < 0.005,  $R^2 < 0.04$ ). Such a small latitudinal trend might stem from a few very strongly responding species, specifically the four species with >20 days decade<sup>-1</sup> advancement (three amphibians and one bird). Surprisingly though, high significance of the trend persisted even when these four most extreme responders were taken out (Fig. 1, shaded circles taken out, P < 0.002). However, while an effect of latitude is present and significant, it is not yet an important predictor of the magnitude of phenological response to climate change.

These results from phenology are in contrast to those from analyses of species' distributions. The very limited data available from population and range dynamics suggest that, in this respect, the expected latitudinal differences in response strength are already appearing. Poleward range shifts have occurred at most latitudes (Parmesan & Yohe, 2003). However, in one study which looked at responses over the entire ranges of 35 butterfly species, a significantly greater proportion of populations at high latitudes had undergone abundance or distributional change compared with more equatorial populations of the same set of species. Sixty-seven percent of northern range boundaries shifted northward (in Finland, Sweden, Great Britain, France and Estonia) compared with only 30% of southern range boundaries contracting northward for the same individual butterfly species (in northern Africa, Spain and France; Parmesan *et al.*, 1999). Further, overall range contractions and population declines appear to be more pronounced, as well as more consistent across species in polar communities, as compared with temperate communities (Parmesan, 2006).

# Taxonomic/functional group effects

In contrast to a weak latitudinal effect, differences among broad taxonomic/functional groups in strength of response were both significant and substantial (analysis of the combined dataset Table 1, Fig. 2). This is not surprising. More than a 100 years of experimentation on temperature tolerances and developmental thresholds, plus field studies in behavioral ecology, have demonstrated strong differences in response to climate and extreme temperatures, both among related species and across broad taxonomic groups (Andrewartha & Birch, 1954; Precht *et al.*, 1973; Weiser, 1973; Woodward, 1987; Parmesan *et al.*, 2000).

Amphibian advance was more than twice as rapid as that of trees, birds and butterflies, and nearly eight times as strong as that for herbs, grasses and shrubs. Failure to find faster change by amphibians in the prior analysis by Retal likely stemmed from errors in incorporating the amphibian data into their database. Data from three out of the four species in Blaustein *et al.* (2001) were omitted by Retal, while their data from Beebee (1995) listed *Rana kl. esculenta, Triturus cristatus,* 

Month	Trend mean					
	Minimum temperature ( °C)	Maximum temperature ( °C)	Precipitation (mm)			
February	-3.4	-2.4	-3.8			
March	-1.2	-0.49	6.6			
April	2.0	1.8	-34.7			

Table 4 Temperature trends from Moonsenee climate station, near Long Point field site for Bufo fowleri in Ontario, Canada

Data all begin at 1980. Data are not available for all years for all months. Data for temperature goes through 1997 for February, through 1993 for March, and through 1991 for April. Data for precipitation goes through 1998 for February and March, and through 1985 for April. No trends were significant at the  $\alpha = 0.05$  level.

*Triturus helveticus* and *Triturus vulgaris* as having advanced their breeding dates by 5.8, 5.9, 6.0 and 7.8 days decade<sup>-1</sup> (respectively), when the correct values are 12.4, 27.1, 31.8 and 34.1 days decade<sup>-1</sup> (see 'Materials and methods' for an explanation of the discrepancy).

Amphibian responses were particularly diverse as well as particularly strong. The most extreme advancement (about a month advancement of breeding per decade) was shown by three congeneric amphibians (Triturus) studied over 17 years in England (Beebee, 1995). However, amphibians also provide one of the strongest opposing trends - delayed breeding by 5.3 days decade<sup>-1</sup> for *Bufo fowleri* (Blaustein *et al.*, 2001). This observation of phenological delay may stem simply from the fact that both minimum and maximum temperatures have shown a (nonsignificant) trend toward cooling during the time period over which the *B*. fowleri data were taken. Table 4 shows a slight cooling trend from climate station data in the same general areas as the B. fowleri field site for key months for amphibian breeding (February and March), although there is also a (nonsignificant) warming trend for later in spring (April). Further, amphibian breeding is likely as sensitive to changes in precipitation as in temperature. The region of the B. fowleri study exhibits (nonsignificant) trends in precipitation that are as strong as trends in temperature (Table 4).

In most regions, precipitation has become more extreme. Total precipitation has generally increased globally, but large regions (e.g. northern Africa) have become drier (IPCC, 2001a). For biological systems, as important as mean changes in precipitation is a significant shift in *patterns* of precipitation: rain and snow are falling in fewer, more intense events, causing significant increases in both flood events and in duration of dry periods (Karl *et al.*, 1996; Karl & Knight, 1998; Kunkel *et al.*, 1999; Easterling *et al.*, 2000a, b; IPCC, 2001a; Trenberth *et al.*, 2003). Therefore, it may not be surprising that amphibians, a group likely to be particularly sensitive to changes in pond depth, duration and temperature – all of which would be affected by recent

climatic trends – showed a very strong departure from other groups, as well as from each other. Because sample sizes are still very low (only 16 species of amphibian from five geographic locations), it is unclear to what extent these results reflect amphibian responses globally.

More generally, one possible source of the high level of variation found here among species within each taxonomic group, is resource-associated differences in strength of response. There is some evidence for this effect among insects. A recent study of 16 butterfly species in Spain documented that strength of phenological advancement was related to both family affiliation and to functional grouping of the species' host plant. Species that specialized on grasses had a stronger advancement than did butterflies whose larvae fed on herbs (Stefanescu *et al.*, 2003).

# Changes in trophic synchrony

In the present new analysis, butterfly and bird emergence or migratory arrival show more than three times greater phenological advancement than does the first flowering of herbs. This difference in strength of response may be important because butterflies mostly feed on herbs (both as larval hosts and as adult nectar sources), and differential responses of insect vs. host, or of pollinator vs. flowering plant, could either draw these interactions closer into synchrony or further out of synchrony, depending on the starting point. Datasets which would allow analysis of long-term alteration in synchrony between interacting species at a given location are sparse (Harrington et al., 1999). In a recent review, Visser & Both (2005) found that for seven species pairs out of 11 total (two of which were insectplant), interacting species are currently more out of synchrony than they were at the start of the studies, but that this did not always correspond to fitness loss.

If insects are well adapted to their habitats, we might expect that the historical 'starting point' should be good synchrony. However, this expectation is frequently not met. Before the recent bout of climate warming, Feeny (1970) showed that winter moth (Opheroptera brumata) routinely suffered high mortality in the field (up to 90%) because of phenological mismatches between egg hatch and budburst on the oak trees that served as larval hosts. Likewise, Singer (1972), also working in the 1960s, showed that Edith's checkerspot butterfly (Euphydryas editha) routinely suffered >98% mortality in the field because of phenological mismatches between larval development and senescence of their annual hosts (Plantago erecta). When mismatches such as these form the 'starting point,' insects may be highly vulnerable to small changes in synchrony with their hosts, and flowering plants may be highly vulnerable to small changes in synchrony with their pollinators. Below, I briefly discuss the evidence for historical and current mismatches observed in host relationships of O. brumata and E. editha.

With respect to the winter moth (O. brumata) and climate change, only indirect estimates of changes in synchrony with oak budburst have been possible, due to lack of long-term field data on moth egg-hatch which would complement existing long-term data on oak budburst (Harrington et al., 1999). An experimental study in the United Kingdom indicated that both moth and oak accelerate development in concert with warming, suggesting that timing has advanced in both species, but that synchrony has not been affected (Buse & Good, 1996). Conversely, a Dutch study which derived estimates from phenological models indicated that moth hatching should have advanced faster than oak budburst, suggesting an increasing asynchrony through time (Visser & Holleman, 2001). Without hard empirical data, definitive conclusions about the effects of climate change on oak/moth interactions are elusive (Watt & McFarlane, 2002).

For the second example, Edith's checkerspot butterfly, there is evidence of a climate-change driven range shift in both latitude and elevation (Parmesan, 1996) across an area where the mean temperature had increased by 0.7 °C (Karl et al., 1996). It has been suggested that increasing butterfly-plant asynchrony contributed to this shift (Parmesan, 2003), as well as to the extinctions of populations which had been shown to be phenologically mismatched under historical (1960s) conditions (McLaughlin et al., 2002). We cannot ask directly whether asynchrony has increased, because the populations in which asynchrony was measured in the field nearly 40 years ago are now extinct. However, through field and greenhouse manipulations as well as through analysis of spatial and temporal climate and vegetational variability in multiple populations, it has been documented that higher temperatures or drier conditions than normal speed up host plant senescence

faster than caterpillar development (Singer, 1972; Weiss et al., 1988; Hellmann, 2002). This asymmetry of response causes a shortening of the time window available for insect feeding, a type of asynchrony that causes deaths of those individuals unable to fit their life cycles into the shortened period. Increasing air temperatures by 2 °C, which shortens the window of food availability by about 2 days, can cause 'normal' caterpillar starvation rates of 80-98% to jump to 100% (Weiss et al., 1988). Observed population extinctions of this species have historically occurred immediately following severe droughts and extreme weather events (Singer & Ehrlich, 1979; Ehrlich et al., 1980; Singer & Thomas, 1996; Thomas et al., 1996; McLaughlin et al., 2002). The documented northward and upward range shift of this species in the 20th century (Parmesan, 1996) was comprised of a disproportionately high rate of population extinctions among low-elevation and low-latitude populations, a high proportion of which fed on annual hosts and were subject to the phenological mismatches described here.

# Effects of data-sampling methodologies

*Effects of excluding stable species.* Once we take into account the differences resulting solely from the criteria for study selection used by P&Y and Retal, the two metaanalyses give estimates of mean spring advancement that are not significantly different from each other. Reanalyses of the two datasets here indicate that the apparently stronger spring advancement shown by the Retal study can be explained solely as a consequence of their exclusion of stable (nonresponsive) species from their analysis.

Even after differences in methodologies of P&Y and Retal are accounted for, there remained a nonsignificant tendency for the Retal dataset to display a stronger spring advancement than the P&Y dataset (by a bit  $<1 \text{ day decade}^{-1}$ ). If it is real, this remnant tendency toward stronger spring advancement in Retal could be due to two factors that merit further investigation.

*Effects of time period.* As suggested by Badeck *et al.* (2004), a stronger estimate of advancement would be expected from the greater concentration of the Retal data in more recent, strongly warming decades. A metaanalysis of long-term (48–132 years) datasets showed that for 100% of 44 species, biological trends through time – either in spring phenologies or in geographic location of their northern range boundaries – mirrored decadal temperature trends over the 20th century (Parmesan & Yohe, 2003). For example, with data going back to 1947, McCleery & Perrins (1998) documented that nesting times for the great tit (*Parus major*) in England did not start advancing until the current warming trend began in 1970. In another study, the skylark (*Alauda arvensis*) and the white wagtail (*Motacilla alba*) advanced their arrival to Estonia during the warming trend of the 1930s and 1940s, delayed arrival during the cooling trends of the 1950s and 1960s, and again started arriving earlier as the current warming trend began in the early 1970s (Ahas, 1999). Repeated instances of these patterns across diverse species, in and of themselves, were used to diagnose a climate 'fingerprint' in biological changes that provided a causal link between anthropogenic global warming and biological impacts (Parmesan & Yohe, 2003).

Studies published subsequently continue to support this pattern, although it is not universal across all species. A shift toward stronger spring advancement starting in the mid-1980s was documented for snowdrops (*Galanthus nivalis*), sweet cherry (*Prunus avium*) and lime tree (*Tilia platyphyllos*) (Dose & Menzel, 2004). Similarly, out of 10 plants in a German study, all showed spring advancement since 1984, and eight of these had shown opposite responses (delayed budburst or blooming) during the cool period of 1951–1984 (Schaber & Badeck, 2005).

*Effects of publishing bias.* A stronger estimate of spring advancement would also be expected from the inclusion by Retal of a substantial number of single species, single location studies. Individual species tend to be chosen *a posteriori* as being 'interesting' from a climate change angle. Further, single-species studies that fail to show effects usually remain unpublished. Thus, single-species data are susceptible to a positive publishing bias and likely to be skewed toward stronger effects. The potential for single-species studies to skew estimated response was the reasoning behind P&Y's criterion for studies to be multispecies, with data presented for all species in the category studied irrespective of any observed degree of change.

Indeed, a comparison of the two histograms for responsive species (>1 day decade<sup>-1</sup> change) shows the pattern expected from this potential effect. In P&Y, a very high proportion of responsive species (40%) show weak response (1–2 days decade<sup>-1</sup> advancement), as compared with only 15% in Retal (Fig. 3). In the Retal dataset, only 12.5% of weak responders (1–2 days decade<sup>-1</sup> advancement, *n* = 16 total) are from single-species studies, compared with 33% of strong responders ( $\geq$ 2 days decade<sup>-1</sup> advancement, *n* = 90 total). The difference in strength of response between single-species and multispecies studies was not quite significant (Contingency table test, *G* = 3.21, df = 1, *P* = 0.07). It nonetheless suggests that inclusion of single-species, single-location studies could skew

estimates of overall responses of wild species toward a stronger response to climate warming, compared with estimates derived only from multispecies studies.

# Conclusions

At first sight, there appear to be large differences in estimates of phenological response between between two major global meta-analyses: Retal and P&Y. These studies had differing criteria for data selection and in consequence used moderately nonoverlapping datasets. However, once the use of different methodologies for data inclusion is taken into account, there is remarkable consistency between these studies in the estimated strength of response by wild species to warming temperatures of the past several decades. New analyses here indicate a consensus estimate of mean response between 2.3 and 2.8 days decade<sup>-1</sup> advancement of spring events across all taxa globally (Tables 1 and 3).

Analyses presented here fail to show any important latitudinal trend in responses (Fig. 1). This contrasts with earlier published conclusions (Root *et al.*, 2003). A significant increase in strength of response at higher latitudes *was* found in the current analyses of 203 species reported here, but explained very little of the variation in response. Thus, latitude is not yet an important explanatory variable.

Multispecies studies have documented an enormous variation of response among species within taxonomic groups and across broad taxonomic/functional groups exposed to the same type and intensity of climate change (i.e. emerging from a single study in the same region; Parmesan & Yohe, 2003). Variation among species at a given site is as great (or greater) than variation across geographic regions. This explains why latitude, in itself, is not strongly associated with strength of response, even though latitude *is* associated with strength of warming trends. These two patterns indicate that the absolute strength of warming trend at any given location is a poor predictor of community-wide responses.

There were significant differences in mean response across taxonomic groups, but the largest differences – between amphibians and all other taxa – stem from extremely strong spring advancements of just a few amphibian species, and so may not be generalizable (Table 1, Fig. 2). Stronger advancement of butterflies compared with herbs may portend an increasing asynchrony in insect–plant interactions (Table 1, Fig. 2).

Observed high variation of response among species experiencing similar climatic trends – within latitudes, within regions, within communities and within taxonomic groupings – suggests that projections of impacts will continue to be a challenge. In particular, projections of response across interacting trophic levels will be hampered without an increased investment in empirical data. Only long-term field observations can reveal complex interdependencies between species, an essential component to estimating future responses to global warming.

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