

Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change

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Abstract

Shifts in phenology and distribution in response to both recent and paleontological climate changes vary markedly in both direction and extent among species. These individualistic shifts are inconsistent with common forecasting techniques based on environmental rather than biological niches. What biological details could enhance forecasts? Organismal characteristics such as thermal and hydric limits, seasonal timing and duration of the life cycle, ecological breadth and dispersal capacity, and fitness and evolutionary potential are expected to influence climate change impacts. We review statistical and mechanistic approaches for incorporating traits in predictive models as well as the potential to use phylogeny as a proxy for traits. Traits generally account for a significant but modest fraction of the variation in phenological and range shifts. Further assembly of phenotypic and phylogenetic data coupled with the development of mechanistic approaches is essential to improved forecasts of the ecological consequences of climate change.

1. INTRODUCTION

Predicting species responses to climate change is a challenge central to both maintaining biodiversity and assessing our understanding of constraints on species abundance and distribution. In response to past climate changes, species in a variety of taxa have shifted their phenology (Parmesan 2006), distribution (Davis & Shaw 2001), and abundances (Williams & Jackson 2007) in different directions and to different extents. These individualistic range shifts are inconsistent with the most common technique for predicting species' distribution responses to change—correlative species distribution models (SDMs). These models estimate a species' niche by correlating localities to environmental layers (e.g., temperature and precipitation) in order to define a climate envelope (or environmental niche). Range shifts are predicted by assuming that the species will follow its climate envelope through climate change.

Correlative SDMs require little understanding of organismal biology and are obtainable for a wide variety of organisms, but predictions are coarse and tend to get spatial details wrong (Helmuth et al. 2005, Kearney & Porter 2009, Buckley et al. 2010). Morphological and physiological traits can vary across the range of a species such that the environmental niche estimated by an SDM is an overestimate for any particular individual or population. Further, the associations between multiple abiotic variables may shift over time, leading to spurious estimates of environmental suitability.

In contrast to broad-scale modeling efforts that largely ignore biological details, small-scale experimental studies highlight how complex interactions between organismal traits and environmental conditions can be crucial to determining responses to environmental change (Jentsch et al. 2007). However, the generality and realism of these small-scale studies is uncertain. The studies tend to ignore stochastic environmental fluctuations and the complex context of actual ecosystems. Moreover, studying all species in all environmental conditions in detail is impractical.

Here, we ask what biological details are needed to more accurately predict how species will respond to climate change. Can traits such as individual and population growth rate and ecological generality predict climate change responses? How do predictor traits vary between taxa and regions? Can functional approaches successfully bridge between small-scale experimental studies where the biological details are thought to be crucial and broad-scale modeling efforts where the biological details are ignored? Can we use proxies for biology such as phylogenetic relatedness to inform predictions?

We start by reviewing aspects of the physical environment that can result in traits being central to an organism's response to environmental change. We next consider traits that may govern responses to environmental change. We evaluate whether these traits and evolutionary history can predict whether a species will move, acclimate, adapt, or go extinct in response to environmental change. We conclude by summarizing how the reviewed research should inform the next generation of models for forecasting ecological responses to environmental change.

2. PHYSICAL CONTEXT OF CLIMATE AND CLIMATE CHANGE

The challenge of addressing the particulars of organisms' interactions with the environment has led to increased attention to spatial and temporal patterns of climate and climate change. Characterizing these patterns can identify the aspects of the physical environment relevant to organisms without the uncertainty of accounting for biological details (Ackerly et al. 2010). Describing the geography of climate can address where disappearing and novel climates occur (Williams et al. 2007) and how fast and in what direction an organism would have to move to offset future climate change (Loarie et al. 2009). Climate metrics relevant to biological impacts include patterns of climate change across space and seasons and the incidence of extreme events.

2.1. Shifts in Mean Climate Conditions Vary Across Space and Seasons

The magnitude of climate change varies considerably across locations and seasons. One mid-range climate change scenario predicts that average annual global temperatures will increase by 2.45°C from 1950–1990 to 2070–2100. However, polar and temperate areas (>20°N and S) are expected to incur more pronounced changes than tropical areas (2.51°C versus 2.23°C) [based on climate scenario and data from Deutsch et al. (2008)]. Traditionally, it has been assumed that this differential warming will result in more severe impacts being experienced by polar organisms. However, the lesser climatic seasonality in the tropics may lead to greater thermal specialization. Thus, a lesser magnitude of temperature change may have a more severe impact for tropical organisms as they may easily exceed their narrow thermal safety margins (Tewksbury et al. 2008).

Considering seasonal differences in climate change is also crucial for predicting biological impacts. For example, in boreal regions, winter warming is predicted to be more severe than summer warming, particularly at higher latitudes (Tebaldi et al. 2010). Seasonal climate manipulations in a subarctic peat land found that spring warming and winter snow addition had as much potential to impact plant phenotypes as did summer warming (Aerts et al. 2009). Furthermore, the frequency of cold extremes has been declining more rapidly than the frequency of heat extremes is increasing, and this trend is predicted to continue (Kharin et al. 2010). Although scenarios for future precipitation are less certain, it is likely that precipitation patterns will shift toward less frequent, more intense events (Kharin et al. 2010).

2.2. Climatic Extremes and Novelty

Most research concerning the link between environmental conditions and organismal performance and demography focuses on mean environmental conditions over time (Easterling et al. 2000, Stenseth et al. 2002). Yet, temperature variability and extreme events can substantially impact organismal stress and ultimately survival and fecundity (Helmuth et al. 2005). The incidence of extreme heat and precipitation events is expected to increase in response to climate change. Indeed, in Central Europe, heat waves have doubled in length, and the likelihood of extreme precipitation events has increased from 1.1% to 24.6% over the past century (Jentsch & Beierkuhnlein 2008).

Although extreme events are expected to substantially impact populations, communities, and ecosystems, calls are only now emerging for research to decipher the details of these impacts (Smith 2011). Paleorecords suggest that shifts in mean and extreme events will interact to produce complex biological responses (Jackson et al. 2009). We illustrate this interaction using a model of the responses of *Colias* butterflies in the Rocky Mountains to recent climate change (Buckley & Kingsolver 2012). The duration of flight, which is restricted to a narrow thermal window, is directly related to fecundity as the butterflies lay individual eggs on host plants. Although flight duration is largely a function of mean thermal conditions, egg viability is sensitive to heat extremes: Temperatures exceeding 40°C quarter egg viability (Kingsolver & Watt 1983). In a focal location in Colorado, recent increases in mean temperature are less dramatic than the increasing incidence of extremes (**Figure 1a,b**). Warm temperatures have led to decreases in estimates of available flight time, but the decline in population growth rates is more pronounced when decreases in egg viability due to extreme events are also considered (**Figure 1c,d**).

An additional challenge for predicting biological impacts is that much of Earth will experience novel climates by 2100 (Williams et al. 2007). Organisms are likely to respond to these new combinations of environmental variables such as temperature and precipitation in unexpected ways (Williams & Jackson 2007). Climate novelty presents a particular challenge to species distribution modeling techniques based on defining a multidimensional climatic niche. Assessing

Climate novelty: combinations of environmental conditions, such as temperature and precipitation, without current analogs

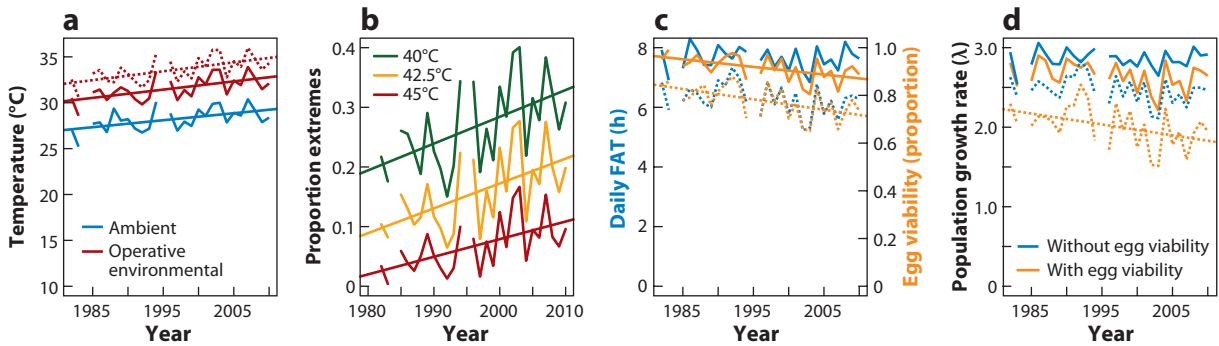


Figure 1

Responses to temperature change for two species of alpine butterflies, *Colias eriphyle* (solid lines) and *C. meadii* (dashed lines). The species display phenotypes adapted to lower and higher elevations, respectively. (a) Mean flight season (June 15–August 15) ambient and operative environmental temperatures have increased since 1980 in Grand Junction, CO (National Weather Service COOP Program #53489). These increases in mean conditions are less dramatic than (b) increases in the incidence of thermal extremes. Predicted (c) available flight time and (d) population growth rates (λ) have remained relatively constant in response to shifts in mean temperature for both species. Notably, decreases in population growth rates are predicted when impacts of extreme events on (c) egg viability are included. Adapted from Buckley & Kingsolver (2012). Lines are depicted for regressions significant at $P < 0.05$. Abbreviation: FAT, flight activity time.

potential niche locations of an organism following climate change requires extrapolation beyond the currently sampled environmental space (Veloz et al. 2012).

3. BIOLOGICAL DETERMINANTS OF CLIMATE CHANGE RESPONSES

The importance of measuring phenotypes for addressing climatic limits on species' distribution and abundance is increasingly being recognized (Helmuth et al. 2005, Gaston et al. 2009, Kingsolver 2009). Here, we review phenotypes governing responses to environmental change. How phenotypes mediate shifts in species interaction due to climate change is complex (Gilman et al. 2010), so we omit community responses despite their likely importance.

3.1. Thermal and Hydric Limits

Thermal performance curves (TPCs) describe the performance of a biological process as a function of temperature (Huey & Stevenson 1979). Processes that are frequently considered include aspects of whole-organism performance—such as rates of locomotion, growth, and feeding—and components of fitness—such as survival, reproductive rate, and generation time (Figure 2). The temperature dependence of performance and fitness is typically unimodal with a single optimal temperature and asymmetric such that performance declines more quickly at temperatures above rather than below the optimum (Figure 2). Classically, performance curves are thought to be constrained by trade-offs. For example, generalist-specialist trade-offs sometimes occur in which species or genotypes may either exhibit high performance over a narrow range of temperatures or low performance over a broad range of temperatures (Gilchrist 1995, Izem & Kingsolver 2005). However, a “hotter is better” phenomenon, in which maximum performance is greater as optimal temperature increases, has been observed for a variety of organisms (Angilletta 2009, Kingsolver 2009).

The temperature sensitivity of performance and fitness can vary considerably. For example, the thermal breadth for assimilation tends to be narrower than that for locomotion

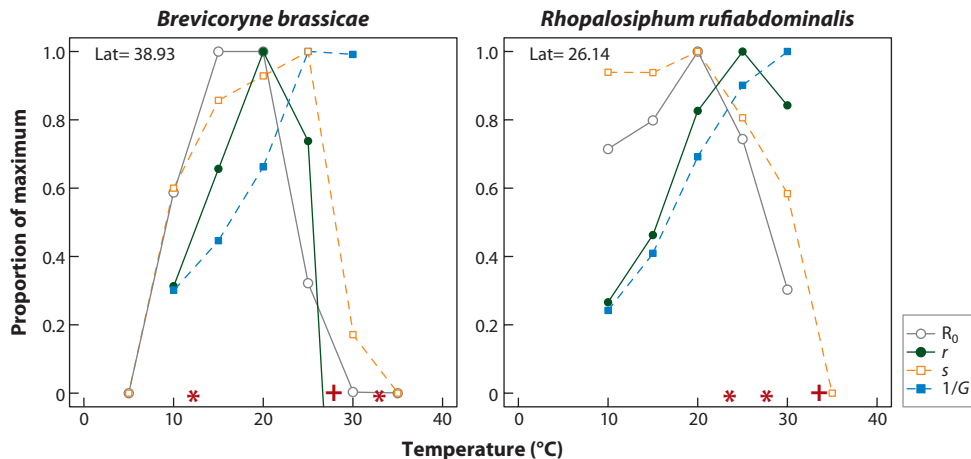


Figure 2

Components of fitness (proportion of maximum) as functions of mean rearing temperature for two aphid insect species: R_0 , net reproductive rate; r , intrinsic rate of population increase; s , survival of juveniles (to adulthood or first reproduction); and $1/G$, generation time (reciprocal). Critical thermal maximum (CT_{max}) for each species is indicated as a plus sign. Mean annual temperature and the mean temperature for the hottest month at each site over the period 1960–2009 are also indicated as asterisks. Adapted from Kingsolver et al. (2011).

(Angilletta 2009). The processes often occur in sequence such that any one process can be a bottleneck for the overall energy balance of an organism. Similarly, different fitness components may differ in both thermal breadth and optimal temperature. For example, thermal breadths for survival probabilities are often wider than for net reproductive rates (Figure 2). Several recent data compilations have produced generalizations regarding geographic variation in TPCs. Thermal breadth tends to be narrower in the tropics, resulting in a smaller thermal safety margin (Huey et al. 2009, Sunday et al. 2010, Clusella-Trullas et al. 2011).

Thermal and water stresses can also have acute impacts on organisms. Water stress during heat extremes is predicted to result in mortality events for taxa including birds (McKechnie & Wolf 2009). A well-documented example of the interaction of acute and accumulated thermal impacts on organisms has been shown in intertidal mussels. Helmuth (2009) has developed a biophysical model for mussels that reveals the importance of the interaction between air temperature and tidal height for determining the incidence of heat mortality events. Due to this interaction, the incidence of thermal stress does not follow a consistent latitudinal gradient. Although the occurrence of thermal stress (confirmed by biophysical models and assessment of heat shock proteins) does successfully predict the distributions of mussels in some regions such as the east and west coasts of the United States, estimates of thermal stress overpredict distributions elsewhere. Historical records reveal that the southern range limit of some European intertidal species are more constrained by long-term energy budgets than by direct thermal stress (Wetthey et al. 2011). How multiple environmental stressors will interact to impact organisms is an important and scarcely addressed question.

3.2. Seasonal Timing and the Life Cycle

At temperatures below the optimum, development rate declines with decreasing temperature and approaches zero at some lower developmental threshold (LDT) temperature. If the thermal

sensitivity of the development rate is approximately linear within this temperature range (cf. $1/G$ in **Figure 2**), then a simple model for development time to adulthood applies: the accumulation of heat (temperature) over time above the LDT. The quantity is known as degree-days and has successfully predicted the development time required for a variety of organisms, including many plants and insects (McMaster & Wilhelm 1997). The acceleration of development, and thus phenological shifts, due to climate change has been successfully predicted for a variety of organisms [e.g., trees (Morin et al. 2009); and grasshoppers (Nufio et al. 2010)].

One complicating factor is that temperature changes have not occurred consistently throughout seasons (see Section 2). Thus, early- versus late-developing species may experience different degree-day augmentation from climate change. For Colorado grasshoppers, the predominance of late-summer warming since 1960 has led to late-season grasshoppers advancing their development more than early-season species (Nufio et al. 2010). Among both European butterflies and moths since 1980 (Altermatt 2010) and North American prairie flowers in a warming experiment (Sherry et al. 2007), early-season flyers and bloomers emerge earlier, whereas late-season flyers and bloomers emerge later in response to warming. Another complicating factor is that many organisms use photoperiodic cues for key developmental events such as diapause, hatching, and emergence. As thermal isoclines shift, the associations between temperature and photoperiod also shift. The resulting mismatches between thermal and photoperiod cues pose a major challenge to organisms (Bradshaw & Holzapfel 2010). Different developmental constraints between predators and prey can also lead to phenological mismatches with detrimental impacts to populations (Visser & Both 2005).

Life stages of a species can also differ in thermal sensitivity and sometimes in habitat requirements. This phenomenon is particularly apparent for insects (Kingsolver et al. 2011). For example, larvae of *Colias* butterflies are cryptically colored and exhibit only limited thermoregulation; optimal temperatures for larval feeding are 20–30°C and variable among species. In contrast, the wing absorptivity of adult *Colias* butterflies varies along elevation gradients and determines their ability to thermoregulate and achieve flight; optimal temperatures for flight are 33–38°C and similar among species (reviewed by Kingsolver et al. 2011). Salmon populations are tightly adapted to local conditions and face diverse selection pressures across their complex life cycles. Consequently, juvenile salmon survival is correlated with summer temperature in some populations and fall streamflow in others (Crozier et al. 2008).

Accelerated development time may also alter the number of generations organisms such as insects are able to complete in a year. For example, 44 of 263 species of butterflies have increased their annual number of generations (i.e., voltinism) and the frequency of second and subsequent generations has increased significantly for multivoltine species since 1980 (Altermatt 2009). The life stage at which organisms overwinter can influence how severely their seasonal timing is altered by climate change. For example, those insects that overwinter at more advanced stages may more readily shift their phenology in response to earlier snow melt and spring warming than those that overwinter as eggs (Altermatt 2010, Diamond et al. 2011). Longer growing seasons and an increased number of generations may augment population growth, but species may risk being exposed to more variable spring temperatures.

3.3. Ecological Breadth and Dispersal

The responses of organisms to climate change depend on their ability to evade shifts in their environmental niches via movement. A substantial number of organisms have demonstrated their ability to use movement to track recent climate shifts (e.g., Tingley et al. 2009). The dependence of niche tracking on organismal characteristics contributes to individualistic range shifts. Different

dispersal abilities among similar species can explain the degree to which particular species have been impacted by recent climate change (Pearson 2006). The ability of an organism to use dispersal to alleviate thermal stress may depend on the relative timing of a dispersal-capable life stage and of climate conditions. For example, it may be the sessile adults that experience thermal stress rather than the mobile larvae, which have the potential to move to evade hot conditions. Development rate, which is tightly constrained by temperature, is a key determinant of dispersal distance for planktivorous marine larvae (O'Connor et al. 2007). An additional challenge is that distribution shifts tend to be influenced more by rare, long-distance dispersal events than by mean dispersal rates (Clark 1998), and shifts may also be impeded by habitat loss (Parmesan 2006, Loarie et al. 2009).

Diet and habitat breadth may be important determinants of the potential for phenological and distribution shifts, but the directionality of these effects is uncertain. A broader niche may facilitate the persistence of species in new environments (including a temporal shift in emergence). Species are also less likely to be constrained by the phenology of species with which they interact (Pelini et al. 2009). However, if the host or prey species of a specialist shifts, the specialist may be more likely to follow. Higher trophic levels may respond less readily to climate change due to being constrained by prey or host availability. However, mismatches in phenological shifts between interacting species are frequently observed (Visser & Both 2005). A number of readily quantified traits such as body and range size and historical locations offer only a limited functional basis for predicting climate change responses but are frequently used when attempting to explain observed responses (see below).

3.4. Fitness and Evolutionary Potential

The mean fitness (e.g., the intrinsic rate of increase, r) of a population is key to understanding the dynamics and trajectory of population change. Data for the thermal sensitivity of r (Figure 2) have been widely used to predict ecological responses to future climate change (Tewksbury et al. 2008, Huey et al. 2009). These studies have emphasized the negative ecological impacts of climate change for tropical insects and lizards, despite smaller predicted climate changes in tropical rather than in high-latitude regions (Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009). However, because of the importance of temporal variation in weather and climate in temperate and high-latitude regions, more detailed models incorporating the thermal sensitivity of multiple fitness components may be required for realistic predictions of the ecological consequences of climate change in these regions (Kingsolver et al. 2011).

In these and similar models, ecologically important phenotypic traits are assumed to be constant and unvarying for a population. Phenotypic and genetic variation in such traits creates the potential for selection and evolutionary responses to climate change. A central issue is whether adaptive evolution can reduce the negative consequences of climate change for the mean fitness of a population, thereby reducing the likelihood of its extinction. Models for the evolution of thermally sensitive traits in response to sustained directional changes in climate yield several important insights (Huey & Kingsolver 1993, Lynch & Lande 1993, Bürger & Lynch 1995). First, there is a critical rate of environmental change beyond which the mean phenotype of the population lags too far behind the optimal phenotype, ensuring rapid extinction. Second, adaptive evolution is more likely to help maintain a population through methods of greater genetic variation, larger initial population size, shorter generation time, and higher maximum reproductive potential, and for slower and less variable rates of climate change. Third, the relationship between selection (reflecting variation in relative fitness) and mean absolute population fitness is critical: If selection is sufficiently strong to reduce mean absolute fitness below replacement, the conditions under which adaptive evolution can rescue the population from extinction are very restrictive (Holt et al.

2004). Understanding the significance of evolutionary responses to climate change for range shifts and population extinction remains a major challenge (Kingsolver 2009, Schoener 2011).

Niche conservatism:
tendency for ecological traits to remain similar over time and, thus, be shared among closely related taxa

4. PREDICTING CLIMATE CHANGE RESPONSES

Species can effectively respond to climate change in three primary ways: moving in space or time to remain in a constant environmental niche, evolutionary adaptation, or phenotypic acclimation or plasticity. If these three response strategies fail, species face extinction. Can we use our knowledge of traits and phylogenetic relatedness to predict the relative importance of different responses to environmental change across different species? The potential for using species' characteristics to assess vulnerability to climate change has long been heralded, but only recently quantitatively assessed. For example, Williams et al. (2008) envisioned a vulnerability framework incorporating biotic vulnerability, exposure to climate change, potential evolutionary and acclimatory responses, and the potential efficacy of management strategies. One challenge is that it is often difficult to relate responses such as phenological shifts to fitness or population growth.

We review three approaches to ecological forecasting. First, traits have been incorporated in regressions attempting to explain recent distribution and phenological shifts. Second, traits have been used to parameterize process-based models that translate environmental conditions into energetics and demography. Third, phylogenetic relatedness may be used as a proxy for phenotypes to predict species responses. The rationale for this approach is that niche conservatism, the tendency for closely related species to share similar traits (Wiens et al. 2010), implies that closely related species will respond similarly to climate change (**Figure 3**).

4.1. Overview of Existing Studies

We searched the literature (through 2011) for studies examining the performance of traits or phylogenies as predictors of phenological or range shifts attributed to recent climate change. How numerous are such studies, and how much variation in climate change responses can they account for? We queried the Thomson Reuters (ISI) Web of Knowledge database and Google Scholar using all combinations of the following three search terms: climate change, phenology or range shift, and phylogeny or trait(s). We excluded studies with less than five species as we were interested in whether trait differences between species can predict differential climate change responses.

We summarize 11 studies of range shifts and 18 studies of phenological shifts in **Table 1** (see **Supplemental Table 1** for more detail; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). The studies are primarily from Europe and North America, and each study includes between 9 and 566 species (mean = 167, median = 90). The average study interval is 58 years (median = 36 years). Most of the studies extracted trait information and phylogenies from published articles and atlases, suggesting that data availability is not a substantial barrier to including such analyses when reporting climate change responses. Traits were generally modeled using multivariate regressions. In cases in which a database was analyzed repeatedly, we included the study with the most thorough investigation of potential explanatory traits (e.g., Angert et al. 2011).

Additional studies have examined whether recent abundance changes can be predicted by traits and phylogeny. We excluded these studies as the link between the predictor variables and climate change responses may be more tenuous owing to other concurrent changes (e.g., land use). One interesting conclusion drawn from these studies is that the demography of shorter-lived species may be more responsive to increased climate variability associated with climate

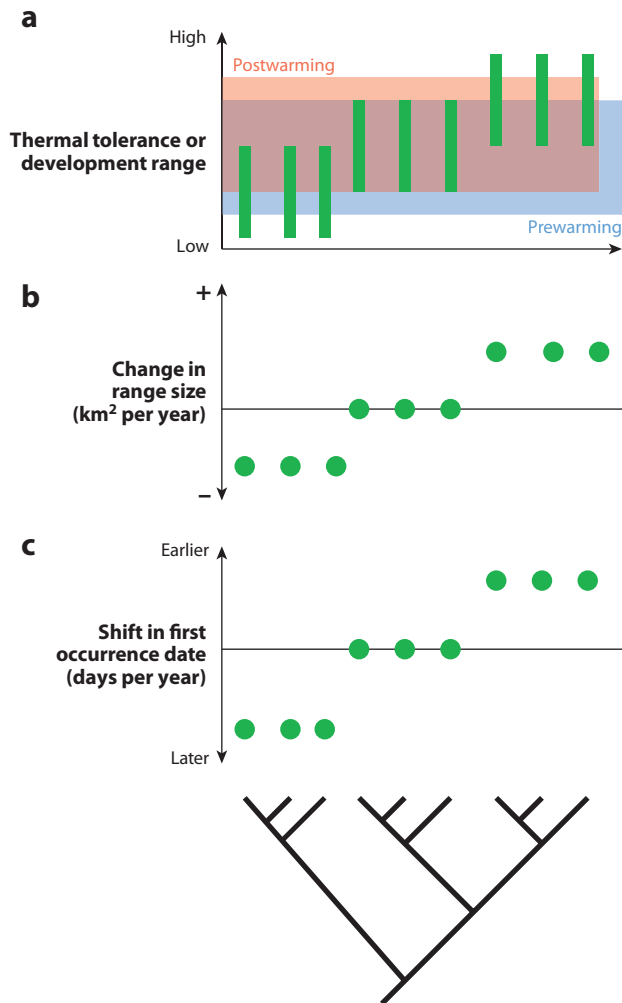


Figure 3

The conservatism of traits relevant to climate change responses may result in the biological impacts of climate change being phylogenetically biased. Climatically relevant traits (e.g., thermal tolerance and thermal limits on development, *green*) are conserved across a hypothetical phylogeny. (a) Shifts in environmental temperatures (from *blue* to *red* shading) may produce phylogenetic clustered responses such as range and phenological shifts. (b) The cool-adapted species may decrease their range size as an increased portion of habitat exceeds their thermal tolerance. The warm-adapted species may increase their range size as habitat warms to within their thermal tolerance range. (c) The cool-adapted species may emerge later as a greater proportion of temperatures exceed their thermal limits for development. The warm-adapted species may emerge earlier as a greater proportion of temperatures enter their thermal limits for development. After Davis et al. (2010).

change (Morris et al. 2008). Many of these studies employ long-term and broad-scale monitoring networks, particularly for European birds (e.g., Davis et al. 2010, Jiguet et al. 2010).

Our classification of utilized predictor traits (**Table 1**) does not correspond directly to the biological attributes that we present as potentially important predictors (Section 3). The discrepancies stem from the ease with which biological attributes resulting in climate sensitivity

Table 1 Studies examining the ability of phylogeny and traits to predict distribution and phenological shifts^a

Taxa	Number of species (N)	Location	Time period	Phylogeny	↑ Earlier season	↑ Growth rate	↑ Dispersal	↑ Ecological generalization	↑ Body or range size	↑ Elevation or latitude	↓ Trophic level	R ²	Reference
Distribution													
Plants	171	Western Europe	1905–2005			+		-					Lenoir et al. 2008
Plants (alpine)	133	Switzerland	1885–2004	1		o	o	o	o	-		0.18	Angert et al. 2011
Butterflies	51	United Kingdom	1970–1999				o	o		o			Hill et al. 2002
Butterflies	48	Finland	1992–2004	3	+	o+	+	× - o	+				Pöyry et al. 2009
Odonata	24	United Kingdom	1960–1995	1		o	o	+	o	o		0.24	Angert et al. 2011
Birds	254	North America	1775–2004	1		o	o	o	o -	o		0.07	Angert et al. 2011
Birds (passerine)	254	North America	1775–2004	1		o	o	+	o	o		0.07	Angert et al. 2011
Birds	55	Peru	1969–2010					o				0.03	Forero-Medina et al. 2011
Fish	90	North Sea	1977–2001			+			-			0.24 ^b	Perry et al. 2005
Fish	28	North Sea	1980–2004							+			Dulvy et al. 2008
Mammals	28	Western North America	1914–2008	1		o		o	o	o -		0.33	Angert et al. 2011
Phenology													
Plants	557	United Kingdom	1954–2000		+	+	-					0.19 ^b	Fitter & Fitter 2002
Plants	478	Eastern United States	1851–2007	5								NA	Willis et al. 2008
Plants	323	United Kingdom	1954–2000	5								NA	Davis et al. 2010
Butterflies/moths	566	Europe	1964–2008	4	+	+		+				0.47 ^b	Altermatt 2010
Butterflies	51	United Kingdom	1976–2010	1	+	o	o	-	-	o		0.52	Diamond et al. 2011
Butterflies	17	Northwest Mediterranean	1988–2002	4	o	o	o	×					Stefanescu et al. 2003
Odonata	37	Netherlands	1995–2004	2								NA	Dingemanse & Kalkman 2008
Odonata	25	United Kingdom	1960–2004	3	+							0.31 ^b	Hassall et al. 2007
Birds	307	Global	1995–2006			o							Gienapp et al. 2007
Birds	184	Europe	1960–2006	5				-				0.18	Rubolini et al. 2007
Birds	117	Eastern Hungary	1969–2007	1		o+	-	o+				0.11 ^b	Vegvari et al. 2010
Birds	103	Eastern United States	1903–1993				-	×				NA	Butler 2003
Birds	100	Europe	1970–2000	1								NA	Davis et al. 2010
Birds	56	Northern Germany	1977–2006	3		o	-	o	o			0.11 ^b	Rubolini et al. 2010
Birds	34	Scandinavia	1980–2004				+						Jonzén et al. 2006
Birds	18	United States	2000–2010				-					0.63	Hurlbert & Liang 2012
Birds	9	Northern Europe	1976–1997	3								0.64	Spottiswoode et al. 2006
Multiple	726	United Kingdom	1976–2005			o		o			+	0.06 ^b	Thackeray et al. 2010
			Total +		5	6	2	4	1	1	1		
			Total o		1	12	7	9	6	6	0		
			Total -		0	0	6	3	3	2	0		

^aThe predictive ability of phylogeny is coded as follows from low to high (*light blue to dark blue*): 1, phylogenetic signal not significant or Pagel's $\lambda < 0.1$; 2, family or subfamily not a significant factor in a regression; 3, regression factors still significant when accounting for phylogeny; 4, family or subfamily is a significant factor in a regression; and 5, significant phylogenetic signal. The predictive ability of traits is coded as follows based on a significance level of $p < 0.05$ (from *light blue to dark blue*): o, no effect; ×, nondirectional difference between groups; -, slower/smaller response; +, accelerated/large response. ^bCoefficient of variation (R²) based on the single explanatory variable with the most explanatory power rather than the full model. Studies with NAs are those that only address phylogeny or that use nonparametric tests, and studies without R² values do not provide sufficient information to estimate R². Abbreviation: NA, not applicable.

can be quantified or grouped as a trait and the difficulty of measuring the trait. Notably, thermal tolerances and water requirements are absent from **Table 1**. Evolutionary potential is not directly assessed but is related to factors such as reproductive rate, generation time, and population size. We also include in **Table 1** some traits such as body size and historical locations that are frequently reported but whose predicted effects for responses to climate change are less clear (see below). In summary of Section 3, we expect that the following characteristics will yield more pronounced responses to climate change:

1. *Early season* species may have greater exposure to warming, which has been concentrated during spring seasons (Menzel et al. 2006), and may be selected to capitalize on an expanded

growing season (Pau et al. 2011). Species of arthropods with more advanced overwintering stages are more mobile and can respond quickly without waiting for further development (Dennis 1993).

2. *Higher individual and population growth rates* enable more rapid evolutionary and demographic responses to climate change (Perry et al. 2005).
3. *Greater dispersal* can enable more pronounced range shifts. However, this greater capacity to track climatic niches may dampen phenological shifts.
4. *Greater ecological generalization* (greater habitat or diet breadth) may release species from being constrained by the distribution or phenology of species they associate with.
5. *Larger body or range size* may correlate directly with dispersal ability, trophic level, environmental tolerance, ecological generalization, and life-cycle duration, and inversely with reproductive rates (Davies et al. 2009). Expectations based on range or body size are complicated by these correlations, but the traits may serve as informative and readily available proxies (Angert et al. 2011).
6. *Higher elevation or more poleward* species may be more responsive to climate change because they may be adapted to cooler temperatures, have experienced a greater magnitude of warming, or be more habitat restricted.
7. *Lower trophic levels* may respond more readily to climate change because they may be less constrained by prey or host availability (Thackeray et al. 2010).

4.2. Phenomenological Phenotypic Approaches

Attempts to relate traits to responses to recent climate change generally find that traits can explain a significant, but modest amount of the variation (**Table 1**). Traits tend to be better predictors of phenological shifts (mean $R^2 = 0.42$, $N = 18$) than of distribution shifts (mean $R^2 = 0.16$, $N = 11$). This may occur because phenology is typically measured as the date of first occurrence, whereas range shifts may be measured in different portions of the range (leading or trailing edge or center). Whether phenomenological approaches can account for a sufficient proportion of the variation to reliably forecast future responses and identify those species most likely to be impacted by climate change is questionable.

In a recent synthesis for multiple taxa, Angert et al. (2011) found that traits could predict a small, but often significant, percent of the variation in shifts of the leading range edge (**Table 1**). Although observed range shifts were generally consistent with their expectations (which parallel ours), models explained only a modest portion of the variation [worst for birds (4–7%) and best for mammals (22–31%)]. Few individual traits were significant predictors of range shifts. North American birds with smaller range sizes exhibited slightly but significantly larger range shifts. Range shifts among British Odonata were best, but modestly, predicted by egg habit. The duration of seed dispersal was a marginally significant predictor variable of elevation shifts in Swiss alpine plants. Small mammals in western North America from lower elevations shifted less.

Other studies have detected somewhat stronger effects of dispersal, life history, and ecological generalization [sometimes using the same data (Sorte & Thompson 2007, Holzinger et al. 2008, Moritz et al. 2008) but different metrics than Angert et al. (2011)]. Marine demersal fishes with smaller body sizes, faster maturation, and smaller sizes at maturity were more likely to shift their ranges (Perry et al. 2005). Grasses and those plant species restricted to mountain habitats experienced more pronounced range shifts in response to twentieth-century climate change (Lenoir et al. 2008). More mobile butterflies shifted their ranges further (Pöyry et al. 2009).

Attempts to predict phenological shifts have been somewhat more successful (Pau et al. 2011). Phenological shifts of butterflies are predicted, albeit sometimes weakly, by traits such as diet,

generation time, overwintering stage, and dispersal ability (Stefanescu et al. 2003, Diamond et al. 2011). A larger study of phenological shifts for 566 European butterflies and moths over the past 150 years explained phenological changes using diet and life-cycle variables [with the strongest predictor variable (flight time) accounting for $\sim 1/2$ of the variation (Altermatt 2010)].

Trait-based expectations for phenology were a mix of consistent, inconsistent, and ambiguous responses compared with the observed responses to climate change (**Table 1**). The most consistent responses were that earlier season species (including those that overwinter in a more advanced stage) and species with a faster growth rate or more rapid life cycle had more accelerated or pronounced responses to climate change. Although some studies did not find a significant effect from earlier seasonality or faster growth rate, no observations reversed this expectation. Dispersal ability was a frequently utilized predictor of phenological shifts, particularly for birds. Notably, birds with smaller dispersal distances tended to exhibit more pronounced phenological shifts (**Table 1**). Long-distance migrants may be accustomed to heterogeneous climate conditions and their tropical wintering grounds may have experienced only limited warming (Rubolini et al. 2010). Additionally, they may have limited plasticity in their migration timing with which to respond to environmental variation (Pulido & Widmer 2005). These taxa-specific exceptions to common expectations highlight the challenges of generalizing phenomenological phenotypic models across taxa and regions.

4.3. Mechanistic Phenotypic Approaches

Other approaches explicitly incorporate traits through describing their influence on performance, energetic balances, and ultimately demography. Biophysical models use traits such as size and solar absorptivity to translate air temperatures (and other environmental variables such as radiation and wind speed) into body temperatures (Helmuth et al. 2005, Kearney & Porter 2009, Buckley et al. 2010). Predicted body temperatures can be compared to organisms' thermal limits to estimate activity time, energy balances, and thermal stress. Estimates of an organism's fundamental niche following climate change can be compared to its current realized niche to predict whether a species will need to move or adjust its phenotype to avoid extinction.

Ecosystem models based on plant functional types are frequently invoked to project ecosystem changes due to climate shifts (Van Bodegom et al. 2012). These models use empirically derived descriptions of the temperature dependence of processes such as survival, development, and photosynthesis to predict abundances and distributions (Moorcroft et al. 2001, Strigul et al. 2008). Although most vegetation models make fairly general predictions, models focused on particular species are emerging. For example, the PHENOFIT model incorporates thermal performance curves for numerous demographic constraints to produce estimates of a plant species' probability of persistence in a given region (Morin & Thuiller 2009). Demographic studies of forests have been used to construct probabilistic models based on individual sensitivities to the environment (Clark et al. 2012).

Analogous models for animals are less well established. As discussed above, Helmuth (2009) have used biophysical models to estimate thermal stress and energetics for intertidal organisms. Porter et al. (2000) have developed biophysical models to estimate body temperatures for a variety of terrestrial organisms. Information on the temperature dependence of development can be coupled with the biophysical model output to predict development rates and, thus, phenology (Kearney et al. 2010b). Body temperatures can be compared to thermal limits to predict activity time; knowledge of the amount of activity required to meet energetic demands can be used to estimate distributions (Kearney & Porter 2004). Recently, the biophysical models have been linked with dynamic energy budget models to produce demographic predictions based on rules of energy

allocation (Kearney et al. 2010a, Kearney 2012). Activity time estimates can also be used to derive demographic predictions by examining energetic yield within an optimal foraging framework (Buckley 2008). Another approach involves documenting thermal performance curves for survival and fecundity to estimate population dynamics (Crozier & Dwyer 2006, Doak & Morris 2010). These mechanistic approaches have found that geographic trait variation can influence distributions substantially (Buckley 2008, Kolbe et al. 2010), highlighting the importance of species' traits for predicting climate change responses.

Mechanistic models generally require detailed biological understanding for their parameterization. A less detailed but promising approach relies on the occurrence of niche conservatism and predictable broad-scale patterns in thermal tolerance to predict responses to climate change (Tewksbury et al. 2008; see also Section 3). For example, Huey et al. (2009) have documented that upper thermal tolerances are tightly constrained among temperate and tropical lizards. As a result, a Puerto Rican anole is predicted to have moved into the forest and to have displaced a forest anole through recent climate changes.

4.4. Phylogenetic Approaches

The conservatism of traits governing a species' environmental niche (Wiens et al. 2010) can result in responses to climate change being likewise phylogenetically conserved (Burns & Strauss 2011). If this is the case, studies of climate change impacts on a few species could be generalized to their relatives. The flip side of this is that if climate impacts (or predictor traits) are phylogenetically conserved, phylogeny must be controlled for in identifying predictor traits because the conservation of multiple traits can produce spurious correlations between particular traits and vulnerability to climate change. Phylogenetic signal can be assessed using metrics (e.g., Pagel's λ or Blomberg's K) or randomization tests (such as repeatedly swapping the tips of the phylogenetic tree). Evolutionary history can be controlled for in trait-based analyses by transforming the data into phylogenetically structured comparisons between sets of related species (independent contrasts). Another approach is to statistically account for expected covariance in trait values due to phylogenetic relatedness (phylogenetic generalized least squares, PGLS) (methods reviewed by Paradis 2006).

Of the analyses relating traits to climate change responses, half (54%) considered phylogeny (**Table 1**). Phylogeny was often controlled for in the trait regressions by using independent contrasts or PGLS. In other cases where phylogenies were unavailable, taxonomic groupings were included as an addition factor in the regression. We focus here on the several studies that examined phylogenetic signal in climate change responses directly using Pagel's λ ($\lambda = 0$, no phylogenetic signal; $\lambda = 1$, complete phylogenetic determination) or randomization tests (Davis et al. 2010). These studies suggest that climate change responses are constrained by phylogeny. Indeed, the degree to which flowering time in Thoreau's Woods (Concord, MA) tracked temperature was similar among closely related species and related to shifts in abundance (**Figure 4**) (Willis et al. 2008, Davis et al. 2010). The phylogenetic signal in flowering time tracking was confirmed for plants in Chinnor, United Kingdom (Davis et al. 2010). Flowering phenology itself tends to be phylogenetically conserved across broad geographic gradients (reviewed by Pau et al. 2011). Among European birds, population declines were phylogenetically clustered, but not fully attributable to phenological changes (Davis et al. 2010). Although the authors (Davis et al. 2010) identified traits (body size, overwintering location, and range latitude) exhibiting phylogenetic signal that might account for similar responses among related species, they did not find phylogenetic signal in phenological shifts, which is the best predictor of bird decline (Møller et al. 2008). Phenological

Phylogenetic signal: recognized when the traits of closely related taxa are more similar than expected under a specified model of trait evolution

shifts were not phylogenetically conserved among butterflies (Diamond et al. 2011) and some birds (Vegvari et al. 2010).

Less evidence exists for the phylogenetic conservatism of range shifts. This may be because range size shows only weak phylogenetic signal (Davies et al. 2009). All but one example we located that controlled for phylogeny in regressions with traits was by Angert et al. (2011). They found very low λ values (absence of significant phylogenetic signal) in their phylogenetic regressions. One other study (Pöyry et al. 2009) showed that the traits remained significant predictors of range shifts when accounting for phylogeny, suggesting that the traits may be robust predictor variables.

Do responses to climate change exhibit phylogenetic signal due to the conservation of traits governing a species' environmental niche? Analyses of phylogenetic signal in thermal tolerances offer a direct assessment of this issue. Similarities in thermal tolerance would provide a functional basis for predicting similar responses to climate shifts among closely related species. A global study of upper and lower thermal limits for a variety of terrestrial and marine taxa (reptiles, arthropods, amphibians, fish, and mollusks) found that including taxonomic nesting as a random effect significantly improved model performance (Sunday et al. 2010). More taxonomically focused analyses have enabled using phylogenies. Huey et al. (2009) found a high degree of phylogenetic signal in the field body temperatures, critical thermal minima and maxima, and optimal temperatures of 70 lizard species. The degree of niche conservatism varied between lineages. Lineages of forest-dwelling, nonbasking species have remained largely restricted to the tropics, whereas open-habitat, basking lineages have extended into temperate zones (Huey et al. 2009). Ants were found to exhibit a high degree of phylogenetic signal ($\lambda \sim 0.9$) in warming tolerance (Diamond et al. 2012). This is notable because ant species with higher critical thermal maxima were more abundant in experimental warming chambers (Diamond et al. 2012a).

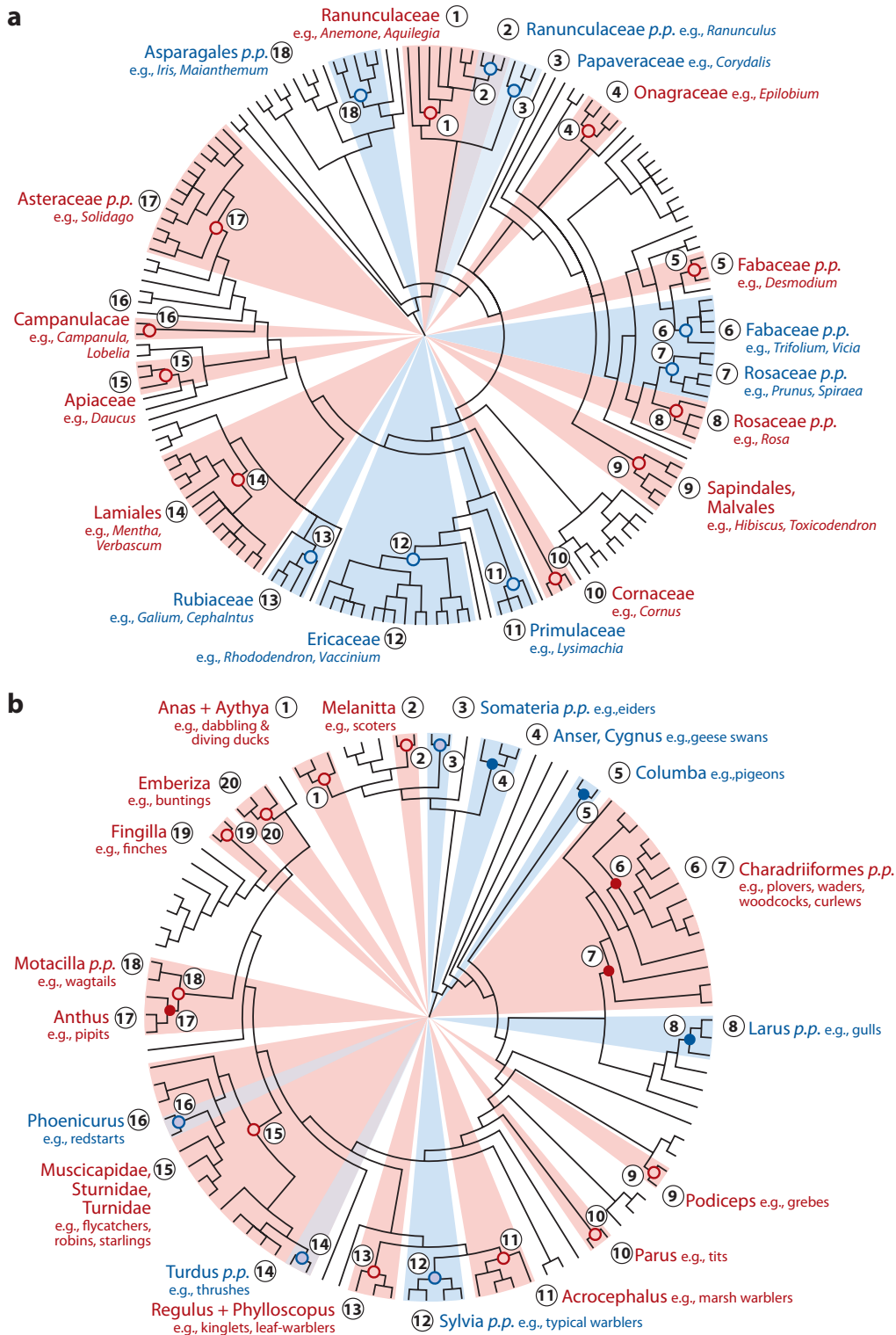
Conservatism of realized climatic niches has been assessed for taxa lacking data on thermal tolerances. Phylogenetic signal has been detected in the realized climatic niches of amphibians (Hof et al. 2010) and mammals (Cooper et al. 2008). Environmental niches tend to be sufficiently conserved to justify predicting similar responses to climate change among closely related species. Yet, the potential to use phylogeny as a predictive tool has seldom been investigated. The tendency for environmental niches to be conserved also highlights the importance of controlling for phylogeny in trait-based analyses.

5. PROSPECTS FOR IMPROVED ECOLOGICAL FORECASTING

Researchers are still largely at a loss in explaining interspecific variation in responses to climate change. More pronounced biological responses do seem to correspond to exposure to greater magnitudes of climate warming (Chen et al. 2011). Attempts to explain the extent of range and phenological shifts have found that traits can account for a sometimes significant, but generally modest, proportion of the variation. In the few cases examined, climate change impacts have been observed to phylogenetically cluster. This highlights the need to control for phylogeny in searches for predictor traits. It also suggests that we may not have yet identified or appropriately quantified the most promising predictor traits given the modest success of trait-based analyses. Perhaps more likely, our often linear expectations for environment-trait interactions may be inadequate

Figure 4

Composite phylogenies depict the phylogenetic clustering of (a) phenological shifts since 1851 for plants from Concord, MA, and (b) changes in population size of European birds since 1970. Red and blue shading and dots at nodes indicate less and more responsive clades, respectively (*solid dots*, significant; *open dots*, marginally significant). Reproduced with permission from Davis et al. (2010).



to account for the complex interactions among suites of traits in heterogeneous and temporally varying environments. Additionally, behavior and acclimation can complicate environment-trait interactions. Evolution can lead to local adaptation that exceeds our coarse geographic knowledge of trait values.

The commonly implemented correlative SDMs are inherently limited in their ability to predict individualistic responses due to their assumption of constant traits across a range, fixed correlations between environmental variables, and persistent and generally simple environment-trait interactions. Extrapolating these models across time and space can be particularly problematic. Efforts to include more organismal biology (by including the output of mechanistic models as predictor variables) have met modest success (Elith et al. 2010, Buckley et al. 2011). Detailed mechanistic models for thoroughly studied species have succeeded in using the details of organismal biology to predict current distributions and climate change responses (Kearney & Porter 2009, Buckley et al. 2010), but how can these techniques be generalized to less studied species?

What aspect of the biology included in the models is responsible for their ability to predict individualistic range shifts? Applying functional and phylogenetic approaches to additional data sets may offer the most promise for addressing this question. Phylogenies and phylogenetic methods are becoming more accessible (e.g., R packages such as ape, CAIC, phylobase, phytools, and Picante; see Paradis 2006), and the assembly of trait data is accelerating (e.g., TRY initiative for plant traits). Most of the studies reviewed here used published phylogenies and trait data to investigate functional and phylogenetic predictors of climate change responses. It is thus our hope that many forthcoming reports of climate change responses will consider the traits and relatedness of species. Although initial functional and phylogenetic approaches demonstrate promise, many more case studies are needed to test our ability to predict responses to past climate change and, thus, provide a reliable basis for predicting future responses.

SUMMARY POINTS

1. Considering physical aspects of climate change beyond shifts in the mean and investigating the interaction of these physical characteristics with traits is central to forecasting impacts. Important considerations include variability in the magnitude of climate change across locations and seasons, increases in the incidences of climate extremes, and the occurrence of novel climates.
2. The complexity of an organism's life cycle along with its seasonal timing will determine its exposure to climate change. An organism's degree of ecological generalization is an important determinant of its ability to modify its timing or distribution. Thermal and hydric limits and evolutionary potential are conceptually important aspects of an organism's phenotype, but they are seldom empirically examined.
3. Traits can account for an often significant but generally modest amount of the variation in phenological and range shifts. Both traits and climate change responses tend to be phylogenetically conserved, suggesting that traits should be considered in an explicit phylogenetic framework. Further case studies and the development of more mechanistic techniques will enhance our ability to forecast the ecological consequences of climate change.

FUTURE ISSUES

1. Understanding and quantifying the phenotypic variation within and between species is becoming increasingly important in the context of climate change. Lab measurements using temperature-controlled environments are providing important insight into thermal limits and thermal constraints on development. Although basic data in constant conditions is crucial, experiments in fluctuating and stochastic environments are also important to understanding responses to climate extremes. Common garden experiments provide essential information on how locally adapted traits interact with the environment to determine performance and demography (e.g., Sexton et al. 2009). Manipulative field experiments directed at understanding responses to shifts in extremes in addition to mean conditions will provide important insight (Jentsch et al. 2007, Smith 2011).
2. Assembling phenotypic data and phylogenies is central to improved ecological forecasting. Investigating phenotypic shifts over time is also central to ecological forecasting. Museum specimens and data compilation are a valuable but largely untapped resource for examining temporal change in phenotypes (Johnson et al. 2011, Lister 2011). For example, recent studies have documented shifts in body size (Gardner et al. 2011) and coloration (linked to fitness as a function of snow cover; Karell et al. 2011) in response to recent climate change.

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Contents

Scalingy Up in Ecology: Mechanistic Approaches <i>Mark Denny and Lisandro Benedetti-Cecchi</i>	1
Adaptive Genetic Variation on the Landscape: Methods and Cases <i>Sean D. Schoville, Aurélie Bonin, Olivier François, Stéphane Lobreaux, Christelle Melodelima, and Stéphanie Manel</i>	23
Endogenous Plant Cell Wall Digestion: A Key Mechanism in Insect Evolution <i>Nancy Calderón-Cortés, Mauricio Quesada, Hirofumi Watanabe, Horacio Cano-Camacho, and Ken Oyama</i>	45
New Insights into Pelagic Migrations: Implications for Ecology and Conservation <i>Daniel P. Costa, Greg A. Breed, and Patrick W. Robinson</i>	73
The Biogeography of Marine Invertebrate Life Histories <i>Dustin J. Marshall, Patrick J. Krug, Elena K. Kupriyanova, Maria Byrne, and Richard B. Emlet</i>	97
Mutation Load: The Fitness of Individuals in Populations Where Deleterious Alleles Are Abundant <i>Aneil F. Agrawal and Michael C. Whitlock</i>	115
From Animalcules to an Ecosystem: Application of Ecological Concepts to the Human Microbiome <i>Noah Fierer, Scott Ferrenberg, Gilberto E. Flores, Antonio González, Jordan Kueneman, Teresa Legg, Ryan C. Lynch, Daniel McDonald, Joseph R. Mihaljevic, Sean P. O'Neill, Matthew E. Rhodes, Se Jin Song, and William A. Walters</i>	137
Effects of Host Diversity on Infectious Disease <i>Richard S. Ostfeld and Felicia Keesing</i>	157
Coextinction and Persistence of Dependent Species in a Changing World <i>Robert K. Colwell, Robert R. Dunn, and Nyeema C. Harris</i>	183
Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change <i>Lauren B. Buckley and Joel G. Kingsolver</i>	205

Rethinking Community Assembly through the Lens of Coexistence Theory <i>J. HilleRisLambers, P.B. Adler, W.S. Harpole, J.M. Levine, and M.M. Mayfield</i>	227
The Role of Mountain Ranges in the Diversification of Birds <i>Jon Fjeldså, Rauri C.K. Bowie, and Carsten Rabbek</i>	249
Evolutionary Inferences from Phylogenies: A Review of Methods <i>Brian C. O'Meara</i>	267
A Guide to Sexual Selection Theory <i>Bram Kuijper, Ido Pen, and Franz J. Weissing</i>	287
Ecoenzymatic Stoichiometry and Ecological Theory <i>Robert L. Sinsabaugh and Jennifer J. Follstad Shab</i>	313
Origins of New Genes and Evolution of Their Novel Functions <i>Yun Ding, Qi Zhou, and Wen Wang</i>	345
Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts <i>Wim H. Van der Putten</i>	365
Inflammation: Mechanisms, Costs, and Natural Variation <i>Noah T. Ashley, Zachary M. Weil, and Randy J. Nelson</i>	385
New Pathways and Processes in the Global Nitrogen Cycle <i>Bo Thamdrup</i>	407
Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton Succession <i>Ulrich Sommer, Rita Adrian, Lisette De Senerpont Domis, James J. Elser, Ursula Gaedke, Bas Ibelings, Erik Jeppesen, Miquel Lüring, Juan Carlos Molinero, Wolf M. Mooij, Ellen van Donk, and Monika Winder</i>	429
Global Introductions of Crayfishes: Evaluating the Impact of Species Invasions on Ecosystem Services <i>David M. Lodge, Andrew Deines, Francesca Gherardi, Darren C.J. Yeo, Tracy Arcella, Ashley K. Baldridge, Matthew A. Barnes, W. Lindsay Chadderton, Jeffrey L. Feder, Crysta A. Gantz, Geoffrey W. Howard, Christopher L. Jerde, Brett W. Peters, Jody A. Peters, Lindsey W. Sargent, Cameron R. Turner, Marion E. Wittmann, and Yiwen Zeng</i>	449
Indexes	
Cumulative Index of Contributing Authors, Volumes 39–43	473
Cumulative Index of Chapter Titles, Volumes 39–43	477

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://ecolsys.annualreviews.org/errata.shtml>