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Plant phenology and distribution in relation to recent climate change

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BERTIN, R. I. (Biology Department, College of the Holy Cross, Worcester, MA 01610) Plant phenology and distribution in relation to recent climate change. J. Torrey Bot. Soc. 135: 126–146. 2008.—This paper summarizes a broad range of studies that have examined influences of recent climate change on plant phenology or distribution. Spring events such as leafing and flowering have typically advanced, some by several weeks, with median advances of 4–5 d per degree Celsius. Autumn events, such as leaf coloring or leaf fall, have usually become delayed, though with more variability than spring events. Changes in summer events have been mixed. Phenological changes have varied geographically, as have recent temperature changes. Most studies of at least several decades duration show the initiation of rapid changes in the 1970s or 1980s, paralleling patterns of temperature change. Plants and animals in a given area have often responded at different rates to temperature change, which is likely to change patterns of interaction between plants and their pollinators and herbivores. Altitudinal changes in plant distributions have been demonstrated in several areas, especially in Scandinavia and in Mediterranean Europe, though these changes lag the measured temperature changes. Latitudinal changes in plant distribution have been demonstrated in only a few instances and it has been suggested that precipitation changes may have limited range shifts in response to warming in some areas. The observed and predicted changes in plant distribution and phenology have major implications for various ecological and evolutionary phenomena, including ecosystem productivity, species interactions, community structure, and conservation of biodiversity.

Key words: climate change, distribution limits, flowering, global warming, leafing, phenology.

Global surface temperature has increased by an estimated 0.74°C over the past century, a change that is widely believed to result primarily from the effects of anthropogenic emissions of carbon dioxide and other greenhouse gases (International Panel on Climate Change, hereafter IPCC, 2007). Many physical changes have been attributed to this warming, including sea level rise, melting of glaciers and ice sheets, decreased snow and ice cover, increased depth to permafrost and changes in patterns of wind, temperature, and precipitation (summarized in IPCC 2007).

Such changes are likely to have considerable biological effects and numerous studies have sought evidence of such biological effects in nature. Several recent papers summarize the results of these studies and conclude that biological effects are already evident and have affected numerous taxa in different geographical areas (Walther et al. 2002, Parmesan and Yohe 2003, Menzel et al. 2006, Parmesan 2006).

My goal in this paper is to summarize a broad sampling of field studies that have examined changes in plant distribution or phenology in relation to recent climate change. It is not my intention to conduct a meta-analysis of the data, of which several are available in the literature (Parmesan and Yohe 2003, Root et al. 2003, Menzel et al. 2006, Parmesan 2007). I also omit the large literature on experimental warming studies. Rather I wish to bring to a botanical audience a literature on botanical field studies that has appeared primarily in climatological journals, and to briefly discuss some ecological and evolutionary consequences of the observed and projected changes.

Phenology. METHODOLOGY AND COVERAGE. Many biological phenomena are episodic and at least partly dependent on weather patterns, some of the most familiar being migration of birds, emergence of insects, flowering and leafing out of plants. Changes in phenology have long been regarded as sensitive indicators of climatic change. The recording of phenological observations has a long history, nowhere more evident than in the several centuries of records of cherry blossoming in Japan (Menzel and Dose 2005, Aono and Kazui, 2008). While such observations were "once the hobby of the leisured classes"

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(Sparks et al. 1997), this idle pleasure now contributes importantly to our understanding of the effects of recent climate changes. Sparks and Menzel (2002) contend that ''phenology is the most responsive aspect of nature to warming and the simplest to observe.''

The sensitivity of at least spring phenophases to temperature is consistent with the observation that heat sums for the late winter or spring months often are accurate predictors of phenophase timing (Sparks and Carey 1995, Diekmann 1996, Kai et al. 1996, Heikinheimo and Lappalainen 1997, Thórhallsdóttir 1998, Schwartz 1999, Spano et al. 1999, Van Vliet et al. 2002, Galán et al. 2005). Menzel and Fabian (1999) found that 70% of interannual variation in bud break in a group of European species was explained by daily temperature patterns, and average February and March temperatures explained 75% of the variation in flowering time of Japanese cherries (*Cerasus* spp., Miller-Rushing et al. 2007). Certainly other variables influence timing of at least some phenophases. Timing of snow melt can be an important variable for early spring phenophases in northern and alpine climates (Saavedra et al. 2003, Molau et al. 2005). While snow melt is strongly influenced by temperature, it is also influenced by amount of precipitation and other factors. Flowering of many plant species is responsive to photoperiod (Raven et al. 2005) and precipitation influences the timing of various plant phenophases, especially in dry or seasonally dry habitats (Keatley et al. 2002, Kramer et al. 2000).

The principal approach for documenting phenological changes in plants is direct observation of particular taxa over periods of decades to centuries. A minimum observation period of two decades is recommended by Sparks and Menzel (2002), and most time series used to examine the issue of temporal change have been at least this long. Some observations were recorded by single or multiple observers at single locations and others as part of phenological networks, where multiple observers record observations of the same species from different locations. A recent approach has been to compare current observational records to older records documented by either photographs or herbarium specimens (Miller-Rushing et al. 2006). Springtime events have received the most attention.

Satellite imagery has provided useful large-scale information, especially the Normalized Difference Vegetation Index (NDVI), based on measurements of short wavelength radiation (Myneni et al. 1997). Such data are useful primarily to document general patterns of leafing out in spring, and are not useful for evaluating phenology of particular species. Satellite measurements have the advantage of broad geographical coverage, though their utility is limited by the lack of older records (pre-1980s). Additionally, correlations with ground-based observations have been described as ''modest'' (Badeck et al. 2004), though the strength of the correlation varies with which ground-based observations are used (Studer et al. 2007). Other issues concerning satellite measurements are the long intervals between successive flyovers of a given location, the need for adjustments due to changes in orbital and atmospheric conditions, and possible influences of late snow cover on the resultant data (Schwartz 1999, Schwartz and Reed 1999, Badeck et al. 2004, Schwartz et al. 2006, Studer et al. 2007).

All methods of measuring phenology are subject to various sources of error (reviewed by Dose and Menzel 2004) and the extent of these potential errors is not precisely known. Criteria for recording a particular phenological event (e.g., peak flowering) can be interpreted differently by different observers. Genetic variation is inevitable in studies of natural and most cultivated specimens, though all but somatic variation is eliminated in those studies using material asexually propagated from a single clone. Plant age often varies among sites, with unknown effects on phenology. Environmental and cultural condition such as soil type, soil moisture, aspect, and exposure cannot be precisely controlled. Trends in several variables, such as precipitation or an urban heat island effect, sometimes accompany and potentially confound temperature trends. Urban effects can be substantial. Contributions of urbanization to flowering advancement have been estimated at 4 d over 30 y in central Europe (Roetzer et al. 2000) and 4–6 d in the past century in China and Japan (Yoshino and Ono 1996). Comparisons of temperature changes in rural and urban sites in Massachusetts suggested that urban effects accounted for half of the total change in greater Boston (Primack et al. 2004).

Other issues affect the interpretation of results. Different studies have different starting dates, ending dates, durations, and frequencies of observation, and temperature change has not been constant over the past few centuries. Calculated rates of change vary depending on what time period is included in the particular set of records (Menzel 2000, Roetzer et al. 2000, Sparks and Menzel 2002, Badeck et al. 2004, Dose and Menzel 2004). Menzel et al. (2006) eliminated this problem in their comprehensive analysis of European phenological records by standardizing the time period over all sites.

The most common method of analysis has been to regress date of a phenological event on year. This procedure allows calculation of a rate of change in the phenological event over time though, as noted above, the result depends on whether the series covers just a period of relatively rapid change (e.g., post-1970s or post-1980s) or includes a period of stable or declining temperatures (e.g., 1940–1970). Temperature data (typically monthly means) are often recorded from nearby weather stations. Numerous studies have examined the relationship between phenological events and temperature over several seasons to derive predictive relationships between temperature and timing of a phenophase. Such functions are typically used as the basis for predicting phenological changes likely to be associated with future temperature changes, with a linear relationship generally assumed. Sparks et al. (2000) note that the plant response to temperature, even if linear over a certain range, must inevitably taper off, though we do not know at what temperature this is likely to occur. Several papers have used other methods, including dynamic factor analysis (Gordo and Sanz 2005), chronological clustering (Doi 2007), and Bayesian methods (Dose and Menzel 2004, 2006) to investigate phenological changes, and these have been helpful in separating out different parts of a single time series that show different patterns.

Sagarin (2001) points out that the common method of expressing date in phenological studies (days from the start of the year, or Julian days) is problematic because the starting date in this sequence (January 1) is somewhat arbitrary. This date does not correspond to a particular relationship between sun and earth and varies by nearly a day over the course of the century relative to a celestially determined event such as a solstice or an equinox. Use of Julian days leads to overestimates of advancing spring events with a 1–5% bias in late 20th century studies and a bias of up to 10% in studies covering a century. He argues instead for using the vernal equinox as a more meaningful point of reference.

A further potential bias in phenological studies is the possibility that studies showing certain patterns of change are more likely to be published than those showing no change or a change opposite to the expected direction (Kozlov and Berlina 2002, Menzel et al. 2006). Such bias could result from the greater likelihood of a paper's acceptance if it shows clear patterns of change or it could reflect a tendency on the part of a researcher to delay or avoid submission of a manuscript not showing expected patterns. While the interpretation of a significant result can be straightforward, a non-significant result could mean either that no trend exists or that the method used was insufficient to resolve the pattern, and uncertainty over which of these is correct may reduce the likelihood a paper is submitted. This problem is eliminated by analyzing one or more entire sets of records with all results reported, as done by Menzel et al. (2006) for numerous European records and in meta-analyses by Parmesan and Yohe (2003) and Parmesan (2007).

Geographical coverage of phenological series is very uneven. Europe has the greatest coverage (Table 1), reflecting the International Phenological Gardens operating in multiple countries since the 1950s and the tradition of recording phenology among hobbyists. Temperate North America has somewhat less extensive coverage, and records from other parts of the world are few. Despite these various limitations of data and analysis, attempts at comprehensive and standardized analyses have been made (Menzel et al. 2006, Schwartz et al. 2006) and robust patterns have emerged.

RESULTS. Advances of springtime phenological events have been documented in the vast majority of published studies (Table 1). Particularly compelling evidence is provided by broad scale studies using satellite imagery (Schwartz et al. 2006) and by several meta-analyses (Parmesan and Yohe 2003, Root et al. 2003, Menzel et al. 2006). Average advanc-

es in spring phenophases have been 1–3 days per decade during the last several decades in temperate regions of the Northern Hemisphere (Menzel 2000, Walther et al. 2002, Parmesan and Yohe 2003, Wolfe et al. 2005, Menzel et al. 2006, Schwartz et al. 2006, Parmesan 2007), though studies of particular species or particular regions give much more variable results (Scheifinger et al. 2002, Menzel et al. 2006). The emergence of patterns in so many individual phenological studies is impressive given the large year-to-year variation evident in most long phenological series (Hulbert 1963, Ahas 1999, Aono and Kazui 2008).

While the overall pattern unequivocally points to advancement of most springtime phenological events, several studies have sought but not found temporal changes in phenology. These include some that cover time periods when little change in global average temperatures were evident (Keatley et al. 2002, references in Roetzer et al. 2000) and others that occurred during periods of global warming, but in regions where temperatures were constant or declining (Kozlov and Berlina 2002, Shutova et al. 2006). A few occurred at places and times when temperature changes were occurring, but were unable to document significant changes in phenology (Schwartz and Chen 2002). The presence of some studies showing unchanging or even delayed phenologies in such a large sample is not surprising and could be due either to chance or to real biological phenomena as discussed below.

Several generalizations follow from phenological studies published in the last decade or so:

1. Spring phenophases have advanced much more consistently than summer or autumn phenophases, and early spring phenophases show greater advances than those in later spring or early summer (Sparks et al. 1997, Bradley et al. 1999, Menzel 2000, Defila and Clot 2001, Fitter and Fitter 2002, Scheifinger et al. 2002, Sparks and Menzel 2002, Van Vliet et al. 2002, Walther et al. 2002, Zhao and Schwartz 2003, Dose and Menzel 2004, Gordo and Sanz 2005, Wolfe et al. 2005, Schaber and Badeck 2005, Ahas and Aasa 2006, Menzel et al. 2006, Miller-Rushing et al. 2007). This pattern is at least partly explained by the fact that in most locations winter and early spring temperatures have risen more rapidly than those at other times of year (Myneni et al. 1997, Ahas 1999, Luckman and Kavanagh 2000, Roetzer et al. 2000, Cayan et al. 2001). In central and western Europe, for example, the early spring flowering of *Corylus avellana* and *Tussilago farfara* has advanced 10–20 days compared to an advance of 5–15 days for later spring phenophases of *Syringa*, *Malus*, *Tilia* and *Betula* (Ahas et al. 2002). Also of potential importance is that early phenophases are typically more strongly influenced by timing of snowmelt than are later phenophases (Inouye and McGuire 1991, Henry and Molau 1997, Price and Waser 1998, Molau et al. 2005), and time of snowmelt has advanced in many northern hemisphere locations (Ahas 1999, Burns et al. 2007, Hüttich et al. 2007). Also relevant is that independent of any consistent trends in phenology, early phenophases often show more variation than later phenophases, indicating a greater sensitivity to yearly environmental variations (Hulbert 1963, Sparks and Menzel 2002, but see Molau et al. 2005, Miller-Rushing et al. 2007).

Among phenological series that begin before the recent period of rapid warming (i.e., before the 1970s or 1980s) and extend through at least the 1990s, reported changes in spring phenophases range from negative or zero up to over 40 d (Abu-Asab et al. 2001, Defila and Clot 2001, Fitter and Fitter 2002). Some of the greatest changes partially reflect urban heat island effects (Landsberg 1981) as well as broader climatic changes. Some of the largest advances reported from more rural areas are 55 d and 35 d for the flowering of *Lamium album* and *Cymbalaria muralis*, respectively, in England (Fitter and Fitter 2002), 30–37 d for leaf unfolding of several tree species in Spain (Peñuelas et al. 2002), and 26 d for the flowering of *Populus tremuloides* in Alberta (Beaubien and Freeland 2000). Conversely, the largest reported delay seems to be 36 d for the flowering of *Buddleja davidii* in England (Fitter and Fitter 2002). Expressed in terms of phenological change per degree Celsius of temperature change, most springtime records show advances of 1–8 d (Table 2), but range from a delay of 4 d for flowering of *Colchicum autumnale* to an advance of 10 d for flowering of *Convovulus sepium* (Sparks et al. 2000). The temperature measurements

Table 1. Observations of phenological series in plants.

Location	Time Period	Taxa	Events	Results	Reference
Europe					
England	1736–1925	17 phenophases	flowering, leafing	advanced up to 25 d	Sparks and Carey 1995
England	1947–1996	4 tree species	leafing	advanced 8 d	Sparks et al. 1997
Hungary	1851–1994	*Robinia pseudoacacia*	flowering	advanced 5–7 d	Walkovszky 1998
Estonia	1919–1996	4 species	flowering	advanced 3–14 d	Ahas 1999
Europe	1959–1993	clones of woody species	various	spring advanced, autumn delayed	Menzel and Fabian 1999
Estonia	1946–1998	*Secale*, 6 tree species	flowering & others	advanced	Jaagus and Ahas 2000
Europe	1951–1996	numerous species	flowering, leafing	most spring events advanced	Menzel 2000
Central Europe	1951–1995	4 species	flowering	most advanced	Roetzer et al. 2000
Switzerland	1800s–2000	*Aesculus*, *Prunus*	flowering, bud burst	advanced 7–44 d	Defila & Clot 2001
Switzerland	1951–1998	13 species	flowering & others	most advanced	Defila & Clot 2001
Europe	1951–1998	6 species	flowering, leafing	advanced 5–20 d	Ahas et al. 2002
Europe	1969–1998	4 tree species	leafing	advanced 8 d	Chmielewski and Rötzer 2002
England	1954–2000	385 species	flowering	most advanced	Fitter and Fitter 2002
Russia	1930–1998	3 species	flowering, leafing	spring unchanged, autumn advanced	Kozlov and Berlina 2002
Spain	1952–2000	numerous species	various	spring advanced, autumn delayed	Peñuelas et al. 2002
Central Europe	1951–1998	17 phenophases	various	spring advanced, autumn various	Scheifinger et al. 2002
Netherlands	1969–2000	14 taxa	pollen release	10 advanced significantly	Van Vliet et al. 2002
Germany	1951–1999	*Betula*, *Quercus*	bud burst	advanced	Badeck et al. 2004
Ireland	1970–2000	*Tilia cordata*	leafing	advanced at 2 of 4 sites	Donnelly et al. 2004
Germany	1896–2002	*Galanthus*, *Prunus*, *Tilia*	flowering	advanced recently	Dose and Menzel 2004
Russia	1948–2003	*Quercus robur*	leafing	advance approaching significance	Askeyev et al. 2005
Spain	1982–2002	*Olea europea*	pollen release	advanced	Galán et al. 2005
Spain	1943–2000	46 taxa	various	spring advanced	Gordo and Sanz 2005
Estonia	1951–1999	753 phenophases	various	86% of phenophases advanced	Ahas and Aasa 2006
Europe	1971–2000	542 species	various	78% of spring phenophases advanced	Menzel et al. 2006
Northern Europe	1964–2003	*Betula pubescens*	leafing, yellowing	various	Shutova et al. 2006
North America					
North Dakota	1960s–1990s	*Syringa*	flowering	spring advanced	Schwartz 1994
E. North America	1900–1995	terrestrial ecosystems	leafing	advanced recently	Schwartz 1998
Wisconsin	1936–1998	36 species	flowering	10 had significant advances	Bradley et al. 1999
Western Canada	1973–1996	3 woody species	flowering	advanced 8+ d	Beaubien & Freeland 2000
North America	1959–1993	*Syringa*	flowering, leafing	advanced 5–6 d	Schwartz and Reiter 2000
Washington, D.C.	1970–1979	100 species	flowering	most advanced	Abu-Asab et al. 2001
Western U.S.	1957–1994	*Syringa*, *Lonicera*	flowering, leafing	advanced 7–10 d	Cayan et al. 2001
Wisconsin	1965–1998	multi-species indexes	flowering	most advanced	Zhao and Schwartz 2003
Massachusetts	various	woody species	flowering	advanced 8 d	Primack et al. 2004
North America	1960–2001	*Malus*, *Syringa*, *Malus*	flowering, leafing	advanced	Wolfe et al. 2005

Table 1. Continued.

Location	Time Period	Taxa	Events	Results	Reference
Australasia					
China	1982–1993	integrated measure	leafing	advance at 1 of 3 sites	Chen et al. 2001
Australia	1940–1962	4 *Eucalyptus* species	flowering	no significant trends	Keatley et al. 2002
Northern China	1963–1993	*Syringa*	flowering, leafing	no significant trends	Schwartz and Chen 2002
Japan	1953–2000	*Ginkgo biloba*	bud break & leaf fall	budding advanced, leaf fall delayed	Matsumoto et al. 2003
Japan	1953–2005	*Prunus mume*	flowering	advanced, mostly after 1989	Doi 2007
Japan	1981–2005	*Cerasus* spp.	flowering	advanced 5–6 d	Miller-Rushing et al. 2007
Global					
Land 45°–75°N	1981–1991	terrestrial ecosystems	leafing	spring advanced, autumn delayed	Myneni et al. 1997
World-wide	various	numerous taxa	various	most advanced (a meta-analysis)	Root et al. 2003

Table 2. Changes in timing of springtime plant phenological events per °C of temperature change. Positive changes represent advances.

Taxon	Event	Days Change per °C	Location	Typical Season	Source
Amelanchier alnifolia	flowering	4–5	western Canada	May	Beaubien and Freeland 2000
Anemone nemorosa	flowering	4–7	England	March	Sparks and Menzel 2002
Betula pubescens	leafing	4–6	Kola Peninsula	June	Shutova et al. 2006
Betula pubescens	bud burst	3–8	northern Fennoscandia	May–June	Karlsson et al. 2003
Cerasus spp.	flowering	3–5	Japan	March–April	Miller-Rushing et al. 2007
Ginkgo biloba	bud burst	3	Japan	April	Matsumoto et al. 2003
Olea europea	pollen release	4–6	Mediterranean	May	Osborne et al. 2000
Populus tremuloides	flowering	5	western Canada	April	Beaubien and Freeland 2000
Prunus virginiana	flowering	7	western Canada	May	Beaubien and Freeland 2000
Prunus yedoensis	flowering	3–6	Japan, Korea	April	Yoshino and Ono 1996
Quercus robur	leafing	7	England	March–April	Cannell et al. 1999
Robinia pseudoacacia	flowering	7	Hungary	May	Walkovszky 1998
Syringa vulgaris	flowering	5	western North America	March–June	Cayan et al. 2001
Tilia cordata	leafing	6	Ireland	April	Donnelly et al. 2004
Multiple taxa	flowering	3–8	Japan	mostly spring	Kai et al. 1996
Multiple taxa	flowering	(−4) 2–10	England	mostly spring	Sparks et al. 2000
Multiple taxa	flowering	6	Europe	spring	Menzel and Fabian 1999
Multiple taxa	leafing index	10	Europe	spring	Chmielewski and Rötzer 2001, 2002
Multiple taxa	flowering	4	Massachusetts	spring & summer	Primack et al. 2004
Multiple taxa	various	1–4	Europe	spring & summer	Menzel et al. 2006

used in these analyses vary, but are typically the mean temperatures for one or more months preceding the event recorded. The several advances of 20–55 d reported above suggest that phenophases of some species may be much more sensitive to temperature changes than the typical 4–5 d, but these await more detailed analysis. Fewer studies report rates of change in autumn events in relation to temperature increases, but most reported delays are 3–5 d per degree Celsius (Kai et al. 1996, Matsumoto et al. 2003).

Changes in summer and autumn phenophases are less consistent in direction and magnitude than changes in spring phenophases (Walther et al. 2002), though the most typical response of autumn phenophases is a slight delay. In a large series of observations covering the late 1950s through the 1990s from the International Phenological Gardens in Europe, spring events advanced an average of 6 days, while fall events were delayed an average of 4–5 days (Menzel and Fabian 1999, Menzel 2000). Ahas and Aasa (2006) found that most phenophases exhibiting a delay in a sample of 753 series were for autumn events. From an examination of 17 phenophases in Europe during 1951–1998, Scheifinger et al. (2002) report changes of 0.2 to 0.6 d/y in early spring phenophases, 0.0 to 0.3 d/y in late spring phenophases and +0.2 to −0.2 d/y in autumn phenophases. The exhaustive compilation by Menzel et al. (2006) revealed advances in 78% of flowering and leafing phenophases but in only 48% of leaf coloring (autumn) phenophases. The difference in degree of change between spring and fall phenophases could reflect either less climatic change during summer or fall, or less sensitivity of the phenophases to the changes that are occurring. The former explanation seems to partly explain the results from Estonia, where fall temperatures have been changing less than those in spring (Ahas and Aasa 2006). In line with the second explanation are observations by Estrella and Menzel (2006) that leaf color changes in four deciduous trees in Germany are only weakly correlated with summer or fall temperatures.

2. Geographic variation exists in patterns and degree of phenological change. In Estonia, Ahas (1999) reported that flowering times of four species advanced twice as fast in coastal regions as in inland areas, and Ahas and Aasa (2006) noted a greater advancement of *Betula* leaf unfolding in the central part of the country than in the northwestern part. Advances of several spring phenophases during 1951–1998 were generally higher in western Europe than in central or eastern Europe, a difference attributed to changes in atmospheric circulation due to the North Atlantic Oscillation (Scheifinger et al. 2002). In fact, spring in easternmost Europe appears to have retreated by a week or two during this period. The timing of snow and ice melt on the Kola Peninsula in northernmost European Russia has become later, though the three spring phenophases examined showed no significant change (Kozlov and Berlina 2002). In the same region, leafing and leaf yellowing of *Betula pubescens* exhibited small and variable trends between 1964 and 2003 (Shutova et al. 2006). Phenological changes in the Balkans appear to differ from those in central and northern Europe, a difference suggested to reflect regional differences in chilling conditions during the dormant period resulting from differences in winter temperatures (Menzel 2000, Menzel and Fabian 1999). In North America, Schwartz and Reiter (2000) found somewhat greater advancement of leafing and flowering of *Syringa vulgaris* in the West than in the East, and Zhao and Schwartz (2003) found differences in phenological change of a multi-species index in different regions of the continent.

Altitudinal or latitudinal patterns have been sought in a few cases. Data from Switzerland suggest a greater advance in phenophases at higher elevations than those at lower elevations (Defila and Clot 2001). A slight trend towards more change at higher latitudes than low latitudes was found in meta-analysis by Root et al. (2003), but when data were reanalyzed by Parmesan (2007) no significant latitudinal pattern was seen. Parmesan (2007) did find a small effect in her own analysis of an overlapping data set, though latitude explained only 4% of overall variation in phenological change. Neither Matsumoto et al. (2003) nor Doi (2007) found correlations between latitude and advancement of

Table 3. Plant distributional changes attributed to or potentially related to climate change.

Location	Time Period	Taxa	Events and Results	Reference
Altitude				
New Zealand	1860s–1990s	tree line	raised by tens of meters	Wardle and Coleman 1992
Austrian and Swiss Alps	1910s–1990s	vascular plants	species richness increased on summits	Grabherr et al. 1994
Canadian Rockies	1600s–1990s	tree line	increased at only some sites	Luckman and Kavanagh 2000
Bulgaria	1955–1998	*Pinus peuce* treeline	increased 200 m	Meshinev et al. 2000
Sweden	1950s–1990s	tree line	raised by up to several hundred meters	Kullman 2001, 2002, 2003
Spain	1945–2001	several communities	beech loss at lower elevations, upward extension of oak forests	Peñuelas and Boada 2003
Spain	1957–1991	high elevation communities	alpine communities replaced by shrub communities typical of lower elevations	Sanz-Elorza et al. 2003
Switzerland	1900s	*Viscum album*	upper limits increased	Dobbertin et al. 2005
Italian Alps	1950–2003	grassland, shrub communities	upper limits increased	Cannone et al. 2007
Sweden	1990s–2000s	thermophilic tree species	upper limits increased	Kullman 2007
Latitude				
Northern Canada	1300s–1980s	*Picea mariana*	tree ring width did not change	Payette et al. 1989
Sub-Antarctic islands	1960s–1990s	*Colobanthus*, *Deschampsia*	increased range and abundance	Fowbert and Lewis Smith 1994, Lewis Smith 1994
Sub-Antarctic islands	1965–1990s	non-native species	most were spreading	Gremmen and Smith 1999
Spain	1990s	*Pinus sylvestris*	decline accompanying increased herbivory at southern edge of range	Hódar et al. 2003
Spain	1970s–2001	*Frangula alnus*	decline at southern edge of range	Hampe 2005
Italy	1970s–1990s	*Pinus sylvestris*	growth decline at southern edge of range	Piovesan et al. 2005
Switzerland	1900s	*Pinus sylvestris*	high mortality at southern edge of range	Bigler et al. 2006
Spain	1975–2003	*Fagus grandifolia*	decreased growth at lower elevations	Jump et al. 2006
Mediterranean France	1880s–2001	Eurosiberian flora	decline at southern edge of range	Lavergne et al. 2006
Sub-Antarctic islands	1992–2004	*Sphagnum falcatum*	decreased abundance	Whinam and Copson 2006

phenological stages of *Ginkgo biloba* and *Prunus mume*, respectively, in Japan, perhaps because these studies did not extend into polar regions. In general we expect the greatest phenological changes at high latitudes, where global circulation models predict warming will occur soonest and with greatest intensity (Kennedy 1995, Henry and Molau 1997, Robinson et al. 2003). Examination of this issue is complicated by the different time periods examined in different studies, the variation in responses among species at a given site and regional variation in climatic changes that are independent of any general latitudinal effect.

3. Phenological changes over the past few decades (usually starting in the 1970s or 1980s, depending on location) are much greater than those from the previous several decades (Sparks et al. 1997, Peñuelas et al. 2002). An examination of 17 phenophases at 6500 stations in central Europe revealed "almost no trend" prior to marked changes taking place after the late 1980s in most areas (Sheifinger et al. 2002). Observations of *Robinia pseudoacacia* in Hungary during three periods (1851–1930, 1952–1981, 1983–1994) revealed substantial changes between the second and third periods but little change prior to the second period (Walkovszky 1998). Examining a group of 34 relatively long time series in Germany, Schaber and Badeck (2005) found relatively little change before 1931, advancement until 1948, delay until 1984 followed by strong advancement through 1999. Flowering of *Prunus mume* trees in Japan showed little change up to 1989 but conspicuous advancement thereafter (Doi 2007).
4. Studies of multiple species show differences among species in extent of phenological change. Among 751 springtime phenological series recorded in Europe's International Phenological Gardens in Europe, 22% show significant advances and 5% show significant delays (Menzel 2000). Of 100 species examined from 1970–1999 in Washington, D.C., flowering advanced in 89 (significantly in 76, the greatest advance being 46 days) and retreated in 11, the greatest delay being 10 days (Abu-Asab et al. 2001). Among 385 species observed in central England, 16% showed a significant advance in flowering time and 3% showed a significant delay (Fitter and Fitter 2002). Of 60 regressions of phenophase timing on year in central Europe, 11 showed significant advances and 2 showed significant delays (Roetzer et al. 2000). In the comprehensive European study by Menzel et al. (2006), 31% of leafing and flowering stages showed significant advances and 3% showed significant delays during the period 1971–2000. One factor contributing to this variation is the different flowering or leafing seasons of different species. If, as noted above, greatest temperature changes have occurred in winter and early spring, one would expect the flowering time of early-flowering species to change the most. However other variables are also involved. While many spring phenological events can be predicted using heat sums (e.g., Beaubien and Freeland 2000), this is not true for all. Flowering of *Tussilago farfara* exhibited a correlation of only 0.30 with the best heat sum, while correlations of other species were 0.66–0.90 in a group of species studied in Finland (Heikinheimo and Lappalainen 1997). Furthermore, mid- and late-season events, such as flowering of summer and fall blooming species, may be strongly influenced by photoperiod or other factors. While delays of phenological events (especially spring events) during a period of warming might seem counterintuitive, and perhaps be considered chance results in a large sample, reasonable biological explanations can be advanced. The need to meet a chilling requirement may delay phenological events where warmer winter temperatures lengthen the period required to meet this requirement (Schwartz et al. 2006). Also, temperature increases at high latitudes may be accompanied by increased snowfall (Shutova et al. 2006). Given that timing of snow melt can have a major influence on timing of spring phenophases, increases in snowfall could negate effects of higher temperatures. At present, we simply do not know how much of the observed interspecific variation is real and how much reflects uncontrolled factors. This issue is only likely to be resolved by multiple studies of similar or overlapping groups of species or by detailed studies observational or experimental studies of factors controlling phenology in particular taxa.

Distribution. Small shifts in mean temperature translate into substantial shifts in isotherms in terms of either latitude or altitude. The mean global increase of 0.7°C in the past century translates to a shift of roughly 100 km in latitude and over 100 m in elevation at temperate latitudes. A middling estimate of 3°C warming over the next century would translate into shifts of over 300 km and 500 m, respectively (Hughes 2000). Temperature changes in some regions exceed the global averages, and in some cases plants respond to temperature variables other than the mean (e.g., minimum temperatures) which have often increased faster than mean temperatures (Easterling et al. 1997). However, distributional changes are likely to be much slower than the virtually instantaneous phenological changes. In several studies, for example, detrimental effects of extreme winters have been shown to persist for years or decades, even as conditions ameliorate (Kullman 1996, Askeyev et al. 2005). Peñuelas and Boada (2003) suggested that changes in plant distributions may be easier to detect than changes in animal distributions because the latter often have larger annual fluctuations. However, the pace of shifts in plant ranges is likely to be much slower than among animals because of the latter's mobility and, in some species, relatively short generation times. More poleward shifts have been documented in animals than in plants (Hickling et al. 2006, Parmesan 2006).

Temperature may exert effects on distribution through any of several biological processes, including reproduction, recruitment and mortality, and these processes may differ in their sensitivity to climatic factors. If recruitment is more sensitive than adult mortality to climate change, a population may persist for decades or centuries through the survival of established individuals even if no recruits join the population. Jump et al. (2006) argued that changes at the advancing edge of a species distribution will be faster than changes at the retreating edge because reproduction and recruitment are likely to be more sensitive to environmental changes than mortality of established individuals.

The most conspicuous evidence of climatically-induced distributional changes is to be sought at latitudinal or altitudinal range limits. Relevant data include changes in plant numbers, cover, reproductive output, recruitment, growth, or mortality. A thoughtful discussion of expected changes at the tree line was provided by Holtmeier (1994), and many of his arguments would also apply to other range limits. He emphasized that vegetation changes are likely to be complex and are more likely to respond to changes in temperature extremes rather than means. Numerous other environmental factors are likely to exert influences, and their effects can be difficult to separate from those of temperature. These include changes in precipitation, herbivory, fire regimes and patterns of human land use.

Elevational Studies. Several studies have examined changes at the altitudinal tree line. In 1994, Holtmeier stated that "no definite evidence" linked recent climate changes to improved tree growth or regeneration. At the same time, Petersen (1994) cited several studies showing increased conifer growth in mountainous western North America but concluded that information was insufficient to distinguish possible influences of temperature from effects of carbon dioxide, precipitation, atmospheric nitrogen fertilization, and natural stand dynamics. Since that time, however, several studies have documented advancing altitudinal tree lines in areas where the climate has warmed.

One of the earliest documented rises in an elevational tree line in recent times comes from the South Island of New Zealand, where mean temperatures have increased about 0.5°C since the 1860s. Here young, vigorously growing individuals of several tree species were recorded tens of meters above an older tree line (Wardle and Coleman 1992).

The *Pinus peuce* treeline has also been rising in the Central Balkan Mountains of Bulgaria (Meshinev et al. 2000). Analysis of age structure near the treeline revealed that the 1970 treeline was at about 1800 m but that progressively younger individuals could be found up to at least 2100 m. The authors suggested that this growth above the former treeline was related to rising minimum winter temperatures since 1970. They did not observe increases in elevational limits of two other species, *Fagus sylvatica* and *Picea abies*.

Several studies have investigated altitudinal limits of trees in the Scandes Mountains of Sweden. The upper limits of the common species (*Betula pubescens*, *Pinus sylvestris*, *Picea abies*) have risen, with increases of 75–

375 m reported in different studies (Kullman 2001, 2002, 2003). Previously unforested alpine areas in the southern Scandes have become "entirely covered with mixed birch/conifer stands." However, the general advance has been interrupted by periods of stasis or decline, with a retreat of 15 m for *Picea abies* between 1974 and 1994 (Kullman 1996) accompanying cooler temperatures in both winter and summer. Greater winter exposure as a result of decreasing snow cover also appears to have influenced the treeline and birch, particularly, has declined in some areas. Summer temperatures have been particularly important in the overall advance, with 73% of the variation in initiation of new stems explained by mean June–August temperatures (Kullman 2001). Kullman (2003) concluded that the extent and rate of recent change in the tree line is unprecedented in the past 3500 y.

In North America, increases in the altitudinal *Picea glauca* tree line since the 1800s were reported at some sites in Alaska (Lloyd and Fastie 2003). Complex patterns were reported from the Canadian Rocky Mountains, where mean annual temperature has increased 1.5°C over the past century. Winter temperatures have increased the most, and summer temperatures have actually declined by 0.5°C in the past few decades. At one of three sites, establishment of seedlings led to a rapid upwards migration of the tree line. At a second site, a few slow-growing seedlings have established above the previous tree line, and at a third site a retreating glacier has exposed potential colonization sites, but tree seedlings had not become established at the time of the study (Luckman and Kavanagh 2000).

Changes in alpine communities have also been demonstrated. In the Italian Alps, Cannone et al. (2007) found upward movement of alpine grasslands and montane shrub communities between 1950 and 2003, generally increasing cover (1.9% per decade) and somewhat inconsistent patterns in the highest elevation occurrence of early successional species. During this time interval regional temperature increased by at least 1°C, precipitation increased, though with considerable variation, and the duration and thickness of snow cover decreased. Also in the Alps, plant species numbers on most of a sample of 26 Austrian and Swiss summits were greater in the 1990s than 40–90 y previously (Grabherr et al. 1994). The authors explained this pattern as a result of upwards migration of plant species in response to the observed 0.7°C increase in mean annual temperature. The mean migration of nine of these alpine plants was 0.4 m/y.

Numerous changes have also been recorded at somewhat lower elevations. The upper elevational limit of mistletoe (*Viscum album*) in the Rhone Valley of Switzerland rose 200 m in the past century, during which time the mean winter temperature increased by 1.6°C. (Dobbertin et al. 2005). The host plant, *Pinus sylvestris*, has suffered high mortality in these alpine valleys (Bigler et al. 2006 and references therein) where the pines are near their southern range limit. However, it is not clear whether this is related to mistletoe infestation.

Vegetation shifts have also been observed in mountainous regions of Spain (Peñuelas and Boada 2003). In the Montseny Mountains, beech forests have moved 70 m upwards in the past 55 y (accompanying a temperature rise of over 1°C) and are being replaced by oak at lower altitudes, especially on south-facing slopes, where the health of remaining beech trees is poor. Oak is also moving upwards into *Calluna* heathlands at middle elevations. Land use changes, including a decrease in burning after the site became a national park in 1977, are a potentially confounding factor, though the authors believe that climatic changes were paramount. In central Spain, alpine grassland communities have been replaced by shrubby vegetation (especially *Juniperus communis* and *Cytisus oromediterraneus*) characteristic of lower elevations (Sanz-Elorza et al. 2003). These changes have occurred during a period of climatic warming and changes in the annual distribution of rainfall. Decreased frost damage and a longer growing season along with possible reductions in snow cover are implicated in the changes. Influences of changes in grazing patterns and other land use changes are not evident but cannot be ruled out.

Permanent transects at mid-elevations in the Scandes mountains reveal upwards spread of several relatively thermophilic species, including *Alnus glutinosa*, *Betula pendula*, *Quercus robur*, *Ulmus glabra*, and the alien *Acer platanoides* (Kullman 2008). Areas currently being invaded by more thermophilic trees have not supported these species for at least 8000 y.

An interesting question concerning altitudinal changes is whether the rate of change is limited by rising temperatures or by plant

dispersal abilities. Kullman (2002) suggested dispersal would not limit elevational expansion, citing work by Molau and Larsson (2000) that showed occasional dispersal of *Betula tortuosa* seeds to 300 m above the highest reproductive individuals. However, Peñuelas and Boada (2003) found an upwards shift of only 70 m in Spanish beech forests, compared to a predicted shift of 240–280 m based on observed temperature changes. Temperature increases in New Zealand correspond to a rise of about 100 m, though most tree species have advanced only 30–80 m. The one species that was closely tracking the temperature rise is dispersed by pigeons (Wardle and Coleman 1992). Grabherr et al. (1994) calculated that temperature changes in the Alps would correspond to movement at a rate of 0.8–1.0 m/y, in contrast to the 0.4 m that they measured for a group of alpine species. The emerging picture is that species with good dispersal (wind, birds) can probably keep pace with temperature changes, while species with more limited means of dispersal will lag behind.

Latitudinal Studies. Several studies have examined plant distribution or performance near the southern limit of plant distribution in the sub-Antarctic region. Smith (1994) reported dramatic increases in two native vascular plant species, *Colobanthus quitensis* and *Deschampsia antarctica*, between the 1960s and 1990s. Summer temperatures increased during this period, and plants responded not only by increasing density but by colonizing new areas (Fowbert and Lewis Smith 1994, Lewis Smith 1994). The temperature increases were thought likely to have increased both seed production and rates of seed germination. Gremmen and Smith (1999) examined range changes in several non-native species on two sub-Antarctic islands. Most species were spreading, most at 100 to 300 m/y. One possible explanation was that they were favored by temperature increases. Mean temperatures rose 1°C between 1970 and the end of their study and the growing season was thought to have lengthened by 15% over 20 y. However, they note that other explanations are possible, including increased foot traffic or simply a greater elapsed time since introduction. On Macquarie Island, another sub-Antarctic island, casual observations suggested spread of *Sphagnum falcatum* during the 1980s. However, more careful monitoring between 1992 and 2004 revealed decreases during a period of rising temperatures and declining precipitation, a pattern that is projected to continue with further global warming (Whinam and Copson 2006).

A detailed examination of rare species in the Mediterranean region of France found that the abundance of species having a primarily Mediterranean distribution had not changed greatly in the past 115 y, whereas species with primarily Eurosiberian distributions had declined dramatically. The Eurosiberian species were near their southern range limits, and their decline was attributed to regional warming (Lavergne et al. 2006).

Also in the Mediterranean region, Jump et al. (2006) report a decline in the radial growth of *Fagus sylvatica* near the southern end of the species range in Spain. Among individuals at lower elevations, the basal area increment declined 49% between 1975 and 2003. Beech trees growing at higher elevations were unaffected. These changes were coincident with a regional warming trend. Growth of beeches in central Italy also declined beginning in the 1970s, which investigators attributed to drier conditions resulting from a tendency of the North Atlantic Oscillation to remain in a positive phase (Piovesan and Schirone 2000, Piovesan et al. 2005).

Yet another Mediterranean study reported a decline of *Frangula alnus* near the southern edge of its range in Spain, an area where temperatures have increased and precipitation has decreased over the past century (Hampe 2005). A critical period of late season reproduction was especially sensitive to the observed climatic changes.

In addition to direct effects of climatic variables, climate change could also act through effects on herbivores. An example involves isolated, high elevation, southern populations of *Pinus sylvestris* in Spain. These have been declining as herbivory by the caterpillar *Thaumetopoea pityocampa* has increased, apparently in response to climate change (Hódar et al. 2003).

Studies near the treeline in the northern hemisphere have had mixed results. Northward shifts have been reported in northern Canada, involving a 12 km displacement of *Picea mariana* trees since the late 1800s (Lescop-Sinclair and Payette 1995) and in Sweden, where a northward expansion of

Picea abies has accompanied recession of permafrost (Kullman 2001). North of the Brooks Range in Alaska, the extent and density of *Picea* forests near the tree line has increased, and the height and diameter of shrubs increased at some but not all sites (Sturm et al. 2001). Several other studies show little or no response in recent decades (Payette et al. 1989, Lescop-Sinclair and Payette 1995, Briffa 1998, Barber et al. 2000) even where responses to early 20th century warming occurred. One possible explanation of this difference is that recent warming has often been accompanied by decreased precipitation, in contrast to some earlier periods of warming (Barber et al. 2000, Parmesan 2006). Another possibility is that the patterns of change (or lack thereof) are sensitive to the pre-existing ecosystem state, as suggested by Payette et al. (1989) to explain the lack of emergence of tree-sized *Picea mariana* in or northward of *Picea mariana* krummholz in northern Canada. The starting community during the present period of warming was low krummholz, contrasting with the high krummholz vegetation that preceded periods of favorable growth during the late Middle Ages.

Parmesan and Yohe (2003) provide one of the few comprehensive estimates of poleward advancement of northern species, with a mean figure of 6.1 km per decade for the past few decades. However, this estimate is based mostly on ranges of birds and butterflies and is not necessarily representative of plants, which are likely to have slower range extensions than more mobile animals.

Ecological and Evolutionary Implications. Changes in plant phenology and distribution have potential implications for both human affairs and various biological phenomena. Among the former are agricultural threats from weeds and patterns and timing of high concentrations of airborne allergens (Peñuelas and Filella 2001, Sparks and Menzel 2002, Van Vliet et al. 2002, Emberlin et al. 2007). Below I comment briefly on several ecological and evolutionary implications of changes in plant distributions and phenology.

PRODUCTIVITY. A reasonable hypothesis is that phenological changes associated with warming will increase ecosystem productivity. Growing seasons in several areas have lengthened by 1–3 weeks over the past century (Gremmen and Smith 1999, Menzel and Fabian 1999, Zhou et al. 2001, Schwartz and Chen 2002, Matsumoto et al. 2003, Kimball et al. 2006, Walther and Linderholm 2007). Areas with longer growing seasons have greater average productivity than those with shorter growing seasons unless moisture or another limiting factor intervenes (Leith 1975). Of course the actual result for a particular area or species will be influenced by several variables, especially changes in carbon dioxide levels, precipitation, decomposition, nitrogen fixation and herbivory, and the relative effects of temperature change on photosynthesis and respiration (Rustad et al. 2001). Using satellite data to examine productivity in the latitudes 45–70°N during 1981–1991, Myneni et al. (1997) reported an overall increase in terrestrial photosynthesis, which they attribute in part to an observed 12 d increase in the growing season. Kimball et al. (2006) argued that timing of spring thaw strongly influences productivity in Arctic ecosystems and that the substantial warming that has taken place may be sufficient to account for the apparent increases in productivity of Arctic ecosystems since the 1980s. Price and Waser (1998) make a similar argument for alpine ecosystems, noting that primary productivity is "strongly limited by the snow-free growing season" at high elevations in the temperate zone. In the shortgrass prairie of northeastern Colorado, however, Alward et al. (1999) found a complex pattern, with a decline in productivity of the dominant grass (the native C_4 species *Bouteloua gracilis*) but increases in productivity of a C_3 sedge and a group of C_3 forbs, including non-native species. These changes accompanied increases in the daily minimum temperature. An examination of 49 forest studies by Boisvenue and Running (2006) led them to the conclusion that climate change has had a generally positive effect on productivity except in forests where water is limiting. In short, increases in the growing season can be expected to increase ecosystem productivity, but only if other factors, especially precipitation, do not work against it. It is unlikely, however, that we can isolate the effects of phenology from the many other variables that can affect productivity.

SPECIES INTERACTIONS AND COMMUNITY PATTERNS. Because different species respond to climate change at different rates and to different degrees, the makeup of communities

and the nature of species interactions must inevitably change (Harrington et al. 1999, Hughes 2000, Peñuelas and Filella 2001, Fitter and Fitter 2002, Root et al. 2003, Parmesan 2007). Plant competitive relationships are likely to change, not only as a result of different phenological responses, but also as a result of different responses to variables such as precipitation and carbon dioxide levels. While such effects have been demonstrated in numerous experimental studies, I know of no examples yet reported from nature.

Relationships with pollinators, herbivores and pathogens may shift because some of these animals are likely to respond to different phenological cues than their associated plants. Such a mismatch could work to a plant's benefit or detriment depending on the nature of the relationship. Rising winter temperature may in some cases delay the leafing out of plants that have chilling requirements, though they could advance egg hatching and development of associated insects if these variables are more closely tied to heat sums (Harrington et al. 1999). Abu-Asab et al. (2001) noted the possibility that changes in flowering phenology may not be correlated with changes in pollinator phenology or (for forest understory species) with changes in canopy closure, affecting reproductive success of the flowering species. Wall et al (2003) showed that primary pollinators of *Clematis socialis* change according to the timing of flowering, which in turn reflects late winter temperatures. Kudo et al. (2004) showed that seed set in two bee-pollinated spring ephemerals declined in a warm year. They suggested that bumblebee emergence was tied to daily temperature maxima in the hibernating areas, producing a different phenology than in plants responding to heat sums and loss of snow cover. Several dominant New Zealand grasses exhibit mass flowering or mast seeding after hot summers, phenomena associated with decreased herbivory (McKone et al. 1998). The authors suggest that if climate change is associated with decreased amplitude of yearly temperature variation and hot summers occur with greater regularity, herbivore populations may increase, with detrimental effects on grass reproductive success. Recent increases in spring temperatures in The Netherlands are associated with poor synchronization between egg hatching of winter moths (*Operophtera brumata*) and bud burst of the oaks (*Quercus* spp.) on which they feed (Visser and Holleman 2001). Honeybee emergence advanced more than flowering seasons of spring-blooming plants in Spain (Gordo and Sanz 2005). In her meta-analysis, Parmesan (2007) found that phenophases of herbaceous plants did not advance as much as those of butterflies and birds. She and Peñuelas and Filella (2001) suggested that prediction of effects of global warming on community patterns will be difficult given the different responses of different taxa to climate change.

Evolution. Evolutionary responses by plants to changing climatic regimes are expected since environmental change invariably initiates directional selection, though present knowledge is insufficient to predict most changes. The main selection pressures would occur where a population's phenology is shifted relative to the timing of other events critically important to its fitness. Thus for a partner that benefits in an interaction (e.g., plant or pollinator in a pollination interaction or an herbivore in a plant/herbivore interaction) strong selection should favor resynchronization of the relevant phenophase. Conversely, desynchronization should be favored for a partner bearing costs as a result of a species interaction (e.g., either member of a competitive pair or the plant in a plant/herbivore interaction). The precise course of such evolutionary changes will of course be affected by the overall impact of the particular relationship on a species' fitness, the existence of other, opposing, selection factors, and genetic linkages among traits (Etterson and Shaw 2001). In few, if any, cases do we have a sufficient understanding of a population's ecology to predict with confidence the evolutionary consequences of phenological changes. Other evolutionary results are also possible. Fitter and Fitter (2002) suggested that increased hybridization among related species may occur in a warmed world because some related species will flower more synchronously than previously. While some have argued for "a substantive role of evolution in mitigating negative impacts of future climate change," Parmesan (2006) points out that the Pleistocene glaciation appeared to cause populations to shift distribution rather than "remaining stationary and evolving new forms." In experimental work with *Chamaecrista fasciculata*, Epperson and Shaw (2001) predicted a

slow rate of response to climatic change despite the presence of substantial heritability of most of the relevant traits because of correlations among traits that opposed the expected direction of selection. The capacity for genetic change before extinction will also be limited by the rapid rate of the predicted environmental changes. The populations at greatest risk may be marginal populations, which are often small and isolated, and, while their collective genetic diversity may be high, their individual genetic diversity is likely to be low. Their ability to respond evolutionarily to climate changes may therefore be low and their ability to adapt could be swamped by gene flow from central populations (Parmesan 2006).

DIVERSITY. Species extinctions are likely to result from climatic changes, and high elevation species in montane areas seem to be especially at risk (Sanz-Elorza et al. 2003, Miller-Rushing and Primack 2004). Temperature increases would, in effect, force species adapted to particular climatic zones to move up the mountains, but if warming is sufficient, suitable habitat will become unavailable on particular peaks or in particular mountain ranges, resulting in local extinction. Rull and Vegas-Vilarrúbia (2006) project that species losses among endemic vascular plants in the Guayana Highlands of northern South America would range from 10% to 33% with the 2–4°C temperature rise expected by 2100. Thuiller et al. (2005) also predicted high extinction rates in the European montane flora, with over 20% of a sample of European species predicted to lose at least 80% of appropriate habitat by 2080. However, the relatively coarse scale of their analysis necessarily overlooks the possibility of small refugia that could be important in species survival. A finer scale analysis by Guisan (2006) predicts lower but still considerable losses among the montane flora. Projections for the Austrian Alps are that a 2°C temperature change would cause severe loss and fragmentation of habitat for alpine species (Dirnböck et al. 2003).

Habitat fragmentation will pose problems across much of the landscape because of the barriers that it poses to dispersal. Distributional responses to climate change can be seen as a race between the dispersal abilities of plants and the rate of change in the physical environment. Anything that slows dispersal increases the threat to species persistence.

Hampe and Petit (2005) have argued that the loss of peripheral populations from the rear edge of a species' range during a range shift may have important genetic and evolutionary implications. They suggest that peripheral populations at a stable species range margin, may, in aggregate, contain a disproportionate share of a species' genetic diversity owing to genetic drift and local adaptation during a period of prolonged isolation. Thus population losses accompanying climate change could result in losses of genetic diversity that are disproportionately large relative to the proportion of a species' range that is lost.

ALIENS. Climate changes inevitably provide opportunities for establishment of non-native species (Dukes and Mooney 1999). If we assume that the species in an area are generally those best suited to the climatic conditions of the recent past, then any change in those conditions is likely to create an environment better suited for at least some species not currently there (Walther et al. 2002). Several species of ornamental woody plants in Switzerland seem to have spread more in recent warm conditions than in previous cooler conditions (Walther 2000), as would be expected of thermophilous garden plants (Walther et al. 2002). Ontario populations of the invasive *Lythrum salicaria* showed more rapid growth and earlier flowering, but no difference in biomass or inflorescence size, in atmospheric conditions associated with El Niño-Southern Oscillation (ENSO) than in more typical conditions (Dech and Nosko 2004). Although such conditions appear to have become more common in the past century, it is not clear whether this results from global climatic change (Nyenzi and Lafale 2006). Increased rainfall in the southwestern United States has been linked to increases in alien grasses (Burgess et al. 1991), though we cannot yet be sure whether anthropogenic climate change will cause precipitation increases in this area. Kullman (2002, 2008) recorded elevational increases of the alien *Acer platanoides* in the Swedish Scandes Mountains. Experiments by Lewis Smith (2001) suggest that warming will increase opportunities for establishment of aliens in the cold climate of the sub-Antarctic islands. Robinson et al. (2003) note that these islands receive a steady supply of exotic

spores, and a milder climate will allow more of these species to become established. Populations of some alien species are also likely to decrease as the environment in previously invaded areas or areas subject to invasions becomes less suitable (Beerling et al. 1995).

Plant movements in response to rapid climatic changes may force us to refine our notions of alien and native. A species entering areas adjacent to its current range as a result of normal patterns of reproduction, dispersal, and recruitment in a changed climate is clearly not in the same category as a species from another continent that escapes from cultivation. The former species may join a community that shares numerous features with its earlier one, and it may be interacting with many of the same pollinators, pathogens, herbivores, and competitors. This is unlikely for the latter species. It seems reasonable to retain the term alien or non-native for the latter species. An alternative label should be sought for species in the former group, perhaps "climate change migrants."

Conclusion. The majority of the studies summarized above are correlational in nature. Particular changes in patterns of phenology or distribution have been observed to accompany temporal changes in average temperature and sometimes other variables. A basic axiom of data interpretation is that correlation does not demonstrate causation, and it is possible that some of the reported patterns (particularly those involving distribution) are unrelated to global climate change.

For phenological studies, the sheer volume of studies provides convincing evidence of plant responses to recent climatic changes. This impression is confirmed by those meta-analyses that have included only studies reporting results for every species in a group of species (Parmesan and Yohe 2003, Parmesan 2006), thereby circumventing the problem of non-reporting of non-significant trends.

Distributional studies provide a less compelling picture than phenological studies, with altitudinal changes better documented than latitudinal changes. Distributional studies are fewer in number than phenological studies and include a higher percentage (though still a minority) that do not reveal clear changes. Differences between regional and global effects are more difficult to separate, and effects of changes in precipitation and land use may contribute to some of the observed plant changes. The difference between phenological and distributional studies is to be expected given that the former involve rapid physiological responses, while the latter usually involve population phenomena like recruitment, mortality and reproduction. If climatic projections over the next decades become reality, conspicuous distributional changes will emerge.

Interesting research questions are legion, because so many processes could be influenced by changes in phenology and distribution, because different regions experience different amounts and patterns of change, and because different species respond differently to climatic changes. No one would dispute that plant phenology can be a sensitive indicator of climatic change, allowing one to be used almost as a proxy for the other. A logical next step is to get some measure of repeatability or reliability in our assessments of species responses. Determining whether the interspecific variation in response observed in a multi-species study has predictive value requires examining overlapping suites of species in separate studies to see if the observed patterns are consistent across studies. Beyond that, study of the phenologies of interacting groups of species and exploring the potential genetic and evolutionary consequences of phenological changes are of particular interest.

Most work on distributional influences has occurred in a few areas: near alpine and Arctic treelines, in the sub-Antarctic region, and in mountainous regions north of the Mediterranean Sea. Much remains to be documented and learned from these regions, but a broader geographical coverage is desirable. The floras of most regions of the world include some species near their northern limits or southern limits, and almost any area with at least a few hundred meters of relief is also likely to contain altitudinal limits. Any such area whose floristics have been thoroughly documented in the past would present opportunities for examining distributional changes. As patterns emerge as to what taxa are or are not changing, studies designed to elucidate the causes of such patterns are in order.

The challenges for conservation are both conceptual and practical. The conceptual issues include how much effort should be devoted to preservation of particular species in conservation areas as the climate becomes increasingly unsuitable. Conversely, how

should managers respond to the arrival of species from nearby areas as the climate changes? Practical issues include how best to protect rare species in the face of climate change and how to minimize the spread of undesirable aliens favored by climate change. A critical initial step for conservation areas is to obtain thorough inventories of their current biota. A logical subsequent step is to identify species for which climate change might pose a risk and to establish monitoring programs to provide accurate information on their population status. A network of such programs, if well-designed, could provide information of value to the broader scientific community.

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