

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/308994259>

Climate change is advancing spring onset across the U.S. national park system

Article in *Ecosphere* · October 2016

DOI: 10.1002/ecs2.1465

CITATIONS

0

READS

53

8 authors, including:



Nicholas A. Fisichelli

Schoodic Institute at Acadia National Park

37 PUBLICATIONS 201 CITATIONS

[SEE PROFILE](#)



Toby Rollin Ault

Cornell University

50 PUBLICATIONS 925 CITATIONS

[SEE PROFILE](#)



Mark Schwartz

University of Wisconsin - Milwaukee

107 PUBLICATIONS 4,850 CITATIONS

[SEE PROFILE](#)



John E. Gross

National Park Service, Ft Collins, CO

62 PUBLICATIONS 2,861 CITATIONS

[SEE PROFILE](#)

Climate change is advancing spring onset across the U.S. national park system

WILLIAM B. MONAHAN,^{1,2,†} ALYSSA ROSEMARY,^{3,4} KATHARINE L. GERST,^{3,4} NICHOLAS A. FISICHELLI,^{5,6}
TOBY AULT,⁷ MARK D. SCHWARTZ,⁸ JOHN E. GROSS,⁵ AND JAKE F. WELTZIN⁹

¹*Inventory and Monitoring Division, National Park Service, Natural Resource Stewardship and Science, 1201 Oakridge Drive, Fort Collins, Colorado 80525 USA*

²*Forest Health Technology Enterprise Team, USDA Forest Service, 2150A Centre Avenue, Suite 331, Fort Collins, Colorado 80526 USA*

³*National Coordinating Office, USA National Phenology Network, 1311 E 4th Street, Tucson, Arizona 85721 USA*

⁴*School of Natural Resources and the Environment, University of Arizona, 1311 E 4th Street, Tucson, Arizona 85721 USA*

⁵*Climate Change Response Program, National Park Service, Natural Resource Stewardship and Science, 1201 Oakridge Drive, Fort Collins, Colorado 80525 USA*

⁶*Forest Ecology Program, Schoodic Institute at Acadia National Park, P. O. Box 277, Winter Harbor, Maine 04693 USA*

⁷*Department of Earth and Atmospheric Sciences, Cornell University, 1113 Bradfield, Ithaca, New York 14853 USA*

⁸*Department of Geography, University of Wisconsin–Milwaukee, P. O. Box 413, Milwaukee, Wisconsin 53201 USA*

⁹*U.S. Geological Survey, Tucson, Arizona 85721 USA*

Citation: Monahan, W. B., A. Rosemary, K. L. Gerst, N. A. Fisichelli, T. Ault, M. D. Schwartz, J. E. Gross, and J. F. Weltzin. 2016. Climate change is advancing spring onset across the U.S. national park system. *Ecosphere* 7(10):e01465. 10.1002/ecs2.1465

Abstract. Many U.S. national parks are already at the extreme warm end of their historical temperature distributions. With rapidly warming conditions, park resource management will be enhanced by information on seasonality of climate that supports adjustments in the timing of activities such as treating invasive species, operating visitor facilities, and scheduling climate-related events (e.g., flower festivals and fall leaf-viewing). Seasonal changes in vegetation, such as pollen, seed, and fruit production, are important drivers of ecological processes in parks, and phenology has thus been identified as a key indicator for park monitoring. Phenology is also one of the most proximate biological responses to climate change. Here, we use estimates of start of spring based on climatically modeled dates of first leaf and first bloom derived from indicator plant species to evaluate the recent timing of spring onset (past 10–30 yr) in each U.S. natural resource park relative to its historical range of variability across the past 112 yr (1901–2012). Of the 276 high latitude to subtropical parks examined, spring is advancing in approximately three-quarters of parks (76%), and 53% of parks are experiencing “extreme” early springs that exceed 95% of historical conditions. Our results demonstrate how changes in climate seasonality are important for understanding ecological responses to climate change, and further how spatial variability in effects of climate change necessitates different approaches to management. We discuss how our results inform climate change adaptation challenges and opportunities facing parks, with implications for other protected areas, by exploring consequences for resource management and planning.

Key words: climate change; landscape context; monitoring; national parks; phenology; protected areas; Special Feature: Science for Our National Parks' Second Century; spring index; United States.

Received 29 July 2016; **accepted** 1 August 2016. Corresponding Editor: D. P. C. Peters.

Copyright: © 2016 Monahan et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** wmonahan@fs.fed.us

INTRODUCTION

U.S. national parks—from Alaska to the South Pacific and across the conterminous states and the Caribbean—are already experiencing climate change (Monahan and Fisichelli 2014). Changes in climate are evident across parks of all designations, including National Parks containing large wilderness areas receiving the highest level of protection, National Preserves allowing resource extraction, and National Lakeshores and National Battlefields providing protection for sites of recreational and historical significance, respectively. Despite such pervasive patterns, the complexities of climatic changes underway require the U.S. National Park Service (NPS) to steward its areas and resources for “continuous change that is not yet fully understood” (National Park System Advisory Board 2012). As the NPS celebrates its centennial in 2016, the next century of stewardship and science will require us to understand how climate and other forms of broadscale environmental change are impacting park resources and values (Hansen et al. 2014, 2016, National Park Service 2015). Here, we evaluate the effects of climate change on spatial and temporal trends in timing of spring onset (i.e., start of spring) in national parks, as defined by the first leaf and bloom dates of indicator plant species.

Phenology, the study of seasonal life-history stages of plants and animals (e.g., leafing and flowering in plants, migration and reproduction in animals) and their interactions with environmental drivers, is a valuable and traceable biological indicator of the ecological consequences of climate change (Menzel et al. 2006, IPCC 2014, Melillo et al. 2014). Numerous studies have found a shift in recent years toward an earlier spring and a longer growing season (Parmesan and Yohe 2003, Schwartz et al. 2006, Inouye 2008). However, divergence exists in both the direction and the magnitude of phenological responses through time among species within communities (Davis et al. 2010, Cleland et al. 2012, Cook et al. 2012, Wolkovich et al. 2012, Mazer et al. 2015). For example, in tallgrass prairie of the United States, the direction of phenological change depends on whether species flower before or after peak summer heat (Sherry et al. 2007). Such changes in temperature are likely the result of both climate forcing from human activity as well as

from long-term fluctuations generated internally by the climate system itself (Ault et al. 2015a). Managers of protected areas require an understanding of phenological patterns and trends to gain more insight into the likely consequences of climate change as it unfolds over the coming century (Miller-Rushing et al. 2011).

The “Spring Indices” are climate-based empirical models of phenological events—developed from a 60-yr data set of in situ lilac and honeysuckle phenology—that predict leaf and bloom dates for a suite of species and provide insight into historical patterns of spring warming (Schwartz 1997, Rosemartin et al. 2015). The models used day of year, chilling hours, heat accumulation, and number of high-energy synoptic events (i.e., large-scale warm spells) to develop indices of first leaf (FLI) and first bloom (FBI) dates for a cloned lilac cultivar (*Syringa x chinensis* “Red Rothomagensis”) and two cloned honeysuckle species (*Lonicera tatarica* “Arnold Red” and *L. korolkowii* “Zabeli”) (Schwartz 1997, Schwartz et al. 2006). Recent work has extended these indices across the continental United States, from high-latitude regions to subtropical environments, by removing the chilling requirement and leveraging gridded climate products (Schwartz et al. 2013, Ault et al. 2015a).

Importantly, the spring indices are based purely on temperature thresholds for mesophytic shrubs, but high temperatures can in some cases delay phenology (Sherry et al. 2007). In addition, water availability may be a more important driver of phenology in dryland parks (Bowers and Dimmitt 1994). Despite these limitations, the spring indices are highly correlated with phenological events in a variety of native plant species and crops (Schwartz et al. 2013, Allstadt et al. 2015), as well as with the spring greening (i.e., leaf development at landscape scales) of ecosystems (Schwartz 1990, Schwartz et al. 2006). Furthermore, the lilac and honeysuckle species used to derive the spring indices are found in over 30% of parks (National Park Service 2016). The spring indices have also shed light on long-term trends in climate, as well as decadal variability resulting from climate modes (Schwartz et al. 2006, Ault et al. 2015a). As such, FLI and FBI effectively bracket a spectrum of the timing of spring onset for a wide range of plant species important to parks, ranging from forested

wilderness areas (e.g., Rocky Mountain National Park in Colorado) to working landscapes (e.g., Tallgrass Prairie National Preserve in Kansas) to culturally significant landscapes and gardens (e.g., Saint-Gaudens National Historic Site in New Hampshire).

Many parks are already experiencing changes in key climatic drivers of phenology, as determined by comparing their recent climates measured over the past few decades to those measured over the course of more than a century (Monahan and Fisichelli 2014). The historical range of variability (HRV) from 1901 to 2012, our long-term reference, is important to understand the degree to which management can respond to phenological change, and to help establish plausible “desired future conditions” that can serve as targets for strategically planning management actions (Morgan et al. 1994, Keane et al. 2009). Here, using an analytical framework that compares recent phenological conditions to their HRV, we assess the timing of spring onset in 276 natural resource national parks over the past 112 yr (1901–2012). We consider parks within the context of their surrounding landscapes (park + surrounding 30 km) and evaluate the two spring indices (FLI, FBI) over multiple climatic- and management-relevant time periods. Although our spring indices are spatially coarse, they are broad in spatial extent and cover most parks, thus offering a consistent examination of potential climate change impacts that may inform adaptation planning at individual parks as well as regionally and nationally. Our analyses address three primary questions: (1) When has spring been starting in recent years? (2) How has this recent timing changed with respect to the 1901–2012 HRV? and (3) which parks and regions are most impacted by these changes? We conclude by discussing how the spring indices and a better understanding of phenological changes can help U.S. national parks and other protected areas prepare for and adapt to climate change.

METHODS

Study sites

Of the 413 park units currently administered by the NPS, about 300 are considered “natural resource parks” because natural resources are explicitly recognized in their enabling legislation.

Our analyses were performed for all natural resource parks in the conterminous United States and Alaska ($n = 276$), including a 30-km buffer around each park's boundary (National Park Service 2011). For each park, we buffered the vector polygon representing the administrative boundary and dissolved areas by park name (e.g., Saguaro National Park in Arizona is separated into two districts; the overlapping buffers from the two districts were dissolved to form a single contiguous polygon we used to represent the park in a landscape context). We refer to these areas of analysis as “parks.” The 30-km buffer was selected because of the relatively coarse spatial resolution of the gridded phenology data, as well as to approximate the protected area-centered ecosystems (PACES) of parks (Hansen et al. 2011); park PACES and 30-km buffers overlap, on average, by 60%. Long, linear parks, such as trails, parkways, and rivers (e.g., Appalachian National Scenic Trail), are challenging to analyze and visualize. Rather than attempting to separate them into arbitrary sections, we include raw data and results for all parks (see Data S1), so that readers may compare to other parks that fall on or near the same latitudinal and longitudinal transects.

Spring indices

We analyzed “Spring Indices” (SI- x) as described in Ault et al. (2015b), gridded at 1 degree (latitude and longitude) spatial resolution for the northern hemisphere using the “Berkeley Earth” daily minimum and maximum surface temperature data product (Ault et al. 2015a). The “ x ” in SI- x refers to an “extended” version of the model, whereby the minimum cold exposure (i.e., accumulated chilling hours) that certain plant species need to initiate spring growth was removed, thus enabling estimations to be made not just across temperate and high-latitude environments, but subtropical environments as well (Schwartz et al. 2013). The two primary model outputs computed by SI- x are the “first leaf index” (FLI), the average date when first leaves emerge from buds on the indicator species, and the “first bloom index” (FBI), the average date when blossoms first appear; “average” dates are calculated across the three indicator plant species. FLI is estimated by accumulated growing degree-days above 0.6°C, and “high-energy synoptic weather events” (warm spells measured as the number of times

three consecutive days' heat accumulation exceeds a threshold: 637 growing degree hours for FLI and 2001 growing degree hours for FBI), beginning 1 January each year. FBI uses FLI as the start date and includes additional accumulated growing degree-days. Additional details of the model are provided in Ault et al. (2015b).

Statistical analysis

For each spring index (FLI and FBI), over the entire time series (1901–2012), we used three moving windows (10, 20, and 30 yr) to calculate a series of running means. Hereafter we refer to these as “moving window means”; we use these statistical distributions to estimate HRV. For example, for the 10-yr moving window, we calculated the mean for 103 windows (1901–1910, 1902–1911, ..., 2003–2012) to create the HRV distribution. We selected these three windows because they encompass both near- and long-term management and planning considerations, as well as important climatic periods and cycles (Monahan and Fisichelli 2014). Strategic planning in the NPS tends to focus on a 10- to 20-yr planning horizon (National Park Service 2004), whereas traditional climate summaries and normals span periods of 30 yr (MetOffice 2016). Furthermore, major climate cycles such as the Pacific Decadal Oscillation and North Atlantic Oscillation tend to operate roughly on decadal to multidecadal scales (Stenseth et al. 2003).

For each index and moving window size (i.e., length of window time series), we calculated the area-weighted mean for each park, based on the spatial intersect of park areas of analysis with the SI-x grid. For example, if the park area of analysis spanned two SI-x grid cells, intersecting 3% of one cell with a value of day 100 and 97% of the other cell with a value of day 102, the area-weighted mean would be day 101.5, in contrast to the arithmetic nonweighted mean of day 101. Most parks intersected only a few SI-x grid cells (mean = 4.1 cells, median = 4 cells, range = 1–43 cells), but the use of the area-weighted mean was desirable because it allowed us to most accurately relate the high-resolution park vector polygons to the coarse-resolution SI-x gridded data.

Using the area-weighted means, we first estimated the recent timing and variability of spring onset. We computed both the mean and the standard deviation (SD) in annual FLI and FBI

over each most recent moving window, and then averaged each across moving windows (i.e., we averaged the mean and SD across 2003–2012, 1993–2012, and 1983–2012). This averaging was performed to summarize and present results of overall patterns; detailed results for all windows are also provided (see Data S1). We used Pearson product-moment correlations to assess correlations between the mean and SD of FLI and FBI with latitude, elevation, and Euclidean distance from park centroids to the nearest coast. FLI and FBI should be correlated with elevation and latitude; we report the correlations purely for the purposes of confirming and describing spatial patterns.

Second, we estimated recent change in the timing of spring onset. We computed the percentile of the mean SI-x value for each most recent window (2003–2012, 1993–2012, 1983–2012) from the corresponding distribution of moving window values for each park (i.e., its HRV). In other words, we quantified recent conditions as the percentile of the most recent moving window values relative to the entire distribution of moving window values for each spring index and window size (e.g., a 90th percentile for the most recent 10-yr moving window of FLI signifies that the value of this spring index during this time period was greater [i.e., later] than 90% of all FLI 10-yr moving window values). Hereafter we refer to these estimates as “recent percentiles.”

We then averaged the recent percentiles of the most recent 10-, 20-, and 30-yr moving windows (“recent mean percentiles”) and computed the maximum difference in percentile (max Δ) among windows; this resulted in—for each park and index—both an overall measure of recent change in the timing of spring onset with respect to HRV and an estimate of how sensitive that measure was to trends in the past 30 yr by comparing the different moving window sizes (see Data S1 for results of all windows). Following Monahan and Fisichelli (2014), we refer to recent mean percentiles that are <5% as “extreme” early or advancing, those that are >95% as “extreme” late or delaying, and all other intervening percentiles as either early (5–25%), average (25–75%), or late (75–95%). Similarly, we categorize results for max Δ as low sensitivity to moving window size (<5%), moderate or medium sensitivity (5–25%), and high sensitivity (>25%). Raw data (SI-x

rasters of moving window means) and computer code written in R (Hijmans and van Etten 2015, R Core Team 2015) for computing recent percentiles on HRV and max Δ values are also provided to facilitate additional analyses using different thresholds (see Data S1).

An example of these methods is shown for Tallgrass Prairie National Preserve (Fig. 1). The percentiles associated with the most recent FLI windows (computed over 10, 20, and 30 yr) are highly variable (Fig. 1A, B), ranging from 4% (30 yr) to 34% (20 yr) (see location of red asterisks in boxplot distributions; Fig. 1B). The overall mean across the three moving windows is 22%, indicating that the park has experienced a slight advance in the timing of spring onset according to FLI. The max Δ for FLI is 30%, revealing a high degree of sensitivity to moving window size. Meanwhile, the percentiles associated with the most recent mean FBI windows are all <5% (mean = 2%), showing that the recent timing of spring onset based on FBI is at the extreme early end of the entire distribution of moving windows (Fig. 1C, D). The max Δ for FBI is relatively small (3%), confirming that recent conditions have been very advanced across all three window sizes.

Lastly, given that FLI and FBI are used here as a proxy to bracket the timing of spring onset for a wide variety of plant species and ecosystems (Schwartz 1990, Schwartz et al. 2006, 2013, Allstadt et al. 2015), we applied a threshold-based classification of recent mean percentiles to assist with interpreting ecological consequences for parks. In this analysis, we used our thresholds of <5% and >95% to tally for each park whether one or both spring indices were extreme early (<5%) or extreme late (>95%). This resulted in a total of nine possible ecological response categories (Table 1). We identified parks as experiencing significant climate change impacts if one or both spring indices were extreme (e.g., as for the Tallgrass Prairie National Preserve example in the prior paragraph, where FBI was <5%). Parks experiencing significant trends in FLI or FBI were further characterized by their rates of change in the timing of spring onset. Rates of change were estimated by first calculating average FLI and FBI over each of the three most recent moving windows (10, 20, and 30 yr), and then subtracting the corresponding average of the moving window means for the 1901–2002, 1901–1992, and

1901–1982 periods. Using the midpoints of each time period, where “historical” and “recent” midpoints were separated by 56 yr, we calculated the rate of change in days per year, and multiplied by 10 so that units were in days per decade and comparable to Ault et al. (2015a). We used a Pearson product-moment correlation to assess the degree of correlation between the rates of change in FLI and FBI, averaged across moving windows.

RESULTS

The recent timing of spring onset, averaged over the past 10, 20, and 30 yr, is positively associated with latitude (FLI and FBI: $r = 0.84$, $P < 0.001$), elevation (FLI: $r = 0.48$, $P < 0.001$; FBI: $r = 0.51$, $P < 0.001$), and proximity to the coast (FLI and FBI: $r = 0.41$, $P < 0.001$). Across parks in the conterminous United States ($n = 260$), the recent mean FLI is day of year (DOY) 70 ($\pm 1\text{SD} = 29$ d; range = DOY 13–132), whereas the recent mean FBI is DOY 103 (SD = 32 d; range = DOY 26–169) (Fig. 2A, B). FLI and FBI in Alaska ($n = 16$ parks) are later relative to the conterminous United States by about 70 d. In Alaska, the recent average FLI for parks is DOY 140 (SD = 11.4 d; range = DOY 106–156), while the recent average FBI is DOY 171 (SD = 8.1 d; range = DOY 154–186).

Recent variability in the timing of spring onset within parks, as measured by the SD in annual FLI and FBI over the past 10, 20, and 30 yr, is similar in both the conterminous United States and Alaska (mean = 6–8 d). However, it varies geographically among parks in important ways (Fig. 2A, B). High recent interannual variability (SD > 10 d) in both FLI and FBI occurs in the northwestern region of the conterminous United States. In contrast, low variability (SD < 5 d) in both indices occurs in parks in the southern United States, coastal California, and northern Alaska.

Recent departures from HRV indicate that many parks are tending toward an earlier spring (Fig. 3). Recent mean percentiles of departure from HRV for both spring indices in the conterminous United States are on average 18%, while in Alaska they are 7% (i.e., earlier than 82% and 93% of the historical range of conditions, respectively). In the conterminous United States and

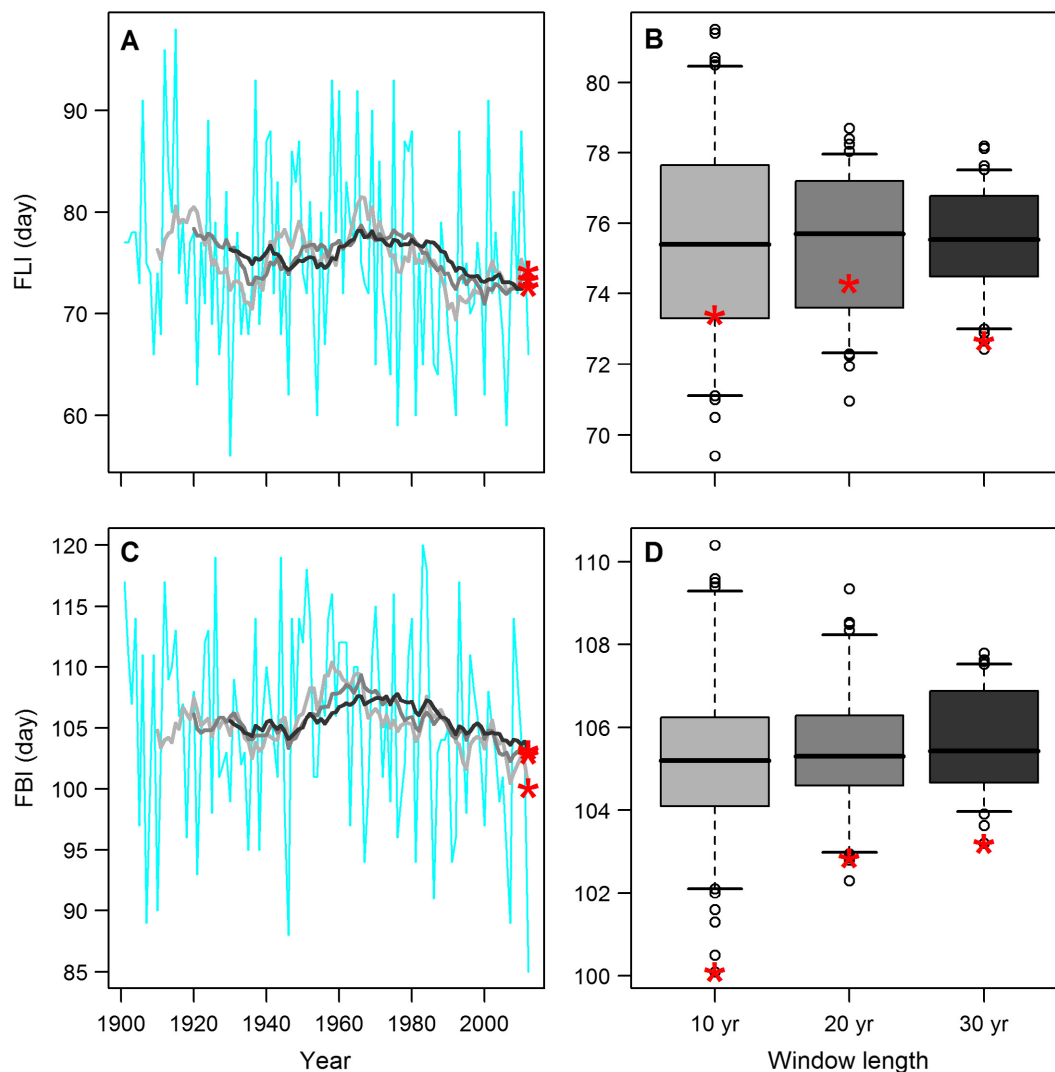


Fig. 1. Example moving window time series used to estimate historical range of variability (HRV) and recent percentiles shown for the first leaf (FLI: A, B) and first bloom (FBI: C, D) indices, Tallgrass Prairie National Preserve (with 30-km buffer), Kansas. Three moving windows—10 yr (light gray), 20 yr (medium gray), and 30 yr (dark gray)—are calculated from the annual time series (blue, A and C). Values associated with each index for the most recent windows (2003–2012 [10 yr], 1993–2012 [20 yr], 1983–2012 [30 yr]) are indicated by the red asterisks. Boxes in B and D are the 25th–75th percentiles (median or 50th percentile = thick horizontal line), dashed lines the 5th to 25th and 75th–95th percentiles, and dots the outliers (<5th percentile or >95th percentile). Recent percentiles are calculated for the red asterisks, which are determined by rank-sorting the statistical distribution of FLI or FBI values within each moving window class (10, 20, and 30 yr) and then calculating the percentage of individual windows in the time series that fall below the FLI or FBI value associated with the most recent window.

Alaska, 82 parks show recent extreme early onset (<5th percentile) for FLI, with most of these parks (73%) having very low sensitivity to moving window size (max Δ <5%). Similarly, for FBI in the conterminous United States and Alaska, 113

parks have extreme early onset and most of these parks (84%) have maximum delta values that are less than 5%. These parks are thus all experiencing extreme early springs, regardless of moving window size. By broadening the definition

Table 1. Number of parks (out of 276) that exhibited recent extreme early (<5th percentile) or extreme late (>95th percentile) first leaf index (FLI), first bloom index (FBI), both, or neither.

Category	Number of parks
Only FLI extreme early	32
Both FLI and FBI extreme early	50
Only FBI extreme early	63
FLI extreme early, FBI extreme late	0
Only FBI extreme late	0
Both FLI and FBI extreme late	0
Only FLI extreme late	0
FLI extreme late, FBI extreme early	0
Neither FLI nor FBI extreme ("not extreme")	131

of early spring onset to the 25th percentile, an additional 128 parks (FLI) and 98 parks (FBI) are experiencing earlier springs. Thus, when we consider either index and percentiles <25%, about three-quarters of parks (76%) are experiencing earlier springs relative to the range of historical conditions going back to 1901. In contrast, only one park (FLI) and 11 parks (FBI) are experiencing late springs (i.e., are in the 75th–95th percentile). The remaining 65 parks (FLI) and 54 parks (FBI) have not changed (i.e., are in the 25th–75th percentile). These parks that have not changed are generally also exhibiting the greatest sensitivity to moving window size (large max Δ ; Fig. 3), meaning that certain moving windows exhibit recent percentiles that are considerably greater or less than 50%.

Of the nine possible ecological response categories (Table 1), 145 parks (53%) are presently experiencing an extreme early spring (Fig. 4); in other words, spring is occurring in the earliest 5% of 1901–2012 observations, in terms of first leaf, first bloom, or both. No parks are experiencing extreme delays in spring onset (Table 1). The remaining 131 parks (47%) are not experiencing extreme change in either FLI or FBI ("not extreme"; Table 1). Importantly, many of these "not extreme" parks also show an advance in the timing of spring onset (Fig. 3; in the 5th–25th percentile). Of the parks that are experiencing extreme early springs under one or both indices, those with extreme early FBI (orange in Fig. 4) occur in the southern and northeastern United States, while those with extreme early FLI (red in Fig. 4) occur predominantly in the southwestern

and northern United States. Parks exhibiting both extreme early FLI and FBI (brown in Fig. 4) are generally situated at the boundaries of regions with parks that have either extreme early FLI or FBI, as well as in coastal California and Alaska.

The ecological response categories are also characterized by considerable rates of change in the timing of spring onset (Fig. 5). On average, extreme early spring parks based on FLI are advancing 0.86 d/decade, which is 79% faster than parks in the "not extreme" category. Similarly, extreme early spring parks according to FBI are advancing 0.80 d/decade (56% faster than parks in the "not extreme" category). The Pearson correlation (r) between estimates of recent change in FLI and FBI is 0.58 ($P < 0.001$). Importantly, a number of the "not extreme" parks are still experiencing earlier springs, some at rates that on average exceed 1 d/decade (Fig. 5). However, these parks also tend to exhibit greater interannual variation in the timing of spring onset, where SDs are 9 d, which is about 2 d greater than the extreme early parks.

DISCUSSION

An overwhelming majority of parks (81%) are already at the extreme warm end of their 1901–2012 historical temperature distributions (Monahan and Fisichelli 2014). Here, we demonstrate an important ecological consequence of ongoing climate change: The timing of spring onset is advancing in about three-quarters of parks (76%), and longer term projections suggest that all regions containing parks will experience advances in the timing of spring onset by mid-century (Allstadt et al. 2015). Furthermore, in 53% of parks, average spring commencement is already earlier than 95% of the historical range of spring onset dates since 1901. Thus, managers who have worked in these parks for the past one to three decades are already working under anomalous conditions.

While these indices of spring onset were developed for lilac and honeysuckle, other plant species are expected to respond similarly to the same temperature cues, with indirect effects for animals reliant on maintaining phenological synchrony with plants (e.g., Wood and Pidgeon 2015). An advancing spring has the potential to impact the timing of many park operations, events, and

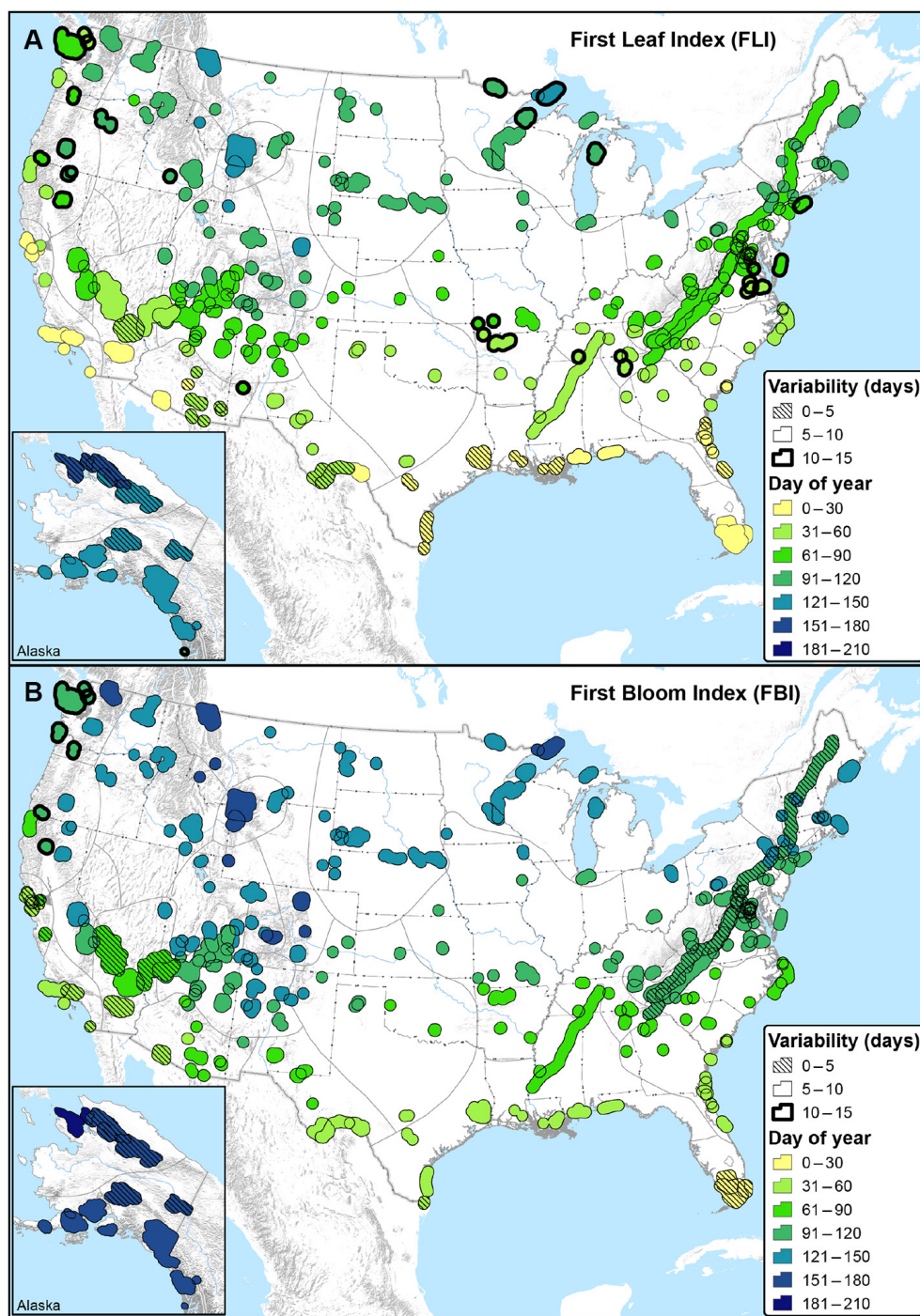


Fig. 2. The recent timing of spring onset in national parks over the past 10 to 30 yr. (A) First leaf index (FLI). (B) First bloom index (FBI). Recent values, measured in day of the year, are calculated as the mean FLI and FBI of the most recent 10 (2003–2012)-, 20 (1993–2012)-, and 30 (1983–2012)-yr moving windows. Similarly, variability is the SD in FLI and FBI, averaged over the same time periods. In both panels, as well as in Figs. 3 and 4 (below), solid gray outlines denote NPS Inventory and Monitoring Network boundaries, which closely align with ecoregions.

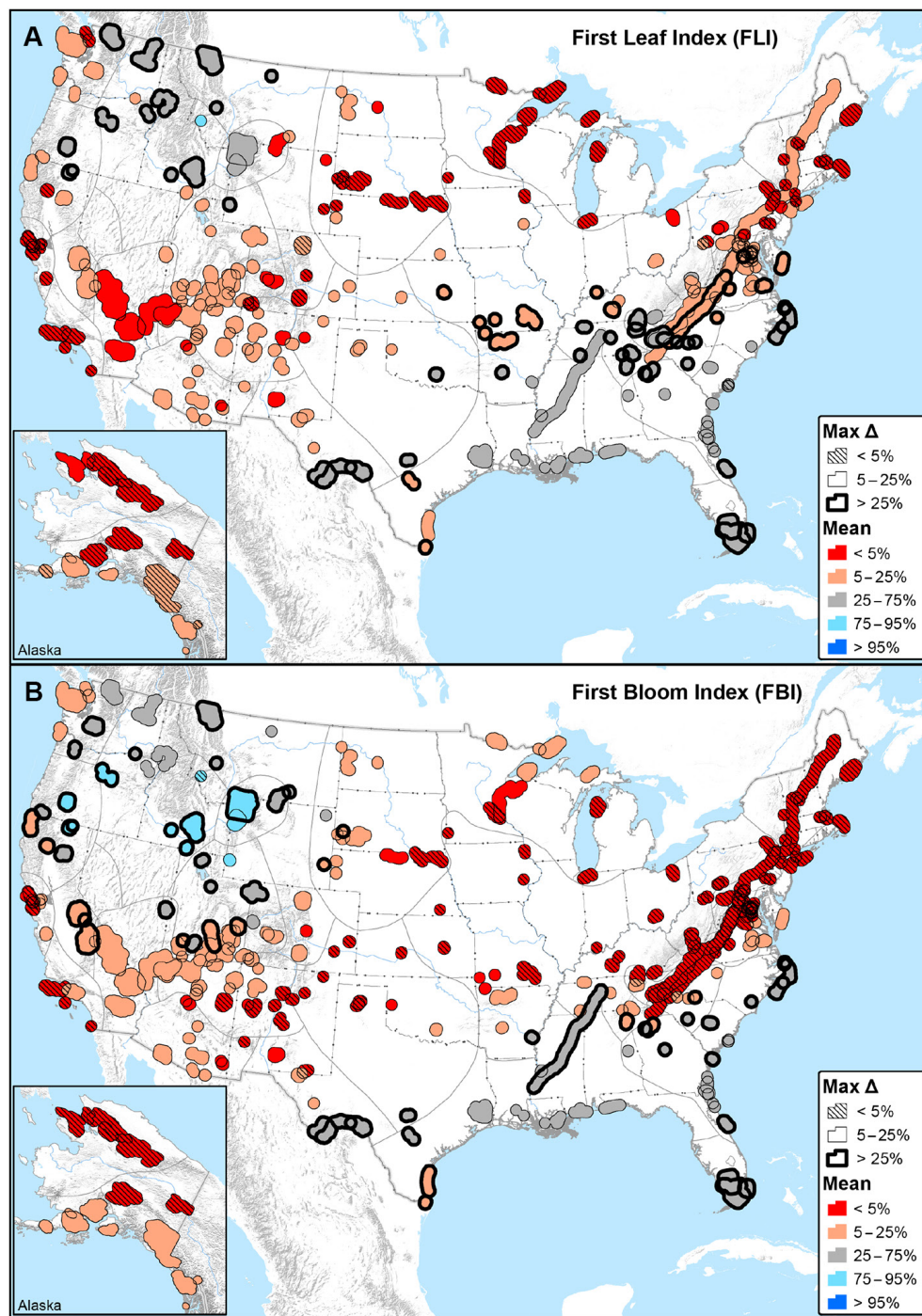


Fig. 3. Recent changes in the timing of spring onset relative to the 1901–2012 historical range of variability (HRV). (A) First leaf index (FLI). (B) First bloom index (FBI). Mean values provide an overall measure of recent (past 10-, 20-, and 30-yr windows) change in the indices with respect to 1901–2012 HRV. Max Δ is the largest difference in percentiles among the most recent 10-, 20-, and 30-yr windows and thus measures sensitivity to moving window size (smaller values are less sensitive).

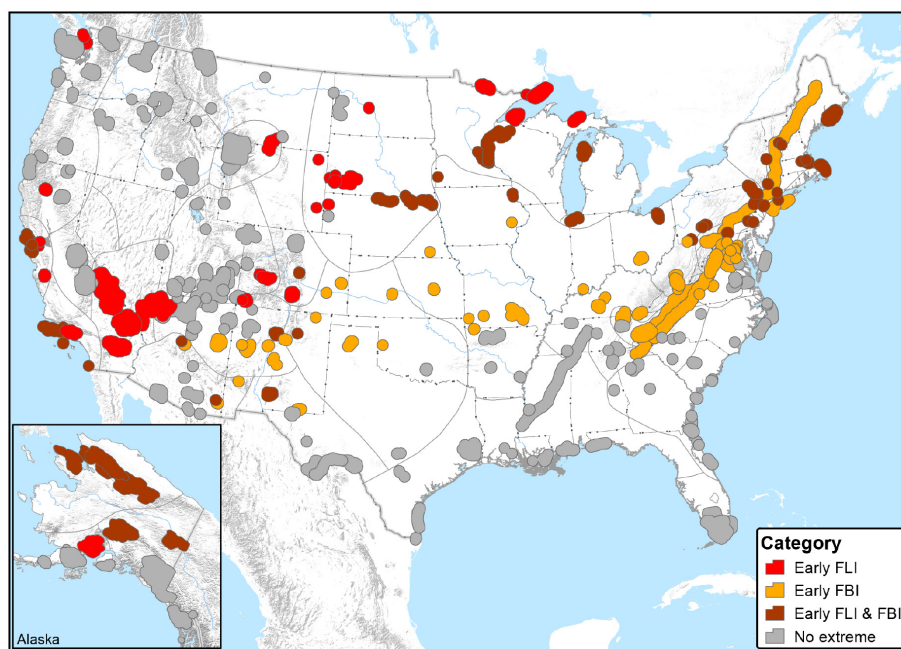


Fig. 4. Categories of ecological response to changes in the first leaf (FLI) and first bloom (FBI) indices of national parks, based on recent mean percentiles. Parks are categorized as “early” under one or both indices if the recent timing of spring onset is occurring earlier than 95% of the range of historical conditions going back to the year 1901. See Table 1 for all possible categories, as well as the total number of parks in each category.

visitor uses, including road openings, flower festivals, and backcountry recreation. Importantly, our findings emphasize how interpretation of some ecological responses to climate change requires understanding seasonal, not just annual, changes in climate, and further that spatial variability in climate and phenological changes will require different management tactics. Below, we explore potential ecological and management implications, articulate connections between spring timing and park monitoring, and identify avenues for future research and synthesis.

Ecological implications

Despite the earlier springs occurring in most parks, two regions of the United States are notable because the timing of spring onset has remained roughly constant or experienced delays. The absence of a change in spring timing in the southeastern United States is consistent with the “warming hole” identified in other studies (Meehl et al. 2012), whereas in the northern U.S. Rocky Mountains the delayed timing for FLI and FBI may have been caused by influences of

the Pacific Decadal Oscillation (PDO) (McCabe et al. 2013). The most recent PDO was in a negative phase through 2012, which tends to result in later springs (Ault et al. 2015a). Nevertheless, projections for mid-century suggest all regions containing parks will experience advances in the timing of spring onset (Allstadt et al. 2015). If this is true, and assuming patterns of interannual to decadal variability persist, the number of parks experiencing extremely early springs will increase in the coming years. These trends emphasize the need for parks to prepare for important ecological changes.

Species-specific phenological models will ultimately be required to understand the ecological implications for particular parks, particularly those with plant communities that respond strongly to variability in climate drivers, including temperature and precipitation. While phenological plasticity (or adaptive capacity) may enable certain species to persist under climate change (Anderson et al. 2012, Cleland et al. 2012), the potential for phenological mismatches among interacting species is recognized as a

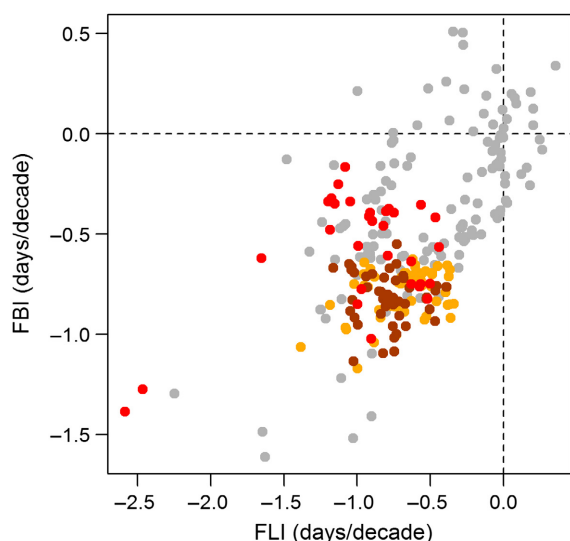


Fig. 5. Recent change in the timing of spring onset, expressed in days per decade, according to the first leaf (FLI) and first bloom (FBI) indices. Colors correspond to the same ecological response categories shown in Fig. 4. As reference, the two extreme early FLI parks in the lower left are Ebey's Landing National Historical Reserve and San Juan Island National Historical Park, both in Washington.

threat to population dynamics and community structure (Both et al. 2006, Chuine 2010, Miller-Rushing et al. 2010). Mismatches can occur when species in a community respond to different climatic or environmental cues to initiate phenological activity. Interactions that can be affected by such mismatches include plant-pollinator interactions (Hegland et al. 2009), plant-herbivore interactions (Post et al. 2008), and competitive interactions (Willis et al. 2010). These can strongly influence and disrupt multitrophic interactions (Both et al. 2006, 2009). Shifts in phenology can have cascading impacts on large-scale ecosystem processes, such as carbon cycling, because of changes in the duration of the growing season or changes in the timing and intensity of peak leaf production (Richardson et al. 2013). Earlier spring onset can also lead to an increased risk of "false springs," when emergent plant tissues are damaged by hard freezes occurring after FLI or FBI (Fisichelli et al. 2014, Allstadt et al. 2015). Parks require ecological monitoring if they are to document and potentially respond to these types of

ecological changes induced by changes in the timing of spring onset.

Park monitoring

The NPS Inventory and Monitoring Program uses a select set of information-rich "vital signs" to track the overall condition or ecological "health" of park natural resources (Fancy et al. 2009). The top-ranked vital sign is weather/climate, identified by 246 of the original 270 natural resource parks as fundamental to informing resource management (Fancy and Bennetts 2012). The spring indices inform this vital sign and offer an NPS-wide indicator system at the granularity of parks, similar to indicators effectively implemented at broader scales (US Environmental Protection Agency 2014, US Global Change Research Program 2014).

Existing ground-based phenology monitoring efforts could help explicitly extend the SI-x model approach to species other than lilac and honeysuckle. The NPS Inventory and Monitoring Program, NPS Climate Change Response Program, NPS Research Learning Centers, and approximately 30 individual parks are already working with the USA National Phenology Network (USA-NPN) to develop monitoring programs (e.g., Haggerty et al. 2013, A. T. Seasons 2016) and protocols (Tierney et al. 2013, Matthews et al. 2014). Citizen science—a major priority of the NPS Centennial (National Park Service 2015)—is central to many of these efforts and it can dramatically increase the quantity of data collected. For example, the California Phenology Project used trained citizen scientists, resource managers, and interns to collect over 860,000 phenology observations in parks throughout the state (Mazer et al. 2015, as of July 2016, the total number of records collected NPS-wide was 1.8 million). This project demonstrates how parks can collaborate with one another and external partners to better understand and share phenological information, even within a physiographically complex region that extends from the Mojave Desert to the Sierra Nevada Mountains and to the coast redwood forests. Additional monitoring efforts to understand phenology for climate change adaptation at parks include observations from phenology cameras (Brown et al. 2016), remote sensing (Talbert et al. 2013, Duarte et al. 2014), and other species-specific techniques (Roland and Nicklen 2011).

Resource management decision making

A critical need for parks and other protected areas in an era of climate change is the timely synthesis of existing science into working hypotheses that inform action (Bobowski et al. 2016). Climate change adaptation will help parks moderate harm and exploit beneficial opportunities, such as those arising from phenological responses to climate change (Enquist et al. 2014, Morellato et al. 2016). An important early step in the Climate-Smart Conservation Cycle (CSCC, Stein et al. 2014), a guide for land managers from diverse agencies and institutions attempting to manage their areas and resources in response to climate change, is to evaluate climate change vulnerabilities and their causes (Glick et al. 2011, Beever et al. 2015, Hansen et al. 2016). Our use of SI-x is best applied as a “coarse-filter” component of the climate change vulnerability of parks (Glick et al. 2011), meaning that it is a broadscale indicator of potential climate change impacts (Gross and Noon 2015). A coarse-filter approach can be highly informative to prioritize where and how to invest in more detailed, site-specific, and costly phenological and climate change studies. Furthermore, parks and other protected areas increasingly are encouraged to “scale up” and manage within a landscape context (National Park System Advisory Board 2012, National Park Service 2015); often this necessitates a coarse-filter approach (Tingley et al. 2014, Theobald et al. 2016).

Landscape-scale information on historical patterns of change and on recent variability in the arrival of spring provides a backdrop against which parks can both reevaluate management goals and consider management options (steps 3 and 4 of CSCC; Stein et al. 2014). If the timing of spring onset is well within HRV, or the temporal trend in start of spring is small with respect to the magnitude of interannual or decadal variation, a park might decide that no immediate action is required, or that they will establish an early warning system by monitoring climate change exposure and the population dynamics of phenological indicator plant (or animal) species. Conversely, early springs may threaten the persistence of some species within park boundaries, either through direct response or mediated through interactions with other species, such as facilitation of the spread of invasive species.

Management actions may include protecting populations inhabiting naturally cool microenvironments that exhibit refugial characteristics (Heller and Zavaleta 2009, Keppel and Wardell-Johnson 2012, Morelli et al. 2016). Protected microenvironments may further be managed in ways that reduce nonclimate stressors, thereby reducing cumulative impacts (West and Julius 2014).

Our results can support more specific recommendations and strategies for managing resources that may respond to phenological changes in parks. National parks are ecologically diverse, and consequently, there are many ways that our coarse-filter results can inform decision making. Generally, areas that experience extreme early springs are likely more susceptible to ecological mismatches and invasions because they promote expression of phenological variability among species in response to warming. In these situations, the differences in phenological response between species that track seasonality well and those that do not will be large. These areas are also most likely to have operational mismatches between their monitoring or maintenance practices and the timing of the phenomena they are intended to target.

Invasive species tend to have more “flexible” phenologies than their native counterparts, thus enabling invasives to better track earlier and more variable springs (Willis et al. 2010, Wolkovich and Cleland 2011). Invasive plant control can take advantage of the early green-up of undesirable species by broadcast spraying foliar herbicides prior to leaf out of native species. Many parks will need to plan both earlier and more flexible monitoring and control windows for invasives, including hiring seasonal exotic plant management personnel earlier in the year to coincide with invasive species advancing their phenologies (Marushia et al. 2010). For example, the Appalachian Trail Conservancy has needed to adjust removal treatments of garlic mustard (*Alliaria petiolata*) to accommodate earlier springs in some years, but planning the timing of treatments has been complicated by high interannual variability (M. Orlousky, *personal communication*). These changes to operations can come at significant additional cost. At Acadia National Park in Maine, the invasive species management season is longer now than it was historically—so long that it extends into the academic school year. As

a result, the park must pay field crews longer (A. Miller-Rushing, *personal communication*).

Advances in the timing of spring also impact visitor services. Parks see high levels of visitation in periods of warm (but not hot) weather, and visitation across the park system is projected to increase with warming (Fisichelli et al. 2015). Given the relationship between visitation and air temperature, advancing springs portend earlier and longer visitation seasons for many parks, with many implications for operations. Changes may be particularly notable at parks where spring events are key attractions (e.g., wildflower blooms, seasonal waterfalls, bird migrations). Parks with an increasing interannual variability in the arrival of spring in recent years may need to plan a longer window around cultural events. For example, the Cherry Blossom festival in Washington, DC, has evolved from a single-day to a multiweek celebration; in 2012, it was broadened to 5 weeks to capture variation in spring onset as measured by peak bloom of cherry trees (Chung et al. 2011, US Environmental Protection Agency 2015). Similarly, the Memorial Day lilac festival near Saint-Gaudens National Historic Park typically no longer overlaps with the bloom time of lilacs (Rockman 2015). Observers in citizen science programs may also miss key events, as occurred recently when HawkWatch participants missed peak migration at Acadia National Park (A. Miller-Rushing, *personal communication*).

Future needs and opportunities

Managers of parks and other protected areas ultimately require phenological data and results at higher spatiotemporal resolutions than those analyzed and reported here (Hansen et al. 2016). For example, many of the parks examined are mountainous, and the elevational gradients both within and extending out from a park can have large effects on the magnitude and seasonality of temperature, precipitation, and snowmelt timing, and thus on phenology. Such phenological changes in parks also offer benchmarks for comparing to surrounding areas that have altered species composition in part because of human land use intensification. The USA-NPN now produces SI-x at finer spatial (~2.5 km) and temporal (daily) scales, including short-term (6-d) forecasts, which will assist in identifying and prioritizing management actions within park

boundaries (T. Crimmins et al., *unpublished data*). Finer resolution phenological data and models will also help identify landscapes surrounding parks that support park biodiversity at ecologically relevant scales (e.g., phenological gradients that influence seasonal migration to critical habitats outside of a park). The use of phenological indices such as the SI-x will be further enhanced as we develop a more detailed understanding of their correlations with specific plant species and habitats in and around parks. This requires scaling up the collection of ground observations, such as through field-based monitoring protocols and programs, which may be expanded and accelerated through citizen science (McKinley et al. 2015). Future work integrating phenological predictions from climate products (e.g., SI-x) with ground observations and remote sensing holds great potential (e.g., Schwartz and Hanes 2010, Bradley 2014, Elmore et al. 2016, Melaas et al. 2016).

According to Jonathan Jarvis, Director of the National Park Service, climate change is "... the greatest threat to the integrity of our national parks that we have ever experienced" (National Park Service 2010). Already we are seeing the effects of climate change in parks from the tropics to the arctic (Monahan and Fisichelli 2014), and models suggest that impacts will only become greater in the future (Melton et al. 2016). Despite the challenges, opportunities exist for ensuring the protection and relevance of parks, and for using science to inform climate adaptation decision making (Gross and Olliff 2016). NPS programmatic long-term ecological monitoring is a core science that will consistently and reliably support decision making at parks (Fancy et al. 2009). The NPS Inventory and Monitoring Program, while still relatively young in relation to its long-term mission, endeavors to support natural resource stewardship and science through the next century and beyond.

ACKNOWLEDGMENTS

This work was supported by the NPS landscape dynamics monitoring project, NPScape, the NASA-NPS Landscape Climate Change Vulnerability Project (NASA Applied Sciences program award number 10-BIOCLIM10-0034), and by Cooperative Agreement (G14AC00405) from the United States Geological

Survey to the University of Arizona. The SI-x models were developed using phenological data that are now available from the National Phenology Database at the USA National Phenology Network. We thank reviewers and colleagues who provided comments that greatly improved an earlier version of this manuscript: Timothy Assal, Jherime Kellermann, Abraham Miller-Rushing, Jeff Morissette, David Thoma, and John Paul Schmit. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.

LITERATURE CITED

- A. T. Seasons. 2016. Tracking Phenology from Georgia to Maine. USA National Phenology Network. <https://www.usanpn.org/appalachian/>
- Allstadt, A. J., S. J. Vavrus, P. J. Heglund, A. M. Pidgeon, W. E. Thogmartin, and V. C. Radeloff. 2015. Spring plant phenology and false springs in the conterminous US during the 21st century. *Environmental Research Letters* 10:104008.
- Anderson, J. T., D. W. Inouye, A. M. McKinney, R. I. Colautti, and T. Mitchell-Olds. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society of London B: Biological Sciences* 279:3843–3852.
- Ault, T. R., M. D. Schwartz, R. Zurita-Milla, J. F. Weltzin, and J. Betancourt. 2015a. Trends and natural variability of spring onset in the coterminous United States as evaluated by a new gridded dataset of spring indices. *International Journal of Climate* 28:8363–8378.
- Ault, T. R., R. Zurita-Milla, and M. D. Schwartz. 2015b. A Matlab® toolbox for calculating spring indices from daily meteorological data. *Computers and Geosciences* 83:46–53.
- Beever, E. A., et al. 2015. Improving conservation outcomes with a new paradigm for understanding species' fundamental and realized adaptive capacity. *Conservation Letters* 9:131–137. <http://dx.doi.org/10.1111/conl.12190>
- Bobowski, B., I. Ashton, and W. B. Monahan. 2016. Chapter 14: Perspectives on responding to climate change in Rocky Mountain National Park. Pages 277–301 in A. J. Hansen, W. B. Monahan, D. M. Theobald, and S. T. Olliff, editors. *Climate change in wildlands: pioneering approaches to science and management*. Island Press, Washington, D.C., USA.
- Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83.
- Both, C., C. A. M. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. B. Foppen. 2009. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London B: Biological Sciences*. <http://dx.doi.org/10.1098/rspb.2009.1525>
- Bowers, J. E., and M. A. Dimmitt. 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. *Bulletin of the Torrey Botanical Club* 121:215–229.
- Bradley, B. A. 2014. Remote detection of invasive plants: a review of spectral, textural and phenological approaches. *Biological Invasions* 16:1411–1425.
- Brown, T. B., et al. 2016. Using phenocams to monitor our changing Earth: toward a global phenocam network. *Frontiers in Ecology and the Environment* 14:84–93.
- Chaine, I. 2010. Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365:3149–3160.
- Chung, U., L. Mack, J. I. Yun, and S. H. Kim. 2011. Predicting the timing of cherry blossoms in Washington, DC and mid-Atlantic states in response to climate change. *PLoS ONE* 6:e27439.
- Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* 93:1765–1771.
- Cook, B. I., E. M. Wolkovich, and C. Parmesan. 2012. Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences USA* 109:9000–9005.
- Davis, C. C., C. G. Willis, R. B. Primack, and A. J. Miller-Rushing. 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3201–3213.
- Duarte, L., A. C. Teodoro, and H. Gonçalves. 2014. Deriving phenological metrics from NDVI through an open source tool developed in QGIS. *Proceedings of SPIE 9245, Earth Resources and Environmental Remote Sensing/GIS Applications V*, 924511, Amsterdam, The Netherlands.
- Elmore, A. J., C. D. Stylinski, and K. Pradhan. 2016. Synergistic use of citizen science and remote sensing for continental-scale measurements of forest tree phenology. *Remote Sensing* 8:502.
- Enquist, C. A., J. L. Kellermann, K. L. Gerst, and A. J. Miller-Rushing. 2014. Phenology research for natural resource management in the United

- States. *International Journal of Biometeorology* 58: 579–589.
- Fancy, S. G., and R. E. Bennetts. 2012. Institutionalizing an effective long-term monitoring program in the US National Park Service. Pages 481–497 in R. A. Gitzen, J. J. Millspaugh, A. B. Cooper, and D. S. Licht, editors. *Design and analysis of long-term ecological monitoring studies*. Cambridge University Press, Cambridge, UK.
- Fancy, S. G., J. E. Gross, and S. L. Carter. 2009. Monitoring the condition of natural resources in US national parks. *Environmental Monitoring and Assessment* 151:161–174.
- Fischelli, N. A., G. W. Schuurman, W. B. Monahan, and P. S. Ziesler. 2015. Protected area tourism in a changing climate: Will visitation at US national parks warm up or overheat? *PLoS ONE* 10: e0128226. <http://dx.doi.org/10.1371/journal.pone.0128226>
- Fischelli, N. A., T. Vor, and C. Ammer. 2014. Broad-leaf seedling responses to warmer temperatures 'chilled' by late frost that favors conifers. *European Journal of Forest Research* 133:587–596.
- Glick, P., B. A. Stein, and N. A. Edelson, editors. 2011. *Scanning the conservation horizon: a guide to climate change vulnerability assessment*. National Wildlife Federation, Washington, D.C., USA.
- Gross, J. E., and B. R. Noon. 2015. Application of surrogates and indicators to monitoring natural resources. Pages 169–178 in D. Lindenmayer, P. Bartonand, and J. Pierson, editors. *Indicators and surrogates of biodiversity and environmental change*. CSIRO Publishing, Clayton South, Victoria, Australia.
- Gross, J. E., and S. T. Olliff. 2016. Chapter 2: Effectively linking climate science and management. Pages 17–32 in A. J. Hansen, W. B. Monahan, D. M. Theobald, and S. T. Olliff, editors. *Climate change in wildlands: pioneering approaches to science and management*. Island Press, Washington, D.C., USA.
- Haggerty, B. P., E. R. Matthews, K. L. Gerst, A. G. Evenden, and S. J. Mazer. 2013. The California Phenology Project: tracking plant responses to climate change. *Madroño* 60:1–3.
- Hansen, A. J., C. R. Davis, N. Piekielek, J. Gross, D. M. Theobald, S. Goetz, F. Melton, and R. DeFries. 2011. Delineating the ecosystems containing protected areas for monitoring and management. *BioScience* 61:363–373.
- Hansen, A. J., W. B. Monahan, D. M. Theobald, and S. T. Olliff, editors. 2016. *Climate change in wildlands: pioneering approaches to science and management*. Island Press, Washington, D.C., USA. 384 pp.
- Hansen, A. J., N. Piekielek, C. Davis, J. Haas, D. M. Theobald, J. E. Gross, W. B. Monahan, T. Olliff, and S. W. Running. 2014. Exposure of US national parks to land use and climate change 1900–2100. *Ecological Applications* 24:484–502.
- Hegland, S. J., A. Nielsen, A. Lázaro, A. L. Bjerknes, and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184–195.
- Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142:14–32.
- Hijmans, R. J., and J. van Etten. 2015. raster: geographic analysis and modeling with raster data. R package version 2.5-2. <http://CRAN.R-project.org/package=raster>
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- IPCC. 2014. *Climate change 2014: mitigation of climate change*. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Keane, R. E., P. F. Hessburg, P. B. Landres, and F. J. Swanson. 2009. The use of historical range and variability (HRV) in landscape management. *Forest Ecology and Management* 258:1025–1037.
- Keppel, G., and G. W. Wardell-Johnson. 2012. Refugia: keys to climate change management. *Global Change Biology* 18:2389–2391.
- Marushia, R. G., M. W. Cadotte, and J. S. Holt. 2010. Phenology as a basis for management of exotic annual plants in desert invasions. *Journal of Applied Ecology* 47:1290–1299.
- Matthews, E. R., et al. 2014. California Phenology Project (CPP) plant phenological monitoring protocol: version 1. Natural Resource Report. NPS/PWR/NRR–2014/763. National Park Service, Fort Collins, Colorado, USA.
- Mazer, S. J., K. L. Gerst, E. R. Matthews, and A. Evenden. 2015. Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem. *Ecosphere* 6:1–27.
- McCabe, G. J., J. L. Betancourt, G. T. Pederson, and M. D. Schwartz. 2013. Variability common to first leaf dates and snowpack in the western conterminous United States. *Earth Interactions* 17: 1–18.
- McKinley, D. C., et al. 2015. Investing in citizen science can improve natural resource management and environmental protection. *Issues in Ecology* 19: 1–27. <http://www.esa.org/esa/wp-content/uploads/2015/09/Issue19.pdf>

- Meehl, G. A., J. M. Arblaster, and G. Branstator. 2012. Mechanisms contributing to the warming hole and the consequent U.S. east-west differential of heat extremes. *Journal of Climate* 25: 6394–6408.
- Melaas, E. K., M. A. Friedl, and A. D. Richardson. 2016. Multiscale modeling of spring phenology across deciduous forests in the Eastern United States. *Global Change Biology* 22:792–805.
- Melillo, J. M., T. T. Richmond, and G. W. Yohe, editors. 2014. Climate change impacts in the United States: the third national climate assessment. US Global Change Research Program. <http://nca2014.globalchange.gov/>
- Melton, F., J. Xiong, W. Wang, C. Milesi, S. Li, A. Quackenbush, D. M. Theobald, S. J. Goetz, P. Jantz, and R. Nemani. 2016. Chapter 7: Potential impacts of climate and land use change on ecosystem processes in the Great Northern and Appalachian Landscape Conservation Cooperatives. Pages 119–150 in A. J. Hansen, W. B. Monahan, D. M. Theobald, and S. T. Olliff, editors. *Climate change in wildlands: pioneering approaches to science and management*. Island Press, Washington, D.C., USA.
- Menzel, A., et al. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- MetOffice. 2016. Climate averages. <http://www.metoffice.gov.uk/public/weather/climate>
- Miller-Rushing, A., A. Evenden, J. Gross, B. Mitchell, and S. Sachs. 2011. Parks use phenology to improve management and communicate climate change. *Park Science* 28:65–71.
- Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3177–3186.
- Monahan, W. B., and N. A. Fisichelli. 2014. Climate exposure of US national parks in a new era of change. *PLoS ONE* 9:e101302. <http://dx.doi.org/10.1371/journal.pone.0101302>
- Morellato, L. P. C., et al. 2016. Linking plant phenology to conservation biology. *Biological Conservation* 195:60–72.
- Morelli, T. L., et al. 2016. Managing climate change refugia for climate adaptation. *PLoS ONE* 11: e0159909. <http://dx.doi.org/10.1371/journal.pone.0159909>
- Morgan, P., G. H. Aplet, J. B. Haufler, H. C. Humphries, M. M. Moore, and W. D. Wilson. 1994. Historical range of variability: a useful tool for evaluating ecosystem change. *Journal of Sustainable Forestry* 2:87–111.
- National Park Service. 2004. Program Standards: Park Planning. https://www.nature.nps.gov/water/planning/Planning_pdfs/park.pdf
- National Park Service. 2010. National Park Service climate change response strategy. NPS Climate Change Response Program, Fort Collins, Colorado, USA.
- National Park Service. 2011. NPScape NPS boundary-derived areas of analysis SOP: park, 3 km, and 30 km areas of analysis. Natural Resource Program Center, Fort Collins, Colorado, USA. <https://irma.nps.gov/App/Reference/Profile/2170522?Inv=True>
- National Park Service. 2015. A call to action – preparing for a second century of stewardship and engagement. https://www.nps.gov/calltoaction/PDF/C2A_2015.pdf
- National Park Service. 2016. NPSpecies: information on species in National Parks. <https://irma.nps.gov/NPSpecies/>
- National Park System Advisory Board. 2012. Revisiting Leopold: resource stewardship in the national parks. National Park System Advisory Board, Washington, D.C., USA. http://www.nps.gov/calltoaction/PDF/LeopoldReport_2012.pdf
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Post, E., C. Pedersen, C. C. Wilmsers, and M. C. Forchhammer. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proceedings of the Royal Society of London B: Biological Sciences* 275: 2005–2013.
- R Core Team. 2015. R: a language and environment for statistical computing. Version 3.2.3 (2015-12-10). R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169:156–173.
- Rockman, M. 2015. An NPS framework for addressing climate change with cultural resources. *George Wright Forum* 32:37–50.
- Roland, C. A., and E. F. Nicklen. 2011. Aspen phenology monitoring in the Central Alaska Network of the National Park Service: progress report 2010. Natural Resource Technical Report NPS/CAKN/NRTR–2010/501. National Park Service, Fort Collins, Colorado, USA.
- Rosemartin, A., E. G. Denny, J. F. Weltzin, R. L. Marsh, B. E. Wilson, H. Mehdipour, R. Zurita-Milla, and

- M. D. Schwartz. 2015. Lilac and honeysuckle phenology data 1956–2014. *Nature Scientific Data* 2:1–8.
- Schwartz, M. D. 1990. Detecting the onset of spring: a possible application of phenological models. *Climate Research* 1:23–29.
- Schwartz, M. D. 1997. Spring index models: an approach to connecting satellite and surface phenology. Pages 23–38 in H. Lieth and M. D. Schwartz, editors. *Phenology in seasonal climates I*. Backhuys Publishers, Leiden, The Netherlands.
- Schwartz, M. D., R. Ahas, and A. Aasa. 2006. Onset of spring starting earlier across the northern hemisphere. *Global Change Biology* 12:343–351.
- Schwartz, M. D., T. R. Ault, and J. L. Betancourt. 2013. Spring onset variations and trends in the continental United States: past and regional assessment using temperature-based indices. *International Journal of Climatology* 33:2917–2922.
- Schwartz, M. D., and J. M. Hanes. 2010. Intercomparing multiple measures of the onset of spring in eastern North America. *International Journal of Climatology* 30:1614–1626.
- Sherry, R. A., X. Zhou, S. Gu, J. A. Arnone III, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences USA* 104:198–202.
- Stein, B. A., P. Glick, N. Edelson, and A. Staudt, editors. 2014. *Climate-smart conservation: putting adaptation principles into practice*. National Wildlife Federation, Washington, D.C., USA.
- Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K. S. Chan, N. G. Yoccoz, and B. Ådlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London B: Biological Sciences* 270: 2087–2096.
- Talbert, C., T. Kern, J. Morissette, D. Brown, and K. James. 2013. MODIS phenology image service ArcMap toolbox. U.S. Geological Survey Open-File Report 2013–1250. <http://pubs.usgs.gov/of/2013/1250/>
- Theobald, D. M., W. B. Monahan, D. Harrison-Atlas, A. J. Hansen, P. Jantz, J. E. Gross, and S. T. Olliff. 2016. Chapter 6: Assessing vulnerability to land use and climate change at landscape scales using landforms and physiographic diversity as coarse-filter targets. Pages 95–115 in A. J. Hansen, W. B. Monahan, D. M. Theobald, and S. T. Olliff, editors. *Climate change in wildlands: pioneering approaches to science and management*. Island Press, Washington, D.C., USA.
- Tierney, G., et al. 2013. Phenology monitoring protocol: Northeast Temperate Network. Natural Resource Report. NPS/NETN/NRR—2013/681. National Phenology Network, Fort Collins, Colorado, USA.
- Tingley, M. W., E. S. Darling, and D. S. Wilcove. 2014. Fine-and coarse-filter conservation strategies in a time of climate change. *Annals of the New York Academy of Sciences* 1322:92–109.
- US Environmental Protection Agency. 2014. Climate change indicators in the United States, 2014. Third edition. EPA 430-R-14-004. www.epa.gov/climatechange/indicators
- US Environmental Protection Agency. 2015. Technical documentation: cherry blossom bloom dates in Washington, D.C. http://www3.epa.gov/climatechange/pdfs/cherry-blossoms_documentation.pdf
- US Global Change Research Program. 2014. National climate assessment. <http://nca2014.globalchange.gov/>
- West, J. M., and S. H. Julius. 2014. Choosing your path: evaluating and selecting adaptation options. Pages 141–152 in B. Stein, P. Glick, N. Edelson, and A. Staudt, editors. *Climate-smart conservation: putting adaptation principles into practice*. National Wildlife Federation, Washington, D.C., USA.
- Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable climate change response explains non-native species' success in Thoreau's woods. *PLoS ONE* 5:e8878.
- Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: a community ecology. *Frontiers in Ecology and the Environment* 9:287–294.
- Wolkovich, E. M., et al. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494–497.
- Wood, E. M., and A. M. Pidgeon. 2015. Climatic extremes influence spring tree phenology and migratory songbird foraging behavior. Pages 117–131 in E. M. Wood and J. L. Kellermann, editors. *Phenological synchrony and bird migration: changing climate and seasonal resources in North America*. Studies in Avian Biology (no. 47). CRC Press, Boca Raton, Florida, USA.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1465/supinfo>