

Deciduous forest responses to temperature, precipitation, and drought imply complex climate change impacts

Yingying Xie^{a,1}, Xiaojing Wang^b, and John A. Silander Jr.^a

^aDepartment of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043; and ^bDepartment of Statistics, University of Connecticut, Storrs, CT 06269-4120

Edited by William H. Schlesinger, Cary Institute of Ecosystem Studies, Millbrook, NY, and approved September 23, 2015 (received for review May 21, 2015)

Changes in spring and autumn phenology of temperate plants in recent decades have become iconic bio-indicators of rapid climate change. These changes have substantial ecological and economic impacts. However, autumn phenology remains surprisingly little studied. Although the effects of unfavorable environmental conditions (e.g., frost, heat, wetness, and drought) on autumn phenology have been observed for over 60 y, how these factors interact to influence autumn phenological events remain poorly understood. Using remotely sensed phenology data from 2001 to 2012, this study identified and quantified significant effects of a suite of environmental factors on the timing of fall dormancy of deciduous forest communities in New England, United States. Cold, frost, and wet conditions, and high heat-stress tended to induce earlier dormancy of deciduous forests, whereas moderate heat- and drought-stress delayed dormancy. Deciduous forests in two eco-regions showed contrasting, nonlinear responses to variation in these explanatory factors. Based on future climate projection over two periods (2041–2050 and 2090–2099), later dormancy dates were predicted in northern areas. However, in coastal areas earlier dormancy dates were predicted. Our models suggest that besides warming in climate change, changes in frost and moisture conditions as well as extreme weather events (e.g., drought- and heat-stress, and flooding), should also be considered in future predictions of autumn phenology in temperate deciduous forests. This study improves our understanding of how multiple environmental variables interact to affect autumn phenology in temperate deciduous forest ecosystems, and points the way to building more mechanistic and predictive models.

Land-surface phenology | dormancy date | frost | New England

Plant phenological shifts in recent decades are iconic bio-indicators of climate change (1–4). These phenological changes in turn have cascading ecological effects on species demography, biotic interactions, and ecosystem functions (5–8). Whereas mechanisms of spring phenology (i.e., bud burst, leafing out, and flowering) are well studied (9–13), fall phenology (i.e., leaf senescence and dormancy, indicated by visual signals from leaf coloration and leaf drop) remains little studied (14–16). Changes in timing of autumn phenology play a significant role in growing season length prediction, C and N cycling, and biotic interactions (8, 17–19). Furthermore, delayed leaf coloration and more muted autumn foliage in response to climate change will likely significantly affect the multibillion dollar fall foliage ecotourism industry (20–22). Although delayed leaf coloration and leaf drop in deciduous forests have been observed across the northern hemisphere in recent decades (14, 23, 24), the full range of environmental triggers and how they influence fall phenological changes now or in the future remain poorly understood.

Autumn phenology of deciduous woody plant species in temperate regions is the timing of the developmental stages of leaf senescence and dormancy. Plant physiologists demark leaf senescence beginning with onset of leaf coloration, and dormancy with leaf drop and the development of dormant apical meristems (25, 26). As detected by remotely sensed satellite images, autumn phenology dates describe the timing of loss of leaf greenness. Leaf senescence dates correspond

to when greenness starts to decrease (i.e., onset of leaf coloration) and dormancy dates occur when greenness reaches a minimum value (brown leaves with leaf drop) (27) (*SI Appendix*, Figs. S1 and S2). Currently, most studies consider short day length and low temperature as the primary or only external triggers of autumn phenology (28, 29). However, over the past 60 y (25, 30, 31), researchers studying the physiology of leaf senescence and dormancy have enumerated a range of other environmental conditions that may influence autumn phenology, including frost, moisture conditions, and extreme weather events (e.g., drought- and heat-stress, and flooding). Although the effects of a subset of these factors on plant leaf coloration and leaf drop were reported by a handful of physiological experiments (32, 33), few studies have quantified the response of fall phenology to a full suite of potential explanatory factors. Ongoing climate changes are likely to introduce higher frequency and intensity of climatic stress factors (34), so it is important to include these in developing more predictive, mechanistic models of fall phenology.

To study landscape-scale forest phenology, we used satellite remotely sensed autumn dormancy dates of deciduous forests in New England, United States, from the Moderate Resolution Imaging Spectroradiometer (MODIS) data product (27) (*SI Appendix*, Fig. S1). Greenness of forest canopy reaches the minimum values at the dormancy date (27), a proxy for plant fall dormancy (*SI Appendix*, Figs. S1 and S2). We examined dormancy dates of deciduous forest communities in two eco-regions (NH, Northeastern Highlands; NCZ, Northeastern Coastal Zone) from 2001 to 2012 (Figs. 1 and 2). Multiple environmental factors affecting fall forest dormancy were identified representing spatially and temporally varying chill and frost-stress, heat-stress, drought-stress, precipitation,

Significance

Autumnal phenological shifts (leaf senescence and dormancy) because of climate change bring substantial impacts on community and ecosystem processes (e.g. altered C and N cycling and phenological mismatches) and the fall foliage ecotourism industry. However, the understanding of the environmental control of autumn phenology has changed little over the past 60 y. We found that cold, frost, wet, and high heat-stress lead to earlier dormancy dates across temperate deciduous forest communities, whereas moderate heat- and drought-stress delayed dormancy. Divergent future responses of fall dormancy timing were predicted: later for northern regions and earlier for southern areas. Our findings improve understanding of autumn phenology mechanisms and suggests complex interactions among environmental conditions affecting autumn phenology now and in the future.

Author contributions: Y.X. and J.A.S. designed research; Y.X. and J.A.S. performed research; X.W. contributed new reagents/analytic tools; Y.X. and X.W. analyzed data; Y.X., X.W., and J.A.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. Email: yingying.xie1@gmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1509991112/-DCSupplemental.

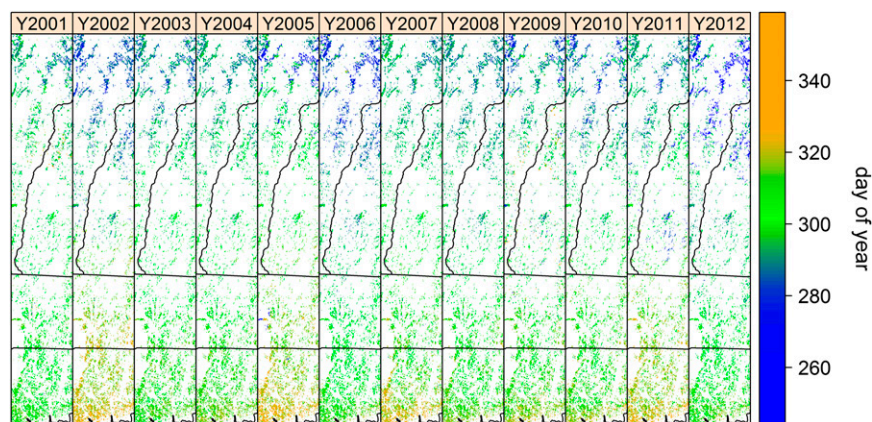


Fig. 2. Dormancy dates (day of year) for deciduous forests across study area from 2001 to 2012. Small values (blue pixels) indicate early dormancy dates and large values (orange pixels) indicate late dormancy dates. Black lines are state boundaries (Connecticut at the bottom, Massachusetts next, then Vermont upper left, and New Hampshire upper right). White areas indicate nondeciduous forest area; see also study area shown in Fig. 1.

Appendix, Figs. S4 and S5). However, there are also antagonistic factors operating at the same time that lead to earlier fall dormancy: that is, in the future higher heat-stress, slightly less drought, and significant interaction effects between moderate heat-stress and summer rainfall. The heat-stress effects were stronger than the lower chill effects in NCZ eco-region, leading to earlier dormancy dates (*SI Appendix, Fig. S5*). Although warmer autumn may extend forest growing season, earlier leaf dormancy can be forced under higher heat-stress during the summer from climate change. This finding suggests that multiple impacts from projected climate with more identified stresses, in addition to warming, will in concert affect autumn phenology of deciduous forest trees in the future. Recent studies pointing out the positive correlation between spring and fall phenology (51, 52), further support our finding that autumn phenology responds to weather spanning the full growing season.

Moreover, these responses will be spatially and temporally complex: different phenological responses will likely occur in different regions, given the spatial variation in climate variables across the landscape.

From the variable selection methods, the very slight difference in predictor coefficients, model selection criteria, and RMSE (*SI Appendix, Tables S1 and S2*) suggested that multicollinearity does not significantly affect model fitting or predictions. RMSE in model validation (2011–2012) suggested predictive uncertainties were about 14.2 (NH) and 6.7 (NCZ) days (*SI Appendix, Tables S1 and S2*), which include data uncertainty in the MODIS and climate data because of data quality and model uncertainties; this is within the limits of the temporal resolution of MODIS phenology data summarized at 8-d intervals.

We encourage further investigations on physiological responses of autumn phenology to multiple environmental stresses, including interactions among stresses and nonlinear effects, and collecting long-term datasets across more species, communities, and ecosystems, including field observations and physiological experiments, to better inform future predictions and narrow model uncertainties. Species-specific phenological responses also need to be integrated into forest community phenology models in the future to better predict individual species- and community- or landscape-level responses (53). Indeed the bimodality in dormancy responses for the NH (Fig. 3) may reflect this issue.

Materials and Methods

Study Area. A rectangular area (72.6°W to 71.8°W, 41.3°N to 45°N) was selected in New England, United States as the study area (Fig. 1). This area covers two ecological regions: the Northeastern Highlands (NH) and Northeastern Coastal Zone (NCZ) (archive.epa.gov/wed/ecoregions/web/html/na_eco.html). These two eco-regions are geographically and ecologically different representing a large variation of landscape, species composition, and environmental conditions in deciduous forest communities in New England (*SI Appendix, Fig. S6*). The NH is a mountainous area with elevations up to 1,000 m higher than the NCZ, which comprises coastal plains with hills rising to about 400 m, and overall the NH has a cooler and wetter climate than the NCZ. For forest tree species composition, deciduous forests in the NH are dominated by maples and birches, whereas the NCZ deciduous forest is dominated by oaks (*SI Appendix, Table S3*).

Data and Processing. The MODIS Land Cover Dynamics (MCD12Q2) product (the NASA Land Processes Distributed Active Archive Center, US Geological Survey/Earth Resources Observation and Science Center) provides estimates of the timing of vegetation phenology at regional to global scale based on the remotely sensed vegetation index summarized at 8-d temporal resolution. The MODIS data product derives four phenological transition dates (green-up, maturity, senescence, and dormancy) from 2001 to 2012 with a spatial resolution of 500 m (28) (*SI Appendix, Fig. S1*). This study focuses on dormancy dates in fall. By using 30-m resolution land cover data from National Oceanic and Atmospheric Association's Coastal Services Center C-CAP 2001 dataset (coast.noaa.gov/dataregistry/search/collection/info/ccapregional), we extracted MODIS pixels corresponding to deciduous forest in the study area. The percentage of deciduous forest cover in each MODIS grid cell was calculated by combining land cover and phenology data. MODIS pixels with at least 75% deciduous forests were retained for analysis. We

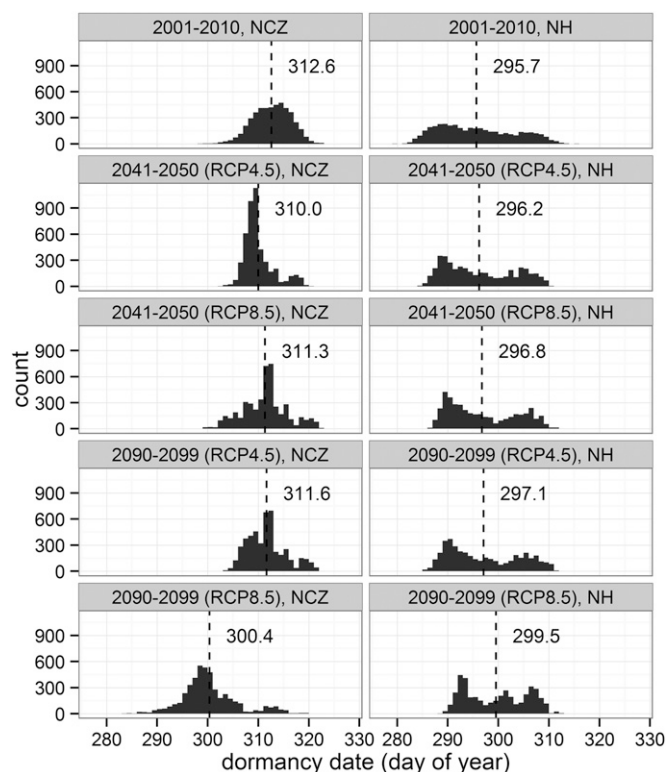


Fig. 3. Histogram of 10-y averaged dormancy dates in three 10-y periods (current: 2001–2010, and projected future: 2041–2050, 2090–2099) with two climate change projection scenarios (RCP 4.5 and RCP 8.5) across the two eco-regions (NCZ and NH). Dashed lines and numbers indicate mean values of predicted dormancy dates.

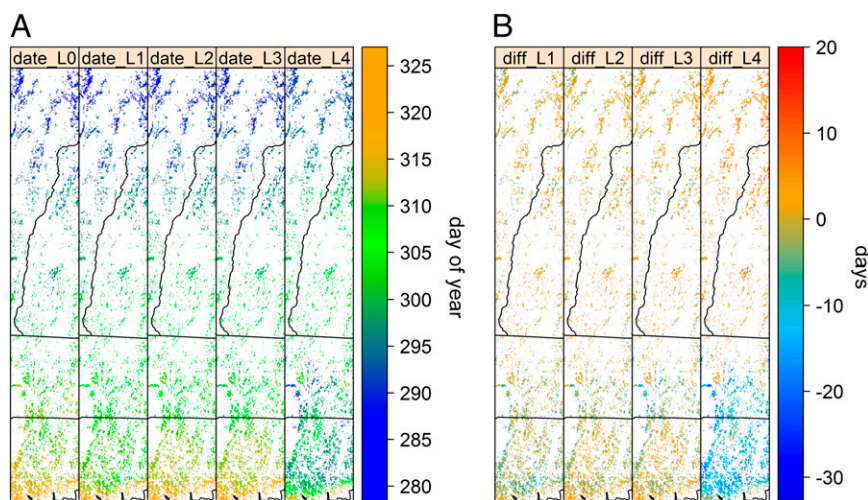


Fig. 4. (A) Maps of 10-y averaged dormancy dates for deciduous forests across the region over different 10-y periods with two climate change projection scenarios. L0: 2001–2010; L1: 2041–2050, RCP 4.5; L2: 2090–2099, RCP 4.5; L3: 2041–2050, RCP 8.5; L4: 2090–2099, RCP 8.5. (B) Difference of dormancy dates between current period and predicted periods in study area. Positive values (warm color) indicate delayed dormancy dates in the future compared with the current period, and negative values (cold color) indicate earlier dormancy dates in the future. In both plots, black lines are state boundaries and white areas indicate nondeciduous forest areas; see also study area shown in Fig. 1.

removed outliers from the analyses that showed dormancy occurring before Julian day 244 (September 1 or August 31) or after Julian day 360 (December 26 or 25). These outliers are less than 1% of the MODIS phenology data in the deciduous forest region, and are likely because of subpixel patches of agricultural fields being plowed, forest patches being defoliated or harvested, or the occurrence of grassy areas that remain green well into the winter. The final phenology data set included about 9,500 grid cells for each year for two eco-regions. Digital elevation data (srtm.csi.cgiar.org) with a spatial resolution of 90 m were aggregated to generate elevation data for the 500-m MODIS grid cells.

We used gridded daily weather data from 2001 to 2012 obtained from PRISM climate group to develop the explanatory weather variables. The data included daily mean, maximum, and minimum temperature and daily precipitation with a spatial resolution of 4 km (54), which can be used to summarize a broad range of different weather indices (55). Statistically downscaled climate projection data for one global climate model (GCM, GFDL-ESM2G) with two future scenarios (RCP 4.5 and RCP 8.5) were obtained from Multivariate Adaptive Constructed Analogs group for model predictions (37). We used daily maximum and minimum temperature and daily precipitation over two 10-y periods (2041–2050 and 2090–2099) with a spatial resolution of 4 km, which is comparable to the PRISM data.

To find the relationships between environmental factors and dormancy of deciduous forests, we first built a list of weather variables of potential environmental conditions that may affect fall phenology including cold, frost, heat, rainfall, drought, and flood events (Table 1 and *SI Appendix*, Fig. S6). Accumulating CDDs (28, 56) and decreasing day length that occur in fall have long been considered as the primary triggers of leaf senescence and dormancy. Because day length does not have year-to-year variation, we did not investigate the effect of day length effect; rather this effect is taken into account in the latitudinal variation (57). The other variables in Table 1 represent environmental/weather stressors potentially affecting tree performance (55, 58, 59). Plant responses to stresses may differ depending on when stresses occur in different seasons, and the specific species involved (56, 60–62). The physiological requirements of trees may also differ in different phenophases (62, 63). We calculated three sets of weather variables, growing season drought, rainy days, and heavy rainy days, for three periods (May 1 to June 30, July 1 to August 31, and September 1 to November 15). For CDD, we examined the effects of three different base temperatures (10°, 15°, and 20 °C) and starting dates (July 1, August 1, and September 1) to determine which period of CDD with what base temperature may best explain dormancy timing variation across the deciduous forest landscape. The end date of CDD was set as November 15, the 90th percentile of dormancy dates in the whole study region. We also used different threshold temperatures (32° and 35 °C) for hot days and we found hot days only occurred in July and August in the study area. There was no frost between June 30 and September 1 in study area, so we only calculated FD for two periods (April 1 to May 31 and September 1 to November 15), representing spring and fall growing season frosts.

Statistical Modeling. Datasets from two eco-regions were analyzed separately because dormancy dates in two eco-regions fall in two different normal

distributions. Data from 2001 to 2010 were used as model training data, and data from 2011 to 2012 were used in model validation. From initial exploratory data analyses, we selected one CDD variable with the highest correlation coefficient with dormancy dates plus other variables with a limited number of quadratic and interaction terms between predictors for each eco-region in subsequent analyses. Large number of explanatory variables from a large-scale dataset with multicollinearity among variables (e.g., correlations between temperature and latitude, latitude, and elevation) make variable selection and interpretation quite challenging (64). Thus, in addition to multiple linear regression, we used several complementary statistical methods to select important predictors explaining variation in dormancy dates. Variable selection methods include penalized regression methods, BMA (35), and Bayesian spike and slab regression (36). The penalized regression methods used were: ridge regression (65), Bayesian Least Absolute Shrinkage and Selection Operator (Bayesian LASSO) (66), the Elastic Net (67), and Pairwise Absolute Clustering and Sparsity method (PACS) (68). Penalized regression methods apply penalties to estimate coefficients with shrinkage effects of driving coefficients to be zero, which can simultaneously select important variables and estimate coefficients in the model. PACS and Elastic Net can especially select groups of correlated variables to deal with multicollinearity (67, 68). BMA provides a coherent mechanism to take account of model uncertainty by determining the coefficient of each variable using the weighted average of the parameter's posterior estimate in each model on the entire model space (35). To choose a model for future prediction, the model consisting of those variables that have overall posterior inclusion probability equal to or greater than 0.5 was considered as the optimal predictive model (38); this is termed the "posterior median model" and is easily found in BMA procedures. Bayesian spike and slab regression used a mixture of "slab distribution" (e.g., normal distribution) and "spike distribution" (e.g., a probability mass at zero) as a prior distribution to segregate the variable coefficients to be exactly zero in the induced posterior (36). Data were analyzed using software R (69) (see *SI Appendix* for R codes).

The Akaike Information Criterion (AIC) (70), Bayesian Information Criterion (BIC) (71), and RMSE were used for model selection. Models from all eight methods were used to predict dormancy dates for 2011–2012 as model validation. AIC, BIC, and RMSE were calculated for model estimation (2001–2010) and validation (2011–2012) (*SI Appendix*, Tables S1 and S2). Best models were selected by smallest AIC, BIC, and RMSE indicating best model fitting and prediction. Based on future climate projection data, dormancy dates of deciduous forests in two eco-regions were predicted by the best models for two 10-y periods, 2041–2050 and 2090–2099, with two scenarios (RCP 4.5 and RCP 8.5). We calculated 10-y average dormancy dates of period, 2001–2010, as a base line, and then compared these to 10-y averaged dormancy dates in future periods.

ACKNOWLEDGMENTS. We thank R. Primack, J. Allen, M. Aiello-Lammens, C. Merow, E. Adams, and two anonymous reviewers for helpful comments. This study was supported in part by National Science Foundation Grant DEB 0842465 (to J.A.S.).

- Peñuelas J, Filella I (2001) Phenology. Responses to a warming world. *Science* 294(5543):793–795.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421(6918):37–42.

- Miller-Rushing AJ, Primack RB (2008) Global warming and flowering times in Thoreau's Concord: A community perspective. *Ecology* 89(2):332–341.
- Ibáñez I, et al. (2010) Forecasting phenology under global warming. *Philos Trans R Soc Lond B Biol Sci* 365(1555):3247–3260.

5. Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. *Trends Ecol Evol* 22(7):357–365.
6. Cook BI, Wolkovich EM, Parmesan C (2012) Divergent responses to spring and winter warming drive community level flowering trends. *Proc Natl Acad Sci USA* 109(23):9000–9005.
7. Ovaskainen O, et al. (2013) Community-level phenological response to climate change. *Proc Natl Acad Sci USA* 110(33):13434–13439.
8. Estiarte M, Peñuelas J (2014) Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: Effects on nutrient proficiency. *Glob Change Biol* 21(3):1005–1017.
9. Chuine I (2000) A unified model for budburst of trees. *J Theor Biol* 207(3):337–347.
10. Körner C, Basler D (2010) Plant science. Phenology under global warming. *Science* 327(5972):1461–1462.
11. Polgar CA, Primack RB (2011) Leaf-out phenology of temperate woody plants: From trees to ecosystems. *New Phytol* 191(4):926–941.
12. Clark JS, Melillo J, Mohan J, Salk C (2014) The seasonal timing of warming that controls onset of the growing season. *Glob Change Biol* 20(4):1136–1145.
13. Allen JM, et al. (2014) Modeling daily flowering probabilities: Expected impact of climate change on Japanese cherry phenology. *Glob Change Biol* 20(4):1251–1263.
14. Estrella N, Menzel A (2006) Responses of leaf colouring in four deciduous tree species to climate and weather in Germany. *Clim Res* 32(3):253–267.
15. Vitasse Y, Porté AJ, Kremer A, Michalet R, Delzon S (2009) Responses of canopy duration to temperature changes in four temperate tree species: Relative contributions of spring and autumn leaf phenology. *Oecologia* 161(1):187–198.
16. Gallinat AS, Primack RB, Wagner DL (2015) Autumn, the neglected season in climate change research. *Trends Ecol Evol* 30(3):169–176.
17. Weih M (2009) Genetic and environmental variation in spring and autumn phenology of biomass willows (*Salix* spp.): Effects on shoot growth and nitrogen economy. *Tree Physiol* 29(12):1479–1490.
18. Fridley JD (2012) Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature* 485(7398):359–362.
19. Pépino M, Proulx R, Magnan P (2013) Fall synchrony between leaf color change and brook trout spawning in the Laurentides Wildlife Reserve (Québec, Canada) as potential environmental integrators. *Ecol Indic* 30:16–20.
20. Spencer DM, Holecek DF (2007) A profile of the fall foliage tourism market. *J Vacation Marketing* 13(4):339–358.
21. Rustad L, et al. (2011) *Changing Climate, Changing Forests: The Impacts of Climate Change on Forests of the Northeastern United States and Eastern Canada*. USDA Forest Service Northern Research Station General Technical Report NRS-99. (US Department of Agriculture, Forest Service, Newtown Square, PA) 48 pp.
22. Ge Q, Dai J, Liu J, Zhong S, Liu H (2013) The effect of climate change on the fall foliage vacation in China. *Tour Manage* 38:80–84.
23. Doi H, Takahashi M (2008) Latitudinal patterns in the phenological responses of leaf colouring and leaf fall to climate change in Japan. *Glob Ecol Biogeogr* 17(4):556–561.
24. Dragoni D, Rahman AF (2012) Trends in fall phenology across the deciduous forests of the Eastern USA. *Agric For Meteorol* 157:96–105.
25. Paul LK, Rinne PL, van der Schoot C (2014) Shoot meristems of deciduous woody perennials: Self-organization and morphogenetic transitions. *Curr Opin Plant Biol* 17:86–95.
26. Hänninen H, Tanino K (2011) Tree seasonality in a warming climate. *Trends Plant Sci* 16(8):412–416.
27. Zhang X, et al. (2003) Monitoring vegetation phenology using MODIS. *Remote Sens Environ* 84(3):471–475.
28. Archetti M, Richardson AD, O'Keefe J, Delpierre N (2013) Predicting climate change impacts on the amount and duration of autumn colors in a New England forest. *PLoS One* 8(3):e57373.
29. Jeong S-J, Medvigy D (2014) Macroscale prediction of autumn leaf coloration throughout the continental United States. *Glob Ecol Biogeogr* 23(11):1245–1254.
30. Lim PO, Kim HJ, Nam HG (2007) Leaf senescence. *Annu Rev Plant Biol* 58:115–136.
31. Samish RM (1954) Dormancy in woody plants. *Annu Rev Plant Physiol* 5(1):183–204.
32. Rosenthal SI, Camm EL (1997) Photosynthetic decline and pigment loss during autumn foliar senescence in western larch (*Larix occidentalis*). *Tree Physiol* 17(12):767–775.
33. Fracheboud Y, et al. (2009) The control of autumn senescence in European aspen. *Plant Physiol* 149(4):1982–1991.
34. Garcia RA, Cabeza M, Rahbek C, Araújo MB (2014) Multiple dimensions of climate change and their implications for biodiversity. *Science* 344(6183):1247579.
35. Hoeting JA, Madigan D, Raftery AE, Volinsky CT (1999) Bayesian Model Averaging: A tutorial. *Stat Sci* 14(4):382–417.
36. Ishwaran H, Rao JS (2005) Spike and slab variable selection: Frequentist and Bayesian strategies. *Ann Stat* 33(2):730–773.
37. Abatzoglou JT, Brown TJ (2012) A comparison of statistical downscaling methods suited for wildfire applications. *Int J Climatol* 32(5):772–780.
38. Barbieri MM, Berger JO (2004) Optimal predictive model selection. *Ann Stat* 32(3):870–897.
39. Günthardt-Goerg MS, Vollenweider P (2007) Linking stress with macroscopic and microscopic leaf response in trees: New diagnostic perspectives. *Environ Pollut* 147(3):467–488.
40. Cooke JE, Eriksson ME, Junttila O (2012) The dynamic nature of bud dormancy in trees: Environmental control and molecular mechanisms. *Plant Cell Environ* 35(10):1707–1728.
41. Jibrán R, A Hunter D, P Dijkwel P (2013) Hormonal regulation of leaf senescence through integration of developmental and stress signals. *Plant Mol Biol* 82(6):547–561.
42. Leuzinger S, Zotz G, Aschhoff R, Körner C (2005) Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiol* 25(6):641–650.
43. Larcher W (2003) *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups* (Springer, New York), 4th Ed.
44. Carvalho HH, et al. (2014) The molecular chaperone binding protein BiP prevents leaf dehydration-induced cellular homeostasis disruption. *PLoS One* 9(1):e86661.
45. Naschitz S, Naor A, Wolf S, Goldschmidt EE (2014) The effects of temperature and drought on autumnal senescence and leaf shed in apple under warm, east Mediterranean climate. *Trees (Berl)* 28(3):879–890.
46. Xu Y, Huang B (2007) Heat-induced leaf senescence and hormonal changes for thermal bentgrass and turf-type bentgrass species differing in heat tolerance. *J Am Soc Hortic Sci* 132(2):185–192.
47. Rivero RM, et al. (2007) Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *Proc Natl Acad Sci USA* 104(49):19631–19636.
48. Pääkkönen E, Vahala J, Holopainen T, Kärenlampi L (1998) Physiological and ultrastructural responses of birch clones exposed to ozone and drought stress. *Chemosphere* 36(4):679–684.
49. Hinkley TM, Dougherty PM, Lassoie JP, Roberts JE, Teskey RO (1979) A severe drought: Impact on tree growth, phenology, net photosynthetic rate and water relations. *Am Midl Nat* 102(2):307–316.
50. Caspersen JP, Kobe RK (2001) Interspecific variation in sapling mortality in relation to growth and soil moisture. *Oikos* 92(1):160–168.
51. Fu YSH, et al. (2014) Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proc Natl Acad Sci USA* 111(20):7355–7360.
52. Keenan TF, Richardson AD (2015) The timing of autumn senescence is affected by the timing of spring phenology: Implications for predictive models. *Glob Chang Biol* 21(7):2634–2641.
53. Diez JM, et al. (2012) Forecasting phenology: From species variability to community patterns. *Ecol Lett* 15(6):545–553.
54. PRISM Climate Group (2004) *Prism Climate Data*, Available at prism.oregonstate.edu. Accessed June 25, 2014.
55. Wilson AM, Silander JA, Jr (2014) Estimating uncertainty in daily weather interpolations: A Bayesian framework for developing climate surfaces. *Int J Climatol* 20(8):1251–1263.
56. Richardson AD, Bailey AS, Denney EG, Martin CW, O'Keefe J (2006) Phenology of a northern hardwood forest canopy. *Glob Change Biol* 12(7):1174–1188.
57. Forsythe WC, Rykiel EJ, Stahl RS, Wu HI, Schoolfield RM (1995) A model comparison for day length as a function of latitude and day of year. *Ecol Modell* 80(1):87–95.
58. Duque AS, et al. (2013) Abiotic stress responses in plants: Unraveling the complexity of genes and networks to survive. *Abiotic Stress—Plant Responses and Applications in Agriculture*, eds Vahdati K, Leslie C (InTech, Rijeka, Croatia), pp 49–55.
59. Niinemets Ü (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *For Ecol Manage* 260(10):1623–1639.
60. Bréda N, et al. (2006) Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Ann Sci* 63(6):625–644.
61. Primack RB, et al. (2009) Spatial and interspecific variability in phenological responses to warming temperatures. *Biol Conserv* 142(11):2569–2577.
62. Wilczek AM, et al. (2010) Genetic and physiological bases for phenological responses to current and predicted climates. *Philos Trans R Soc Lond B Biol Sci* 365(1555):3129–3147.
63. Hwang T, et al. (2014) Divergent phenological response to hydroclimate variability in forested mountain watersheds. *Glob Change Biol* 20(8):2580–2595.
64. Dormann CF, et al. (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36(1):27–46.
65. Hoerl AE, Kennard RW (1970) Ridge regression: Biased estimation for nonorthogonal problems. *Technometrics* 12(1):55–67.
66. Park T, Casella G (2008) The Bayesian LASSO. *J Am Stat Assoc* 103(482):681–686.
67. Zou H, Hastie T (2005) Regularization and variable selection via the elastic net. *J R Stat Soc, B* 67(2):301–320.
68. Sharma DB, Bondell HD, Zhang HH (2013) Consistent group identification and variable selection in regression with correlated predictors. *J Comput Graph Stat* 22(2):319–340.
69. R Core Team (2015) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria).
70. Akaike H (1973) Information theory and an extension of the maximum likelihood principle. *Proceedings of the Second International Symposium on Information Theory*, eds Petrov BN, Caski S (Akademiai Kiado, Budapest, Hungary), pp 267–281.
71. Schwarz G (1978) Estimating the dimension of a model. *Ann Stat* 6(2):461–464.