Climate or disturbance: temperate forest structural change and carbon sink potential

Travis Andrews[1], Michael Dietze[2], Robert Booth[1]

Summary paragraph

Terrestrial ecosystems are the single largest flux in the global carbon cycle[1] but correctly anticipating forest responses to changing climate requires understanding the interaction of long-term successional processes and integrating these processes across regional-to-continental spatial scales[2,3]. Estimates of existing forest structure and biomass are improving globally[4]; however, vegetation models continue to show substantial spread in predictions of future land carbon uptake[1,2,5] and the roles of forest structural change and demography are increasingly being recognized as important[6]. Here we reveal a coherent, cyclic pattern of change in temperate forest mean tree size, density and carbon predicted by successional theory and identify significant sensitivity to climate anomalies using large datasets. For example, in the eastern US above average temperature (+1.0^{o}C) was associated with a -29% (-0.55±0.08 Mg C ha^{-1} yr^{-1}) reduction in net primary productivity attributed to higher rates of disease (+31%) and weather disturbance (+42%). Projections of future C sink potential suggest vegetation carbon would be lowest on managed lands (72±2.2 Mg C ha^{-1}) and highest when larger trees survive in undisturbed conditions (152.7±20.6 Mg C ha^{-1}). Results provide robust comparisons for global vegetation models, valuable projections for carbon mitigation efforts, and context for management.

Structural changes in forests have long-term implications for the terrestrial carbon sink[6], but remain a challenge to predict due to the complex interactions of succession, disturbance, and climate sensitivity[3,5-7]. To identify mechanisms that drive change in tree size, density and carbon, we need a better understanding of forest structural trajectories and the factors that affect those

[1]Earth & Environmental Sciences, Lehigh University, Bethlehem, Pennsylvania 18015, USA. [2]Earth & Environment, Boston University, Boston, Massachusetts 02215, USA.

trajectories. As succession proceeds, resource limitation bounds the possible combinations of stem density and mean tree size, though the relative influence of disturbance remains poorly constrained[3]. Given this uncertainty, even anticipating relatively simple climate-induced structural changes in forests, such as changes in density or carbon accumulation, are challenging using traditional ecological approaches, which have often been spatially and temporally limited[8]. Furthermore, spatial heterogeneity in land use has led to considerable variability in forest ages[4,9]. Climate change will play out against this variable mosaic, which for much of the world is not at a landscape-scale steady-state[10].

Here we empirically quantify successional processes and identify the influence of changing climate and disturbances on tree growth, density and carbon accumulation. Ecological succession is one of the most enduring concepts of forest ecology, describing how resources, competition, and disturbance influence tree establishment, growth, and mortality. To quantify successional structural change we use the US Forest Service Forest (USFS) Forest Inventory and Analysis (FIA) database to map how stem density, radial tree growth, and net primary productivity (NPP) change as a function of mean diameter and relative density (stocking) over time for a broad range of common temperate forest densities. These relationships form the empirical succession mapping (ESM). Forest plots were grouped by mean diameter and relative density at the initial survey as proxies for successional status and to facilitate comparisons across species and environments. Relative density integrates stem density, tree size, tree species, and site index (environmental quality) relative to an optimum at that location for timber production, and can be estimated using USFS algorithms[11]. The ESM was then used as the basis for comparative and predictive models to assess the influence of climate and disturbance on forest structure and carbon accumulation.

The ESM reveals mean tree diameters and stem density change in a coherent, cyclic pattern predicted by successional theory (density model, Fig. 1A). Patterns generally highlight the primary processes likely driving change, including early successional establishment and growth, self-thinning, and gap filling (Fig. 1A inset). The majority of forests in the eastern US are recovering from past disturbance and/or management and increased stem density and accumulated carbon during the census interval (+4.2±0.1 stems ha^{-1} yr^{-1}, +1.7±0.01 Mg C $\text{ha}^{-1}\text{yr}^{-1}$; respectively). In Fig. 1, vectors with the largest vertical component represent the maximum average early successional tree recruitment (i.e. crossing the 12.7 cm diameter threshold) and carbon accumulation (Fig. 1B) occurring in forests with small mean diameters (+73.6±15.4 stems ha^{-1} yr^{-1}, +2.4±0.7 Mg C $\text{ha}^{-1}\text{yr}^{-1}$; respectively). At larger mean diameters (i.e. > 18.5 cm), rapid recruitment (+10.3±0.3 stems $\text{ha}^{-1}\text{yr}^{-1}$) in forests with low stem densities (relative density < 20) resulted in sharp reductions of mean diameter over the census interval. At higher stem densities (i.e. > 60% relative density), mortality exceeds recruitment and these forests begin self thinning[12]. As one of the earliest quantified relationships in ecology, the -3/2 self thinning power law describes the upper boundary of plant size-density relationships[13]. The overall ESM density distribution closely approximated this power law (equation 1) with a scaling exponent, b = 1.4±0.1, using a 0.99-quantile regression. We suggest more constrained thinning (e.g. Fig. 1A dashed line, b = -1.75; and as related to metabolic scaling[14,15]) best delineates exceptional forests at the tails of the size-density distribution but poorly describes the bulk of thinning relationships that maintain the center of this distribution through continual density cycling. Forests with the largest mean diameters (i.e. > 35 cm; 1.8% of the dataset) have slowed or reversed mean diameter change and carbon accumulation, as existing tree growth, resource limitation, disturbance, and recruitment were roughly balanced during the census interval.

Of the many factors that influence forest structure and carbon accumulation, the response of forests to changing climate is of particular concern[1-4,7,16]. For example, higher temperatures are widely associated with drought stress, increased pathogen and insect infestations, increased tree mortality and selective recruitment[7]. To assess the ESM sensitivity to climate, we examined structural change that occurred during anomalous moisture and temperature conditions. The climate conditions experienced by each forest over the 5-year census interval were derived from 0.5^{o} x 0.5^{o} gridded mean summer (June, July, and August) historic climate data for 5-year mean precipitation and surface temperature, and 1-year maximum/minimum soil moisture (Extended Data Table 2, esrl.noaa.gov/psd). From the climate data associated with each forest census interval, we utilize the difference between conditions over the different census intervals (1998-2012) that occurred within each grid cell to determine the median and difference from the median (anomalous climate; see Extended Data Table 2 for condition values). We compare forests that experienced near median conditions (50^{th} ±20 percentile; null model) spatially weighted to match forests that experienced the top or bottom 17^{th} and 3^{rd} percentile of climate conditions (chosen to correspond with +0.5°C and +1.0°C warming respectively), or as noted (i.e. Fig. 2 & Extended Data figs. 1-5).

Temperature and moisture anomalies were associated with significant change ($p < 0.05$) in carbon accumulation, stem density and radial tree growth in eastern US forests (Fig. 2). Forests that experienced summer temperature anomalies +1.0 °C (SD: ±0.15 °C) above average over the 5-year census interval were associated with higher rates of disease (+31±12%), weather disturbance (+42±16%) and were nearly twice as likely to also experience anomalously wet or dry summers. These warmer conditions correlated to a reduction in NPP by -29% (-0.55±0.08 Mg C ha^{-1} yr^{-1}, n = 378). Cool and wet climate conditions were associated with large positive influences on forest carbon accumulation, with 5-year wet periods substantially increasing NPP by up to +32% (+0.52±0.08 Mg C ha^{-1} yr^{-1}, n = 513) with +0.68 (SD: ±0.11) mm day^{-1} more summer precipitation. Over 5-year periods NPP was substantially reduced in dry conditions and less substantially to insignificantly reduced with 1-year dry summer conditions, in part because sapling stem density had the opposite response of larger trees. Stem density and radial growth were generally more sensitive to moisture than warming; excluding disturbances and saplings, warming had little effect on carbon accumulation (Extended Data Fig. 1). Deciduous and coniferous dominated forests had similar NPP relationships to climate conditions (Extended Data Figs. 2 & 3). Results suggest near-term direct forest growth response to moderate warming will be limited compared to indirect responses through intensified disease and insect infestations and sapling dynamics in the eastern US. Notably, increased disease and insect infestations had a stronger association to warming, rather than drying conditions as commonly suggested[7] (Extended Data Table 3), potentially because eastern US forests are not generally moisture limited[17] despite being sensitive indicators of drought and pluvials[18].

A challenge for climate mitigation planning and forest management is to predict future carbon sequestration and density of forests recovering from historic land use in the context of climate change[4]. We used ESM as a basis for projecting current forest change into the future under different disturbance regimes and climate conditions. Here we take a simple approach and connect all plot level vectors by matching the ending density (mean diameter and relative density) of each plot to the starting density of a similar plot, in a space for time substitution. When run forward in 5-year increments, the density of every plot changes to follow the trajectory of the connected plot and the average of all plots progresses toward steady-state (Extended Data Fig. 4). Notably projections do not include future CO_2 fertilization. Under current conditions, average unmanaged forests of the eastern US would reach a steady-state density in ~145 years gaining +43.5 Mg C ha^{-1} for a maximum vegetation carbon sink of 112±7 Mg C ha^{-1}, with a density of 281±10 stems ha^{-1}, mean tree diameter of 34.2±0.7 cm (Figs. 1 & 3). Management (i.e. logging), changing climate, and disturbance regimes produced substantial differences in future sink potential ranging from 72.2±2.2 Mg C ha^{-1} with current eastern US logging regimes (excluding permanently unmanaged forests) to 152.7±20.6 Mg C ha^{-1} in undisturbed forests (Extended Data Fig. 4). We found the future carbon steady-states were primarily related to the size of trees that died in self thinning forests ($p < 0.001$, $r^2 = 0.98$; Fig. 3). This relationship applied to scenarios that both enhanced forest growth (e.g. wet summers) and reduced forest growth (e.g. 5-yr dry periods), which suggests mortality influences long-term carbon storage in living biomass more than growth. Much work remains to understand why disturbances and climate changes are associated with variable tree mortality size in a global context and how these relationships will change in the future.

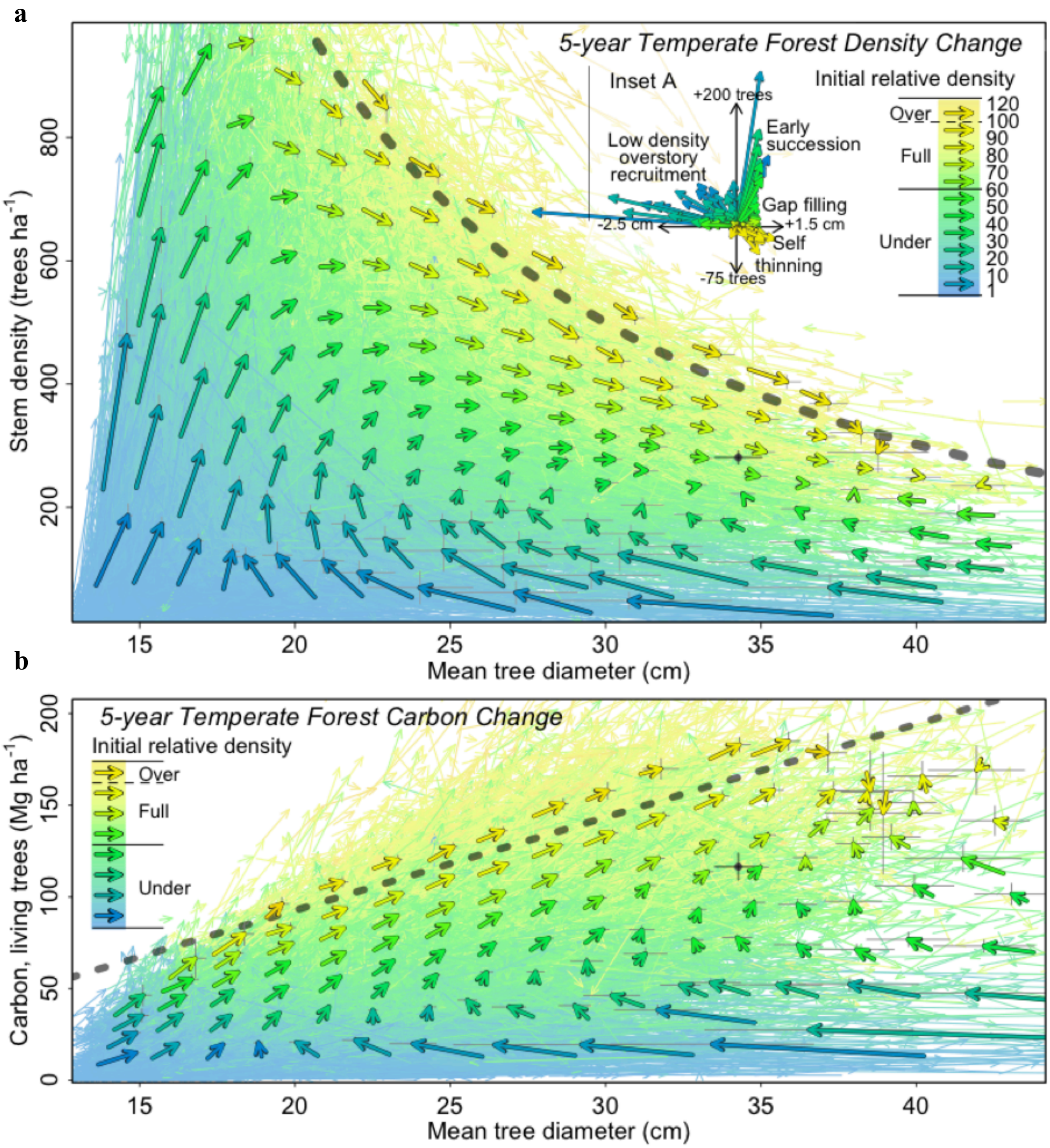


Figure 1. Empirical Succession Mapping for a) density and b) carbon. Measured changes in the number, size, and carbon stored in trees (n = 38,857) were independently averaged at increments of initial mean diameter and initial relative density (bold vectors) with bootstrapped error (±2SE; 1000 iterations, solid black lines); except for forests with initial mean diameters greater than 32 cm, where moving averages were used due to high probability of mortality (30%) and recruitment (35%) making forests with these large mean diameters unlikely (4.5% of dataset). Inset A on panel A compiles mean density change vectors and highlights likely ecological processes driving observed changes. Grey points show projected mean steady-state density and carbon under current conditions with model uncertainty.

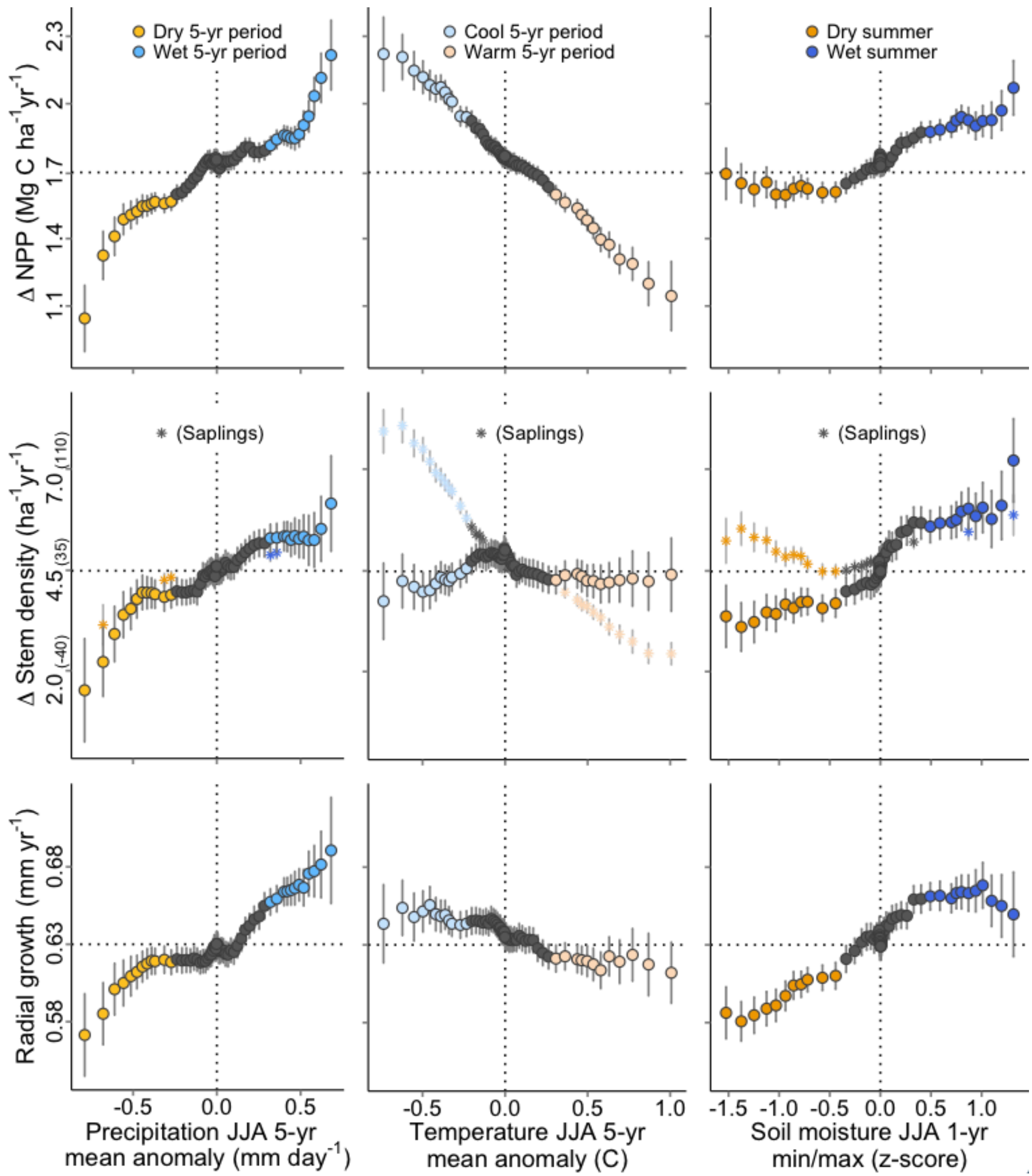


Figure 2. Influence of changing climate on forest structure. Change in net primary productivity, stem density and radial tree growth in forests that experienced unusually wet, dry, warm or cool summer (June-August) climatic conditions relative to a comparison null model (represented by the horizontal dotted line showing mean conditions of the null model). Points are a 20-percentile moving average (n > 350) with bootstrapped error. Sapling stem density is shown when relative change trends diverge with y-axis values shown in parentheses.

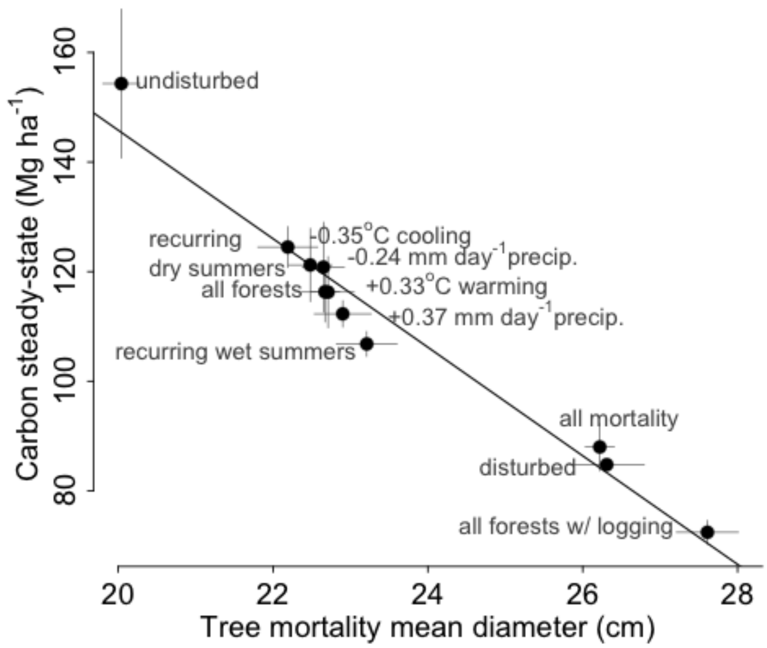


Figure 3. Projected vegetation carbon steady-states relationship to tree mortality size. The mean diameter of trees that die in self thinning forests ($D_{mortality}$; relative density > 60) under climate and disturbance conditions with error (±1.96SE) and the vegetation carbon steady-state for each scenario projected by the forward model (C_{sink}; Extended Data Figure 4) with model uncertainty (±1.96SD) were linearly related ($C_{sink} = -9.24D_{mortality} + 327$; $r^2 = 0.98$).

References

1 Change, I. P. o. C. *Climate Change 2013: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press, 2014).

2 Purves, D. & Pacala, S. Predictive models of forest dynamics. *Science* **320**, 1452-1453 (2008).

3 Seidl, R., SCHELHAAS, M. J. & Lexer, M. J. Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology* **17**, 2842-2852 (2011).

4 Pan, Y. *et al.* A large and persistent carbon sink in the world's forests. *Science* **333**, 988-993 (2011).

5 Bellassen, V. & Luyssaert, S. Carbon sequestration: Managing forests in uncertain times. *Nature* **506**, 153-155 (2014).

6 Friend, A. D. *et al.* Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO2. *Proceedings of the National Academy of Sciences* **111**, 3280-3285 (2014).

7 Anderegg, W. R., Kane, J. M. & Anderegg, L. D. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change* **3**, 30-36 (2013).

8 Foster, J. R. *et al.* Evidence for a recent increase in forest growth is questionable. *Proceedings of the National Academy of Sciences* **107**, E86-E87 (2010).

9 Caspersen, J. P. *et al.* Contributions of land-use history to carbon accumulation in US forests. *Science* **290**, 1148-1151 (2000).

10 Turner, M. G., Romme, W. H., Gardner, R. H., O'Neill, R. V. & Kratz, T. K. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology* **8**, 213-227 (1993).

11 Arner, S. L. *et al.* National algorithms for determining stocking class, stand size class, and forest type for Forest Inventory and Analysis plots. *Internal Rep. Newtown Square, PA: US Department of Agriculture, Forest Service, Northeastern Research Station. 10p* (2001).

12 Cochran, P., Geist, J., Clemens, D., Clausnitzer, R. R. & Powell, D. C. *Suggested stocking levels for forest stands in northeastern Oregon and southeastern Washington*. (US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 1994).

13 Reineke, L. H. Perfecting a stand-density index for even-aged forests. (1933).

14 Enquist, B. J. & Niklas, K. J. Invariant scaling relations across tree-dominated communities. *Nature* **410**, 655-660 (2001).

15 West, G. B., Enquist, B. J. & Brown, J. H. A general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences* **106**, 7040-7045 (2009).

16 Schellnhuber, H. J. *et al.* Turn down the heat: why a 4 C warmer world must be avoided. (World Bank, 2012).

17 Hanson, P. J., Todd, D. E. & Amthor, J. S. A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. *Tree physiology* **21**, 345-358 (2001).

18 Martin-Benito, D. & Pederson, N. Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. *Journal of Biogeography* (2015).
19 Team, R. C. (ISBN 3-900051-07-0, 2012).
20 Jenkins, J. C., Chojnacky, D. C., Heath, L. S. & Birdsey, R. A. National-scale biomass estimators for United States tree species. *Forest Science* **49**, 12-35 (2003).

Acknowledgments:

We acknowledge the immense field and data management efforts provided by FIA staff that made these analyses possible. Thanks to Ben Felzer, the Walt Cason lab, and numerous US Forest Service staff in the Northeastern Area office, for early review. MCD supported by NSF Macrosystems 1318164.

Author Contributions: T.D.A., M.C.D. and R.K.B designed the project. T.D.A. performed analyses and wrote the initial paper. All authors revised and commented on the manuscript.

Author Information: FIA data are publicly available from apps.fs.fed.us/fiadb-downloads/datamart.html. Climate data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at http://www.esrl.noaa.gov/psd/. Analysis R code is accessible via Github (github.com/wanderswest/ESM-FIA). Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to tda210@lehigh.edu.

Methods:

All data filtering, statistical analyses, and figure creation were performed using R version 3.1.2[19]. The commented R code and filtered dataset used for all analyses are available on Github (github.com/wanderswest/ESM-FIA). All raw data is publicly available with links provided below.

FIA data: The US Forest Service has measured or calculated hundreds of characteristics associated with millions of trees in a regular gridded sampling of forests across the US. Over the last decade these measurements have been standardized and repeated for forest plots on an approximate 5 year cycle. Measurements are made for trees larger than 12.7 cm diameter at breast height (DBH) on 0.067 ha plots (subplots). We subset the FIA (downloaded on 7/2013 from *http://apps.fs.fed.us/fiadb-downloads/datamart.html*) using the criteria in Extended Data Table 1 to create a robust dataset suitable to answer questions in this paper. FIA surveys are performed at the state level and due to the high quality standards, Louisiana, Florida, and West Virginia have less dense sampling than adjacent states, which is not expected to impact analyses presented here. Environmental characteristics (e.g. soil quality, microclimates) are expected to have a consistent influence on forest structure during the census interval.

We filtered the FIA to 38,857 forest interior plots composed of ~1.0 million trees (minimum diameter 12.7 cm) in the US east of -95W longitude, resurveyed at a 5.0±0.01 (mean±SE) year census interval between 1998-2012. We excluded seedlings, planted forests, and forests with edge effects (see criteria in Extended Data Table 1). Saplings (2.54-12.7 cm diameter) were excluded except for carbon calculations and as a response variable to climate conditions. Harvested plots (n = 4452) were used only in one future carbon sink projection. Vegetation carbon was estimated in the FIA for above and below ground portions of living trees greater than 2.54 cm in diameter, excluding foliage, and for dead trees greater than 12.7 cm in diameter, based on allometric relationships[20]. Carbon in saplings that die during the census interval is not estimated by the FIA, and instead was approximated using the initial survey carbon estimate, thereby making no contribution to net primary productivity (NPP) during the census interval. Therefore in plots with extensive sapling mortality, NPP is conservatively estimated. NPP was calculated for each plot over the census interval as the difference between carbon stored in living biomass at the initial survey and living and dead biomass at the second survey.

Plot-scale disturbance is denoted in the FIA as AGENTCD, identified by technicians in the field. Here we include disturbances that caused mortality of one or more trees during the census interval associated with insects, disease, fire, animals, weather. Specifically, disturbed trees were alive at the initial survey and dead at the resurvey with the AGENTCD identified as the cause of mortality, which impacted 31.0% of all forest plots and 34.3% of self thinning plots. Mortality associated with vegetative suppression/competition and unknown causes were expected to be largely associated with autogenic succession and were not considered disturbance. Notably, unknown disturbances were common, attributed to 45.4% of tree mortalities. Since disturbances (fire, insect, disease, animal, weather) may be difficult to identify and attribute to mortality in the field, undisturbed forest thinning rates may be conservatively estimated.

Climate conditions data: We used monthly 0.5^o x 0.5^o gridded datasets of historic climate data for 5-year mean precipitation (PREC/L) and surface temperature (GHCN_CAMS 2m), and 1-year maximum/minimum soil moisture (CPC), produced by NOAA from land-based instrument records spanning the last century (esrl.noaa.gov/psd). In the Eastern US, rolling 5-year average June, July, and August (JJA) summer climate conditions over the past two decades were identified for each grid cell. Summer climate was chosen as the most relevant period of growth and climate induced stress for forests of the Eastern US. Wet and dry 5-year water-year averages were also compared with similar results to Figure 3 except with larger error and less significance. For the one-year summer wet and dry anomalies, soil moisture was chosen as a more accurate measure than precipitation to infer forest water stress during extreme events. The soil moisture data is derived from a simple bucket model that integrates observations of temperature and precipitation to model water height equivalent in the top meter of soil. Soil moisture z-scores were calculated for each grid cell using the period from 1991-2012. Specific definitions of climate conditions used in each analysis are in Extended Data Table 2. Numerous additional climate condition comparisons, such as temperature variability and nighttime temperatures, could be assessed in future work.

Climate conditions during the census interval were assigned to each forest. Due to the dense and on-going nature of the FIA program, within each 0.5^o x 0.5^o grid cell, several forests have been surveyed over several different time periods. Here we exploit differences in climate between different survey periods within each grid cell to determine climate anomalies. Anomalies are differences of plot climate conditions from the median climate conditions of all forest plots within the grid cell. Anomalies were selected as quantiles of the overall dataset. The top and bottom 17th and 3rd percentiles (chosen because they are associated with 0.5^{o}C and 1.0^{o}C warming) were generally used to describe conditions associated with the climate anomalies (Extended Data Tables 2 & 3) except in Fig. 2 that uses a 20-percentile moving average and in the future projections steady-state model where approximately the top and bottom 30th percentile were used for increased data density.

Analysis Methods

Empirical Succession Mapping (ESM) models: The ESM is simple and similar to climatology where means are taken of many samples at the smallest representative resolution, which can then be used for comparison. The ESM density model averages changes in forest plot mean diameter and stem density along increments of mean diameter and relative density over the census interval of approximately 5.0 ± 0.005 years. Mean diameter is related to stand age however it is expected to be a superior proxy for successional status, particularly in mixed age forests. Notably however, the 500 forests believed to be the oldest, 122-255 years old, had a wide range of mean diameters, which suggests the steady-state density of an individual late successional forest follows a long-term, large-scale circulation of densities. Early testing of the ESM included building the density model using density change measured over two consecutive resurveys, which produced a similar but less well defined ESM due in part to a smaller dataset.

Figure 1 is the visual portrayal of ESM density and carbon models primarily valuable for displaying forest ecological concepts. The bold dashed lines on Figure 1 are the best fit to delineate the boundary between fully-stocked and overstocked forests. In the density model, the best fit power law in the form of equation (1), is b = -1.75 and Y_0 = 189632. The function was identified using a linear quantile regression through log-transformed self-thinning forests (i.e. relative density > 60). The 0.9 quantile was chosen to visually delineate the fully-stocked boundary best.

$$\textit{Stem density} = Y_0 \cdot \textit{Mean diameter}^{(b)} \qquad (1)$$

Early successional forests were generally defined by small diameter trees and a rapid recruitment into the 12.7 cm minimum diameter size class (Fig. 1A inset) and rapid carbon accumulation. Because recruitment and carbon accumulation transition gradually throughout the ESM, without clear boundaries between successional phases, stem density and carbon accumulation change associated with early succession provided in the main text were the maximum mean change rates found in the ESM models. Surprisingly, simply considering all forests with small diameters (i.e. <18.5 cm) as early successional, resulted in carbon accumulation rates nearly identical to the average of all forests, which may suggest rapid carbon accumulation is more common at mean diameters smaller than 12.7 cm and that many small mean diameter/low density forests accumulate carbon slowly.

The best fit line for Fig. 1B is linear with a slope of 5.6 and intercept of -19.4. The line represents the combined allometric equations for forests of the eastern US.

Climate sensitivity: The ESM models were created as a basis for comparison of density and carbon change under specific conditions (conditional data). Generally, comparisons of thinning rates were robust across temperate forest types and mean temperatures, however, magnitude of density change is sensitive to these factors. Specifically, building ESM null models for magnitude comparisons of small influences, such as observed climate anomalies, required a few additional considerations to maximize sensitivity and minimize biases. Null models were based on forests that experienced non-anomalous climate with conditions between the 30th to 70th percentile. We expect climate anomalies had a consistent effect across microclimates. Null models used mean change vectors at even 2-cm increments of mean diameters and even 10 unit increments of relative density, with a minimum mean vector sample size of $n > 25$, which produces a model nearly identical to the general pattern in Fig. 1 with some exclusion of fringe vectors due to small sample sizes. Data for null models is selected from the same 0.5^{o}x0.5^{o} grid cells with the same weighted frequency of sampling as in the conditional data. Spatial weighting was based on a simple weighted average using the proportion of conditional data to null data within each grid, such that change in null model variables better reflected change associated with the condition rather than spatial covariates such as temperature. Simply put, a spatial weighting factor was derived from the number of conditional data points in each grid divided by the total number of points in that grid cell. The null model is then built with data that is multiplied by the associated spatial weighting factor and divided by the average spatial weight within each mean diameter/relative density grouping. (Refer to Appendix A for exact implementation). Analyses were also run without spatial weighting, which produced similar results with larger uncertainty. A separate warming climate sensitivity analysis was also run comparing change in NPP at each conditional plot to change in the three closest plots (in distance) without warming that were of similar mean diameter, relative density and forest type (deciduous or coniferous). Results of this analysis showed reductions in NPP associated with warming were within error of the previous results.

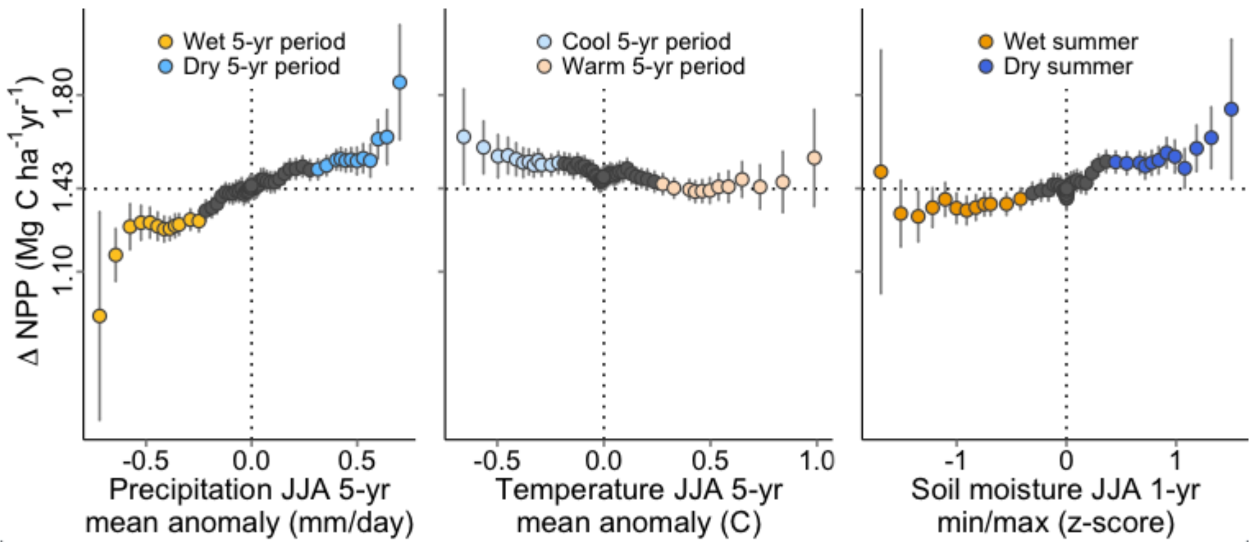
Rates of change are generally calculated per year by dividing change by the census interval. Note however, linear rates of change likely oversimplify the impact of dry and wet summers that are 1-year events within a 5-year census interval. Bootstrapped confidence intervals (1.96SE, 1000 iterations) were applied to the difference between the trajectories of all the conditional data from the associated null model. Conditional datasets were smaller than null models with larger standard error, and as such, significance was determined if conditional data confidence intervals did not overlap the null model mean represented by the horizontal dashed line in Fig. 2. Radial tree growth is featured in Fig. 2 as a useful measure that exclusively looks at the influence of climate conditions on diameter growth of living trees rather than mean diameter change that integrates growth, mortality and recruitment.

Climate conditions are expected to influence forest change through direct mechanisms (e.g. Q10 relationships) and by correlating with disturbance and other climate conditions (e.g. drought during warm periods). In Extended Data Table 3, for each climate condition, the likelihood of also experiencing specific disturbances or alternative climate conditions relative to the likelihood of occurrence in the null dataset is given ("Difference (%)") with the number of occurrences ("n"). Null dataset values were weighted to match the spatial distribution of the conditional dataset. Here the ESM was not used as the basis for comparison. The difference between the datasets indicates whether the disturbance agent or climate condition is more or less common in the conditional dataset.

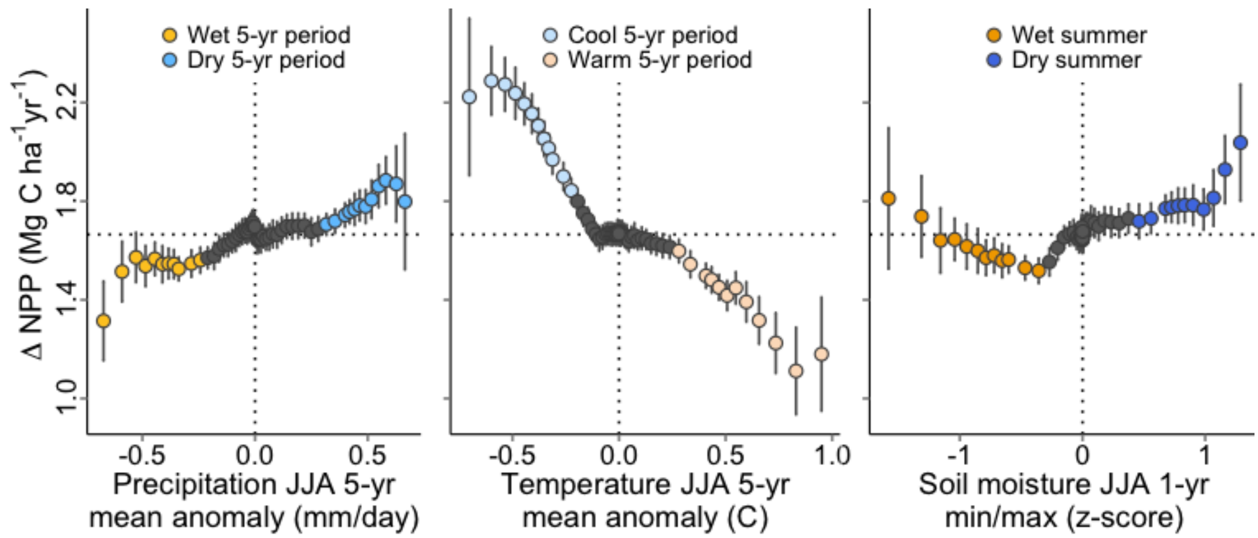
Forward steady-state model: Future vegetation carbon and structural projections were made using a forward modeling-type method. The forward model is merely a computationally intensive weighting process of existing empirical data and no new data were manufactured. The method starts by connecting the end of all resurvey vectors that underlie the ESM carbon model to the start of a nearby vector; then repeating the connection process with the new vectors for the desired number of iterations. Nearby is defined as within a gridded bounding box with increments of 0.5 cm mean diameter and 10 relative density up to overstocked forests that were grouped together as the largest relative density increment. To avoid missed connections in forests with mean diameters larger than 32 cm, the grid was enlarged to increments of 2 cm mean diameter and 20 relative density; and all forests with mean diameters greater than 40 cm were put into the 40 cm mean diameter bin. The 40 cm truncation was determined to be the largest mean diameter that allowed all vectors to connect with each other. Without this truncation, the carbon trajectory and sink potential of average forests was similar although there was a considerable loss of data where vector ends had no nearby starting vector. Lumping forests with diameters greater than 40 cm assumes these forests have similar likelihood for growth and disturbance. Within each connection grid, start vectors were randomly selected. If more vectors ended in the connection grid than started, start vectors were randomly repeated. Finally, in the rare occurrence that any vectors ended without trees, they were started in the grid cell with the smallest mean diameters and lowest relative density. This process of restarting forest growth assumes the presence of large saplings, which if saplings are not present or if the land will not return to forest, may slightly overestimate or underestimate average eastern US forest density, respectively. Starting with the whole forest dataset, each scenario was implemented by connecting exclusively to forests with that condition. Climate scenarios were ramped up in intensity and the maximum intensity that reached a steady-state were used. Climate conditions were generally mild because extreme conditions (e.g. +1.0^{o}C warming) did not have enough data to cycle density and therefore did not reach steady-state. The model was run for 60, 5-year iterations and most scenarios reached a density steady-state within 150 years generally composed of 1/3 unique original vectors. Model uncertainty was assessed by running each scenario 10 times using equal sized data sets (n=7202; i.e. 95% of the smallest dataset) randomly selected at each iteration and then taking the standard deviation of the final steady-state densities (each based on the final 10 iterations).

Each of the climate scenarios were implemented gradually over the first four iterations (20-year linear ramp) to mimic slow projected change in climate over the next few decades. Climate scenarios were considerably less extreme than those expected in the distant future but were useful to assess controls on steady-state density.

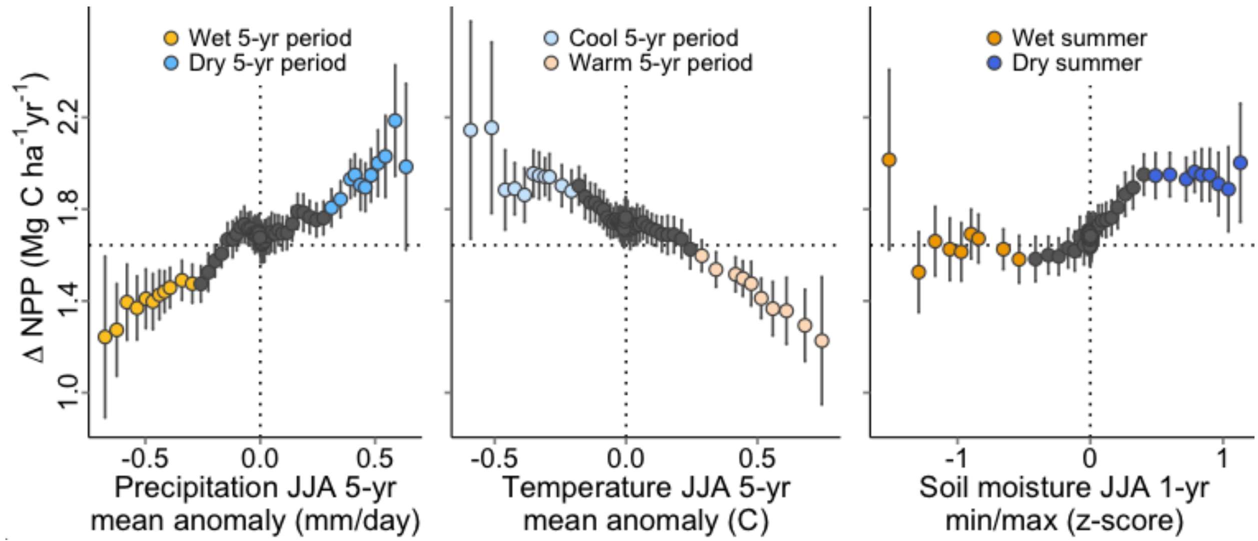
Extended Data:



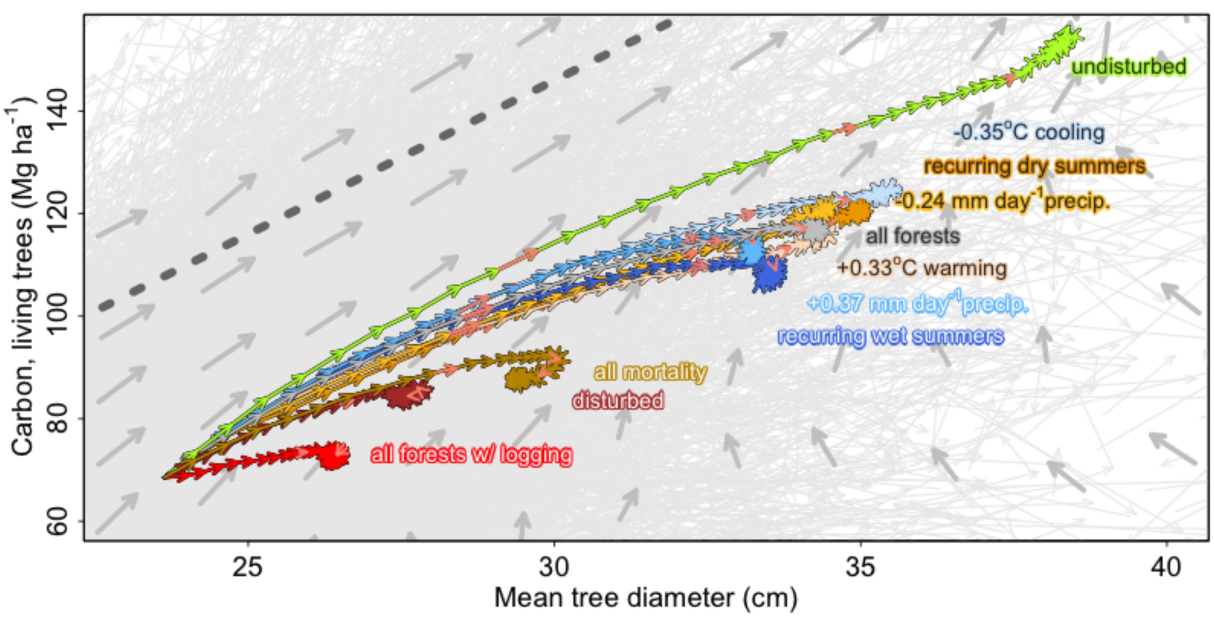
Extended Data Figure 1. Change in net primary productivity for forests without disturbances and excluding saplings for climate conditions relative to a comparison null model (represented by the horizontal dotted lines). Points are a 20 percentile moving average (n > 5) and rates of change are per year with bootstrapped error (±1.96SE; 1000 iterations, solid black lines.



Extended Data Figure 2. Deciduous forest change in net primary productivity for climate conditions relative to a comparison null model (represented by the horizontal dotted lines). Points are a 20 percentile moving average (n > 10) and rates of change are per year with bootstrapped error (±1.96SE; 1000 iterations, solid black lines).



Extended Data Figure 3. Coniferous forest change in net primary productivity for climate conditions relative to a comparison null model (represented by the horizontal dotted line). Points are a 20 percentile moving average (n > 10) and rates of change are per year with bootstrapped error (±1.96SE; 1000 iterations, solid black lines. Notably, a dominant forest species was not attributed by the FIA to 15% of the dataset.



Extended Data Figure 4. Eastern US temperate forest vegetation carbon forward steady-state model results for unmanaged forests (all forests), all forests under moderate climate conditions, forests with mortality, forests with plot-level disturbance, and all forests including those harvested during the census interval (all forests w/ logging). Scenarios are run forward 300 years and each vector represents change over 5-years with salmon colored vectors indicating 50-year increments. Each scenario reaches steady-state where density remains fairly constant.

Extended Data Table 1. FIA data filters used to select forest plots for density change analysis.

Data filter goal	**FIA filter method**	**FIA/R reference**
Sample forest interiors and exclude sharp edge ecotones	Plots have only 1 condition	CONDmax = 1
Plots have tree(s) that have been resurveyed	Plots had at least one tree at first survey	PREV_STOCKING > 0
Exclude plots with previous survey error(s)	Exclude plots with reconciled trees i.e. RECONCIDCD>4	STATUSCD ≠ 0 or 3
Exclude plots with trees unknown to be alive or dead	All trees must have a status	STATUSCD = 1 or 2
Plots are all the same size	Plots are all national standard FIA design	DESIGNCD = 1
Plots resurveyed after ~5 years and outliers removed	Exclude plots resurveyed over less than 3 years or more than 9.5 years	REMPER ≥ 3 and ≤ 9.5
Exclude saplings and seedlings	Exclude trees with DIA<5in. (12.3 cm)	DIA ≤ 5
Eastern US defined as east of -95 W longitude	Exclude trees west of -95W	LON < -95
Only plots used by USFS to calculate growth	Merge subset data with all live trees from the TREE_GRM_ESTN table	ESTN_TYPE = AL
Use only breast height tree diameter measurements	Use DIA measurements from TREE_GRM_ESTN table	DIA = DBHcalc
Exclude artificially regenerated forests	Select only naturally occurring forests	STDORGCD = 0
Exclude trees not part of the resurvey plot	Exclude any trees not used in the TREE_GRM_ESTN table	P2A_GRM_FLG ≠ "N"

Extended Data Table 2. Climate anomaly descriptions, mean condition values and number of samples.

Climate condition	Description	Steady-state model (Ss)	17^{th} percentile	3^{rd} percentile	n (Ss/17^{th}/3^{rd})
Wet 5-year period	Anomalously high mean June-August precipitation during the five-years prior to forest resurvey.	0.37 mm/day	0.44 mm/day	0.68 mm/day	9979/ 4970/ 513
Wet summer	Maximum z-scored mean June-August soil moisture that occurred between 1-5 years prior to forest resurvey.	0.69 (z-score)	0.8 (z-score)	1.32 (z-score)	7582/ 4110/ 750
Dry 5-year period	Anomalously low mean June-August precipitation during the five-years prior to forest resurvey.	-0.24 mm/day	-0.39 mm/day	-0.61 mm/day	15484/ 5541/ 985
Dry summer	Minimum z-scored mean June-August soil moisture that occurred between 1-5 years prior to forest resurvey.	-0.53 (z-score)	-0.78 (z-score)	-1.37 (z-score)	14450/ 4568/ 1481
Warm 5-year period	Anomalously high mean June-August temperature during the five-years prior to forest resurvey.	+0.33°C	+0.50°C	+1.0°C	10308/ 4945/ 378
Cool 5-year period	Anomalously low mean June-August temperature during the five-years prior to forest resurvey.	-0.35°C	-0.36°C	-0.62°C	8593/ 5023/ 1161

Extended Data Table 3. Comparison of disturbance and climate condition binary frequencies that occurred in forests with top/bottom 17^{th} or 3^{rd} percentiles of climate conditions relative to forests with 30^{th}-70^{th} percentile of climate conditions (null model). Bootstrapped standard error (1000 iterations) of the difference calculation is provided and bold values indicate significance ($p < 0.05$).

		17^{th} percentile			**3^{rd} percentile**		
Disturbance/climate	Climate Condition	n	Difference (%)	SE	n	Difference (%)	SE
Fire mortality	5-yr Dry period	56	32.9	40.5	17	219	243.1
	5-yr Wet period	47	15.9	31.2	10	10	76.1
	Cool period	48	48.2	49.7	15	103	1036
	Warm period	59	94.2	68.9	20	122	508.6
Insect mortality	Dry summer	169	**-52.2**	14.5	-	-	-
	Wet summer	218	-37.5	25.9	-	-	-
	5-yr Dry period	246	**-17.6**	8.1	54	-5	18.4
	5-yr Wet period	335	**36.8**	13.9	67	84	39.7
	Cool period	312	**24.8**	12.1	86	44	25.8
	Warm period	254	-1.2	8.7	55	-3	19.9
Disease mortality	Dry summer	844	-28.4	16	155	-26	26.3
	Wet summer	849	-12.7	17.6	-	-	-
	5-yr Dry period	1091	7.5	5	251	10	9.9
	5-yr Wet period	1031	**25.2**	6.2	201	**36**	14.0
	Cool period	866	7	5.8	207	22	13.3
	Warm period	1299	**37.8**	6.5	342	**31**	11.8
Animal mortality	5-yr Dry period	49	6.3	29	8	-4	56.3
	5-yr Wet period	61	35.1	34.5	16	31	55.9
	Cool period	39	15.3	29.5	10	242	272.1
	Warm period	51	56.4	37.2	-	-	-
Weather mortality	Dry summer	614	**-51.5**	10.4	122	**-59**	12.3
	Wet summer	751	**-41.6**	13	153	**-60**	18.2
	5-yr Dry period	775	10.1	6	136	10	13.4
	5-yr Wet period	869	**41.5**	8	202	**90**	21.5
	Cool period	854	**21.8**	6.6	197	27	14.0
	Warm period	927	**31.0**	7.4	238	**42**	16.6
Dry summer	5-yr Dry period	1829	**100.4**	9.3	452	**176**	25.0
	5-yr Wet period	795	**-10.9**	5.2	166	-9	9.7
	Cool period	1086	**86.4**	10.8	269	**140**	36.3
	Warm period	1432	**142.3**	13.8	294	**121**	27.4
Wet summer	5-yr Dry period	555	5.5	6.6	75	-4	14.4
	5-yr Wet period	2098	**391.6**	25.5	516	**748**	95.9
	Cool period	1471	**156.6**	15.2	369	**205**	36.0
	Warm period	1324	**104.4**	11.3	345	**94**	20.1
5-yr Dry period	Dry summer	1742	**236.9**	79.6	518	619	389.9
	Wet summer	468	**-73.7**	4	46	**-48**	23.8
	Cool period	820	**103.9**	11.8	283	**349**	60.7
	Warm period	2224	**379.5**	25.3	531	**623**	78.0
5-yr Wet period	Dry summer	416	**-64.6**	5.1	77	**-52**	12.9
	Wet summer	1719	**-35.8**	7.2	385	**-47**	9.2
	Cool period	1699	**137.1**	12.3	260	**93**	22.3
	Warm period	455	**-42.6**	3.5	7	**-97**	1.2