BULLETIN

New Evidence of Tree Species on the Move

MAY 31, 2017 / BY JENNIFER HUSHAW

There has been significant debate and research about where, how quickly, and to what degree our forests will shift with the changing climate. These questions have primarily been tackled through modeling (e.g., see Modeling Future Forests bulletin) or studying plant response in the distant past through paleoecology. Quite a bit of uncertainty remains because we do not have complete information about the physiological limits, tolerances, and life history traits of all species, or a good understanding of how changes in relative competiveness will play out (Corlett & Westcott 2013). The paleo record offers us a few examples of vegetation response to abrupt climatic change, but we are generally limited to episodes that were far more gradual than the relatively rapid warming we see today (Williams & Burke *in press*). There is also the confounding factor of human influence on the landscape, via land use, forest management, wildlife management, introduction of new species, and so on.

Given this uncertainty, researchers have used recent observational data to detect early signs of tree species migration and ecosystem shifts. The results have been mixed, as to whether large-scale shifts are underway and whether they are due to climate change. In this bulletin, we highlight a noteworthy new study in the eastern U.S. that shows evidence of significant changes in abundance for a number of tree species. We look at how these results compare with previous research, highlight some overarching themes, and conclude with action items for managers.

New Evidence of Tree Species Shifts

A recently published study by Fei et al (2017), entitled *Divergence of species responses to climate change*, found "prominent westward and poleward shift in abundance for most tree species in the eastern United States during the last 30 years." The study provides evidence that eastern tree species are responding to recent changes in climate, and the details of their findings highlight the individual responses of different species groups.

WHAT THEY DID

Researchers used tree abundance data from the U.S. Forest Inventory & Analysis (FIA) program for 86 species/groups in the eastern U.S. They looked at shifts in abundance between two inventory periods: 1980-1995 (depending on the state) and 2015 (the most recent completed year)—with an average window of about 30 years. They analyzed the relationship between observed species shifts and climate (specifically, mean annual temperature (MAT), total annual precipitation (TAP), and Palmer Drought Severity Index (PDSI)), as well as forest succession status. They also looked at whether there were differences in species response depending on functional traits (drought tolerance, wood density, and seed weight) or evolutionary lineage.

WHAT THEY FOUND

- **Distinct spatial patterns**
    - 73% of species shifted their abundance centers westward *
    - 62% of species shifted their abundance centers poleward **
    - Shifts were primarily due to changes in subpopulations at the leading edges
    - There were regional differences in the primary direction of abundance shifts:
        - Northern Hardwood = poleward
        - Central Hardwood = westward
        - Southern Pine-Hardwood = westward
        - Forest-Prairie Transition = westward
    - Sapling abundance shifted in higher proportions (and farther) than adult tree abundance
    - Longitudinal shift was 1.4 times faster than latitudinal
    - Observed a poleward shift rate of 11.0 km per decade, similar to estimates from previous studies
- **Influence of climate and succession**
    - Changes in abundance were more strongly related to moisture (precipitation and drought index) than temperature
        - "…changes in mean annual precipitation alone explained about 19% of the variability in species abundance change and spatial shift."
    - Early successional forests had more gains in abundance than forests in late successional stages
- **Different shifts depending on traits and evolutionary lineage**
    - Influence of physiological tolerance and dispersal ability
        - Generally, species that shifted westward had larger seed size and higher wood density than species that shifted eastward
        - Species with medium to high drought tolerance shifted westward at a faster rate than those with low drought tolerance
        - Species that shifted northward were associated with lower annual precipitation and lower wood density than southward shifting species
        - Wind-pollinated species primarily shifted northward, while animal-pollinated shifted southward ****
    - Influence of phylogeny (evolutionary lineage)
        - 81.5% of angiosperms (hardwoods/flowering plants) shifted westward ***
        - 71.4% of gymnosperms (softwoods/non-flowering plants) shifted northward, along with all poplar and most birch species

* 65% of these were statistically significant
** 55% of these were statistically significant
*** 52.3% of these were statistically significant
**** Similar northward shifts occurred in New England 10–8K years ago (during the early Holocene)

WHAT IT MEANS

The results of this study suggest some interesting implications for tree species migration in the eastern U.S., including the following highlights from the discussion section:

- Vegetation dynamics appear to be a more sensitive to moisture than temperature, at least in the near-term.
- While the western portion of the study area is drier than the east, it experienced an increase in total annual precipitation over the study period, suggesting that drought tolerant species shifted westward because they could more readily take advantage of the increased moisture.
- Poleward shifts were more prominent at higher latitudes, where the greatest warming has taken place to date.
- The stronger trend observed for saplings supports the idea that saplings will respond more quickly to climatic change and exhibit greater sensitivity to drought than adults.
- Results support the idea that initial changes will be most prominent at species range margins, particularly the leading edge.
- Gymnosperms have less efficient water transport systems that lead to lower maximum growth rates (compared with angiosperms), so their primarily northward shift may be due to a lack of competitiveness in the drier western region of the study area.
- Seed size may be an important factor because it is linked to different colonization, tolerance, and competitive strategies used by different species.
- Higher wood density is often associated with greater survival, which may explain the preferential shift of high wood density species into the droughty (southern) and relatively dry (western) portions of the study area.
- Non-climatic factors also played a role, including successional processes, forest densification related to fire suppression, and (potentially) infestations (of pests, plants, and pathogens), forest conservation, and plantation efforts.

Previous Research

Numerous studies have documented species range shifts that are consistent with what we would expect in a warming world, namely upward shifts in elevation and latitude, for plants and many other types of organisms (Root et al 2003; Parmesan & Yohe 2003; Parmesan 2006; Chen et al 2011). For tree species, in particular, these types of elevational or poleward shifts have been previously documented in temperate (Lenoir et al 2008; Beckage et al 2008; Woodall et al 2009; Wright et al 2016), boreal (Soja et al 2007), and even tropical (Feeley et al 2011) biomes.

Although, the studies that have detected changes (including Fei et al 2017) show discernible shifts for only some fraction of species. Not all tree species are responding (yet), and some are responding in ways we might not expect, including instances of downhill shifts (Crimmins et al 2011) and the expansion of some species into more southerly areas (Woodall et al 2009). This is due to the complex array of factors that influence where and how tree species will grow, and researchers have cited a number of these to explain the apparent lack of movement or counterintuitive shifts among some species, including competition from established species, changes in moisture availability, adaptation, and so on.

In some cases, we also see contradictory results. For example, a 2012 study by Zhu and colleagues examined FIA data for over 90 species in the eastern U.S. and they found that only ~20% of species showed a pattern of northward shift (with close to 60% exhibiting evidence of range contraction) and no apparent relationship between these observed patterns and seed size, dispersal characteristics, or degree of climate change, which is in contrast to the findings of Fei et al (2017). However, the two studies used different methodologies, which may explain the difference. In fact, the issue of methodology has been pointed to as a partial explanation for the lack of evidence of species shifts to date. Shifts may be happening that our methods can't sufficiently detect because of challenges with accurately identifying species range margins and data availability across entire species' distributions (Jump et al 2009).

In fact, previous studies have used a variety of a different approaches to determine whether species are on the move, including comparing the average latitude of tree biomass with the average latitude of seedlings for a given species (Woodall et al 2009), comparing the 5th and 95th percentile latitudes for seedlings and trees (Zhu et al 2012), assessing change in the average elevation of recruitment over time (Wright et al 2016), and others. Fei et al (2017) is different from many preceding studies in using abundance data throughout the species range, rather than focusing solely on range margins for detecting changes.

Take Homes

Despite the inherent uncertainty in forecasting future forests, current scientific understanding suggests some general rules-of-thumb regarding tree species shifts, such as:

- Tree species will respond independently, not as cohesive forest types
- Significant time lags are likely
- There is potential for faster change with mortality from extreme events
- Changing moisture availability will likely be more important than changing temperature for driving species shifts in the near-term
- Most species will experience climate conditions that are novel for that species (in some portion of their range)
- Look for initial forest composition changes at range margins
- Look for initial changes in regeneration, rather than the overstory
- Uncertainty is not *if* tree distributions and abundance will shift, but exactly *where* and *when*
- Generally, we expect…
    - Range expansion at the leading edge (northern and higher elevations)
    - Range contraction at the trailing edge (southern and low-altitudinal limits)

The Fei et al (2017) study supports many of these and also provides a useful illustration of how to think about these types of changes. This is often framed as a question of whether a particular species will disappear from the landscape in the next 50 to 100 years (e.g. Will all the sugar maple disappear from New England?), but the more relevant question(s) should be things like:

- Will the species become more or less prevalent (in terms of relative abundance)?

- How will changes in relative competitiveness manifest?
- Will the species experience growth declines due to less optimal climate conditions and/or a reduced capacity to fend off threats, such as insect infestation?
- Is the overall species range likely to shift, contract, or expand in the long-term?

Things to Do

Two important things managers can do are (1) monitor and (2) promote regeneration. Monitoring includes watching for changes in the forests you manage (e.g. changes in moisture availability or in regeneration success, relative abundance, and/or competitiveness among species) and keeping an eye on the results of large-scale studies like the new research highlighted here. This is especially important in light of the distinct regional differences observed by Fei and colleagues. This will also be an important component of the Resiliency Assessment Framework that is currently under development, which is designed to provide informative metrics for detecting the impacts of climate change on North American forests.

Regeneration is the phase when species have the best opportunity to express adaptation to new climate conditions through phenotypic plasticity and it is the mechanism of species migration, so promoting regeneration can be the first step in moving a forest stand toward a condition/composition that may be more resilient in the face of changing climate conditions.

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