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PERSPECTIVE

Who is the new sheriff in town regulating boreal forest growth?

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Climate change appears to be altering boreal forests. One recently observed symptom of these changes has been an apparent weakening of the positive relationship between high-latitude boreal tree growth and temperature at some sites (D'Arrigo *et al* 2008). This phenomenon is referred to as the 'divergence problem' or 'divergence effect' and is thought to reflect a non-linear relationship between temperature and tree growth, where recent warming has allowed other factors besides growing-season temperature to emerge as dominant regulators of annual growth rates.

Figure 1 demonstrates this divergence phenomenon with records of tree-ring widths collected from 59 populations of white spruce in Alaska¹. Key tendencies among these populations include: (1) growth is most sensitive to temperature during relatively cold growing seasons (figure 1(a)), (2) populations at colder sites are more sensitive to temperature than those at warmer sites are (figure 1(a)), and (3) growth at warmer sites may respond negatively to increased temperature beyond some optimal growing-season temperature (figure 1(b)). Since temperature is rising rapidly at high latitudes, one interpretation of figures 1(a) and (b) is that warming has promoted increased growth at colder sites, but caused growth to plateau or slow at warmer sites. Corroborating this interpretation, satellite imagery and tree-ring data indicate increasing vegetation productivity near the forest-tundra boundary but declining productivity in warmer regions within forest interiors (e.g., Bunn and Goetz 2006, Beck and Goetz 2011, Beck *et al* 2011, Berner *et al* 2011).

Will continued warming cause a northward migration of boreal forests, with mortality in the warmer, southern locations and expansion into the colder tundra? This question is difficult to answer because many factors besides temperature influence boreal forest dynamics.

Widespread productivity declines within interior boreal forests appear to be related to warming-induced drought stress (Barber *et al* 2000). Notably, this response may be more complicated than simply a decline in soil moisture. Even when soil moisture is plentiful, warming can negatively impact plant growth and survival by causing increased respiratory consumption of stored carbohydrates (McDowell 2011) and decreased stomatal conductance due to hydraulic limitation (Flexas *et al* 2004). Some degree of acclimation may be occurring, as white spruce populations that experience moderate temperatures and precipitation have lower optimal growth temperatures than populations at warmer, drier sites do (figure 1(c)). Yet, populations at the warmest or driest sites show strong growth declines during warm periods, consistent with a decline in the viability of these populations in some regions (Goetz *et al* 2005, Beck and Goetz 2011, Beck *et al* 2011). Can interior boreal forests acclimate to the current era's rapid warming? Or will temperatures within interior boreal forests outpace or extend beyond the adaptive capabilities of boreal tree species? The answer remains a mystery, partly because important aspects of acclimation are still poorly understood, and partly because of other important processes such as wildfire and increases in CO₂ concentration, nitrogen deposition, growing-season length, and tropospheric ozone concentration.

¹ Tree-ring data: <ftp.ncdc.noaa.gov/pub/data/paleo/treering>. Climate data: <snap.uaf.edu/downloads/alaska-climate-datasets>.

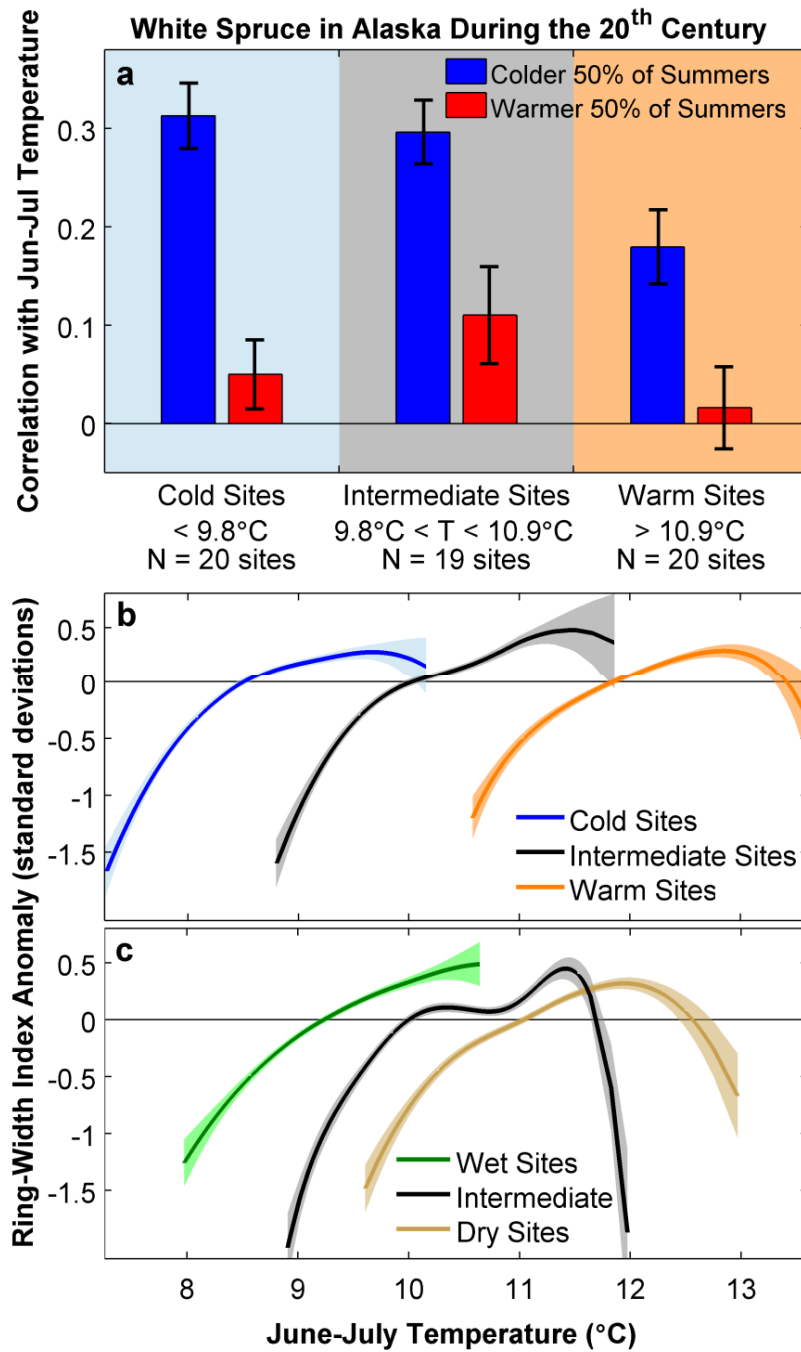


Figure 1. Relationships between white spruce tree-ring widths and climate at 59 sites in Alaska. (a) Annual correlation between ring-width index and June–July average temperature during years when June–July temperature was colder (blue bars) and warmer (red bars) than average. Pairs of bars represent the coldest 20 sites (left), 19 sites with intermediate temperature (middle) and the warmest 20 sites (right). (b) Spline curves that represent the best-fit relationship between temperature (*x*-axis) and ring-width index variability (*y*-axis) at cold sites (blue line), intermediate sites (black line) and warm sites (orange line). (c) Same as (b) but for the wettest 20 sites (green line), 19 sites with intermediate annual precipitation (black line) and the driest 20 sites (brown line). Error bars in (a)–(c) are standard errors.

Perhaps an even bigger mystery is what the future has in store at the cold ecotone where boreal forest gives way to arctic tundra. Just as for warmer sites, there tends to be a temperature threshold at cold and intermediate sites, above which further warming no longer positively influences growth rate (figures 1(a) and (b)). Rather than reverse sign once this threshold is surpassed, growth–temperature relationships at cold and intermediate sites tend to simply disappear or at least diminish. This is because metabolic rates are slow in the cold, but are optimal under moderately warmer conditions (Tjoelker *et al* 2009). As temperature increases into a range of variability that no longer limits metabolic rate, a host of other climatic and soil-related factors can limit or promote growth and seedling recruitment. At some cool treeline sites, rapidly rising temperatures may have already surpassed the level that supports optimal growth, as negative relationships have emerged between temperature and growth rate in most decades (McGuire *et al* 2010).

In a recent contribution to this important body of research, Andreu-Hayles *et al* (2011) studied growth–temperature relations within a white spruce population growing at the northern treeline in Alaska. Consistent with observations elsewhere in boreal forests, Andreu-Hayles *et al* discovered that a positive and significant relationship between ring widths and June–July temperature during 1901–1950 disappeared during 1951–2000. Interestingly, ring widths and temperature both increased throughout the 20th century at this treeline site, in contrast to recent trends at many other sites in Alaska where warming is outpacing ring widths (e.g., D’Arrigo *et al* 2008). At the site studied by Andreu-Hayles *et al*, it seems recent warming has caused a release of white spruce growth from temperature limitation and there is now a new sheriff in town regulating annual growth rate. Who this new sheriff is, however, remains an open and important question.

Another interesting result in the Andreu-Hayles *et al* study is that the relationship between temperature and density of tree-ring latewood (the dark band formed at the end of the growing season) was stable throughout the 20th century. This means that although temperature may no longer be the primary factor governing annual growth, it still has an important physiological impact at the end of the growing season. The stability of the latewood density–temperature relationship also offers a promising implication for dendroclimatic studies. While non-linear relationships between ring widths and temperature may make it difficult to use ring widths to infer information about historical temperature variability for some sites, Andreu-Hayles *et al* add to the evidence (e.g., Barber *et al* 2000, Davi *et al* 2003, D’Arrigo *et al* 2009) that latewood density may be particularly useful in reconstructing historical temperature at high latitudes.

While the divergence problem and new contribution by Andreu-Hayles *et al* are interesting on their own, they are also important because they highlight the current limits to our understanding of the mechanisms driving boreal forest growth and survival. As Allen *et al* (2010) pointed out, understanding and predicting the consequences of climate changes on forests is emerging as a grand challenge for global change scientists. This is particularly true at high latitudes because boreal forests store ~32% of Earth’s terrestrial forest carbon, more than twice that of temperate forests (Pan *et al* 2011). Will continued warming turn boreal forests into a sink or source of atmospheric CO₂? And will boreal forest growth and distribution change enough to significantly impact the energy balance of high latitude landscapes and thereby influence large-scale atmospheric circulation?

To answer these questions, it is critical to understand the factors influencing boreal forest growth under warmer conditions and how the relative contributions of these factors vary spatially. Our understanding of these factors can be improved through research campaigns that integrate field-measurements, remote sensing and ecological modeling (Goetz *et al* 2011). Field-studies that measure the physiological responses of trees to manipulations of environmental variables such as temperature, soil moisture, soil nutrients and insolation are critical for

informing ecological models that predict forest responses to various scenarios of climate and environmental change. Remote sensing is critical in validating modeled projections of forest growth. At present, ecological models do poorly at characterizing observed trends in boreal-forest productivity in some regions (Beck *et al* 2011). It will be exciting in the coming years to see how field measurements, modeling and remote sensing can work together to resolve the mysteries of the divergence problem, how warming will influence the overall productivity and distribution of boreal forests, and how changes in boreal-forest characteristics may influence regional and global climates.

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