

# NEW APPROACHES TO FIA DATA FOR UNDERSTANDING DISTRIBUTION, ABUNDANCE, AND RESPONSE TO CLIMATE CHANGE

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**Abstract.**—We are using Forest Inventory and Analysis data to examine evidence for tree responses to climate change. By comparing seedling and tree occurrence data, we found that there is not yet evidence that tree populations in the eastern half of the United States are shifting geographic ranges to higher latitude in response to warming temperature. We are developing novel statistical methods to quantify seedling abundance in relation to climate and biotic variables, and to compare seedling and tree responses. We summarize how combining abundance data for seedlings and trees is allowing us to identify differences in how trees respond to climate change in the eastern half of the United States.

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## INTRODUCTION

Forest Inventory and Analysis (FIA) data provide evidence for the effects of climate variation at broad geographic scales. We are using FIA data to quantify relationships between tree distributions and environmental variation as part of a larger study on the consequences of climate change.

First, to determine whether trees shift ranges to track warming climates, we compared geographic distributions of juvenile and adult trees based on the assumption that a migrating population is characterized by offspring extending beyond adults at leading edges and the opposite at trailing edges. Through comparisons of approximately 100 species

having range limits within the eastern United States (all states from Minnesota south to Louisiana and eastward), we found that there is not yet evidence for climate-mediated migration.

Second, to better interpret climate variables important for recruitment, we developed a novel zero-inflated statistical model for seedling counts with extreme incidence of zero observations. FIA seedling counts at plot level contain too many zeros to allow accurate inference using current models. Our zero-inflated general model, with  $k$  layers of zero-inflation ( $k$ -ZIG model) allows more flexible handling of both the zero-inflation and the nonzero counts. Whereas current zero-inflated models perform poorly, the  $k$ -ZIG model shows that seedling abundances can be explained by climate despite high proportions of zeros.

The third area we summarize here concerns the possibility that trees undergo ontogenetic niche shifts. We quantified the differences between juvenile and adult trees' climate relationships based on the FIA seedling and tree data. We are in the process of determining whether there are different patterns of ontogenetic niche expansion and contraction from juveniles to adults.

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## RANGE SHIFTS AND GEOGRAPHIC DISTRIBUTIONS

Anticipating whether species' geographic ranges can track climate change is a goal of global change research. Mean annual temperatures increased substantially during the 20th century in the Midwest and Northeast, but have only recently begun to show substantial change in the Southeast, where warming summers were balanced by cooling winters in the past (Fig. 1a). When viewed in terms of a climate change velocity, i.e., the ratio of temporal change over spatial gradient, regions in the Northeast and Upper Midwest have undergone climate shifts of more than 100 km during the 20th century (Fig. 1b).

Can tree distributions keep pace with the rapid climate warming? We used FIA data to directly compare seedling and tree 5th- and 95th-percentile latitudes for approximately 100 species for more than 40,000 plots across the eastern United States, and their relationship with climate change during the 20th century (Zhu et al. 2012). Our analysis is based on the rationale

that a population that is migrating north in response to warming is expected to have offspring extending to higher latitudes than adults in regions that have warmed over the last century, but not in regions where climate has remained essentially constant. Likewise, a population retreating from a warming southern boundary is expected to have adults south of the southern extent of new recruitment by offspring.

We found that there is essentially no evidence that latitudinal migration has yet occurred for more than half of the approximately 100 tree species in eastern U.S. forests and there is a substantial migration lag behind climate change velocity (Fig. 2). In fact, results suggest that approximately 60 percent of the tree species examined show the pattern expected for a population undergoing range contraction, rather than expansion, at both northern and southern boundaries. Fewer species show a pattern consistent with a northward shift and fewer still with a southward shift. Only about 4 percent are consistent with expansion at both range limits. Comparing results with the 20th-century climate changes that have occurred at the

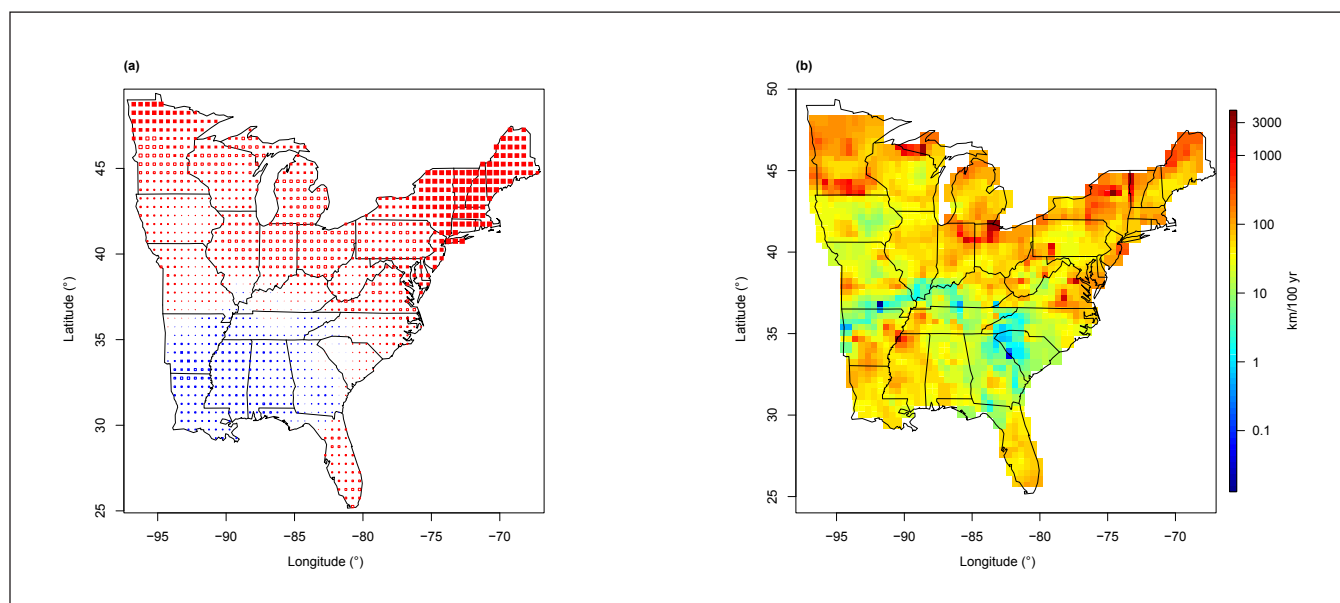


Figure 1.—Temperature change in time and space during the 20th century in the eastern United States. Data are extracted from 10 decadal mean annual temperatures from the Climate Research Unit dataset, 1901-2000 (Mitchell and Jones 2005). Squares in (a) denote the slope of the linear regression of decadal data (red – increasing trend, blue – decreasing trend); square size is proportional to the absolute value of the slope. Spatial velocity of temperature change (b) is defined as the quotient of the temporal gradient (a) and the north-south directional spatial gradient of temperature distribution (Loarie et al. 2009). Adapted from Zhu et al. (2012).

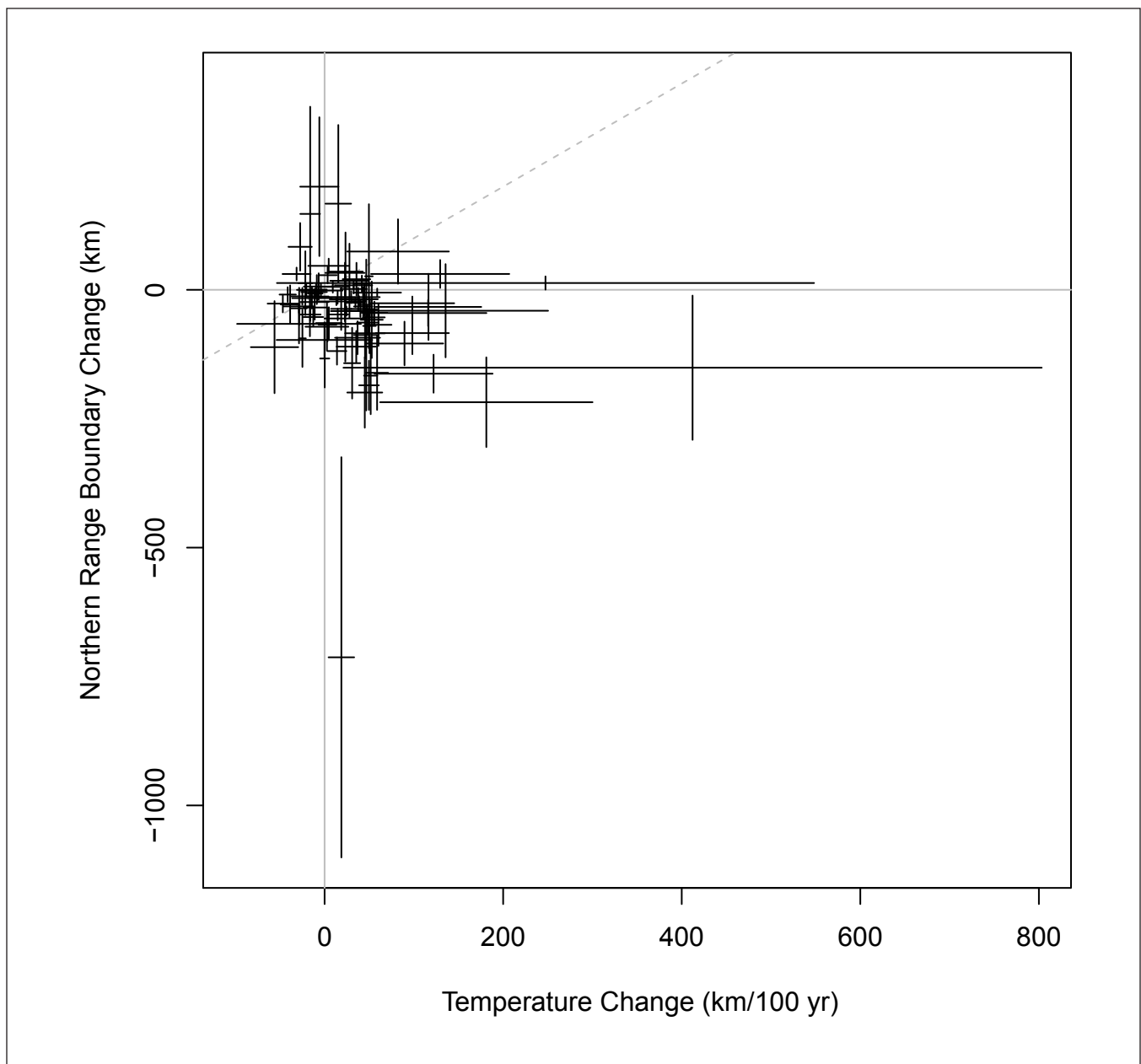


Figure 2.—Temperature change during the 20th century in comparison with latitudinal difference between seedlings and trees at northern range boundary. Each crosshair is a species with mean  $\pm$  standard error. Positive temperature change means temperature distribution is moving to the north; negative, moving to the south. Positive northern range boundary change means species is consistent with expansion at the northern range limit; negative means contraction. Species above the 1:1 line (gray dashed) may be tracking temperature change. Adapted from Zhu et al. (2012).

range boundaries themselves, we find no consistent evidence that population spread is greatest in areas where climate has changed most, nor are patterns related to seed size or dispersal characteristics. The fact that the majority of seedling extreme latitudes are south of those for adult trees should increase concerns for the risks posed by climate change.

## SPECIES ABUNDANCE AND CLIMATE RELATIONS

To explore the relationship between seedling abundance and variables that might be especially important for recruitment, we developed a novel zero-inflated statistical model for seedling counts with extreme incidence of zero observations. All species in the FIA data are absent in at least 60 percent of seedling plots, and some are absent from more than 90 percent of seedling plots.

In the statistical literature, zero-inflated count models, in particular, the zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) models, along with Poisson and negative binomial hurdle models, are commonly used to address this problem. However, these models struggle to explain extreme incidence of zeros (e.g., > 80 percent), especially to find important covariates. In fact, the ZIP may struggle even when the proportion is not extreme. To redress this problem we developed the class of  $k$ -ZIG models (Ghosh et al. 2012). These models allow more flexible modeling of both the zero-inflation and the nonzero counts. The models are fitted within a Bayesian framework.

For the FIA data, we fit the model for seedling abundance of two representative species: red maple (*Acer rubrum*) and yellow-poplar (*Liriodendron tulipifera*), with 62.7 and 93.8 percent of zeros, respectively. We used climate (winter temperature and annual precipitation) and biotic variables (basal areas of conspecific and all species) as covariates. Whereas current ZIP and ZINB models perform poorly, the  $k$ -ZIG model shows that, despite high proportions of zeros, the seedling counts could be explained by both types of variables.

## SPECIES' RESPONSES TO CLIMATE CHANGE

Biogeographic responses of plant species to climate change are determined by the requirements of juveniles, which can limit spread to new environments. However, most models of climate response are calibrated to adults, which may not reflect the climate that determined their original establishment. Despite a large literature on ontogenetic niche shifts in animals, there is little direct evidence for plants that could provide insight on the consequences of climate change for migration potential. Using the FIA data, we built a species distribution model to jointly quantify juvenile and adult trees' abundance distributions in relationship with the two most commonly used climatological variables, temperature and precipitation. To accommodate the mismatch between fine-scale biological processes and coarse-scale climate variables we introduced an aggregation approach to climate calibration. The fitted model allowed us to compare differences between juveniles and adults in climate relationships.

Adults and juveniles of a given species respond differently: some species showed broader climate calibrations for adults, whereas others showed broader climate calibration for juveniles. The differences could be partly because of ontogenetic niche shifts and partly because of other factors that impact climate response. For example, American hornbeam (*Carpinus caroliniana*) juveniles tend to be abundant in cold and dry climates relative to adults (Figs. 3a,b). The relative recruitment intensity, i.e., the ratio of seedling counts over tree basal areas, also shows cold and dry climate benefits juveniles while warm and wet climate benefits adults (Fig. 3c). Finally, the 90-percent volume under the fitted surface within the geographic range suggests a broader climatic niche for juveniles than adults (Fig. 3d). This pattern could be consistent with ontogenetic niche contraction, but there are alternative explanations as well.

Both types of ontogenetic niche differences could have important ecological implications. Niche expansion would be suggested when adult niches are broader

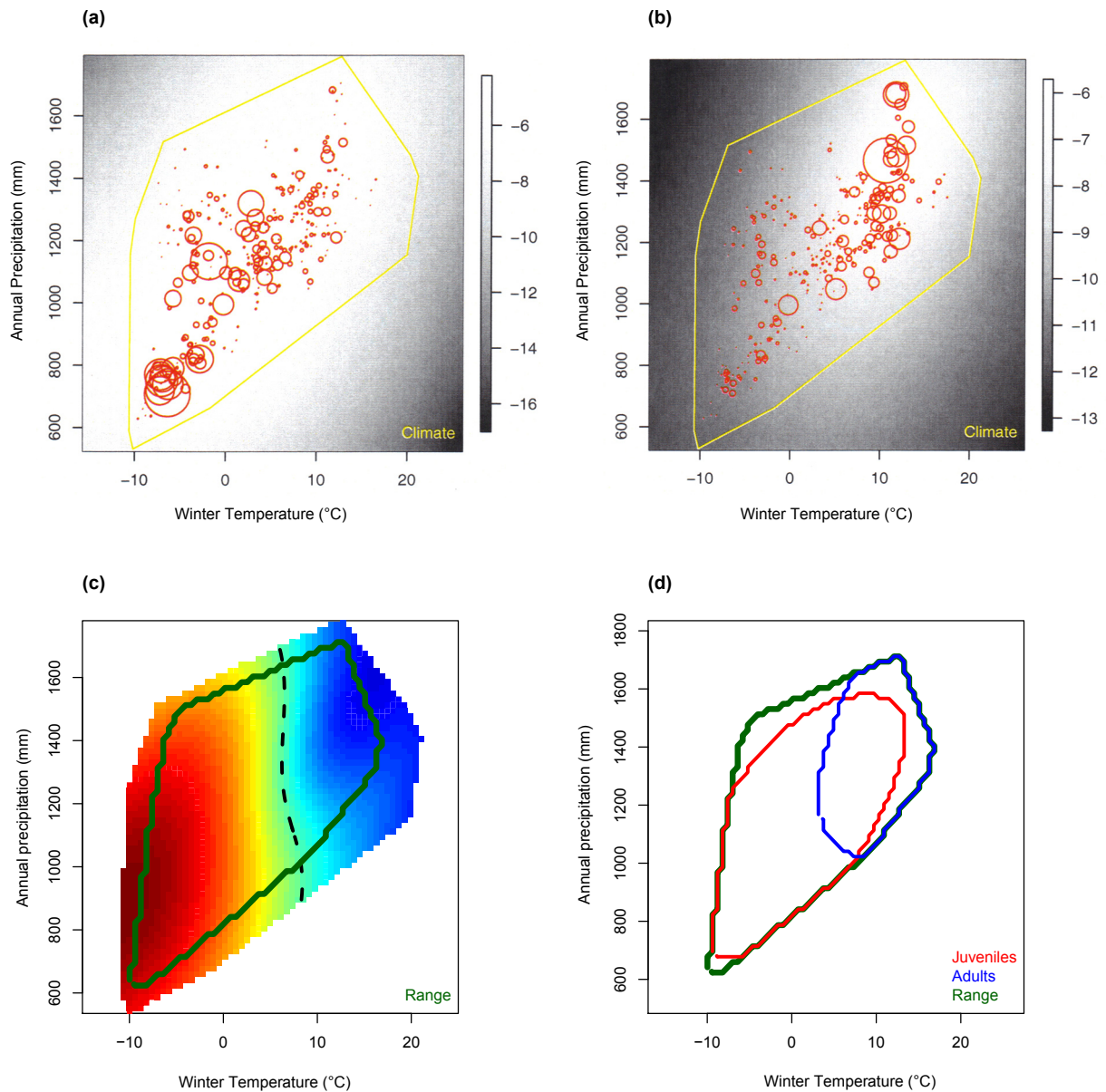


Figure 3.—Comparison of juvenile vs. adult of American hornbeam (*Carpinus caroliniana*) abundance surfaces as an example of ontogenetic niche shift. (a) is the observed (red bubble) and fitted (gray surface) seedling counts on log scale, with all available climate (yellow box) in the eastern United States. (b) is the observed (red bubble) and fitted (gray surface) tree basal areas on log scale, with the same climate boundary (yellow box). (c) is the relative recruitment intensity, defined as the ratio of seedling counts over tree basal areas on log scale. Warm colors show high values, cold colors show low values, and black dashed line shows zero references. It was calculated only within the available climate, superimposed with the actual geographic range mapped into the climatic space (green box). (d) is the 90 percent volume under the fitted surface within the geographic range (green box), where a large contour suggests a flat surface, and a small contour suggests a peaked surface. It approximates different climatic niche requirements for juveniles (red) and adults (blue).

than juvenile niches. This expansion could be expected if adults integrated over fluctuating windows for juvenile establishment in the past, while juveniles more narrowly reflect the current climate conditions. Seedlings can have narrower niche requirements owing to limited root systems, low carbon reserves, and reduced photosynthetic capacity. In contrast, niche contraction could be suggested by adult niches that appear narrower than those of juveniles. Contraction could occur if seeds can establish in sink populations, where they ultimately do not replace themselves due to competition or herbivory. We are examining a large number of species across the eastern United States to determine how climate calibrations of both adults and juveniles are impacted by climate change and the emerging role of new competitive environments and natural enemies.

## ACKNOWLEDGMENTS

The authors thank Chris Woodall for database assistance. The study was supported by National Science Foundation grants CDI 0940671 and Coweeta Long Term Ecological Research.

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