# Assessing the stability of tree ranges and influence of disturbance in eastern US forests

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## ABSTRACT

Shifts in tree species ranges may occur due to global climate change, which in turn may be exacerbated by natural disturbance events. Within the context of global climate change, developing techniques to monitor tree range dynamics as affected by natural disturbances may enable mitigation/adaptation of projected impacts. Using a forest inventory across the eastern U.S., the northern range margins of tree distributions were examined by comparing differences in the 95th percentile locations of seedlings to adults (i.e., trees) by 0.5° longitudinal bands over 5-years and by levels of disturbance (i.e., canopy gap formation). Our results suggest that the monitoring of tree range dynamics is complicated by the limits of forest inventory data across varying spatial/temporal scales and the diversity of tree species/environments in the eastern U.S. The vast majority of tree and seedling latitudinal comparisons across measurement periods and levels of disturbance in the study were not statistically different from zero (53 out of 60 comparisons). A potential skewing of ranges towards a northern limit was suggested by the stability of northern margins of tree ranges found in this study and shifts in mean locations identified in previous work. Only a partial influence of disturbances on tree range dynamics during the course of the 5-years was found in this study. The results of this study underscore the importance of continued examination of the role of disturbance in tree range dynamics and refined range monitoring techniques given future forest extent and biodiversity implications.

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## 1. Introduction

Given the importance of climate as a driver of numerous forest ecosystem functions (Stenseth et al., 2002), current and forecasted changes in climate (IPCC, 2007) have the potential to substantially affect forest ecosystem attributes and functioning (Ryan et al., 2010). The culmination of numerous climate change effects may ultimately be reflected in the contraction/expansion of tree species ranges (Walther et al., 2002; Malcolm et al., 2002; Parmesan and Yohe, 2003; Botkin et al., 2007; Chen et al., 2011). Tree ranges are dynamic with substantial documentation of their change over the course of millennia (Clark et al., 1998; Davis and Shaw, 2001; McLachlan et al., 2005; Pearson, 2006), as well as over recent decades (Woodall et al., 2009; Lenoir et al., 2009). In light of contemporary climate change, several observational investigations on plant species have indicated that current rates of range shifts may be greater than historic rates with a predominant focus on responses across elevation as opposed to latitude (Walther et al., 2005; Beckage et al., 2008; Holzinger et al., 2008; Kelly and Goulden, 2008; Lenoir et al., 2008; Harsch et al., 2009; Lenoir et al., 2009; Crimmins et al., 2011; Feeley et al., 2011; Van Bogaert et al., 2011). Correspondingly, it has been suggested that climate may change at a rate beyond the adaptability of tree species resulting in range contractions or extirpations (Clark et al., 1998; Malcolm et al., 2002; McLachlan et al., 2005; Iverson et al., 2008; Bertrand et al., 2011a). Unfortunately, latitudinal range shifts are poorly understood due to the requirement of large datasets across broad geographic scales (Woodall et al., 2009; Murphy et al., 2010; Zhu et al., 2012). Given the profound effects that climate change may have on forest biodiversity (Botkin et al., 2007) or even forest extent, monitoring the status and dynamics (e.g., effects of invasive species or disturbance effects) of tree ranges is paramount.

Due to the complex ecosystem dynamics that define current tree ranges, determining the causal agents of tree range shifts is difficult with individual tree species responding in an apparent idiosyncratic manner to climate change (Lenoir et al., 2008; Doak and Morris, 2010). The migratory response of tree species to climate

change events may depend on genetic attributes (Potter and Woodall, 2012), habitat quality/continuity (i.e., forest fragmentation; Schwartz et al., 2001), demography (Anderson et al., 2009), modes of seed dispersal (Iverson et al., 2008), competition (Moorcroft et al., 2006), and response to natural disturbance (i.e., canopy gap formation; Leithead et al., 2010). The monitoring of tree species ranges can be advanced by examining their variability over short time-steps and how factors such as forest disturbance influence them.

Within closed canopy forests, there is a wider suite of temperate tree species (e.g., *Acer rubrum*) that show preferential colonization in large canopy gaps compared to species that are more common to boreal environments (e.g., *Picea mariana*) in eastern North America (Leithead et al., 2010). Thus, habitat quality, competition, demography, and species-level adaptation likely interact to affect rates of species migration. Forest canopy gaps (i.e., tree fall gaps) are caused by the death and fall of a tree of sufficient size to result in an opening of the overstory canopy (Denslow, 1980). While canopy gaps may change tree competition dynamics in a rapid manner (Scheller and Mladenoff, 2005; Leithead et al., 2010), our understanding of the effects of disturbances such as forest canopy gaps on tree range shifts at large spatial scales have often been limited to simulation studies (Scheller and Mladenoff, 2005), with only localized, empirical examinations of the effects of canopy gaps on range shifts (Leithead et al., 2010). As such, there are key knowledge gaps related to the range-wide impact of canopy gaps on changes in tree species distributions.

Several approaches have been used to empirically assess large-scale shifts in current tree ranges, including examinations of tree occurrence across elevational gradients (Kelly and Goulden, 2008; Lenoir et al., 2008), comparisons of tree ranges from historical and contemporary inventories (Woodall et al., 2008), and comparisons of seedling and adult tree extent (Lenoir et al., 2009; Woodall et al., 2009), or some combination thereof. Numerous aspects of tree ranges have been examined, such as measures of tree range central tendency (Woodall et al., 2009) or tree range limits (Zhu et al., 2012). Taken together, refined understanding of the variability of tree range margins over short time-steps may be acquired through development of techniques that empirically assess tree range expansion/contraction and naturally occurring interactions across large scales. Using a large-scale forest inventory to examine northern range limits by life stage (i.e., seedlings versus adults; see Woodall et al., 2009), while considering the effect of recent tree canopy gaps, offers the potential to refine the monitoring of tree latitudinal ranges. Therefore, the two objectives of this study were (1) to evaluate the stochasticity (i.e., range expansion or retreat) of northern range limits of eastern U.S. tree species by comparing latitudinal occurrences of trees and their associated seedlings by individual tree species at 0.5-degree lines of longitude in eastern U.S. forests and (2) to determine if said stochasticity is influenced by forest disturbance (i.e., canopy gaps).

## 2. Methods

### 2.1. Study tree selection

The selection of tree species for the purpose of evaluating indicators of range shifts can influence study results (Woodall et al., 2010). Numerous species selection criteria were established in an effort to objectively accomplish study objectives. First, lists of the most common tree species in the eastern U.S. were determined: top 50 in terms of tree abundance and top 50 in terms of seedling abundance (for a total of 62 tree species). Second, species were eliminated from this list of common tree species whose range (according to Little, 1971) substantially extended beyond the

49th parallel into Canada. At most, tree species could only have portions of their northern limits well-below the 49th parallel (e.g., southeastern Ontario). It is hoped that this criterion would negate many of the statistical censorship issues inherent with tree ranges that extend into Canada as there is no consistent forest inventory across the international border. Third, all tree species were ordered according to the forecasted range expansion/contraction as simulated within Prasad et al.'s (2007–ongoing) future potential tree habitat models using the low emission Hadley climate scenario (B2). Through combination of all these criteria, two study species lists (10 species each) were created: (a) common tree species with no substantial component of their range in Canada and likely to experience either a loss in range or minimal range expansion in the U.S. under a future climate scenario and (b) common tree species with no substantial component of their range in Canada and likely to experience substantial range expansion in the U.S. under a future climate scenario (Table 1). It can be hypothesized that trees forecasted to have the greatest future range expansion or contraction (i.e., future range change) might demonstrate the greatest contemporary northern margin variability potentially exacerbated by disturbances.

### 2.2. Data

The USDA Forest Service's Forest Inventory and Analysis (FIA) program is the primary source for information about the extent, condition, status and trends of forest resources across all ownerships in the U.S. (Bechtold and Patterson, 2005). FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships in the entire nation (Bechtold and Patterson, 2005). FIA operates a multi-phase inventory based on an array of hexagons assigned to separate interpenetrating, non-overlapping annual sampling panels. In Phase 1, land area is stratified using aerial photography or classified satellite imagery to increase the precision of estimates using stratified estimation. Remotely sensed data may also be used to determine if plot locations have forest land cover; forest land is defined as areas at least 10% stocked with tree species, at least 0.4 ha in size, and at least 36.6 m wide. In Phase 2, permanent fixed-area plots are installed in each hexagon when field crews visit plot locations that have accessible forest land. Field crews collect data on more than 300 variables, including land ownership, forest type, tree species, tree size, tree condition, and other site attributes (e.g., slope, aspect, disturbance, land use) (USDA Forest Service, 2008). Plot intensity for Phase 2 measurements is approximately one plot for every 2428 ha of land (roughly 125,000 plots nationally) which is remeasured every five years in the eastern U.S. Briefly, the plot design for FIA inventory plots consists of four 7.2-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center. All trees, with a diameter at breast height (d.b.h.) of at least 12.7 cm, are inventoried on forested subplots. Within each subplot, a 2.07 m microplot offset 3.66 m from subplot center is established. Within each microplot, all live tree seedlings are tallied according to species. Additionally, all trees with a d.b.h. between 2.5 and 12.7 cm are inventoried. Conifer seedlings must be at least 15.2 cm in height with a root collar diameter less than 2.5 cm. Hardwood seedlings must be at least 30.5 cm in height with a root collar diameter less than 2.5 cm. Individual subplots with no anthropocentric disturbances (e.g., harvest) and fully occupied by a forest condition (i.e., no other land uses such as agricultural) at both measurement times were considered individual study observations. As an objective of this study is to evaluate the effect of disturbance (e.g., canopy gap formation) on seedling/tree range variability across northern range margins, it was felt that subplots needed to be examined individually as opposed to pooling data from all the subplots within one FIA inventory plot.