GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 16 (2015) 231–238
Basic and Applied Ecology
www.elsevier.com/locate/baae

Latitudinal range shifts of tree species in the United States across multi-decadal time scales

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Received 19 November 2013; accepted 10 February 2015
Available online 19 February 2015

Abstract

It is expected that some species will shift poleward in range due to climate change. However, despite numerous publications that project species distributions under climate change scenarios, there is less evidence for current latitudinal shifts by tree species, in part because ranges are dynamic and complex to measure. We developed a method to compare tree ranges using continental USDA Forest Service Forest Inventory and Analysis tree surveys during an interval of approximately 28 years. We analyzed compositional differences in ecological subsections within latitudinal bands using repeated measures ANOVA and considered differences in bands at the outer northern and southern range edges combined with increased area to indicate range expansion. Out of a pool of 74 relatively common species, we detected 12 species that had significant increases and expansion in the northern outer band, 13 species that had significant increases and expansion in the southern outer band, and one species that increased and expanded in both northern and southern bands. However, seven species with significant increases in the northern outer band in the contiguous United States had distributions that extended within Canada so that shifts do not represent increases in the northernmost latitudinal band for these species. Uniform poleward migration was not detectable and the number of species shifting southward suggests influence of other driving factors than climate change, including assisted migration of tree species through landscaping and a cascade of range shifts along ecotonal boundaries due to fire exclusion and land use.

Zusammenfassung

Man erwartet, dass einige Arten ihre Verbreitungsgebiete als Folge des Klimawandels polwärts verschieben. Trotz zahlreicher Veröffentlichungen, die die Verbreitung von Arten in Klimawandel-Szenarien vorhersagen, gibt es wenige Befunde für gegenwärtige latitudinale Verschiebungen bei Baumarten. Dies liegt z.T. daran, dass die Verbreitungsgebiete dynamisch und schwer zu messen sind. Wir entwickelten eine Methode, um die Verbreitungsgebiete von Bäumen während eines Zeitraums von etwa 28 Jahren zu vergleichen, indem wir Daten aus den kontinentalen Erhebungen des Forest Inventory and Analysis Programms (USDA Forest Service) nutzten. Wir analysierten Unterschiede in der Zusammensetzung von ökologischen Untereinheiten innerhalb von latitudinalen Bändern mit Hilfe von ANOVA mit wiederholten Messungen und bewerteten mit einer Flächenzunahme verbundene Veränderungen in den Bändern am nördlichen bzw. südlichen Rand des Verbreitungsgebiets als Indikatoren einer Ausdehnung des Verbreitungsgebietes. Von 74 relativ weit verbreiteten Arten zeigten 12 Arten eine signifikante Zunahme und Expansion im nördlichsten Band, 13 Arten breiteten sich nach Süden aus und eine Art dehnte sich sowohl nach Norden als auch nach Süden aus. Indessen hatten sieben Arten mit signifikanter Ausdehnung im nördlichsten Band in den Grenzstaaten der

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http://dx.doi.org/10.1016/j.baae.2015.02.002
1439-1791/

USA Verbreitungen, die bis nach Canada hineinreichen, so dass Ausdehnung bei diesen Arten keine Zunahme im nördlichsten Band darstellt. Eine einheitliche Wanderung nach Norden konnte nicht festgestellt werden, und die Zahl der Arten mit Ausdehnung nach Süden legt nahe, dass andere Steuerfaktoren als der Klimawandel Einfluss nehmen. Dazu gehören Wanderungen von Baumarten, die unterstützt werden durch Landschaftsgestaltung und eine Abfolge von Verbreitungsänderungen entlang von Grenzbereichen, die durch Feuerausschluss oder Landnutzung entstehen.

Keywords: Assisted migration; Climate change; FIA; Fire; Horticultural; Land use; Landscaping

Introduction

It is axiomatic that ranges of some species will shift poleward due to climate change. Ranges of species have shifted in the past and will shift in the future. Indeed, particularly because of short-term variation and oscillations in weather, it is not clear that species ranges are ever in equilibrium with climate. However, rapid forcing of climate change by burning of fossil fuel may result in mismatches between climate envelopes of species and climate. Assisted migration therefore may be necessary for some species to track climate boundaries.

Because of expected range shifts, numerous research papers are published each year that project future distributions of species, generally trees or birds, based on climate change scenarios (Clark, Gelfand, Woodall, & Zhu 2014; Iverson, Prasad, Matthews, & Peters 2011). Most of the species projections are species distribution models, based on statistical methods and current distributions of species, without incorporation of dynamic processes other than climate change although the models are becoming increasingly sophisticated (Clark et al. 2014; Iverson et al. 2011). In contrast to numerous projections of future changes in species distributions, evidence is sparse for current changes in species distributions. Some butterfly and bird species appear to have tracked temperature northward (Walther et al. 2002), and indeed, climatic envelope researchers commonly cite Parmesan et al. (1999), a study of 35 non-migratory European butterflies, where 63% shifted northward in range and 3% shifted southward in range. As for more sedentary taxa, such as trees, altitudinal range shifts have been documented (Bertin 2008; Walther et al. 2002). Another approach to detect change in tree ranges is through demographical change in location, by comparing location of seedling to adult trees (Woodall et al. 2013; Zhu, Woodall, & Clark 2012). This method may produce few results for several reasons, including limited survey duration and low survey intensity for seedlings combined with great mortality; seedling presence may not be a good predictor of survival because juveniles have dispersed away from where adults were successful.

Studies that demonstrate latitudinal range shifts in adult trees are rare. It is not clear whether species simply are not shifting in range or researchers have not quantified range shifts because ranges are complex. Ranges do not conform to a continuous shape that increases in density to the center and shifts as a unit. Species can expand in range while rarefying in density and conversely, contract in range while densifying. Therefore, ranges are difficult to describe and test for differences. Even definition of a range is not clear. For example, most tree species have been planted outside of their natural distribution, complicating range delineation. Tree expansion up a mountain is more clearly demarcated and can be captured in a small study. Tree expansion across a continent is not visibly bounded because for many species, there are millions of trees covering millions of ha. The northernmost or southernmost individuals may not have been marked over time and individuals that have been surveyed may represent (1) viable populations on the leading edge of migration, (2) planted trees that are outside of their realized distribution and thus may not be able to survive and reproduce, (3) differing sampling intensity, i.e., unrecorded individuals of a species in past surveys. Statistically, ranges at different time intervals overlap, producing variation that confounds simple tests to compare significant differences in range. In addition, short term oscillations in temperature and precipitation may produce advances and retreats in range boundaries.

Given the lack of studies about current range shifts and expectation of poleward range shifts, we used USDA Forest Service Forest Inventory and Analysis (FIA) tree surveys, a dataset that covers the United States, to quantify latitudinal changes in tree species distributions suggested by increased area and changes in outer latitudinal bands. Due to inconsistent USDA FIA survey methods (Woodall, Oswalt, Westfall, Perry, & Nelson 2009; Bechtold & Patterson 2005), we developed a methodology to adjust for sampling changes over time. For common species, we defined range as presence at $\geq$0.5% of total species composition in by ecological subsection (Ecomap 1993, Fig. 1, see below for greater detail). Our objective was to determine latitudinal range shifts in adult trees using a new methodology to examine long term, continental surveys and in particular, we were interested in whether species were migrating predominantly poleward, which indicates a strong climate change signal.

Materials and methods

The USDA Forest Service Forest Inventory and Analysis (FIA DataMart, www.fia.fs.fed.us/tools-data) measures sample forest plots located nationwide about every 2000–2500 ha