

Dual impacts of climate change: forest migration and turnover through life history

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Abstract

Tree species are predicted to track future climate by shifting their geographic distributions, but climate-mediated migrations are not apparent in a recent continental-scale analysis. To better understand the mechanisms of a possible migration lag, we analyzed relative recruitment patterns by comparing juvenile and adult tree abundances in climate space. One would expect relative recruitment to be higher in cold and dry climates as a result of tree migration with juveniles located further poleward than adults. Alternatively, relative recruitment could be higher in warm and wet climates as a result of higher tree population turnover with increased temperature and precipitation. Using the USDA Forest Service's Forest Inventory and Analysis data at regional scales, we jointly modeled juvenile and adult abundance distributions for 65 tree species in climate space of the eastern United States. We directly compared the optimal climate conditions for juveniles and adults, identified the climates where each species has high relative recruitment, and synthesized relative recruitment patterns across species. Results suggest that for 77% and 83% of the tree species, juveniles have higher optimal temperature and optimal precipitation, respectively, than adults. Across species, the relative recruitment pattern is dominated by relatively more abundant juveniles than adults in warm and wet climates. These different abundance-climate responses through life history are consistent with faster population turnover and inconsistent with the geographic trend of large-scale tree migration. Taken together, this juvenile–adult analysis suggests that tree species might respond to climate change by having faster turnover as dynamics accelerate with longer growing seasons and higher temperatures, before there is evidence of poleward migration at biogeographic scales.

Keywords: abundance, biogeography, climate change, Forest Inventory and Analysis, range shift, seedling, species distribution model, tree migration

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Introduction

Biogeographic responses of plants to climate change will be largely determined by the niche requirements of juveniles, which can limit the capacity of plant species to colonize new environments (Clark *et al.*, 2001; Ibanez *et al.*, 2008, 2009). If juveniles and adults respond differently to climate variations, then niche models calibrated to adult distributions may provide limited guidance for species climate responses. This potential importance of juvenile requirements could be dismissed on the grounds that, where there are adults, there were once juveniles – adult distributions thus integrate effects of climate on both life stages. However, adults can be abundant as a result of climate trends or fluctuations that affected recruitment in the past (Agee, 1993; Clark, 1996). Because adult abundance accumulates the effects

of past climate variation, models based on current climate–adult abundance might misrepresent the critical relationships between life history and climate. Incorporating juvenile distribution information together with that of adults could provide insight that directly relates to species response to climate change.

Ontogenetic shifts in species environmental requirements occur when organisms occupy different niches at different life history stages (Chase & Leibold, 2003). Despite a large literature on ontogenetic shifts in animals (reviewed by Werner & Gilliam, 1984), there is little direct evidence for how it affects migration potential of plants (Young *et al.*, 2005). Field experiments provide support for ontogenetic shifts in physiology (Parrish & Bazzaz, 1985; Donovan & Ehleringer, 1991; Cavender-Bares & Bazzaz, 2000; Thomas & Winner, 2002; Bansal & Germino, 2010; Kulmatiski & Beard, 2013), demography (Poorter, 1999; Eriksson, 2002; Miriti, 2006; Warren & Bradford, 2011), phenology (Yang & Rudolf, 2010), and functional traits (Butterfield & Briggs, 2011; Heralult *et al.*, 2011; Houter & Pons, 2012; Palow *et al.*, 2012), but few studies investigate biogeographic responses

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(Stohlgren *et al.*, 1998; Quero *et al.*, 2008; Bertrand *et al.*, 2011; Urbietta *et al.*, 2011). For tree species, seedlings and adult trees are usually not part of the same analysis. Previous studies concentrate on either trees greater than a minimum diameter (e.g., Iverson & Prasad, 1998; Canham & Thomas, 2010) or on seedlings (e.g., Ibanez *et al.*, 2008, 2009). Thus, there is little opportunity to directly compare responses of large and small trees and to infer ontogenetic shifts.

Species distribution models (SDMs) are the main tool used to study climate change impacts on forest biodiversity at regional scales (Botkin *et al.*, 2007; Elith & Leathwick, 2009; McMahon *et al.*, 2011; Bellard *et al.*, 2012), yet few consider responses from both juvenile and adult trees (Bykova *et al.*, 2012). One of the fundamental assumptions for SDMs is that species niches are retained over time, that is, niche conservatism (Wiens & Graham, 2005; Pearman *et al.*, 2008; Wiens *et al.*, 2010; Peterson, 2011). Niche conservatism has been studied in the context of species invasion (Broennimann *et al.*, 2007; Beaumont *et al.*, 2009; Gallagher *et al.*, 2010; Petitpierre *et al.*, 2012) and evolution (Maiorano *et al.*, 2013), but not at different life history stages. The notion of niche conservatism leads to the prediction that species will shift their ranges poleward in latitude and upward in elevation in response to climate warming, a pattern that is evident for some species in some regions (Walther *et al.*, 2005; Beckage *et al.*, 2008; Kelly & Goulden, 2008; Lenoir *et al.*, 2008; Gottfried *et al.*, 2012; Pauli *et al.*, 2012).

In the eastern United States, the northern range limits of most tree species appear to be stable through time, which is contrary to the predictions of SDMs under climate change (Iverson & Prasad, 1998; McKenney *et al.*, 2007; Iverson *et al.*, 2008). Among the few empirical studies on latitudinal tree migration, Woodall *et al.* (2009) found that juveniles have higher mean latitudes than adults for northern species, suggesting northward range shifts, but not for southern species. They recognized that all their northern species have distributions that are truncated at the US-Canada border, so the use of mean latitude might not reflect species actual distributions. By comparing range edge distributions of juveniles vs. adults, Zhu *et al.* (2012) found that there is not yet evidence for latitudinal migration for more than half of the 92 tree species analyzed in the eastern US forests. More recently, Woodall *et al.* (2013) combined the juvenile–adult geographic analysis with forest disturbance metrics, and confirmed the stability of tree northern range margins. All these empirical juvenile–adult analyses in geographic space suggest that large-scale tree northward migration, especially along northern range margins, has not yet occurred. A more mechanistic understanding of why responses may be

slow requires new approaches to the effects of climate on adults and juveniles (Jackson *et al.*, 2009). Therefore, we propose to extend the geographic comparison into climate space.

In this analysis, we investigate how juveniles and adult trees differ in their relationships with regional climate variation, focusing on two hypotheses. Recognizing that adult distributions represent recruitment of the past, latitudinal migration suggests that juveniles will be more concentrated in cold climates than adults – these are areas warm enough for contemporary colonization that were not previously suitable when mature individuals became established. Alternatively, if species are not migrating, then we might observe juveniles concentrated in warm climates simply because higher temperature implies higher turnover rate. The rationale is based on the observation that growth is promoted by long growing seasons, and rapid growth increases competition and mortality rates (Assmann, 1970; Clark, 1990). Specifically, we evaluate the following two hypotheses:

1 *Migration hypothesis.* A population migrating northward in response to a warming climate will have juveniles located further north than adults. When mapped in climate space, juveniles would be relatively more abundant than adults in cold and dry climates, as low temperature is usually associated with low precipitation because of high correlation. Driven by constant climate–distribution relationships and future climate scenarios, northward shift in habitat is one of the predictions of SDMs based on distribution and abundance data from adults (Iverson & Prasad, 1998; McKenney *et al.*, 2007; Iverson *et al.*, 2008). By incorporating juvenile distribution and abundance, we can compare the difference between juveniles and adults in climate space and geographic space.

2 *Turnover hypothesis.* Increasing temperature and precipitation could increase turnover rates, that is, rapid growth, increased mortality, and elevated recruitment. The most obvious cause for this phenomenon is a prolonged growing season, but it could also result if growth increases with temperature and precipitation during the growing season. The latter occurs if individuals are below their temperature optima and they are not limited by drought or other factors. Juveniles could be relatively more abundant than adults in warm and wet climates if increased mortality increases recruitment opportunities. Higher turnover in warm and wet climate is suggested by a legacy of physiological experiments (Saxe *et al.*, 2001), a global meta-analysis on population dynamics across latitude and elevation (Stephenson & van Mantgem, 2005), and long-term demographic observations in tropical forests (Phillips & Gentry, 1994; Phillips *et al.*, 2004). This prediction of

high recruitment, and thus high turnover, in warm and wet climates is contrary to the pattern expected by northward migration hypothesis – recruitment shifted to higher latitudes than adults.

In this study, we evaluate one of the most extensive sources of biogeographic information on juvenile and adult tree species to quantify climate differences through life history and consider its role for potential change. We make use of species abundance data from the Forest Inventory and Analysis (FIA) program of the USDA Forest Service, with millions of tree observations and a consistent sampling scheme for a continuum of size classes. We adopt the usual assumption that species distributions in geographic space correspond to the realized niches in climate space, recognizing that those relationships are influenced by interactions with other species (Pulliam, 2000; Soberon & Nakamura, 2009; Peterson *et al.*, 2011; Wiens, 2011). Our modeling strategy differs from previous approaches in which we jointly analyze juveniles and adults to understand the interactions that contribute to distributions at biogeographic scale. We compare the abundance-climate response surfaces between juveniles and adults for each species, and synthesize overall patterns among all species.

Materials and methods

We combined forest inventory and climate data to construct a joint SDM, and we compared juvenile vs. adult abundance in climate space. First, we aggregated data to regional scales to understand species biogeographic responses to climate. Instead of modeling all observations, we focused on nonzero observations where species are present, because we were interested in whether abundance within the range varies along climate gradients, and previous analysis of occurrence (zeros and non-zeros) did not provide evidence that populations are migrating in response to climate change. To test the migration and turnover hypotheses, we directly compared the optimal climate conditions for juveniles and adults. We then calculated the ratio of juvenile to adult abundance, that is, relative recruitment intensity, in climate space. Finally, we synthesized results across species to a relative recruitment score by standardizing relative recruitment intensity of each species.

Forest inventory data

The FIA program is the primary source for information about the extent, condition, status, and trends of forest resources in the United States (Smith *et al.*, 2009). FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships across the United States, resulting in national sample intensity of one plot per 2428 ha (Bechtold & Patterson, 2005). Classified satellite imagery is used to stratify sampling. Forested land

is defined as areas with at least 10% covered by tree species canopies, at least 0.4 ha in size, and at least 36.6 m wide. FIA inventory plots consist of four, 7.2 m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Bechtold & Patterson, 2005). All trees (standing live and dead) 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 radius microplot offset 3.66 m from subplot center is established where only live trees with a d.b.h. between 2.5 and 12.7 cm are inventoried. Within each microplot, all live tree seedlings are tallied according to species. 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. Note that they are often well established stems, typically not first-year seedlings.

In this analysis, FIA data were extracted from the recent annual inventories (1999–2008) in 31 eastern states for a total of 43 396 inventory plots from FIADB version 4.0 on 16 March 2010 (available online <http://fia.fs.fed.us/>). Because we were interested in tree species abundance within their respective ranges in climate space, we focused on species with substantial sample sizes in the eastern United States. We used the species list from Iverson & Prasad (1998) to further restrict analysis to 65 species, by excluding genus-level species and riparian/hydric species (Table 1 includes the complete species list). These 65 common species span major plant functional types in North America. To compare species abundance in different life stages, we followed the FIA sampling design to divide the data into two size classes: (i) seedling (d.b.h. < 2.54 cm) and (ii) tree (d.b.h. ≥ 2.54 cm). For each species, we extracted the seedling count and tree basal area in each plot. The condition delineation in FIA database was used to identify fully forested, non-plantation plots that have both seedling and tree surveys.

Climate and ecoregion data

Climate data in this study were extracted from the 800 m resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) data set (available online <http://www.prism.oregonstate.edu/>). Recognized as a high quality spatial climate data set in the United States, PRISM is an interpolation of meteorological station data to produce continuous, digital grid estimates of climatic parameters, with consideration of location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly *et al.*, 2008). We used long-term average climate data (1990–2010) corresponding to each FIA plot as the climate covariates. We extracted annual mean temperature (°C), ranging from 0 °C to 25 °C, and annual precipitation (mm), ranging from 550 mm to 1650 mm. We used these two variables because they are important to species distributions (Peterson *et al.*, 2011), commonly used in SDMs (Elith & Leathwick, 2009), and are highly correlated with other climate variables.

Table 1 Model fit measures and optimal climate conditions for all 65 species. Model fit is summarized by the goodness-of-fit (Eqn 3), ranging from 0 to 1, for seedlings (R_Y^2) and trees (R_Z^2) at ecoregion and plot scales. For each species, the ecoregion-level model performs better than the plot-level model. Optimal climate is calculated as the annual mean temperature (\bar{T}) and annual precipitation (\bar{P}) weighted by the predicted seedling and tree abundances (Eqns 4 and 5). For the majority of species, the turnover hypothesis is supported as the seedling surface has higher optimal temperature and/or precipitation than the tree surface ($\bar{T}_Y > \bar{T}_Z$ and/or $\bar{P}_Y > \bar{P}_Z$)

Species	Model fit				Optimal climate					
	Seedling (R_Y^2)		Tree (R_Z^2)		Annual mean temperature (\bar{T} , °C)			Annual precipitation (\bar{P} , mm)		
	Ecoregion	Plot	Ecoregion	Plot	Seedling	Tree	Hypothesis	Seedling	Tree	Hypothesis
<i>Abies balsamea</i>	0.64	0.15	0.52	0.03	4.56	5.01	Migration	1200	1150	Turnover
<i>Acer pensylvanicum</i>	0.65	0.05	0.58	0.01	5.39	5.95	Migration	1230	1220	Turnover
<i>Acer rubrum</i>	0.11	0.03	0.27	0.08	18.60	7.41	Turnover	1430	1050	Turnover
<i>Acer saccharum</i>	0.50	0.21	0.35	0.06	11.80	11.10	Turnover	1390	1260	Turnover
<i>Betula alleghaniensis</i>	0.68	0.03	0.61	0.02	9.16	6.96	Turnover	1320	1270	Turnover
<i>Betula lenta</i>	0.45	0.03	0.47	0.01	11.40	11.00	Turnover	1450	1340	Turnover
<i>Betula papyrifera</i>	0.36	0.01	0.35	0.01	4.29	4.79	Migration	1020	1080	Migration
<i>Carpinus caroliniana</i>	0.27	0.13	0.14	0.04	18.10	17.50	Turnover	1520	1450	Turnover
<i>Carya alba</i>	0.56	0.02	0.41	0.01	16.10	14.90	Turnover	1380	1320	Turnover
<i>Carya cordiformis</i>	0.49	0.04	0.35	0.01	16.20	11.90	Turnover	1420	1100	Turnover
<i>Carya glabra</i>	0.52	0.01	0.27	0.00	14.70	13.70	Turnover	1280	1270	Turnover
<i>Carya ovata</i>	0.43	0.02	0.38	0.00	17.10	15.10	Turnover	1480	1340	Turnover
<i>Celtis occidentalis</i>	0.36	0.02	0.21	0.00	19.70	18.40	Turnover	1490	1380	Turnover
<i>Cercis canadensis</i>	0.48	0.01	0.44	0.00	18.60	17.30	Turnover	1550	1450	Turnover
<i>Cornus florida</i>	0.60	0.07	0.46	0.00	18.30	17.10	Turnover	1590	1460	Turnover
<i>Diospyros virginiana</i>	0.37	0.01	0.18	0.02	20.10	19.10	Turnover	1610	1500	Turnover
<i>Fagus grandifolia</i>	0.69	0.36	0.43	0.03	11.30	8.53	Turnover	1370	1230	Turnover
<i>Fraxinus americana</i>	0.47	0.05	0.34	0.02	11.80	9.44	Turnover	1210	1120	Turnover
<i>Fraxinus nigra</i>	0.65	0.04	0.54	0.01	5.79	6.40	Migration	777	777	Migration
<i>Fraxinus pennsylvanica</i>	0.43	0.08	0.25	0.00	16.70	11.90	Turnover	1390	811	Turnover
<i>Gleditsia triacanthos</i>	0.14	0.04	0.22	0.05	19.20	18.60	Turnover	1470	1440	Turnover
<i>Ilex opaca</i>	0.38	0.09	0.16	0.02	16.20	17.50	Migration	1340	1480	Migration
<i>Juglans nigra</i>	0.43	0.01	0.49	0.01	14.70	13.20	Turnover	1310	1200	Turnover
<i>Juniperus virginiana</i>	0.42	0.10	0.18	0.01	17.50	16.70	Turnover	1430	1370	Turnover
<i>Liquidambar styraciflua</i>	0.51	0.01	0.48	0.00	18.80	19.10	Migration	1390	1430	Migration
<i>Liriodendron tulipifera</i>	0.46	0.01	0.33	0.03	14.60	13.80	Turnover	1300	1260	Turnover
<i>Maclura pomifera</i>	0.48	0.12	0.30	0.02	16.90	16.40	Turnover	1320	1300	Turnover
<i>Magnolia virginiana</i>	0.39	0.01	0.15	0.04	22.80	21.40	Turnover	1510	1500	Turnover
<i>Morus rubra</i>	0.30	0.07	0.21	0.02	18.20	16.90	Turnover	1550	1510	Turnover
<i>Nyssa sylvatica</i>	0.51	0.02	0.30	0.01	18.50	17.30	Turnover	1610	1480	Turnover
<i>Ostrya virginiana</i>	0.33	0.02	0.17	0.00	16.40	14.40	Turnover	1410	1230	Turnover
<i>Oxydendrum arboreum</i>	0.54	0.01	0.54	0.01	15.30	14.00	Turnover	1410	1330	Turnover
<i>Pinus echinata</i>	0.43	0.05	0.21	0.02	17.40	16.30	Turnover	1480	1400	Turnover
<i>Pinus elliotii</i>	0.39	0.00	0.56	0.00	23.10	22.70	Turnover	1480	1440	Turnover
<i>Pinus palustris</i>	0.49	0.09	0.15	0.00	21.00	20.60	Turnover	1500	1460	Turnover
<i>Pinus resinosa</i>	0.52	0.05	0.29	0.00	6.18	7.35	Migration	799	800	Migration
<i>Pinus strobus</i>	0.45	0.11	0.40	0.01	12.00	11.20	Turnover	1480	1320	Turnover
<i>Pinus taeda</i>	0.77	0.00	0.51	0.00	19.30	18.80	Turnover	1530	1460	Turnover
<i>Pinus virginiana</i>	0.64	0.04	0.44	0.01	15.90	15.40	Turnover	1460	1450	Turnover
<i>Populus deltoides</i>	0.39	0.01	0.20	0.06	19.00	11.10	Turnover	1450	1020	Turnover
<i>Populus grandidentata</i>	0.37	0.01	0.34	0.02	6.70	7.55	Migration	845	858	Migration
<i>Populus tremuloides</i>	0.64	0.03	0.62	0.05	5.17	5.38	Migration	813	822	Migration
<i>Prunus serotina</i>	0.41	0.09	0.32	0.09	11.60	11.10	Turnover	1130	1140	Migration
<i>Quercus alba</i>	0.38	0.06	0.54	0.05	16.80	15.30	Turnover	1570	1410	Turnover
<i>Quercus coccinea</i>	0.55	0.01	0.57	0.02	13.10	13.00	Turnover	1320	1310	Turnover
<i>Quercus falcata</i>	0.48	0.00	0.38	0.01	18.40	17.30	Turnover	1560	1480	Turnover

Table 1 (continued)

Species	Model fit				Optimal climate					
	Seedling (R_Y^2)		Tree (R_Z^2)		Annual mean temperature (\bar{T} , °C)			Annual precipitation (\bar{P} , mm)		
	Ecoregion	Plot	Ecoregion	Plot	Seedling	Tree	Hypothesis	Seedling	Tree	Hypothesis
<i>Quercus laurifolia</i>	0.58	0.12	0.55	0.01	20.60	21.80	Migration	1280	1360	Migration
<i>Quercus macrocarpa</i>	0.32	0.05	0.30	0.02	12.30	11.90	Turnover	1100	1090	Turnover
<i>Quercus marilandica</i>	0.41	0.08	0.15	0.02	19.40	18.20	Turnover	1630	1530	Turnover
<i>Quercus muehlenbergii</i>	0.49	0.02	0.31	0.00	18.20	16.90	Turnover	1490	1430	Turnover
<i>Quercus nigra</i>	0.54	0.02	0.60	0.00	20.60	20.60	Migration	1580	1500	Turnover
<i>Quercus palustris</i>	0.44	0.23	0.17	0.01	8.83	9.03	Migration	861	889	Migration
<i>Quercus phellos</i>	0.45	0.08	0.19	0.01	20.10	19.10	Turnover	1610	1530	Turnover
<i>Quercus prinus</i>	0.62	0.07	0.45	0.00	13.80	13.70	Turnover	1480	1370	Turnover
<i>Quercus rubra</i>	0.28	0.03	0.50	0.04	13.50	12.40	Turnover	1380	1280	Turnover
<i>Quercus stellata</i>	0.49	0.05	0.25	0.07	18.20	17.90	Turnover	1550	1460	Turnover
<i>Quercus velutina</i>	0.46	0.08	0.58	0.05	16.00	15.40	Turnover	1540	1400	Turnover
<i>Robinia pseudoacacia</i>	0.18	0.04	0.42	0.01	10.10	12.30	Migration	1100	1210	Migration
<i>Sassafras albidum</i>	0.40	0.02	0.44	0.04	16.50	15.50	Turnover	1490	1400	Turnover
<i>Thuja occidentalis</i>	0.54	0.12	0.30	0.04	3.85	4.25	Migration	989	893	Turnover
<i>Tilia americana</i>	0.47	0.02	0.52	0.03	10.60	10.60	Migration	1000	937	Turnover
<i>Tsuga canadensis</i>	0.47	0.11	0.55	0.03	12.80	12.50	Turnover	1490	1400	Turnover
<i>Ulmus alata</i>	0.50	0.02	0.30	0.00	20.10	19.20	Turnover	1600	1530	Turnover
<i>Ulmus americana</i>	0.50	0.01	0.31	0.00	17.10	13.90	Turnover	1370	999	Turnover
<i>Ulmus rubra</i>	0.54	0.03	0.30	0.00	19.20	17.10	Turnover	1570	1410	Turnover

Since the actual FIA plot coordinates are not publicly available, the longitude and latitude of plot locations have been perturbed in an unbiased direction not exceeding 1.67 km, and typically within a 0.8 km radius of the actual plot location, so as to facilitate study repeatability without introducing bias (McRoberts *et al.*, 2005). The spatial resolution of PRISM data is similar to that of the FIA perturbed plot locations. We therefore used the publicly available perturbed plot coordinates to match the FIA plot location with the PRISM climate data.

We performed our analysis at an aggregated regional scale, not at the individual FIA plot scale, because regional climate and local species abundance data are misaligned. Tree abundance varies along climate gradients at regional scales (Iverson & Prasad, 1998), but not at plot scales (Canham & Thomas, 2010). This incongruity is expected due to the fact that regional climate data are not resolved at the plot scale, but microclimate, drainage, and competition vary locally. Therefore, we followed an alternative option similar to that of Iverson & Prasad (1998) to aggregate plot-level FIA data to a scale more compatible with regional climate data. The ecological subsection (hereafter *ecoregion*) is essentially a collection of plots where each unit defines a region of unique ecological characteristics of surficial geology, lithology, geomorphic process, soil groups, subregional climate, and potential natural communities that differs from neighboring units in the United States (Cleland *et al.*, 1997; Keys *et al.*, 2007; McNab *et al.*, 2007). In our study area of the eastern United States, we aggregated the plot-level data ($n = 43\,396$) into the ecoregion-level data ($n = 427$) by averaging seedling densities (#/ha), tree

basal areas ($\text{m}^2 \text{ha}^{-1}$), annual mean temperature (°C), and annual precipitation (mm) of plots within each ecoregion.

Species distribution model

We adopted the framework from S. Ghosh, K. Zhu, A.E. Gelfand & J.S. Clark (unpublished data) to jointly model seedling densities as juvenile response and tree basal areas (BAs) as adult response, based on the rationale that tree BAs depend on climate, and seedling densities depend on both climate and tree BAs through reproduction. Tree BAs could affect seedling densities through both reproduction (a positive effect) and competition (shading, a negative effect). We constructed a SDM for ecoregions using plots with nonzero seedling densities and tree BAs. At the ecoregion scale, a zero observation indicates absence from all 100 seedling and tree plots located in a geographic area over 7000 km². The SDM is constructed and fitted in a Bayesian framework to allow interdependence and coherent inference.

In ecoregion i , we modeled the tree BA (Z_i) as a lognormal distribution with mean linked to climate,

$$Z_i \sim \text{Lognormal}(\mu_i, \sigma^2) \quad (1)$$

$$\mu_i = X_i \alpha$$

where $X_i = [1, T_i, P_i, T_i^2, P_i^2, T_i P_i]$ is the climate design matrix (temperature T_i and precipitation P_i), with the climate coefficients $\alpha = [\alpha_0, \alpha_1, \alpha_2, \alpha_3, \alpha_4, \alpha_5]^T$. Likewise, we modeled the seedling density (Y_i) as a lognormal distribution with mean

linked to climate and tree BA (Z_i) in the corresponding ecoregion i ,

$$\begin{aligned} Y_i &\sim \text{Lognormal}(\lambda_i, \delta^2) \\ \lambda_i &= X_i\beta + Z_i\gamma \end{aligned} \quad (2)$$

where the climate design matrix (X_i) is the same as in Eqn (1), with the climate coefficients $\beta = [\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5]^T$, and γ as the coefficient linking seedling density to tree BA.

We used the standard semi-conjugate noninformative priors on $\alpha, \beta, \gamma \sim \text{Normal}(0, 10^2)$ and $\sigma^2, \delta^2 \sim \text{InvGamma}(0.05, 0.05)$. Climate covariates were centered and scaled to unit standard deviation. Implemented in the full Bayesian framework, parameter posterior distributions were simulated using Markov chain Monte Carlo (MCMC). Convergence was checked by both visually assessing trace plots and Geweke diagnostics after 100 000 iterations for each species.

To compare the ecoregion-level and plot-level models, we implemented the same SDM to data at both scales. We checked model performance using in-sample predictions by composite sampling from Eqns (1) and (2). We summarized model fit by goodness-of-fit measures, R_Y^2 for seedling density and R_Z^2 for tree BA,

$$\begin{aligned} R_Y^2 &= 1 - \frac{\sum_i (Y_i - \hat{Y}_i)^2}{\sum_i (Y_i - \bar{Y})^2} \\ R_Z^2 &= 1 - \frac{\sum_i (Z_i - \hat{Z}_i)^2}{\sum_i (Z_i - \bar{Z})^2} \end{aligned} \quad (3)$$

where Y_i and Z_i are observed seedling density and tree BA, \hat{Y}_i and \hat{Z}_i are predicted seedling density and tree BA in ecoregion/plot i , \bar{Y} and \bar{Z} are average observed seedling density and tree BA. Both R_Y^2 and R_Z^2 range from 0 to 1, with greater values indicating better model fit.

Response surface comparisons

We used the fitted SDM to predict species abundance in a gridded climate space ($T \times P$) as species response surfaces. In other words, a species has predicted seedling densities (#/ha) and tree BAs ($\text{m}^2 \text{ha}^{-1}$) within its geographic range mapped in the climate space of annual mean temperature ($^\circ\text{C}$) and annual precipitation (mm). To compare the difference of seedling vs. tree response surfaces, we first calculated the optimal climate conditions as the temperature and precipitation weighed by the predicted abundances. For seedling response surfaces, the optimal temperature (\tilde{T}_Y) and precipitation (\tilde{P}_Y) are

$$\begin{aligned} \tilde{T}_Y &= \frac{\sum_j \hat{Y}_j T_j}{\sum_j \hat{Y}_j} \\ \tilde{P}_Y &= \frac{\sum_j \hat{Y}_j P_j}{\sum_j \hat{Y}_j} \end{aligned} \quad (4)$$

where \hat{Y}_j is the predicted seedling density (#/ha) in climate grid j , with annual mean temperature T_j ($^\circ\text{C}$) and

annual precipitation P_j (mm). Likewise, for tree response surfaces, the optimal temperature (\tilde{T}_Z) and precipitation (\tilde{P}_Z) are

$$\begin{aligned} \tilde{T}_Z &= \frac{\sum_j \hat{Z}_j T_j}{\sum_j \hat{Z}_j} \\ \tilde{P}_Z &= \frac{\sum_j \hat{Z}_j P_j}{\sum_j \hat{Z}_j} \end{aligned} \quad (5)$$

where \hat{Z}_j is the predicted tree BA ($\text{m}^2 \text{ha}^{-1}$) in climate grid j , with annual mean temperature T_j ($^\circ\text{C}$) and annual precipitation P_j (mm). Ontogenetic niche shifts are suggested by the differences in the optimal climate conditions between seedling and tree response surfaces. For each species, the migration hypothesis is supported if the seedling surface has lower optimal temperature and/or precipitation than the tree surface ($\tilde{T}_Y < \tilde{T}_Z$ and/or $\tilde{P}_Y < \tilde{P}_Z$). In contrast, the turnover hypothesis is supported if the seedling surface has higher optimal temperature and/or precipitation than the tree surface ($\tilde{T}_Y > \tilde{T}_Z$ and/or $\tilde{P}_Y > \tilde{P}_Z$).

To identify the climate conditions that relatively benefit seedlings over trees, we then calculated the relative recruitment intensity (R_j) in climate space,

$$R_j = \frac{\hat{Y}_j}{\hat{Z}_j} \quad (6)$$

where \hat{Y}_j is the predicted seedling density (#/ha), \hat{Z}_j is the predicted tree BA ($\text{m}^2 \text{ha}^{-1}$) in climate grid j . Relative recruitment intensity (R_j , #/m²) is large in climate conditions where seedling abundance is relatively higher than tree abundance. For each species, the migration hypothesis is supported if its relative recruitment intensity is high in cold and dry climates. In contrast, the turnover hypothesis is supported if its relative recruitment intensity is high in warm and wet climates. This index (R_j) in the entire climate space gives more comprehensive understanding than the optimal temperature (\tilde{T}_Z) and precipitation (\tilde{P}_Z) summaries of the seedling and tree response surfaces.

To summarize the differences of seedling vs. tree response surfaces, we finally calculated a standardized score for all 65 species. For each species, the relative recruitment intensity (R_j) was standardized by subtracting its mean and dividing by its SD,

$$\tilde{R}_{jk} = \frac{R_{jk} - \text{mean}_j(R_{jk})}{\text{sd}_j(R_{jk})} \quad (7)$$

where \tilde{R}_{jk} is the standardized relative recruitment intensity (unitless) in climate grid j , for species k . This index is comparable among species after standardization (Eqn 7). It was then averaged across species to obtain the relative recruitment score (S_j),

$$S_j = \text{mean}_k(\tilde{R}_{jk}) \quad (8)$$

in climate grid j , for species k . A higher score (S_j , unitless) identifies climate conditions where seedlings are relatively more abundant than trees. Across all species, the migration hypothesis is supported if the relative recruitment score is

high in cold and dry climates. In contrast, the turnover hypothesis is supported if the relative recruitment score is high in warm and wet climates. This score in the entire climate space summarizes seedling and tree response surfaces for all species.

All analyses were performed in R version 2.15.0 (R Development Core Team, 2012).

Results

For each species, our SDM predicts seedling and tree abundance at the ecoregion scale, but not at the plot scale. We checked model fit using in-sample prediction

for seedling densities and tree BAs at two scales, and we summarized model fit using the goodness-of-fit measures (Eqn 3). As an example species, *Pinus taeda* (loblolly pine) seedling and tree abundances within its range are well predicted by the model at the ecoregion scale (Fig. 1a and b), with goodness-of-fit $R^2_Y = 0.77$ for seedlings and $R^2_Z = 0.51$ for trees. However, the same model has no predictive capacity at the plot scale (Fig. 1c and d), with goodness-of-fit $R^2_Y = 0.0017$ for seedlings and $R^2_Z = 0.0013$ for trees. This pattern – that climate can predict abundance at the ecoregion but not at the plot scale – is true for all 65 species (Table 1).

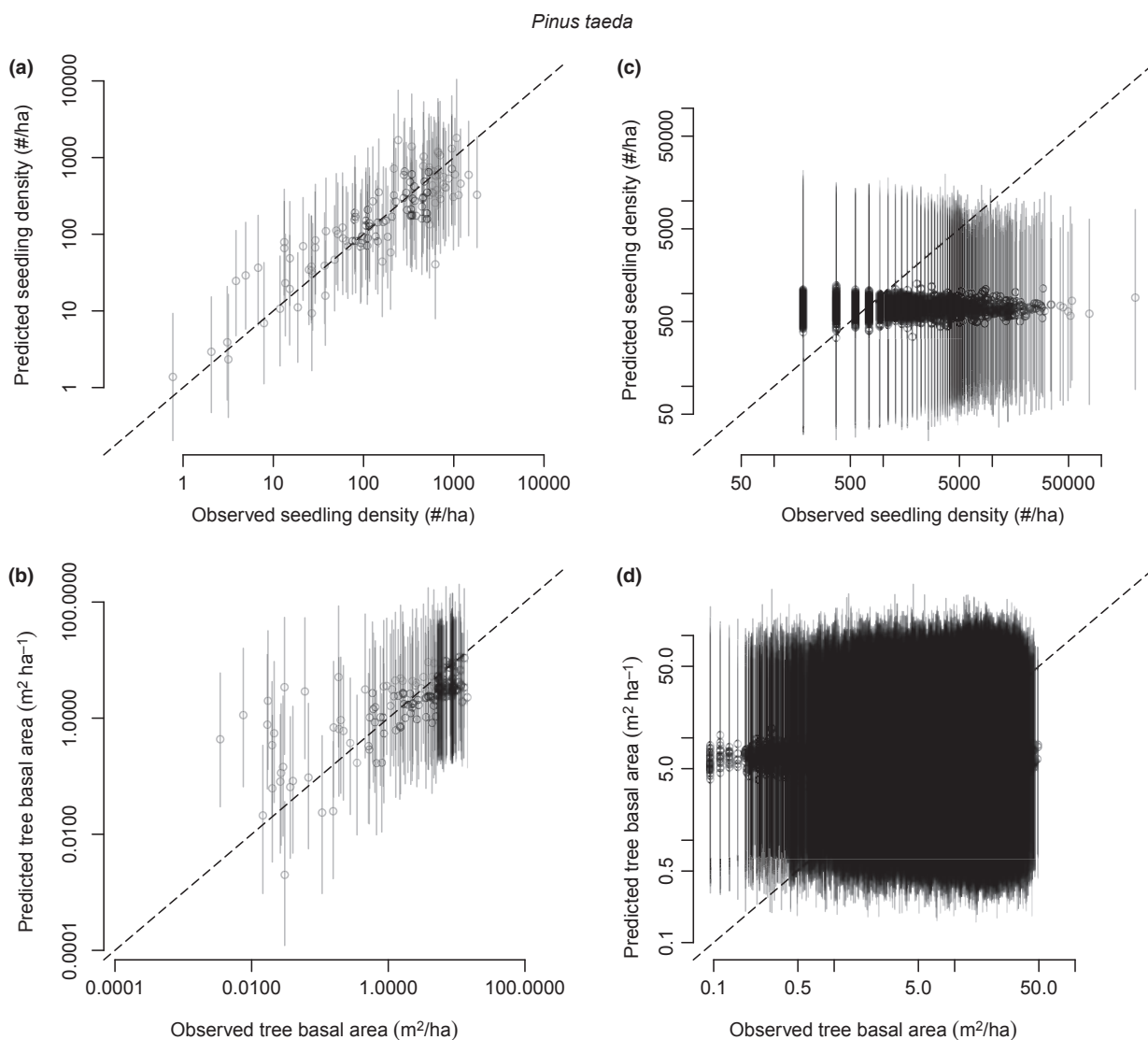


Fig. 1 Model checking (in-sample prediction) of an example species, *Pinus taeda*, at ecoregion (a, b) vs. plot scale (c, d). Points and solid lines are posterior predictive means and 95% credible intervals, and dashed lines are the 1 : 1 reference. The ecoregion-level model performs significantly better than the plot-level model for both seedling density (a vs. c) and tree basal area (b vs. d), because regional climate and plot-level species abundance are spatially misaligned. All the subsequent figures are results from the ecoregion-level model.

This result does not mean that seedling densities and tree BAs are unresponsive at the plot scale; rather climate data are misaligned, being smoothed at geographic scales much coarser than individual plots, and there are additional local variables that affect plot-level data. The ecoregion-level model aggregates FIA data at a scale that is in closer alignment with climate. Hereafter, we focus on results from the ecoregion-level models.

At the ecoregion scale, the fitted SDM predicts change in species abundance along climate gradients. For example, *Pinus taeda* seedling density and tree BA are both abundant in warm (15–20 °C annual mean temperature) and wet (1400–1600 mm annual precipitation) climates (surfaces in Fig. 2a and b). The optimal climates for the seedling response surface (Eqn 4) are $\tilde{T}_Y = 19.30$ °C and $\tilde{P}_Y = 1530$ mm. The optimal climates for the tree response surface (Eqn 5) are $\tilde{T}_Z = 18.80$ °C and $\tilde{P}_Z = 1460$ mm. In this case, the turnover hypothesis is supported because the seedling surface has higher optimal temperature ($\tilde{T}_Y > \tilde{T}_Z$) and precipitation ($\tilde{P}_Y > \tilde{P}_Z$) than the tree surface. The relative recruitment intensity, that is, ratio of seedling density vs. tree BA (Eqn 6), indicates that seedling recruitment is more concentrated in warm and wet climates than adult abundance (Fig. 2c). This result does not mean that cold and dry climates are detrimental for either seedlings or trees; rather it demonstrates how recruitment varies with climate relative to adult abundance. This trend in relative recruitment intensity is consistent with the hypothesis that warm and wet climates have high population turnover. It is inconsistent with northward migration.

An alternative example is *Ilex opaca* (American holly) with both seedlings and trees being abundant in moderate (15 °C annual mean temperature and 1400 mm annual precipitation) climates (surfaces in Fig. 3a and b). The optimal climates for the seedling response surface (Eqn 4) are $\tilde{T}_Y = 16.20$ °C and $\tilde{P}_Y = 1340$ mm. The optimal climates for the tree response surface (Eqn 5) are $\tilde{T}_Z = 17.50$ °C and $\tilde{P}_Z = 1480$ mm. In this case, the migration hypothesis is supported because the seedling surface has lower optimal temperature ($\tilde{T}_Y < \tilde{T}_Z$) and precipitation ($\tilde{P}_Y < \tilde{P}_Z$) than the tree surface. The relative recruitment intensity (Eqn 6) is concentrated in cold climates (Fig. 3c). This trend appears to suggest northward migration for this species.

Taken across all species, the turnover hypothesis is predominately supported by the optimal temperature and precipitation comparisons between seedling and tree response surfaces. For optimal temperature, 50 of 65 species (77%) support the turnover hypothesis ($\tilde{T}_Y > \tilde{T}_Z$), but only 15 of 65 species (23%) support the

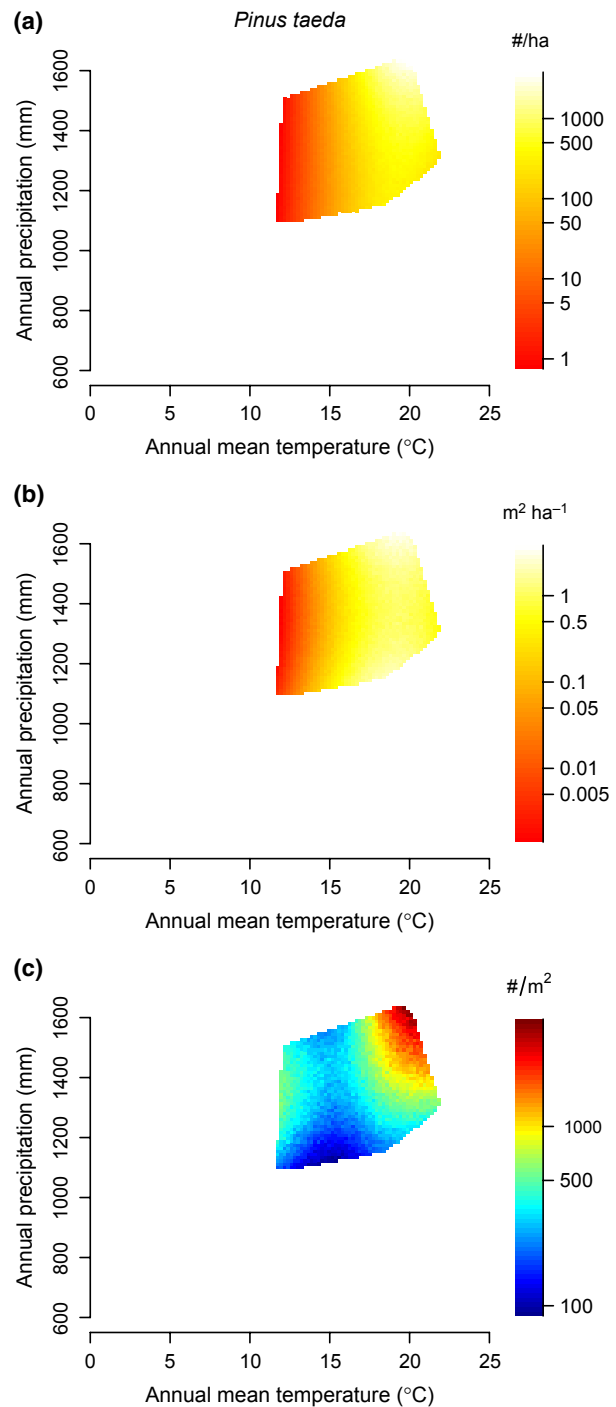


Fig. 2 Abundance response surfaces for seedling density (a), tree basal area (b), relative recruitment intensity (c) from the fitted ecoregion-level model of an example species, *Pinus taeda*. Abundance response surfaces of seedlings (a) and trees (b) show clear patterns within species range (colored images) in the climate space (annual mean temperature and annual precipitation). Relative recruitment intensity (c), calculated as the ratio of (a) over (b), as in Eqn (6), identifies the climate conditions that relatively benefit seedlings over trees. In this case, warm and wet climates benefit *Pinus taeda* recruitment.

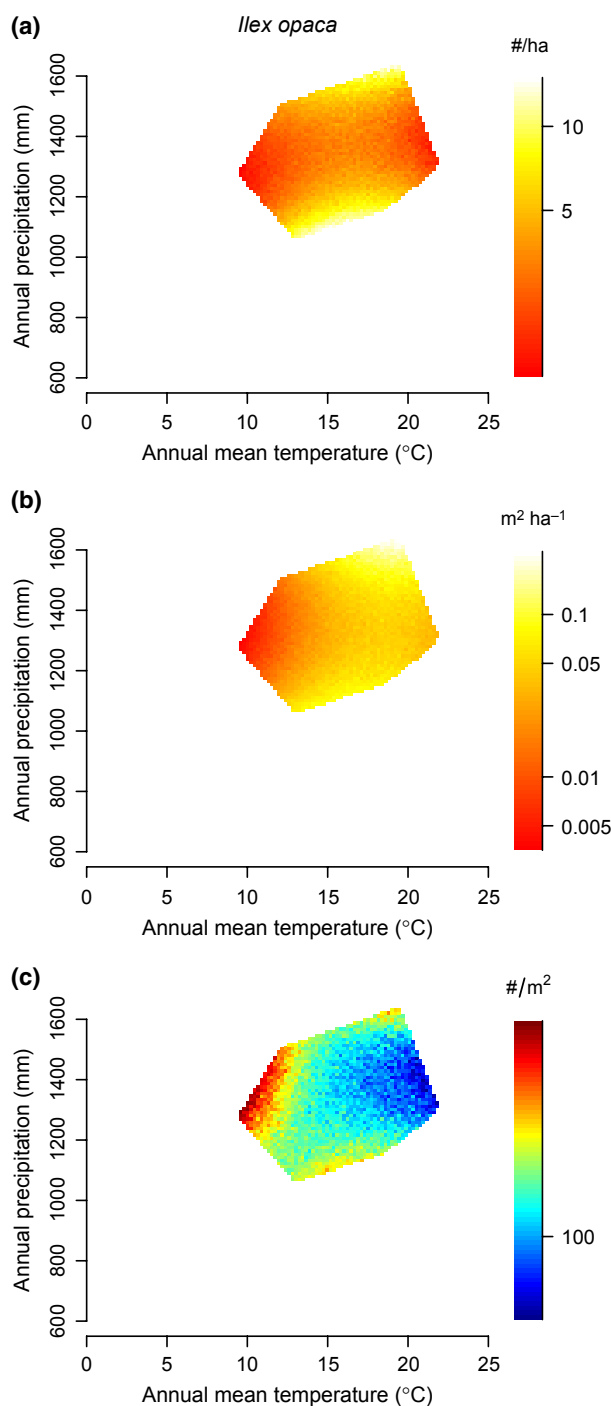


Fig. 3 Abundance response surfaces for seedling density (a), tree basal area (b), relative recruitment intensity (c) from the fitted ecoregion-level model of an example species, *Ilex opaca*. Symbolism follows Fig. 2. In this case, cold climates benefit *Ilex opaca* recruitment.

migration hypothesis ($\tilde{T}_Y < \tilde{T}_Z$). For optimal precipitation, 54 of 65 species (83%) support the turnover hypothesis ($\tilde{P}_Y > \tilde{P}_Z$), but only 11 of 65 species (17%)

support the migration hypothesis ($\tilde{P}_Y < \tilde{P}_Z$). The differences between seedling and tree surfaces are also consistent with ontogenetic niche shifts in species climate-abundance relationships, indicating seedlings and trees respond differently to this regional climate variation. We include the optimal climates and supports for migration or turnover hypothesis for each species in Table 1.

Synthesized over all species, the turnover hypothesis is supported by patterns in the relative recruitment score, where warm and wet climates have relatively higher seedling than tree abundance (Fig. 4). The relative recruitment score is a standardized summary of relative recruitment intensity for all 65 species (Eqns 7 and 8). It offers an alternative perspective from the individual view of the optimal climates (Eqns 4 and 5). Across 65 species, the climates that benefit most seedlings than trees are roughly at 20 °C annual mean temperature and 1500 mm annual precipitation. In contrast, temperatures below 10 °C generally have relatively low seedling than tree abundance. In summary, the turnover hypothesis is supported by the majority of individual species (optimal climates, Table 1) and by the synthesis across species (relative recruitment score, Fig. 4).

Discussion

By comparing juvenile vs. adult tree abundance in climate space, we found that regional-scale recruitment

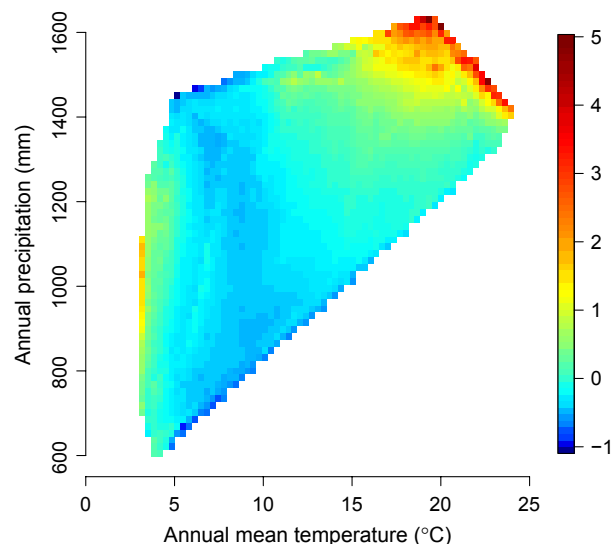


Fig. 4 Relative recruitment score from the fitted ecoregion-level models across all 65 species. Relative recruitment score is calculated as the species average of standardized relative recruitment intensity, as in Eqns (7) and (8). On average, warm and wet climates benefit species recruitment.

across species is relatively more abundant in warm and wet climates in the eastern United States. Distributions of juveniles vs. adults differ in ways that are more consistent with geographic trends in turnover but less with migration in response to climate change. These results are consistent with the previous geographic analysis of range limits, which did not show evidence of large-scale latitudinal migration either (Zhu *et al.*, 2012). High turnover in warm and wet climates per se does not mean that populations are threatened by climate warming. Rather, it is consistent with the effects of more rapid dynamics that are possible when growing seasons are long, resulting in faster maturation, more rapid thinning, and elevated recruitment. However, failure to migrate is a clear concern in the face of rapid climate change. For some species, the differences between juveniles and adults suggest ontogenetic shifts in species climatic requirements, which challenge the assumption of niche conservatism through life history. In addition, we identified several key issues in modeling species distributions including local vs. regional scales and zero abundance observations.

Forest responses to climate change

The turnover hypothesis is supported by the fact that relative recruitment dominates in warm and wet climates both for the majority of individual species (Table 1) and the synthesis of all species (Fig. 4). Most species (ca. 80%) show patterns like *Pinus taeda*, having higher optimal temperature and/or precipitation for juveniles than adults, and few (ca. 20%) show patterns like *Ilex opaca*, having lower optimal temperature and/or precipitation for juveniles than adults (Table 1). Results of these two example species are consistent with the geographic analysis at local scales that indicates *Ilex opaca* has a tendency of northward migration (fig. 4a and b, and table S1 in Zhu *et al.*, 2012), but *Pinus taeda* does not (table S1 in Zhu *et al.*, 2012). Among all these common eastern US species, the turnover hypothesis is supported by many genera (*Acer* spp., *Betula* spp., *Carya* spp., *Pinus* spp., *Quercus* spp., *Ulmus* spp.) and species (*Carpinus caroliniana*, *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Ostrya virginiana*). Furthermore, the relative recruitment score, a standardized metric of juvenile–adult abundance ratio for all species, also suggests that warm and wet climates have relatively high recruitment (Fig. 4). In this case, the turnover hypothesis applies to not only individual species but also total recruitment. If dynamics are accelerated in warm or wet regions, the species that benefit will change with the overall change in turnover. We do not expect recruitment of all species to increase uniformly, but we

do expect that overall growth, mortality, and recruitment will increase.

Faster tree population turnover in warm and wet climates is supported by a range of theoretical, experimental, and observational studies. Theory predicts that rapid tree growth results in thinning and turnover (Clark, 1991), which is promoted by fertility, growing season length, and moisture. Experiments at boreal and temperate latitudes show that rising temperatures affect all major chemical and biological processes that can influence forest dynamics, including photosynthesis, respiration, soil nutrient availability, and ontogenetic development (Saxe *et al.*, 2001). A synthesis of observations from many sites across the globe consistently supports higher recruitment and mortality rates in tropical than temperate forests and declining turnover with elevation, that is, a proxy of temperature (Stephenson & van Mantgem, 2005). Long-term monitoring in tropical forests reveals increasing tree population turnover rates through time (Phillips & Gentry, 1994; Lewis *et al.*, 2004b; Phillips *et al.*, 2004), but the global change agents have not yet been identified because the data are sparse both spatially and temporally (Lewis *et al.*, 2004a). The massive, consistently sampled temperate forest inventory data set available for this analysis provides clear evidence that relative recruitment rates increase with geographic gradients in temperature and precipitation.

The juvenile–adult comparison in geographic space (Zhu *et al.*, 2012) and climate space (this analysis) both show that large-scale poleward tree migration is not yet evident even in a data set as exhaustive as FIA. In geographic space, a poleward migration would be characterized by juveniles that are shifted to the north of adults. On the contrary, we found that most species are not experiencing northward migration at their northern range limits (i.e., high latitudes) where temperatures have increased most during the 20th century (fig. 6 in Zhu *et al.*, 2012). In climate space, the migration hypothesis predicts that juveniles would be more abundant than adults in cold and dry climates. Here, we demonstrate that patterns of juveniles and adults are inconsistent with a climatically driven migration signal. Instead, we found that recruitment is relatively more abundant in warm and wet climates. Insights gained from climate envelope projections of large-scale northward shift in habitat (Iverson & Prasad, 1998; McKenney *et al.*, 2007; Iverson *et al.*, 2008) could be updated with this evidence from juvenile–adult relationships.

Our comparisons between juvenile and adult responses show markedly different abundance–climate relationships through life history. Apparent regional-scale ontogenetic shifts in climatic requirements from

this FIA analysis are consistent with plot-scale observations (Harper & White, 1974; Grubb, 1977). The difference between juvenile and adult responses challenges the assumption of niche conservatism through life history stages. As one of the pivotal assumptions of SDMs, niche conservatism suggests that species niches are retained over time. In a biogeographic setting like ours, species realized niches are approximated by distribution-environment relationships (Peterson *et al.*, 2011). Our relative recruitment intensities indicate that the regeneration niche can look different from those of adults even when observed at the regional scale. Transplant experiments also suggest that adult abundance might provide a poor indication of the niche requirements, and cast doubt upon SDMs based solely on adult distribution data (Warren & Bradford, 2011). Among the factors that can produce these life history differences are strong interactions between climate and competition, which differs for seedlings and adult trees. Clark *et al.* (2011b) found that the effects of both temperature and drought interact with light and local moisture availability. Because seedlings of most species are subject to lower light levels, these interactions provide reasons to expect a shift in the climate impacts with age. These results highlight the importance of recognizing differences between juveniles and adults in biogeographic studies (McLaughlin & Zavaleta, 2012; Mok *et al.*, 2012; Bell *et al.*, in press).

We recognize some of the important caveats that can influence interpretation of these relationships. In addition to climate, differences between distributions of juveniles and adults can result from regional-scale patterns in succession. We have not found differences between early vs. late successional species in our results (Table 1), and our aggregation from plots to ecoregions also reduces the influence of successional trends. However, we feel that this issue must still be considered in the future. Land use legacies could play a role. To minimize its effects, we only included FIA plots that are natural (nonplantation) and fully forested. However, there is still a strong tendency toward stands of a limited age range, dating from 19th century reforestation in the eastern United States. Note that source-sink population dynamics is not an important consideration in this analysis, because we focused on regional scale, not local scale, species abundance-climate relationships. Finally, relative recruitment scores at the edge of the climate space (Fig. 4) should be interpreted with caution, because evidence is weakest there.

Regional species distribution modeling

We found that models fitted at the ecoregion scale predict abundance, but those fitted at the plot scale do not

(Fig. 1; Table 1). Others have noted lack of predictive capacity from models at this scale and interpret it as lack of response (Canham & Thomas, 2010). Iverson & Prasad (1998) resolved the misalignment between plot data and smoothly varying climate by county-level aggregation (ca. 100 000 ha). Likewise, Boucher-Lalonde *et al.* (2012) found that a single, simple model could predict North American tree occurrence in climate space at a coarse scale (ca. 40 000 ha). Apparent contradiction results from spatial misalignment of coarse scale climate and fine scale tree data. Biogeographic responses are not limited to coarse spatial scales; they are simply not available from aggregated data.

The scale alignment of individual- and aggregated-level data has been recognized as a widespread and oft-ignored phenomenon termed the *ecological fallacy* or *Simpson's paradox*. It often leads to confusing and even paradoxical interpretations of ecological data (Clark *et al.*, 2011a). In the context of species distribution modeling, it can occur when regional temperature and precipitation data do not capture local microclimate relationships that result from drainage, slope, aspect, albedo, wind fields, etc. If climate data are spatially smoothed and interpolated, then those data can be most productively applied to species distribution data aggregated at a similar scale.

The misalignment problem is especially relevant for spatial data at biogeographic scales, and it has long been recognized by statisticians (Banerjee *et al.*, 2004) and geographers (Scott *et al.*, 2002). Analyses with SDMs often take particular care with the scale of data (Hallett *et al.*, 2004; Pearson *et al.*, 2004; Diez & Pulliam, 2007; Trivedi *et al.*, 2008; Randin *et al.*, 2009; Seo *et al.*, 2009; McGill, 2010; Franklin *et al.*, 2013). In our context, species abundance and distribution are aggregations of individual demographic and physiological performance, while regional climate marginalizes local weather over space and time. Tree species do not directly respond to climate, rather individuals respond to weather. Local microclimate data are important (Dobrowski, 2011), but yet unavailable for FIA plots. Rather than using an epidemiological approach to investigate individual tree health at fine scales (Clark *et al.*, 2011b, 2012), we adopted an alternative approach, similar to Iverson & Prasad (1998), to aggregate FIA data from plots to ecoregions, a scale more compatible with regional climate.

At the ecoregion scale, we focused the analysis on nonzero observations, because we were interested in abundance pattern within a species' geographic range. On the one hand, we assumed our aggregated ecoregion data has only one source of zero observations: the species is located outside of its range so it cannot occur.

In an average ecoregion, a zero observation implies zero seedling density or tree BA in all of the approximately 100 plots located in a geographic area over 7000 km². On the other hand, focusing on nonzero observations greatly simplified the model and identified clear climate signals in species abundance data. Handling both zero and nonzero abundance using zero-inflated distributions is more challenging, as we found in a separate analysis (S. Ghosh, K. Zhu, A.E. Gelfand & J.S. Clark, unpublished data). Future studies on modeling zero-inflated data may be needed in this context.

Conclusions

The comparisons of juvenile vs. adult in both geographic space at local scale (Zhu *et al.*, 2012) and climate space at regional scale (this analysis) suggest that tree species are not yet migrating to track climate change, in agreement with modeling studies (Clark *et al.*, 2001) and increasing evidence from observational studies (Corlett & Westcott, 2013). Instead, here we show that the overall tendency is toward faster population turnover in warm and wet climates, consistent with physiological experiments (Saxe *et al.*, 2001), and observations across space (Stephenson & van Mantgem, 2005) and time (Phillips & Gentry, 1994; Phillips *et al.*, 2004). At biogeographic scales, eastern US forests are responding to climate change with faster turnover rates, and not yet with appreciable northward migration.

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References

Agee JK (1993) *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC.

Assmann E (1970) *The Principles of Forest Yield Study*. Pergamon Press, New York, NY.

Banerjee S, Carlin BP, Gelfand AE (2004) *Hierarchical Modeling and Analysis for Spatial Data*. Chapman & Hall/CRC, Boca Raton, FL.

Bansal S, Germino MJ (2010) Variation in ecophysiological properties among conifers at an ecotonal boundary: comparison of establishing seedlings and established adults at timberline. *Journal of Vegetation Science*, **21**, 133–142.

Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions*, **15**, 409–420.

Bechtold WA, Patterson PL (2005) *The Enhanced Forest Inventory and Analysis Program: National Sampling Design and Estimation Procedures*. USDA Forest Service, Southern Research Station, Asheville, NC.

Beckage B, Osborne B, Gavin DG, Pucko C, Siccamo T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences*, **105**, 4197–4202.

Bell DM, Bradford JB, Lauenroth WK (in press) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, doi: 10.1111/geb.12109.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Bertrand R, Gégout J-C, Bontemps J-D (2011) Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. *Oikos*, **120**, 1479–1488.

Botkin DB, Saxe H, Araujo MB *et al.* (2007) Forecasting the effects of global warming on biodiversity. *BioScience*, **57**, 227–236.

Boucher-Lalonde V, Morin A, Currie DJ (2012) How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography*, **21**, 1157–1166.

Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

Butterfield BJ, Briggs JM (2011) Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia*, **165**, 477–487.

Bykova O, Chuine I, Morin X, Higgins SI (2012) Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography*, **39**, 2191–2200.

Canham CD, Thomas RQ (2010) Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. *Ecology*, **91**, 3433–3440.

Cavender-Bares J, Bazzaz FA (2000) Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia*, **124**, 8–18.

Chase JM, Leibold MA (2003) *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, IL.

Clark JS (1990) Integration of ecological levels: individual plant growth, population mortality and ecosystem processes. *Journal of Ecology*, **78**, 275–299.

Clark JS (1991) Disturbance and tree life history on the shifting mosaic landscape. *Ecology*, **72**, 1102–1118.

Clark JS (1996) Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *American Naturalist*, **148**, 976–996.

Clark JS, Lewis M, Horvath L (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist*, **157**, 537–554.

Clark JS, Bell DM, Hersh MH *et al.* (2011a) Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecology Letters*, **14**, 1273–1287.

Clark JS, Bell DM, Hersh MH, Nichols L (2011b) Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. *Global Change Biology*, **17**, 1834–1849.

Clark JS, Bell DM, Kwit M, Stine A, Vierra B, Zhu K (2012) Individual-scale inference to anticipate climate-change vulnerability of biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 236–246.

Cleland DT, Avers PE, McNab WH, Jensen ME, Bailey RG, King T, Russell WE (1997) National hierarchical framework of ecological units. In: *Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources* (eds Boyce MS, Haney A), pp. 181–200. Yale University Press, New Haven, CT.

Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? *Trends in Ecology and Evolution*, **28**, 482–488.

Daly C, Halbleib M, Smith JI *et al.* (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, **28**, 2031–2064.

Diez JM, Pulliam HR (2007) Hierarchical analysis of species distributions and abundance across environmental gradients. *Ecology*, **88**, 3144–3152.

Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, **17**, 1022–1035.

Donovan LA, Ehleringer JR (1991) Ecophysiological differences among juvenile and reproductive plants of several woody species. *Oecologia*, **86**, 594–597.

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.

Eriksson O (2002) Ontogenetic niche shifts and their implications for recruitment in three clonal *Vaccinium* shrubs: *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Vaccinium oxycoccos*. *Canadian Journal of Botany*, **80**, 635–641.

Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L (2013) Modeling plant species distributions under future climates: how fine-scale do climate projections need to be? *Global Change Biology*, **19**, 473–483.

- Gallagher RV, Beaumont LJ, Hughes L, Leishman MR (2010) Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *Journal of Ecology*, **98**, 790–799.
- Gottfried M, Pauli H, Futschik A *et al.* (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111–115.
- Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, **430**, 71–75.
- Harper JL, White J (1974) The demography of plants. *Annual Review of Ecology and Systematics*, **5**, 419–463.
- Herauld B, Bachelot B, Poorter L *et al.* (2011) Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology*, **99**, 1431–1440.
- Houter NC, Pons TL (2012) Ontogenetic changes in leaf traits of tropical rainforest trees differing in juvenile light requirement. *Oecologia*, **169**, 33–45.
- Ibanez I, Clark JS, Dietze MC (2008) Evaluating the sources of potential migrant species: implications under climate change. *Ecological Applications*, **18**, 1664–1678.
- Ibanez I, Clark JS, Dietze MC (2009) Estimating colonization potential of migrant tree species. *Global Change Biology*, **15**, 1173–1188.
- Iverson LR, Prasad AM (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*, **68**, 465–485.
- Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, **254**, 390–406.
- Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences*, **106**, 19685–19692.
- Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences*, **105**, 11823–11826.
- Keys JE, Cleland DT, McNab WH (2007) *Delineation, Peer Review, and Refinement of Subregions of the Conterminous United States*. USDA Forest Service, Washington, DC.
- Kulmatiski A, Beard KH (2013) Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia*, **171**, 25–37.
- Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.
- Lewis SL, Malhi Y, Phillips OL (2004a) Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 437–462.
- Lewis SL, Phillips OL, Baker TR *et al.* (2004b) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 421–436.
- Maiorano L, Cheddadi R, Zimmermann NE *et al.* (2013) Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. *Global Ecology and Biogeography*, **22**, 302–317.
- McGill BJ (2010) Matters of scale. *Science*, **328**, 575–576.
- McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF (2007) Potential impacts of climate change on the distribution of North American trees. *BioScience*, **57**, 939–948.
- McLaughlin BC, Zavaleta ES (2012) Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). *Global Change Biology*, **18**, 2301–2312.
- McMahon SM, Harrison SP, Armbruster WS *et al.* (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology and Evolution*, **26**, 249–259.
- McNab WH, Cleland DT, Freeout JA, Keys JE Jr, Nowacki GJ, Carpenter CA (2007) *Description of "Ecological Subregions: Sections of the Conterminous United States"*. Washington, DC, USDA Forest Service.
- McRoberts RE, Holden GR, Nelson MD *et al.* (2005) Estimating and circumventing the effects of perturbing and swapping inventory plot locations. *Journal of Forestry*, **103**, 275–279.
- Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, **94**, 973–979.
- Mok H-F, Arndt SK, Nitschke CR (2012) Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of South-Eastern Australia. *Global Change Biology*, **18**, 1053–1072.
- Palow DT, Nolting K, Kitajima K (2012) Functional trait divergence of juveniles and adults of nine Inga species with contrasting soil preference in a tropical rain forest. *Functional Ecology*, **26**, 1144–1152.
- Parrish JAD, Bazzaz FA (1985) Ontogenetic niche shifts in old-field annuals. *Ecology*, **66**, 1296–1302.
- Pauli H, Gottfried M, Dullinger S *et al.* (2012) Recent plant diversity changes on Europe's mountain summits. *Science*, **336**, 353–355.
- Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. *Trends in Ecology and Evolution*, **23**, 149–158.
- Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography*, **27**, 285–298.
- Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.
- Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton, NJ.
- Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. *Science*, **335**, 1344–1348.
- Phillips OL, Gentry AH (1994) Increasing turnover through time in tropical forests. *Science*, **263**, 954–958.
- Phillips OL, Baker TR, Arroyo L *et al.* (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 381–407.
- Poorter L (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology*, **13**, 396–410.
- Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Quero JL, Gomez-Aparicio L, Zamora R, Maestre FT (2008) Shifts in the regeneration niche of an endangered tree (*Acer opalus* ssp. *granatense*) during ontogeny: using an ecological concept for application. *Basic and Applied Ecology*, **9**, 635–644.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org> (accessed 1 May 2012).
- Randin CF, Engler R, Normand S *et al.* (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557–1569.
- Saxe H, Cannell MGR, Johnsen B, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369–399.
- Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (eds.) (2002) *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, DC.
- Seo C, Thorne JH, Hannah L, Thuiller W (2009) Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters*, **5**, 39–43.
- Smith WB, Miles PD, Perry CH, Pugh SA (2009) *Forest Resources of the United States, 2007*. USDA Forest Service, Washington Office, Washington, DC.
- Soberón J, Nakamura M (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, **106**, 19644–19650.
- Stephenson NL, van Mantgem PJ (2005) Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters*, **8**, 524–531.
- Stohlgren TJ, Bachand RR, Onami Y, Binkley D (1998) Species-environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. *Plant Ecology*, **135**, 215–228.
- Thomas SC, Winner WE (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology*, **22**, 117–127.
- Trivedi MR, Berry PM, Morecroft MD, Dawson TP (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology*, **14**, 1089–1103.
- Urbietta IR, Garcia LV, Zavala MA, Maranon T (2011) Mediterranean pine and oak distribution in southern Spain: is there a mismatch between regeneration and adult distribution? *Journal of Vegetation Science*, **22**, 18–31.
- Walther GR, Berger S, Sykes MT (2005) An ecological 'footprint' of climate change. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1427–1432.
- Warren RJ, Bradford MA (2011) The shape of things to come: woodland herb niche contraction begins during recruitment in mesic forest microhabitat. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1390–1398.
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics*, **15**, 393–425.
- Wiens JJ (2011) The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2336–2350.

- Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.
- Wiens JJ, Ackerly DD, Allen AP *et al.* (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.
- Woodall CW, Oswald CM, Westfall JA, Perry CH, Nelson MD, Finley AO (2009) An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management*, **257**, 1434–1444.
- Woodall CW, Zhu K, Westfall JA, Oswald CM, D'Amato AW, Walters BF, Lintz HE (2013) Assessing the stability of tree ranges and influence of disturbance in eastern US forests. *Forest Ecology and Management*, **291**, 172–180.
- Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters*, **13**, 1–10.
- Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters*, **8**, 662–673.
- Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, **18**, 1042–1052.