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RESEARCH ARTICLE

Multi-model comparison on the effects of climate change on tree species in the eastern U.S.: results from an enhanced niche model and process-based ecosystem and landscape models

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Abstract

Context Species distribution models (SDM) establish statistical relationships between the current distribution of species and key attributes whereas process-based models simulate ecosystem and tree species dynamics based on representations of physical and biological processes. TreeAtlas, which uses DISTRIB SDM, and Linkages and LANDIS PRO, process-based ecosystem and landscape models, respectively, were used concurrently on four regional climate change assessments in the eastern Unites States.

Objectives We compared predictions for 30 species from TreeAtlas, Linkages, and LANDIS PRO, using two climate change scenarios on four regions, to derive a more robust assessment of species change in response to climate change.

Methods We calculated the ratio of future importance or biomass to current for each species, then compared agreement among models by species, region, and climate scenario using change classes, an ordinal agreement score, spearman rank correlations, and model averaged change ratios.

Results Comparisons indicated high agreement for many species, especially northern species modeled to lose habitat. TreeAtlas and Linkages agreed the most but each also agreed with many species outputs from

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LANDIS PRO, particularly when succession within LANDIS PRO was simulated to 2300. A geographic analysis showed that a simple difference (in latitude degrees) of the weighted mean center of a species distribution versus the geographic center of the region of interest provides an initial estimate for the species' potential to gain, lose, or remain stable under climate change.

Conclusions This analysis of multiple models provides a useful approach to compare among disparate models and a more consistent interpretation of the future for use in vulnerability assessments and adaptation planning.

Keywords Climate change · Eastern United States · Multi-model comparison · TreeAtlas · DISTRIB · LANDIS PRO · Linkages · Forests

Introduction

Average global land temperatures have risen approximately 1 °C since the mid-1950s (Rohde et al. 2012) and increasingly rapid warming is projected to occur during the twenty first century (IPCC 2014). Predictions of future precipitation also indicate seasonal changes, but the timing and magnitude of precipitation events are not well understood. A more vigorous hydrologic cycle is expected to result in heavy precipitation events that will increasingly provide a larger proportion of the total annual precipitation. Indeed, this pattern has been observed across the eastern United States with an increase of 27, 37, and 71 % of precipitation falling in very heavy events (the heaviest 1 %) from 1958 to 2012 for the Southeast, Midwest, and Northeast, respectively (Melillo et al. 2014). The increased frequency of these events is expected to result in more runoff and floods (Lenderink and van Meijgaard 2008) as well as more and longer periods without rain and droughts (IPCC 2014). Indeed, the elevated number, severity, and impact of disastrous heat and precipitation events have been linked to the human influence on climate (Coumou and Rahmstorf 2012) and amplified heating of the Arctic (Seminov 2012).

Climate is the primary driving force at a coarse scale for the location, composition, and productivity of forests (Woodward and Williams 1987), and past changes in climate and tree distributions, responding individually as species (not communities) are evident in the paleoecological record (e.g., Webb III and Bartlein 1992; DeHayes et al. 2000). There is already evidence that tree species have moved to higher altitudes (Beckage et al. 2008; Holzinger et al. 2008; Lenoir et al. 2008) and latitudes (Woodall et al. 2009; Boisvert-Marsh et al. 2014; Reich et al. 2015) in recent decades, and future climate changes are expected to result in further range shifts.

A number of different modeling approaches have been developed to project future distributions of trees and forests under a changing climate. Species distribution models (SDMs) establish a statistical relationship between the current distribution of species and key attributes of their habitats and are used to predict how species distributions might shift as climate change affects those attributes. SDMs are computationally inexpensive and typically provide projections for many species over large areas. SDMs carry caveats, discussed elsewhere, that limit their scope to the realized niche (the habitat currently occupied) rather than fundamental niche (the habitat that could potentially be occupied in the absence of competitors, diseases, or herbivores) and fail to consider migration or successional patterns of forest growth (e.g., Wiens et al. 2009; Iverson and McKenzie 2013). Rather, SDMs assess whether species will be exposed to bioclimatic conditions outside their realized ranges into the future, suggesting a potential for changes to suitable habitats.

Process models simulate ecosystem and tree species dynamics based on mathematical representations of physical and biological processes. Process models can simulate future change in tree species dispersal, succession, biomass and nutrient dynamics over space and time, often with competition considered among several species; they most often operate at a finer pixel size and require more computational power than a SDM. Process models also have assumptions and uncertainties that should be taken into consideration when applying results to management decisions (Lawler et al. 2006; Kennedy and Ford 2011). For example, they rely on species parameterization and empirical and theoretical relationships that are specified by the modeler using imperfect knowledge, and any uncertainties in these relationships can be compounded over time and space, leading to potential biases.

SDM and process models have forecasted tree habitats to move variously, but generally poleward, with climate change (Iverson et al. 2008b; Keith et al. 2008; Dobrowski et al. 2011; McKenney et al. 2011). Changes in potential tree habitat are often modeled to show much larger changes that can be expected to be colonized within 100 years through unassisted migration (e.g., Iverson et al. 2004; Serra-Diaz et al. 2014). Uncertainty in data inputs and model outputs, as well as other challenges will continue to confront species modeling (Pearson et al. 2006; Thuiller et al. 2008; Xu et al. 2009). Meanwhile, multiple approaches are being developed in attempts to improve projections (Morin and Thuiller 2009; Franklin 2010; Iverson et al. 2011; Matthews et al. 2011). Assuredly, within the landscape of interest, managers and decision makers will need to use model outputs in concert with an evaluation of legacies in land use, past ecological trends, and local conditions prior to determining a management prescription. For example, identification of potential refugia for species losing habitat or possible sites for encouraging species expansion or new establishment may be important.

As part of a Climate Change Response Framework that is being applied across the Northeastern United States (Swanston and Janowiak 2012), the predictions from TreeAtlas (SDM) and process models Linkages and LANDIS PRO were applied using consistent climate and forest inventory data sets and future climate scenarios to assess changes in tree species importance at the end of this century. Projects within this area have been the focus of extensive ecosystem vulnerability assessment and synthesis efforts coordinated by the Northern Institute of Applied Climate Science (Brandt et al. 2014; Butler et al. 2015). These efforts effectively created a platform for scientists and managers to provide early feedback on model outputs in each region, thereby improving model results, and were also the basis for adaptation efforts towards informed forest management in the face of climate change (Janowiak et al. 2014).

Our goal was to derive a robust assessment of potential changes in trees species importance or abundance in response to climate change through multi-model inference. We compared predictions from a species distribution model (TreeAtlas, or DISTRIB), a hybrid empirical-process model (Linkages), both of which projected habitat suitability in 2100, and a process-based landscape change model (LANDIS PRO), which projected forest composition and structure in 2100 and 2300, for four regions of the eastern United States using two climate change scenarios. We modeled predictions for two 'bookends' of climate scenarios for each forest change model, and assessed species change that were not dependent on any one model framework. This allowed us to address uncertainties in future climate by considering climate scenarios with lesser and greater amounts of change in precipitation and temperature. We hypothesized that TreeAtlas and Linkages, both projecting suitable habitat, should be more in agreement with each other than with the LANDIS PRO succession model outputs, but that as succession is allowed to proceed within LANDIS PRO, agreement with the suitable habitat outputs would improve. Furthermore, we expected LANDIS PRO and Linkages predictions to be in closer agreement over longer time periods as stand dynamics equilibrated because species specific establishment probabilities and maximum growing space were parameterized in LANDIS based on Linkages predictions for each climate scenario.

Methods

Study areas

The study area consisted of much of the forested land in the central and northern portions of the eastern United States (Fig. 1). The area was modeled in four regions: the Central Hardwoods (CH), Central Appalachians (CA), Mid-Atlantic (MA), and New England (NE). The MA and NE are much larger in area and had more species (24) modeled than the other two regions (20 for CH and 15 for CA, Table 1) in this study. The climates in the regions represented north–south and east–west gradients. Mean annual temperatures ranged from 13.0 °C in CH to 6.4 °C in NE at present (1981–2010) and are projected to increase to 14.2–17.5 °C in CH and 7.6–10.3 °C in NE, depending on scenario, by the end of century (Table 1). Estimates of annual precipitation did not vary widely across regions or scenarios, although CH is modeled to have higher precipitation under the mild scenario of climate change and lower under the harsh scenario, while the other regions had estimates of level or slightly higher annual precipitation under either scenario. However, with the warmer conditions, and larger precipitation events followed by longer drought periods, greater physiological "hot droughts" can be

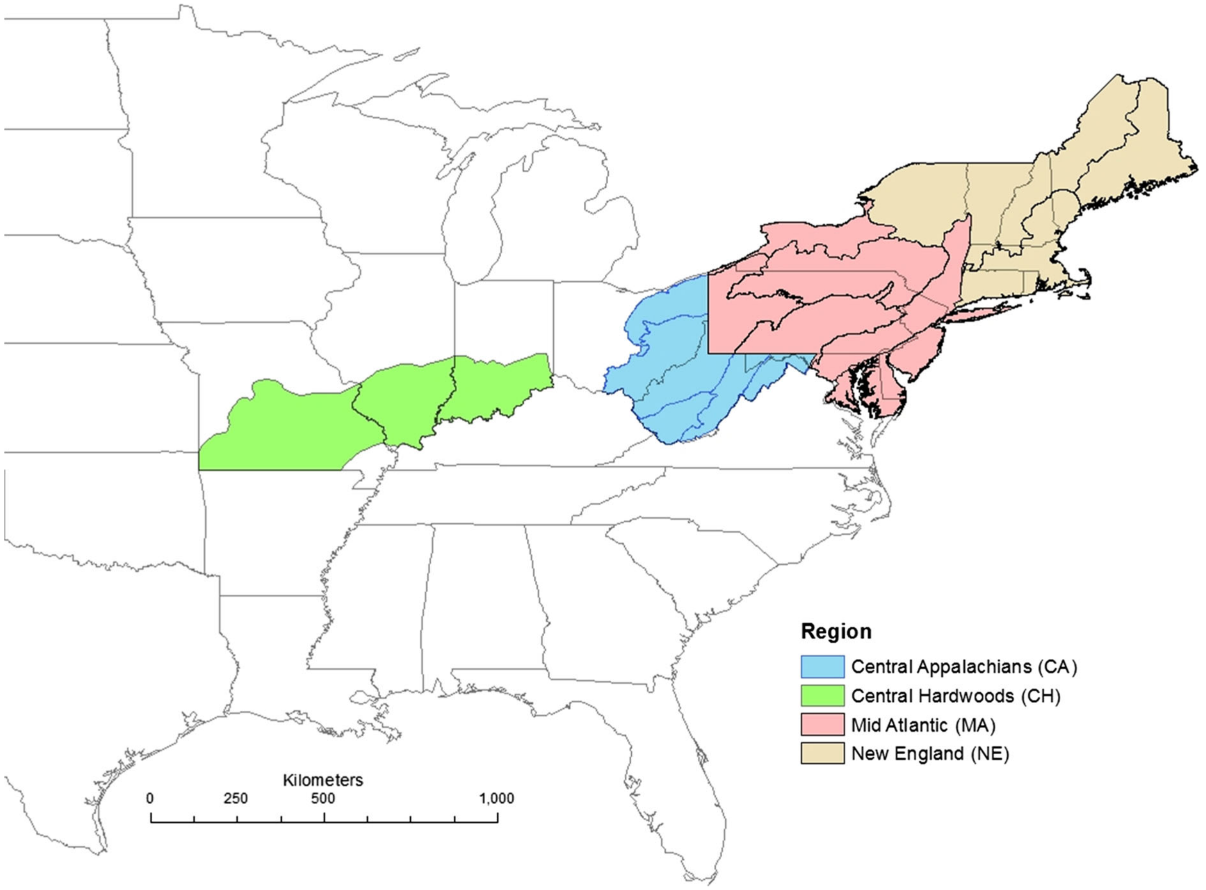


Fig. 1 Locations of the four study regions in the eastern United States for which we compare projected changes in tree species importance

Table 1 Attributes of each region

	CH	CA	MA	NE
Area (km^2 × 1000)	170.10	116.00	245.20	212.30
Mean center, latitude	38.1	39.4	41.1	44.2
Mean center, longitude	−90.0	−81.1	−76.8	−71.5
Number of species represented	20	15	24	24
Mean annual temperature (°C)	13.0	10.8	9.6	6.4
Mean annual precipitation (mm)	1139	1099	1106	1172
PCM mean annual temperature (°C)	14.2	11.7	10.7	7.6
PCM mean annual precipitation (mm)	1184	1144	1158	1170
GFDL mean annual temperature (°C)	17.5	15.0	13.7	10.3
GFDL mean annual precipitation (mm)	1037	1102	1161	1206
Mean maximum elevation (m)	288	570	439	482
Clay (%)	33.9	27.9	19.1	10.8
Organic matter (%)	0.8	1.8	2.5	8.8
Available water supply (mm)	21.3	16.2	15.5	16.7
pH	5.81	5.48	5.45	5.41

Climate and soil parameters were generated by aggregating 10 × 10 km data within each region. *CH* Central Hardwoods, *CA* Central Appalachians, *MA* MidAtlantic, *NE* New England expected to increase forest mortality (Allen et al. 2015). Elevations are substantially higher and more variable in the CA (mean maximum elevation of 570 m) and lower in the CH (288 m mean maximum elevation). Edaphic variables also provide important features which describe ecological conditions and, in the models, create variation across the regions (Table 1).

Data sources

The same climate scenarios and downscaled climate data were used for the TreeAtlas, Linkages, and LANDIS PRO models. We selected two climate scenarios that generally spanned the range of potential future conditions by pairing general circulation models (GCM) with emission scenarios. The Parallel Climate Model (PCM, the mild scenario) has relatively low sensitivity to changes in greenhouse gas concentrations (PCM, Washington et al. 2000) and was combined with the B1 emission scenario, which represented a rapid conversion by humans to low carbon energy sources (Nakicenovic et al. 2000). The Geophysical Fluid Dynamics Laboratory (GFDL, the harsh scenario) is moderately sensitive to changes in greenhouse gas concentrations (Delworth et al. 2006) and was combined with the A1FI emission scenario, which predicted the highest greenhouse gas emissions (Nakicenovic et al. 2000). Therefore our PCM-B1 and GFDL-A1FI scenarios represent bookends to potential future climates out to 2100. A statistically downscaled dataset at ~12 km resolution was used to calculate daily precipitation and mean, maximum, and minimum temperature through 2100 for the two scenarios (Stoner et al. 2013), which provided the climate inputs to the forest models described here. All three model approaches used U.S. Forest Service Forest Inventory and Analysis data (FIA) to model current habitat or initialize current conditions for simulations (Woodall et al. 2010).

TreeAtlas

TreeAtlas is a collection of DISTRIB models that use a statistical approach (Random Forest) to predict current and potential future suitable habitat (Prasad et al. 2006). Model inputs include US Forest Service forest inventory data and other environmental variables (Iverson et al. 2008b; Prasad et al. 2016). Each species model was given a reliability rating, using four statistical and spatial metrics, to provide an indication of the quality of the species model; species with fewer FIA observations tended to have lower reliability (Iverson et al. 2011). Each species also was rated, via literature, on 9 biological characteristics that may assist in adaptation to climate change as well as its capacity to deal with 12 disturbance types (Matthews et al. 2011). The outputs are presented in a web-based Climate Change Tree Atlas, which incorporates a diverse set of information about potential shifts in the distribution and abundance of tree species' habitat in the eastern United States over the next century (Landscape Change Research Group 2014). Importantly, TreeAtlas projects where suitable habitat may change for a particular species, but does not project how long it may take for a species' range to change. The actual rate of migration into newly suitable habitat will be influenced by large time lags, dispersal and establishment limitations, and availability of refugia. These have been evaluated in other work for a few species through our model SHIFT and the multi-stage approach, but were not used here because of insufficient numbers of modeled species (Iverson et al. 2004; Prasad et al. 2013, 2016).

The models use inputs of tree abundance, climate, and the environment to simulate species' habitats into 20 × 20 km cells; details are presented elsewhere (Iverson et al. 2008b; Landscape Change Research Group 2014; Butler et al. 2015). Because the forest inventory plots are non-biased and extensive across the eastern US, the 30 common species reported here have high model reliability within TreeAtlas.

Linkages

Linkages is a hybrid empirical-physiological model that simulates forest ecosystem functions such as soil–water balance, litter decomposition, nitrogen cycling, soil hydrology, and evapotranspiration to predict tree establishment, growth, and death. Model inputs include daily maximum and minimum temperature, precipitation, wind speed, solar radiation, soil moisture capacity for multiple soil layers, wilting point, percent rock, percent clay, percent sand, initial organic matter, and nitrogen contents (Wullschleger et al. 2003; Dijak et al. in press). We used Linkages to model the relative performance of individual tree species for the ecological subsections and climate scenarios we considered in this study (for details see Brandt et al. 2014; Butler et al. 2015; Wang et al. (in press); Wang et al. 2015). We predicted the maximum biomass reached for individual species based on 20 replicate simulations for 30 years starting from bare ground on virtual plots that represented 8–10 landforms in each subsection under current climate (1980–2009) and each future climate scenario (2070–2099). We aggregated the biomass estimates from these studies from landforms to subsections and subsections to sections using area-weighted means and calculated change ratios as the quotient of future biomass divided by current biomass. Like TreeAtlas, this application of Linkages provided a prediction of the change in future habitat suitability for individual tree species and is not a simulation of actual forest change.

LANDIS PRO

LANDIS PRO (hereafter Landis) is a forest landscape model that projects changes in forest composition and structure due to processes occurring at species-, stand-, and landscape-levels (Wang et al. 2013, 2014a). We used Landis to simulate changes in forest composition and structure due to succession, dispersal, windthrow, harvest, and climate change for each region and climate scenario (for details see Brandt et al. 2014; Butler et al. 2015; Wang et al. 2015). Landis simulates tree growth, longevity-caused mortality, competition-caused mortality (self-thinning), disturbance-caused mortality, resprouting, fecundity, seed dispersal, and establishment (He et al. 2005). It tracks the number of trees and diameter at breast height (DBH) by species and age cohort in each 270-m raster cell and after establishing initial forest conditions at year 2000 from 1995 to 2005 FIA data including trees >2.54 cm (Wang et al. 2014b). Landis does not directly consider climate, however; effects of climate change were incorporated by estimating climate change impacts on species establishment probabilities (SEP), which affect species colonization, and resources availability (measured as maximum growing space, MGSO), which, in turn, affects tree mortality as a function of climate, soil, and terrain. MGSO and SEP were modeled using Linkages under current climate and each future climate scenario, then linearly interpolated from current climate to the end of the century. We calculated species importance values for each cell at the start of simulations and at year 2100 (hereafter Landis100) and 2300 (hereafter Landis300) under each scenario and the ratio of future to current importance values. However, because the climate scenarios only forecasted climate change through 2100, simulations for years 2100–2300 did not consider climate change beyond 2100 and held SEP and MGSO at year 2100 levels. We recognize the high degree of uncertainty around 300 year projections; indeed a recent publication reports immense climatological changes should humans continue to burn fossil fuels to 2300 (Tokarska et al. 2016). However, we wished to demonstrate the effects of an additional 200 years of stand dynamics in response to the climate change that occurred through 2100 because species turnover can take a long time (Wang et al. 2015). Unlike TreeAtlas and Linkages, Landis simulated stand dynamics, colonization, and extinction; representing projections of expected change in forest composition and structure at 2100 and 2300. We simulated the current level of tree harvest and approximated the silvicultural methods used in the region to make our simulations as realistic as possible (Wang et al. 2015). We created regional management units and parameterized the level of harvest based on FIA data and we varied the amount of basal area harvested in a stand to simulate clearcutting or partial harvest at the pixel level. In addition, we simulated windthrow as a stochastic gap-scale disturbance that affected the oldest trees on an average of 1.4 % of pixels per decade. (Wang et al. 2015,).

Model assumptions

All models have limitations and assumptions, and are approximations of reality. Each of these models carry the assumptions for the climate change scenarios for GFDL and PCM, and that the FIA data captures the distribution and abundance for the species under study. For TreeAtlas, we assume that the selected variables do in fact reflect the niche requirements of a species, that species are in equilibrium with their suitable habitat, that predictions can be made into novel climates and land covers, that the effects of adaptation and evolution are minimal, and that the effects of biotic interactions (including human interactions) are minimal. For Linkages, we assume that the variables selected and the parameterization of those variables accurately drive the establishment, growth, and death of individual tree species over the first 30 years of growth from bare ground. For Landis, we assume that we have correctly parameterized life histories and physiologies for each species, captured the complexity of interacting biotic and disturbance factors, and controlled cumulative errors associated with the sheer number and diverse spatio-temporal scales of parameters. Despite these limitations, this study represents a pathway to further understand the range of possibilities for tree species under a changing climate.

Analysis

We calculated a future:current change ratio as the ratio of a species' future importance values (as calculated equally from tree density and basal area in TreeAtlas and Landis, and as biomass in Linkages) to current importance values or biomass. For example, the future:current ratio for species X according to TreeAtlas and GFDL scenario = modeled future importance value for species X at 2100 according to GFDL scenario/current importance for species X. Future values were calculated for 2100 (100 years) for TreeAtlas and Linkages and 2100 and 2300 (100 and 300 years) for Landis. If the change ratio is close to one (i.e., 0.8–1.2), essentially no change in suitable habitat is projected by the models. If the ratio exceeds 1.2, an increase is projected, while if the ratio is less than 0.8, a decrease is projected. We created the following change classes based on change ratios to facilitate interpretation of some results: Large Increase (>2), Small Increase (1.2–2.0), No Change (0.8–1.2), Small Decrease (0.5–0.8), Large Decrease (<0.5). Change ratios were derived using each model in each region for the two climate scenarios to assess overall species vulnerability.

We tallied agreement between the following pairs of models based on change ratios: (1) TreeAtlas & Linkages, (2) TreeAtlas & Landis100, (3) TreeAtlas & Landis300, (4) Linkages & Landis100, (5) Linkages & Landis300, and (6) Landis100 & Landis300. To present a simple, single metric with higher values indicating higher agreement, we created an ordinal scale of 0–4 and assigned 4 points if both change classes were identical = full agreement; 3 points if one class apart (e.g., No Change and Small Increase or Small Decrease); 2 points if two classes apart but still trending in same direction (e.g., No Change and Large Increase or Large Decrease); 1 point if Small Decrease & Small Increase (opposite trend); and 0 points if opposite trend and one or both are Large Decrease or Large Increase. In this way, we assign increasing penalties as the classes are more in disagreement.

We also calculated Spearman's rank correlations of future:current ratios among combinations of models and scenarios as another measurement of agreement. We report correlations and p-values for the hypothesis that change ratios from a pair of models were not positively correlated and used Holm's method to adjust p-values to account for familywise error rate with multiple comparisons (Holm 1979), a fairly restrictive adjustment.

To assess association of potential change to their geographic location for the 30 species, we evaluated the mean centers of the species distribution, now and into the future, against the geographic centers of each of the four regions. We calculated the weighted mean centers of species' current and future habitats based on importance values reported within TreeAtlas (www.nrs.fs.fed.us/atlas/tree/meancenter_latlong2f.html), then calculated the difference between a species center of distribution and the geographic center of our study regions (species mean center—region mean center = mean offset from range center) to assess if a species center was North (>2°N), Central (2°N to 2°S) or South (>2°S) with respect to centers of the four regions. For example, balsam fir is a species with a species mean center to the far North (latitude 46.2°N), while the geographic center for the study region MA is at 41.2°N, a mean offset of 5°, so that the species is classed as North for this region. For species intersecting Canada, only the US portion (for which importance values are available) was used for calculating mean centers, which compressed some latitude differences, but results were robust relative to the regional locations. We included the mean offset from range center in our correlation analysis, and summarized future:current ratios by North, Central, or South latitude classes to assess relationships between model outputs and species geographic positioning.

Lastly, we calculated mean future:current ratios across species and for each model system for both PCM and GFDL scenarios. These ratios represent single estimates of change derived from all three models and the range between PCM and GFDL can be interpreted as a measure of uncertainty across scenarios.

Results

By tabulating change classes for species by region, model, and climate scenarios, some general patterns in species changes were apparent: (1) substantially less change was projected by the models under PCM than GFDL for all models; (2) Landis100 has small changes under both scenarios but Landis300 shows larger changes; (3) more species show projected declines than increases, with a possible exception in New England (Fig. 2).

TreeAtlas-Linkages had the highest agreement scores on our 0–4 ordinal scale when averaged across species, with 3.4 for PCM and 3.16 for GFDL (Table S1). Next in agreement was Landis100-Landis300 (3.07–3.11), followed by Linkages-Landis300, Linkages-Landis100 ≅ TreeAtlas-Landis300, and TreeAtlas-Landis100. TreeAtlas-Landis300 tended to agree the most for the GFDL scenario (2.78 vs. 2.48 on PCM), while Linkages-Landis300 agreed relatively more for the PCM scenario (2.92 vs 2.60 on GFDL). These relationships generally held across regions. Among the 30 species, there was a variation in agreement, with some of the northernmost species (e.g., black spruce, balsam fir, northern white cedar, and red spruce) showing maximum agreement among models (Table 2, Note: scientific names for all species are presented in Table 2). On the low end of agreement are several pines (shortleaf, pitch, loblolly, and Virginia—the latter two with low prominence in these regions), quaking aspen, post oak, tulip poplar, yellow birch, and American beech. Quaking aspen had model outputs in NE with large increases under Landis100/300 and large decreases in TreeAtlas and Linkages, while the reverse was true for shortleaf pine, and to a lesser extent, post oak, in CH. Many of the oaks, hickories, and maples tended to have moderate agreement; for example, most models show a decline in sugar maple especially in the more southerly regions of CH and CA.

There were 83 species-region combinations when we pooled species for the correlation analysis. The highest correlations between model-scenario pairings were between Landis100 PCM and Landis100 GFDL (Fig. 3; Table S2), which was not surprising because change is predominately driven by succession, not climate, in the first 100 years in Landis (Wang et al. 2015). Landis100 versus Landis300 were also highly correlated regardless of scenario, but especially so within the same scenario. High correlations also occurred between PCM and GFDL scenarios within both TreeAtlas and Linkages across most combinations of species and regions, except for CA with its low species count of 15 (Table S2). There were also highly significant correlations between TreeAtlas and Linkages outputs for both scenarios except for in the CA (Table S2).

Importantly, however, correlations between TreeAtlas and Landis increased as Landis simulations increased from 100 to 300 years, especially under the GFDL scenario where the correlation increased from 0.23 to 0.25 ($P > 0.05$) for 100-year to 0.48-0.51 ($P < 0.0001$) for 300-year Landis simulations (Fig. 3, Table S2). An increase in correlation would be expected over time because of the role of the Linkages outputs as inputs to Landis, and because Linkages and TreeAtlas outputs were quite highly correlated ($r = 0.60$–0.77). The same pattern of increasing correlation over time is true for both Linkages and TreeAtlas throughout regions although not always significantly so (Fig. 3; Table S2). Notably however, rank correlations between Landis even at 300 years and the habitat suitability models did not attain very high values, probably because certain species that did not model well fell in highly variable ranks among the models.

There was also a highly significant negative correlation between the latitude difference and change ratios from TreeAtlas and Linkages across species-region combinations (~ -0.8, Fig. 3; Table S2). This pattern indicates that as the distance between mean centers of the species and the region center increased, the future:current ratios (~habitat suitability) decreased. The relationship was also highly significant for Landis300 GFDL but not the other outputs from Landis, again indicating a progression towards the habitat models given harsh conditions and 300-year Landis simulations.

When species were evaluated according to their latitudinal differences between the region and mean centers, the 16 species/region combinations categorized as North had very low future:current ratios under both PCM (average = 0.68) and especially GFDL (average = 0.23) scenarios (Table 3). Those combinations categorized as South had future:current ratios >1, indicating increasing tendencies for habitat within their region, while the Central class was between these extremes but tended towards decreasing habitat, especially under GFDL. Graphically, future:current ratios

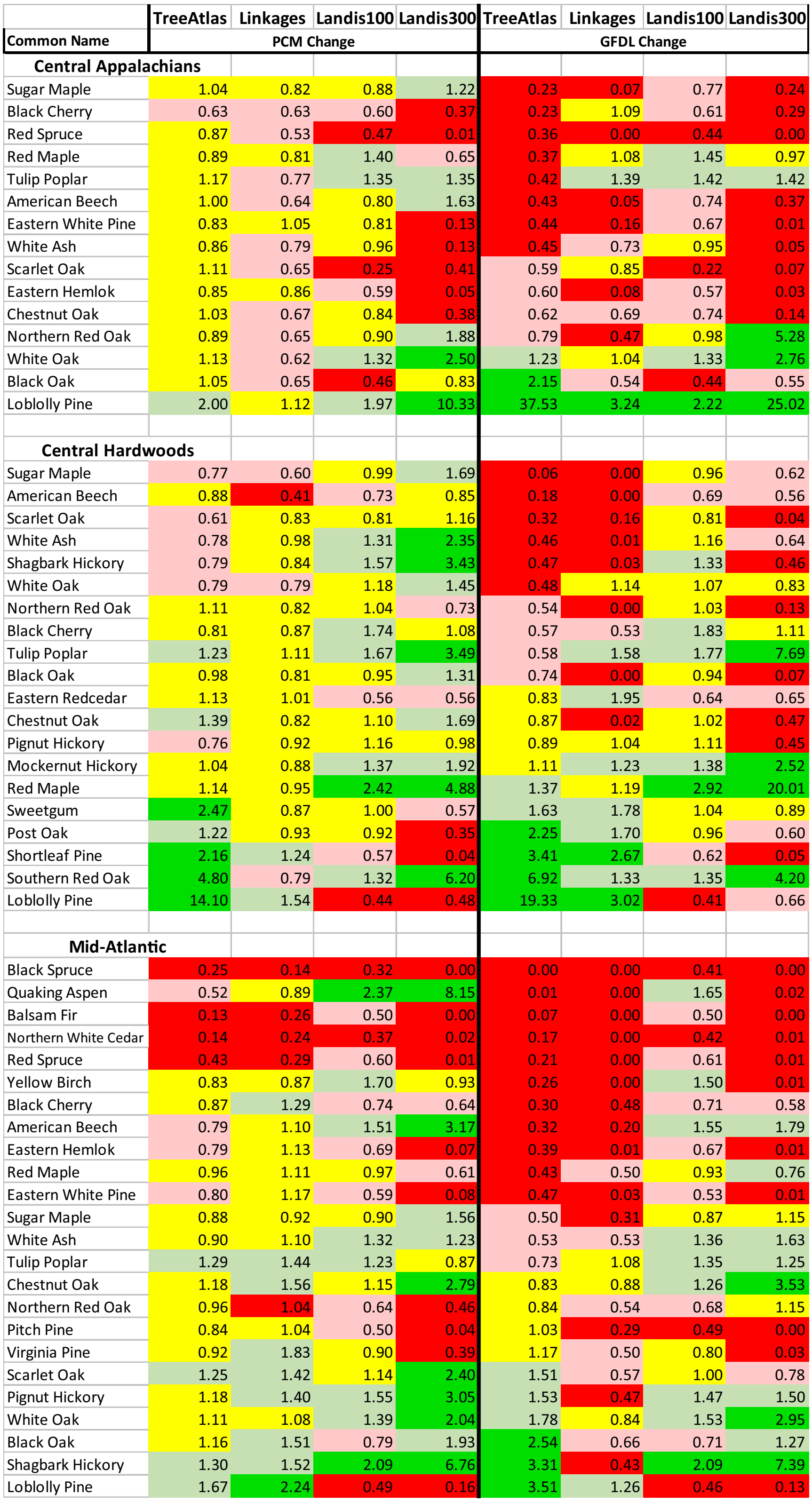
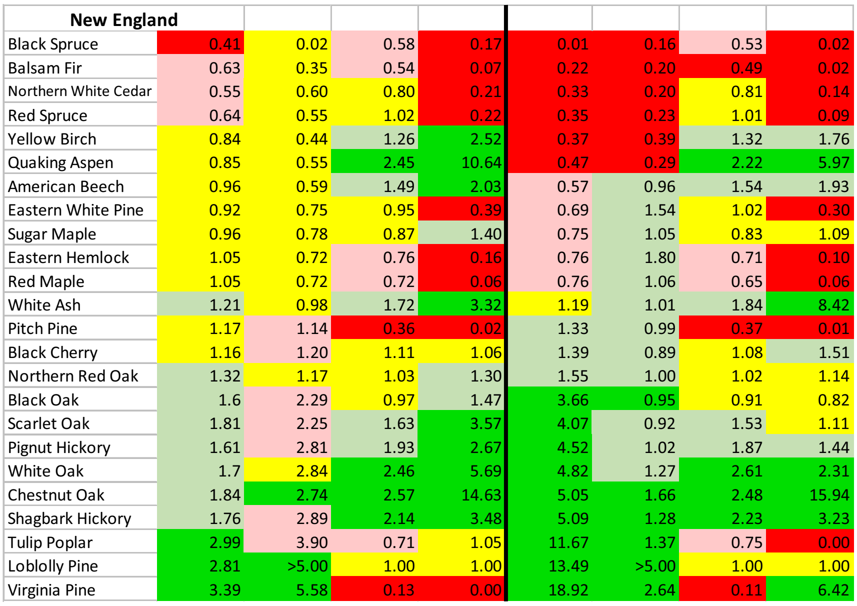


Fig. 2 Comparison of change classes for 30 species for TreeAtlas, Linkages, and Landis100 and Landis300 for PCM and GFDL climate change scenarios, for the New England (NE, N = 24), MidAtlantic (MA, N = 24), Central Appalachians (CA, N = 15), and Central Hardwoods (CH, N = 20) regions. *Numbers* indicate the future:current ratios, while *colors* represent the change class, where *red* = Large Decrease (future:current ratio <0.5), *pink* = Small Decrease (future:current ratio >0.5 and <0.8), *yellow* = No Change (future:current ratio >0.8 and <1.2), *light green* = Small Increase (future:current ratio >1.2 and <2.0), and *darker green* = Large Increase (future:current ratio >2.0)

	TreeAtlas	Linkages	Landis100	Landis300	TreeAtlas	Linkages	Landis100	Landis300
Common Name	**PCM Change**				**GFDL Change**			
Central Appalachians								
Sugar Maple	1.04	0.82	0.88	1.22	0.23	0.07	0.77	0.24
Black Cherry	0.63	0.63	0.60	0.37	0.23	1.09	0.61	0.29
Red Spruce	0.87	0.53	0.47	0.01	0.36	0.00	0.44	0.00
Red Maple	0.89	0.81	1.40	0.65	0.37	1.08	1.45	0.97
Tulip Poplar	1.17	0.77	1.35	1.35	0.42	1.39	1.42	1.42
American Beech	1.00	0.64	0.80	1.63	0.43	0.05	0.74	0.37
Eastern White Pine	0.83	1.05	0.81	0.13	0.44	0.16	0.67	0.01
White Ash	0.86	0.79	0.96	0.13	0.45	0.73	0.95	0.05
Scarlet Oak	1.11	0.65	0.25	0.41	0.59	0.85	0.22	0.07
Eastern Hemlok	0.85	0.86	0.59	0.05	0.60	0.08	0.57	0.03
Chestnut Oak	1.03	0.67	0.84	0.38	0.62	0.69	0.74	0.14
Northern Red Oak	0.89	0.65	0.90	1.88	0.79	0.47	0.98	5.28
White Oak	1.13	0.62	1.32	2.50	1.23	1.04	1.33	2.76
Black Oak	1.05	0.65	0.46	0.83	2.15	0.54	0.44	0.55
Loblolly Pine	2.00	1.12	1.97	10.33	37.53	3.24	2.22	25.02
Central Hardwoods								
Sugar Maple	0.77	0.60	0.99	1.69	0.06	0.00	0.96	0.62
American Beech	0.88	0.41	0.73	0.85	0.18	0.00	0.69	0.56
Scarlet Oak	0.61	0.83	0.81	1.16	0.32	0.16	0.81	0.04
White Ash	0.78	0.98	1.31	2.35	0.46	0.01	1.16	0.64
Shagbark Hickory	0.79	0.84	1.57	3.43	0.47	0.03	1.33	0.46
White Oak	0.79	0.79	1.18	1.45	0.48	1.14	1.07	0.83
Northern Red Oak	1.11	0.82	1.04	0.73	0.54	0.00	1.03	0.13
Black Cherry	0.81	0.87	1.74	1.08	0.57	0.53	1.83	1.11
Tulip Poplar	1.23	1.11	1.67	3.49	0.58	1.58	1.77	7.69
Black Oak	0.98	0.81	0.95	1.31	0.74	0.00	0.94	0.07
Eastern Redcedar	1.13	1.01	0.56	0.56	0.83	1.95	0.64	0.65
Chestnut Oak	1.39	0.82	1.10	1.69	0.87	0.02	1.02	0.47
Pignut Hickory	0.76	0.92	1.16	0.98	0.89	1.04	1.11	0.45
Mockernut Hickory	1.04	0.88	1.37	1.92	1.11	1.23	1.38	2.52
Red Maple	1.14	0.95	2.42	4.88	1.37	1.19	2.92	20.01
Sweetgum	2.47	0.87	1.00	0.57	1.63	1.78	1.04	0.89
Post Oak	1.22	0.93	0.92	0.35	2.25	1.70	0.96	0.60
Shortleaf Pine	2.16	1.24	0.57	0.04	3.41	2.67	0.62	0.05
Southern Red Oak	4.80	0.79	1.32	6.20	6.92	1.33	1.35	4.20
Loblolly Pine	14.10	1.54	0.44	0.48	19.33	3.02	0.41	0.66
Mid-Atlantic								
Black Spruce	0.25	0.14	0.32	0.00	0.00	0.00	0.41	0.00
Quaking Aspen	0.52	0.89	2.37	8.15	0.01	0.00	1.65	0.02
Balsam Fir	0.13	0.26	0.50	0.00	0.07	0.00	0.50	0.00
Northern White Cedar	0.14	0.24	0.37	0.02	0.17	0.00	0.42	0.01
Red Spruce	0.43	0.29	0.60	0.01	0.21	0.00	0.61	0.01
Yellow Birch	0.83	0.87	1.70	0.93	0.26	0.00	1.50	0.01
Black Cherry	0.87	1.29	0.74	0.64	0.30	0.48	0.71	0.58
American Beech	0.79	1.10	1.51	3.17	0.32	0.20	1.55	1.79
Eastern Hemlok	0.79	1.13	0.69	0.07	0.39	0.01	0.67	0.01
Red Maple	0.96	1.11	0.97	0.61	0.43	0.50	0.93	0.76
Eastern White Pine	0.80	1.17	0.59	0.08	0.47	0.03	0.53	0.01
Sugar Maple	0.88	0.92	0.90	1.56	0.50	0.31	0.87	1.15
White Ash	0.90	1.10	1.32	1.23	0.53	0.53	1.36	1.63
Tulip Poplar	1.29	1.44	1.23	0.87	0.73	1.08	1.35	1.25
Chestnut Oak	1.18	1.56	1.15	2.79	0.83	0.88	1.26	3.53
Northern Red Oak	0.96	1.04	0.64	0.46	0.84	0.54	0.68	1.15
Pitch Pine	0.84	1.04	0.50	0.04	1.03	0.29	0.49	0.00
Virginia Pine	0.92	1.83	0.90	0.39	1.17	0.50	0.80	0.03
Scarlet Oak	1.25	1.42	1.14	2.40	1.51	0.57	1.00	0.78
Pignut Hickory	1.18	1.40	1.55	3.05	1.53	0.47	1.47	1.50
White Oak	1.11	1.08	1.39	2.04	1.78	0.84	1.53	2.95
Black Oak	1.16	1.51	0.79	1.93	2.54	0.66	0.71	1.27
Shagbark Hickory	1.30	1.52	2.09	6.76	3.31	0.43	2.09	7.39
Loblolly Pine	1.67	2.24	0.49	0.16	3.51	1.26	0.46	0.13

Fig. 2 continued



New England								
Black Spruce	0.41	0.02	0.58	0.17	0.01	0.16	0.53	0.02
Balsam Fir	0.63	0.35	0.54	0.07	0.22	0.20	0.49	0.02
Northern White Cedar	0.55	0.60	0.80	0.21	0.33	0.20	0.81	0.14
Red Spruce	0.64	0.55	1.02	0.22	0.35	0.23	1.01	0.09
Yellow Birch	0.84	0.44	1.26	2.52	0.37	0.39	1.32	1.76
Quaking Aspen	0.85	0.55	2.45	10.64	0.47	0.29	2.22	5.97
American Beech	0.96	0.59	1.49	2.03	0.57	0.96	1.54	1.93
Eastern White Pine	0.92	0.75	0.95	0.39	0.69	1.54	1.02	0.30
Sugar Maple	0.96	0.78	0.87	1.40	0.75	1.05	0.83	1.09
Eastern Hemlock	1.05	0.72	0.76	0.16	0.76	1.80	0.71	0.10
Red Maple	1.05	0.72	0.72	0.06	0.76	1.06	0.65	0.06
White Ash	1.21	0.98	1.72	3.32	1.19	1.01	1.84	8.42
Pitch Pine	1.17	1.14	0.36	0.02	1.33	0.99	0.37	0.01
Black Cherry	1.16	1.20	1.11	1.06	1.39	0.89	1.08	1.51
Northern Red Oak	1.32	1.17	1.03	1.30	1.55	1.00	1.02	1.14
Black Oak	1.6	2.29	0.97	1.47	3.66	0.95	0.91	0.82
Scarlet Oak	1.81	2.25	1.63	3.57	4.07	0.92	1.53	1.11
Pignut Hickory	1.61	2.81	1.93	2.67	4.52	1.02	1.87	1.44
White Oak	1.7	2.84	2.46	5.69	4.82	1.27	2.61	2.31
Chestnut Oak	1.84	2.74	2.57	14.63	5.05	1.66	2.48	15.94
Shagbark Hickory	1.76	2.89	2.14	3.48	5.09	1.28	2.23	3.23
Tulip Poplar	2.99	3.90	0.71	1.05	11.67	1.37	0.75	0.00
Loblolly Pine	2.81	>5.00	1.00	1.00	13.49	>5.00	1.00	1.00
Virginia Pine	3.39	5.58	0.13	0.00	18.92	2.64	0.11	6.42

versus latitude difference by species (for TreeAtlas and GFDL scenario) generally shows higher future:current ratios (gains or less loss in habitat) for the most northerly region (NE) and less gain or more loss for the southerly regions CH and CA (Fig. 4). With data from these graphs and the latitude of the mean centers (imbedded on the graph), users can, for the majority of the 24 species presented, be given a crude idea of the habitat tendencies based on their latitude of interest. For example, sugar maple has a mean center latitude of 42.1°N (Fig. 4). For someone interested in a location at 40°N (i.e., $42.1-40 = \sim+2$ difference in latitude), a straight line interpolation from the sugar maple graph on Fig. 4 would yield a future:current ratio of ~0.35, or roughly a loss of 65 % of habitat, and presumably the ecosystem services it provides, by 2100 under the GFDL scenario. In contrast, the habitat for black oak would roughly double at that same latitude (Fig. 4). Exceptions to the north to south trend were with loblolly pine, a large gainer in the MA relative to other regions, and red maple with much higher gains in CH, an artifact because this species is already prevalent in the other three regions) (Fig. 4). Landis300 versus GFDL showed similar trends except that northern red oak follows the trend of loblolly pine and tulip poplar follows the trend of red maple shown in Fig. 4 (Fig. S1).

We compared the mean and ranked future:current change ratios for each species across all four models, all four regions, and under PCM, GFDL, or both scenarios (Table 4), and based on all output data (Table S3). Seven northern conifers were predicted to decline the most under climate change: black spruce, balsam fir, northern white cedar, red spruce, eastern hemlock, eastern white pine, and pitch pine. All had future:current ratios <0.8 so were categorized as small to large decreasers. Some species had a wide variation among models, including trends of opposite sign (future:current change ratio both <1 and >1) among models. Most striking is pitch pine, with Landis300 projecting a complete collapse in the NE and MA regions, while TreeAtlas and Linkages project small increases in NE. Sugar maple would only decrease slightly under PCM but lose substantial habitat, especially in the more southern CA and CH regions, under GFDL. Many of the hardwoods and southern pines show overall average increases in future:current ratios across regions and models (Tables 4, S3). However, some averages are skewed by very high ratios caused by very low current importance under one or more models (e.g., Virginia and loblolly pine), and there is a wide variation including substantial losses in some regions under some models.

Discussion

This comparative study, a first of its kind as far as we know, standardizes outputs from three unique forest

Table 2 Mean agreement scores among model projections sorted by decreasing agreement for species across four regions in the eastern United States

Species	Scientific name	No. regions modeled	All combinations	TreeAtlas-Linkages-Landis300		
			PCM&GFDL	PCM&GFDL	PCM	GFDL
Black Spruce	*Picea mariana*	2	3.75	4.00	4.00	4.00
Balsam Fir	*Abies balsamea*	2	3.58	3.83	3.67	4.00
Northern White Cedar	*Thuja occidentalis*	2	3.50	3.83	3.67	4.00
Red Spruce	*Picea rubens*	3	3.28	3.67	3.33	4.00
Sugar Maple	*Acer saccharum*	4	3.21	3.17	3.00	3.33
Mockernut Hickory	*Carya tomentosa*	1	3.17	3.00	3.33	2.67
Chestnut Oak	*Quercus prinus*	4	3.17	3.04	2.92	3.17
Black Cherry	*Prunus serotina*	4	3.15	3.21	3.50	2.92
Pignut Hickory	*Carya glabra*	3	3.08	2.78	3.11	2.44
Eastern Hemlok	*Tsuga canadensis*	3	3.06	2.94	2.56	3.33
Scarlet Oak	*Quercus coccinea*	4	3.00	3.00	3.17	2.83
Eastern White Pine	*Pinus strobus*	3	2.97	2.83	2.56	3.11
Northern Red Oak	*Quercus rubra*	4	2.97	2.83	2.92	2.75
Eastern Redcedar	*Juniperus virginiana*	1	2.92	2.83	3.33	2.33
Red Maple	*Acer rubrum*	4	2.88	2.92	3.00	2.83
White Oak	*Quercus alba*	4	2.88	2.63	2.42	2.83
Sweetgum	*Liquidambar syraciflua*	1	2.83	2.50	1.67	3.33
Shagbark Hickory	*Carya ovata*	3	2.78	2.94	2.78	3.11
White Ash	*Fraxinus americana*	4	2.71	2.71	2.58	2.83
Black Oak	*Quercus velutina*	4	2.63	2.83	3.50	2.17
Southern Red Oak	*Quercus falcata falcata*	1	2.58	2.33	1.33	3.33
Virginia Pine	*Pinus virginiana*	1	2.56	2.76	3.00	2.53
American Beech	*Fagus grandifolia*	4	2.52	2.38	2.00	2.75
Yellow Birch	*Betula alleghaniensis*	2	2.42	3.00	3.33	2.67
Pitch Pine	*Pinus rigida*	2	2.42	2.33	2.67	2.00
Tulip Poplar	*Lireodendron tulipifera*	4	2.40	2.17	2.75	1.58
Post Oak	*Quercus stellata*	1	2.17	1.50	1.67	1.33
Loblolly Pine	*Pinus taeda*	3	1.92	1.83	1.56	2.11
Quaking Aspen	*Populus tremuloides*	2	1.92	2.33	2.00	2.67
Shortleaf Pine	*Pinus echinata*	1	1.17	1.17	1.00	1.33

Agreement was scored on an ordinal scale of increasing agreement from 0 to 4 where 0 represented opposite trends and 4 identical change classes

landscape models across spatial (four regions) and temporal (2000, 2100, 2300) scales, a range of climate scenarios (PCM B1 and GFDL A1fi), species (30 total, most common species; region totals varied from 15 to 24), and evaluation metric (future:current ratios). Standardizing in this manner enables an increased understanding of underlying drivers of differences across models that use diverse approaches and assumptions. Divergence among models for certain species could indicate insufficient knowledge of the species' life history traits or ecological complexities, a mismatch between current tree distributions and ecological drivers selected for modeling, or individual model biases. Divergence indicators provide fodder for further investigations into model behavior versus drivers. Agreement common to models could indicate a better understanding of species and their drivers, or could be indicative of a systemic bias among all models. The three models represent different approaches to assess potential species changes.

Table 3 Mean ratios of future:current species importance or biomass for all species and regions categorized as North, Central, or South in relation to the a regions center

Species-latitude class	Number of species	Latitude difference	PCM future:current ratio					GFDL Future:Current Ratio				
			TreeAtlas	Linkages	Landis100	Landis300	Average	TreeAtlas	Linkages	Landis100	Landis300	Average
North	16	3.21	0.79	0.71	0.77	0.45	0.68	0.22	0.00	0.68	0.02	0.23
Central	36	−0.06	0.89	0.87	0.93	0.91	0.90	0.74	0.49	0.94	0.51	0.67
South	30	−4.19	1.46	1.23	1.13	1.44	1.31	2.39	1.50	1.06	1.26	1.55

TreeAtlas provides a robust statistical approach to model projected habitat, assuming the trees are where they are currently due to ecological and legacy conditions that will hold true into the future. Linkages also projects habitat as a hybrid empirical-physiological model working at the species level, and also feeding into Landis, which is a forest succession model estimating expected species importance through time.

Going into this study, we expected, based on what we know about the models, that (1) species with very low IV or biomass in the region will likely have less reliable models, and therefore less consistency among models; (2) Landis outputs will be dominated by current growth and succession of existing vegetation, and those legacies will persist; (3) migration does not occur in TreeAtlas or Linkages (only movement of suitable habitat), while migration within Landis will be extremely slow, even out 300 years; (4) the scenario with the least climate change, PCM, should also have the least predicted changes in IV or biomass; and (5) each of the models have a set of assumptions and limitations that need to be taken into account upon application (Iverson and McKenzie 2013).

Overall estimated impacts on species

With exceptions, there was overall agreement among models on species expected to do poorly under climate change in the future, especially under the hotter, drier GFDL scenario (see Table 1 for temperature and precipitation forecasts by region and scenario). The northern conifers of black spruce, balsam fir, northern white cedar, eastern hemlock, and red spruce are modeled to have large reductions in the future (Fig. 2). In the near term, however, red spruce has been shown to be expanding due to release from earlier human pressures (Foster and D'Amato 2015). This expanding trend may not continue for long because it favors cool, no-fire, and low spruce budworm conditions (Blum 1990), all conditions forecast to change to opposing trends in future. Historically, the southern margin of spruce and to some degree, fir, was likely limited by summer heat and drought, and they have only existed prominently in New England over the past 1000–1500 years, a time when July temperatures were perhaps 1 °C cooler than present (DeHayes et al. 2000). Thus, the warning of large future reductions for spruce and fir is warranted.

Table 4 Model averaged ratios of future:current species importance or biomass across all regions and by climate change scenario (PCM or GFDL) and both scenarios combined

Species	PCM		GFDL		Combined average
	Average	Range	Average	Range	
Black Spruce	0.27	0.08–0.45	0.13	0.01–0.47	0.20
Balsam Fir	0.32	0.04–0.57	0.17	0.01–0.5	0.25
Northern White Cedar	0.35	0.12–0.58	0.25	0.05–0.62	0.30
Red Spruce	0.52	0.08–0.88	0.36	0.04–0.8	0.44
Eastern Hemlock	0.65	0.09–1.02	0.41	0.05–0.76	0.53
Eastern White Pine	0.74	0.29–1.07	0.61	0.24–1.13	0.68
Pitch Pine	0.67	0.02–1.17	0.87	0.01–1.76	0.77
Sugar Maple	1.03	0.79–1.47	0.59	0.28–0.99	0.81
Black Cherry	0.90	0.67–1.21	0.84	0.53–1.28	0.87
Eastern Redcedar	0.81	0.56–1.13	1.02	0.64–1.95	0.91
American Beech	1.17	0.66–1.93	0.74	0.21–1.28	0.96
Yellow Birch	1.24	0.83–2.11	0.69	0.17–1.63	0.96
Northern Red Oak	0.98	0.69–1.34	1.08	0.51–2.25	1.03
Post Oak	0.86	0.35–1.22	1.38	0.6–2.25	1.12
Scarlet Oak	1.27	0.81–2.06	0.97	0.45–1.81	1.12
Black Oak	1.12	0.76–1.47	1.14	0.48–2.32	1.13
Pignut Hickory	1.28	0.84–1.92	1.23	0.61–1.99	1.25
White Ash	1.24	0.68–1.99	1.31	0.4–3.04	1.28
Sweetgum	1.23	0.57–2.47	1.33	0.89–1.78	1.28
Shortleaf Pine	1.00	0.04–2.16	1.69	0.05–3.41	1.35
Mockernut Hickory	1.30	0.88–1.92	1.56	1.11–2.52	1.43
Red Maple	1.22	0.57–2.11	2.16	0.51–5.88	1.69
White Oak	1.65	0.9–2.92	1.78	1.03–2.92	1.71
Tulip Poplar	1.46	0.87–2.32	2.28	0.43–5.53	1.87
Shagbark Hickory	2.22	1.23–4.31	2.36	0.95–4.47	2.29
Quaking Aspen	3.34	0.69–9.4	1.32	0.12–3.81	2.33
Chestnut Oak	2.26	1.05–5.04	2.57	0.87–5.31	2.41
Southern Red Oak	3.28	0.79–6.2	3.45	1.33–6.92	3.36
Loblolly Pine	2.48	0.53–6.91	6.26	0.77–15.44	4.37
Virginia Pine	1.53	0.2–3.24	7.66	0.07–17.23	4.59

Sugar maple is a species modeled to stay roughly constant under the mild PCM scenario with all models, but likely to diminish substantially at the southern portions of its range under GFDL. In NE, it may stay relatively constant even under GFDL as it has some buffering because of its positive modification factors (Matthews et al. 2011). The red maple models show a large increase projected for the CH and more of a tendency to decline in the other three regions (Fig. 2), but it is the most adaptive species of all 134 species evaluated in TreeAtlas and should generally do fine under climate change (Matthews et al. 2011).

The oaks and hickories as a group generally show agreement across the modeling approaches, lending more support that, as a group, they may fare better under climate change, with the overall future:current averages for these species consistently above 1.0 (increase in importance or biomass) (Fig. 2, Table S3). They are often projected to have increased habitat or expanded ranges in the northern regions (NE and MA) but fare less well in the southern regions (CA and CH) where their southern limits are reduced within the region. With exceptions (e.g., northern red oak), this group of species is physiologically favored to withstand drought and heat (Johnson et al. 2009) and should be competitive under hotter and drier conditions of GFDL. However, succession of oak-dominated stands in the eastern United States is currently leading to 'mesophication' and dominance by maple (Nowacki and Abrams 2008), potentially due to lack of fire (Brose et al. 2014) and a more moist climate regime in the past century (Pederson et al. 2014). In much of the oak-hickory forests of the eastern United States, current management often relies upon increased fire and harvest to restore oak-hickory communities in locations otherwise trending towards maple (Hutchinson et al. 2005; Iverson et al. 2008a; Brose et al. 2013). A hotter climate may assist in enabling oak regeneration, but management to favor oak will likely still be needed because the highly competitive capabilities of maple (Abrams 1998; Matthews et al. 2011).

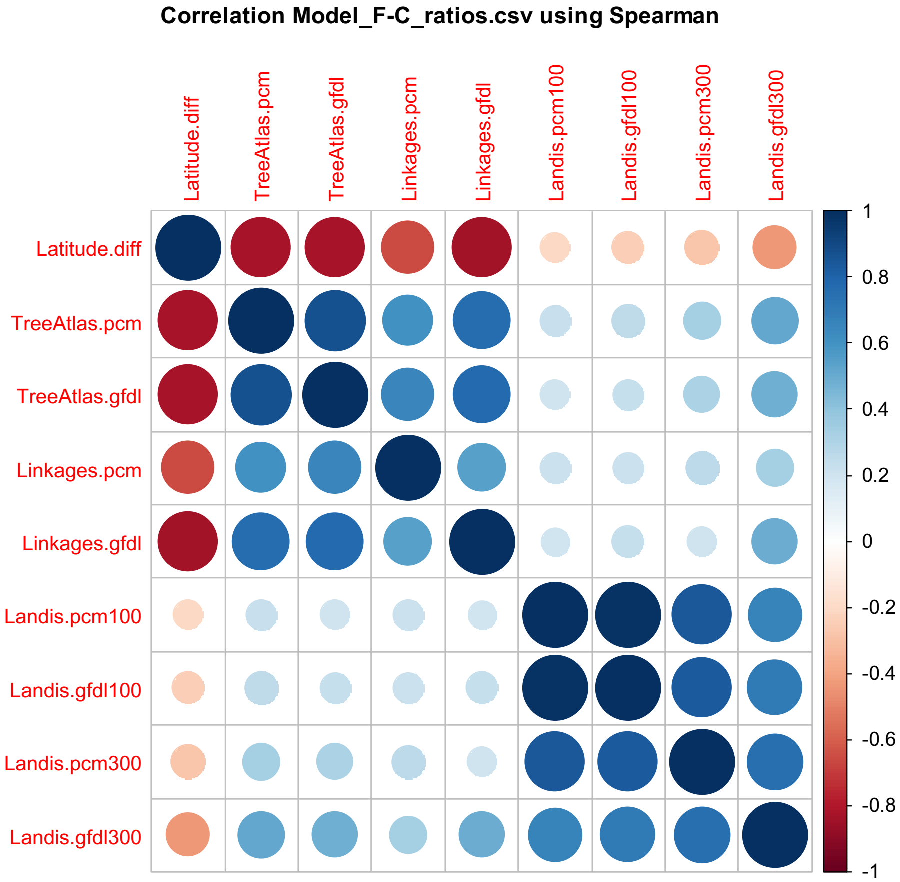
The pines generally have the most variable species projections among the models. The southern loblolly and Virginia pines have very low densities currently in these regions which cause less reliable future:current ratios for Landis and Linkages (the TreeAtlas models are built from entire eastern US distribution). Expansion by natural dispersal from low density populations is very slow within Landis. Pitch pine requires fire which is not directly included in the models, though may be indirectly included in the TreeAtlas model as a historic component of its current distribution. Eastern white pine generally shows a decreasing status in future.

Agreement among models

Several metrics were used to assess agreement among models. We hypothesized that TreeAtlas and Linkages, both projecting suitable habitat, should be more in agreement than with the Landis succession model outputs. All of our metrics appear to align with this hypothesis. A side-by-side visual comparison (Fig. 2), the agreement metric by species (Table 2) and region (Table S2), along with the Spearman rank coefficients (Fig. 3; Table S2), all point to the greatest overall agreement between the TreeAtlas and Linkages models. Therefore, for many species-region combinations with high agreement, uncertainty is lessened and confidence is built indicating probable tendencies of species behavior in coming decades. As in a similar study comparing Linkages and TreeAtlas for southern Missouri (Schneiderman et al. 2015), we found highest correlations under the scenario with the most change, GFDL (Spearman $r = 0.77$), compared to PCM ($r = 0.60$) for 83 species-region combinations. However, there was a large variation among regions: correlations were highest for 24 species simulated in NE ($r = 0.91$–0.96, $P < 0.0001$), followed by 24 species in the MA ($r = 0.75$–0.88, $P < 0.01$–0.0001), 20 species in the CH ($r = 0.35$–0.77, P = NS - < 0.05), and 15 species in the CA ($r = 0.02$–0.40, P = NS). We attribute much of the reduction in correlation to lower sample sizes in CH and CA. A further analysis of model sensitivity to species parameters would allow a more complete assessment of those species-region combinations showing disagreement between the two habitat models, but currently these disagreements underscore uncertainty for those combinations (Fig. 2; Table S3). Importantly, combinations of uncertainty between TreeAtlas and Linkages also indicate more uncertainty for Landis outputs because Linkages provide species establishment probabilities and maximum growing space inputs into Landis.

Some key differences between the two habitat models (TreeAtlas and Linkages) and Landis are attributed to the added components of succession and dispersal accounted for in Landis. For example, TreeAtlas and Linkages project large increases for loblolly pine habitat in CH and MA while Landis projects small to large decreases. This species currently has limited distributions in those regions and are constrained by natural dispersal. Of course, the future picture would change towards the habitat model projections should assisted migration of loblolly pine be implemented (Iverson and McKenzie 2013). In NE, TreeAtlas and Linkages predict large decreases in quaking aspen but Landis predicts increases because aspen, as an early successional species, fills growing space vacated by other northern species that are removed through harvest or are more severely affected by climate change. These differences illustrate the strength of a multi-model approach especially when the outcomes necessitate clear interpretability such as when being applied to regional vulnerability assessments. The importance of successional dynamics is a key ecological process that will regulate future forest transitions, yet the drivers of such change are dynamic and precise predictions are untenable. Therefore, by being able to evaluate side-by-side results originating from different approaches, one can begin to formulate

Fig. 3 Spearman rank correlations future:current ratios of predicted tree species importance or biomass by three models (TreeAtlas, Linkages, Landis) and two climate scenarios (PCM B1, GFDL A1FI) for the four regions (CA, CH, MA, NE) pooled together. Landis was modeled to 2100 (e.g., Landis.gfdl100) and 2300 (Landis.gfdl300). Latitude difference is also included



quantitative and biologically informed assessments of likely outcomes, while clearly acknowledging potential sources of uncertainty.

We also hypothesized that Landis outcomes should move towards the habitat suitability outputs of TreeAtlas and Linkages as time moves from 100 to 300 years out. The metrics we used bore this out, but primarily with the harsh GFDL model (Figs. 2, 3; Tables S1, S2). Both the Spearman rank statistic, showing a large increase in correlations going from TreeAtlas and Linkages versus Landis100 to Landis300 (Fig. 3), and the class agreement scores, higher for TreeAtlas/Landis300 than for TreeAtlas/Landis100 (Table S1), showed these trends for GFDL but inconsistently so for PCM. Because Landis is a succession model, and a high proportion of established tree cohorts are likely to stay in place through 2100, most species will not see drastic changes by that time. However, most tree cohorts will be replaced by 2300 in Landis, by which time climate conditions (through Linkages) will dictate a greater similarity to the habitat suitability outcomes from Linkages and TreeAtlas. Landis simulations for the CH and CA indicated that the amount of variation in tree importance explained by succession and harvest decreased from 80 to 67 %, and by climate increased from 13 to 26 %, from 2100 to 2300 (Wang et al. 2015). Therefore, since TreeAtlas and Linkages did not consider succession and harvest, we expected agreement with Landis to increase as climate became more important over time and in the harsher GFDL scenario.

As for the higher correlations with the harsher, GFDL scenario, we suggest that the greater extremes in temperature and moisture, as analyzed through a daily database through 2100 (Matthews et al. in press), creates conditions likely to hasten succession and disturbance such that Landis300 will approximate changes in suitable habitat much faster than in the moderated climatic conditions projected through the PCM scenario. Notably, the large contrast between

GFDL and PCM in this regard again points to the value of global society holding down emissions in coming decades (IPCC 2014).

The only disturbances we simulated in Landis were tree harvest and windthrow. In reality, additional disturbances from pests, pathogens, more frequent and hotter droughts, fires, floods, warm springs followed by late spring frosts, and wind damage are all expected to increase under climate change, and more so under the harsh scenario than the mild scenario (Dale et al. 2001; IPCC 2014; Melillo et al. 2014). Therefore, these disturbances will likely hasten transitions so that Landis300 along with TreeAtlas and Linkages projections of habitat may be closer to expectations by 2100. We emphasize the need to review species outputs, be they potential suitable habitat changes or succession models, in concert with other species and locality information, such as the TreeAtlas modification factors, so that disturbance and biological features of the species can be included into interpretations for management going forward (Iverson et al. 2011).

Relationships depending on geographic location

With these analyses, we confirm that the geographic position of the species range in comparison to the area of interest influences the potential for the species to thrive or not under a changing climate. Species that are already centered north of the region of interest are more likely to undergo a loss in habitat, as shown by the 16 species-region combinations classed as 'North' (species center is >2°N of region center) in Table 3; this pattern is consistent across all models and is much worse for the harsh GFDL scenario than the PCM scenario. Similarly, those species with mean centers >2°S of the region centers (in this case 30 species-region combinations averaging 4.2°S of region centers) had future:current ratios above 1 for all models and would be expected to increase in importance under climate change. For the 36 species-region combinations falling between 2°N and 2°S, the tendency is for a slight loss in importance according to all models, especially under GFDL, so the fate of these species may depend more on local conditions and specific attributes of the species.

Further confirmation of these geographic trends, by species, shows that, for TreeAtlas (Fig. 4) and Landis300 (Fig. S1), most species follow an expected north to south trend, with high future:current ratio/northerly latitude differences trending to low ratio/southerly latitude differences going from NE to MA to CA to CH. The exceptions to the pattern, such as red maple and loblolly pine for both TreeAtlas and Landis300, can be explained by a huge spatial niche becoming suitable in one of the regions (CH for red maple and MA for loblolly pine), creating a proportionately greater boost in those particular regions. The same can be said for some of the oaks and hickories in the Landis300 graphs. The geographic analysis presented here may therefore be a simple way for managers to get a perspective on tendencies for how species may fare in coming decades in their area of interest. By comparing the latitude of interest to the mean center latitude for the species, and then extrapolating to the points on species graphs of future:current ratio versus difference in latitude on Fig, 4, one can obtain an estimate of potential climatic pressures on the species by 2100 at that location. It is important to calculate mean centers based on both abundance and occupancy, not just presence so that a realistic center of species is generated. Low abundance and occupancy in expanding edges of the range may limit a species capacity to migrate (Iverson et al. 2004; Prasad et al. 2013), while low abundance at the trailing, or southern latitude edges, may result in range erosion and regional extirpation of suitable habitats. Examples of the former may be black oak in NE (i.e., rare propagules available to migrate into NE) while of the latter may be sugar maple in the CH (i.e., large loss of habitat in the species' southern range) in this examination. Murphy et al. (2010), using TreeAtlas data, examined abundance–occupancy distributions across the geographic ranges of 102 eastern U.S. trees and found that 62 % of the species tended towards higher capacity to respond to climate change in the northern latitudes of their range but that most species were found to have range contraction in the south and limited range expansion in the north. Evaluating mean center positions of species importance (available on the TreeAtlas web site, cited in Methods) simultaneously with area of interest can thus provide a first look at potentials for species changes.

Informing management decisions

Our approach can help forest managers who are interested in adapting their management to current and future climate change (Janowiak et al. 2015). We have

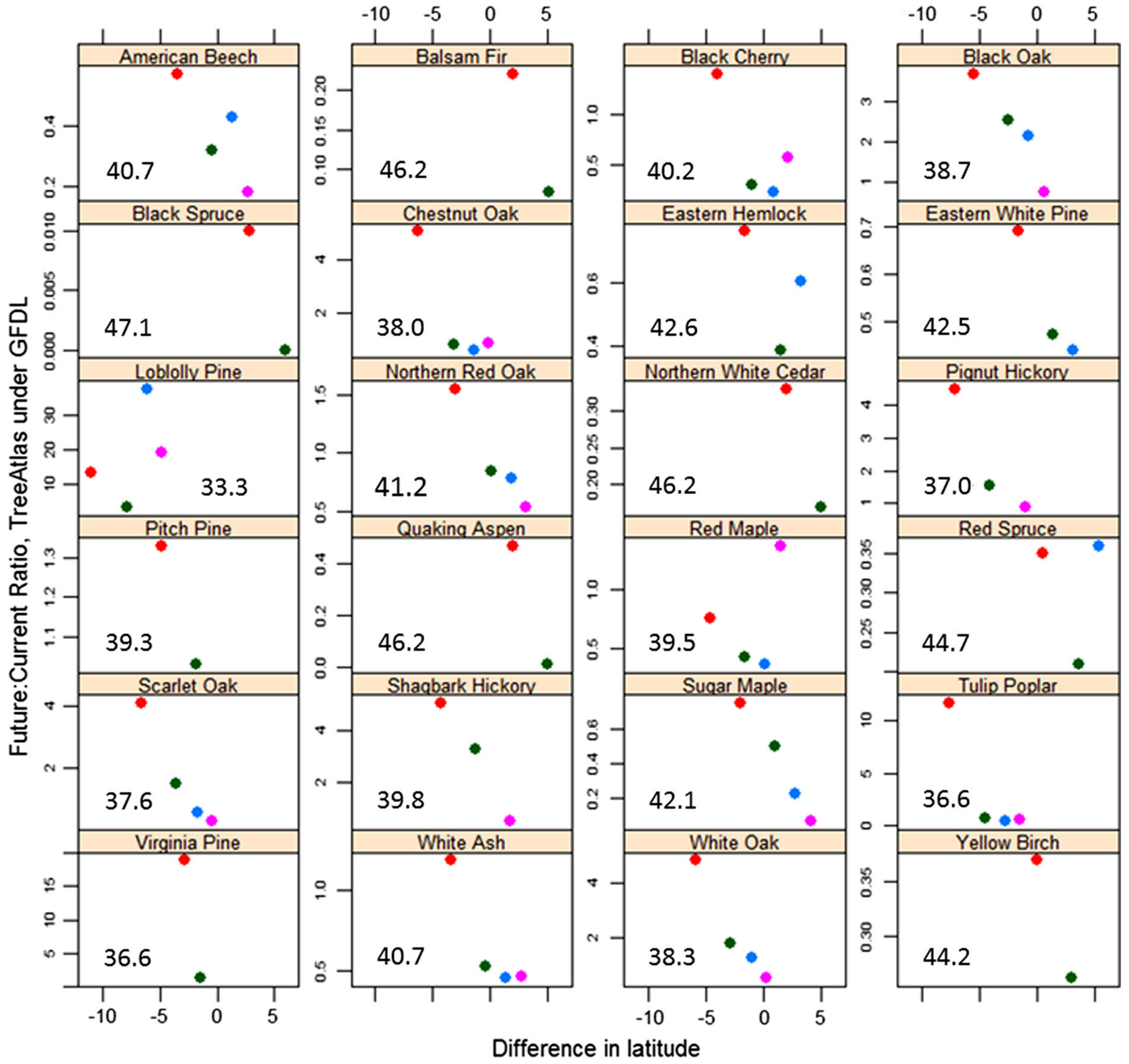


Fig. 4 The relationship of difference in latitude to future:current ratios, by region (*red* = NE; *green* = MA, *pink* = CH, *blue* = CA) for each of 24 species as forecast by TreeAtlas for 2100 under the GFDL climate scenario. Numbers in each species block indicate current mean latitude. Difference in latitude is calculated as (region mean center)—(species mean center), such that species mean centers to the north of region center have negative numbers

successfully incorporated the comparison of these models into climate change vulnerability assessments designed to support forest management decision-making (Brandt et al. 2014; Butler et al. 2015). The use of this information varies by individual management objectives, local site conditions, and differences in model projections by species and location. When there is greater agreement among models for a species of interest in a particular location, managers may choose to favor a species projected to do well or disfavor a species that is projected to do poorly in a manner than supports their land management objectives. When there is less agreement among models in the timing or direction of change, managers may choose alternative strategies such as favoring a greater diversity of species or choosing a mix of strategies in different areas (Swanston and Janowiak 2012). These areas of greater uncertainty can also provide an indication of when additional modeling, scientific evidence, ancillary information such as the modification factors, or just plain expertise gained from local, on-the-ground experience is needed to help inform decisions.

Conclusions

We evaluated three models and four model outcomes, for 30 common species and across four regions in the eastern United States, for agreement and enriched interpretation for forest management. Comparisons indicated high agreement for many species, especially northern species modeled to lose habitat in coming decades. TreeAtlas and Linkages outputs had the greatest agreement, but each had reasonable agreement with many species outputs from Landis, particularly when Landis was simulated to 2300. Most differences in projected change could be rationalized based on whether models considered realized versus fundamental niches, inclusion or not of succession, disturbance, and dispersal components, and the errors associated with incomplete knowledge and model constructs of ecological drivers, species parameters, and species interactions. Clearly there is still uncertainty imbedded in each of the models, such that any application stemming from them requires a thorough vetting through the lens of experts. A geographic analysis provided evidence that a simple calculation of mean center of species versus location of interest provides a basic idea on potential for the species under climate change. Of course the mantra “all models are wrong, but some are useful” (Box and Draper 1987) holds here but we suggest a unified analysis of multiple models provides a more consistent interpretation of the future for use in vulnerability assessments and adaptation planning.

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