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RESEARCH ARTICLE

Comparison of a species distribution model and a process model from a hierarchical perspective to quantify effects of projected climate change on tree species

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Abstract

Context Tree species distribution and abundance are affected by forces operating across a hierarchy of ecological scales. Process and species distribution models have been developed emphasizing forces at different scales. Understanding model agreement across hierarchical scales provides perspective on prediction uncertainty and ultimately enables policy makers and managers to make better decisions.

Objective Our objective was to test the hypothesis that agreement between process and species distribution models varies by hierarchical level. Due to the top-down approach of species distribution models and the bottom-up approach of process models, the most agreement will occur at the mid-level of the hierarchical analysis, the ecological subsection level, capturing the effects of soil variables.

Methods We compared projections of a species distribution model, Climate Change Tree Atlas, and a process model, LINKAGES 2.2. We conducted a correlation analysis between the models at regional, ecological subsection, and species level hierarchical scales.

Results Both models had significant positive correlation ($\rho = 0.53$, $P < 0.001$) on the regional scale. The majority of the ecological subsections had greater model correlation than on the regional level when all climate scenarios were pooled. Correlation was poorest for the analysis of individual species. Models had the greatest correlation at the regional scale for the GFDL-A1fi scenario (the scenario with the most climate change). Species near their range edge generally had stronger correlation (loblolly pine, northern red oak, black oak).

Conclusion Our general hypothesis was partly accepted. This suggests that uncertainties are relatively low when interpreting model results at subsection level.

Keywords Climate change · LINKAGES 2.2 · Climate Change Tree Atlas · Hierarchical · Process model · Species distribution model

Introduction

Tree species distribution and abundance are affected by forces operating across a hierarchy of ecological scales (Diez and Pulliam 2007). At the regional level,

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climate variables such as temperature and precipitation may have the greatest control. At the intermediate levels, such as the ecological subsection, landform and soil may show a dominant effect. At the species level, biotic interactions such as inter- and intra-species competition may affect the local variations of species extinction and colonization. Hierarchy theory provides a perspective for organizing the complexity of ecological systems (O'Neill et al. 1989) from which different types of models are developed. Models used to study climate change have been created utilizing hierarchy theory, emphasizing forces at different scales. Process-based simulation models (hereafter process models) and species distribution, niche, or envelope models (hereafter species distribution models) are the most common approaches used to assess climate change impacts on forests at large spatial scales (Morin and Thuiller 2009).

Process models simulate the behavior of a system based on interactions between physiological mechanisms and functional components and their interaction with the environment, generally represented as mathematical equations (Mäkelä et al. 2000; Landsberg and Sands 2011). They use a bottom up approach beginning with simulating site-scale (e.g. individual plots within ecological subsections) species and environmental (soil and climate) interactions and expanding to regional scales that account for broader climatic patterns. Process models are able to take into account species response to environmental conditions by utilizing biological processes calibrated by observations on individuals in natural environments (Morin and Thuiller 2009). They are better equipped for predicting species responses to novel environment conditions than niche models by simulating mechanisms affecting species (Gustafson 2013).They may require parameter values that are difficult to obtain (Landsberg and Gower 1997) as well as more computational power and time than species distribution models, which could result in consideration of fewer species in assessments (Brandt et al. 2014).

Species distribution models use a species' observed distribution or biological characteristics to predict future distribution (Iverson and McKenzie 2013). They use a top-down approach beginning with using climatic variables at the regional scale and adding local (ecological subsection) soil information to improve prediction realism. This approach emphasizes abiotic controls (climate and soil) so that the predicted outcomes reflect statistical associations between the occurrence and abundance of species and predictor environmental variables that may influence suitability of habitat (Iverson and McKenzie 2013). A species niche can be described by climate tolerance levels or thresholds, expressed in terms of climate variables (Gallego-Sala et al. 2010). These variables are considered key attributes of a species habitat. The degree that climate affects these attributes determines how the species will then react (Pearson and Dawson 2003). Species distribution models can fit complicated geographic ranges (Iverson and McKenzie 2013). Another benefit is they tend to require less computer capability or processing time than process models, so they are capable of projecting greater numbers of species response to climate change over very large areas (Brandt et al. 2014).

Comparing process and species distribution models in terms of their assumptions, approaches, and results provides perspective on prediction uncertainty and ultimately enables policy makers and managers to make better decisions (Beaumont et al. 2007; Marcot et al. 2012). When different approaches result in similar predictions, more confidence is attained. When disagreement occurs between models, assumptions can be challenged and new directions for analysis studied (Iverson and McKenzie 2013). Research of this type has shown that when process and species distribution models are compared to observed data, there is overlap in assumptions, validation and reproducibility challenges (Dormann et al. 2012). Research has highlighted problems related to estimating species distributions as well as uncertainty in making future projections (Keenan et al. 2011; Cheaib et al. 2012), and has found agreement in the ability to show large scale range contractions of some species (Cheaib et al. 2012). More studies are necessary to improve current and future models. Understanding model dynamics on multiple scales is one area that is beneficial.

We hypothesize that agreement between process and species distribution models varies by hierarchical level. Specifically, because of the top-down approach of species distribution models and the bottom-up approach of process models, the most agreement will occur at the mid-level of the hierarchical analysis, the ecological subsection level, capturing the effects of soil variables. Our objective was to use Climate Change Tree Atlas (Landscape Change Research Group 2014), which utilizes the species distribution model DISTRIB, and the process model LINKAGES 2.2 (Wullschleger et al. 2003) to assess climate change impacts on tree species in Missouri and to compare results of these two approaches on a hierarchical level. We hereafter refer to Climate Change Tree Atlas as a species distribution model because of the DISTRIB portion. We chose LINKAGES 2.2 and Climate Change Tree Atlas for our analysis because they have been widely used (Pastor and Post 1985; He et al. 1999, 2005; Iverson et al. 2008; Dale et al. 2009; Matthews et al. 2011) to predict effects of climate change. Specifically, we compared the change in biomass predicted by LINKAGES and Importance Values predicted by Tree Atlas for current climate and future climate projections. We were interested in understanding how well the models agreed across the following hierarchy of scales: regional, ecological subsection, and species level. We conducted a correlation analysis between the changes predicted by each model across this hierarchy.

Methods

Study area

The study area encompassed the Southern 2/3 of Missouri, USA, and was at the westernmost edge of the Central Hardwood Region, historically a transition zone between forest and prairie. Latitude ranged from 36.42 to 39.11 and longitude ranged from −89.80 to −94.58 (Fig. 1). The area was 11695,575 ha, of which 5049,920 ha was forested. The elevation ranged from 70 to 540 m. It was composed of the Ozark Highlands ecological section (Bailey 1995). The area was further subdivided into seven ecological subsections (Fig. 1) based on similar soil characteristics and landforms. We chose this area because we were interested in understanding how ecological pattern in the transition zone was affected by climate change.

Missouri has a continental climate with strong seasonality Temperature and precipitation follow a general gradient along a diagonal line from northwest to southeast (Nigh and Schroeder 2002). The mean annual temperature range in the study area is 6.3–19.2 °C. The annual precipitation range in the study area is 101.8–138 cm (Stoner et al. 2011).

Tree species analyzed

We selected nine tree species for analysis: white oak (*Quercus alba*), northern red oak (*Quercus rubra*), black oak (*Quercus velutina*), shortleaf pine (*Pinus echinata*), loblolly pine (*Pinus taeda*), eastern redcedar (*Juniperus virginiana*), sugar maple (*Acer saccharum*), American elm (*Ulmus americana*), and flowering dogwood (*Cornus florida*). We selected these species because they met at least one of three criteria: they were abundant; they had high economic value; or they were at the northern or southern extent of their range (Fig. 2) and were poised to expand or reduce their range with climate change.

LINKAGES 2.2

LINKAGES 2.2 is an ecosystem process model derived from JABOWA (Botkin et al. 1972) and simulates ecosystem processes based on vegetation and resources present. The basic premise of LINKAGES is that variation in amounts of ecosystem nitrogen and carbon retention and cycling can be explained by biogeochemical processes affecting nitrogen present, biogeographical processes that determine availability of water, and demographics of plant species. Climate and edaphic conditions affect feedback between vegetation and nitrogen present, and vegetation and light available. The model simulates individual tree establishment, growth, and death within a stand. Competition, climate, and soil variables are used to determine the life history factors for species present (Pastor and Post 1985). Wood decay of tree cohorts is also simulated. Population dynamics are affected by temperature and soil water content, also affecting soil nitrogen availability and light presence through canopy. Temperature, precipitation, initial size of tree, death, and recruitment are all variable stochastically around mean values (Pastor and Post 1988).

LINKAGES 2.2 simulations

Ecological subsection and landform creation

We divided each subsection into eight landforms to capture variation in soil characteristics used by

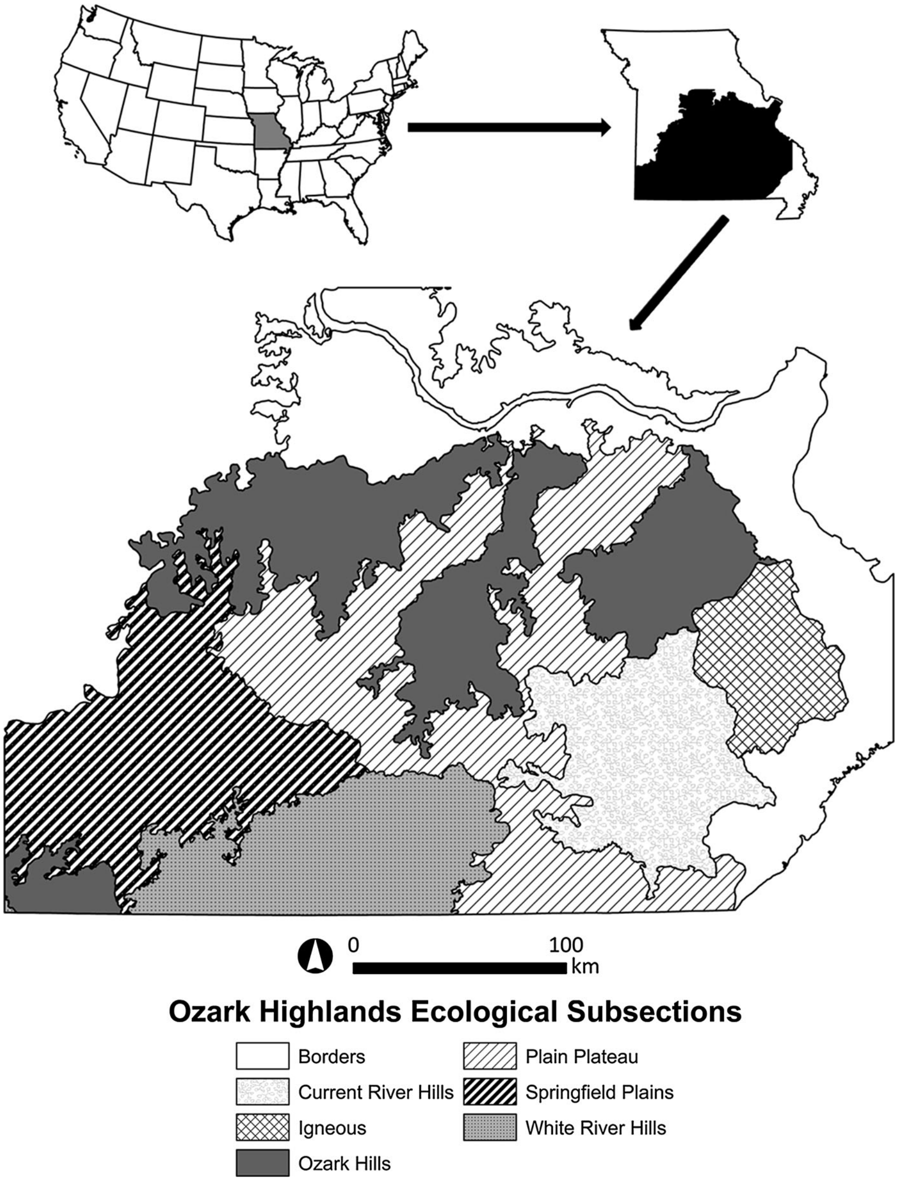

Fig. 1 Study area

LINKAGES: south and west slopes, north and east slopes, ridges, upland drainages, bottomlands, grasslands, water, and non-forest. We classified landforms from a 30 m resolution digital elevation model (DEM) using a topographic position index (TPI), which we calculated as a cell's elevation minus the mean elevation of cells within a moving window neighborhood divided by the standard deviation of the window's mean cell elevation. Slope and aspect layers were also created from the DEM, and used to further subset landform classes. Thresholds for the classification were based on those determined by Dijak and Rittenhouse (2009). Our goal was to capture differences in moisture gradients related to landforms. The output from the TPI, when overlayed on a topographic map, follows the basic breaklines for the ecological land classifications described by (Miller 1981), created specifically for the Ozark Plateau Region of Missouri. We only used south and west slopes, north and east slopes, ridges, upland drainages, and bottomlands (the potentially forested landforms) for our simulations.

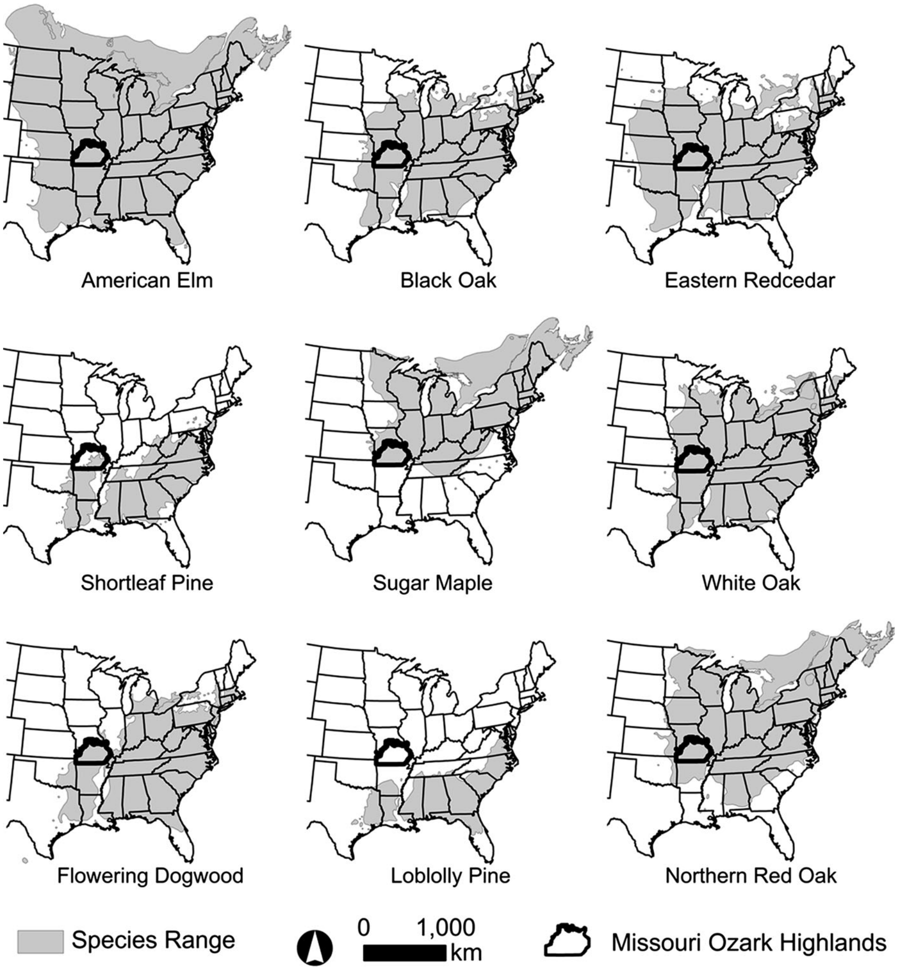

Fig. 2 Distribution of analysis species (Little 1971)

Climate scenarios

We used three general circulation models (GCM) combined with emission scenarios for years 2080–2099 to create climate scenarios that captured the full range of potential climate projections represented by Intergovernmental Panel on Climate Change (IPCC) (2007) models. Different GCMs may not produce the same projections. This makes it necessary to consider several GCMs and emission scenarios that will provide a full range of future climate projections (Newman et al. 2011). The parallel climate model (PCM), Geophysical Fluid Dynamics Laboratory Coupled Model version 2.1 (GFDL), and Hadley Centre Coupled Model version 3 (Hadley) represent the extreme ranges of climate projections for our study area, when combined with high (A1fi) and low (B1) end emission scenarios (Stoner et al. 2011). We also used a current climate scenario based on actual climate during 1980–2003.

We required daily values for maximum and minimum temperature (°C), precipitation (mm), wind speed (m/s), and solar radiation (MJ/m^2) for the LINKAGES 2.2 model. We used values associated with the center point of each subsection. We obtained information for current climate for temperature, precipitation, and solar radiation from Daily Surface Weather and Climatological Summaries (Daymet) (Thornton et al. 2012) and wind speed from the National Oceanic and Atmospheric Administration-National Climatic Data Center (2011). A modified statistical asynchronous regression downscaling method was used at a 12 km resolution to obtain daily temperature and precipitation values for the PCM-B1, GFDL-A1fi, and Hadley-A1fi climate scenarios for the end of the century (Stoner et al. 2011). All three future climate scenarios projected higher temperatures than current climate. Overall, minimum and maximum annual temperature increased the most in the Hadley-A1fi scenario (+6.6, +7.2 °C respectively), followed by GFDL-A1fi (+5.2, +5.4 °C respectively) and PCM-B1 (+1.8, +1.8 °C respectively). PCM-B1 projected higher growing season precipitation (+4.2 cm) than current climate. Hadley-A1fi and GFDL-A1fi (−20 cm) were projected to have less precipitation than current climate. Growing season minimum and maximum temperatures were highest for the GFDL-A1fi scenario (14, 27.3 °C respectively) (Stoner et al. 2011).

Soil input variables

We obtained physical variables (wilting point, field moisture capacity, nitrogen, organic matter, rock fragment, clay, and sand content) for the uppermost 1 m layer of soil from the Natural Resources Conservation Service soil survey (Soil Survey Staff, Natural Resources Conservation Service 2013) for each landform within each subsection. We converted soil polygons to raster data (90 m cell) and combined it with landform and subsection raster data to determine the most common soil type on each landform within each subsection. From this we derived soil characteristics for 12 vertical soil layers for input into LINKAGES 2.2.

Model simulation

We simulated the nine species individually for each of the five landforms, within each of the ten subsections, under the four climate scenarios because we were interested in the potential establishment and growth of each species without interspecific competition. Species were simulated individually to observe their fundamental niche (physiological growth). We also simulated LINKAGES using Tree Atlas' 20 km pixel grid to see if the scale of analysis caused differing results. LINKAGES simulated the birth, death, and growth of all trees larger than 1.43 cm diameter at breast height within a 1/12 ha plot (Pastor and Post 1985); we created virtual plots representing each combination of landform and subsection (as well as Tree Atlas' 20 km pixels). All plots were void of trees at year zero of the simulation. We set the initial number of trees planted within each plot to 200 saplings ha^{-1}. We ran the model for 30 years, with 200 replications approximating 200 plots evenly distributed across the simulated landform. We determined that year 30 was a good analysis point because the output indicated that a species either disappeared from the landscape or reached a stable trend by this point. The simulation results were averaged for each subsection by landform.

We used biomass as a measure of tree species productivity and establishment under each climate scenario. Understanding tree species establishment (a synthesis of a tree species' response to climate change) is critical to the study of the effects of climate change on forest ecosystems (He et al. 1999). The resulting tree species biomass was based on potential to grow (under current or future climate), not whether the species currently existed in the area. For example, subsections that do not currently have loblolly pine present exhibited the potential to sustain this species, producing biomass values.

The landform analysis was appropriate for simulating LINKAGES, to properly capture ecological processes. To be sure differences between the two models' predictions were not due to differences in analysis unit, we also performed this analysis at the 20 km scale, the scale used by Tree Atlas, and compared the results. All climate data were similarly downscaled and soil data similarly aggregated.

Climate change tree atlas

We obtained raster format results for the Climate Change Tree Atlas (Louis R. Iverson and Matthew P. Peters personal communication 2013) for the same tree species and climate scenarios we simulated with LINKAGES. Tree Atlas predictions were represented as projections of future Importance Values (IV) for tree species (Landscape Change Research Group 2014):

$$\begin{aligned}\mathrm{IV}_{\mathrm{SpeciesA}} = \Big\{ & \big[\big(50 * \text{Basal Area}_{\mathrm{SpeciesA}}\big) \\ & /\text{Basal Area}_{\mathrm{AllSpecies}}\big] \\ & + \big[\big(50 * \text{Stems}_{\mathrm{SpeciesA}}\big)/\text{Stems}_{\mathrm{AllSpecies}}\big]\Big\}.\end{aligned}$$

Tree Atlas has analyzed 134 tree species in the eastern United States. Importance values were calculated for each species for 20 km × 20 km cells from

U. S. Forest Service Forest Inventory and Analyis data (Woodall et al. 2010). 38 predictor variables were developed to determine suitable condition for each species. Predictor variables described climate, elevation, soil class, soil properties, land use and fragmentation (Landscape Change Research Group 2014). Regression tree analysis (RTA) was used to estimate IV from the predictors, followed by Bagging Trees (Breiman 1996) to determine stability of the RTA simulations. Random Forest (Breiman 2001) was next utilized to create current IV based on 1000 perturbed trees, as well as IV for future climate scenarios (Iverson and Prasad 1998; Iverson et al. 2008). Distributions are further evaluated for factors not analyzed in the statistical models. This allows Tree Atlas to identify when an individual species may do better or worse than model projections (Matthews et al. 2011).

Data analysis

Quantification of difference between future climate and current climate

We calculated the difference between future climate (PCM-B1, GFDL-A1fi, and Hadley-A1fi scenarios) and current climate biomass and IV for each ecological subsection. We estimated biomass for each subsection as the area weighted average of LINKAGES biomass estimates for each landform within each subsection. To ensure that the 20 km scale LINKAGES results had uniformity with our landform analysis, we also analyzed the 20 km scale results with a stratification of subsections. Although the change in LINKAGES biomass estimates and Tree Atlas IV are different measures, they both represented measures of species performance under the same climate scenarios.

We subtracted the IV and biomass output of future climate scenarios by the output of the current climate for each ecological subsection. Positive values indicated an increase in habitat suitability. Negative values indicated a decrease in suitability.

Comparison between Climate Change Tree Atlas and LINKAGES 2.2

We calculated Spearman's rank correlations between the LINKAGES change in biomass and Tree Atlas change in IV to determine the degree of similarity in model predictions. We used a rank correlation because the two models predicted different measures of tree abundance, making a correlation of actual values inappropriate. We expected significant positive correlations ($\alpha = 0.05$) if the models were performing similarly (Sheskin 2000).

Relationships between pattern and process differ based on the scale of analysis (Turner 1989, 2005). Proper organization of scale relationships is imperative. Hierarchy theory provides a method for organizing the complexity of ecological systems (Turner et al. 2001). Essentially, at a given level of resolution, a system is made of interacting lower level entities, and is a component of a larger system (Klopatek and Gardner 1999). We investigated the correlation between models at three hierarchical scales: regional (entire study area), ecological subsection, and species level. At the regional level we examined the correlation in change for all climate scenarios, ecological subsections, and species combined as well as each climate scenario independently. At the ecological subsection level we conducted two analyses: all species and climate scenarios combined for each individual subsection, and all species combined for each individual subsection for each individual climate scenario. At the individual species level we conducted two analyses: all climate scenarios and subsections combined, and each individual climate scenario with subsections combined.

Results

Change in biomass and importance values

Our LINKAGES results showed differing levels of future climate suitability for our analysis species. Sugar maple biomass for all future scenarios was less than current biomass. Biomass for all other species was greater than current climate levels under the PCM-B1 scenario. Red and black oak biomass was the least for the GFDL-A1fi and Hadley-A1fi scenarios. Shortleaf and loblolly pine biomass for GFDL-A1fi and Hadley-A1fi was greater than current levels. White oak, American elm, and Eastern redcedar had less biomass under GFDL-A1fi, but improved for Hadley-A1fi. Flowering dogwood biomass changed little, but overall was greater for all future climate scenarios versus current levels (Fig. 3).

Tree Atlas data indicated pine species would have an overall increase in IV for all future climate scenarios. Conversely, sugar maple showed an overall decline in IV under the future climate scenarios. Results were mixed for Eastern redcedar: half of the subsections increased and half decreased for GFDL-A1fi, and the majority of subsections decreased for PCM-B1 and Hadley-A1fi. Black, red and white oak were projected to have a decrease in IV for GFDL-A1fi and Hadley-A1fi scenarios. White oak was projected to do poorly for the PCM-B1 projections. Black and red oak were projected to improve for PCM-B1 in most subsections, and decrease in a few. American elm had an overall decrease in IV for GFDL-A1fi and Hadley-A1fi, and stayed the same or improved in IV for PCM-B1. Flowering dogwood had an overall decrease in IV for all future climate scenarios (Fig. 3).

Regional level

There was a strong positive correlation between models for all climate scenarios, ecological subsections, and tree species combined ($\rho = 0.53$, $P < 0.001$). The correlation between models was similarly strong and positive at the regional level for each individual climate scenario (Table 1).

Ecological subsection level

Our hypothesis that the most model correlation would occur at the ecological subsection level was accepted for the pooled climate scenarios. Correlation was higher for the individual climates, although the significance mostly was greater than $\alpha = 0.05$, rejecting the hypothesis.

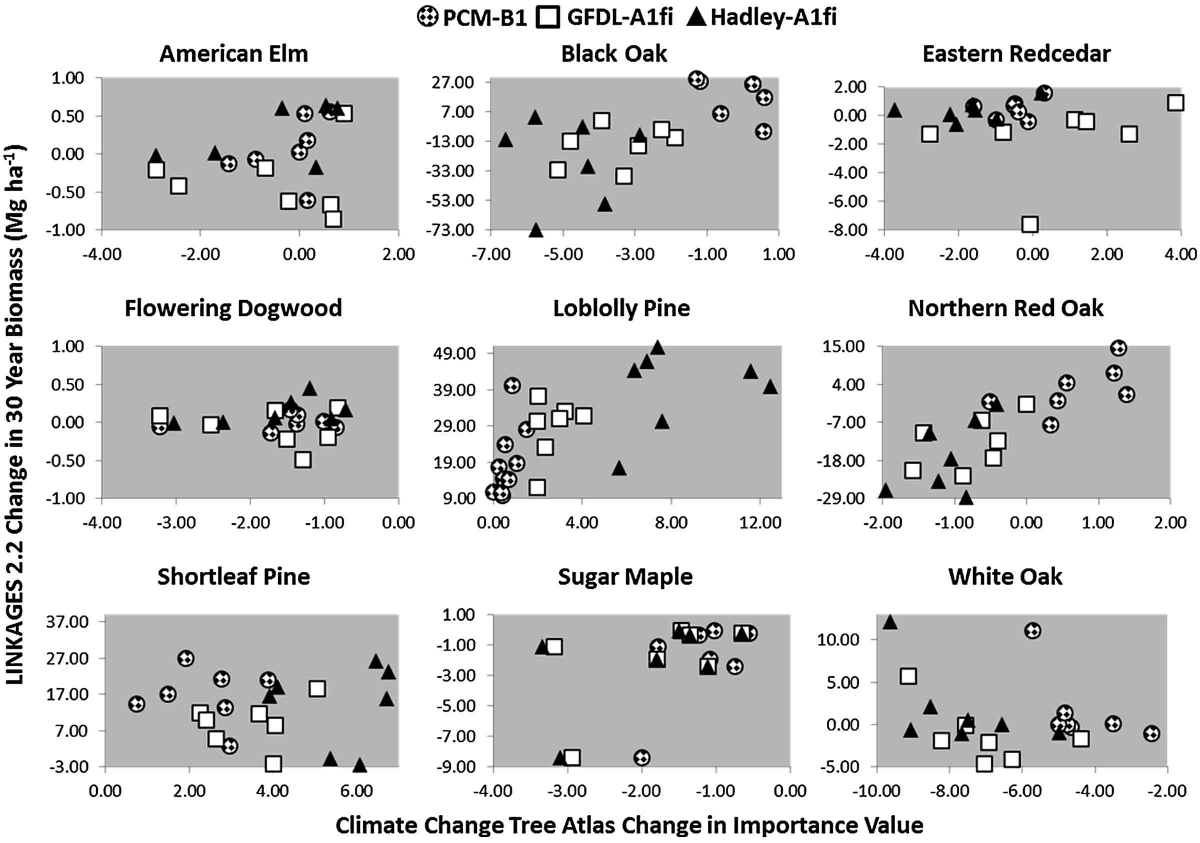

Fig. 3 Relationships between change in importance values from the Climate Change Tree Atlas and change in biomass values predicted by LINKAGES 2.2 for nine tree species within the seven ecological subsections of the Missouri Ozark Highlands, for three climate scenarios

Table 1 Spearman's rank correlation (ρ) for regional level analysis between predicted change in importance values from the Climate Change Tree Atlas and change in biomass predicted by LINKAGES 2.2 across all species, subsections, and climate scenarios, as well as individual climate scenario

Level analyzed	ρ	*P*
All species, subsections, climate scenarios[a]	0.53	<0.001
All species, subsections, PCM-B1[b]	0.50	<0.001
All species, subsections, GFDL-A1fi[b]	0.51	<0.001
All species, subsections, Hadley-A1fi[b]	0.50	<0.001

[a] (9 species) × (7 subsections) × (3 climate scenarios) = 189 analysis values

[b] (9 species) × (7 subsections) = 63 analysis values

There was a positive correlation between models at the subsection level across all climate scenarios and species; the Borders subsection had the greatest correlation (ρ = 0.69) and the Springfield Plain the lowest correlation value (ρ = 0.35) (Table 2). Statistically significant correlations between models were greatest under the GFDL-A1fi and PCM-B1 scenarios. Under the PCM-B1 scenario, the greatest correlation was for the Borders subsection (ρ = 0.85), and the lowest value was for the Current River Hills (ρ = 0.37). The greatest correlation for the GFDL-A1fi scenario was in the Plain Plateau subsection (ρ = 0.78), and the lowest correlation was in the Springfield Plain (ρ = 0.18). The highest correlation for the Hadley-A1fi scenario was in the Igneous subsection (ρ = 0.75), and the lowest in White River Hills (ρ = 0.33) (Table 2).

Species level

Model correlations were notably less for individual species across subsections (species level, Table 3). Three of nine species had significant positive correlations between models across all climate scenarios and subsections: Northern red oak (ρ = 0.82), black oak (ρ = 0.60), and loblolly pine (ρ = 0.70). Sugar maple had a high positive correlation (ρ = 0.41) but was not statistically significant. The remaining species had low correlations that were not significant (α > 0.05).

20 km Scale analysis

The 20 km scale results exhibited similar trends as the landform analysis, with some exceptions. On the regional scale, correlation was positively correlated and slightly more for PCM-B1 (ρ = 0.51 versus ρ = 0.50) and GFDL-A1fi (ρ = 0.53 versus ρ = 0.51), but still close to those of the landform analysis. Hadley-A1fi was positively correlated and less than the landform analysis (ρ = 0.25 versus ρ = 0.50) (Table 1 of supplementary material).

There was a positive correlation between models at the subsection level across all climate scenarios and

Table 2 Spearman's rank correlation (ρ) for ecological subsection level analysis between predicted change in importance values from the Climate Change Tree Atlas and change in biomass predicted by LINKAGES 2.2 across all ecological subsections and climate scenarios, as well as individual climate scenario

	All species, All climate scenarios[a]		All species, PCM-B1[b]		All species, GFDL-A1fi[b]		All species, Hadley-A1fi[b]	
	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*
Borders	0.69	<0.001	0.85	0.004	0.45	0.224	0.63	0.067
Current river hills	0.38	0.052	0.37	0.332	0.28	0.46	0.32	0.406
Igneous	0.61	0.001	0.62	0.077	0.6	0.087	0.75	0.02
Ozark hills	0.56	0.002	0.52	0.154	0.48	0.188	0.48	0.188
Plain plateau	0.62	0.001	0.72	0.03	0.78	0.013	0.53	0.139
Springfield plain	0.35	0.078	0.42	0.265	0.18	0.637	0.5	0.171
White river hills	0.51	0.007	0.47	0.205	0.77	0.016	0.33	0.381

[a] (9 species) × (3 climate scenarios) = 27 analysis values

[b] (9 species) = 9 analysis values

Table 3 Spearman's rank correlation (ρ) for species level analysis between predicted change in importance values from the Climate Change Tree Atlas and change in biomass predicted by LINKAGES 2.2 for nine tree species and all climate scenarios combined, as well as individual climate scenario

	All climate scenarios, Ecological subsections[a]		PCM-B1, all Ecological subsections[b]		GFDL-A1fi, all Ecological Subsections[b]		Hadley-A1fi, all Ecological subsections[b]	
	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*
American Elm	0.14	0.224	0.51	0.248	−0.14	0.760	0.32	0.482
Black Oak	0.60	0.004	−0.70	0.078	0.32	0.482	−0.18	0.702
Flowering Dogwood	0.19	0.415	0.14	0.76	−0.04	0.939	0.61	0.148
Loblolly Pine	0.70	<0.001	0.54	0.215	0.54	0.215	0.00	1.000
Eastern Redcedar	0.05	0.823	0.18	0.702	0.43	0.337	0.39	0.383
Northern Red Oak	0.82	<0.001	0.75	0.052	0.54	0.215	0.54	0.215
Shortleaf Pine	0.01	0.978	−0.18	0.702	0.00	1.000	0.25	0.589
Sugar Maple	0.41	0.062	0.46	0.294	0.36	0.432	0.36	0.432
White Oak	−0.18	0.444	−0.71	0.071	−0.43	0.294	−0.50	0.253

[a] (3 climate scenarios) × (7 ecological subsections) = 27analysis values

[b] (7 ecological subsections) = 7 analysis values

species. The correlations between models were greatest, on average, under the GFDL-A1fi scenario, and lowest for Hadley-A1fi (Table 2 of supplementary material).

Four of nine species had significant positive correlations between models across all climate scenarios and subsections: Northern red oak (ρ = 0.63), black oak (ρ = 0.58), loblolly pine (ρ = 0.69), and sugar maple (ρ = 0.62). The remaining species had low or negative correlations that were not significant (α > 0.05) (Table 3 of supplementary material).

Discussion

We highlighted differences and similarities, across a hierarchy of ecological scales, in predictions by a process model and a species distribution model. Some differences were likely due to inherent contrasts in how process and species distribution models function, whereas other differences were likely related to the way LINKAGES and Tree Atlas were applied in this study. We explained discrepancies between models based on differences in each approach and potential implications to ecological understanding and conservation as it is not possible to determine which model projections would represent future status.

Our hypothesis that agreement between process and species distribution models varies by hierarchical level, with the most agreement occurring at the ecological subsection level (middle hierarchical level) was partly accepted. The ecological subsection level captured the effects of the soil variables used, allowing for higher model correlation due to soil boundaries being more likely to coincide with ecological subsection boundaries (Soil Survey Staff, Natural Resources Conservation Service 2013). When all climate scenarios were pooled, correlation between the models was higher for the majority of ecological subsections than the regional level. When individual climate scenarios were analyzed, correlation between the models was higher for the majority of the subsections, but was not statistically significant. Morin and Thuiller (2009) concluded that although extinction and colonization may be a region-wide phenomenon, it occurred at local scale, coinciding with the ecological subsection. In many cases species geographic range shift only occurred at the boundaries or edge areas (Iverson et al. 2004; Morin and Thuiller 2009; Meier et al. 2012). Explanation as to why lower correlation occurred for some subsections may relate to model parameters utilized. Although similar soil variables were used by both models (e.g. organic matter), There were also variables not used for both. Tree Atlas required input of soil pH, soil erodibility factor, and landuse change (Landscape Change Research Group 2014), while LINKAGES used variables such as soil nitrogen and wilt point (Wullschleger et al. 2003).

Under the broad-scale regional analyses, all species and scenarios were combined and ranked. The species that were well correlated between the models compensated for the poor correlation of other species. This resulted in a higher level of monotonic distribution (indicative of high correlation) (Fig. 4) as compared to a single species analysis with poor correlation (American elm, Fig. 3) (Sheskin 2000). Similar trends were also reported in (Liang et al. 2013, 2014) that responses at fine-scale landform can be averaged out at the coarser landscape scales. High correlation was also likely due to both models utilizing some similar large-scale climate variables, such as precipitation and temperature, which allowed for some common overlap of observations between the two models at the regional hierarchical level.

Correlation between the models on the species level was noticeably less than that for the ecological subsections, whether climate scenarios were pooled or considered individually, consistent with our hypothesis. This suggests that there was more variation in species responses to the individual climate scenarios than there was in responses by species across ecological subsections. When analyzing smaller systems (e.g. plot-level), differences in the forces acting upon them become more evident, resulting in more variability. Also, at the species level, intra-species competition was not simulated within Tree Atlas (Landscape Change Research Group 2014), whereas it was simulated in LINKAGES (Wullschleger et al. 2003), potentially resulting in poorer agreement. Another source of variation may have come from the method in which the two models utilized temperature and precipitation. LINKAGES utilized daily measurements (Wullschleger et al. 2003), while Tree Atlas used monthly (Landscape Change Research Group 2014). Monthly or greater averages of these values may not capture drought events in the predicted climate scenario, producing discrepancies among species (Gustafson et al. 2015).

Another potential reason for differences between model results may lie in differences in how geochemical processes are represented. Species response to drought and soil characteristics such as low nitrogen is accounted for in the models in different ways. LINKAGES accounts for these factors through biogeochemical processes and Tree Atlas accounts for them indirectly based on species abundance from historical patterns of drought and low nitrogen soils. These differences can be seen in Flowering dogwood. Flowering dogwood is intolerant to low nitrogen soil levels (Pastor and Post 1986), and Tree Atlas may not have similarly captured the effects of changes to soils characteristics since changes in nitrogen availability

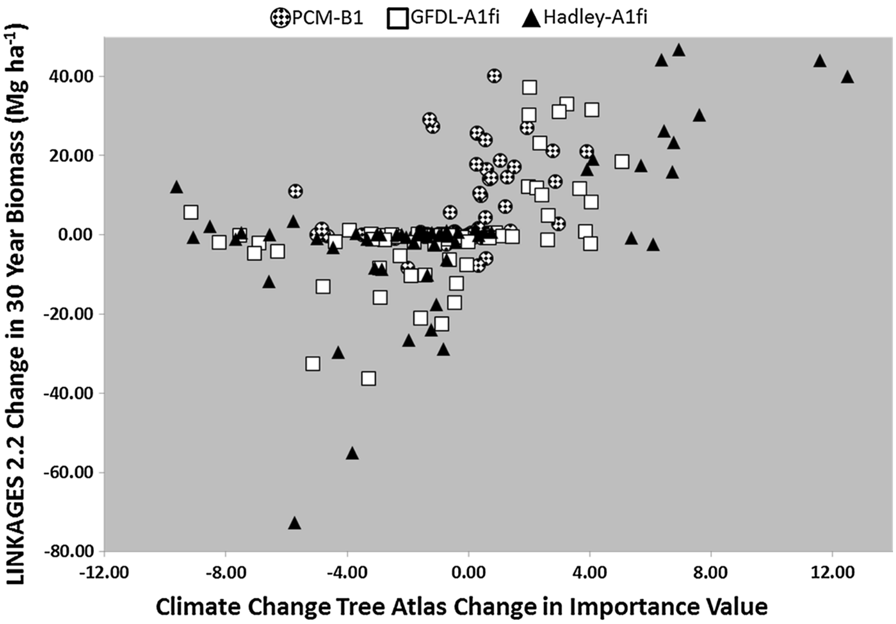

Fig. 4 Regional scale relationships between change in importance values from the Climate Change Tree Atlas and change in biomass values predicted by LINKAGES 2.2 for nine tree species within the seven ecological subsections of the Missouri Ozark Highlands, for three climate scenarios

due to climate change is not readily available to incorporate in Tree Atlas. Eastern redcedar and shortleaf pine, species with poor model correlation, were classified as xeric (based on the fraction of growing season drought days that a species can tolerate before annual growth is prevented) (Pastor and Post 1986). Model correlation may have been poor because their extreme suitability to dry conditions was not being fully captured by tree atlas due to the lack of water dynamics being simulated.

Our research showed GFDL-A1fi, the most extreme climate scenario, resulted in the greatest correlation between the models. GFDL-A1fi was the driest scenario during the growing season and had the highest correlation and agreement between models. This has implications for future modeling, as Zimmermann et al. (2009) similarly reported that models utilizing climate extremes in their construction tend to improve spatial pattern accuracy for tree species. Models results were also generally similar for species at or near the edge of their range. The northern edge of range for loblolly pine was immediately south of the study area (Fig. 2) and these species were highly correlated. Model results were also similar for northern red oak and black oak, which were at the edge of their range (Fig. 2). Species response to changing environments is often largely determined by population response at the leading and rear edge of their range (Hampe and Petit 2005; Thomas 2010).

Our results indicated that the differences between the two models' predictions were likely not due to different analysis units (landforms vs. 20 km pixel), because results for both methods indicated there were several similar trends in model correlation (see supplement). Therefore, the differences seen should be related to the difference between how the models function. We feel analysis of LINKAGES at the landform scale was more appropriate because this better represented ecological processes due to landforms being ecologically defined and representing more homogeneous soil conditions. The 20 km analysis for LINKAGES represented averages of arbitrarily defined cells overlapping subsections which may have contained more or less landform and soil diversity.

Conclusion

Our general hypothesis that agreement between process and species distribution models varies by hierarchical level, with the most agreement occurring at the ecological subsection was partly accepted. We only saw this trend when all climate scenarios were combined.

Our comparison of the application of a process-based model and a statistical model for predicting changes in tree species abundance under alternative climate scenarios provided insight into the uncertainty in predicted changes and potential reasons for model disagreement. Stronger correlation was seen for most species that were near the edge of their range, and for extreme climate scenarios with greater level of predicted change. We suggest further investigation into where models disagreed such as simulations to examine model sensitivities to key parameters. An investigation into model agreement for additional species, based on a priori hypotheses generated from our study, would provide additional insight. Analysis of additional species distribution and process models would also be beneficial in diminishing uncertainty with regard to climate projections.

Our research benefits the discipline of landscape ecology through the understanding of climate change's effect on tree species pattern over forest landscape at different scales. This will also help to understand forest landscape sustainability under the stress of climate change. Our research methods can be applied to other landscapes and landscape models, making it relatable to other geographic locations and allowing for further understanding of climate changes' effects on landscape processes.

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