



Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors

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ABSTRACT

Species distribution models (SDMs) to evaluate trees' potential responses to climate change are essential for developing appropriate forest management strategies. However, there is a great need to better understand these models' limitations and evaluate their uncertainties. We have previously developed statistical models of suitable habitat, based on both species' range and abundance, to better understand potential changes of 134 tree species habitats in the eastern United States (<http://www.nrs.fs.fed.us/atlas>). Our focus here is to build on these results via a more robust assessment framework called modification factors (ModFacs) that is made up of five components. ModFac 1 addresses nine biological characteristics (e.g., shade tolerance and seedling establishment) that quantify the influence of species life-history traits. ModFac 2 considers 12 disturbance characteristics (e.g., insect pests, drought, and fire topkill) which address the capacity of a species to tolerate and respond to climate-induced changes in habitat. ModFac 3–5 distill the tree SDM results and facilitate communication of model uncertainty; we quantified the variability in projected change for General Circulation Models (GCM) and emissions scenarios (ModFac 3), the extent to which each species' habitat intersects novel climate conditions (ModFac 4), and accounted for long-distance extrapolations beyond a species' current range (ModFac 5). The life-history components of ModFacs 1 and 2 demonstrate the marked variability among species in terms of biological and disturbance characteristics, suggesting diverse abilities to adapt to climate change. ModFacs 3–5 show that the information from the SDMs can be enhanced by quantifying the variability associated with specific GCM/emission scenarios, the emergence of novel climates for particular tree species, and the distances of species habitat shifts with climate change. The ModFacs framework has high interpretive value when considered in conjunction with the outputs of species habitat models for this century. Importantly, the intention of this assessment was not to create a static scoring system, but to broadly assess species characteristics that likely will play an important role in adaptation to climate change. We believe these scores based on biological, disturbance, and model synthesis factors provide an important expansion of interpretive and practical value to habitat model projections.

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1. Introduction

Climate change has disrupted ecological systems worldwide, and is predicted to intensify by mid-century (Intergovernmental Panel on Climate Change [IPCC], 2007). Management decisions made in the face of climate change will play a critical role in how forests and individual tree species will respond. Managing natural systems with high uncertainty of future conditions requires adaptive management approaches, yet we first need to understand how species and ecological communities may react to changing climates (Aitken et al., 2008). Models and simulations

are the primary tools for evaluating potential responses of biota to changing and uncertain climates (Guisan and Thuiller, 2005). Major modeling efforts have been undertaken worldwide to identify possible trends for forests and tree species, and much of this work relies on species distribution models (SDMs) (Franklin, 2009).

All models are, of course, only approximations of reality and must be treated with caution, especially when projecting into an uncertain future and into new locations. Most SDMs have been built with statistical/empirical approaches and carry numerous assumptions. These assumptions have been reviewed by critics and SDM modelers alike, and include (1) unlimited dispersal capability, (2) equilibrium with environment, (3) biotic interactions, (4) CO₂ effects, (5) key environmental variables unidentified or unsupported by data, (6) adaptation, (7) inability to incorporate disturbance, (8) uncertainties in General Circulation Models (GCM) projections, and (9) variations associated with SDM algorithms

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(Pearson and Dawson, 2003; Hampe, 2004; Iverson et al., 2011; Franklin, 2009; Wiens et al., 2009). Some of these assumptions have been addressed with process-based or hybrid approaches (Morin et al., 2008; Scheller and Mladenoff, 2008; Kearney and Porter, 2009; Keenan et al., 2011), in which temporal stochasticity and individual physiological mechanisms can be better simulated and interpreted. For example with tree species, the main barriers to mechanistic approaches are an inadequate understanding of ecophysiological processes across a species' entire range and then a lack of sufficient data, resources, and time to appropriately parameterize such models for multiple species (Lawler et al., 2006) across these broad geographic extents. Several applications, however, warrant the extra time and effort: (1) developing hypotheses about particular species' limits, (2) modeling invasive or other species markedly out of equilibrium, (3) assessing physiological constraints to future novel environments, and (4) assessing suitability of potential translocation sites (Kearney and Porter, 2009).

Ultimately, all models suffer from insufficient knowledge on how multiple species will respond to and interact in an uncertain future. Nonetheless, managers considering model uncertainties around projected species' responses must keep in mind (1) the risks of taking no action or the wrong action, and (2) the reality that ignoring potential future outcomes is not an option (Wiens et al., 2009). Therefore, to increase the usefulness of projected

impacts of climate change, managers should be equipped with a toolbox that provides more specific indications of possible outcomes in light of site-specific and local management decisions.

Many researchers have been using SDMs with statistical methods to better understand the potential future distributions of different organisms in the face of climate change (e.g., Franklin (2009) and citations within). Our assessment framework first uses the DISTRIB model (Iverson et al., 2008c), a decision-tree based ensemble model using the randomForest approach (Breiman, 2001), in conjunction with current and future climate data, environmental data (e.g., soil properties), and tree species abundance data, to create potential suitable habitat maps under three GCMs and two emission scenarios for the eastern United States. Outputs from this effort are detailed on our website <http://www.nrs.fs.fed.us/atlas>, and published elsewhere (Iverson et al., 2008b,c). Next, the SHIFT migration model is used to assess the potential for tree species to colonize the newly derived habitat by considering Holocene tree migration rates and the current fragmented state of the landscape (Iverson et al., 1999, 2004a,b; Schwartz et al., 2001). The combination of DISTRIB and SHIFT outputs indicate how suitable tree habitats may shift, and the potential of individual species to colonize newly available habitats within about 100 years. Lessons learned from this research of 16 years are detailed in a recent paper (Iverson et al., 2011).

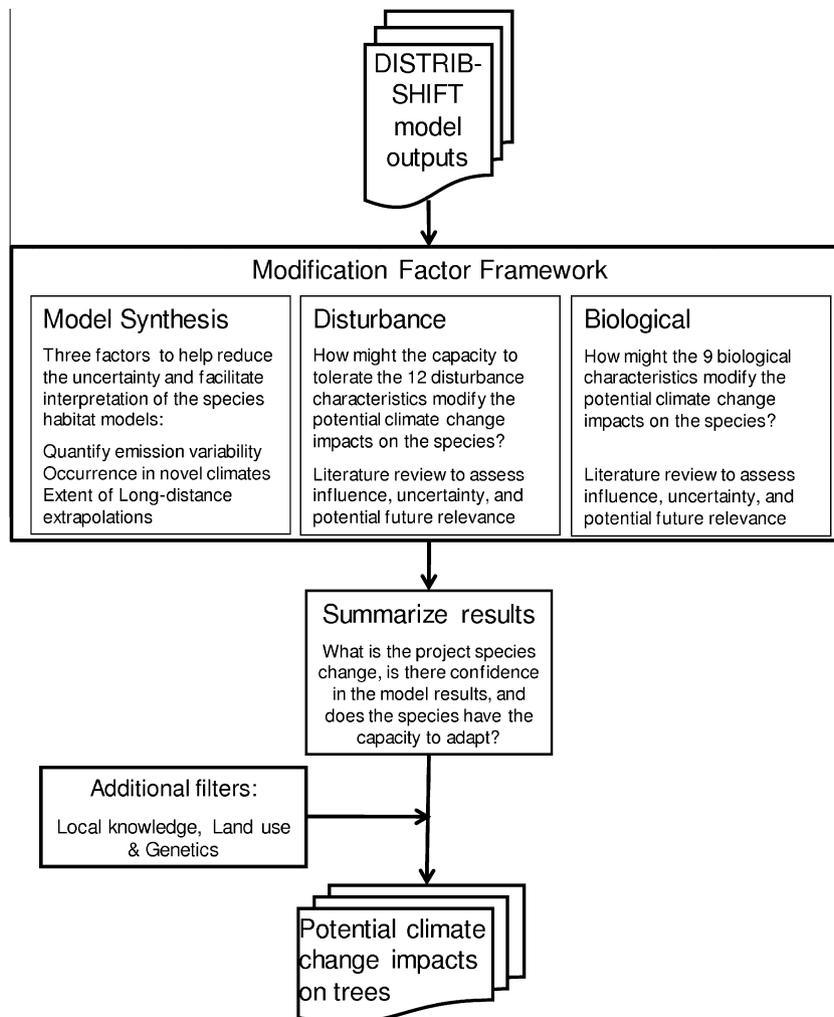


Fig. 1. Graphic depicting the ModFacs framework. The results presented here reflect the main pathway of incorporating the modification factors with the habitat models to provide a broad-scale assessment of species vulnerabilities. However, biological and disturbance factors can be changed to reflect local knowledge and specific management strategies.

The objective of this paper is to further enhance the approach and make results more accessible to management decisions. Specifically, we aim to introduce, explain, and incorporate several modifying factors (hereafter referred to as ModFacs) that add to the interpretative value of DISTRIB or DISTRIB/SHIFT results and give users more reliable potential outcomes in light of a large suite of variables that may or may not be related to climate (Fig. 1). The development of multi-criteria ecological monitoring programs (Manley et al., 2000) provides a logical conceptual model on which to build a climate change assessment framework for tree species. Contemporary challenges of identifying risks to conservation and nature reserves require the synthesis of multi-layered information. The goal is to provide information to a broad audience of decision makers in regards to climate change impacts that helps establish a structured system for developing science-based planning (Manley et al., 2000) to forest management.

The ModFacs framework aims to address uncertainties of tree species' responses to climate change that are not well accounted for in current SDMs. Two factors address life-history characteristics that influence and shape species patterns beyond the environmental determinants used to describe species' distributions. These life-history characteristics reflect the importance of plant trait variability as expressed through performance filters, which influences the occurrence of plant communities (Webb et al., 2010). Specifically we focus on nine biological characteristics of species that may influence their population persistence and adaptation capacity under climate change, and 12 disturbance influences, including many that are expected to increase under climate change (Dale et al., 2001; Scheller and Mladenoff, 2005). In addition to the biological and disturbance factors, three model synthesis factors were developed to quantify important information, beyond measures of changing species' distributions, contained within the species habitat models and to better understand associated uncertainties. These factors are (1) emissions variability, the variation of projected changes in species' habitats derived from the differences in precipitation and temperature according to emissions scenarios used by the IPCC (Nakicenovic et al., 2000) and from variations in sensitivity to atmospheric carbon dioxide within the various GCMs

(Real et al., 2010); (2) novel climate, locations that the species does not now occupy where the species' capacity to grow and survive may be challenged because of disrupted temperature–precipitation regimes (Williams et al., 2007; Gallagher et al., 2010); and (3) long-distance extrapolations, the extent of potentially suitable habitat beyond the species current distribution boundary according to the model projections.

These five components of the ModFacs framework were evaluated for each of 134 tree species in the eastern United States so that the species can be compared relative to each other as well as providing a better understanding of, and alternative approaches to, the potential pitfalls of uncritically accepting the outputs from the SDM models. While this application of considering tree species as the foundation of the framework differs from the development of multi-criteria to identify monitoring plans, the approaches have a similar global objective: to create a better toolbox for researchers, managers, and decision-makers challenged with the need to manage landscapes under a changing climate.

2. Material and methods

2.1. Biological and disturbance factors

To evaluate the potential of species to adapt to and tolerate disturbances under the predicted future changing climates, we assessed nine biological and 12 disturbance characteristics for each species (Table 1, see Appendix A for scoring criteria). The biological characteristics were; CO₂/productivity, CO₂/water use efficiency, shade tolerance, edaphic specificity, environmental habitat specificity, dispersal, seedling establishment, vegetative reproduction, and fire regeneration. The disturbance characteristics were; disease, insect pests, browse, invasive plants, drought, flood, ice, wind, fire topkill, harvest, temperature gradients, pollution. Each of these characteristics cannot typically be directly captured in SDMs. The biological capacities may increase, decrease, or not affect the species' adaptability to or tolerance of climate change. In addition, changes in disturbance intensities and patterns can be attributed to climate disruption, and many are likely to increase over the

Table 1
Default modification factor scores. Biological and disturbance scores were determined based on a size class impact of seedlings and saplings (SS) and/or Pole and Sawtimber (PS). The characteristic score was the product of literature score × uncertainty × future relevance and the factor was the mean biological and disturbance score. Model syntheses scores are described in methods.

| Modification factor | Factor score | Size class | Char. names | Lit. score | Uncertainty | Future relevance | Char. score |
|-----------------------------|--------------|---------------------------|-----------------------------------|------------|-------------|------------------|-------------|
| Biological | 0.89 | SS/PS | CO ₂ /PROD | 1 | 0.50 | 1 | 0.50 |
| | | SS/PS | CO ₂ /WUE | 1 | 0.75 | 2 | 1.50 |
| | | SS/PS | Shade tolerance | 0 | 0.75 | 3 | 0.00 |
| | | SS/PS | Edaphic specificity | 0 | 0.75 | 2 | 0.00 |
| | | SS/PS | Environmental habitat specificity | 0 | 0.75 | 3 | 0.00 |
| | | PS | Dispersal | 1 | 0.50 | 3 | 1.50 |
| | | SS | Seedling establishment | 1 | 0.75 | 4 | 3.00 |
| | | SS/PS | Vegetative reproduction | 1 | 0.75 | 2 | 1.50 |
| | | SS | Fire regeneration | 0 | 0.75 | 2 | 0.00 |
| Disturbance | −1.43 | SS/PS | Disease | −1 | 0.75 | 2 | −1.50 |
| | | SS/PS | Insect pests | −2 | 0.50 | 4 | −4.00 |
| | | SS | Browse | −1 | 0.75 | 1 | −0.75 |
| | | SS | Invasive plants | −2 | 0.50 | 4 | −4.00 |
| | | SS/PS | Drought | −1 | 0.75 | 4 | −3.00 |
| | | SS/PS | Flood | −1 | 0.75 | 1 | −0.75 |
| | | PS | Ice | −1 | 0.50 | 1 | −0.50 |
| | | PS | Wind | −1 | 0.75 | 2 | −1.50 |
| | | PS | Fire topkill | −1 | 0.75 | 3 | −2.25 |
| | | SS/PS | Harvest | 1 | 0.50 | 2 | 1.00 |
| | | SS/PS | Temperature gradients | 1 | 0.75 | 2 | 1.50 |
| | | SS | Pollution | −1 | 0.75 | 2 | −1.50 |
| | | GCM emissions variability | 1.00 | | | | |
| Novel climate | 1.00 | | | | | | |
| Long-distance extrapolation | 1.00 | | | | | | |

coming century (Dale et al., 2001). For example, increasing fire impacts have been recorded in the western United States (Westerling, 2006; Littell et al., 2009). Increasing mortality of pines in the Rocky Mountains has been attributed to warmer winters and higher survival of the mountain pine beetle, *Dendroctonus ponderosae* (Logan et al., 2003; Kurz et al., 2008). Increasing droughts have been shown to be responsible for wide-scale mortality in *Pinus edulis* in the southwestern United States (Breshears et al., 2009). Thus, we add an important link between the rigorous (and often complex) modeling of climate impacts and the data needed to inform management decisions (Loehle, 2000).

For both biological and disturbance factors, we conducted a literature assessment; the primary sources are the USDA Forest Service Silvics Manual (Burns and Honkala, 1990a,b), USDA National Resources Conservation Service Plants Database (<http://www.plants.usda.gov/>), USDA Forest Service Climate Change Tree Atlas (<http://www.nrs.fs.fed.us/atlas>), and USDA Forest Service Fire Effects Information System (<http://www.fs.fed.us/database/feis/plants/tree>). These sources were largely compiled from the primary literature, and thus represent a broad assessment of species' characteristics. For some species, additional literature was used to fill in gaps, but we could not do a complete literature review for each species. To assess whether species follow a pattern associated with functional types associated with their regeneration guild, we classified each species into one of three classes: persistent, opportunistic, or pioneer (Burns and Honkala, 1990a,b; Sutherland et al., 2000). The regeneration guild identification for each species are available at <http://www.nrs.fs.fed.us/atlas>. In this way, we could determine the tendency of species to cluster (or not) with the biological and/or disturbance characteristics.

The scoring system involved developing a standardized set of variables (Table 1) and variable definitions (Appendix A), and then compiling pertinent information for each species based primarily on the four sources above. Once these data were collected for each species, each biological or disturbance characteristic was given three scores. In developing the scoring criteria, we evaluated standard social science protocol, e.g. (Bright et al., 2000) and developed several scores from the compiled literature. First, and foremost, a "literature" score was assigned on a bi-polar Likert-style score, ranging from –3 to 3 (strongly negative to strongly positive) influence on the species' capacity to withstand the disturbance or tolerate a biological condition. This score establishes the direction and magnitude of the likely impact on the species. Two multipliers, to account for uncertainty in a characteristic's influence and the likely relevance of the characteristic under projected climate change, were applied to modify this score. The uncertainty score was assigned which could only reduce or maintain the initial score; its only possible values were 0.5, 0.75, or 1. Therefore, as this value increases, the certainty around the initial score was higher (e.g., the information content from the sources was adequate, clear, and consistent as to the direction and magnitude of a characteristic's influence on the species). When adequate information was not found for a characteristic, estimates were made based on a species' closest known relatives, and the uncertainty multiplier score was either 0.5 or 0.75. The future relevance score, which ranged from 1 to 4, was then used as a multiplier to account for the expectation that the variable will be more or less relevant with respect to climate change in the future, i.e., how much will the variable change due to climate changes? The four-point range was used to allow finer distinction of the characteristics. For example, as mentioned earlier, increased drought, insect pests, and fire activity have already been attributed to climate change (Westerling, 2006); these variables are projected to be more prevalent on the landscape and thus receive high future relevance scores (see Appendix A). In terms of the biological ModFac, the future relevance for seedling establishment receives the highest score, as the ability of a species

to establish new seedlings will be vital for persistence within its current occupied zone, the successful reproduction will serve to encourage greater genetic heterogeneity, and it will be necessary to facilitate movement to new location under climate change.

For each characteristic (Table 1) and for all 134 species, author scoring was used for the three scores (literature, uncertainty, and future relevance) based on the surveyed literature. Though the scoring necessarily was largely subjective, the evaluation of the scoring criteria was calibrated using repeated independent evaluations followed by review until consensus among the authors was achieved. We also preserve the score rational recorded for each characteristic to serve as an archive. For example, the biological characteristic of seedling establishment has high future relevance and thus was assigned a 4 (Table 1) because a species' ability to occur in the face of shifting habitats will hinge on its ability to establish in new areas. In the case of *Acer rubrum*, statements found in Burns and Honkala (1990a) and other sources point to the species broad germination niche, resulting in a +3 seedling establishment score with little uncertainty (assigned 1). In the case of *Abies balsamea*, there were inconsistencies across sources but a more negative statement such as low seed viability with variation contingent upon age and light, resulting in an assigned –1 score with high uncertainty (0.5). However, managers can (and should) change these scores as they consider local conditions for each of these characteristics (Fig. 1). With local knowledge of site-specific processes, managers will be better suited to interpret the potential suitable habitat models after considering these ModFacs. In addition, this approach encourages decision-makers' to include silvicultural knowledge and to take an active role in managing tree habitats under projected future climatic conditions. We are endeavoring to open a clearer path to incorporate climate change impacts into an adaptive management framework (Mawdsley et al., 2009) within the context of local knowledge, genetics, and land-use patterns.

2.2. Model synthesis factors

The three remaining factors, described below, address uncertainty inherent in 134 tree species distribution models and the results from the DISTRIB methodology (Iverson et al., 2008c). The spatial extent of the analysis consists of the conterminous United States east of the 100th meridian with a resolution of a 20 × 20 km grid. The response variable in this analysis was a continuous variable, importance values (hereafter, IV), based on the basal area and number of stems of each species on Forest Inventory Analysis plots that were aggregated and averaged for each 20 × 20 km cell. Importance value ranges from 0 to 100 with the maximum value being a pure stand of a species. To evaluate the potential habitat response of the 134 tree species, we projected the species current distribution models onto three GCMs: HadleyCM3 model (hereafter abbreviated HAD), the Geophysical Fluid Dynamics Laboratory (GFDL CM2.1) model, and the Parallel Climate Model (PCM). These GCMs were considered under two emissions scenarios established by the IPCC (Nakicenovic et al., 2000): the A1fi (high emissions, hereafter termed "hi") assumes that currently increasing emission trends continue for several decades, and the B1 (hereafter termed "lo") assumes a high level of conservation and reduction of CO₂ emissions.

2.2.1. GCM emissions variability factor

A key step in any modeling effort must be to confront the uncertainty inherent in projecting current climate conditions forward (Araujo and New, 2007). It is essential that we evaluate our habitat models under various projected outcomes, especially to present a range of realistic possibilities based on the IPCC scenarios (Nakicenovic et al., 2000; Beaumont et al., 2008). In doing so, we create

multiple habitat models for each species. While this provides a range of possibilities of how species' habitats may change, it also adds complexity for interpretation. Here we provide a synthesis of the two main sources of variation in climate change models as they relate to the 134 tree SDMs: the variability between different GCMs and the differences between emissions scenarios. For each species, we quantify the areas of agreement and disagreement among the model outputs.

The emissions factor was, therefore, developed to determine, for each species, if there is greater variability in projected habitat changes between the two ("hi" vs. "lo") emissions scenarios than in the projected change among the three GCM outputs. This factor provides a means to quantify variability in a species' projected habitat response under climate change. For each 20×20 km grid cell, we record the difference between the projected IV under high and low emissions for each of the three GCM models. The mean difference for each cell was then calculated from these three difference values, and the ratio of this mean difference to the projected change in IV under any given GCM/emission projection was calculated and mapped. When the ratio ≥ 1 , the variability between emission scenarios is equal to or greater than the projected habitat change according to the particular GCM/emission projection. Conversely, a ratio < 1 indicates a relatively smaller variation between the high and low-emission scenarios. To capture a distribution-wide assessment for each species, the summary of the cell-by-cell values are reported as the mean ratio and used here to quantify emissions variability. According to these model results, the higher the ratio, the greater the influence humans have in the future distribution of the species' habitat, in that the high emissions scenario (A1fi) generally produces more dramatic changes in suitable habitat.

2.2.2. Novel climates factor

To explore species' potential responses to climate change, it is common to use a variety of climate variables to capture the climate associations for a species. These links have served as foundations in biogeography and have helped explain patterns of contemporary

species distributions. However, both paleohistoric evidence and current GCMs suggest that as the climate changes, the components of climate that we typically evaluate (temperature and precipitation) are not expected to respond in a similar manner, and new climate space may emerge (Hargrove and Hoffman, 2004; Williams et al., 2007). This mismatch of climate conditions, or novel climates, may cause additional stresses on the organisms living there, especially if the novel conditions are hotter and drier than currently (or importantly, historically) experienced.

Following Hargrove and Hoffman (2004), we performed *k*-means cluster analysis for each of the 9767 pixels (20×20 km cells) defining the eastern United States. These clusters were derived from a principal component analysis (PCA) of the seven current climate variables used in our SDMs (see website for maps of the seven variables, http://www.nrs.fs.fed.us/atlas/tree/map_predictors.html). The first two principal component axes captured 92 percent of the variance, and loadings reflected a temperature-driven *x* axis and a precipitation-dominated *y* axis. *K*-means clusters was then used to identify 20 unique clusters, based on 1000 runs with randomly assigned starting positions performed until less than 1% of cells showed cluster switching. We selected 20 clusters based on exploration of the stabilization and visual inspection from 5 to 30 clusters. With less than 20 clusters, important regions such as the Great Smoky Mountains were lost and using more than 20 clusters was unsupported given the spatial resolution of 20×20 km cells. These clusters, evaluated in data space, were then related back to geographic space to map the spatial distribution of the current climate clusters. Next, we projected the PCA onto a GCM and emissions scenario (using the most extreme and mildest climate scenarios in our modeling set, HADhi and PCMlo, respectively) following the same clustering methodology. The distance (in data space) to the closest current climate cluster analog was then recorded and transformed from data space back to geographic space to map how the climate clusters across the eastern United States may change (Fig. 2). The Euclidian distance between cluster centroids provides a good measure of climate representativeness (Hargrove and Hoffman, 2004). We identified the cluster as being

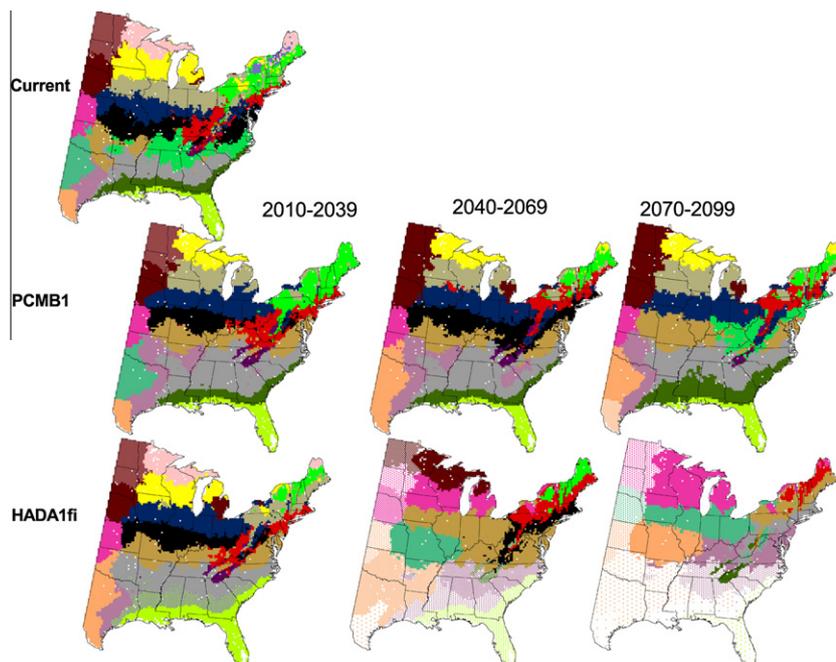


Fig. 2. Novel climate condition based on 20 clusters of five temperature and two precipitation variables through 2100. The color of the clusters was based on current climate conditions. Therefore, under HADhi and PCMlo, the color is assigned to the nearest contemporary climate cluster. The stippling of colors reflects where the Euclidian distance between the nearest contemporary climate cluster exceeds the present mean between cluster center minimum distance ($d_{\min} = 1.40$) and as this distance increases the amount of white space increases.

a novel climate cluster where the minimum Euclidian distance between a current cluster center and a future cluster was greater than the mean minimum Euclidian distance between all current clusters ($d_{\min} = 1.40$).

We extended this methodology by overlaying each species' current and future habitat geographic distribution onto the 20 clusters. This step allowed us to quantify the amount of each species' summed IV that resided in each cluster, and then calculate the proportion of the species' projected future IV that occurs within climate clusters that it presently occupies. We use this proportion as the factor score. When a high proportion of the species' future habitat occurs in unique climates, which could be either current clusters that it does not now reside in or climates novel to the eastern United States, greater care should be taken in interpreting how the species may respond.

2.2.3. Long-distance extrapolations factor

Lastly, a factor was developed to assess the projected future habitat for each tree species relative to the distance beyond its current range boundary. Future habitats were derived by mapping where individual species habitats would be suitable with projected climate change. The potential for colonization of these future habitats has been investigated for several species using a model called SHIFT (Iverson et al., 2004a,b). In that work, we calculated that less than 15% of new suitable habitat had even a 2% probability of colonization within 100 years, demonstrating the challenges species face when moving across a fragmented landscape under a shifting climate. In this factor, we are not assessing the colonization potential, which the SHIFT model calculates; rather we quantify accessibility of the future habitat.

The procedure was first to create range boundaries for the species (as "presence contours") using the species current and future IV distributions. To eliminate outlier cells of species occurrence, we excluded isolated 'islands' where there were less than 10 contiguous 20 × 20-km cells. Next, the minimum Euclidian distance from each cell along the current range boundary to the nearest future boundary cell was calculated. We report the mean minimum distance to quantify the overall distance. Next, to further the interpretive capacity of this factor, we identified the proportion of the future summed IV that was within 200 km of the current range boundary. The 200-km distance was identified as a key distance from the SHIFT model outputs, beyond which there was very limited potential for colonization within 100 years (Iverson et al., 2004a).

2.3. Overall assessment

To build a comprehensive tool to aid in predicting and responding to climate change impacts for eastern United States tree species, we performed a final scaling of all five factors individually as a means to standardize units of the metrics. However, we resisted the urge to calculate a final weighting of the factors into one metric as the individual factor scores should be considered on their own. This approach follows logic similar to that of Hierl et al. (2008) in their assessment of management plans, as management decisions should consider the relative influence of each factor in light of potential changes in species habitats under climate change. Especially noteworthy is the difference between the disturbance and biological information as compared to the three model synthesis factors. Nevertheless, it is vital that the different factors can be easily compared both within and among species, so for each factor we set the median to 0 and distribute the values from -3 to +3, using

$$\tilde{x}_i = \frac{(x_i - \min(x)) * 6}{\max(x) - \min(x)} - 3$$

where $\min(x)$ and $\max(x)$ are the minimum and maximum raw scores, respectively, for all species and (x_i) is the score for the i th species, calculated separately for each of the five factors, and (\tilde{x}_i) is the resulting normalized score. These scores were plotted on five-sided star graphs to visualize the score of each factor, by species. By calculating the area occupied within the star graph, and viewing the sorted set of graphs, one can visualize one means of ranking of each species' vulnerability to climate change. The higher the area inside the plotted surface for the two life history factors, the more resilient to climate change the species can be considered, and for the three model synthesis factors, greater area lends to higher confidence in the species habitat models and resulting map outputs.

3. Results

To illustrate the utility of the framework, we included specific results for *Acer rubrum*, *Abies balsamea*, *Prunus serotina*, and *Quercus falcata*, as well as summaries of the ModFacs framework across all 134 tree species. Because these results complement published research exploring potential climate change impact for the 134 tree species (e.g., Iverson et al., 2008c), we show the habitat results for only one GCM emissions scenario. We selected our highest emission scenario (HADhi) for demonstration, as recent data suggest that emissions are tracking at higher levels than projected even in the most severe A1fi scenario used in the HADhi model (Canadell et al., 2007).

3.1. Biological and disturbance factors

The 134 tree species exemplify a broad diversity of life-history tradeoffs and this variability was captured in part in the nine biological characteristics evaluated. The summary of the individual characteristics shows the great variability among species; standard deviations for six of the nine scores overlapped zero (Fig. 3). For example, there was a large contrast among species with respect to shade tolerance, their ability to disperse, or their capacity to regenerate following an intense fire. Similarly, disturbance characteristics show marked variation, with scores for drought, fire top-kill, and temperature gradients showed the greatest variability among species (Fig. 3). Next, across all species the mean biological score was +0.96 (SD = 1.3), but it ranged widely, from -2.03 to +4.89 (Fig. 4, Appendix B). The 12 disturbance characteristics also show substantial variation among species with the mean score of -1.2, and ranged from -3.27 to 0.35 (SD = 0.71, Fig. 4, Appendix B). Even functional groups as evaluated based on regeneration guild varied markedly within groups (Fig. 4). When viewed together, the biological and disturbance ModFac scores illustrate the potential adaptability of a species under climate change. With those species showing positive biological and disturbance scores occupying the upper right quadrant of Fig. 4 and likely in a better position to adapt with climate change, while species in the lower left quadrant showing substantial vulnerabilities based on their life history characteristics.

The real interpretive value of both disturbance and biological factors was captured at the species level, where they can be interpreted in conjunction with the habitat change models. For example, the severe projected loss (-86%) of suitable habitat for *Abies balsamea* within the eastern United States may even be underestimated because of its negative disturbance (-3.0) and biological scores (-0.35) (Appendix B). In contrast, *Acer rubrum* was projected to lose 41% of its habitat (mostly importance value IV, not area) under HADhi and has the most positive biological (+3.0) and disturbance (+3.0) profile of all species evaluated. As such, even though *Acer rubrum* was projected to decline according to

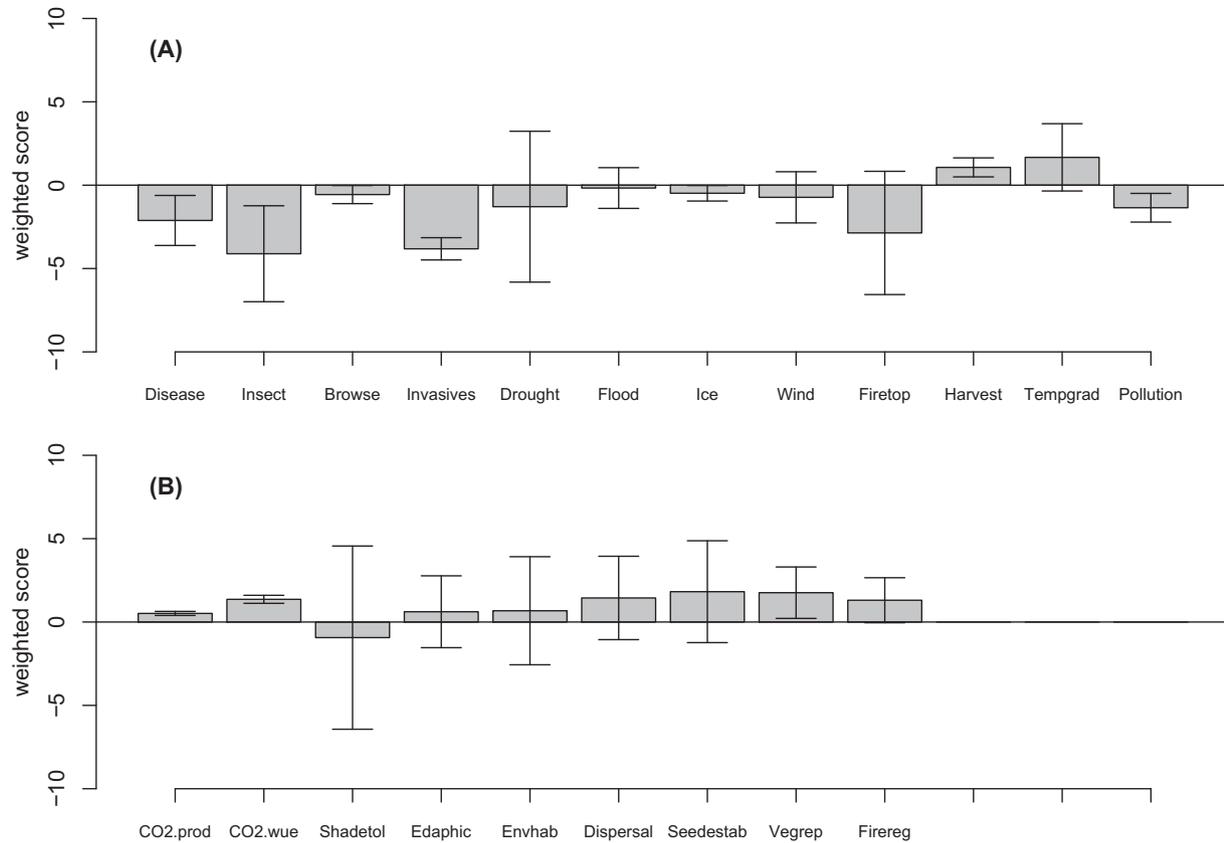


Fig. 3. Mean and SD of biological (A) and disturbance (B) scores across the each of the 21 characteristics. The scores reflected here were based on the literature score, the uncertainty around that score and the potential future relevance of the factor. The maximum (or minimum) value possible was +12, with a literature score of +3, an uncertainty score of one and a future relevance score of four.

the habitat models, its capacity to withstand change and exploit opportunities creates the potential to counterbalance the habitat shifts. It may even do quite well under climate change, especially in places where sufficient moisture remains.

3.2. GCM emissions variability

The differences between high and low-emission projected changes in species habitat reflected both species-specific and regional variability (Fig. 5, emissions variability). The green portions of these maps indicate areas of very low variability in emissions, where there is full agreement between the A1fi emissions (harsh) and B1 emissions (mildest) scenarios. Many species, however, show large spatial variation, with high emissions variability especially in the northern zones of their distribution where the A1fi scenarios project substantially warmer temperatures than B1 scenarios (Fig. 5). Because of the large proportion of low variability (“green” areas on the maps), the mean values were low at 0.31 (SD = 0.17), within a broad range of 0.02–0.78 across the 134 tree species (Appendix B). Where there is consistency across the high and low emissions (i.e., low ratios), there is greater confidence as to how a species habitat may change. For example, *Abies balsamea* is projected to decline by 86% in habitat across its eastern United States distribution, and the various GCM models are very consistent in their projections (mean ratio of 0.11), with only a few pixels in New York showing marked divergence (Fig. 5D). On the other hand, *Prunus serotina*, while showing similarity across much of its distribution (mean ratio = 0.35), has some areas where the difference between high and low emissions was more than twice that of the projected change in the species IV under

the averaged high-emissions model (Fig. 5B). For example, *Prunus serotina* in northern Wisconsin the mean ratio = 1.2, while in northwestern Pennsylvania the mean ratio = 0.6. Next, *Prunus serotina* and many other species, most of the widest disparity between emissions scenarios occurs at the margins of the species distribution, reflecting the differences between the two CO₂ emissions trajectories. For species such as *Q. falcata*, however, differences occur not only at the margins but also within the core of the species distribution (Fig. 5A).

3.3. Novel climates

We found that on average under HADhi, only 38% (SD = 28%) of all the species' potential future habitats occur within climates (temperature and precipitation regimes) that they currently occupy in the eastern United States. Again, the high standard deviation reflects the vast species-specific variability, as it ranged from zero for several uncommon, southern species to 95% for *Tsuga canadensis* (Appendix B). For *Acer rubrum*, over 61% of its projected future area-weighted IV occurs in the same climate clusters that it now occupies (Fig. 5C). In contrast, *Q. falcata* has just 33% of its future IV in common current climates clusters and only an additional 11% in clusters with current eastern United States climate analogs (Fig. 5A). These low percentages for *Q. falcata* reflect that the species remains most abundant in the southern portion of the eastern United States, where the expansive zone of novel climate occurs under HADhi and corresponds to climates that are hotter and drier than those experienced today in the eastern United States. In contrast, the novel climate factor is less extreme for species having

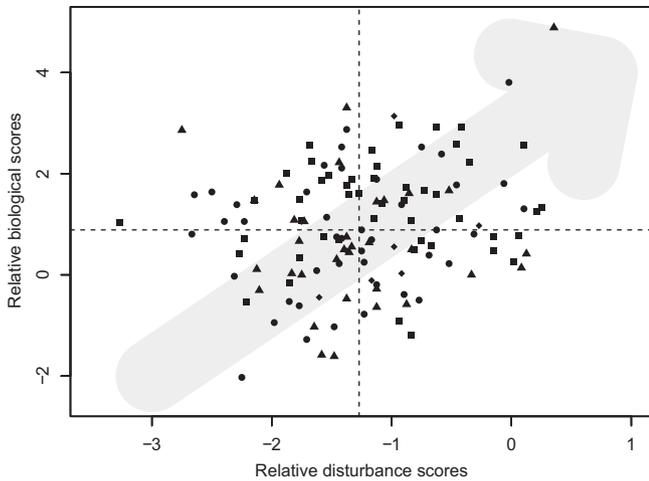


Fig. 4. Disturbance and biological ModFac scores across all 134 tree species. As species move towards upper right quadrant, both factors indicate greater adaptability potential. Dashed lines represent median scores for each factor. Species are classified by regeneration functional group; squares = persistent guild, circles = opportunistic guild, triangles = pioneer guild, diamonds = unclassified.

broad distributions and a greater proportion of their IV in the northern portion of the country (e.g., *Prunus serotina* = 58%).

3.4. Long-distance extrapolations

Across all species, the mean distance from the species' current range to the potential future boundary ca. 2100 was 328 km under

HADhi, but the mean proportion of potential future habitat that is within 200 km of the species' present range boundary was 0.79 (SD = 0.24). This factor allows for a quick assessment of models where a substantial amount of the potential future habitat was far beyond the species' current range. For *Q. falcata* (which represents a species near the mean, with a distance of 386 km and a proportion of 0.77, Appendix B), we see that much of northern New England lies far beyond its current range so it cannot be considered likely for future occupancy without assisted migration (Fig. 5A). In terms of regional filtering and assessments of potential assisted migration, it may be useful to calculate the minimum distance between the species' current range boundary and particular areas of interest.

3.5. Results across species

Each of the five factors within the ModFacs framework contains a wealth of information and, in many cases, can be used to identify specific characteristics that may inhibit or facilitate potential responses to climate change (e.g., a species with limited competitiveness for regeneration may have more difficulty establishing in newly available habitat). However, a cumulative picture of all five scores along with the results from the habitat model provides the best assessment of a species' vulnerability to climate change (Fig. 6, Appendix B). The biological and disturbance factors provide an independent source of information for each species, suggesting additional pathways (beyond the habitat models) along which a species may respond to climate change. The total area contained within the star graphs of the ModFacs based on the scaled five factors (Fig. 6) is weakly and negatively associated with projected changes in habitat under HADhi (Spearman correlation = -0.3, $p \geq 0.001$). This correlation suggests that many species projected

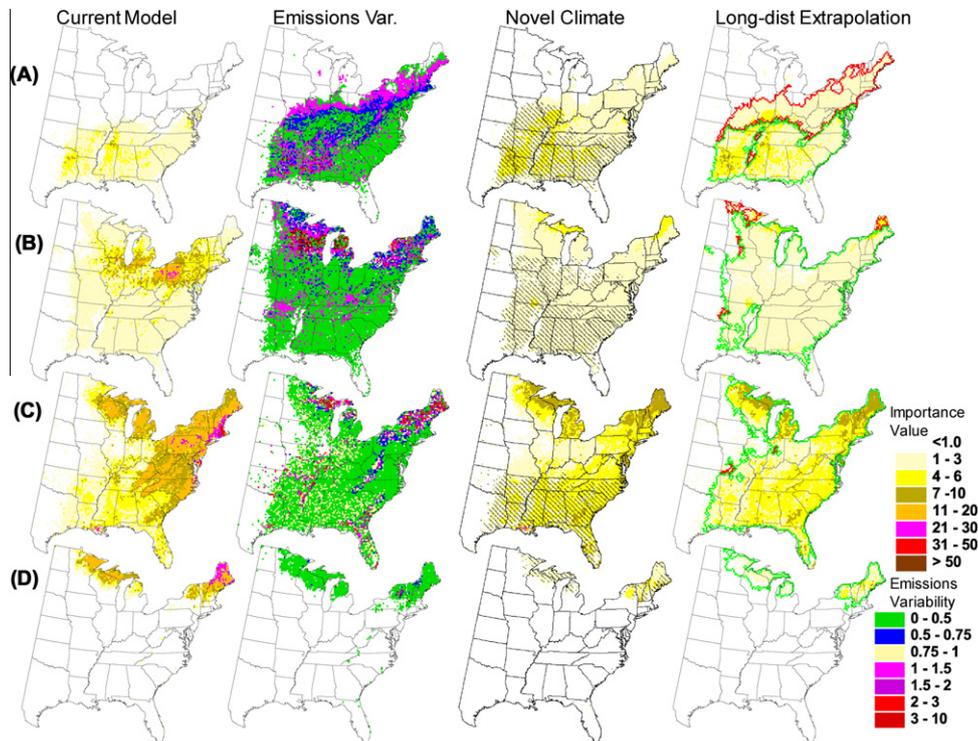


Fig. 5. Maps depicting the species current modeled distribution, emissions variability, novel climates, and long-distance extrapolations for (A) *Q. falcata*, (B) *Prunus serotina*, (C) *Acer rubrum*, and (D) *Abies balsamea*. Importance values (metric of abundance) ranging from 0 to 100 are provided on all maps. For emissions variability (range 0–10), we plot the ratio of variation between emissions scenarios by change in habitat under high emissions, as values get larger, greater variability exists among models than for projected habitat change under high emissions. For novel climate, HADhi IV is in red with stippling reflecting areas of novel climate for that species. For long-distance extrapolations, the green is the current species range boundary and red is the potential future boundary under HADhi, thus showing the disparity between current and future range boundary.

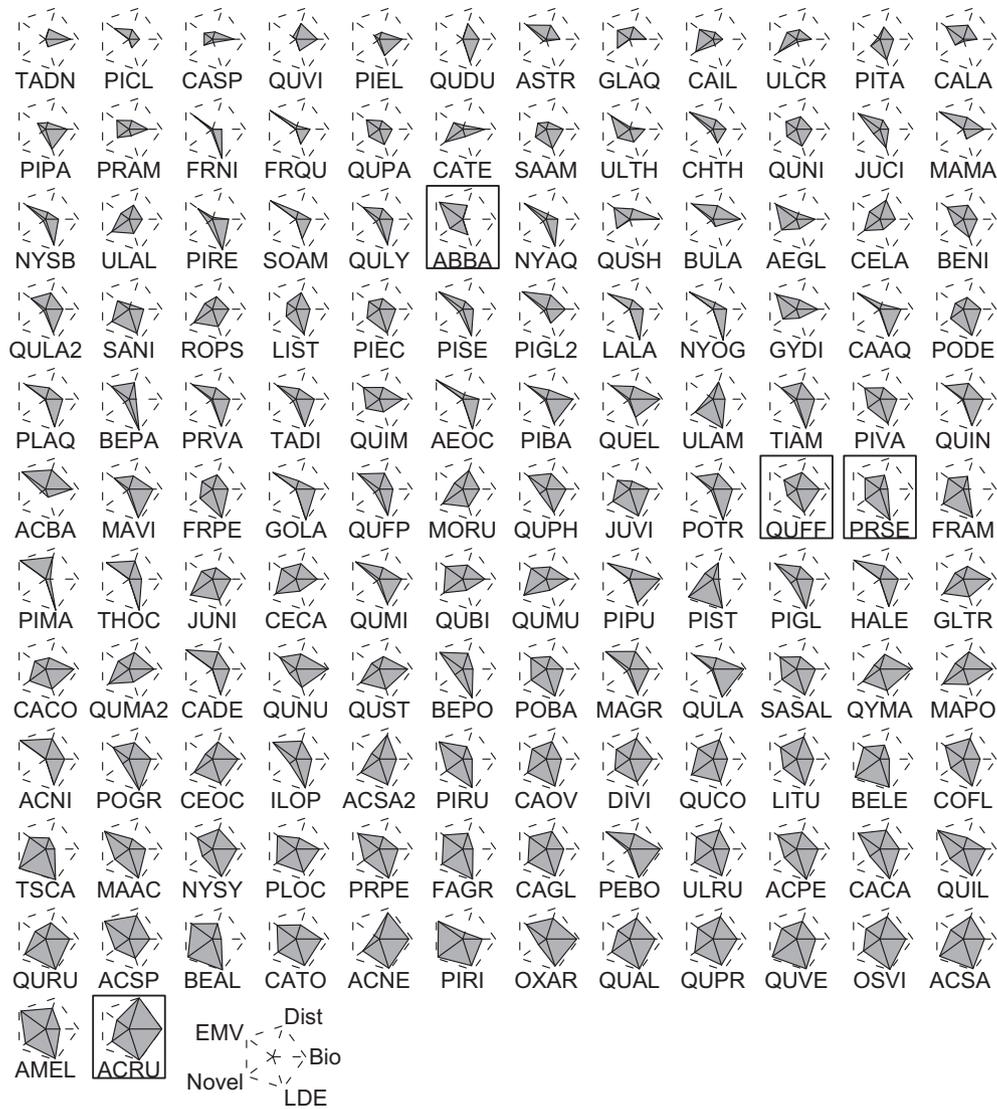


Fig. 6. Combination of the scaled five modification factor (ModFacs) metrics plotted on a five-sided star graph with the outer boundary of each equal to a score of three. The five metrics include the disturbance factor (Dist), biological factor (Bio), long distance extrapolation factor (LDE), novel climates factor (Novel), and emissions variability factor (EMV). The filled interior represents the species-specific score for each factor. The species were sorted based on the total occupied area within the star. Focal species, discussed throughout text, include QUFF (*Quercus facata*), PRSE (*Prunus serotina*), ACRU (*Acer rubrum*), and ABBA (*Abies balsamea*).

to have large increases in habitat may not be able to occupy them. On the other hand, many species with projected declines in suitable habitat may have a relatively higher capacity to tolerate climate-induced changes. However, there is marked variation around this weak association, and many species, such as *Abies balsamea* and *Fraxinus nigra*, show serious projected declines in both the habitat models and ModFacs assessments.

4. Discussion

The approach taken within the ModFac framework demonstrates the need to go beyond basic SDM results as we build a comprehensive perspective of how tree species may respond to climate change. The use of SDM's allows us to consider the potential changes in habitat across a diverse array of tree species within the eastern United States. To make these results relevant to forest management and policy, we must not only report the results with careful consideration of the assumptions but also strive to present the information in ways that facilitates the communication of uncertainty. Unfortunately, a complete reporting of results can make planning for climate change seem daunting and amorphous.

Therefore, we base this synthesis on five main directions to complement the habitat models. Once an overall assessment is prepared within a region, it will be necessary to further investigate specific features of the priority species, and develop an adaptive management strategy to address the uncertainty inherent in climate change projections.

4.1. Biological and disturbance factors

The biological and disturbance factors add a new dimension to the modeling strategy of SDMs. They bring to light the importance of species' traits and filters in shaping species communities (Webb et al., 2010). The nine biological characteristics, averaged across all species, suggest an overall positive influence on the capacity to adapt to climate change impacts (Appendix B). Of course, individual species have very different life-history strategies that are likely to be enhanced or diminished in the face of climate change. For example, many species are adapted so that vegetative reproduction, including regeneration after fire, can occur readily; these species may be available to migrate to new northerly or upslope sites in a changing climate (Kellomaki and Vaisanen, 1995; Middleton,

2009). They may be able to outcompete less-adapted species to take advantage of new unoccupied habitat opening on particular sites. In many cases, biological traits may be more positive or negative based on the local conditions and this regional variability in the scores is not reflected in our range-wide analysis. For example, many seeds may have limited dispersal capacity overall, but regional patterns of dispersing agents may compensate for such negative scores. A good example of this situation occurs where the white-tailed deer has been shown to be an effective long-distance disperser for plants including on occasion woody species (e.g., *Betula lenta*) in New York, USA (Myers et al., 2004).

The one characteristic that shows the greatest variability across species is shade tolerance and it is likely to be a key variable in how species will respond to climate change. The ability of trees in the understory to tolerate shade (or not) can be critically important as new suitable sites emerge for some species and become less suitable for others (Valladares and Niinemets, 2008). A prime example of the influence of shifting disturbance regimes is with the dramatic increases in mesophytic species in the eastern forests (Nowacki and Abrams, 2008). The trend in shifting disturbances has been to the detriment of oaks; one factor besides fire that appears to drive these processes has been the disparity in light availability (Iverson et al., 2008a). The ability of *Acer rubrum* to grow under shade and take advantage of multiple environmental conditions is reflected in its growing dominance across the eastern United States, and these characteristics also favor its future position under climate change scenarios despite projected losses in suitable habitat.

The disturbance factors, unlike the biological factors, had a negative average score (−1.2). A negative mean value was expected as many of the characteristics, such as disease and insect pests, have negative impacts across all species. Unfortunately, most, if not all, of the 12 disturbance characteristics, including disease, insect pests, invasive plants, drought, flood, ice (in certain locations), fire, temperature gradients, and pollution, are expected to increase and cause significant biological changes under most climate change scenarios (Dale et al., 2001; Westerling, 2006; Hellmann et al., 2008; Dukes et al., 2009; van Mantgem et al., 2009; Wittig et al., 2009; Kleinbauer et al., 2010). Many of these characteristics have the capacity to supersede the relevance of any climate change projections, as they can act on a much reduced timeframe. For example, exotic pests such as the emerald ash borer (*Agrilus planipennis*) and hemlock woolly adelgid (*Adelges tsugae*) are currently proving that their disruptive capacity will supplant any climate-induced shifts in habitat for these tree species. While these threats are clearly on the minds of those developing management options under climate change, it does help to have this broad suite of information at hand. In addition, by looking across all characteristics, we can identify those species that would appear to have the greatest challenges adapting to climate change. In fact, the top 10 species with the most negative disturbance profile (*Abies balsamea*, *Picea mariana*, *Fraxinus americana*, *Pinus strobus*, *Betula papyrifera*, *Prunus serotina*, *Juglans cinerea*, *Betula alleghaniensis*, *T. canadensis*, and *Fraxinus nigra*) are all projected to decline in habitat (Appendix B). This projection indicates that these species are confronted not only with shifting suitable habitat, but also with negative responses to many critical disturbance threats. *Fraxinus nigra* is the only species to rank in the bottom 10 for both biological and disturbance factors; it has seven individual characteristics that are distinctly negative (i.e., literature score is at least −2 and future relevance is at least 3). In addition to its vulnerability to pests such as the emerald ash borer, this species is sensitive to drought and fire. Collectively, these factors likely will substantially reduce the species' importance in the future. On the positive side, both *Acer rubrum* and *Acer negundo* rank in the top 10 for both biological and

disturbance scores, and thus should be more adaptable to changing conditions going forward.

This assessment provides a broad-scale perspective of characteristics that likely are important in allowing species to adapt to climate change. However, it is important to stress that the scores assigned to the biological and disturbance characteristics may change with location specific knowledge or improved species information, including genetic information, to arrive at a regionally tailored assessment (Fig. 1). Importantly, many of the factors not only will show regional variation but also can be greatly influenced by local managers, and the ModFac assessment allows a semi-quantified evaluation of these management potentials. Oak regeneration provides an example in the eastern United States. A broadly distributed species such as *Quercus alba* has relatively high biological and disturbance scores across the 21 characteristics. Within many portions of its range, however, regeneration is a major limiting characteristic. The root cause of this has been the focus of much research (Hutchinson et al., 2008; Kabrick et al., 2008). In certain regions, the suppression of fire and changes in management regimes can be attributed to some of the compositional changes observed in eastern forests (Hutchinson et al., 2008). Intensive silvicultural treatments such as harvesting (Kabrick et al., 2008) or a combination of fire and thinning (Brose et al., 1999), can counteract oaks' shade intolerance by creating favorable light conditions (Iverson et al., 2008a).

Managers will play an important role in adaptation to climate change. In fact, to enhance tree species' adaptability, managers can manipulate nine of the 21 characteristics, including: shade tolerance, dispersal, fire and seedling regeneration, seedling establishment, habitat specificity, fire topkill, browsing, and harvesting. By using the ModFacs framework that incorporated broad-scale climate change habitat models with some qualification of relevant life history characteristics, we anticipate that managers will find it easier to meet the challenges of managing with uncertainty in species' response. Instead of providing only a top down point of view of how species' habitat may respond to climate change (i.e., broad-scale distributions with change driven by global shifts in climate) and forcing managers to work outside their domain of balancing multiple management dimensions, we can open a new channel by integrating a climate change perspective into contemporary management decisions.

4.2. Model synthesis factors

With the GCM emissions variability, novel climate, and long-distance extrapolation factors, we again focus on the habitat models and have shown how additional information can be gleaned from the multiple projections of habitat change. These projections attempt to bring critical information to the forefront of our multi-stage modeling approach (Iverson et al., 2011) by highlighting the implications of key assumptions inherent in the SDM habitat models. In addition, the value of each three ModFacs not only resides at the distribution level but also can be partitioned at regional extents to provide more management relevant summaries of regional patterns.

4.2.1. GCM emissions variability

The reality that the climate is changing has become much clearer, but the ability to project exactly what the climate and the resulting impacts might look like will remain a moving target as the climate models project into novel space. Therefore, we must develop ways to use multiple projections of how a species habitat may respond. Though a recent paper states that the uncertainty associated with the various GCMs and emission scenarios precludes the use of SDMs for policy planning (Real et al., 2010), we agree with Wiens et al. (2009) that doing nothing until uncertainty

in the climate modeling is sufficiently reduced is not an option. Real et al. (2010) made their conclusions based on one amphibian, one reptile, one bird, and one mammal, two GCMs, and two emission scenarios over mountainous terrain in a portion of Spain for their analysis; this limited evaluation also limits broad generalizations. In our analysis of variability associated with GCM and emissions, many tree species show little variation between the harshest and the mildest scenario, and many other species had high uncertainty only for a small portion of their range. Understanding where areas of high and low variation within a species range are critical as these results are summarized into specific management regions. Because the ratio was calculated at each cell and summarized across the species distribution, the low mean value of emissions variability could be an artifact of these severely skewed distributions. However, the mean of the third quartile across species was only 0.51, suggesting that for most species, 75% of the cells are less than half as variable (differences between high and low emissions) as the projected habitat change under the high emissions scenarios. In many cases, the largest differences occur at the northern-range boundaries where the consequences of a high emissions trajectory become clear.

Of course, it remains important that species models are built with multiple GCM and emissions scenarios, but this level of detail must be balanced with practical reporting. This is the stage where nested and interactive tools for evaluating climate change impacts are important. With the 134 tree species we studied, an initial sorting of emissions variability by species can highlight which species have agreement or not across models. From here, it will be important that the individual maps of different climate change scenarios are available (see <http://www.nrs.fs.fed.us/atlas/>) for more detailed examination of species' potential changes.

4.2.2. Novel climates

Our analysis of novel climates shows that these will appear throughout the southern portion of our study area, especially under the HADhi scenario, where temperatures would be substantially higher. This pattern is in contrast to the mildest scenario we evaluated, that of PCMlo, which showed very little novel climate by 2100. The PCMlo scenarios suggest that if humans can reduce emissions to the B1 level, the biota of the region may require less adaptation to new climate regimes. Though this phenomenon of potential future novel climates provides an additional level of uncertainty with respect to species' capacity to adapt under climate change, a recent Australian study reported that, of 26 plant species introduced from other continents, 20 were thriving in novel climates (Gallagher et al., 2010). Thus, there is some probability that the species currently occupying zones that will have novel climates may be able to adapt to those new conditions in situations of limited competition from species more tolerant of those new conditions. The Australian study however also establishes an additional danger of climate change, that being the concomitant influx and flourishing of invasive plants (Hellmann et al., 2008; Dale et al., 2009; Dukes et al., 2009; Hartley et al., 2010). Also important is the physiological impacts on plant establishment and growth if temperatures increase greatly (as projected under HADhi) while precipitation changes little, resulting in more evaporative loss, and leading to greater physiological stress on the biota (Allen et al., 2010). The potential shift in water balance in the southern portion of the eastern United States is expressed under high-emission projections with the process model MAPSS, which includes potential changes in water use efficiency (Neilson, 1995). Thus there is potential for trees in some regions to be subjected to new levels of stress under climate change, even to the point of reducing or eliminating the potential to sustain forests.

How then can we utilize the information of novel climate ModFacs for species? First, in areas where the species continues to occupy climates that are similar to its current distribution, we can have greater confidence that the species will likely be able to locate and live in suitable habitat. Secondly, as reported for Hadhi, which is more closely aligned with current trends in carbon emissions (Canadell et al., 2007), and especially in the south, we can determine the amount of the species distribution contained in locations that may be climatically unique by the end of the century. We can then evaluate each species' biological and disturbance characteristics to identify species that may have greater adaptive capacity. Of course, genetic variability in the species' populations is a key variable in whether the species will be able to adapt to new climate conditions (Rehfeldt et al., 1999; Lu et al., 2003). The result that climatic clusters will likely move independently of species, indicates a clear need to understand genetic variation of species. By gaining a firmer understanding of genetic heterogeneity of populations, it might become possible for a more mechanistic quantification of how species can adapt to new climate conditions.

4.2.3. Long-distance extrapolations

One key criticism of SDMs for forecasting climate change impacts has been the lack of accounting for dispersal. The inherent assumption of SDM's is unlimited dispersal. Of course, this is beyond the domain of most empirical models, and their inference should merely focus how suitable habitat may change, rather than on a species' ability to colonize a new location. Others using SDMs have addressed this challenge by presenting results with and without dispersal (Lawler et al., 2006). Allowing the models to predict suitable habitat without limiting distance provides a clearer picture of how habitat for a species can change, yet we must take into account the assumption of unlimited dispersal when considering the results. To do so, we applied a limiting dispersal buffer to quantify the amount of potential future habitat availability. This approach follows Lawler et al. (2010) where dispersal was separated into several ordinal categories. In the assessment of long-distance extrapolations of 134 tree species models, most species have a large proportion of their potential future habitat within the 200-km buffer (mean = 0.78) of their current distribution. However, for species with a greater proportion of their summed IV beyond 200-km from their current distribution boundary, an interpreter is required to add an additional level of scrutiny. If the model reliability (see Iverson et al., 2008c for an explanation of how model reliability was calculated) was low, or even medium, we would be very cautious in accepting the long-distance movement of suitable habitat. A prime example of this situation occurs with *Ulmus crassifolia*, where the species model reliability is low and the long-distance extrapolation value (proportion of a species' projected range within 200-km of current range) is among the lowest of all species. This pattern strongly suggests poor model fit and likely over-predicts the species' potential future habitat. Even with high model reliability and confidence in the current model output, colonization of potential future habitat can still be unlikely. Based on our earlier and ongoing work with the SHIFT model, e.g. (Iverson et al., 2004b, 2011), there is only a very small likelihood of tree species' long-distance migration via non-human assisted mechanisms. Thus, these species could be considered as candidates for assisted migration if it is a viable management option upon evaluation of other ModFacs and species-specific criteria.

5. Conclusions

We have presented a framework to assess species for their capacity to adapt to changing conditions, especially those

associated with climate change. These modification factors greatly expand the applicability of our earlier work on modeling potential suitable habitats for tree species, by incorporating species traits and model nuances into the considerations and interpretations needed to plan for climate change. The individual and collective ModFacs can also be used independently in other applications to compare among species or groups of species.

We believe that researchers, managers, and others agencies can benefit from the comprehensive ModFacs evaluation framework when it is viewed in conjunction with the models of potential changes in suitable habitat. This multi-criteria modeling approach reflects the need for more information than SDMs can provide on their own as we consider climate change impacts (Franklin, 2010). From the results presented here, lists of potential “decreasers” or “increasers” for a particular region can be evaluated with locally filtered modification factors to arrive at more logical and inclusive lists of potential species changes. By providing broad-scale results that can incorporate local knowledge, our study creates a strong link to silvicultural decisions via an adaptive management pathway to sustain our forest resources in a changing climate.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.06.047.

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