Landscape Ecol (2016) 31:2187–2204
DOI 10.1007/s10980-016-0369-7

A multistage decision support framework to guide tree species management under climate change via habitat suitability and colonization models, and a knowledge-based scoring system

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Received: 4 June 2015 / Accepted: 16 March 2016 / Published online: 6 April 2016

Abstract

Context No single model can capture the complex species range dynamics under changing climates—hence the need for a combination approach that addresses management concerns.

Objective A multistage approach is illustrated to manage forested landscapes under climate change. We combine a tree species habitat model—DISTRIB II, a species colonization model—SHIFT, and knowledge-based scoring system—MODFACs, to illustrate a decision support framework.

Methods Using shortleaf pine (*Pinus echinata*) and sugar maple (*Acer saccharum*) as examples, we project suitable habitats under two future climate change scenarios (harsh, Hadley RCP8.5 and mild CCSM RCP4.5 at ~2100) at a resolution of 10 km and assess the colonization likelihood of the projected suitable habitats at a 1 km resolution; and score biological and disturbance factors for interpreting modeled outcomes.

Results Shortleaf pine shows increased habitat northward by 2100, especially under the harsh scenario of climate change, and with higher possibility of natural migration confined to a narrow region close to the current species range boundary. Sugar maple shows decreased habitat and has negligible possibility of migration within the US due to a large portion of its range being north of the US border. Combination of suitable habitats with colonization likelihoods also allows for identification of potential locations appropriate for assisted migration, should that be deemed feasible.

Conclusion The combination of these multiple components using diverse approaches leads to tools and products that may help managers make management decisions in the face of a changing climate.

Keywords Decision support system · Tree habitat suitability model · Tree species migration model · Tree species distribution model · Forest management · Climate change

Introduction

There is increasing need to develop models and decision support systems to facilitate forest management in the era of rapid climate change. Forest

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Electronic supplementary material The online version of this article (doi:10.1007/s10980-016-0369-7) contains supplementary material, which is available to authorized users.

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managers are facing mandates by state and federal governments to adaptively manage forested landscapes for resilience under current and future threats, taking into account disturbances augmented from climate change. Building on our previous experience in developing models for predicting future suitable habitats under climate change (e.g., Iverson et al. 2008; Iverson et al. 2011; Matthews et al. 2011; Prasad et al. 2013), we provide a newer multistage combination approach that we illustrate in this paper.

Species distribution models (SDMs—also called habitat distribution models, niche-based models) have been used extensively to unravel the effects of climate and other abiotic factors on the distribution of tree species habitats. It comes with assets and liabilities that need to be adequately addressed in order to effectively fulfill its role (Araújo and Peterson 2012; Peterson and Soberón 2012). SDMs are quite suitable for macroscale approaches where finer scale species interactions are modeled as aggregate properties of regression-based models using relevant predictors (Diniz-Filho and Bini 2008; Kühn et al. 2008; McGill 2010; Bradter et al. 2013; Svenning et al. 2014; Belmaker et al. 2015; Jackson and Fahrig 2015). Therefore in a macroscale study involving tree species ranges for large regions like the eastern United States, an SDM approach that includes variation in abundance via relevant environmental correlates is quite useful for exploring broad-scale dynamics of habitat ranges (Morin and Thuiller 2009; Dormann et al. 2012; Franklin 2013; Merow et al. 2014).

SDMs can be improved to provide more comprehensive, yet robust predictions—for example, using relative abundance rather than presence/absence, and including edaphic and topographic variables in addition to climate to address some of the limitations (Iverson et al. 2011, Warren 2012, Rehfeldt et al. 2015). Using robust decision-tree based ensemble models that take into account nonlinearity and interactions also helps match the large-scale processes with the prediction (Elith et al. 2010; Guisan et al. 2013). This approach has also been used to project habitats under future climates with the reasonable assumption that the bias-variance tradeoffs are better addressed by these data- driven ensemble models that use various data partitioning techniques to limit variance (Lawler et al. 2006; Randin et al. 2006; Hastie et al. 2009).

However, when SDMs are used in isolation, some limitations of a purely statistical approach become evident. We are forced to accept that the suitable habitats predicted by SDMs are all colonizable under natural dispersal mechanisms, which obviously is not true. Combining SDMs with colonization models at a finer scale addresses this key limitation of the SDMs—not all suitable habitats depicted by the SDMs can be colonized. Modeling colonization can take several forms—both phenomenological and mechanistic—the former using various fat-tailed probability density distributions and the latter relying on parameterization of species-based seed dispersal values based on sparse empirical data (Clark et al. 1999; Nathan et al. 2008). A simpler but effective way is to simulate long distance dispersals under current land-use and abundance patterns is achieved by using calibration constants that can match historical migration rates across fully forested landscapes. This approach calculates colonization likelihoods (CLs) based on habitat suitability and strength of source abundance.

Once CLs are handled, comes the more difficult task—how much of the colonizable habitats are likely to become established. Answers to this question translate to finer scale queries that local managers need to rely on, such as their experience, the land-use history, and other studies. Fine-scale studies on species interactions and micro-climatic and edaphic assessments, possibly through provenance studies or process-based models, could be helpful in assessing establishment probabilities, but are beyond the scope of the present paper. However, addressing some limitations of CLs can be addressed via non-model approaches at a regional and local level, based on relevant literature and local expertise. Some of the biological and disturbance factors which are difficult for models to handle can be accessed via a knowledge-based scoring system that can modify modeled outcomes.

The purpose of our current effort is to provide forest managers, decision makers and researchers an improved toolbox to aid in management decisions under climate change. Many managers are especially challenged by the need to manage landscapes incorporating climate change as mandated by governments because ignoring future risks is no longer a viable option (Wiens et al. 2009). Our three pronged approach consists of combining SDM, simulated colonization, and knowledge-based scoring system in stages and assembling them into a decision support system. It attempts to achieve a favorable tradeoff between generality, realism and precision (Levins 1966, 1993; Orzack and Sober 1993) by combining macro-scale model-based approaches with a literature-based scoring system.

Methods

The multi-stage combination approach

The decision support system is achieved in multiple stages, by combining: (a) a statistical ensemble model (DISTRIB II); (b) a spatially explicit simulation model (SHIFT), and (c) a knowledge-based scoring system (MODFACs). We briefly describe our newer SDM (DISTRIB II), SHIFT and MODFACs and then assemble figures and table based on their integration that is then used as a decision support tool. We have used this tool in the development of several vulnerability assessments across the eastern United States, as coordinated by the Northern Institute of Applied Climate Science (NIACS) (e.g., Brandt et al. 2014; Janowiak et al. 2014; Butler et al. 2015).

Previously, an older version of the habitat suitability model DISTRIB (Iverson et al. 2008) was applied to the tree species in the eastern United States. In this study, we apply a newer version, DISTRIB II, an enhanced version of the CL simulation model SHIFT (Prasad et al. 2013), and a knowledge-based scoring approach MODFACs (Matthews et al. 2011), to assess current and potential future range dynamics of 134 tree species in the eastern United States. We illustrate this approach using shortleaf pine (*Pinus echinata*) and sugar maple (*Acer saccharum*)—two common, commercially important species; the former with its range within, and the latter mostly within the eastern United States, but also extending into Canada.

DISTRIB II model

The earlier habitat suitability model has been considerably revised to provide a more robust estimate of suitable habitats using newer Forest Inventory and Analysis (FIA) data and newer results from general circulation models (GCM) models. Like the earlier version, DISTRIB II is a statistical, decision-tree based ensemble model that uses RandomForest (RF) to predict current and future habitats under several climate scenarios (Prasad et al. 2006) for the eastern United States, but now at a finer resolution of 10 km (compared to the earlier 20 km). The response variable is the importance value (IV) of each tree species, which is a relativized measure of abundance, calculated from the annualized FIA data (Woudenberg et al. 2010) as follows for each species X in a FIA plot:

$$IV(x) = \frac{50 \times BA(x)}{\sum_{i=1}^{N} BA(i)} + \frac{50 \times NS(x)}{\sum_{i=1}^{N} NS(i)}$$

BA is basal area, NS is number of stems (summed for overstory and understory trees) and N is the total number of species in the plot. If $0 < \text{IV} < 1$, it was assigned to 1 since rounding would have falsely turned species-present cells to species-absent cells. For each species, average IV per 10 km cells was calculated by aggregating the FIA annualized plot-level information.

Based on our previous experience with ensemble models, we screened the predictor variables that explained most of the variation in the model and chose a parsimonious set of 12 variables for our predictors (Table 1)—those we determined to be the most relevant for explaining the variation in abundance at a resolution of 10 km, and were least affected by collinearity, although we deemed the ecological importance of the variable to be of utmost importance.

The selected climatic variables address two key temperature-based constraints to tree species ranges—growing season temperature (May–September) and the temperature of the coldest month (January). An aridity index which is the ratio of May–September precipitation to the potential evapotranspiration index (Thornthwaite and Mather 1957), along with growing season precipitation, adequately captures the moisture constraints (Bucklin et al. 2015; Pederson et al. 2015). With parsimony in mind, we limited the soil variables (Peters et al. 2013a) to six after a model-based screening process that eliminated others that were less explanatory (using RandomForest's R^2) (Table 1). We retained two elevation-based variables (maximum elevation and elevation standard deviation) because these variables are useful in distinguishing between species that prefer low elevation and habitats with rugged terrain.

The current climate data were obtained for the period 1981–2010 from the PRISM climate group (PRISM; Daly et al. 2008). For future climate, we

Table 1 The predictors used in the DISTRIB II model with sources

Climate[a]	
TJAN	Mean January temperature (°C)
TMAYSEP	Mean May–September temperature (°C)
PMAYSEP	May–September precipitation (mm)
GSAI	Growing season aridity index (May–September)
Elevation[b]	
ELV_MAX	Maximum elevation (m)
ELV_SD	Elevation standard deviation
Soil[c]	
CLAY	Percent clay (<0.002 mm)
OM	Organic matter content (% by weight)
PH	Soil pH
SIEVE10	Percent passing sieve no. 10 (coarse)
SIEVE200	Percent passing sieve no. 200 (fine)
SPROD[d]	Soil productivity index

[a] Data for the period 1981–2010 from (PRISM Climate Group), GCM data from NEX-DCP30 (Thrasher et al. 2013)

[b] From the NASA's Shuttle Radar Topography Mission provided at a resolution of 3″ (Guth 2006). We calculated the maximum value and standard deviation at 10 and 20 km^2 grids

[c] From Natural Resource Conservation Service's County Soil Survey Geographic (SSURGO) database (NRCS 2009). Data was processed by Peters et al. (2013a) and aggregated to 10 and 20 km^2 grids

[d] From Schaetzl et al. (2012). Mean productivity at 10 and 20 km^2 were calculated from area-weighted percentages of 240 m^2 values

chose two newer GCMs: Community Climate Systems Model (CCSM4—Gent et al. 2011) and Hadley Global Environment Model (HAD, Jones et al. 2011). Two representative concentration pathways (RCP 4.5 and 8.5) representing greenhouse gas emissions were used to evaluate a range, corresponding to the estimated lower and upper potential changes in climate (Meinshausen et al. 2011). For comparison purposes, we used HAD RCP 8.5 as the "harsh" scenario because it depicted the largest increase in temperature, while CCSM4 RCP 4.5 depicted the least increase in temperature and was chosen as the "mild" scenario; these extremes were used to illustrate the utility of greenhouse mitigation efforts. Future climate variables were included in the habitat models as delta adjusted observations, where 30-year monthly normals (2070–2099) were subtracted from the GCM projections for 1981–2010 and added to PRISM values (Monahan et al. 2013).

In order to ensure good model fit, we screened outliers by eliminating cells having zero or only a single FIA plot with mean IV beyond the interquartile range for that species. This ensured that the Random Forest model was robust and relevant to the FIA data. We used this FIA-plot-present model to impute at 10 km over the entire eastern United States for prediction.

We demonstrate the approach by using one species with model outputs showing an increase in its range within the United States (shortleaf pine) and another which decreases its range within the US and extends into Canada (sugar maple) to illustrate the diverse aspects of future range dynamics. Both species have good model reliability with shortleaf pine having an R^2 of 0.45 and True Skill Statistics (TSS) of 0.87 (Allouche et al. 2006); respective values for sugar maple were 0.44 and 0.78. Shortleaf pine represents the distribution of many tree species which occupy the south, south-western (including the Ozarks), and Appalachian corridors within the eastern United States, with no suitable habitat extending as far north as Canada so that we could adequately gauge the CL. It also represents the loblolly/shortleaf pine forest type and is a major component within the oak-pine forest type. Sugar maple is a very important commercial species that is valued for many ecosystem services including timber and maple syrup. As a widespread and tolerant species, it is a major component of several forest types including maple-beech-birch and northern hardwoods. It is, however, modeled to lose suitable habitat especially in the southern portions of its range.

SHIFT model

The SHIFT model runs at a 1 km resolution and simulates dispersal via a fat-tailed inverse power function and calculates future CLs based on historical tree migration rates and current fragmented landscapes (Schwartz 1992; Iverson et al. 2004; Prasad et al. 2013). The two main parameters affecting the migration are the calibration constant (C) that simulates the historical migration and the generation time of the species that spans approximately 100 years (detailed in Prasad et al. 2013).

The range boundaries for the species are derived from the latest FIA annualized data which depict both increases and decreases from the original Little's range maps (Little 1971), the latter representing a generous notion of known range limits during the late 1960s. A technique based on ESRI's (2015) "delineate built-up areas" tool and the aggregated IV of FIA plots within 10 km cells was used to generate an updated estimate of the 'core' species boundary. This 'core' boundary, based on the current species distribution, was used to depict the source region across which propagules are launched in the SHIFT model.

Forested cells from within the core species boundary ("source") are modeled to contribute propagules into forested cells outside the boundary ("sink"). The source strength is a function of both the propagule production and dispersal capability across the boundary. We used the relative abundance and frequency of the species inside the current boundary to define the source strength; locations with higher species abundance and closer proximity to the boundary will create the highest colonization probabilities near the current boundary. Sinks are forests or woodlots of varying degrees of fragmentation (based on the United States Geological Survey's 2006 National Land Cover Data with at least 10 % forest at 1 km resolution) that provide possible locations for the propagules to colonize under current and future climates. The predicted suitable habitats of the DISTRIB II model provide the future (~2100) suitability of the sink habitats based on projected relative abundance.

Colonization of initially unoccupied cells was estimated as a function of recipient cell forest availability and the sum of the likelihood of each occupied cell sending a propagule to that cell. For each cell outside the current occupied boundary, the model estimates the likelihood that each unoccupied cell will become colonized over a period of 100 years (which, for shortleaf pine, amounts to four generations of mature trees producing large numbers of seeds, and three generations for sugar maple). SHIFT is a 'fat-tailed' dispersal model that allows rare long-distance dispersal events up to 500 km and assumes the release of climatic restrictions to tree growth (Prasad et al. 2013). Although 500 km is a generous window over which colonization can occur, the inverse power function makes the likelihood of colonization decay rapidly from the species front, yet will allow for rare, long-dispersal events over historical periods that can potentially seed colonizations far from the source.

Our approach uses historical information on rates of past migration events (Davis and Shaw 2001) as a guide for future potential migration. SHIFT is calibrated independently for each species through trial runs to achieve migration rates ranging from approximately <25 to >100 km per century (depending on criteria of model runs) under high forest availability (80 % cover, representing nearly fully forested conditions, which more closely approximate Holocene conditions), but with the current level of species abundance. There is uncertainty about the historical migration rates—which range from less than 10 to greater than 100 km/century—although recent molecular analyses point to the range of 10–25 km/century because of glacial refugia effects (McLachlan and Clark 2004; Yansa 2006; Svenning and Skov 2007; Cole 2010; Dobrowski 2011). We chose the entire range of <25 to >100 km/century to illustrate the sensitivity of CL to historical migration rates—although we used 50 km/century to test how this optimistic assumption is going to affect the colonization of suitable habitats.

MODFACs—knowledge-based scoring system

The main goal of MODFACs is to add to the interpretative value of DISTRIB II/SHIFT outputs and give users enhanced information that can be used for better management decisions (Matthews et al. 2011). It scores nine *biological* traits of species that may influence their population persistence and adaptation capacity under climate change, with the key characteristics including shade tolerance, edaphic specificity, environmental habitat specificity, dispersal, seedling establishment, and vegetative reproduction. Also included are twelve *disturbance* influences, many of which are expected to increase under climate change (e.g., disease, insect pests, drought, flood, wind, fire topkill, etc.). Each characteristic was scored on a −3 (highly negative) to +3 (highly positive) scheme based on literature. To arrive at an overall adaptability score for the species that could be compared across all 134 modeled tree species, the mean, rescaled (0–6) values for biological and disturbance characteristics were plotted to form two sides of a right triangle; the hypotenuse was then a combination (disturbance and biological characteristics) metric, ranging from 0 through 8.5 (Matthews et al. 2011; Iverson et al. 2012). The intention of the scoring system was to enhance the interpretation of modeled outcomes in order to make them amenable to regional and local needs, and to account for certain situations that were not captured in the models (for example, emerald ash borer killing ash trees).

The future climate outputs of DISTRIB II are then intersected with the CLs calculated by SHIFT using the optimistic migration rate of 50 km/century for the year 2100. The results from DISTRIB II, SHIFT and MODFACs were assembled to develop a flow diagram of maps as well as a table that quantifies the maps. This illustrates one way in which the decision support framework can be used by managers.

Results

Using shortleaf pine and sugar maple to demonstrate this multistage approach (Fig. 1), we first reclassified DISTRIB II and SHIFT outputs to simplify evaluation: low, medium, and high habitat quality (HQ) or CL (Fig. 2). These combinations resulted in nine HQ–CL classes which are presented in Figs. 3 and 4. To enable comparisons among climate scenarios (see later), the 12 classes were themselves simplified into three HQ–CL classes of low, medium, and high ‘success’ for species attempting to migrate from source into sink locations (Fig. 5). Figures 3 (shortleaf pine) and 4

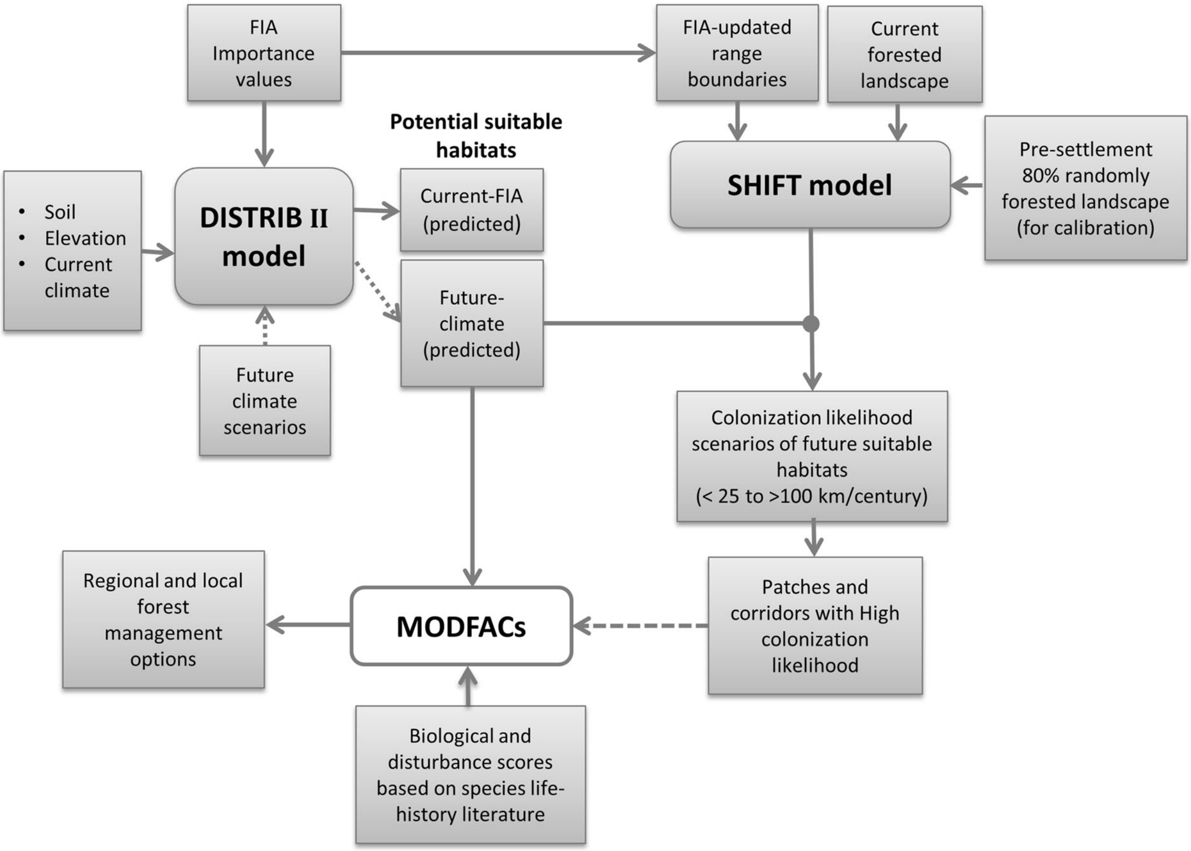

Fig. 1 A schematic depicting the flow of information in the multistage decision support system. DISTRIB II models relative abundance in the form of importance values (IV) based on the Forest Inventory Analysis (FIA) using current and future climate as well as soil and elevation variables to predict current and future suitable habitats. The SHIFT model uses a randomly generated nearly fully forested landscape to simulate historical migration rates to estimate future colonization likelihood based on current IV, the highly fragmented landscapes, and species generation times. When combined with future suitable habitats predicted by DISTRIB II, a reasonable depiction of spatially explicit corridors and patches with varying patterns of colonization likelihoods can be mapped. The MODFACs scoring system, which scores biological and disturbance factors based on species literature, is used in conjunction with outputs of DISTRIB II and optionally SHIFT, to provide a synthetic tool for managers in appraising the adaptation options for forest management in the face of climate change

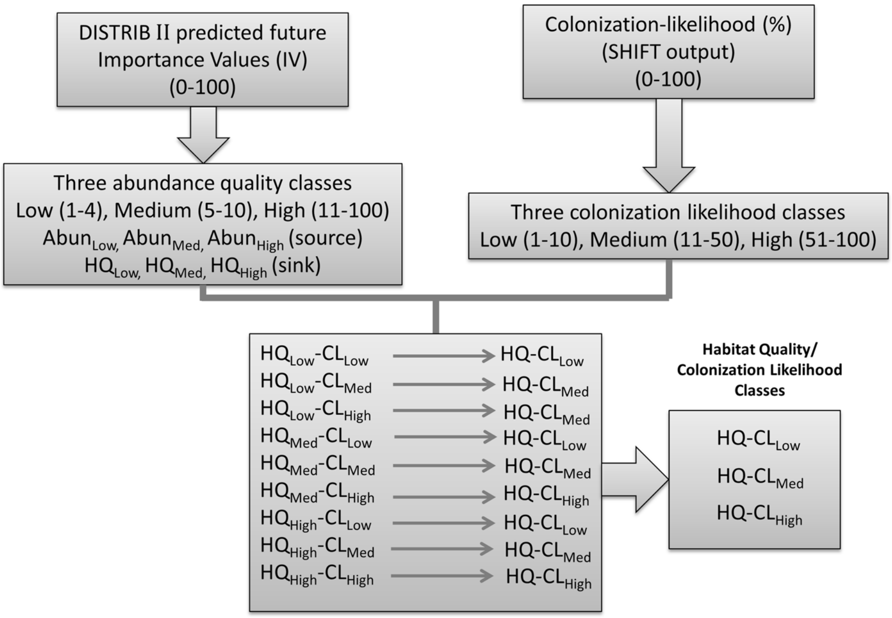

Fig. 2 The reclassification scheme used to reduce the number of classes in DISTRIB II and SHIFT to three categories—low, medium and high. The combination of habitat quality (HQ) and colonization likelihood (CL) classes results in nine HQ–CL classes that have been further reclassified into three HQ–CL classes for mapping purposes

(sugar maple) present mapped outputs produced at each stage of the flow diagram (Fig. 1), and with reclassification schemes from Fig. 2. We then provide a detailed assessment of the metrics available from the analysis (Table 2) along with a narrative to exemplify a process to interpret the findings towards management. The intention of this example analysis is to provide visual and tabular information for managers as they pursue actions relative to securing refugia, advancing silvicultural methods to favor particular species, or encourage migration (natural or assisted) as an adaptation measure for the changing climate.

Shortleaf pine is a commercially important species with a wider range than any other southern pine. It tends to grow well under a variety of soil and climatic conditions. It is classed as a pioneer, dry-site, shade intolerant species, and it competes well in dry sites and in nutrient-poor soils (Lawson 1990). It currently occupies a large portion of the southeastern United States (Fig. 3a, b), but is modeled to increase in habitat throughout the century (Fig. 3c). Sugar maple is also a commercially important, shade tolerant species with most of its high abundance restricted to regions with cool, moist climates (Fig. 4a, b). Although sugar maple does best on well drained loams, it does not grow well in dry, shallow, or swampy soils (Godman et al. 1990). Because of its preference to cooler regions, its habitat is predicted to decrease in the eastern US throughout the century (Fig. 4c), especially under the high emissions scenario.

Shortleaf pine can be classified as an ‘increaser’ species in that northward advances of suitable habitat are likely for both climate scenarios, but especially under the harsh, Hadley RCP 8.5 scenario (Fig. 3d). The large increase in the suitable habitats predicted by DISTRIB II for shortleaf pine is due to the spread of IV to the northeastern and north central regions; the CLs calculated by SHIFT (at ~50 km/century) however, decline rapidly with distance from the range boundary (Fig. 3e). The SHIFT output (Fig. 3e, f) shows that western parts of the range contain the highest likelihoods of colonization (HQ_{High}) because of high values of source abundance near the current range boundary (Fig. 3d). However, in the eastern part of its range, the likelihood of colonization is lower, because of low source abundance near the current range boundary. When the reclassified DISTRIB II habitat quality map (Fig. 3d) is combined with the reclassified CL map (Fig. 3e), the nine resulting classes show combinations of three HQ classes with three CL classes

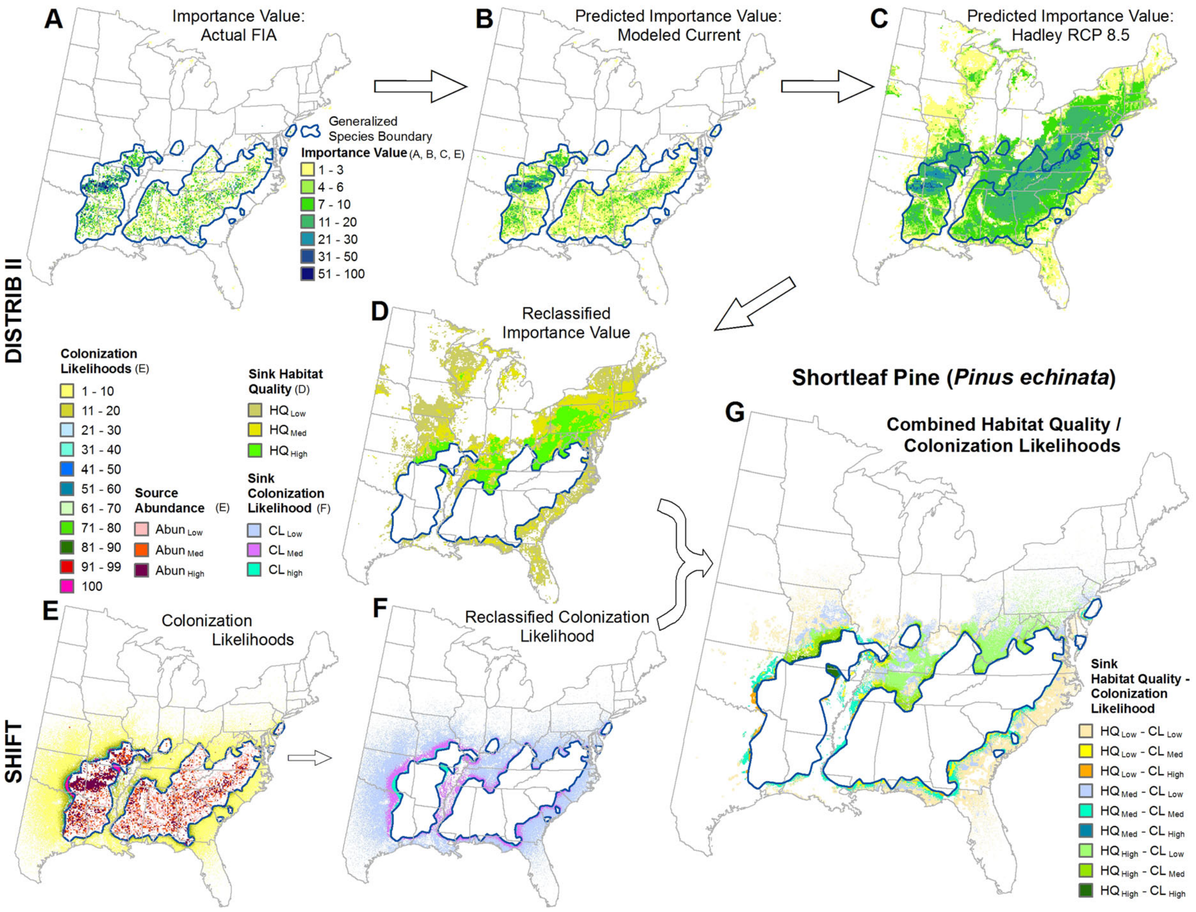

Fig. 3 The map products of DISTRIB II and SHIFT for shortleaf pine for the harsh, Hadley RCP 8.5 scenario. **a** The importance value (IV) distribution (relative abundance) according to Forest Inventory Analysis—they range from 0 to 100. **b** Current IVs as modeled by DISTRIB II using current climate, soil and elevation variables as predictors. **c** Future (~2100) IVs predicted by DISTRIB II using future climate and current soil and elevation variables as predictors. **d** Future IVs reclassified as low, medium and high for the source (within the species range—$\text{Abund}_{\text{low}}$, $\text{Abund}_{\text{med}}$ and $\text{Abund}_{\text{high}}$) and sink (outside the species range—HQ_{low}, HQ_{med}, HQ_{high}) regions. **e** Colonization likelihoods calculated by SHIFT in a 100 years for a historical migration rate of 50 km/century. **f** Colonization likelihoods reclassified as low, medium and high (CL_{low}, CL_{med} and CL_{high}). **g** Combination of 3-class habitat quality and 3-class colonization likelihood (**d**, **f**) to yield a 9-Class combined HQ–CL outputs. The classes that show favorable combinations of habitat quality and colonization likelihoods are the ones most likely to be colonized in the future (see Fig. 2 for the reclassification scheme). The corresponding figures for the CCSM4 RCP 4.5 mild scenario are in Supplemental Figs. S1 and S2

(Figs. 2, 3g). Map flow for shortleaf pine under the mild scenario is in Supplemental Fig. S1.

For sugar maple, which is a 'decreaser' species, the northward advances are not shown because HQ mapping was not conducted into Canada. Much of its habitat also disappears within its current range due to the loss of cooler regions under future climates in the Appalachian region, yet some availability of suitable habitats is noticeable in the west and northwest for the harsh scenario (Fig. 4c). CLs (at ~50 km/century) is higher in the southeast because movement is not restricted in SHIFT (Fig. 4e, f); however, when combined with the suitable habitats predicted by DISTRIB II (Fig. 4d), there are few modeled locations of colonization, in the west and northeast portions of the region (Fig. 4g). These various combinations of HQ and CL (HQ–CL) provide clues regarding potential for migration (natural and assisted) since they represent areas where the species is more or less likely to migrate and thrive into the

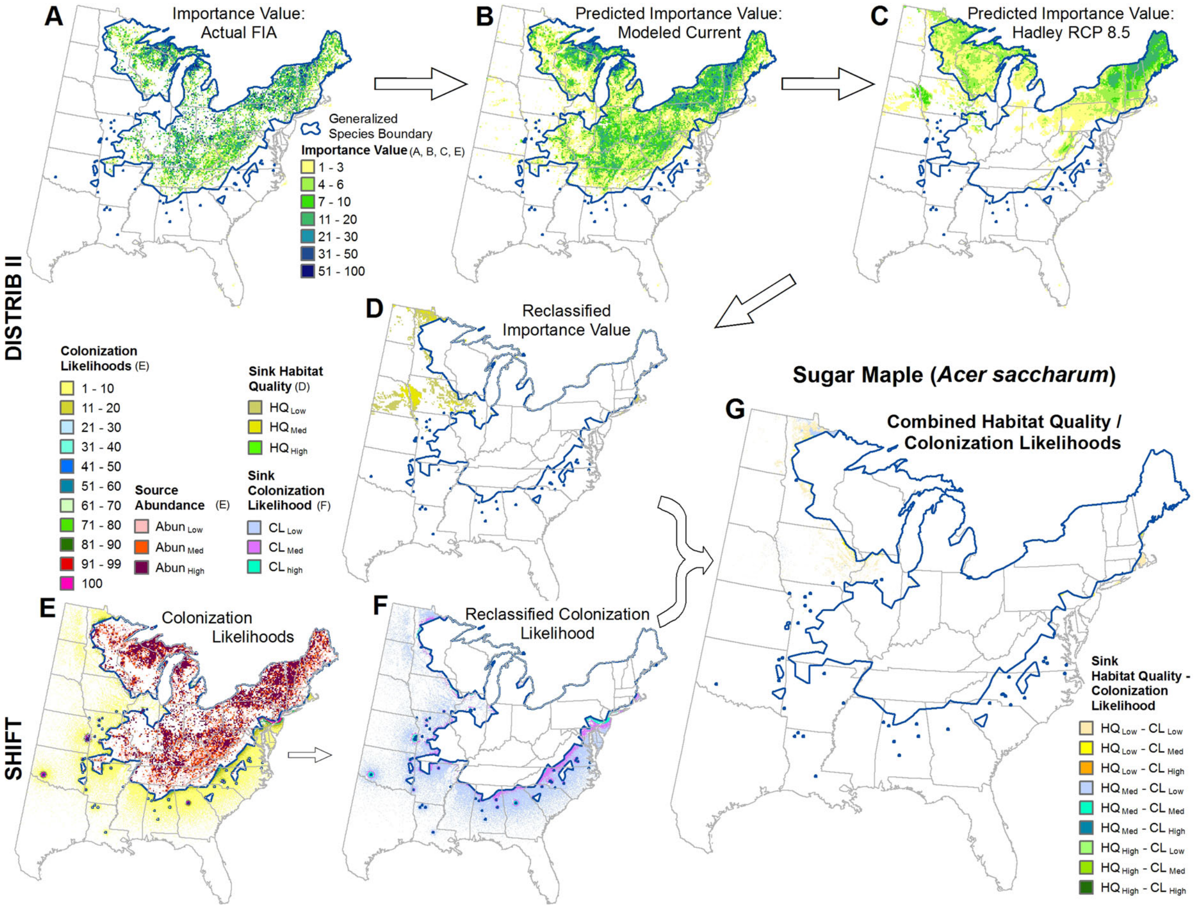

Fig. 4 The map products of DISTRIB II and SHIFT for sugar maple for the harsh, Hadley RCP 8.5 scenario. **a** The importance value (IV) distribution (relative abundance) according to Forest Inventory Analysis—they range from 0 to 100. **b** Current IVs as modeled by DISTRIB II using current climate, soil and elevation variables as predictors. **c** Future (~2100) IVs predicted by DISTRIB II using future climate and current soil and elevation variables as predictors. **d** Future IVs reclassified as low, medium and high for the source (within the species range—$\text{Abund}_{\text{low}}$, $\text{Abund}_{\text{med}}$ and $\text{Abund}_{\text{high}}$) and sink (outside the species range—HQ_{low}, HQ_{med}, HQ_{high}) regions. **e** Colonization likelihoods calculated by SHIFT in a hundred years for a historical migration rate of 50 km/century. **f** Colonization likelihoods reclassified as low, medium and high (CL_{low}, CL_{med} and CL_{high}). **g** Combination of 3-class habitat quality and 3-class colonization likelihood (**d**, **f**) to yield a 9-class combined HQ–CL outputs. The classes that show favorable combinations of habitat quality and colonization likelihoods are the ones most likely to be colonized in the future (see Fig. 2 for the reclassification scheme). The corresponding figures for the CCSM4 RCP 4.5 mild scenario are in Supplemental Figs. S1 and S2

future. Map flow for sugar maple under the mild scenario is in Supplemental Fig. S2.

The nine HQ–CL classes for the two species can be further reclassified to three (Fig. 2) for easier interpretation and comparison between species and between the mild (CCSM4 RCP 4.5) and the harsh (Hadley RCP 8.5) scenario (Fig. 5). One notable feature is that for shortleaf pine, the total area is higher for the harsh scenario compared to the mild scenario because the modeled habitat of the species is largest under the harsh scenario, increasing the suitable habitats available for colonization. This trend is reversed for sugar maple because its habitat decreases less for the mild scenario and therefore shows the potential for migration to be higher in locations outside the current boundary, as compared to the harsh scenario (Fig. 5).

The visual interpretation provided by the maps can be augmented by combining the information of DISTRIB II, SHIFT and MODFACs into a single table that provides quantitative summary of the areas

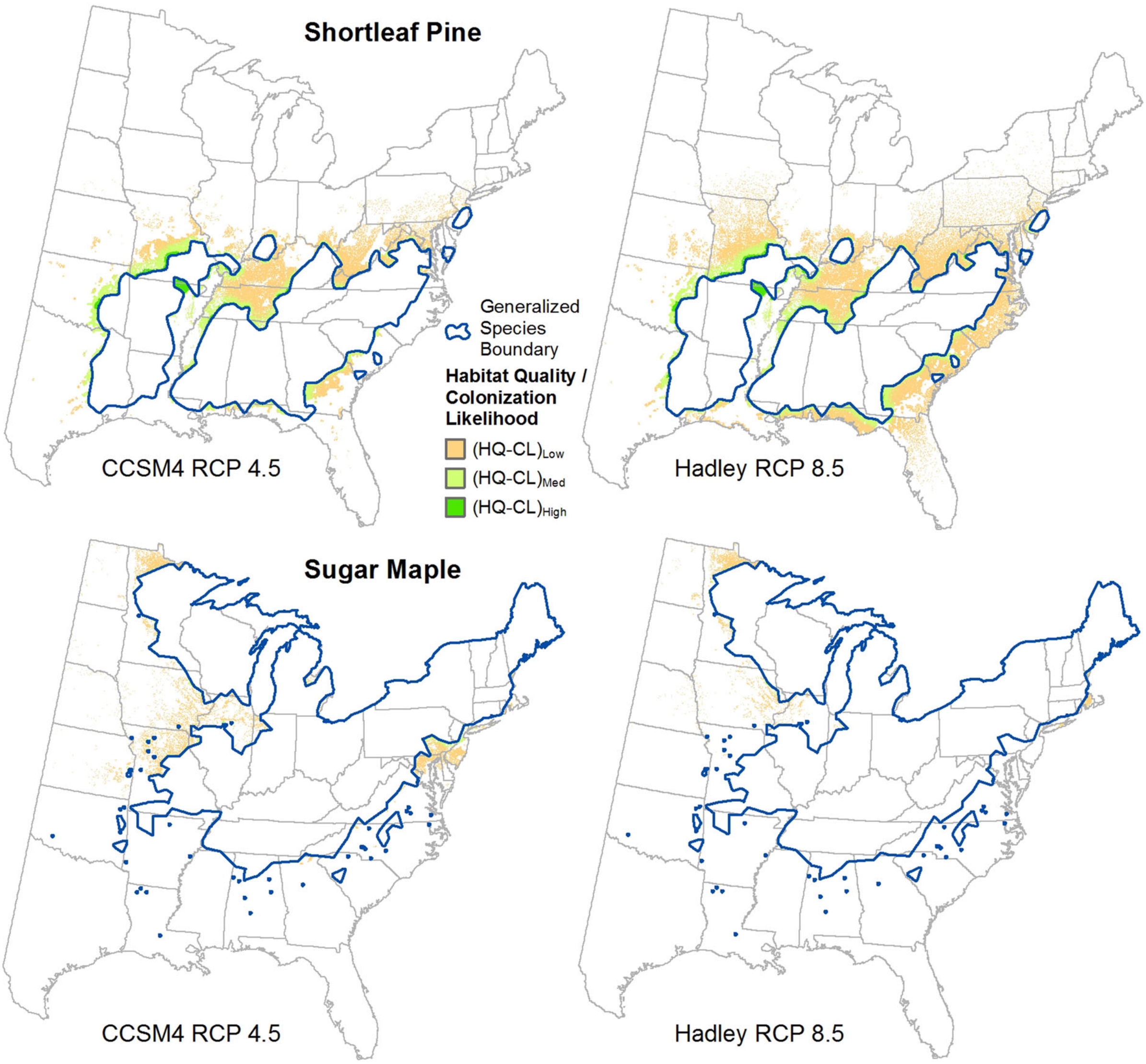

Fig. 5 The combined habitat quality (HQ) and colonization likelihood (CL) map reclassified to three classes (see Fig. 2) for the harsh, Hadley-RCP8.5 and the mild, CCSM4-RCP4.5 scenarios for shortleaf pine and sugar maple. Notice that the HQ–CL_{high}, which depicts the area most likely to be colonized due to the favorable combination of good habitats with high likelihood of colonization, is confined to regions close to the range boundary

represented by each of the maps (Figs. 3, 4), along with derived calculations and a brief synopsis of interpretation (Table 2). These statistics provide a means to compare among species and enable a quantitative path to report trends and relationships.

Table 2A reports areas of suitable habitats for shortleaf pine and sugar maple according to the DISTRIB II model for (a) actual FIA, (b) modeled current, (c) mild future scenario (CCSM4 4.5) and (d) harsh future scenario (Hadley 8.5) for both the source and the sink regions. We have classified the abundance to three IV classes ($Abun_{High} + HQ_{High}$, $Abun_{Med} + HQ_{Med}$ and $Abun_{Low} + HQ_{Low}$) for the source and sink region (Fig. 2) and also report the total area of presence and absence for each. For example, we know from the table that for the harsh scenario, shortleaf pine's combined source and sink habitat, according to the modeled estimates for ~2000, increases from 652 to 2220 thousand km^2 while sugar maple's shrinks from 1443 to 965. These modeled

Table 2 Results from DISTRIB II, SHIFT, MODFACs for shortleaf pine and sugar maple are summarized. The layout of the table is explained below the table

	Shortleaf pine | Sugar maple					
	$\text{Abun}_{\text{High}} + \text{HQ}_{\text{High}}$ (1000 km^2)	$\text{Abun}_{\text{Med}} + \text{HQ}_{\text{Med}}$	$\text{Abun}_{\text{Low}} + \text{HQ}_{\text{Low}}$	Total	Absent	Figure
A. Suitable habitat (DISTRIB II)						
FIA, ~2000						
Within boundary (source)	106 | 345	126 | 234	237 | 282	469 | 861	566 | 913	4 | 5a
Beyond boundary (sink)	0.4 | 0.3	0.3 | 0.2	2 | 0.2	2.2 | 0.7	3163 | 2454	4 | 5a
Total	106 | 345	126 | 234	239 | 282	471 | 861	3729 | 3367	4 | 5a
Modeled, ~2000						
Within boundary (source)	64 | 318	141 | 406	420 | 631	625 | 1355	368 | 349	4 | 5b, d
Beyond boundary (sink)	0.2 | 0.5	0.9 | 4.1	26 | 83	27 | 88	3139 | 2367	4 | 5b
Total	64 | 319	142 | 410	446 | 715	652 | 1443	3507 | 2716	4 | 5b
CCSM4 4.5, ~2100						
Within boundary (source)	200 | 112	461 | 626	241 | 527	903 | 1265	90 | 439	
Beyond boundary (sink)	26 | 1	104 | 38	275 | 230	404 | 269	2762 | 2187	
Total	226 | 113	565 | 665	516 | 757	1307 | 1535	2852 | 2625	
Hadley 8.5, ~2100						
Within boundary (source)	488 | 79	318 | 214	137 | 555	942 | 848	50 | 912	4 | 5c
Beyond boundary (sink)	236 | 0	359 | 28	682 | 88	1277 | 117	1889 | 2283	4 | 5c, d
Total	724 | 79	677 | 242	819 | 644	2220 | 965	1939 | 3194	4 | 5c
B. Habitat ratios, 2100:2000						
CCSM4 4.5	3.53 | 0.35	3.97 | 1.62	1.16 | 1.06	2.01 | 1.06		
Hadley 8.5	11.3 | 0.25	4.76 | 0.59	1.84 | 0.9	3.41 | 0.67		

	CL_{High}	CL_{Med}	CL_{Low}	Total	Figure
C. Colonization likelihood, 100 years (SHIFT)					
SHIFT–sink region	163 | 83	230 | 166	755 | 530	1147 | 779	4f | 5f

	$(\text{HQ–CL})_{\text{High}}$ (1000 km^2)	$(\text{HQ–CL})_{\text{Med}}$	$(\text{HQ–CL})_{\text{Low}}$	Total	Figure
DISTRIB II + SHIFT					
CCSM4 4.5	17.9 | 2.2	110.0 | 15.8	186.6 | 89.9	314.5 | 107.9	6
Hadley 8.5	24.1 | 0.7	132.3 | 6.3	394.0 | 32.9	550.4 | 40.0	6

	Total
D. Ratios of SHIFT:DISTRIB II (proportion of suitable habitat colonized)	
CCSM4 4.5	0.78 | 0.40
Hadley 8.5	0.43 | 0.31
E. Modifying factors (MODFACs)	
Key negative factors	Shade intolerant; drought sensitive; insect pests|none
Key positive factors	Habitat generalist|shade tolerant
Disturbance score	0 | 0.86
Biological score	−0.97 | 1.34
Adaptability score	3.6 | 5.8

Table 2 continued

	Total
F. Interpretation	
DISTRIB II	Shortleaf pine: large increase in suitable habitat (2 × with mild, 3.4 × with harsh scenario)
	Sugar maple: decrease in suitable habitat (1X with mild, −1.5 × with harsh scenario)
DISTRIB II: SHIFT, CCSM4	Shortleaf pine: 315 K of 404 K km^2 (78 %) of new suitable habitat has some chance of colonization, though only 18 K of 404 K km^2 (<1 %) has high likelihood of colonization in high quality habitats
	Sugar maple: 108 K of 269 K km^2 (40 %) of new suitable habitat has some chance of colonization, though only 2.2 K of 269 K km^2 (<1 %) has high likelihood of colonization in high quality habitats
DISTRIB II: SHIFT, Hadley	Shortleaf pine: 550 K of 1277 K km^2 (43 %) of new suitable habitat has some chance of colonization, though only 24 K of 1277 K km^2 (<1 %) has high likelihood of colonization in high quality habitats
	Sugar maple: 40 K of 117 K km^2 (34 %) of new suitable habitat has some chance of colonization, though only 0.7 K of 117 km^2 (<1 %) has high likelihood of colonization in high quality habitats
MODFACs	Shortleaf pine: medium adaptability, models roughly acceptable as is
	Sugar maple: high adaptability, models roughly acceptable as is
Overall	Shortleaf pine will likely have increased habitat northward, and a reasonable portion of that could be colonized in 100 years. The HQ–CL regions especially in HQ–CL$_{\mathrm{High}}$, would also be first candidate places for assisted migration, should that be desired. Best planting places would be in gaps where plenty of light is available and where soil/site is not too droughty
	Sugar maple decreases in habitat especially in the southern portion of its range. Only negligible portion of the future available habitat is colonized because most of the future habitats are beyond the US border. Best planting spaces will be in cool moist areas with partial shade

The table is divided into six sections (A–E) which progressively depict the results of DISTRIB II, SHIFT, DISTRIB II + SHIFT and MODFACs. Section A show areas statistics of source, sink and combined regions for the low, medium and high abundance classes. Section B summarizes the increase/decrease ratios of habitats for the combined source and sinks between 2000 and 2100. Section C reports SHIFT colonization likelihood areas under low, medium and high colonization likelihood classes. It also reports the areas of the colonization likelihood of merged DISTRIB II + SHIFT habitat classes (HQ–CL). Section D reports the proportion of suitable habitat colonized. Section E summarizes MODFACs results. Section F gives a quick overview for managers. Refer to the Fig. 2 for understanding how the various classes are assembled

changes are substantially less for the mild scenario (Table 2A). Table 2 also provides links to the figures (Figs. 3, 4), from which the table values emanate.

Table 2B compares ratios of suitable habitat (combined source and sink) in 2100 under the mild and harsh scenario to that modeled in 2000, thus summarizing whether the species showed increase (>1) or decrease (<1) or roughly remained the same (∼1).

Table 2C compares the CL by about 2100 for SHIFT under the high, medium, and low CL classes and also after combining the DISTRIB II and SHIFT for the harsh and mild scenarios according to Fig. 3. For example, the DISTRIB II + SHIFT tables are useful for gauging how much suitable habitat was colonizable for the best scenario of (HQ–CL)$_{\mathrm{High}}$. Note the small proportion of (HQ–CL)$_{\mathrm{High}}$ relative to total area of modeled suitable habitat for shortleaf pine and especially sugar maple, reflecting in numbers what we saw in the maps of Fig. 5.

Table 2D shows the proportion of suitable habitat colonized under the two scenarios in the sink region (Fig. 5). This ratio is much higher (0.78) for the harsh scenario compared to the mild (0.43) for shortleaf pine. This reflects the fact that for this warm-seeking 'increaser' species, more suitable habitat becomes available in the eastern US under the warmer harsh scenario compared to the mild. This trend is reversed for sugar maple, which prefers cooler conditions (has to migrate north of the border) and hence becomes a 'decreaser' in the eastern US under future warmer conditions. The difference between the mild (0.40) and the harsh (0.31) scenario is low for this species because the habitat available for either scenario is not significantly different inside the eastern US.

Table 2E summarizes the knowledge-based scoring achieved by MODFACs by listing the key negative and positive factors of the species as well the disturbance, biological and adaptability scores. Because sugar maple is shade tolerant, has high biological score (1.34), and the impact of disturbance is minimal, it scores quite high in the adaptability index (5.8 within a range of 1.7–8.5). Therefore it can

Table 3 Area colonized by SHIFT and DISTRIB II + SHIFT under different migration constants under current and future climate scenarios

Migration constant	Area (km^2)			Approximate migration rate (km/century)
	SHIFT–sink region	CCSM4 4.5	Hadley 8.5	
Shortleaf pine				
0.5	958.8	279.3	461.0	<25
1	1147.3	314.5	550.4	~50
1.5	1256.2	331.7	600.3	
2	1331.3	342.9	635.0	
2.5	1390.6	351.3	662.8	
3	1437.4	357.3	684.7	
3.5	1477.7	362.0	704.1	
4	1512.3	365.8	720.2	>100
Sugar maple				
0.5	623.1	85.3	31.6	<25
1	780.4	107.9	40.0	
1.5	885.3	120.0	44.6	
2	968.5	127.5	47.5	
2.5	1037.5	132.5	49.4	~50
3	1099.2	136.6	51.2	
3.5	1153.7	139.4	52.4	
4	1200.5	142.0	53.8	>100

The corresponding maps are in Supplemental Figs. S3 and S4

be expected to do better than modeled in DISTRIB II, and do well in areas of high to medium suitable habitats, as well as survive in lesser suitable habitats. On the other hand, shortleaf pine has an adaptability score of 3.6 indicating an average condition and no particular reasons for adjusting the DISTRIB II model interpretations up or down. These adaptability interpretations may provide users of the information a quick way to assess if the model results are aligned with MODFACs. If there are concerns, the manager can use more information relevant to local conditions to evaluate if further investigations are warranted.

We also include an interpretation (Table 2F) to help managers obtain a quick assessment summary. More broadly the species captured here are representative of general patterns of our models for the eastern US—for 'increasers', the species will have sizable increased habitat northward by 2100, and natural migration could move the species, albeit slowly, northward. For 'decreasers', the possibilities are to shift north-west to west, especially for species that extend beyond the US border. Although SHIFT allows for the possibility of southward migration, it is unlikely that the DISTRIB II + SHIFT combination will find favorable spots in the trailing edge of the range. The mapped locations of $(HQ–CL)_{High}$ are places with highest probability of successful colonization within 100 years (Table 2C), and could also be considered locations where assisted migration of populations (close to current populations) might be most successful, both ecologically and socially. For example, it may be possible to identify and link spatially disparate regions with promising patches and corridors. We illustrate this possibility for shortleaf pine (Fig. 6), where suitable combinations of HQ and CL can be identified and used to locate the most promising places to assist the migration of the species, should society and management find it desirable (Pedlar et al. 2012, Schwartz et al. 2012). For decreasers like sugar maple, we can still track areas outside the current range where possibility exists for assisted migration. However, the focal areas to consider climate change impacts for decreasers will mainly be within their current range where habitat contractions can take two forms, reduction in the extent and suitability of habitat conditions. We have used the optimistic historical migration scenario of

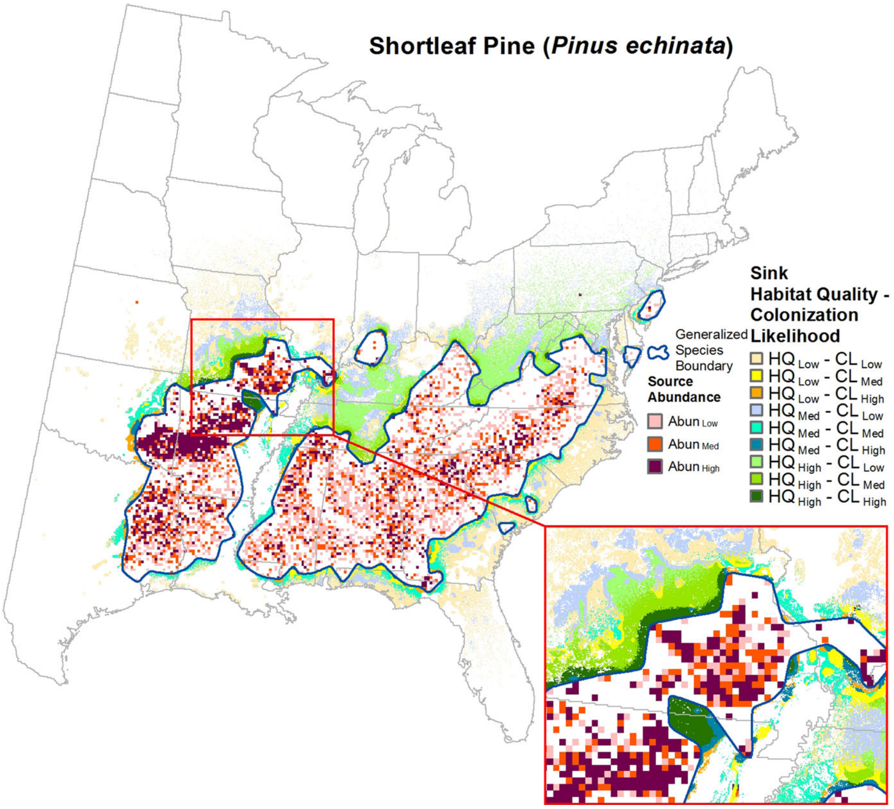

Fig. 6 The habitat-quality and colonization-likelihood combination can depict locations where there is a higher likelihood of colonization. For shortleaf pine, areas suitable for managed relocation can be gauged by looking at the combinations of favorable habitat quality with a higher likelihood of colonization as shown in the zoomed area. The areas depicted as favorable can be analyzed further for suitability based on local conditions

50 km/century for illustrative purposes; however, SHIFT allows for a quick assessment of colonized areas using migration rates below and above that scenario by varying the migration/calibration constant (Table 3; Supplemental Figs. S3, S4).

Limitations

Although our multi-staged approach minimizes some of the limitations of general SDMs, it still carries several assumptions. For example, DISTRIB II model carries with it assumptions common to many SDMs - but we have addressed some of the limitations constraining colonization of suitable habitats via SHIFT, and by using a data-driven multifaceted approach (Iverson et al. 2011). We acknowledge that combining models also may result in error propagation, but we minimize multiplicative errors by modelling DISTRIB II and SHIFT separately (e.g., not using output of DISTRIB II as input to SHIFT) and only later combining the results.

By not explicitly incorporating spatial autocorrelation (SAC), future climate predictions by DISTRIB II may show larger range shifts compared to one that incorporates SAC (Crase et al. 2014, Miller et al. 2007). Comparison of geographic spatial trends among different species showed that the effect varies with species; species having a northern boundary that varies in a definite latitudinal manner shows more SAC effects as compared to species that are dispersed widely.

We also do not account for intraspecific variation in this approach—which becomes important for species which span large north–south areas. A more comprehensive approach that accounts for this *within-species* variation along climatic gradients is under consideration, which will address this increasingly important aspect of the species distribution (Prasad 2015).

Discussion

A synthetic approach that progressively utilizes different types of models as well as a knowledge-based system is a useful way to address current as well as future threats to forested ecosystems. There are inherent limitations and bottlenecks in all types of models—each relevant in a subset of complex situations. Therefore, instead of vainly trying to achieve a one-type-fits-all model, we prefer to leverage the strengths of various approaches at different scales to address the pressing issues that confront forest managers today. There is increasing acknowledgement for the need of a synthetic approach that blends observations, experiments, and narratives, along with statistical, simulation, and conceptual models (Bowman et al. 2015).

In this paper, we focused our description to two species to highlight components and linkages of the approach for species whose ranges are within (shortleaf pine) and extend outside (sugar maple) the eastern United States. Work to extend this approach to the rest of the tree species (134 in the eastern United States), is underway. The difficulty of using SHIFT for species whose range is further north is mainly due to the lack of consistency in inventory data across the US-Canada border, although certain areas beyond the current range within the US can be assessed for most species.

By distinguishing the source region to be within the current range boundary and sink region beyond the species boundary, we were more clearly able to demonstrate the importance of a complementary modeling framework. Key to this approach is the definition of the range boundary. Little (1971) has published the most widely used boundaries for North American species, but these data are now quite old and inventories have since become more comprehensive though still spotty where percent forest is low (such as highly agricultural regions of the Midwestern U.S.). In our case, we expand and shrink the range boundary to conform more closely to the FIA plot data and identify a core region beyond which the species could colonize via a generalized species boundary approach (Peters et al. 2013b).

In spite of the optimistic assumption of 50 km/century migration rate and the fact that after colonization, establishment rates can still be low due to competitive exclusion (Thuiller et al. 2008), the rate of decline with distance is still steep and casts doubt whether the dispersal ability of species can compensate under current fragmented landscapes. Migration rates may vary between wind and animal dispersed seeds, although based on the paleoecological literature (Portnoy and Willson 1993; Higgins et al. 2003), SHIFT assumes no such differences. However, SHIFT allows us to account for historical dispersal rates from <25 to >100 km/century using minimal computing time (using convolution based Fast Fourier Transforms—see Prasad et al. 2013) which enables us to explore a range of historical migration rates and pick the most suitable one of the species based on dispersal mode or other information (Table 3; Supplemental Figs. S2, S3).

One of the advantages of our approach is the ability to target areas where the species have the highest probability of colonization based on the combined information provided by DISTRIB II's suitable habitats and SHIFT's colonization likelihoods. This combined information can be used to assess favorable areas for managed relocation if the situation is of merit.

Another use of our approach is to assess a more realistic mapping of future forest types by taking into account that increases in potential suitable habitats do not translate to colonization of these habitats. Even though exploring the establishment likelihood of the colonizable habitats is beyond the scope of our current macroscale approach, some of the dynamics involved in the modeling of forest types can be modified by the MODFACs scoring system. For example, shortleaf pine is an important component of the loblolly-shortleaf pine and oak-pine forest types. Of these two, the oak-pine forest type shows large increases in suitable habitat in the north if the DISTRIB II model is used in isolation (see: http://www.nrs.fs.fed.us/atlas/tree/ft_summary.html). However, with SHIFT, the CLs of the habitats beyond the first 10–20 km or so are rather low, dampening the possibility of large increases in oak-pine forest type under future climates. When we combine this knowledge with MODFACs, we know that at a regional scale, disease, insect and biotic interactions can still modify outcomes that could give competitive advantage to some species (Nowacki and Abrams 2008). A similar approach can be taken to evaluate the role of sugar maple in the maple-beech forest type.

Outputs of our approach can also be assembled to develop risk matrices that can help managers quickly identify species at risk and prioritize management strategies (Iverson et al. 2012). It would be fruitful to examine the results of our approach with other types of models utilizing different techniques. For example, simulation of migration can be achieved via cost-distance based models using constrained random-walks to limit the migration of the species. Comparison with different modeling techniques allows assessment of where they agree and disagree and the reasons why. A companion study is underway which compares outputs from this approach to outputs from LINKAGES and LANDIS Pro for several regions of the eastern US, as part of vulnerability analyses for the Central Hardwoods (Brandt et al. 2014), Central Appalachians (Butler et al. 2015), Mid-Atlantic (Butler, in prep), and New England (Janowiak, in prep). Early results show that the DISTRIB outputs are similar to LINKAGES at year 2100 and LANDIS Pro at year 2300 (allowing for succession and some migration to occur) (Iverson, personal communication).

In summary, our multistage approach can leverage the strength of different models and narratives, in order to build a decision support system that is hopefully useful to forest managers dealing with multiple issues of climate, land-use and other biotic stressors.

Acknowledgments Thanks to the Northern Research Station, USDA Forest Service, for funding, and external reviewers Maria Janowiak and Laura Leites for their help in improving the manuscript. We declare no conflict of interest to the best of our knowledge.

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