

Lessons Learned While Integrating Habitat, Dispersal, Disturbance, and Life-History Traits into Species Habitat Models Under Climate Change

Louis R. Iverson,^{1*} Anantha M. Prasad,¹ Stephen N. Matthews,^{1,2}
and Matthew P. Peters¹

¹Northern Research Station, US Forest Service, 359 Main Road, Delaware, Ohio 43015, USA; ²School of Environment and Natural Resources, Ohio State University, 2021 Coffey Rd, Columbus, Ohio 43210, USA

ABSTRACT

We present an approach to modeling potential climate-driven changes in habitat for tree and bird species in the eastern United States. First, we took an empirical-statistical modeling approach, using randomForest, with species abundance data from national inventories combined with soil, climate, and landscape variables, to build abundance-based habitat models for 134 tree and 147 bird species. We produced lists of species for which suitable habitat tends to increase, decrease, or stay the same for any region. Independent assessments of trends of large trees versus seedlings across the eastern U.S. show that 37 of 40 species in common under both studies are currently trending as modeled. We developed a framework, ModFacs, in which we used the literature to assign default modification factor scores for species characteristics that cannot be readily assessed in such models, including 12 disturbance factors (for example, drought, fire,

insect pests), nine biological factors (for example, dispersal, shade tolerance), and assessment scores of novel climates, long-distance extrapolations, and output variability by climate model and emission scenario. We also used a spatially explicit cellular model, SHIFT, to calculate colonization potentials for some species, based on their abundance, historic dispersal distances, and the fragmented nature of the landscape. By combining results from the three efforts, we can create projections of potential climate change impacts over the next 100 years or so. Here we emphasize some of the lessons we have learned over 16 years in hopes that they may help guide future experiments, modeling efforts, and management.

Key words: climate change; eastern United States; randomForest; statistical modeling; migration; trees; birds; DISTRIB; SHIFT; ModFacs.

Received 10 December 2010; accepted 11 May 2011;
published online 3 June 2011

Author Contributions: All authors performed research over a 16-year period leading to this point; LRI drafted most of this particular manuscript.

*Corresponding author; e-mail: liverson@fs.fed.us

INTRODUCTION

There has been large effort in recent years to better understand and model potential changes in habitats of organisms due to anthropogenic climate change. As the planet warms and the hydrological

cycle becomes more vigorous, we will likely encounter substantial and ongoing ecosystem changes including changes in forest ecosystem dynamics (Allen and others 2010). Though much uncertainty remains in these predictions, convergence of paleoecological evidence (for example, DeHayes and others 2000) and modeling (Kirilenko and others 2000) suggests that individual tree species will eventually undergo independent, and often radical, changes in distribution (Davis 1981; Webb and Bartlein 1992). Thus, there is clear precedent and need for the modeling of individual species for assessing potential habitat shifts with climate change. Although it is important to recognize that a thorough evaluation of species interactions is not possible with this approach, we must be able to first quantify the changes in potential species habitat. Once these potential changes are adequately quantified, an opportunity arises to assess how species may interact.

Species-based approaches to modeling climate-driven changes in habitat have thus far relied primarily on empirically based statistical models using equilibrium-climate conditions and either presence/absence or abundance-based data. These methods fall under the general methodology nomenclature of species distribution models (SDMs). A thorough review and guide to such models is provided by Franklin (2009), and research has been accomplished to map potential changes in species habitats across many parts of the globe (for example, Box and others 1999; Tchepakova and others 2006; Thuiller and others 2006a, b; McKenney and others 2007; Bu and others 2008; Iverson and others 2008b; Leng and others 2008; Peterson and others 2008; Crookston and others 2010). The limitations of static, empirical models for forecasting possible species changes (or more specifically, habitats of species) under climate change are well known and documented (for example, Pearson and Dawson 2003; Ibanez and others 2006; Pearson and others 2006; Prasad and others 2006; Dormann 2007; Lo and others 2010; Real and others 2010). Care to consider these limitations must be exercised when interpreting and especially incorporating model outputs into on-the-ground management. It is also important to emphasize that there is a wide spectrum of empirically based methods, some of which are more successful than others, and that some of the novel methods used in ecology only since about 2005 are often, but not always, proving to be superior to former methods in species modeling (Elith and others 2006; Prasad and others 2006; Lawler and others 2006; Cutler and others 2007; Franklin 2009).

Though a fully process-driven approach would be preferable to isolate mechanisms and create 'what-if' scenarios, such an approach is presently impossible when considering the detailed parameterization needed for over 100 species, the complexity involved with at least twelve interacting disturbance factors, and the necessary high-resolution modeling over very large areas. When modeling more than a few individual species, it becomes a massive undertaking, because of the lack of knowledge on species life histories and physiologies, to parameterize the species-specific data (Lawler and others 2006). As such, these large-scale, process-based approaches tend to use functional vegetation types rather than species (for example, Bachelet and others 2001; Sitch and others 2003; Gonzalez and others 2010), or have limitations with respect to areal coverage. Indeed, mechanistic models come with their own set of uncertainties, and finally, empirical relationships drive the mechanistic behavior of the models (Bachelet and others 2003). One mechanistic modeling framework showing increasing promise as spectral and machine capabilities grow (but still limited in extent due to computational constraints), is the LANDIS family of models. LANDIS uses species-vital attributes combined with a succession of multiple species cohorts, within a modular approach, to model disturbances including climate change (He and others 1999; Scheller and Mladenoff 2008; Shifley and others 2006). There always will be trade-offs between using complex, mechanistic models versus simple, empirical models to assess possible changes in species habitats resulting from forecasts of environmental change (Thuiller and others 2008). Regardless, all models are simplifications of reality in an uncertain and changing world. The goal is for models to be useful (Box and Draper 1987), and SDMs are proving useful in understanding current and potential future species distributions. In response to critics of SDMs, Wiens and others (2009) stated: "SDMs can provide a useful way to incorporate future conditions into conservation and management practices and decisions, but the uncertainties of model projections must be balanced with the risks of taking the wrong actions or the costs of inaction. Doing this will require that the sources and magnitudes of uncertainty are documented, and that conservationists and resource managers be willing to act despite the uncertainties. The alternative, of ignoring the future, is not an option."

Given the limitations of both empirical and mechanistic modeling, there have been calls for new research efforts to 'go beyond' strictly empir-

ical modeling or strictly mechanistic modeling because of the constraints mentioned above. These include calls for hybrid or other innovative approaches to best address the limitations of each (for example, Ibanez and others 2006; Botkin and others 2007; Beale and others 2008; Thuiller and others 2008; Franklin 2010; Huntley and others 2010). Several groups have been making progress along these lines. For example, Keane and others (2008) used a hybrid approach to combine the spatially explicit, state-and-transition, landscape fire succession model, LANDSUM, with empirically derived successional and disturbance pathways linked to biophysical parameters. Engler and Guisan (2009) and Engler and others (2009) developed MigClim to simulate dispersal in the context of climate change in the Swiss mountain flora. Midgley and others (2010) developed BioMove to simulate plant species' geographic range shifts in response to climate, habitat structure, and disturbance. Anderson and others (2009) used a combination of habitat suitability and metapopulation models to assess potential changes in two hare species. Meentemeyer and others (2008) found that combined habitat niche models and a dispersal kernel resulted in a considerable increase in explanatory power for a model of a forest disease caused by *Phytophthora ramorum*. And Keith and others (2008) coupled suitability models with a population model for two contrasting plant life histories in South Africa. Each of these approaches consider dispersal and land use to arrive at 'potentially colonizable' habitat, rather than strictly 'potentially suitable' habitat.

Since 1994, our group has been using a statistical approach, and later a hybrid approach, to project potential habitat changes for the trees and birds of the eastern United States. For trees, the primary response was based on the U.S. Forest Service's Forest Inventory and Analysis (FIA) data (Iverson and others 1996; Miles and others 2001), whereas for birds, it was based on the Breeding Bird Survey data (Sauer and others 2001). (Note: although this current paper focuses on trees, much of what is described herein was also used for 147 bird species of the eastern United States.) We initially used regression tree analysis at a county resolution for 80 common tree species (Iverson and Prasad 1998; Iverson and others 1999a; Prasad and Iverson 1999), summarized potential changes in suitable habitat under several scenarios of climate change (Iverson and Prasad 2002), and evaluated possible future patterns of species richness and forest types with those data (Iverson and Prasad 2001). Concurrently, we began to develop the SHIFT model

that evaluates migration potential within the newly forming suitable habitat with climate change, first at a 3-km resolution, then with finer-scale inputs and outputs (Iverson and others 1999b, 2004a, b; Schwartz and others 2001). Next we implemented a tri-model approach of regression trees, bagging, and randomForest methods along with revised data and at the 20 × 20 km scale of analysis, which allowed evaluation for an additional 54 species (Prasad and others 2006; Iverson and others 2008a, b). A culmination of this effort for 134 tree species is contained within our tree (Prasad and others 2007) and bird (Matthews and others 2007) atlas Web sites. This long-extended effort has afforded us the opportunity to make mistakes and then make amends as best we can.

In this article, we report the lessons we have learned from modeling species under various scenarios of climate change. It is not intended as a review of modeling approaches or an endorsement of our own work. Instead our objective is to present one thread of scientific inquiry in which we have tried to overcome challenges and learn from our mistakes. Though we have conducted this work only in the temperate forests of the eastern United States, we believe that many of the lessons will be applicable elsewhere, and we hope, helpful for other investigators. In addition, we hope that by laying out the rationale of this approach we demonstrate that empirical modeling for potential changes in species habitats, especially when using the most advanced methods and combined with other research, is a valuable approach to assess climate change impacts at all scales.

MATERIALS AND METHODS

Our overall, multi-stage approach to the modeling is shown in Figure 1. First, the acquisition of high-quality data is paramount. We recognize that we are fortunate in that the tree (Forest Inventory and Analysis, <http://www.fia.fs.fed.us/>) and bird (Breeding Bird Survey, BBS; <http://www.pwrc.usgs.gov/BBS/>) data for the eastern U.S. are very comprehensive, and thus highly appropriate for regional analysis (Lawler and O'Connor 2004). For example with the FIA data, the 100,000+ plots are randomly located in an unbiased fashion and each stem within each of the 0.067-ha plots are identified and measured. Thus, not only are the abundances and basal areas known and statistically unbiased, but the absences within the plots are truly known. Importantly, even though absences are known at the plot scale, there will certainly be a level of unknown absences (and presences) at the

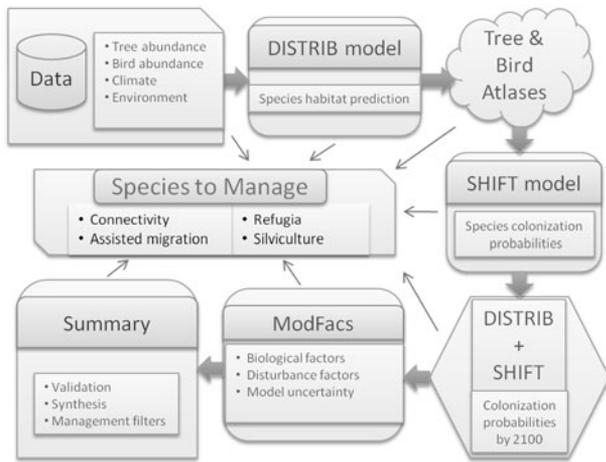


Figure 1. Flow diagram of species modeling approach, all with a focus on assisting with the management of the species under climate change.

scale of the 20×20 km cell, as each plot represents over 2000 ha of forest land. We recognize that the plentiful and statistically relevant data available from FIA and BBS are a luxury that may not be available in many other regions of the globe.

We then use the DISTRIB model (Figure 1), a series of robust statistical models, to build estimates of the potential habitat suitability under various scenarios of climate change, and assess the reliability of each species model (Iverson and others 2008a, b; Prasad and others 2006). These outputs, consisting of roughly 20 maps, 11 charts, and 4 tables for each of 134 tree and 147 bird species, are online (www.nrs.fs.fed.us/atlas). The atlases provide a suite of landscape ecological information for each species depicting both current and future conditions, including details on current species-environment relationships, maps of species abundance, life-history information, predictor importance, potential habitat changes according to three general circulation models and two emission scenarios, and tables of potential changes by ecoregion, state, national park, or national forest (Prasad and others 2009).

The SHIFT model is then used (Figure 1) in conjunction with DISTRIB outputs for trees to model the possible colonization of the new suitable habitat within 100 years (Iverson and others 1999b, 2004a; Schwartz and others 2001). SHIFT is a spatially explicit, 1-km cell-based, simulation model that simulates the dispersal of individual species propagules as a function of the surrounding cells' current abundance, habitat quality (for example, percent forest), and an inverse-power function of distance (so that long-distance dispersal

also occurs occasionally). The rate of dispersal is tied to fossil pollen interpretation of historic migration rates of approximately 50 km/century through unfragmented forest as uncovered from paleoecological data of the Holocene (Davis 1981). The estimate of 50 km/century may be optimistic in light of recent molecular studies (McLachlan and others 2005), however, a key outcome of the SHIFT simulations shows that even at these high end of the Holocene migration rates, the 'advancing front' of the migrating species is likely to be concentrated near the current boundary and not likely to keep pace with projected rates of warming and habitat availability (Iverson and others 2004a). Another important interpretation of SHIFT is that the source-strength (species abundance near the range boundary) has greater weight than the sink strength (percent forest cover). The intersection of SHIFT and DISTRIB then shows how much of the newly suitable habitat may be colonized over a 100-year period (in the absence of human-assisted migration), which typically is a small fraction of the available habitat.

Finally, we use modifying factors (ModFacs, Figure 1), a non-spatial scoring system using life history traits (nine biological factors and twelve disturbance factors) and three post-modeling assessments as an add-on method to increase model usefulness and practicality for managers and researchers (Matthews and others, in press). ModFacs also provides a means to assess each species for their adaptability to the impacts of climate change (see description below). We summarize, synthesize, and validate as best we can with information available, and the overall information is then passed through management filters for local conditions, and adjusted if necessary. The goal is to finally arrive at appropriate information and potential tactics to manage species (Figure 1). Our intention is to provide the best information possible, under the uncertainty of limitations imposed, for decision makers to consider in the face of climate change.

The outputs of the tree and, to a lesser extent, bird models have been used for many assessments, ranging from national to regional. These assessments include the U.S. National Assessment (U.S. National Assessment Synthesis Team 2000); the Northeast Assessment (Frumhoff and others 2007); the Pennsylvania Assessment (Union of Concerned Scientists 2008); the Chicago Assessment (Hayhoe and others 2008); and the northern Wisconsin vulnerability assessment (Swanston and others 2011). With a 20×20 km cell size, the results are intended to provide a relatively coarse, regional

analysis of possible future trends for use by citizens, researchers, and decision makers. Though we have summarized and published results in a number of outlets (see references), the online tree and bird atlases (www.nrs.fs.fed.us/atlas; Prasad and others 2007; Matthews and others 2007) remain the best source for up-to-date information on each species.

LESSONS LEARNED

In this section, we highlight some of the features of our modeling approach and the development of tools to make results useful for ecologists and managers. We hope these 'lessons learned' will prove useful to others involved in similar efforts.

Use machine-learning, data-driven modeling tools

We found that a statistical-empirical approach with a combination of decision trees effectively models the effects of climate, soil, elevation, and landscape predictors on the abundances of the tree species and predicts potential changes in the distribution of potential habitats for future climates (Prasad and others 2006; Iverson and others 2008b). Because the relationship between predictor and response variables is often nonlinear and complex (Austin 2002), they violate most statistical assumptions and traditional parametric statistical approaches generally capture these patterns poorly. Therefore, newer machine-learning, data-driven approaches were used to predict and provide valuable insights into the important predictors influencing species distributions. Specifically, we used a 'tri-model' approach: randomForest (about 1000 decision trees with resampled data and randomized subset of predictors) for prediction, bagging trees (averaging of 30 decision trees with resampling) for assessing the stability among individual decision trees, and a single decision tree to interpret the results if the stability among trees proved satisfactory (Prasad and others 2006). Further, we use the randomForest intermediate products to tease apart much about each variable's impact within the models. To our knowledge, this tri-model approach is unique among researchers to maximize the statistical value of the analyses.

Ensemble methods, which combine the results of many different statistical procedures or many different formulations of the output data, have been shown to improve predictions in some cases (for example, Araujo and New 2007; Franklin 2009). Our experience has shown that great caution is needed when selecting a given modeling

technique, and the outputs must be evaluated independently before an ensemble approach is considered. The use of proven techniques (many of which are only recently developed) should be used when 'fusing' inputs or outputs for species distribution modeling. For modeling of species with ample abundance data (like FIA), we have found that randomForest-bagging decision tree analysis is best for extrapolating to future climates (Breiman 2001; Prasad and others 2006), whereas for presence-only or relatively rare species, MaxEnt may be superior (Elith and others 2010). In addition, generalized boosting methods and adaptive splines (MARS) may be appropriate for some types of data and in some situations. These choices appear to be supported by the thorough review of SDMs by Franklin (2009). As stated by Austin (2002), model types and variables must always be selected based on sound ecological concepts. The above statements should not be construed to mean non-statistical approaches are inappropriate—in fact, because of future data uncertainties as well as problems in model parameterization, a plurality of approaches is recommended.

Use abundance-based information for model building

If possible, there is advantage in using inventory-type, quantitative data (like FIA or BBS) to model relative abundances, unlike limited presence/absence (binary) or presence-only information obtained from traditional sources such as herbaria or county-based records. Because most data used for SDMs are of the presence only or presence/absence type, this has been the focus of most SDM research, especially in Europe (Franklin 2009). Because of the abundance information in our research, we could use powerful regression-based approaches instead of the more common binary/classification approaches for modeling species distributions. The key advantage is that we can make analyses and interpretations based on the core of the species' ranges, rather than the more uncertain range boundaries that are equally weighted in presence/absence data. This distinction is crucial when it comes to modeling habitat responses to climate change. When there is considerable variability around projected changes in climate, a continuous response variable allows the model to focus on core areas of a species distribution where there is greater certainty of species occurrence. Here we present an example of the value of using abundance-based models relative to binary models using sugar maple (*Acer saccharum*). When modeled as presence/absence

using the randomForest classification algorithm, the change in habitat for one climate model is a 90% loss in the extent of the species habitat, but when run with abundance, the loss is only 36% of its current habitat range (Figure 2). This large difference can be attributed to higher sensitivity when including the abundance values, which allows distinguishing the core from the edge of the species range.

Another advantageous feature to using abundance-based models is the ability to interpret to some degree, by species, the possible rate of changes that may occur throughout its range. For example, the DISTRIB models may suggest that the species is a large decreaser, in that the relative abundance in around 2100 may be much less than it is currently, especially towards its southern range boundary. The large change in suitable habitat could indicate a pending population decline due to rather severe limitations to regeneration and even the potential for widespread mortality (as described with drought by Allen and others 2010) to create a relatively rapid change in composition and the

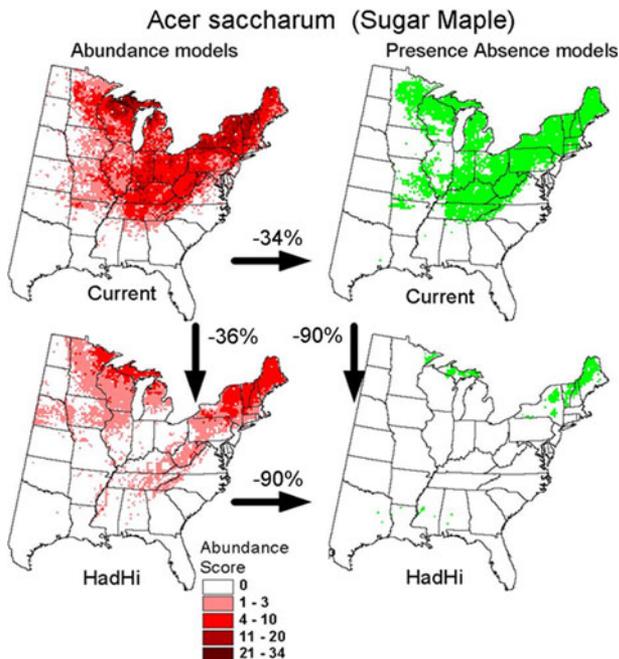


Figure 2. The large disparity of outcomes for sugar maple when comparing abundance-based models to binary (presence/absence) models. “Current” indicates the modeled current abundance or range extent, whereas the “HadHi” maps are based on the HadleyCM3 GCM model (high CO₂ sensitivity) and high emissions (A1fi) scenarios. Abundance score is an importance value based on basal area and number of stems, Iverson and others (2008a, b).

ecosystem. In contrast, a small change in projected relative abundance over time would give an indication of more subtle changes to come.

Use non-climatic variables in combination with climatic variables for stronger models

Our experience has shown great advantage in using relevant non-climatic variables that contribute to the models, in addition to the climatic ones, when modeling most tree and bird species. These variables may represent indirect gradients (for example, soil taxonomy, elevation) but are more commonly direct gradients (for example, soil properties; Austin 1980; Guisan and Zimmermann 2000). For example, the model for *Taxodium distichum* (http://www.nrs.fs.fed.us/atlas/tree/gp_221.html#) is limited by elevation—the highest abundances are in locations of elevation below 1.65 m. This important relationship will not change under climate change (unless sea level rise becomes extreme), and models including only climate variables would not likely catch this. Even though the inclusion of many non-climatic variables may contribute to collinearity and cause some confusion in the choice of the selected variables, our evaluation showed that the benefits outweigh the drawbacks. For example, we were able to accurately delineate certain species, like the example for *Taxodium distichum*, which is not primarily driven by climate. In fact, even though there was no dearth of observations in our dataset, one of the strengths of randomForest is the ability to handle a large number of predictor variables for datasets with limited observations and built-in resistance to overfitting for most types of data (Cutler and others 2007). We, however, realize that not all species models are created equal. We therefore used the same suite of climate and non-climate predictors for multiple species and summarized model performance factors in the ‘tri-model’ approach to evaluate model-reliability among different species.

In the same manner, we found that coupling the outputs from tree models with the bird models provides further evidence to the importance of non-climate variables in SDMs. As with the models of tree species, the bird models benefit greatly by using non-climate variables as potential predictors (Matthews and others 2011).

Provide an assessment of the reliability of each model

Some species are more reliably modeled than others. Rarer species with highly restricted ranges and

low sample sizes (for example, cedar elm, *Ulmus crassifolia*; water locust, *Gleditsia aquatic*) often produce less satisfactory models as compared to more abundant, larger-ranging species (Schwartz and others 2006), and this can be a source of great uncertainty in modeling rare species (and the reason why we do not model the rarest tree species of the eastern United States). On the other hand, some widely dispersed but uncommon species (for example, pawpaw, *Asimina triloba*; Kentucky coffee tree, *Gymnocladus dioicus*) are also difficult to model because they span such a broad climatic gradient. Therefore, large differences exist in the reliability of the predictions among species. The tri-model approach gave us the ability to assess the reliability of the model predictions for each species, which was classified as high, medium, or low depending on the assessment of the stability of the bagged trees and the R^2 in randomForest (see Iverson and others 2008b for details). If the model reliability of a species was high, we could be relatively confident that a single decision tree can be used to assess the interaction among variables and to map the important predictors influencing the distribution geographically, as shown for sugar maple on our Web site (http://www.nrs.fs.fed.us/atlas/tree/gp_318.html). This high rating occurred for 55 of 134 tree and 59 of 147 bird species in our models, whereas 31 trees and 38 birds had the lowest rating. Even if the model reliability was medium or low, randomForest predicts better without overfitting due to its inherent strengths compared to a single decision tree (Cutler and others 2007; Franklin 2009).

Search out independent data to evaluate the models

It is important to evaluate and validate the models as well as possible to enhance credibility and utility. Most SDMs of current distributions can be validated to some degree using independent data or by dividing the original dataset into training and testing data. A thorough review of such methods is found in Franklin (2009). Evaluation of models extrapolating into space or time is more difficult and more development of such methods is needed (Elith and Graham 2009). In certain instances, data may be available to add credence to models that extrapolate into the future. Fortunately, studies conducted by Woodall and others (2009) do just that for many of the tree models we have produced. They used a comparison of the biomass of larger trees (>2.5 cm diameter breast height [dbh]) relative to density of seedlings (<2.5 cm dbh) across each

species' range of latitude to detect possible future trends in distribution. For many of the species, higher regeneration success was evident at the northern edge of their ranges. Of the 40 species Woodall and others (2009) tested, all but three showed trends that agreed with projections of our models. It is also important to retain historic inventory data so that future assessments of trends can be evaluated and multiple potential drivers can be teased apart.

Welcome and compare among multiple approaches in assessing vulnerabilities, estimating impacts, and proposing adaptive management strategies: there is room for all of us in the climate change problem

Models can be evaluated by comparing outputs from other modeling approaches, and then compare, contrast, and analyze the projections toward a better understanding of the entire system (Botkin and others 2007). If two or more models arrive at similar results while using different approaches, the plausibility of the models is increased. Two classic cases were the comparison study of 17 biogeochemical models for evaluating net primary productivity (Cramer and others 1999), and the comparison among 16 SDMs for predicting 226 species distributions across six regions of the globe (Elith and others 2006).

Outputs from our work are being compared with outcomes from other groups modeling trees in the eastern U.S. For example, Mladenoff and Xi are using LANDIS-II to evaluate potential climate change consequences for trees in northern Wisconsin; so far, most results are congruent with ours, with expectations of decreasing northern species and increasing southern species (Swanston and others 2011). Similarly, general agreement on future suitable habitat for many, but not all species has been observed when comparing to outputs from Hargrove and others (2010), who used multivariate spatio-temporal clustering (MSTC) techniques to generate a series of potential future habitat maps for 211 tree species in North America; from McKenney and others (2007), who prepared climatic envelope models of each of 130 tree species across North America; and from Neilson and others (2005), who have generated multiple outputs of plant functional types with their MAPPSS and MC-1 models. The comparison among modeling approaches allows an increase in credibility when the approaches agree (for example, where species habitats will move north or upslope), and when

they depart, a place for further investigation. When there is disagreement, it may be necessary to acquire more specific information to uncover the possible mechanisms behind the differences. For example, the individual-based information and modeling of Clark and others (2011) might provide some clues to such mechanisms.

Combine species into potential community types to provide valuable summaries of overall tendencies

Ferrier and Guisan (2006) present three alternatives to modeling community types: (a) assemble first, predict later; (b) predict first, assemble later; and (c) assemble and predict together. Because the paleoecological record clearly shows that assemblages do not move together in changing climates (Ackerly 2003), alternative (a) is less appropriate in the context of climate change. Alternative (b), used here, has advantage in that it allows the individualistic nature of species to operate, but also suffers in that it assumes that the current species interactions will remain constant into the future. Alternative (c) holds promise, not yet fully achieved, to assess compositional turnover gradients in the context of climate change through tools like generalized dissimilarity modeling (GDM; Ferrier and others 2007).

Although the modeling of species at the individual level has been crucial to our approach, we can capture forest community structure through the use of assembly rules (Keddy 1992), based on measures to combine species importance values. We have prepared maps of 10 forest types that currently occur in the eastern U.S. (http://www.nrs.fs.fed.us/atlas/tree/curr_fortypes.html), and then reassembled these same forest community types based on several scenarios of potential changes in suitable habitat (http://www.nrs.fs.fed.us/atlas/tree/ft_summary.html). These outputs reveal potential loss of the spruce-fir and aspen-birch types and gains in oak-hickory and southern pine types. Such information would be difficult to portray with single-species maps.

Distinguish range from suitable habitat

An early mistake we made is that we inadequately stressed in our writings that the model outputs were forecasted changes in suitable habitats rather than actual changes in species occurrence. Obviously for long-lived trees, there will be large time lags, dispersal and establishment limitations, and refugia which will dictate the rate of migration into

the new suitable habitat as projected by DISTRIB or other SDMs. This limitation of SDMs has perhaps elicited the most criticisms in the literature. By necessity because of data or computational limitations, many SDM analyses of potential climate change effects have evaluated the changes by assuming either complete dispersal or no dispersal (for example, Thomas and others 2004; Guisan and Thuiller 2005), when in reality, it will likely fall somewhere in between. We instead have attempted to elucidate the difference between habitat and species movements, by developing and using a cell-based model, SHIFT, to simulate migration of selected tree species over a 100-year period (Iverson and others 1999b, 2004a, b; Schwartz and others 2001). The output of SHIFT yields a colonization probability of the species over that period of time. The intersection of DISTRIB, which maps the suitability of the habitat, and SHIFT, which maps the probability of migration over 100 years, yields a map of feasible locations for new colonization under various scenarios of climate change (Figure 3). Among five species, less than 15% of the newly suitable habitat was predicted to be potentially colonized within 100 years (Iverson and others 2004b). This result is consistent to that found in the *Banksia* spp. of Western Australia (Fitzpatrick and others 2008). This is an area of active research now by our group and others (for example, Williams and others 2008; Engler and Guisan 2009; Midgley and others 2010), as data and computer limitations are easing.

Consider variations in disturbance, biology, and model issues on each modeled species

No model, statistical or otherwise, can yet include all the life history traits, that is, the biological characteristics of the species or their responses to various disturbances that may influence a species' response to changes in climate. We focus here on some of these types of uncertainty as related to nine biological and twelve disturbance modification factors (ModFacs) that influence species' distribution, as determined from literature surveys (Figure 4, Matthews and others, in press). The biological factors attempt to assess the species capacity to adapt to changing conditions, especially those expected in the future following current trends. For example, higher capacities to regenerate after fire, regenerate vegetatively, or disperse are all positively associated with adaptability to expected climate changes. Similarly, the disturbance factors assess the resilience of the species to twelve

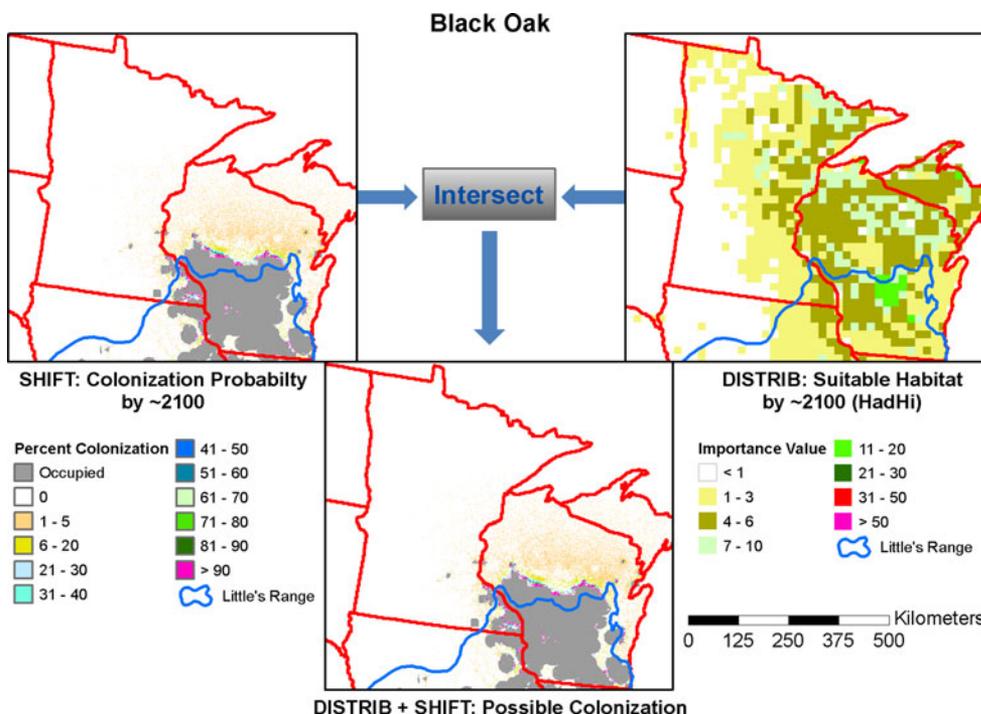


Figure 3. The intersection of DISTRIB with SHIFT provides an indication of potential colonization within the newly suitable habitat within 100 years. Because the potential new suitable habitat encompasses all the area of potential colonization, the two left figures are the same for this species, but this is not the case for many species. The blue line corresponds to the range boundary as identified by Little (1971).

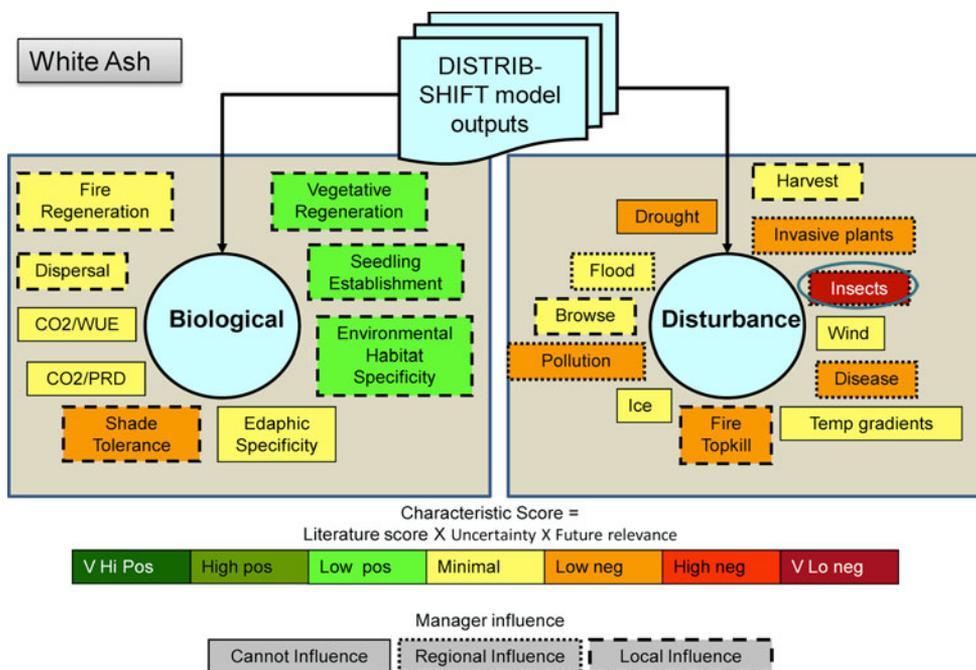


Figure 4. Graphic view of the biological and disturbance modification factors for white ash (*Fraxinus americana*). Factors were scored from very high positive influence (+3) to very high negative influence (−3). Each factor is also evaluated for the potential that managers have to influence it regionally or locally. For this species, the exotic insect, the emerald ash borer (*Agrilus planipennis* Fairmaire), is threatening to destroy the genus in North America (Prasad and others 2010), so any interpretations related to climate change will be obliterated by this modification factor.

disturbance types, or the species' capacity to withstand these disturbances, as best as we can determine from the literature (for example, Burns and

Honkala 1990a, b). Many of the disturbances we evaluated are expected to increase with climate change or other human-influenced stresses and

some are indeed showing signals of such change in the recent past (for example, Allen and others 2010; Breshears and others 2005; Westerling 2006). We assume that the future will bring more drought-related stress, more fire, more flooding events, more wind damage, more ice damage (in northern locations), more air pollutants, more disease, insects, and herbivory, more invasive plants, and more timber harvests (at least in some locations). For each species, key literature was reviewed to arrive, for each factor, a score to one of seven classes (−3 to +3 = very negative to very positive influence) in dealing with expected climate change and associated disturbance impacts (Figure 4). We also scored for future climate relevance and uncertainty within the knowledge base. With the key literature at hand, we scored each species with default values for each of the biological and disturbance modification factors. These values provide baseline information to which users are encouraged to modify based on local knowledge and site conditions, or with revisions based on updated and more comprehensive literature review. The ModFac values can then be used to qualitatively modify, up or down, the projections of the empirically derived DISTRIB model outputs.

Though the ModFacs outputs are not spatially explicit maps, they present the species' overall capability to adapt to the changing conditions predicted with climate change (Figure 4), and better account for the natural processes that influence the final distribution. ModFacs scores may also provide a mechanism to prioritize species when considering management options, for example, which species should be able tolerate particular changing conditions, and which species need management help? Thus, for this reason plus the capability to alter scores based on local knowledge and conditions, the approach encourages decision makers to be actively involved in managing tree habitats under projected future climatic conditions.

Though it might be preferable to have this suite of 21 ModFacs variables be assessed spatially via mechanistic modeling, and some such models are moving toward this goal with a few of these variables (He and others 2008), we are still a long way from adequately modeling all of these variables interacting on 134 intermingling species across half a continent. Instead, this ModFacs method allows a mental and qualitative evaluation of all the factors simultaneously, resulting also in an evaluation of

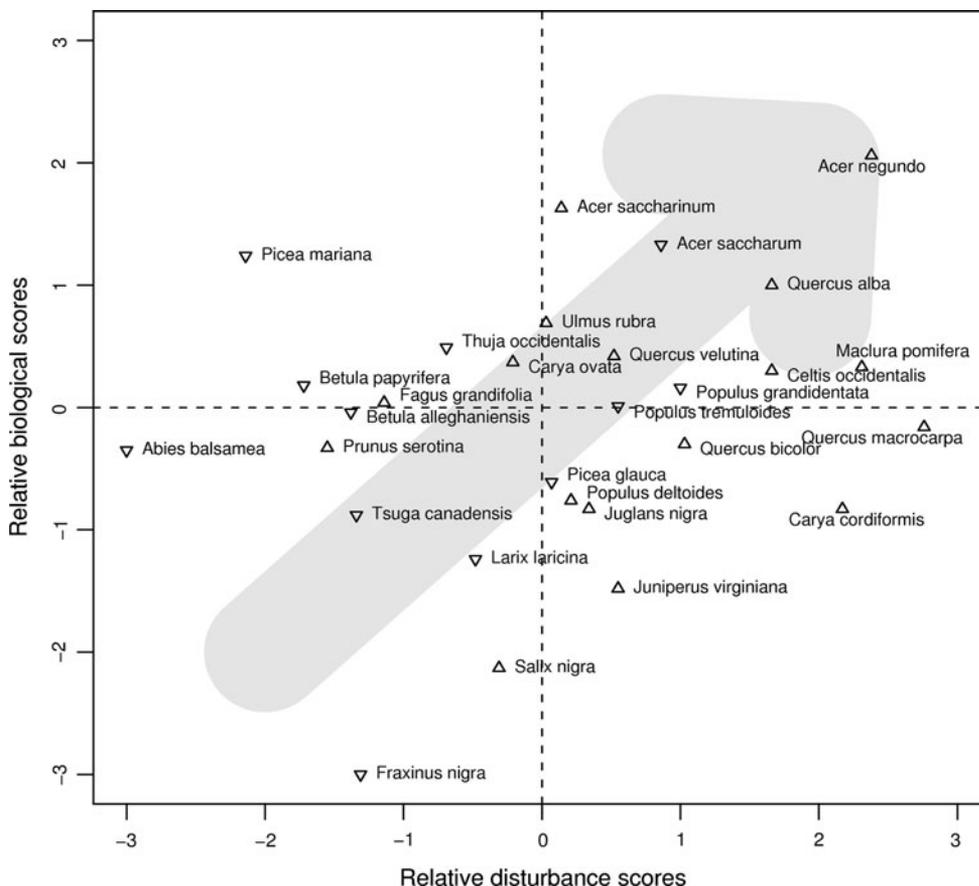


Figure 5. ModFacs averaged and scaled scores for biological versus disturbance factors, for a set of large decrease species (downward facing triangles) and a set of large increase species (upward facing triangles) for the northern third of Wisconsin. The direction of increasing adaptability is in the positive direction on both axes (in the direction of the gray arrow).

the ‘adaptability to climate change’ for each species (Figure 5).

In addition to the disturbance and biological factors, three issues related to the modeling outcomes are addressed in ModFacs: (1) How novel are the climates the species are facing for any particular area? Somewhat akin to the work by Williams and others (2007), this effort uses distance between statistical clusters of seven climate variables to classify each cell into a climate regime. It shows that under the hottest models (for example, Hadley High), much of the southeastern United States will experience climates not witnessed by the current vegetation; (2) What difference does it make for the species’ habitat whether we humans follow the path of low versus high emissions in this century? Some species behave similarly regardless of the decisions humans make on reducing greenhouse gases but most have stark differences in outcomes depending on emission scenario, and contrary to the comments from Real and others (2010) based on a few species from Spain, we do know enough to plan for climate change for many species; and (3) How far would a species have to migrate to reach a particular location, that is, the necessity of long-distance movements? Some species’ models show very large shifts in suitable habitat, so that the chances of that habitat being occupied without human intervention are very remote. The methods for these three metrics cannot be elaborated on here, but the thrust is to quantitatively evaluate these factors to further assist in interpreting the DISTRIB model outputs, and to enhance their usefulness to managers and decision makers.

Consider the scale of influence of environmental variables on species habitats

Scale matters (Wiens 1989). It is important to understand the scale of influence particular environmental variables have on species habitat for interpretation of the SDM outputs and for applying the outcomes to management and decision-making. An advantage of the decision tree approach, amplified via the 1000 trees of randomForest, is the capability to assess the scale of influence of variables via the tree diagram (Moore and others 1991), in that variables appearing at the top of the tree have coarse-scale influences (often temperature in our models), whereas those appearing lower down have finer-scale influences. For example, balsam fir is related highly to climate variables at the regional level, although scarlet oak is more controlled by soil variables at that scale; the reverse

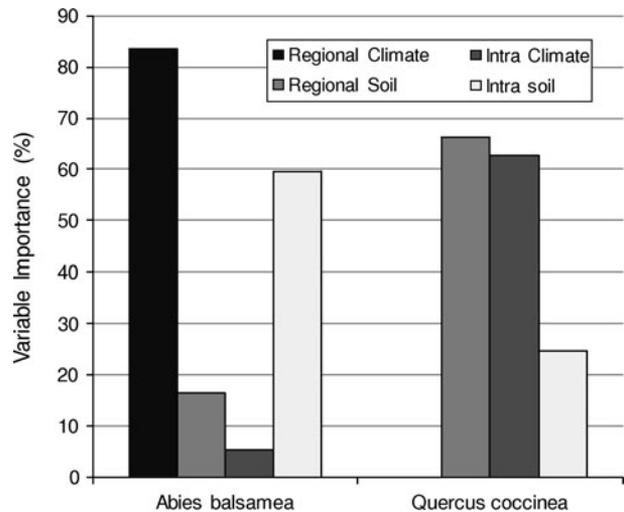


Figure 6. Importance of environmental variable class (soil and climate) as regional vs. local or intra-distributional influences on the current distributions for two species.

is true at the local or intra-distributional level (Figure 6).

Clearly articulate the weaknesses and strengths of the approach

It is important to identify weaknesses and strengths as these must be evaluated when comparing approaches and when applying results to management policies. Important weaknesses to our modeling approach include:

1. The DISTRIB models are correlative and limited in scope to modeling the potential current/future suitable habitats—not their actual future distributions, although SHIFT begins to address the dispersal limitations.
2. The data-driven methods depend on a decent sample size (>~50 cells), and models for very rare species are likely to have limited inference due to lack of data.
3. The methods assume the species are in equilibrium with the environment, so that they are inappropriate for species known to have rapidly changing distributions (for example, invasives).
4. There likely are better environmental predictors that could be used.
5. Not all species have their entire ranges captured with abundance data (that is, we do not have abundance data for Canadian species), so that some artificial boundary limits will be imposed in the modeling process.
6. The DISTRIB models do not account for many life history and ecological community-related

attributes (for example, competition) and disturbance factors that affect species' abundance, although we are attempting to account for these to some extent with ModFacs.

Important strengths of our modeling approach are listed below, the first nine of which have been discussed above:

1. We use extremely robust nonparametric statistical tools using the "tri-model" approach capped by randomForest.
2. FIA and BBS data are extensive, statistically sound, non-biased, and abundance-based. Thus, the analysis and prediction are based on the species' core of distribution via abundances rather than 'fuzzy' range boundaries.
3. The use of 31 non-climate variables to model tree species abundance helps capture possible 'barriers' or 'facilitators' to species' movement.
4. The reliability of individual species models can be evaluated.
5. The models have had some validation via independent studies (Woodall and others 2009) and modeling (Swanston and others 2011) approaches.
6. The models allow production of ranked lists of species that may be in greatest risk or likely to have sufficient suitable habitat for future management, and for combination into forest type projections.
7. The SHIFT models allow for evaluation of potential colonization within new suitable habitat.
8. The ModFacs allow for consideration of unknown or unknowable factors in model outputs.
9. The scale of influence can be evaluated via the products of the randomForest analysis.
10. By combining multiple plots within a 20 × 20 km cell, the models reduce local heterogeneity for more regional accuracy.
11. The nonparametric, statistical models use different variables/parameters to describe primary drivers in different parts of its geographic setting. This is a large advantage over multiple regression approaches that force variables to operate the same everywhere.
12. The DISTRIB models are based on statistical inference and, contrary to most process models, need not be parameterized with a large suite of variables that are imperfectly known or cannot be adequately generalized for a species throughout its range.

RECOMMENDATIONS FOR MANAGERS AND POLICY DECISION MAKERS

We provide the following for researchers, managers, and decision makers to place these results in perspective as they face the difficult challenges of managing under climate change.

1. Regarding climate change predictions: plan for species habitat to change as projected under high emissions (as this is the trajectory the globe is presently on; Canadell and others 2007) but work to encourage lower emissions.
2. It is likely that SDMs produced before the explosion of machine-learning tools (for example, around 2005) will be inferior to those produced later. Insist on robust predicting tools for species-level modeling.
3. Pay attention to the reliability of each species model and even for high reliability models, there still will be errors and uncertainties! Some of these uncertainties can be characterized with the ModFacs.
4. Models involving less common species are more prone to error. Rare species are especially difficult (Schwartz and others 2006).
5. Range boundaries are 'fuzzy', both now and in future. Core areas of higher abundances are more indicative of potential species behavior under climate change.
6. Use species models as guidelines for regional trends. Because of uncertainties and scale, they are not usually appropriate for fine-scale management without the regional context.
7. Consider modifying factors (for example, disturbance, biological) not included in the models as modifiers to model outputs. Use the ModFacs as a starting place for species-specific analysis and planning; local-level variations in the species scores are expected.
8. Concentrate on the factors you can do something about (for example, silvicultural options).
9. Encourage multiple modeling efforts—statistical, process-based, and hybrids—so that where models agree, confidence is strengthened, and where they disagree, a closer look is warranted.

Abiding by these considerations allows for a careful exploration of the species-distribution models. From this, it is possible to learn which species habitats are present, or could occur, in your region now. This includes identifying those that could incur the most risk (for example, local extinction), or even become newly suitable for your location

under climate change. In addition, the models themselves provide opportunities to learn about which environmental factors are likely driving species' suitable habitat, for example, which species are most susceptible to changing climatic factors. Furthermore, with ModFacs, we can identify which factors are most likely to modify model outputs, whether they will increase or decrease the changes projected with the species modeling, and which factors you might be able to influence via management. Finally, with outputs from a model like SHIFT, learn where potential colonization could occur within 100 years. Of course, the pursuit of understanding the determinants of species distributions and climate change responses will continue and healthy debate will push the field to new discoveries and insights. We support and have learned that drawing from the strengths of a multi-pronged approach to overcome individual model assumptions pushes us towards building a comprehensive perspective of how species may respond to climate change.

ACKNOWLEDGMENTS

The authors are grateful to a great number of associates, users, critics, supporters, and reviewers over the years for their help in making this work possible. Funding support has primarily been through the U.S. Forest Service's Northern Global Change Program. Special thanks to Janet Franklin, Matthew Fitzpatrick, Susan Wright, Susan Stout, and two anonymous reviewers for their reviews.

REFERENCES

- Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int J Plant Sci* 164:S165–84.
- Allen C, Macaladyb A, Chenchounic H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshear D, Hoggi E, Gonzalez P, Fensham R, Zhangm Z, Castron J, Demidavao N, Lim J-H, Allard G, Running S, Semerci A, Cobb N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag* 259:660–84.
- Anderson BJ, Akcakaya HR, Araujo MB, Fordham DA, Martinez-Meyer E, Thuiller W, Brook BW. 2009. Dynamics of range margins for metapopulations under climate change. *Proc R Soc B Biol Sci* 276:1415–20.
- Araujo M, New M. 2007. Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–7.
- Austin MP. 1980. Searching for a model for use in vegetation analysis. *Plant Ecol* 42:11–21.
- Austin MP. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol Modell* 157:101–18.
- Bachelet D, Neilson RP, Lenihan JM, Drapek RJ. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* 4:164–85.
- Bachelet D, Neilson RP, Hickler T, Drapek RJ, Lenihan JM, Sykes MT, Smith B, Sitch S, Thonicke K. 2003. Simulating past and future dynamics of natural ecosystems in the United States. *Global Biogeochem Cycles* 17:14–21.
- Beale CM, Lennon JJ, Gimona A. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proc Natl Acad Sci USA* 105:14908–12.
- Botkin DB, Saxe H, Araujo MB, Betts R, Bradshaw RHW, Cedhagen T, Chesson P, Dawson TP, Etterson JR, Faith DP, Ferrier S, Guisan A, Hansen AS, Hilbert DW, Loehle C, Margules C, New M, Sobel MJ, Stockwell DRB. 2007. Forecasting the effects of global warming on biodiversity. *Bioscience* 57:227–36.
- Box G, Draper NR. 1987. *Empirical model-building and response surfaces*. New York: Wiley.
- Box EO, Crumpacker DW, Hardin ED. 1999. Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. *Climatic Change* 41:213–48.
- Breiman L. 2001. Random forests. *Machine Learning* 45:5–32.
- Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J, Anderson JJ, Myers OB, Meyer CW. 2005. Regional vegetation die-off in response to global-change-type drought. *Proc Natl Acad Sci USA* 102:15144–8.
- Bu R, He HS, Hu Y, Chang Y, Larsen DR. 2008. Using the LANDIS model to evaluate forest harvesting and planting strategies under possible warming climates in northeastern China. *For Ecol Manag* 254:407–19.
- Burns RM, Honkala BH. 1990a. *Silvics of North America: 1. Conifers*. Washington, DC: U.S. Department of Agriculture Forest Service.
- Burns RM, Honkala BH. 1990b. *Silvics of North America: 2. Hardwoods*. Washington, DC: U.S. Department of Agriculture Forest Service.
- Canadell JG, Le Quere C, Raupach MR, Field CB, Buitenhuis ET, Ciais P, Conway TJ, Gillett NP, Houghton RA, Marland G. 2007. Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc Natl Acad Sci USA* 104:18866–70.
- Clark JS, Bell DM, Hersh MH, Nichols L. 2011. Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. *Global Change Biol*. doi:10.1111/j.1365-2486.2010.02380.x.
- Cramer W, Kicklighter DW, Bondeau A, Iii BM, Churkina G, Nemry B, Ruimy A, Schloss AL, The Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): Overview and key results. *Global Change Biol* 5(Suppl 1):1–15.
- Crookston NL, Rehfeldt GE, Dixon GE, Weiskittel AR. 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. *For Ecol Manag* 260:1198–211.
- Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ. 2007. Random forests for classification in ecology. *Ecology* 88:2783–92.
- Davis MB. 1981. Quaternary history and the stability of forest communities. In: West DC, Shugart HH, Eds. *Forest succession: concepts and application*. New York: Springer-Verlag. p 132–53.

- DeHayes DH, Jacobson GL, Schaber PG, Bongarten B, Iverson LR, Dieffenbacher-Krall A. 2000. Forest responses to changing climate: lessons from the past and uncertainty for the future. In: Mickler RA, Birdsey RA, Hom JL, Eds. Responses of northern forests to environmental change. Ecological Studies Series. New York: Springer-Verlag. p 495–540.
- Dormann CF. 2007. Promising the future? Global change projections of species distributions. *Basic Appl Ecol* 8:387–97.
- Elith J, Graham CH. 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32:66–77.
- Elith J, Graham CH, Anderson RP, Dudyk M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scabetti-Pereira R, Schapire RE, Sobero'n J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–51.
- Elith J, Kearney M, Phillips S. 2010. The art of modelling range-shifting species. *Methods Ecol Evol* 1:330–42.
- Engler R, Guisan A. 2009. Migclim: Predicting plant distribution and dispersal in a changing climate. *Divers Distrib* 15:590–601.
- Engler R, Randin CF, Vittoz P, Czaka T, Beniston M, Zimmermann NE, Guisan A. 2009. Predicting future distributions of mountain plants under climate change: Does dispersal capacity matter? *Ecography* 32:34–45.
- Ferrier S, Guisan A. 2006. Spatial modelling of biodiversity at the community level. *J Appl Ecol* 43:393–404.
- Ferrier S, Manion G, Elith J, Richardson K. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers Distrib* 13:252–64.
- Fitzpatrick MC, Gove AD, Sanders NJ, Dunn RR. 2008. Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Global Change Biol* 14:1337–52.
- Franklin J. 2009. Mapping species distributions: Spatial inference and prediction. Cambridge, UK: Cambridge University Press. 320p.
- Franklin J. 2010. Moving beyond static species distribution models in support of conservation biogeography. *Divers Distrib* 16:321–30.
- Frumhoff PC, McCarthy JJ, Mellilo JM, Moser SC, Wuebbles DJ. 2007. Confronting climate change in the U.S. Northeast: Science, impacts, and solutions. Synthesis report of the Northeast Climate Impacts Assessment (NECIA). Cambridge (MA): Union of Concerned Scientists.
- Gonzalez P, Neilson RP, Lenihan JM, Drapek RJ. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecol Biogeogr* 19:755–68.
- Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009.
- Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecol Modell* 135:147–86.
- Hargrove WW, Potter KM, Koch FH. 2010. The ForeCASTS project: Forecasts of climate-associated shifts in tree species. Eastern Forest Environmental Threat Assessment Center. USDA Forest Service. http://www.geobabble.org/~hnw/global/treeranges2/climate_change/index.html.
- Hayhoe K, Wuebbles D, Climate Science Team. 2008. Climate change and Chicago: Projections and potential impacts. Chicago (IL): Chicago Climate Action Plan. 33p.
- He HS, Mladenoff DJ, Crow TR. 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecol Modell* 114:213–33.
- He H, Keane RK, Iverson LR. 2008. Forest landscape models, a tool for understanding the effect of the large-scale and long-term landscape processes. *For Ecol Manag* 274:371–4.
- Huntley B, Barnard P, Altwegg R, Chambers L, Coetsee BWT, Gibson L, Hockey PAR, Hole DG, Midgley GF, Underhill LG, Willis SG. 2010. Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. *Ecography* 33:621–6.
- Ibanez I, Clark JS, Dietze MC, Felley K, Hersh M, LaDeau S, McBride A, Welch NE, Wolosin MS. 2006. Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology* 87:1896–906.
- Iverson LR, Prasad AM. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol Monogr* 68:465–85.
- Iverson LR, Prasad AM. 2001. Potential changes in tree species richness and forest community types following climate change. *Ecosystems* 4:186–99.
- Iverson LR, Prasad AM. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. *For Ecol Manag* 155:205–22.
- Iverson LR, Prasad A, Scott CT. 1996. Preparation of forest inventory and analysis (FIA) and state soil geographic data base (STATSGO) data for global change research in the eastern United States. In: Hom J, Birdsey R, O'Brian K, Eds. Proceedings, 1995 meeting of the northern global change program. General Technical Report NE-214, Forest Service, Northeastern Forest Experiment Station, U.S. Department of Agriculture, Radnor, PA, pp. 209–14.
- Iverson LR, Prasad AM, Hale BJ, Sutherland EK. 1999a. An atlas of current and potential future distributions of common trees of the eastern United States. General Technical Report NE-265. Radnor (PA): Northeastern Research Station, USDA Forest Service. 245 p.
- Iverson LR, Prasad AM, Schwartz MW. 1999b. Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: a case study with *Pinus virginiana*. *Ecol Modell* 115:77–93.
- Iverson LR, Schwartz MW, Prasad A. 2004a. How fast and far might tree species migrate under climate change in the eastern United States? *Glob Ecol Biogeogr* 13:209–19.
- Iverson LR, Schwartz MW, Prasad AM. 2004b. Potential colonization of new available tree species habitat under climate change: an analysis for five eastern US species. *Landscape Ecol* 19:787–99.
- Iverson LR, Prasad AM, Matthews SN. 2008a. Modeling potential climate change impacts on the trees of the north-eastern United States. *Mitig Adapt Strat Glob Change* 13:487–516.
- Iverson LR, Prasad AM, Matthews SN, Peters M. 2008b. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *For Ecol Manag* 254:390–406.
- Keane RE, Holsinger LM, Parsons RA, Gray K. 2008. Climate change effects on historical range and variability of two large landscapes in western Montana, USA. *For Ecol Manag* 254:375–89.

- Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *J Veg Sci* 3:157–64.
- Keith DA, Akçakaya HR, Thuiller W, Midgley GF, Pearson RG, Phillips SJ, Regan HM, Araújo MB, Rebelo TG. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol Lett* 4:560–3.
- Kirilenko AP, Belotelov NV, Bogatyrev BG. 2000. Global model of vegetation migration: incorporation of climatic variability. *Ecol Modell* 132:125–33.
- Lawler JJ, O'Connor RJ. 2004. How well do consistently monitored breeding bird survey routes represent the environments of the conterminous United States? *Condor* 106:801–14.
- Lawler JJ, White D, Neilson RP, Blaustein AR. 2006. Predicting climate-induced range shifts: model differences and model reliability. *Global Change Biol* 12:1568–84.
- Leng W, He HS, Bu R, Dai L, Hu Y, Wang X. 2008. Predicting the distributions of suitable habitat for three larch species under climate warming in northeastern China. *For Ecol Manag* 254:420–8.
- Little EL. 1971. Atlas of United States trees. Volume 1. Conifers and important hardwoods. Miscellaneous publication 1146. Washington, DC: U.S. Department of Agriculture, Forest Service.
- Lo Y-H, Blanco JA, Kimmins J. 2010. A word of caution when planning forest management using projections of tree species range shifts. *Forestry Chronicle* 86:312–16.
- Matthews SN, Iverson LR, Prasad AM, Peters MP. 2011. Potential habitat changes of 147 North American bird species to redistribution of vegetation and climate following predicted climate change. *Ecography*. doi:10.1111/j.1600-0587.2011.06803.x.
- Matthews SN, Iverson LR, Prasad AM, Peters MP. 2007. A climate change atlas for bird species of the eastern United States [database]. Northern Research Station, USDA Forest Service, Delaware, OH. www.fs.fed.us/ne/delaware/atlas.
- Matthews SN, Iverson LR, Prasad AM, Peters MP, Rodewald PG. Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history factors. *For Ecol Manag* (in press).
- McKenney DW, Pedlar JH, Hutchinson MF, Lawrence K, Campbell K. 2007. Potential impacts of climate change on the distribution of North American trees. *Bioscience* 57:939–48.
- McLachlan JS, Clark JS, Manos PS. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86:2007–17.
- Meentemeyer RK, Anacker B, Mark W, Rizzo D. 2008. Early detection of emerging forest disease using dispersal estimation and ecological niche modeling. *Ecol Appl* 18:377–90.
- Midgley GF, Davies ID, Albert CH, Altwegg R, Hannah L, Hughes GO, O'Halloran LR, Seo C, Thorne JH, Thuiller W. 2010. BioMove—an integrated platform simulating the dynamic response of species to environmental change. *Ecography* 33:612–16.
- Miles PD, Brand GJ, Alerich CL, Bednar LR, Woudenberg SW, Glover JF, Ezzell EN. 2001. The forest inventory and analysis database: database description and users manual version 1.0. General Technical Report NC-218. St. Paul (MN): North Central Research Station, USDA Forest Service. 130 p.
- Moore DE, Lees BG, Davey SM. 1991. A new method for predicting vegetation distributions using decision tree analysis in a geographic information system. *J Environ Manag* 15:59–71.
- Neilson RP, Pitelka LF, Solomon AM, Nathan RAN, Midgley GF, Fragoso JMV, Lischke H, Thompson KEN. 2005. Forecasting regional to global plant migration in response to climate change. *Bioscience* 55:749–59.
- Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12:361–71.
- Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC. 2006. Model-based uncertainty in species range prediction. *J Biogeogr* 33:1704–11.
- Peterson AT, Stewart A, Mohamed KI, Araujo MB. 2008. Shifting global invasive potential of European plants with climate change. *Plos One* 3(6):e2441. doi:10.1371/journal.pone.0002441.
- Prasad AM, Iverson LR. 1999. A climate change atlas for 80 forest tree species of the eastern United States [database]. Northeastern Research Station, USDA Forest Service, Delaware, OH. www.fs.fed.us/ne/delaware/atlas.
- Prasad AM, Iverson LR, Liaw A. 2006. Newer classification and regression tree techniques: bagging and random forests for ecological prediction. *Ecosystems* 9:181–99.
- Prasad AM, Iverson LR, Matthews S, Peters M. 2007. A climate change atlas for 134 forest tree species of the eastern United States [database]. Northern Research Station, USDA Forest Service, Delaware, OH. www.nrs.fs.fed.us/atlas/tree.
- Prasad A, Iverson L, Matthews S, Peters M. 2009. Atlases of tree and bird species habitats for current and future climates. *Ecol Restor* 27:260–3.
- Prasad A, Iverson L, Peters M, Bossenbroek J, Matthews SN, Sydnor D, Schwartz M. 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. *Landscape Ecol* 25:353–69.
- Real R, Márquez AL, Olivero J, Estrada A. 2010. Species distribution models in climate change scenarios are still not useful for informing policy planning: an uncertainty assessment using fuzzy logic. *Ecography* 33:304–14.
- Sauer JR, Hines JE, Fallon J. 2001. The North American Breeding Bird Survey, results and analysis, 1966–2000. Laurel (MD): USGS Patuxent Wildlife Research Center.
- Scheller RM, Mladenoff DJ. 2008. Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. *Clim Res* 36:191–202.
- Schwartz MW, Iverson LR, Prasad AM. 2001. Predicting the potential future distribution of four tree species in Ohio, USA, using current habitat availability and climatic forcing. *Ecosystems* 4:568–81.
- Schwartz MW, Iverson LR, Prasad AM, Matthews SN, O'Connor RJ. 2006. Predicting extinctions as a result of climate change. *Ecology* 87:1611–15.
- Shifley S, Thompson F, Dijak W, Larson M, Millsbaugh J. 2006. Simulated effects of forest management alternatives on landscape structure and habitat suitability in the midwestern United States. *For Ecol Manag* 229:361–77.
- Sitch S, Smith B, Prentice I, Arneth A, Bondeau A, Cramer W, Kaplan J, Levis S, Lucht W, Sykes M, Thonicke K, Venevsky S. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic vegetation model. *Global Change Biol* 9:161–85.
- Swanston C, Janowiak M, Iverson L, Parker L, Mladenoff D, Brandt L, Butler P, St. Pierre M, Prasad AM, Matthews S,

- Peters M, Higgins D. 2011. Ecosystem vulnerability assessment and synthesis: a report from the climate change response framework at Chequamegon-Nicolet National Forest project, version 1. Houghton, MI: Northern Research Station, USDA Forest Service.
- Tchebakova NM, Rehfeldt GE, Parfenova EI. 2006. Impacts of climate change on the distribution of *Larix* spp. and *Pinus sylvestris* and their climatotypes in Siberia. *Mitig Adapt Strat Glob Change* 11:861–82.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, Van Jaarsveld A, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004. Extinction risk from climate change. *Nature* 427:145–8.
- Thuiller W, Lavorel S, Sykes MT, Araujo MB. 2006a. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Divers Distrib* 12:49–60.
- Thuiller W, Midgley GF, Hughes GO, Bomhard B, Drew G, Rutherford MC, Woodward FI. 2006b. Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biol* 12:759–76.
- Thuiller W, Albert C, Araujo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspect Plant Ecol Evol Syst* 9:137–52.
- Union of Concerned Scientists. 2008. Climate change in Pennsylvania: impacts and solutions for the keystone state. Cambridge (MA): Union of Concerned Scientists.
- U.S. National Assessment Synthesis Team. 2000. Climate change impacts on the United States: the potential consequences of climate variability and change Foundation report. Washington, DC: U.S. Global Change Research Program.
- Webb T, Bartlein PJ. 1992. Global changes during the last 3 million years: climatic controls and biotic responses. *Annu Rev Ecol Syst* 23:141–73.
- Westerling AL. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–3.
- Wiens JA. 1989. Spatial scaling in ecology. *Funct Ecol* 3:385–97.
- Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc Natl Acad Sci USA* 106:19729–36.
- Williams JW, Jackson ST, Kutzbach JE. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proc Natl Acad Sci USA* 104:5738–42.
- Williams NSG, Hahs AK, Morgan JW. 2008. A dispersal-constrained habitat suitability model for predicting invasion of alpine vegetation. *Ecol Appl* 18:347–59.
- Woodall C, Oswalt CM, Westfall JA, Perry CH, Nelson MD, Finley AO. 2009. An indicator of tree migration in forests of the eastern United States. *For Ecol Manag* 257:1434–44.