

Tree-species range shifts in a changing climate: detecting, modeling, assisting

Louis R. Iverson · Donald McKenzie

Received: 18 April 2012 / Accepted: 25 March 2013 / Published online: 4 April 2013
© Springer Science+Business Media Dordrecht(outside the USA) 2013

Abstract In these times of rapidly changing climate, the science of detecting and modeling shifts in the ranges of tree species is advancing of necessity. We briefly review the current state of the science on several fronts. First, we review current and historical evidence for shifting ranges and migration. Next, we review two broad categories of methods, focused on the spatial domain, for modeling potential range shifts and future suitable habitat: empirical species-distribution models and more process-based simulations. We propose long-term demography studies as a complementary approach in the time domain when sufficient data are available. Dispersal and successful migration into newly suitable habitat are key mechanisms constraining range shifts. We review three approaches to estimating these processes, followed by a discussion of the potential for assisted migration. We conclude that there have been significant recent advances on several fronts but there are still large uncertainties that need further research.

Keywords Species distribution models · Process-based · Demography · Assisted migration

L. R. Iverson (✉)
Northern Research Station, US Forest Service,
359 Main Road, Delaware, OH 43015, USA
e-mail: liverson@fs.fed.us

D. McKenzie
Pacific Wildland Fire Sciences Lab, US Forest Service,
400 N 34th St #201, Seattle, WA 98103, USA

Introduction: range shifts are nothing new

Species have always moved about the landscape (Davis and Zabinski 1992; Webb 1992; Davis and Shaw 2001), but in recent decades, evidence is building that species are moving much faster than in historical times (Parmesan and Yohe 2003; Chen et al. 2011; Dobrowski et al. 2011). For example, a meta-analysis of 764 species (mostly arthropods and no tree species) found the average rate of poleward migration to be 16.9 km/decade (Chen et al. 2011). An earlier meta-analysis, using 99 species of birds, butterflies, and alpine herbs, reported a poleward migration of 6.1 km/decade (Parmesan and Yohe 2003). These global estimates across many taxa are much higher than pollen-estimated rates for some tree species of 2–2.5 km/decade between 6,000 to 5,000 years ago (Davis 1989). Consider also that the Holocene migration occurred when species were not slowed by forest fragmentation, which can reduce expected migration rates dramatically (Schwartz 1993; Iverson et al. 2004a). Although there is evidence for upward elevational migration of tree species (Kullman 2002; Beckage et al. 2008; Holzinger et al. 2008; Lenoir et al. 2008), there is a paucity of studies that clearly document poleward migration for trees (Zhu et al. 2011).

Woodall et al. (2009) investigated surrogates for migration among 40 eastern U.S. tree species using Forest Inventory Analysis (FIA) data. They compared the mean latitude of biomass of larger trees [>2.5 cm

diameter breast height (dbh)] to the mean latitude of 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, this analysis indicated higher regeneration success at the northern edge of their ranges. Compared to mean latitude of tree biomass, mean latitude of seedlings was significantly farther north (>20 km) for the northern study species, while southern species had no shift, and general species demonstrated southern expansion. Density of seedlings relative to tree biomass of northern tree species was nearly ten times higher in northern latitudes than in southern latitudes. These results suggest that the process of northward tree migration in the eastern United States is currently underway with rates approaching 100 km/century for many species. Schuster et al. (2008) noted invasions of species from the south and declines of northern species for several species over a 76-year period in a forest in New York, and Treyger and Nowak (2011), also working in New York, noted similar trends inside powerline corridors between 1975 and 2003. Gamache and Payette (2005) found that black spruce (*Picea mariana*) treelines in northern Quebec, Canada expanded significantly in response to climate warming in the past decades. Caccianiga and Payette (2006), working in the same region, also found white spruce (*Picea glauca*) to change from stunted to tree growth forms in recent decades. Lloyd and Fastie (2003) found recent poleward advances by white spruce in interior Alaska corresponding to recent climate warming there. Kharuk et al. (2007) found evidence for climate-driven migration of Siberian pine (*Pinus sibirica*), spruce (*Picea obovata*), and fir (*Abies sibirica*) into the traditional zone of larch (*Larix gmelinii*, *L. sibirica*) dominance in central Asia.

Modeling potential future habitat shifts of trees

We now briefly review modeling approaches, with a very few examples, to assess potential future habitat shifts of trees, remembering that all models are simplifications of reality in an uncertain and changing world. There is a great deal of complexity to consider, as evidenced by the many intrinsic and extrinsic factors that may increase a species' or population's risk of extinction, extirpation, or genetic degradation (Table 1). For models to be useful (Box and Draper

1987), they must enhance our understanding of current and potential future species distributions. Predictive models of vegetation change are often divided into two categories: process-based models, which are usually simulations of vegetation dynamics at the taxonomic resolution of species or life forms, and empirical models that establish statistical relationships between species or life forms and (often numerous) predictor variables. More and more there are hybrid models, extensions to SDMs that include elements of process models that provide additional scope and power to take advantage of the best of both worlds. However, there always will be trade-offs between using complex mechanistic models versus the simpler empirical models to assess possible changes in species habitats resulting from forecasts of environmental change (Thuiller et al. 2008; Fig. 1).

Species distribution models

Species distribution models (SDMs) project future species distributions based on statistical associations

Table 1 Intrinsic and extrinsic factors affecting a species or population of forest trees that may increase its risk of extinction, extirpation, or genetic degradation (revised from Potter et al. 2010)

Intrinsic factors	Extrinsic factors
Limited range	Extensive fragmentation
Small/disjunct populations	Pest/pathogen infestation
Limited to high elevations	Large shift of range with climate change
Long lifespan	Herbivore browsing
Long time to reproduction	Invasive plant competition
Low fecundity	Excessive drought, flood, wind, ice, fire
Physical habitat specialization	Exploitation by humans
Limited seed/pollen dispersal	Exposure to atmospheric pollutants
Low species-wide genetic variation	Geographic dispersal barriers
Late successional species	Anthropogenic dispersal barriers
Dependence on specific disturbance regime	Exposure to sea-level rise
Reliance on interspecific interactions	
Sensitivity to temperature and precipitation change	
Lack of phenological flexibility	

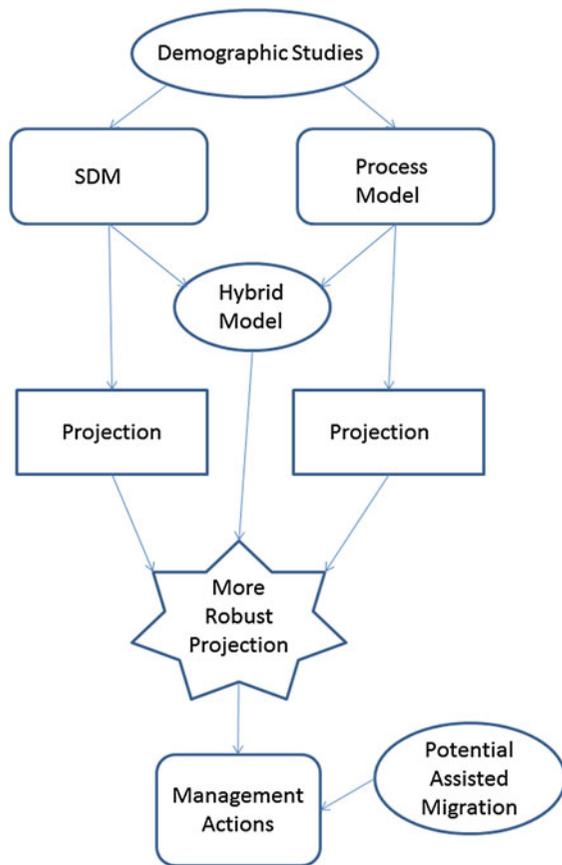


Fig. 1 Steps in data collection, modeling, projection, and management of tree species distributions in a changing climate. Projections are made more robust either by comparing SDMs to process-based models post hoc, or building hybrid models from scratch (see text). *SDM* species distribution models

between species occurrence or abundance and environmental (predictor) variables thought to influence habitat suitability (Franklin 2009). When predictors are chiefly or only climate variables, SDMs are often called climate envelope models (CEMs). Projecting these models onto future climate spaces predicts and maps suitable habitat (though not whether or not a species will reach those habitats). Numerous statistical methods have been used to build SDMs, well reviewed in Franklin (2009). Some of the more recent (since 2005) methods are proving to be more accurate overall than older methods (Elith et al. 2006; Prasad et al. 2006; Cutler et al. 2007; Franklin 2009). For example, machine learning algorithms like Random Forests (Breiman 2001), stochastic gradient boosting (Friedman 2002), or maximum entropy (Elith et al. 2011)

have been shown to perform better in prediction than most other methods (Elith et al. 2006). SDMs have limitations, however, which include the assumptions that the selected variables do in fact reflect the niche requirements of a species, that species are in equilibrium with their suitable habitat, that species will be able to disperse to their suitable locations, that predictions can be made into novel climates and land covers, that the effects of adaptation and evolution are minimal, and that the effects of biotic interactions (including human interactions) are minimal (Ibanez et al. 2006; Pearson et al. 2006; Prasad et al. 2006; Fitzpatrick and Hargrove 2009). Nevertheless, SDMs can still approximate potential species habitat for scores of species using multiple future scenarios of climate and human-based decisions, and thus be useful for conservation and management, especially given that ignoring the inevitability of future changes in a rapidly changing climate is not a realistic option (Wiens et al. 2009).

SDMs are growing in use and influence throughout the world, as evidenced by the number of publications referring to them. A Web of Science inventory, using the same key words as used by Franklin (2009, p. 235) of “species distribution model”, “ecological niche model”, or “climat* niche model”, yielded the following numbers of publications: 26 in 2009, 49 in 2010, 83 in 2011, and 103 in 2012 (plus 10 up to early March 2013). Of these, 60 citations also had the keyword “tree*”, although only 25 truly had tree distribution modeling as the primary topic. We introduce only a very few here but encourage readers to conduct similar searches to capture the breadth of papers on the topic. Several recent studies show an increasing sophistication to the modeling approach, by adding different (and often nonclimatic) variables, using multiple and finer scales of predictors, or inserting methods to incorporate biotic interactions or disturbances.

McKenney et al. (McKenney et al. 2007, 2011) projected an average northward movement of the climate habitat for 130 tree species of roughly 700 km by end of century. Three models (CGCM3.1, CSIRO-MK3.5, CCSM3.0) converged under the A2 emissions scenario, in projecting potential northward shifts of 6°–7° latitude (~700 km), while also projecting large losses of climate habitat in the eastern United States. See <http://planthardiness.gc.ca/index.pl?lang=en> for species-level climate-envelope maps for a series of

scenarios and GCM models. The “ForeCASTS” project (Potter et al. 2010) uses multi-spectral spatial clustering to model environmental niches for current species distributions, with the PCM and HadleyCM3 climate models and A1 and B1 emission scenarios. For example, in the A1 scenario, red spruce (*Picea rubens*) gains habitat through 2050, but then loses from 2050 to 2100 (see http://www.geobabble.org/~hnrw/global/treeranges2/climate_change/Picea_rubens.elev.html). Potter et al. (2010) estimated the straight-line minimum required migration (MRM) distance from each 4 km² grid cell in a species’ current suitable habitat to the nearest favorable future habitat. The greater this distance, the less likely that the species will be able to reach the nearest refuge, and the more likely that the species will become locally extinct.

Iverson et al. (2008) assessed potential future habitat changes in eastern U.S. trees, using 38 environmental variables including seven climate variables. For 134 tree species, the “mean centers” of habitat were predicted to move northeastward by 2100, from up to 400 km for the less CO₂-sensitive model (PCM) with high resource efficiency (B1) to 800 km in the more sensitive (HadleyCM3) model with “business as usual” (A1F1). Under HadleyCM3 A1F1, 66 species would gain and 54 species would lose at least 10 % of their suitable habitat under climate change. A lower emission pathway would reduce both losers and gainers. The iconic sugar maple would lose most of its habitat across the east central U.S. under the most severe scenario (Lovett and Mitchell 2004; Iverson et al. 2008), but it would still maintain a reduced presence throughout (see http://www.nrs.fs.fed.us/atlas/tree/summ6pp_318.html). When species were aggregated to forest types, suitable habitat for spruce-fir (*Picea-Abies*), white-red-jack pine (*Pinus strobus*, *P. resinosa*, *P. banksiana*), and aspen-birch (*Populus-Betula*) was lost, but expanded for oak-hickory (*Quercus-Carya*) (Iverson and Prasad 2001; Iverson et al. 2008, see also http://www.nrs.fs.fed.us/atlas/tree/ft_summary.html). These species models have been enhanced by 21 species-specific modification factors, such as capacities to compete for light or endure fire, drought, flood, or browsing (Matthews et al. 2011). Using these in a large vulnerability assessment for northern Wisconsin, Swanston et al. (2011) found that the most vulnerable species were those in northern part of the range, but although these species’ habitats decline drastically, refugia are

expected to remain in places like coves or low-lying north-facing slopes.

Many other studies have used SDMs throughout the world to assess potential outcomes of climate change on trees. For example, (McLaughlin and Zavaleta 2012) used field data and separate SDMs on juvenile versus adult plants of California valley oak (*Quercus lobata*) and found that juveniles are more sensitive to warming temperatures and that their habitats generally constrict into refugia around water bodies with increasing temperatures. Meier et al. (2012) evaluated 14 European tree species in relation to climate, topography, soil and land-use data to predict current and future tree distributions, and assessed the role of competition and connectivity in potential migration rates of those species. Nabout et al. (2011) assessed the production of “Pequi” fruits in the Brazilian Cerrado under climate change. Hsu et al. (2012) evaluated eight forest types and 237 vascular epiphytes on the Island of Taiwan for potential habitat changes by 2100. Chitale and Behera (2012) developed a SDM to evaluate potential future trends in *Shorea robusta* in India, as did Esteve-Selma et al. (2012) for *Tetraclinis articulata* in southeastern Spain, Luna-Vega et al. (2012) for *Ternstroemia lineata* in cloud forests of Mexico, and Shimazaki et al. (2012) for *Abies mariesii* on Honshu Island, Japan.

Although these studies differed in data and methods, there was generally a consistent pattern of projections of poleward or upslope movement of habitat throughout this century. In an evaluation of many SDMs, Schwartz (2012) asserted that for conservation purposes, they are generally more useful in estimating future habitat (poleward or upslope) than in estimating where current habitat will no longer exist under future states. We agree.

Process-based models

To model species composition changes, a fully process-driven dynamic approach is often thought preferable to SDMs and other equilibrium methods, because it simulates mechanisms, from the physiological to the biogeographic, and can simulate multiple “what-if” scenarios. It is especially true that such models may be superior to SDMs when novel climates are predicted, although there are ways to take the novelty of future climates into consideration upon interpretation of SDM outputs (Matthews et al. 2011).

Process models also are better able to deal with the enhanced productivity possible via elevated CO₂ and increased water use efficiency (Keenan et al. 2011). However, the process-model approach is also limited in that it requires (1) detailed parameterization of life histories and physiologies, (2) capturing the complexity of many interacting disturbance factors, and (3) high-resolution modeling over very large areas (Lawler et al. 2006). Besides these logistical limitations, there are intrinsic problems with controlling cumulative errors associated with the sheer number and diverse spatio-temporal scales of parameters, most of which ultimately being derived from a limited number of empirical studies (Kennedy and Ford 2011). Process-based models are still a valuable tool, however, because much of this uncertainty can be incorporated in reporting projections, such that just as with SDMs, the limits of modeling are clear. A few examples highlight both power and potential of the process modeling approach.

Bachelet et al. (2008) used a dynamic global vegetation model (DGVM), MC1, to predict continental-scale (US) changes in tree life forms and carbon in a warming climate. The warmer and drier scenarios in these experiments show some potential for the habitat of the eastern deciduous and mixed forests to shift to a more open canopy woodland or savanna type while the boreal forests disappear almost entirely from the Great Lakes area by the end of the 21st century (Bachelet et al. 2008). These changes would obviously markedly change the character of these biomes and greatly reduce carbon storage in the eastern U.S. Other studies using DGVMs have shown potential large impacts of climate change in high latitudes (Jiang et al. 2012), over the tropics (Good et al. 2011), on the African continent (Scheiter and Higgins 2009; Sato and Ise 2012), and globally (Heyder et al. 2011).

Ravenscroft et al. (2010) used the spatially dynamic forest landscape model LANDIS to simulate the potential effects of climate change to 2195 in the north-central US and found that two forest types, mesic birch–aspen–spruce–fir and jack pine–black spruce (*Pinus banksiana*–*Picea mariana*), would be substantially altered by the loss of northern species and the expansion of red (*Acer rubrum*) and sugar maple (*A. saccharum*). Xu et al. (2012) coupled LANDIS-II with a forest ecosystem process model, PnET-II, in Minnesota, USA for 13 tree species for the period 2000–2400, and found both competitive and colonization abilities changed over time in response to

climatic change. He et al. (1999) performed early hybrid modeling by combining LANDIS with another process model, LINKAGES, to assess potential changes under climate warming.

Another process-based model that incorporates climate is the Regional Hydro-Ecologic Simulation System (RHESSys) (Tague and Band 2004). In a Sierra Nevada mountain system, Tague et al. (2009) found significant elevational differences in vegetation water use and sensitivity to climate, which will probably be critical for the vulnerability of similar ecosystems under climate change. In these model results, transpiration was consistent across years at the lowest elevations because of topographically controlled high moistures, the middle-elevation transpiration rates were controlled primarily by precipitation, and the high-elevation transpiration rates were controlled primarily by temperatures. These dynamics, along with evidence for reduced snow accumulation and earlier melt of seasonal snowpacks, are expected to influence future species composition in mountainous systems.

These studies generally provide evidence, as with the SDMs, that forest composition and productivity are likely to change, often substantially, as the climate changes during this century and beyond.

Towards maximizing the value of both process models and SDMs

In the last paragraph of her treatise on mapping species distributions as well as her follow-on essay, Franklin entreats the research community to focus on adding mechanistic realism to SDMs with respect to potential climate change impacts (Franklin 2009, 2010). There are an increasing number of studies doing just that, with examples of SDMs being linked to dynamic models of dispersal and species migration, disturbance (landscape dynamics), and demographic processes (population dynamics). Some examples include MigClim of Engler et al. (2012) to model dispersal, colonization, growth, and extirpation of populations inside SDM-derived ranges; BioMove of Midgley et al. (2010) and LANDIS (when initial conditions are established by SDMs, e.g., Franklin et al. 2005), which simulate disturbance and succession; and the linked distribution and population viability models of Lawson et al. (2012), which evaluated scenarios of climate

change, land use change, and altered fire frequency in California, USA.

Another important approach to advancing the science is the value of combining multiple modeling approaches toward common objectives (Dawson et al. 2011; Franklin 2012). Iverson et al. (2011) used SDM, life history traits, and a process model for dispersal together to improve projections and interpretations for trees in the eastern United States. Morin and Thuiller (2009) used a SDM and process model in parallel for 15 species in the eastern United States and found more robust results and accuracy in predictions of range shifts under climate change. Swanston et al. (2011) used this approach as well: when the separate modeling approaches agree, there is more confidence in the predictions; when they disagree, there are specific questions that can be pursued.

Demography studies

To understand and better model the dynamic role of climate in relation to other risk factors such as competition for limited resources, individual variation in physiology and function, and vulnerability to natural enemy attack, individual tree responses at as fine a temporal scale as possible (ideally annually) would be preferable. The extra effort of demographic tracking can determine the vulnerability of individual trees to many risk factors, including climate change over time, variation in abiotic variables over space, and competition. This extra knowledge provides valuable insight for process and “extended” SDMs alike. However, demographic data sets that can provide these knowledge gaps are not common. One study tracked >27,000 individuals of 40 species over 6–11 years to address these interactions over a portion of the southeastern U.S. (Clark et al. 2011). Using state-space models that identified annual varying influences of predictors, they found that the primary climatic controls are spring temperature (regulating species fecundity) and growing season moisture, particularly for species of *Pinus*, *Ulmus*, *Magnolia*, and *Fagus*. *Pinus rigida* tracked both spring temperature and summer drought, *Liriodendron* tracked neither, and *Liquidambar* tracked summer drought but not spring temperature (Clark et al. 2011). Overall, the effect of competition on growth and mortality risk exceeded the effects of climate variation for most species.

Other studies have tracked mortality with an eye towards changing conditions in the recent past. Van Mantgem and Stephenson (2007) and van Mantgem et al. (2009) found increasing mortality in recent decades in the western United States, attributed to regional warming and increased water deficits. Yaussy et al. (2012) found primarily competition, followed by climate (especially warming temperatures) as key drivers of mortality of nearly 48,000 trees in the northeastern United States. Vila-Cabrera et al. (2011) found increasing mortality of Scots pine (*Pinus sylvestris*) due to dryness in the Iberian Peninsula, and a consortium of international colleagues provided evidence for increasing mortality due to heat and drought in forests worldwide (Allen et al. 2010).

Dispersal models

To colonize suitable habitat resulting from a changing climate, each species will need to either migrate or be moved. Modeling seed dispersal has a strong theoretical foundation (Levin et al. 2003); recent approaches have built on this foundation in three distinct ways: mechanistic modeling, stochastic modeling, and raster-based probabilistic simulations. Advances in digital computation and more reliable data from seed dispersal studies have allowed improvement of these models so that they can begin to predict the parameter values of seed dispersal curves as well as the seed distributions.

Mechanistic models draw on ideas from computational fluid dynamics (because of the importance of wind and turbulence), advection–diffusion models, and large-eddy simulations (Bohrer et al. 2008) to create explicit mathematical models of all the processes involved in seed dispersal (Nathan et al. 2011a). For example, Nathan et al. (2011b) modeled 12 North American wind-dispersed tree species for current and projected future spread according to ten key dispersal, demographic, and environmental factors. They found a very low likelihood of any of the 12 species being able to spread on the order of 300–500 m year⁻¹, the rate of change expected under climate change (Loarie et al. 2009).

Recent stochastic models incorporate the intrinsic uncertainty of processes such as long-distance dispersal (LDD), acknowledging that dispersal kernels (probability distributions of dispersal distances of individual seeds) can never be precisely known, but that they can be updated continuously with new observations. Clark

et al. (2003) combined a stochastic (statistical) model with a data-assimilation framework (Hanks et al. 2011) to constrain the LDD of *Acer rubrum*, and showed in the process that most dispersal kernels are over-estimated, leading to over-prediction of species migration rates.

Some models can be built to be more data-driven, which may avoid some of the mathematical formalisms of fully mechanistic or arcane statistical models, and thus reduce the cumulative errors of parameter estimation. For example, the SHIFT simulation model uses historical migration rates and the strengths of the seed sources (its abundance within its current range) and potential future sinks (abundance of potential suitable habitat) rather than poorly understood life-history parameters (Schwartz et al. 2001; Iverson et al. 2004a; Prasad et al. 2013). SHIFT outputs of colonization potentials were combined with a simulation of suitable habitat (DISTRIB model) for five species: *Diospyros virginiana*, *Liquidambar styraciflua*, *Oxydendrum arboreum*, *Pinus taeda*, and *Quercus falcata*. Only 15 % of the newly suitable habitat had any likelihood of being colonized by those species within 100 years (Iverson et al. 2004b). Similarly to Clark et al. (2003) and Nathan et al. (2011b), these results suggest that a serious lag will occur between the potential movement of suitable habitat and species migration into that new habitat, a result also complicated by incompatibilities in soil requirements for many species (Lafleur et al. 2010).

Potential for assisted migration

Assisted migration, or perhaps more appropriately “assisted colonization” (synonyms: managed relocation or managed translocation), may be an approach to help mitigate climate change, by intentionally moving species to climatically suitable locations outside their current ranges (McLachlan et al. 2007; Hoegh-Guldberg et al. 2008; Richardson et al. 2009; Schwartz et al. 2012). The question of assisted migration has been controversial, with some groups advocating for (Minteer and Collins 2010; Vitt et al. 2010) and some against (Ricciardi and Simberloff 2009). Proponents state that these drastic measures are needed to save species that cannot adapt or disperse fast enough. Opponents fear that moving species outside their range may disturb other native species and ecosystems

when these “climate refugees” establish themselves in new environments. Lawler and Olden (2011) clearly identify the tools available for evaluating the pros and cons of a proposed action to assist: projection outputs from models such as those described in this paper, knowledge from previous introductions, experiments and observations, and historical records, paleoecological data, and genetic analyses. They also stress that the goals of assisted migration, the realities of possible success, and the potential to use complementary strategies such as enhancing landscape connectivity need also be considered in such decisions.

We can subdivide assisted migration into “rescue assisted migration” and “forestry assisted migration” (Pedlar et al. 2012). The former, moving species to rescue them from extinction in the face of climate change, is the source of most of the controversy. The latter seeks to preserve traditional forestry values of high levels of productivity and diversity in valuable tree species (Gray et al. 2011; Kreyling et al. 2011). With forestry assisted migration, maintaining forest productivity and ecosystem services are the most obvious desired outcomes. Given the broad distribution of most tree species, and the relatively short distances proposed for tree seed migration, forestry assisted migration typically involves transfers within or just beyond current range limits to locations within a population’s near-future bioclimatic envelope (Gray et al. 2011). The introduction of genotypes to climatically appropriate locations may also improve forest health by establishing vigorous plantations that are less susceptible to forest pests and diseases (Wu et al. 2005). If realized, such an outcome would help ensure the continued flow of ecosystem services provided by forests, such as wildlife habitat, erosion prevention, carbon uptake, and many others (Kreyling et al. 2011). Thus, this forestry form of assisted migration is less controversial than the ‘rescue’ approach, and can be a viable tool for adaptation to climate change in the forestry arena.

Conclusions and research needs

Improved understanding of tree-species range shifts requires integrating the insights from models of habitat, demography, dispersal, and life histories (e.g., Iverson et al. 2011). We report key recent studies in each area, and note that the weight of evidence is increasing that species will move poleward

or upslope in the face of climate change, but that there will be disassociation and re-association of species into potentially novel forest types. Some species will disappear or be restricted to isolated refugia, while others may expand greatly. These generalizations are greatly simplified, and specific efforts in conservation and management will have to address many more subtle, and not so subtle, effects on forest ecosystems that may be unique in space or time.

We encourage continued research to move the science forward on detecting, modeling, and the potential assisting of actual and potential tree range shifts in a changing climate. Many additional advances will be possible by making continued improvements in the integration among the avenues reviewed here. For example, the merger of process models, demography models, and SDMs allows for some of the best attributes of each, in working with suitable habitats into which multiple species must migrate, colonize, compete, and successfully reproduce, all at fine temporal and spatial scales. It is an exciting time for research as the computer-based tools, available data, and methods are simultaneously advancing at a remarkable rate. Meanwhile, we must be diligent to continue to provide the natural history and demography studies (=field work!) to provide the fuel for the modeling and interpretation of model outputs. Many species are poorly known as to their reproductive, competitive, ecological, and adaptability capacities, and how these vary under changing climates, including climates novel to their evolutionary history. There will always be plenty of uncertainty, but we cannot let that stifle our endeavors to bring the best science possible to decision-makers and managers to mitigate and adapt to the coming impacts from climate change.

References

- Allen C, Macaladyb A, Chenchounic H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears 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 Manage* 259:660–684
- Bachelet D, Lenihan J, Drapek R, Neilson RP (2008) VEMAP vs VINCERA: a DGVM sensitivity to differences in climate scenarios. *Glob Planet Change* 64:38–48
- Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proc Natl Acad Sci USA* 105:4197–4202
- Bohrer G, Katul GG, Nathan R, Walko RL, Avissar R (2008) Effects of canopy heterogeneity, seed abscission, and inertia on wind-driven dispersal kernels of tree seeds. *J Ecol* 96:569–580
- Box G, Draper NR (1987) Empirical model-building and response surfaces. Wiley, New York
- Breiman L (2001) Random forests. *Mach Learn* 45:5–32
- Caccianiga M, Payette S (2006) Recent advance of white spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Québec, Canada). *J Biogeogr* 33:2120–2135
- Chen I-C, Hill K, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026
- Chitale VS, Behera MD (2012) Can the distribution of sal (*Shorea robusta* Gaertn. f.) shift in the northeastern direction in India due to changing climate? *Curr Sci* 102:1126–1135
- Clark JS, Lewis M, McLachlan JS, HilleRisLambers J (2003) Estimating population spread: what can we forecast and how well? *Ecology* 84:1979–1988
- Clark JS, Bell DM, Hersh MH, Nichols L (2011) Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. *Glob Change Biol* 17:1834–1849
- Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random forests for classification in ecology. *Ecology* 88:2783–2792
- Davis MB (1989) Lags in vegetation response to greenhouse warming. *Clim Change* 15:75–82
- Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. *Science* 292:673–679
- Davis MB, Zabinski C (1992) Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, pp 297–308
- Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science* 332:53–58
- Dobrowski SZ, Thorne JH, Greenberg JA, Safford HD, Mynsberge AR, Crimmins SM, Swanson AK (2011) Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. *Ecol Monogr* 81(2):241–257
- 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, Scachetti-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* 29:129–151
- Elith J, Phillips SJ, Hastie T, Dudik M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Divers Distrib* 17:43–57

- Engler R, Hordijk W, Guisan A (2012) The MIGCLIM R package: seamless integration of dispersal constraints into projections of species distribution models. *Ecography* 35: 872–878
- Esteve-Selma MA, Martinez-Fernandez J, Hernandez-Garcia I, Montavez J, Lopez-Hernandez JJ, Calvo JF (2012) Potential effects of climatic change on the distribution of *Tetraclinis articulata*, an endemic tree from arid Mediterranean ecosystems. *Clim Change* 113:663–678
- Fitzpatrick MC, Hargrove WW (2009) The projection of species distribution models and the problem of non-analog climate. *Biodiv Conserv* 18:2255–2261
- Franklin J (2009) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge
- Franklin J (2010) Moving beyond static species distribution models in support of conservation biogeography. *Divers Distrib* 16:321–330
- Franklin J (2012) Back of the envelope: climate change and species distribution modelling. *Bull Brit Ecol Soc* 43: 28–30
- Franklin J, Syphard AD, He HS, Mladenoff DJ (2005) Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. *Ecosystems* 8:885–898
- Friedman JH (2002) Stochastic gradient boosting. *Comput Stat Data Anal* 38:367–378
- Gamache I, Payette S (2005) Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. *J Biogeogr* 32:849–862
- Good P, Jones C, Lowe J, Betts R, Booth B, Huntingford C (2011) Quantifying environmental drivers of future tropical forest extent. *J Clim* 24:337–1349
- Gray LK, Gylander T, Mbogga MS, Chen P-Y, Hamann A (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecol Appl* 21:1591–1603
- Hanks EM, Hooten MB, Baker FA (2011) Reconciling multiple data sources to improve accuracy of large-scale prediction of forest disease incidence. *Ecol Appl* 21:1173–1188
- He HS, Mladenoff DJ, Crow TR (1999) Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecol Model* 114:213–233
- Heyder U, Schaphoff S, Gerten D, Lucht W (2011) Risk of severe climate change impact on the terrestrial biosphere. *Environ Res Lett* 6(3). doi:10.1088/1748-9326/6/3/034036
- Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonization and rapid climate change. *Science* 321(5887): 345–346
- Holzinger B, Hulber K, Camenisch M, Grabherr G (2008) Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecol* 195:179–196
- Hsu RCC, Tamis WLM, Raes N, de Snoo GR, Wolf JHD, Oostermeijer G, Lin SH (2012) Simulating climate change impacts on forests and associated vascular epiphytes in a subtropical island of East Asia. *Divers Distrib* 18(4):334–347
- 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* 87:1896–1906
- Iverson LR, Prasad AM (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems* 4:186–199
- Iverson LR, Schwartz MW, Prasad AM (2004a) How fast and far might tree species migrate under climate change in the eastern United States? *Glob Ecol Biogeogr* 13:209–219
- 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* 19:787–799
- Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *For Ecol Manage* 254:390–406
- Iverson L, Prasad AM, Matthews S, Peters M (2011) Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. *Ecosystems* 14:1005–1020
- Jiang YY, Zhuang QL, Schaphoff S, Sitch S, Sokolov A, Kicklighter D, Melillo J (2012) Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. *Ecol Evol* 2(3):593–614
- Keenan T, Maria Serra J, Lloret F, Ninyerola M, Sabate S (2011) Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters! *Glob Change Biol* 17:565–579
- Kennedy MC, Ford ED (2011) Using multi-criteria analysis of simulation models to understand complex biological systems. *BioScience* 61:994–1004
- Kharuk V, Ranson K, Dvinskaya M (2007) Evidence of evergreen conifer invasion into larch dominated forests during recent decades in central Siberia. *Eurasian J For Res* 10–2: 163–171
- Kreyling J, Bittner T, Jaeschke A, Jentsch A, Jonas Steinbauer M, Thiel D, Beierkuhnlein C (2011) Assisted colonization: a question of focal units and recipient localities. *Restor Ecol* 19(4):433–440
- Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J Ecol* 90:68–77
- Lafleur B, Paré D, Munson AD, Bergeron Y (2010) Response of northeastern North American forests to climate change: will soil conditions constrain tree species migration? *Environ Rev* 18:279–289
- Lawler JJ, Olden JD (2011) Reframing the debate over assisted colonization. *Front Ecol Environ* 9:569–574
- Lawler JJ, White D, Neilson RP, Blaustein AR (2006) Predicting climate-induced range shifts: model differences and model reliability. *Glob Change Biol* 12:1568–1584
- Lawson DM, Regan HM, Zedler PH, Franklin J (2012) Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Glob Change Biol* 18(9):2980
- Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771
- Levin SA, Muller-Landau HC, Nathan R, Chave J (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Ann Rev Ecol Evol Syst* 34:575–604

- Lloyd AH, Fastie CL (2003) Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience* 10:176–185
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature* 462(7276): 1052–1055
- Lovett GM, Mitchell MJ (2004) Sugar maple and nitrogen cycling in the forests of eastern North America. *Front Ecol Environ* 2:81–88
- Luna-Vega I, Alcantara-Ayala O, Contreras-Medina R, Rios-Munoz CA (2012) Ecological niche modeling on the effect of climatic change and conservation of *Ternstroemia lineata* DC. (Ternstroemiaceae) in Mesoamerica. *Botany Botanique* 90:637–650
- Matthews SN, Iverson LR, Prasad AM, Peters MP, Rodewald PG (2011) Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history factors. *For Ecol Manage* 262:1460–1472
- 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: 939–948
- McKenney DW, Pedlar JH, Rood RB, Price D (2011) Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. *Glob Change Biol* 17:2720–2730
- McLachlan JS, Hellmann JJ, Schwartz MW (2007) A framework for debate of assisted migration in an era of climate change. *Conserv Biol* 21:297–302
- McLaughlin BC, Zavaleta ES (2012) Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). *Glob Change Biol* 18:2301–2312
- Meier ES, Lischke H, Schmatz DR, Zimmermann NE (2012) Climate, competition and connectivity affect future migration and ranges of European trees. *Glob Ecol Biogeogr* 21:164–178
- 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* 33:612–616
- Minteer BA, Collins JP (2010) Move it or lose it? The ecological ethics of relocating species under climate change. *Ecol Appl* 20:1801–1804
- Morin X, Thuiller W (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90:1301–1313
- Nabout JC, Oliveira G, Magalhaes MR, Terribile LC, de Almeida FAS (2011) Global climate change and the production of “Pequi” fruits (*Caryocar brasiliense*) in the Brazilian Cerrado. *Natureza Conservacao* 9:55–59
- Nathan R, Katul GG, Bohrer G, Kuparinen A, Soons MB, Thompson SE, Trakhtenbrot A, Horn HS (2011a) Mechanistic models of seed dispersal by wind. *Theor Ecol* 4(2):113–132
- Nathan R, Horvitz N, He Y, Kuparinen A, Schurr FM, Katul GG (2011b) Spread of North American wind-dispersed trees in future environments. *Ecol Lett* 14:211–219
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42
- 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(10):1704–1711
- Pedlar JH, McKenney DW, Aubin I, Beardmore T, Beaulieu J, Iverson LR, O'Neill GA, Winder RS, Ste-Marie C (2012) Placing forestry in the assisted migration debate. *BioScience* 62:835–842
- Potter KM, Hargrove WW, Koch FH (2010) Predicting climate change extirpation risk for central and southern Appalachian forest tree species. In: Rentch JS, Schuler TM (eds) Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains, pp. 179–189. Gen Tech Rep NRS-P-64. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA
- Prasad AM, Iverson LR, Liaw A (2006) Newer classification and regression tree techniques: bagging and random forests for ecological prediction. *Ecosystems* 9:181–199
- Prasad AM, Gardiner J, Iverson L, Matthews S, Peters M (2013) Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change. *Glob Change Biol*. doi:10.1111/gcb.12204
- Ravenscroft C, Scheller RM, Mladenoff DJ, White MA (2010) Forest restoration in a mixed-ownership landscape under climate change. *Ecol Appl* 20:327–346
- Ricciardi A, Simberloff D (2009) Assisted colonization is not a viable conservation strategy. *Trends Ecol Evol* 24:248–253
- Richardson DM, Hellmann JJ, McLachlan JS, Sax DF, Schwartz MW, Gonzalez P, Brennan EJ, Camacho A, Root TL, Sala OE, Schneider SH, Ashe DM, Clark JR, Early R, Etterson JR, Fielder ED, Gill JL, Minteer BA, Polasky S, Safford HD, Thompson AR, Vellen M (2009) Multidimensional evaluation of managed relocation. *Proc Natl Acad Sci USA* 106:9721–9724
- Sato H, Ise T (2012) Effect of plant dynamic processes on African vegetation responses to climate change: analysis using the spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM). *J Geophys Res*. doi: 10.1029/2012JG002056
- Scheiter S, Higgins SI (2009) Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Glob Change Biol* 15:2224–2246
- Schuster WSF, Griffin KL, Roth H, Turnbull MH, Whitehead D, Tissue DT (2008) Changes in composition, structure and aboveground biomass over seventy-six years (1930–2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. *Tree Physiol* 28:537–549
- Schwartz MW (1993) Modelling effects of habitat fragmentation on the ability of trees to respond to climatic warming. *Biodiv Conser* 2:51–61
- Schwartz MW (2012) Using niche models with climate projections to inform conservation management decisions. *Biol Conserv* 155:149–156
- Schwartz M, 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* 4:568–581
- Schwartz MW, Hellmann JJ, Jason MM, Sax D, Borevitz JO, Brennan J, Camacho AE, Ceballos G, Clark JR, Doremus

- H, Early R, Etterson JR, Fielder D, Gill JL, Gonzalez P, Green N, Hannah L, Jamieson D, Javeline D, Minter BA, Odenbaugh J, Polasky S, Richardson DM, Root T, Safford HD (2012) Managed relocation: integrating the scientific, regulatory, and ethical challenges. *BioScience* 62:732–743
- Shimazaki M, Tsuyama I, Nakazono E, Nakao K, Konoshima M, Tanaka N, Nakashizuka T (2012) Fine-resolution assessment of potential refugia for a dominant fir species (*Abies mariesii*) of subalpine coniferous forests after climate change. *Plant Ecol* 213(4):603–612
- 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 project in northern Wisconsin. U.S. Department of Agriculture, Forest Service. Northern Research Station, Newtown Square, PA, p 142
- Tague CL, Band LE (2004) RHESSys: Regional hydro-ecologic simulation system—an object-oriented approach to spatially distributed modeling of carbon, water, and nutrient cycling. *Earth Interact* 8:1–42
- Tague CK, Heyn K, Christensen L (2009) Topographic controls on spatial patterns of conifer transpiration and net primary productivity under climate warming in mountain ecosystems. *Ecology* 90:541–554
- Thuiller W, Albert C, Araújo 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(3–4):137–152
- Treyger AL, Nowak CA (2011) Changes in tree sapling composition within powerline corridors appear to be consistent with climatic changes in New York State. *Glob Change Biol* 17:3439–3452
- van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecol Lett* 10:909–916
- van Mantgem PJ, Stephenson NL, Byrne JC et al (2009) Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524
- Vila-Cabrera A, Martínez-Vilalta J, Vayreda J, Retana J (2011) Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. *Ecol Appl* 21:1162–1172
- Vitt P, Havens K, Kramer A, Sollenberger D, Yates E (2010) Assisted migration of plants: changes in latitudes, changes in attitudes. *Biol Conserv* 143:18–27
- Webb TI (1992) Past changes in vegetation and climate: lessons for the future. In: Peters RL, Lovejoy TE (eds) *Global warming and biological diversity*. Yale University Press, New Haven, pp 59–75
- 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* 106:19729–19736
- 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 Manage* 257:1434–1444
- Wu HX, Ying CC, Ju H-B (2005) Predicting site productivity and pest hazard in lodgepole pine using biogeoclimatic system and geographic variables in British Columbia. *Annals For Sci* 62:31–42
- Xu CG, Gertner GZ, Scheller RM (2012) Importance of colonization and competition in forest landscape response to global climatic change. *Clim Change* 110:53–83
- Yaussy DA, Iverson LR, Matthews SN (2012) Competition and climate affects US hardwood-forest tree mortality. *For Sci*. doi:10.5849/forsci.11-047
- Zhu K, Woodall C, Clark J (2011) Failure to migrate: lack of tree range expansion in response to climate change. *Glob Change Biol* 18:1042–1052