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Potential Species Replacements for Black Ash (*Fraxinus nigra*) at the Confluence of Two Threats: Emerald Ash Borer and a Changing Climate

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Abstract

The emerald ash borer (*Agrilus planipennis*; EAB) is causing widespread mortality of ash (*Fraxinus* spp.) and climate change is altering habitats of tree species throughout large portions of North America. Black ash (*F. nigra*), a moist-soil species common in the Northwoods of Minnesota, Wisconsin, and Michigan, USA, is under a double threat of losing habitat from climate change and near annihilation from EAB. Because black ash often occurs in nearly pure stands, planting non-ash species is a management strategy already underway or being planned for thousands of acres. Tools are needed to assist managers in prioritizing sites for early treatment and to select potential species to replace black ash. This study explores the implications of threats to black ash ecosystems using analyses of field data and models to assess both the threats to, and potential replacement species for, black ash in Minnesota. For our analysis we (1) assessed the status of ashes and co-occurring species in forest inventory plots throughout Minnesota; (2) modeled the risk of EAB attack for multiple years in Minnesota; (3) modeled potential impacts of climate change on tree species with current or potential future habitat in Minnesota; (4) evaluated species co-occurring with black ash in plots in Ohio and Michigan, southeast of Minnesota; and (5) synthesized these results to provide a classification for candidate replacement species, both from within Minnesota and from points farther south. Though this process is demonstrated for black ash in Minnesota, the elements to be considered and modeled would be similar for any other location with a pest or pathogen threat for a species which simultaneously faces a changing climate.

Key words: assisted range expansion; invasive insect spread model; climate change; emerald ash borer; multiple forest threats; restoration; species distribution models.

Introduction

Two of the most significant issues facing natural resource managers are invasive species and climate change. The globalization of trade and transport accelerates risk of invasions (Lodge and others

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2006). Invasions usually carry a more immediate threat to forest ecosystems (Stohlgren and others 2014), but climate change poses a threat that is also underway now and likely to accelerate within this century with subsequent impacts on forest composition and health (IPCC 2014). Beyond considerable ecological effects, economic costs from these stressors are high; annual costs for *each* stressor have been estimated to be about 5% of the global economy (Pimentel and others 2001; Stern 2006). These estimates provide a sense of the enormity of the issues, even if the actual numbers are gross estimates. Combining the two threats may magnify the intensity associated with both issues, as climate change may reduce the resilience of ecosystems to resist invasion, while invasions can reduce the resilience of ecosystems (and economies) to deal with the changing climate. Thus, efforts to consider both threats simultaneously provide a way forward for managers to assess the threats and develop strategies to deal with them. Here, we present a model system with a serious forest pest threatening the dominant forest species in a region undergoing the greatest temperature changes within the conterminous United States.

North America is plagued by alien insect pests that are dramatically changing the ecology of forests, including gypsy moth (*Lymantria dispar*), hemlock woolly adelgid (*Adelges tsugae*), emerald ash borer (*Agrilus planipennis*; EAB) (Gandhi and Herms 2010), Asian long-horned beetle (*Anoplophora glabripennis*), sirex woodwasp (*Sirex noctilio*), and redbay ambrosia beetle (*Xyleborus glabratus*) (Koch and others 2011). The threat of invaders continues, with Koch and others (2011) predicting that an average of about 2 alien forest insect species are being established somewhere in the US each year and a 'significant' pest is established every 5–6 years.

Emerald ash borer has caused widespread mortality of ash (*Fraxinus* spp.), with little discrimination based on tree health, tree size, or ecological setting (Herms and McCullough 2014). In the wake of EAB, not only the fate of North American ash species, but also the fate of those ecosystems carrying significant quantities of ash, is in question. So far, EAB has caused more than 99% mortality of black (*F. nigra*), green (*F. pennsylvanica*), and white (*F. americana*) ash trees with stem diameters greater than 2.5 cm in forests of southeastern Michigan (MI; Klooster and others 2014; Herms and McCullough 2014). Furthermore, the ash seed bank was quickly depleted and new recruitment of ash ceased (Klooster and others 2014). Even regenerated stump sprouts of ash were shown to be rare in forested conditions (Klooster and others 2014), or quickly recolonized by EAB (Petrice and Haack 2011).There is some hope via breeding for resistance (Koch and others 2012), finding surviving individuals (Knight and others 2012b; Koch and others 2015), regeneration (and escape of EAB secondary invasion) of ash through survival of seedlings initially too small to be colonized (Kashian and Witter 2011; Klooster and others 2014), or inhibition of spread by cold temperatures in high latitudes (DeSantis and others 2013a, b), but by many indicators, the ashes throughout the continent are seriously threatened. Since its discovery in the Detroit, MI, area in 2002, the pest has girdled and killed millions of ash trees. As of June 2015, EAB had been detected in 25 US states and two Canadian provinces, and continues to spread (updated maps of EAB presence are located at www.emeraldashborer.info). In Minnesota (MN), EAB has so far been detected only along the eastern edge of the state, though the state is progressively planning for its spread and adaptive management (University of Minnesota Extension and MNDNR 2011).

EAB spreads via two primary mechanisms—either general diffusion from its core area via insect flight or by assisted dispersal from human activities (for example, by riding in wood cargo or just hitchhiking on vehicles), often along major highways. These two mechanisms, when simulated via modeling, have been shown to provide valid projections of EAB spread in Ohio (Iverson and others 2010; Prasad and others 2010). New infestations are often detected earlier in urban locations (more eyes per tree!) and Sydnor and others (2005) have published a guide on some potential replacements in urban areas. Detection and replacement of ash will generally be more attainable in urban settings than in forested settings because of the limited number of trees and the wider array of species/cultivars available as replacements in boulevards relative to the primary forest settings. A key objective of this study is to evaluate the risk of EAB spread across MN within the next few years in conjunction with an evaluation of potential species that may be suitable replacement species, most often planted prior to decimation by EAB, in newly or imminently invaded native or urban forest stands.

Simultaneously with this EAB invasion, the climate is changing. Within the conterminous USA, MN has seen some of the most dramatic shifts in temperature over the last few decades, exemplified by minimum winter (mean monthly minimum temperatures for December through February)

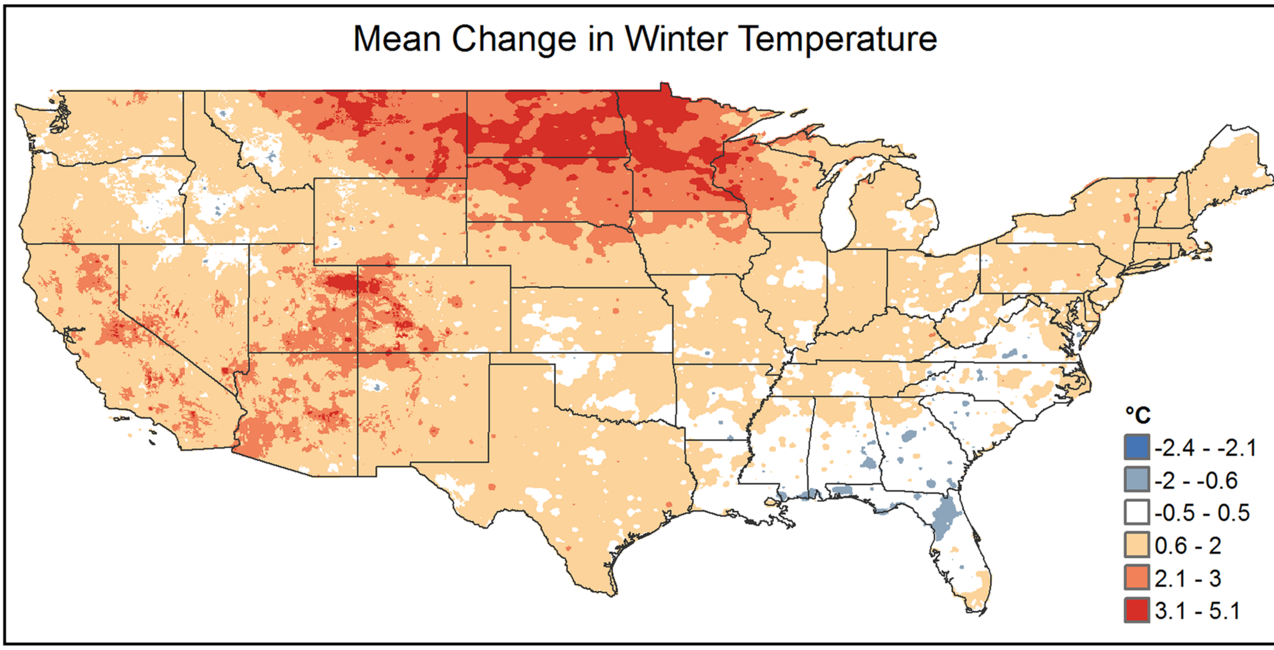

Figure 1. Trends in mean minimum winter temperature (December–February) between 1965–1975 and 1995–2005, depicting large warming over Minnesota (extracted from data from PRISM 2013).

temperatures rising more than 2 °C between the 1965–1975 decade and the 1995–2005 decade (Figure 1). According to Intergovernmental Panel on Climate Change (IPCC) predictions, the climate will continue to warm in this century, with estimated winter minimum temperature increases of an additional 2.6 to 5.9 °C in northern MN, depending on the general circulation model and scenario used (Handler and others 2014). Associated with general winter warming may be warm periods in winter followed by cold spells that can damage plants and animals alike in their reproductive success (Pryor and others 2014), although Sobek-Swant and others (2012) found that such events would not likely limit eventual EAB spread to a great degree. Extreme conditions, including droughts, floods, and storms, are also predicted to continue increasing in frequency (Saunders and others 2012). Although past changes in eastern forests are more closely linked to changes to land-use and management (Nowacki and Abrams 2015; although see also Pederson and others 2015), such changes in climate, especially after mid-century, will likely cause changes in forest composition and ecosystem processes, including eventual changes in suitable habitat for species currently residing in the Northwoods and species that may find newly suitable habitat in the region (Iverson and others 2008; Handler and others 2014). Indeed, several important boreal Minnesota species have been experimentally shown to be physiologically susceptible to warming conditions, while more temperate species are benefited by warming (Reich and others 2015).

Minnesota is the leading state for total ash biomass (Miles and Brand 2007; Miles and others 2007; Flower and others 2013). Estimates of volume from forest inventory for the three species of ash native to the state are 26.3, 10.2, and 0.3 million cubic meters of black ash, green ash, and white ash, respectively, during 2001–2005 (Miles and Brand 2007). Further, growing stock volume of these species has increased in recent decades (Hanberry and others 2013) with black ash increasing in growing stock volume by more than 50% between 1977 and 2005 (Miles and others 2007). Maps of the current distributions of the various ash species across the eastern USA and their potential suitable habitat under several climate change scenarios are presented in our online Climate Change Tree Atlas (www.nrs.fs.fed.us/atlas, Landscape Change Research Group 2014).

Black ash is a native North American hardwood tree species generally found in wetlands or on poorly drained soil (Wright and Rauscher 1990). Ash seed and twigs are valuable food for wildlife (Anderson and Nelson 2003), and the wood provides pulpwood, multiple wood products, and material for Native Americans' traditional basket making (Wright and Rauscher 1990). Palik and others (2011) reported that black ash has been on the decline in the northern USA, even without EAB, with the healthiest stands being younger and located on relatively drier sites and farther from roads. In northern forests, black ash often occurs in nearly pure stands, with very little regeneration of other tree species (Chippewa National Forest Silviculturist Gary Swanson, personal communication; Palik and others 2012). There is concern that the death of the black ash trees in these ecosystems will lead to a transition to non-forest conditions perpetuated by the presence of shrubs (Palik and others 2012), invasive herbaceous plants (Gary Swanson, WNDR Forest Ecologist/Silviculturist Greg Edge, personal communication; Minnesota Department of Natural Resources 2003), and the rise of the water table due to reduced evapotranspiration (Slesak and others 2014).

Many managers and local, state, and federal entities are already engaged in or considering planting non-ash tree species in thousands of acres of forested areas dominated by black ash (Gary Swanson, WDNR Forest Ecologist/Silviculturist Colleen Matula, Greg Edge, personal communication; Slesak and others 2014; Looney and others 2015) and other ash species (Knight and others 2012a, 2012b; WDNR Forester Nick Koltz, USACE Environmental Section Manager Randall Urich, personal communication) currently infested or at risk of infestation by EAB as a proactive response to this threat. Underplanting containerized or bareroot non-ash species beneath the canopy of healthy ash trees prior to infestation by EAB is a strategy that allows the non-ash trees to become established prior to canopy opening from dead ash trees. This strategy has been used successfully in bottomland ash and other similar bottomland ecosystems (Knight and others 2012a; Nick Koltz, Randall Urich, U. Vermont Assoc. Prof. Anthony D'Amato, personal communication). Direct seeding, including aerial seeding, is also under consideration for very large-scale diversification efforts (Gary Swanson, personal communication). Managers and decision-makers desire additional information to identify potential tree species for planting and to prioritize locations for planting (Gary Swanson, Colleen Matula, personal communication) and extension entities have begun responding to this need for information (University of Minnesota Extension and MNDNR 2011). One goal of this study is to provide additional tools and resources for managers, policy makers, and local, state, and federal entities already engaged in or considering these management options.

Future management of black ash ecosystems will need to consider threats from both EAB and climate change; here we demonstrate a combined process to model near-term risk to EAB and long-term risk to climate change. These risk maps feed into our overarching objective to evaluate possible replacement species for selected locations should managers desire to augment, via silviculture or assisted range expansion, the black ash stands before or at first inclination of EAB invasion. We seek to build a hierarchical list of possible replacement species based on each species' current associational status with black ash, in MN or elsewhere, and its potential for suitable habitat as climate changes in the coming decades. A candidate species should include the following traits: (a) it already co-occurs with black ash, either in MN or in locations generally south (for example as studied here, in Ohio [OH] or MI); (b) it has potential to grow successfully under predicted climate scenarios according to model outputs; and (c) it has biological traits and resilience against disturbances such that it is positioned to adapt well to conditions predicted from climate change.

The intention of the study is to provide a process to guide researchers and managers through similar situations when a species is threatened by a pest or pathogen in concert with the ongoing changing climate. We select MN to demonstrate the process because it, in some ways, could be considered an 'epicenter': 1) it will be an epicenter for impacts of loss of ash due to the abundance of black ash in MN and the particular challenges with the types of habitats it occupies there (for example, the water table rise expected with loss of black ash in swamps); 2) it may also be an epicenter for effects of climate change on major tree species (Handler and others 2014; Reich and others 2015). Thus, the choice of MN is an area of regional importance not only for these two issues with respect to EAB and black ash, but also represents a process that can be applied to any system undergoing simultaneous invasions and climate change threats.

Methods

The study integrates the following analyses to better assess the status and trends for black ash, and to evaluate potential replacements for black ash in MN and similar habitats elsewhere: an analysis of the US Forest Service's Forest Inventory and Analysis (FIA) plots for MN, OH, and southern MI including evaluation of co-occurring species with black ash, a field assessment of current co-occurring species within black ash ecosystems in OH and MI, an evaluation of near-term risk of invasion by EAB, and an assessment of species attributes and

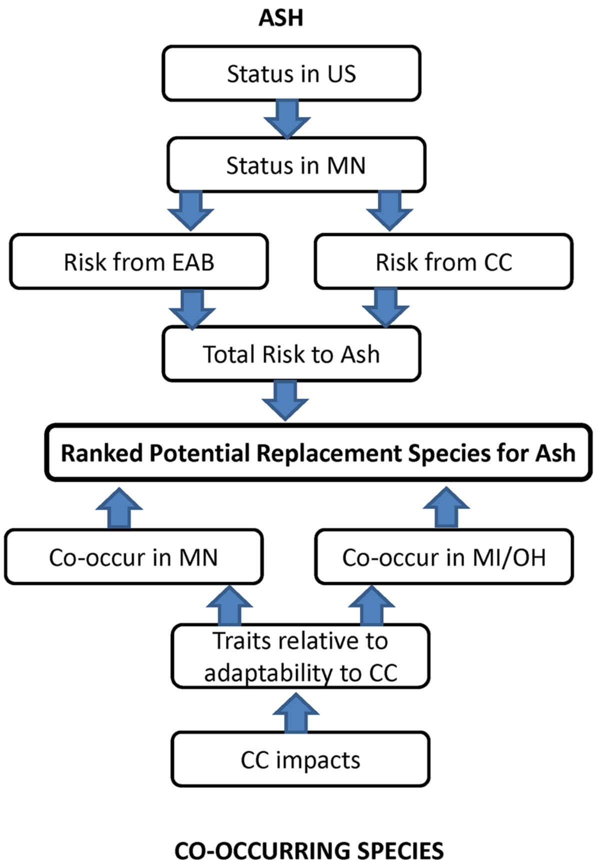

Figure 2. Flow diagram of pieces involved with arriving at the ranked list of potential replacement species. *MN* Minnesota. *OH* Ohio. *MI* Michigan. *CC* climate change.

habitat suitability under changing climatic conditions throughout this century (Figure 2). The flow diagram shows the dual approach used to arrive at these candidate species; we rely on a series of field plots, models, and species traits to develop a ranked set of potential replacement species. These species could be selected through a variety of management techniques depending on the species, such as encouraging natural regeneration or assisted range expansion and infilling through planting.

The Status of Ash and Co-occurring Species with Forest Inventory Data

The current distribution of black ash occupies most of the region between 39° and 50°N latitude and between 65° and 97°W longitude in the northeast quadrant of North America, with the greatest density and frequency present in the northern regions of MN (Figure 3). The loss of black ash in this region would likely have a large and widespread impact, due to the abundance of this species, thus we focused on these ecosystems to represent potential areas where replacement species for black ash would be of great concern. Species distribution and abundance data for MN were acquired from the FIA data portal (www.fia.fs.fed.us) for the period 2008 to 2012. We evaluated all stems larger than 2.5 cm on both plots and subplots for co-occurrence with black ash. Each FIA plot consists of four 7.3 m diameter subplots, arranged with one subplot in the middle and three adjacent subplots at 120°, 240°, and 360° and centered 36.6 m from the plot center. Thus, the plot covers 4× the area, but the subplots provide the more proximal co-occurring species with black ash. A total of 6341 plots were used to summarize the status of black ash in the state. Plots and subplots containing black ash were identified and used in further analysis to extract the co-occurring species within those subplots.

Modeling the Risk of Spread of Emerald Ash Borer in Minnesota

The intended outcome of this effort is a set of potential species that may be suitable for planting in the face of EAB and climate change. These species would be most influential toward maintaining ecosystem function, for at least carbon (Flower and others 2013) and hydrology (Slesak and others 2014), if already established and available for gap infilling at the time of ash decline and death. Obviously, any planting treatments would only be economically feasible on a very small proportion of the landscape, and spatial and temporal prioritization will be necessary. Therefore, it is valuable to undergo an effort to model the risk of EAB spread spatially across MN to identify areas more (or less) likely to succumb in the near future. To do so, we built upon earlier work to create EAB risk maps for OH and MI (Iverson and others 2010; Prasad and others 2010). In this work, we modeled and combined both the insect's flight and short-range dispersal (''insect flight'') and human-facilitated, long-range dispersal (''insect ride'') to create an overall assessment of risk of EAB spread across the study area. This hybrid model required estimates of EAB abundance, ash abundance, traffic density and other parameters for major roads, campground size and usage, distance from the core infested zone, wood products industry size and type of wood usage, and human population density. At that time, we estimated the risk map for OH to be 'useful for about 2–4 years, although it will be useful to re-run and potentially improve the model periodically as new data on outbreaks and other information become available' (Prasad and others 2010). As a test

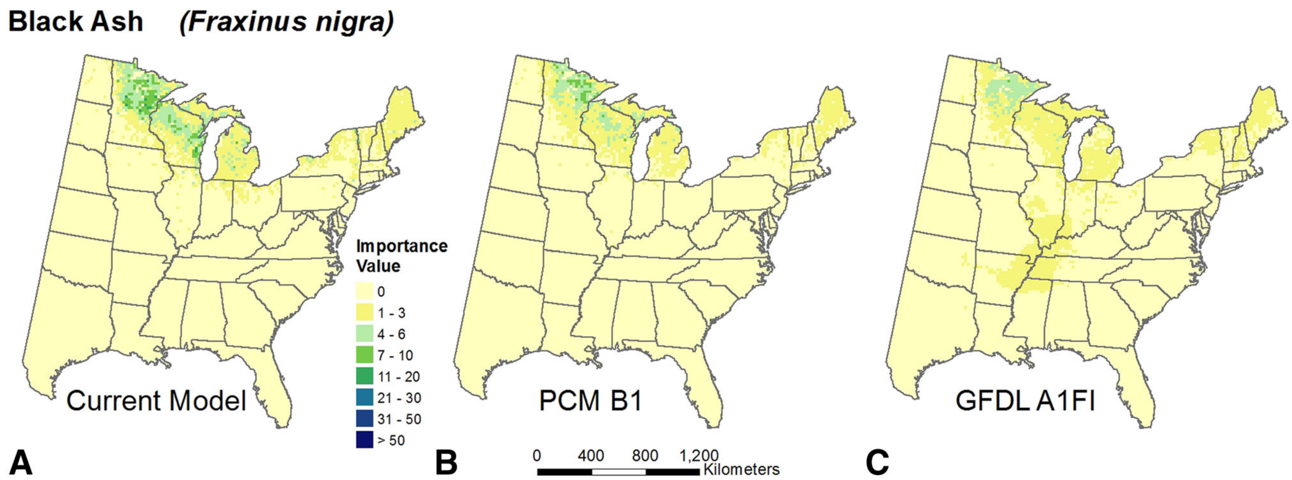

Figure 3. Climate change habitat suitability model outputs for black ash. **A** Current distribution of suitable habitat; **B** suitable habitat for end of century according to the PCM B1 scenario; **C** suitable habitat for end of century according to the GFDL A1FI scenario. Further information on these scenarios is available online (www.nrs.fs.fed.us/atlas).

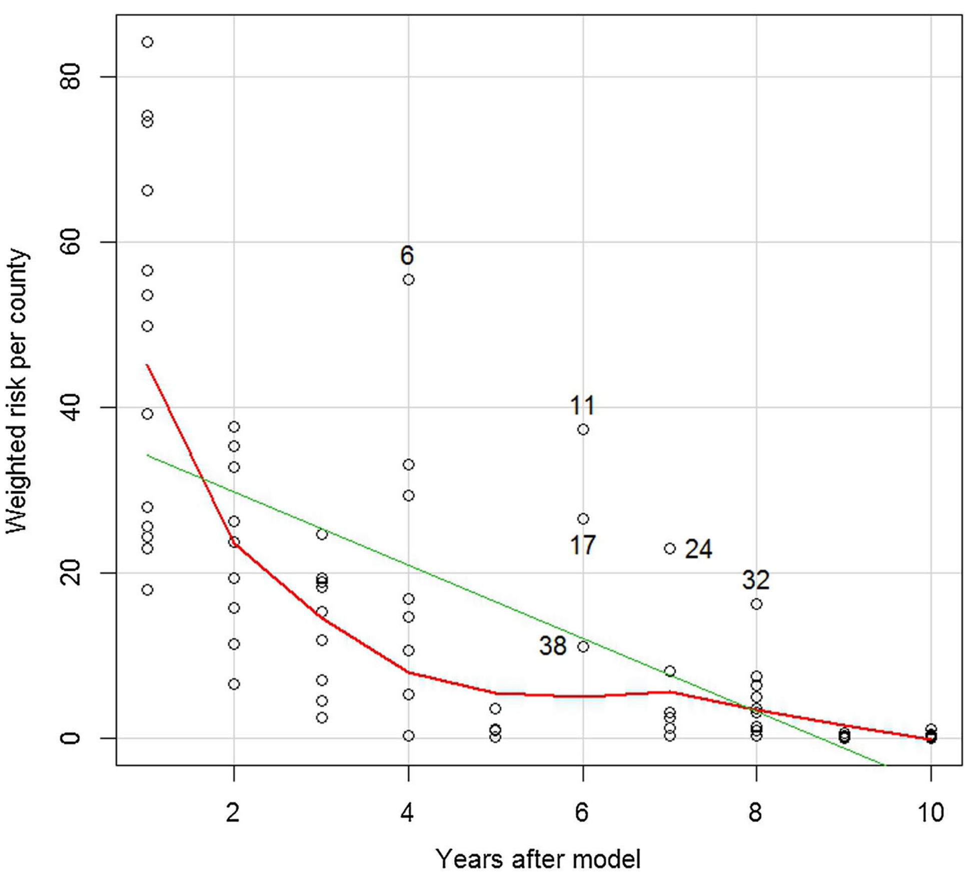

Figure 4. Relationship between OH risk to EAB (as modeled in early 2006) to year of first certified identification of EAB in the county for the following 10 years. Outlier counties were located in northeast Ohio, where invasion occurred slower than modeled (6 = Summit, 11 = Lake, 17 = Geauga, 24 = Crawford, 32 = Stark, 38 = Trumbull).

for validity of the model, we compared the weighted mean risk of EAB invasion for each county in OH from our model run in early 2006 (reported in Prasad and others 2010) to the number of years since 2006 in which the county recorded its first certified identification of EAB through 2014. For the last 6 counties not yet recorded as invaded as of December 30, 2014, an assumption of invasion during 2015 (year 10 after modeling) was made. As shown in Figure 4, the model generally predicted risk of invasion well (linear regression $R^2 = 0.45$, $P < 7e^{-12}$), with the exception of 4–6 counties (labeled on the graph) in northeast Ohio where recorded invasion was slower than the modeled risk level would indicate. Working with the MN Departments of Natural Resources and Agriculture and other sources, we obtained appropriate data to run the model based on known EAB locations as of autumn 2011, 2012, and 2013. Inputs for MN, along with their point values (maximum of 150 points) for the model were (1) major roads, scored by average density of traffic (60 points maximum for 0–1 km buffer, 30 points maximum for 1–2 km buffer); (2) roads likely to bring EAB from other states, scored by the number of out-of-state campground reservations into state parks (40 points maximum for 0–1 km buffer, 20 points maximum for 1–2 km buffer); (3) campgrounds (20 points maximum for 0–1 km buffer, 10 points maximum for 1–2 km buffer); (4) sawmills (10 points maximum); (5) population density by ZIP code (10 points maximum); and (6) number of firewood vendors by ZIP code (10 points maximum). The points attained with the above six layers (0–123 points) were used as a multiplier on ash basal area for the likelihood of ash invasion by EAB. Our earlier work in OH (Prasad and others 2010) indicated the large weighting for roads was justified. The total ash basal area map from the FIA unit of the US Forest Service's Northern Research Station was generated by nearest-neighbor imputation techniques on FIA plots (Wilson and others 2012).

Fortunately, EAB had not spread widely within MN as of autumn 2014, having been detected only in the following two loci on the eastern edge of the state plus one just over the border: the Twin Cities (Minneapolis-St. Paul) area, extreme southeastern MN, and just into Wisconsin at the southern tip of Lake Superior near Duluth, MN. The EAB ''occupied zone'' (sensu Prasad and others 2010) was generated by using a 2-km buffer around known locations of EAB. Because the ''occupied zones'' were so small, the ''insect flight'' model directly contributed very little to the overall risk. However, the current EAB presence in the most populated and densely traveled part of the state greatly increases the chances that it will be established as outliers along the roads via the ''insect ride'' model. By having three successive years of near-term risk maps, one can begin to visualize the increasing risk through time for this region.

Modeling the Risk of Climate Change on Ash and Associates

We previously created models of potential changes in suitable habitat under climate change for 134 tree species in the eastern USA, available at www.nrs.fs.fed.us/atlas. These models were generated from FIA-based estimates of importance value (based on basal area and number of trees on each plot) information, along with 38 environmental variables, to create suitable habitat models for the species using the RandomForest statistical modeling tools (Prasad and others 2006). Resultant model outputs of current distribution were also compared to FIA data, and several metrics were used to generate a reliability score for each model (Iverson and others 2008). We then modeled the suitable habitat for each species under various scenarios of climate change for ~2040, 2070, and 2100. The model outputs were intended to indicate potential changes in suitable habitat for tree species that may eventually occur under climate change. For display in this paper, we selected two scenarios to represent a large range of plausible future climates: (1) a ''mild'' outcome with the Parallel Climate Model (PCM; Washington and others 2000), a model of less sensitivity to atmospheric greenhouse gas concentrations, and with an optimistic scenario of a reduction in human greenhouse gas emissions early in this century (the B1 scenario, Nakicenovic and others 2000); and (2) a ''harsh'' outcome with the Geophysical Fluid Dynamics Laboratory (GFDL) model (Delworth and others 2006), a model with more sensitivity and coupled with a scenario of our current trajectory of emissions (the A1FI scenario). Based on ratios of projected future suitable habitat to current habitat, species were ranked into these classes: large decreaser, small decreaser, no change, small increaser, large increaser, new species habitat under harsh scenario, or new habitat only under the harsh scenario (Handler and others 2014).

The Climate Change Atlas uses statistical modeling and, therefore, cannot model ecosystem processes such as disturbances or competition. Therefore, to augment the models, we used literature-based modification factors to better interpret how a given species might respond to climate change (Matthews and others 2011). Though it would perhaps be preferable to have realistic mechanistic models for anticipating future outcomes, the ecological modeling community is a long way from adequately modeling all biological and disturbance variables interacting among 134 intermingling species across half a continent. Thus, we derived a qualitative approach in which we used multiple literature sources to score (−3, highly negative influence on future success to +3, highly positive influence) 9 biological and 12 disturbance characteristics for their positive or negative impacts on the species' capacity to cope with the many changes (for example, more disturbance impacts, like floods, droughts, and pests in future) associated with climate change. These values provide baseline information that users are encouraged to modify based on local knowledge and site conditions, or to revise based on updated and more comprehensive literature review. The values can then be used to qualitatively modify, up or down, the projections of the empirically derived DISTRIB model outputs. Scores were averaged for the biological (n = 9) and disturbance (n = 12) characteristics and then combined and scaled in two dimensions to arrive at an adaptability score ranging from 1.7 to 8.5 for the 134 species (see Iverson and others 2011; Figure 5). An example of the importance of these literature-based modification factor scores is the situation with native ashes. No model could have predicted the tremendous changes in ash resources caused by the EAB invasion; therefore, any climate impact model output would vastly overestimate future distribution and abundance of ash species.

The Status of Ash and Co-occurring Species in Plots Farther Southeast

Potential replacement species for black ash may currently occur far south of the current center of black ash abundance in northern Minnesota, as climate change may change the distribution of suitable habitat for tree species. Ohio and southern Michigan occur at the southern edge of the range of black ash. In this region, black ash is not frequently

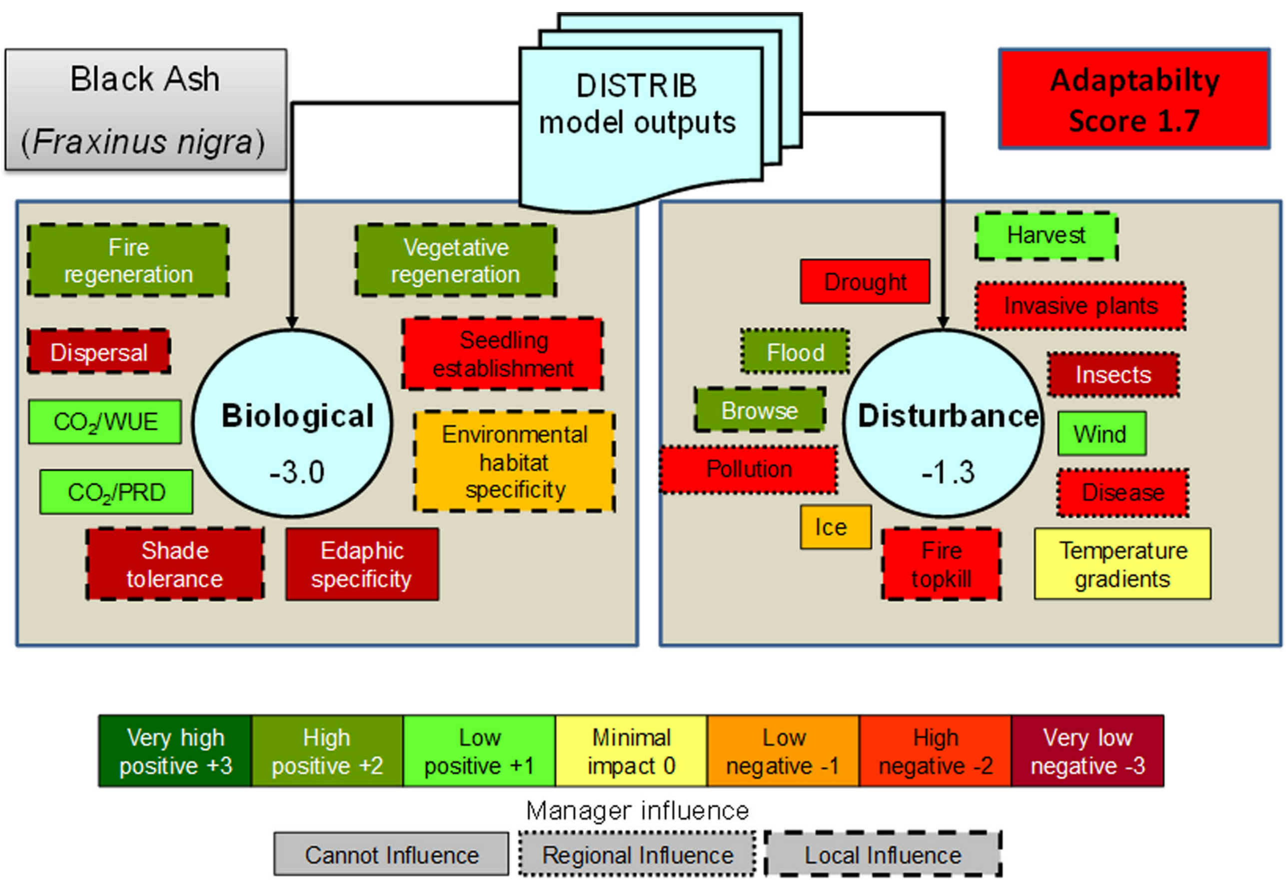

Figure 5. Graphic view of the biological and disturbance modification factors for black ash. Factors were scored from very high positive influence (+3) to very high negative influence (−3). Overall biological and disturbance scores were scaled −3 to +3 over 134 species. Black ash had the lowest adaptability score (1.7) of all species, indicating poor adaptability for the species in coming decades. Emerald ash borer is threatening to destroy the genus in North America, so any interpretations related to climate change will be overwhelmed by the effects of this insect.

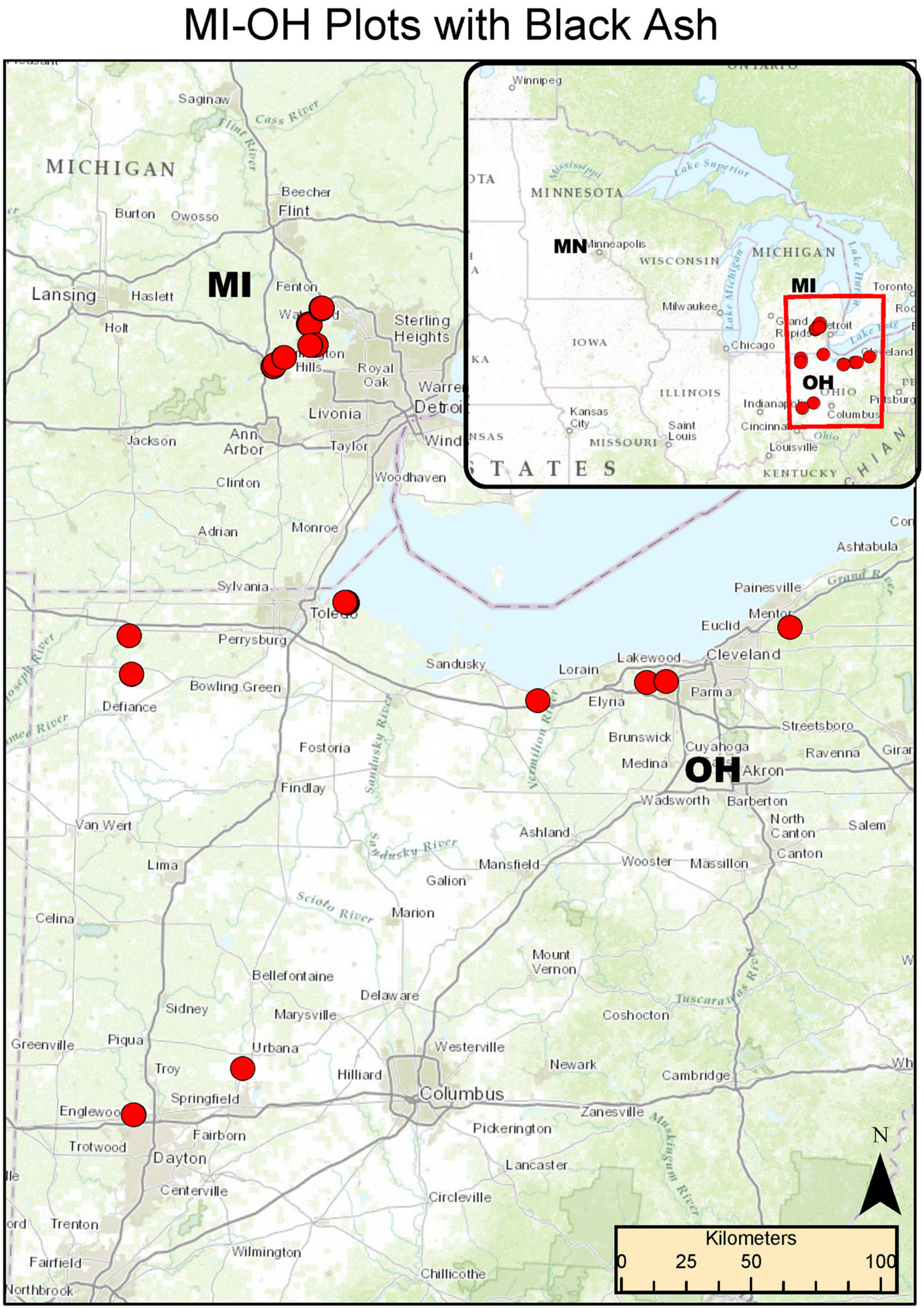

Figure 6. Location of plots containing black ash in Ohio (OH) and Michigan (MI). Inset map shows general location of Minnesota (MN) along with the Ohio and Michigan plots.

encountered on the landscape (Figure 3). In the occasional habitats where black ash is found, it is mixed with some species in common with northern MN black ash habitats as well as some southern species not found in MN. Because black ash is uncommon at this southern edge of its range, it is infrequent in FIA plots. We evaluated 19,808 FIA subplots from all of OH and the 20 southernmost counties of MI that encompass the region of OH and MI plots. Of these, only 39 subplots contained black ash, insufficient to gain an appreciation for the species that could co-occur with black ash and thus the need for additional plots targeted on black ash sites within the region. We used two similar datasets from plots established in ash habitats in OH and MI to represent black ash habitat at the southern edge of its range. The plots, located 250–900 km farther south than the concentration of black ash in MN, were originally established to study the effects of EAB on forest ecosystems (Knight and others 2013; Klooster and others 2014; Smith and others 2015). The plots were specifically placed in stands of each ash species that occurred in this region prior to, or during, EAB infestation (Figure 6). Forested stands containing each ash species were located in 2004–2008, and three circular plots (400 m^2 each in OH and 1014 m^2 each in MI) were placed in each stand in homogeneous habitat (not straddling two distinct habitats or land management regimes) to include at least two mature ash trees (typically many more) per plot. These plots were characterized before, or in some cases, during, EAB invasion for species composition, including density of seedlings, saplings, and overstory trees, to assess potential community composition of the forest following widespread ash mortality (for complete methods see Knight and others 2014). From this dataset, we used only the plots that contained black ash trees larger than 3 cm DBH to examine species (both trees and saplings) co-occurring with black ash. A total of 24 plots in OH and 38 plots in MI included black ash trees, with a total of 329 black ash trees and saplings and a total of 4869 co-occurring non-ash trees along with 2956 ashes other than black ash.

Habitat types for OH and MI black ash plots (wet or mesic) were chosen to correspond to MN community type soil conditions (Minnesota Department of Natural Resources 2003). Specifically, sites with muck or peat soils were categorized as wet, and those with frequently saturated mineral soils were categorized as mesic. Species were categorized as ''mesic,'' ''wet,'' or ''mesic/wet,'' depending on their prevalence as trees (>10 cm in diameter in OH and >12.5 cm in diameter in MI) on plots so categorized. If more than 75% of the trees of a species (normalized for sampling intensity in that habitat type) were present in either the mesic or wet habitat type, the species was reported as predominantly occurring in that habitat type. If the species occurred roughly equally in both habitat types, it was reported as mesic/wet.

Identifying Potential Species Replacements for Black Ash in Minnesota

We coupled each of the above four analysis steps in order to contemplate potential lists of species that may be appropriate for experimentation as to their suitability as possible replacements if replacement is a management option. To build such lists, we sought to categorize species based on commonness, estimated suitable habitat, and estimated adaptability to additional disturbances under climate change. We also aimed to consider the ecological function and resultant functional redundancy of each species to help identify those appropriate for assisted range expansion and infilling if that option is deemed necessary (Montoya and others 2012; Lunt and others 2013). The rules and results for each category are presented in the results section (''Combining Data and Models for Potential Species Replacements for Ash'' section). Fifty-one species were classified into six classes.

Results

Species Currently Co-occurring with Ash

From FIA plots in Minnesota

Forest inventory data from 2008 to 2012 indicate that an estimated 1.088 billion live ash trees larger than 2.5 cm in diameter existed in MN (http://apps.fs.fed.us/fia/fido/index.html). This is a slight increase in total live ash stems as compared to the estimate of 0.975 billion live stems from 2004 to 2008, with almost all of the increase in the smallest size class. Ash also represents 7.8% of the estimated 14 billion total live trees in the state, and an estimated 40.2 billion kg aboveground dry weight of biomass (9.2% of total). Of the ash, about 79% are black ash, 21% green ash, and 0.25% white ash (http://apps.fs.fed.us/fia/fido/index.html).

The FIA data also provided detailed information on abundance of species co-occurring with black ash. Of the 6431 total plots measured between 2008 and 2012, 1600 plots (24.9%) had black ash. Of the 18,527 unique subplots evaluated, 3158 (17%) contained black ash. These data indicate that

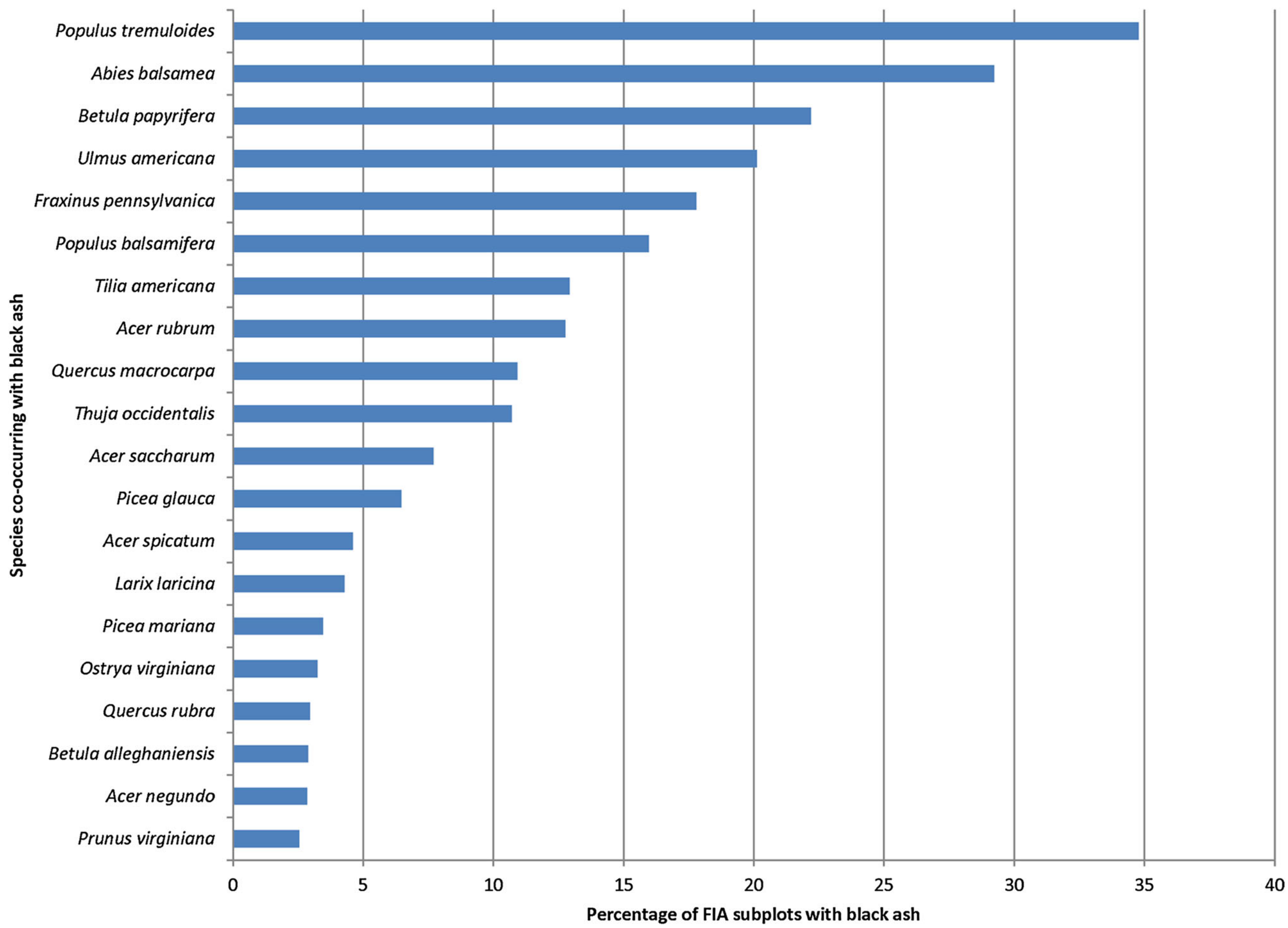

Figure 7. Frequency of species co-occurring with black ash according to FIA data for Minnesota, 2008–2012, for 20 species (out of 55 total species) co-occurring with at least 2.5% of the black ash subplots.

black ash often exists in small patches and typically is absent from one to three of the four subplots within a plot. From this subset of plots, 55 species were associated with black ash on at least one FIA plot, whereas 49 co-occurring species were present on at least one subplot, and 20 species were present on at least 2.5% of the subplots (Figure 7). The primary co-occurring species, in decreasing order, were quaking aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), American elm (*Ulmus americana*), green ash, balsam poplar (*Populus balsamea*), American basswood (*Tilia americana),* red maple (*Acer rubrum*), bur oak (*Quercus macrocarpa*), and northern white-cedar (*Thuja occidentalis*) (Figure 7). These species form the core list of likely candidates to replace black ash, because they already exist in those locations in MN. However, some are less viable candidates because of declining conditions currently and into the future with climate change (for example, quaking aspen and paper birch), or susceptibility to current diseases or insects (for example, American elm and green ash).

From FIA and targeted plots in Michigan and Ohio

The 39 FIA subplots with black ash (out of 19,808 in the MI-OH study area) contained a total of 155 trees, but over 40% (63) were ashes. Other species with over 2.5% of the non-ash trees included, in descending order: *Ulmus americana*, *Acer rubrum*, *Betula alleghaniensis*, *A. saccharum*, *Carya ovata*, *Quercus bicolor*, *Tilia americana*, *Carpinus caroliniana*, *and Q. rubra*. With the exception of *B. alleghaniensis* and *C. caroliniana* which were present but below the 2.5% cutoff on targeted plots, the FIA data concur with the targeted plots (Figure 8). Within the targeted plots, a wide variety of tree species co-occurred with black ash. Black ash often occurred in a mixture with green ash in MI and both green and pumpkin (*F. profunda*) ash in OH. As OH is at the southern edge of the distribution of black ash,

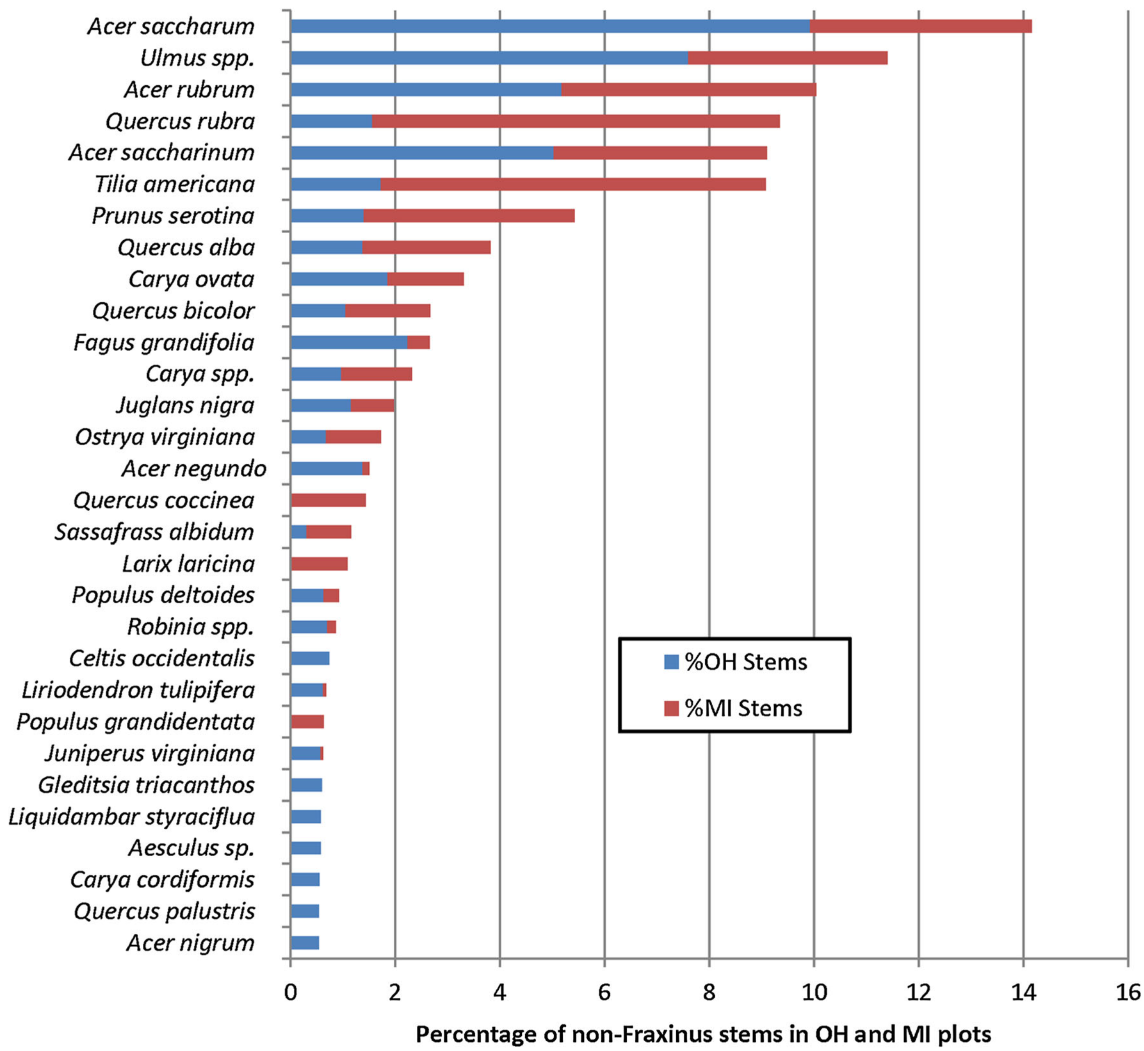

Figure 8. Frequency of species co-occurring with black ash in plots in Ohio (OH) and Michigan (MI), 2004–2009.

populations were often small and isolated. Major co-occurring tree species in the OH-MI, black ash-dominated plots were primarily elms (*Ulmus* spp., mostly *U. americana*) and maples (red, silver: *A. saccharinum*, sugar: *A. saccharum*) in OH, and maples, oaks, and basswood in MI. (Figure 8). The lowland habitat varied from occasionally flooded mesic hardwood sites to wet swamps with mucky soils. Some sites were within river floodplains while others were simply low level sites where soils were often saturated. As ash trees have been killed by EAB, other tree species in the mid-story, and occasionally herbaceous plants, have grown to fill the canopy gaps. In northwest OH, maple and elm species exhibited the greatest growth response as the ash trees died (Flower and others 2013). Red and sugar maple have rapidly responded to the decline and mortality of ash trees with diameter growth of released trees averaging 2–3.5 mm per year (K.C. Costilow, US Forest Service, unpublished data).

Climate Change Potentials on Ash in Minnesota

The previously derived models of suitable habitat under climate change scenarios (as depicted on the website www.fs.fed.us/nrs/atlas), predict that the range of black ash, classed as a highly reliable model sensu Iverson and others (2008), would substantially contract in the eastern USA by 2100 even when excluding the direct impacts of EAB (Figure 3). Across the eastern USA, the model shows a loss of about one-third of its suitable habitat under either PCM B1 or GFDL A1FI scenarios by 2100 (http://www.fs.fed.us/nrs/atlas/tree/tree.php?spp=543).

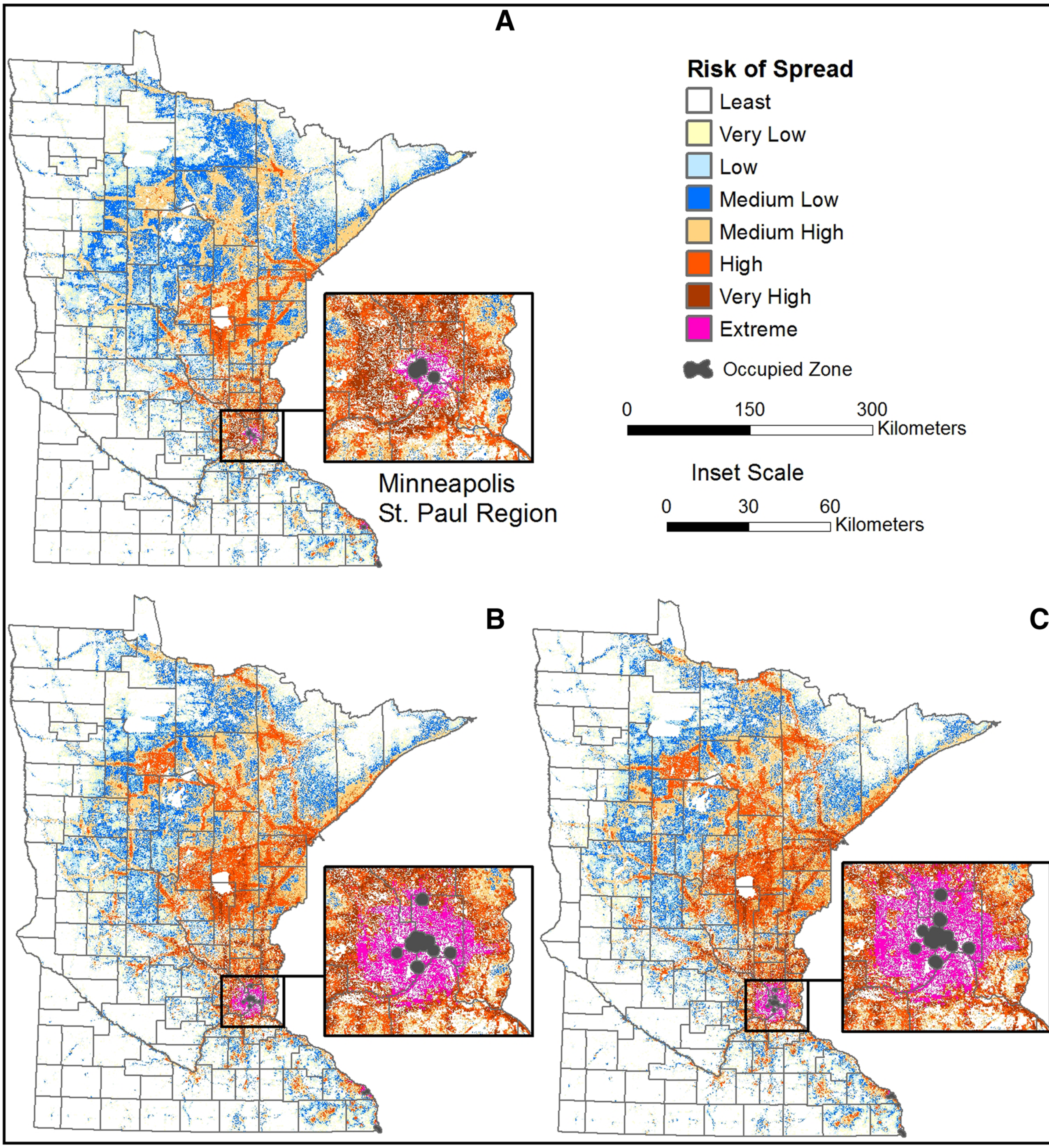

Figure 9. Modeled risk levels associated with the spread of EAB throughout Minnesota, built from EAB occupancy data for **A** 2011; **B** 2012; and **C** 2013. Each map represents risk levels over approximately the next 2–4 years.

Besides suitable habitat, however, we must consider the 9 biological and 12 disturbance modification factors as scored on a −3 (negative) to +3 (positive) scale for black ash (Figure 5, fully explained in Matthews and others 2011). The modification factors present the species' overall capability to adapt to the changing conditions predicted with climate change, and scores were applied while considering the entire eastern US range of the species. Although other factors detract from ash's capacity to adapt to climate change (dispersal restrictions, specificity to particular edaphic conditions, drought, and fire susceptibility; Figure 5), by far the most important factor is the comprehensive

Table 1. Modeled Risk of EAB for Minnesota, Based on Hybrid Flight and Ride Simulations and Represented by Total Area for Each Risk Category from 2011 to 2013

	2011	2012	2013
Class	Area (km^2)		
Least	121,861	119,742	119,327
Very low	11,786	9653	9255
Low	18,167	14,590	13,768
Medium low	28,109	22,843	21,217
Medium high	26,552	28,106	27,902
High	10,364	19,208	21,410
Very high	1405	3381	4402
Extreme	186	777	959
Occupied zone	93	223	282

Also presented is the estimate of area occupied by EAB in each year

mortality of ashes caused by EAB. This situation, of course, greatly reduces these species' ''adaptability'' to expected climatic conditions throughout this century. Though averaging reduces the individual influence of any of the 21 modification factors, black ash has an adaptability score of 1.7, the lowest of all 134 tree species presented in the Climate Change Atlas (Iverson and others 2011) and indicative of a very low ability to adapt to the anticipated changes.

Potential for Risk of EAB Spread in Minnesota

The models for three consecutive years outlining risk of EAB invasion for MN predict a slow, but increasing, risk for the ash in the state (Figure 9). An analysis of the maps shows that as the invaded zone slowly grows and spreads, areas of high risk expand while areas of low risk are diminished (Table 1). The models are intended to represent risk into the near-term future, perhaps with a 2–4 years outlook after which the model should be re-run with newer data (Prasad and others 2010); these rates of documented spread were validated in OH (Figure 4). However, contrary to OH and MI mapping for risk, there is evidence that winter cold temperatures may dampen the rate of spread to a greater degree in MN (Crosthwaite and others 2011; Sobek-Swant and others 2012; DeSantis and others 2013a, b), and as such, areas ranked as ''high'' risk may not see infestation for some time. Nonetheless, the small documented spread in the Twin Cities from 2011 to 2013 leads also to slightly elevated risk outside that metropolitan area (Figure 9). Though there is a vast amount of black ash in the northern half of MN, EAB so far has been detected only in the eastern edge of the state. Major highways are limited in their connections between areas currently known to be infested by EAB and the expansive areas of high black ash density, which generates a relatively low risk in the model, at least for the time being. The model predicts the formation of new populations outside the occupied zone which diminish with increasing distance from the known infested zone. But if there is direct traffic from the occupied zone, the model predicts that chances of becoming infested increase greatly, even for areas far removed from the infestations in the Twin Cities. Aside from the highest risk areas adjacent to the known EAB infestation in the Twin Cities and in southeastern MN, the model predicts that the greatest risk occurs near the Mille Lacs Lake area (large white body in east central MN in Figure 9 maps) because of the high traffic flow from the Twin Cities (i.e., summer cabins for city dwellers) and the large amount of ash present. Once EAB is established in that region, abundant host material will likely facilitate spread unassisted by humans.

Although there is some evidence that winter cold temperatures or large temperature swings may limit population growth of EAB in this area of MN (Venette and Abrahamson 2010; Sobek-Swant and others 2012; DeSantis and others 2013a, b), these conditions are unlikely to have a lasting effect on the ultimate spread of the species. Those EAB that survive may have extremely low supercooling points and are somehow positioned to withstand cold and large temperature swings (Sobek-Swant and others 2012). Thus, they could potentially have progeny that are even more resistant to future cold spells, assuming there is sufficient genetic variation in this trait. If limited degree-day accumulation in the growing season generally results in a two-year life cycle in this region, this could also slow the intrinsic rate of EAB population growth relative to warmer climates, where EAB generally completes its life cycle in a single year (Wei and others 2007).

Combining Data and Models for Potential Species Replacements for Ash

Tree species co-occurring with black ash, their replacement class code, and their potential response to climate change are presented in Table 2. Also provided is an indication of how commonly these species co-occur with black ash in MN according to FIA subplots and in OH and MI based on data from the plots established there, as well as an indication of their adaptability to climate

Table 2. Species Co-occurring with Black Ash in MN, or with Black Ash on MI or OH Plots

FIA num	Common name	Species	Class code[1]	Percent in MN FIA[2]	Percent stems in MI-OH[3]	Climate change class[4]	Adaptability score[5]	FWS[6]	MDNR[7]	Wetness in MI & OH[8]	D'Amato[9]
543	Black ash	*Fraxinus nigra*	Y	100.00	8.6#	Sm. Dec.	1.69	W	WF FF MH	M/W	
544	Green ash	*Fraxinus pennsylvanica*	Y	17.80	41.0#	Sm. Inc.	3.97	W	FF MH WF	M/W	
541	White ash	*Fraxinus americana*	Y	0.03	28.4#	Lg. Inc.	2.65		MH	M	
746	Quaking aspen	*Populus tremuloides*	Z	34.77	0.2	Lg. Dec.	4.66	W	FD MH WF	M	X
12	Balsam fir	*Abies balsamea*	Z	29.23	0.0	Lg. Dec.	2.65		WF FD FP MH		
375	Paper birch	*Betula papyri/era*	Z	22.20	0.0	Lg. Dec.	3.43		MH FD WF FP	M	
741	Balsam poplar	*Populus balsamifera*	Z	15.96	0.0	Lg. Dec.	3.95		WF	M	X
241	Northern white-cedar	*Thuja occidentalis*	Z	10.70	0.0	Lg. Dec.	4.18	W	WF FP MH		X
94	White spruce	*Picea glauca*	Z	6.46	0.0	Lg. Dec.	3.88		FD WF MH		
319	Mountain maple	*Acer spicatum*	Z	4.59	0.0	Lg. Dec.	5.87				
95	Black spruce	*Picea mariana*	Z	3.45	0.0	Lg. Dec.	4.33	W	FP AP WF		X
761	Pin cherry	*Prunus pensylvanica*	Z	0.35	0.0	Lg. Dec.	4.16				
972	American elm	*Ulmus americana*	A	20.11	11.4*	Lg. Inc.	3.97	W	FF MH WF	M/W	X
951	American basswood	*Tilia americana*	A	12.92	9.1	No Change	4.58		MH FF WF	M/W	
316	Red maple	*Acer rubrum*	A	12.76	10.0	Sm. Inc.	8.49	W	MH FD WF	M/W	X
823	Bur oak	*Quercus macrocarpa*	A	10.92	0.3	No Change	6.43		MH FF FD	M/W	
318	Sugar maple	*Acer saccharum*	A	7.69	14.2	Sm. Inc.	5.81		MH FF	M	
701	Eastern hophornbeam	*Ostrya virginiana*	A*	3.23	1.7	Sm. Inc.	6.38		MH	M	
833	Northern red oak	*Quercus rubra*	A*	2.94	9.3	Sm. Inc.	5.39		MH FD	M	
313	Boxelder	*Acer negundo*	A*	2.85	1.5	Lg. Inc.	7.39	W	FF		
762	Black cherry	*Prunus serotina*	A*	0.82	5.4	Lg. Inc.	3.04		FD	M	
743	Bigtooth aspen	*Populus grandidentata*	A*	0.76	0.6	No Change	5.11		MH FD	M	
975	Slippery elm	*Ulmus rubra*	A*	0.44	11.4*	Lg. Inc.	4.77		FF MH	M/W	
71	Tamarack	*Larix laricina*	B	4.27	1.1	Sm. Dec.	3.07	W	FP AP WF	M/W	X
371	Yellow birch	*Betula alleghaniensis*	B	2.88	0.5	Sm. Inc.	3.38	W	WF MH	W	X
763	Chokecherry	*Prunus virginiana*	B	2.53	0.0	Sm. Dec.	3.83				
129	Eastern white pine	*Pinus strobus*	B	0.70	0.3	Sm. Inc.	3.30		FD MH		
105	Jack pine	*Pinus banksiana*	B	0.57	0.0	Sm. Dec.	5.18		FD		
125	Red pine	*Pinus resinosa*	B	0.47	0.0	No Change	3.90		FD		
809	Northern pin oak	*Quercus ellipsoidalis*	C	0.03	0.0	Lg. Inc.	6.04		FD		
317	Silver maple	*Acer saccharinum*	C	0.85	9.1	Lg. Inc.	5.59	W	FF	W	
402	Bitternut hickory	*Carya cordiformis*	C	0.38	0.6	Lg. Inc.	5.61		MH		
922	Black willow	*Salix nigra*	C	0.38	0.2	Lg. Inc.	2.83	W			
391	Musclewood	*Carpinus caroliniana*	C	0.28	0.3	Lg. Inc.	5.08		MH	M/W	
742	Eastern cottonwood	*Populus deltoides*	C	0.16	0.9	Lg. Inc.	3.93	W	FF	M/W	X
802	White oak	*Quercus alba*	C	0.13	3.8	Lg. Inc.	6.14		MH	M	

Table 2. continued

FIA num	Common name	Species	Class code[1]	Percent in MN FIA[2]	Percent stems in MI-OH[3]	Climate change class[4]	Adaptability score[5]	FWS[6]	MDNR[7]	Wetness in MI & OH[8]	D'Amato[9]
602	Black walnut	*Juglans nigra*	C	0.09	2.0	Lg. Inc.	3.99		FF		
68	Eastern red cedar	*Juniperus virginiana*	C	0.09	0.6	Lg. Inc.	3.87		FD		
462	Hackberry	*Celtis occidentalis*	C	0.25	0.7	Lg. Inc.	5.71		FF		X
407	Shagbark hickory	*Carya ovata*	D	0.00	3.3	Lg. Inc.	4.38		FD		
837	Black oak	*Quercus velutina*	D	0.00	0.5	Lg. Inc.	4.90		FD	M	
901	Black locust	*Robinia pseudoacacia*	D	0.00	0.9	New-Both	3.85				
552	Honey locust	*Gleditsia triacanthos*	D	0.00	0.6	New-Both	5.49				
804	Swamp white oak	*Quercus bicolor*	D	0.00	2.7	New-High	4.86		FF	M/W	X
331	Ohio buckeye	*Aesculus glabra*	D	0.00	0.6	New-High	3.55				
403	Pignut hickory	*Carya glabra*	D	0.00	2.3	New-High	4.68			M	
531	American beech	*Fagus grandifolia*	D	0.00	2.6	New-Both	3.56			M	
621	Yellow poplar	*Liriodendron tulipifera*	D	0.00	0.7	New-High	5.29				
931	Sassafras	*Sassafras albidum*	D	0.00	1.2	New-High	4.20			M/W	

Species are classed into six classes according to commonness in MN and MI/OH, potential change of habitat by 2100 with climate change, resilience to climate change, and affinity to wetness.
1. Class Codes reflect six categories of replacement potential and are detailed in Results.
2. Percent of black ash subplots also containing this species in the whole of Minnesota according to FIA.
3. Percent of tree stems within all plots in Michigan and Ohio.
4. Climate Change Classes reflect ratio of future to current suitable habitat (Methods), detailed in Handler and others (2014).
5. Adaptability Scores are explained in the text, with more detail in Matthews and others (2011).
6. US Fish and Wildlife determination of wetland species, according to Cowardin and others (1979). W indicates wetland species.
7. Species are listed as canopy or subcanopy species within the community type for northern Minnesota. Codes according to the Native. Plant Communities in Minnesota document (MDNR 2003). Wet Forest (WF), Floodplain Forest (FF), Mesic Hardwoods (MH), Acid Peatland (AP), Forested Rich Peatland (FP), Fire Dependent (FD).
8. Michigan and Ohio black ash plots were classified as mesic (M) or wet (W). Tree habitat occurrence is listed based on these scores. If the species was predominantly found on mesic sites, it was classed as M (same for W). If the species had roughly equal numbers of stems present on M and W sites, it was classed as M/W.
9. Species was planted in D'Amato and Palik experiment (D'Amato, personal communication; also detailed in Looney and others 2015).
 # For Fraxinus, the percentage relates to only the three ashes.
** For Ulmus, we report the same value on U. americana and U. rubra - in reality it is a mix, but mostly U. americana.*

change. As black ash is a keystone species in many northern wet forest ecosystems, the table also reports information from three sources as to whether the species is particularly adapted to wetland environments: the Native Plant Communities of Minnesota documents (MDNR 2003), the US Fish and Wildlife Service documents (Cowardin and others 1979), and the field assessment of wetland status from the MI and OH ash plots. Finally, we report if the species have been planted in an experiment led by Tony D'Amato and Brian Palik to evaluate their suitability as possible future replacements for black ash in the Chippewa National Forest of north central MN (Beyers 2013; Looney and others 2015).

Class Y

These *Fraxinus* species are in Class Y by themselves as they are the species that will require replacement if they experience widespread mortality from EAB (Table 2).

Class Z

Most of these species are common in MN now as a co-associate with black ash, but climate change is expected to substantially reduce future suitable habitat for them, especially under the harsh climate scenario. Although these species are worthy of planting experimentally to compare against model projections and to assess fine-scale nuances of adaptability to a changing climate, the models suggest that their long-term success is uncertain under climate change. The nine ''large decreaser'' species include many of the iconic species of the Northwoods, and are projected to be seriously affected by climate change by the end of this century. These key species are quaking aspen, paper birch (*Betula papyrifera*), balsam fir, and balsam poplar, all of which currently co-occur with black ash at least 16% of the time on FIA subplots across MN (Table 2).

*Class A and A**

This group of species contains some key candidates for replacing black ash (Table 2). These 11 species currently co-occur with black ash in MN and are well adapted to predicted climate change scenarios; thus, they are the most likely candidate replacements. All of these species also co-occur with black ash on plots in MI or OH, at least to some degree. Rules for this class are: species co-occurs with black ash somewhere in MN, such that at least 5% (and often much more) of the black ash subplots have the species currently; suitable habitat is projected to increase or remain stable under climate change; modification factors are somewhat favorable (Adapt > ~4); and species co-occurs in MI/OH plots. Five species match these criteria (labeled A). Another six species (labeled A*) infrequently co-occur in subplots with black ash (but are more common in plots, so are fairly close to black ash) but do have the other attributes of projected increases in suitable habitat and somewhat favorable modification factors (with the exception of black cherry: Adapt = 3.04). Several species, such as red maple, American elm, American basswood, and slippery elm (*U. rubra*) are quite tolerant of wetland conditions. Some of the others, such as sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), and boxelder (*A. negundo*), may not tolerate very wet conditions but could be suitable replacements in less wet habitats.

Class B

Though this class was a bit of a catch-all group, these species currently co-occur with black ash in MN, but are not so well adapted to current or predicted future climate scenarios (Adapt <3.9 except for *Pinus banksiana* with Adapt = 5.2), and suitable habitat is modeled to remain rather constant (small decrease, no change, or small increase) in this century (Table 2). Rules for this class are: species co-occurs with black ash in subplots somewhere in MN, but less than 5% of the time; it is rare or absent in MI/OH plots; climate change will not greatly change the species' habitat; and modification factors are generally less favorable than Class A species (Adapt mostly 3–4). Two species in this class that are also tolerant of wet conditions are tamarack (*Larix laricina*) and yellow birch (*Betula alleghaniensis*).

Class C

These species currently but rarely (<1%) co-occur with black ash in MN, but are presumably able to grow as potential black ash replacements because they do co-occur with black ash both in MN subplots and plots located 250–900 km farther south in MI/OH (Table 2). Primarily these species are modeled to have large increases in suitable habitat in MN with climate change. Rules for this class are species co-occurs with black ash in MI/OH, and also to a limited extent somewhere in MN; climate change is expected to create substantially more suitable habitat in MN; modification factors are somewhat favorable (Adapt > 3.85 except for black willow [*Salix nigra*], with Adapt = 2.83).

Though northern pin oak (*Q. ellipsoidalis*) was not present in MI/OH plots, it is found in the region and met all other criteria so was added to this class. The 10 Class C species all are classified as ''large increaser'' species by the climate change analysis, and have reasonably high adaptability to climate change. However, only three are noted as facultative wetland species potentially suited to the wet conditions common in the black ash swamps: silver maple (*A. saccharinum*), eastern cottonwood (*Populus deltoides*), and black willow.

Class D

Rules for the 10 species in this class are species co-occurs with black ash in MI or OH, or both, but not in MN; climate change is expected to create newly suitable habitat in MN by century's end, under either the harsh climate scenario or both scenarios; modification factors are somewhat favorable (Adapt > 3.5). These would be the most risky species to plant, as presumably they do not *currently* have suitable habitat in MN (eight species). For two additional species, shagbark hickory (*Carya ovata*) and black oak (*Q. velutina*), there is currently evidence that they grow in MN, just not in the subplots with black ash. Thus, they are coded as ''large increaser'' for climate change class (Table 2). Though more common in upland habitats, they were noted with black ash in MI/OH. We believe that picking species in Class D is more reasonable than picking other random southern species because they at least are co-associates with black ash in wet or mesic habitats. Other potential species include swamp white oak (*Q. bicolor*), American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), and sassafras (*Sassafras albidum*). Of this group, however, only swamp white oak is a noted wetland species.

Discussion

This paper uses a series of studies that, when considered collectively, provides a more synthetic approach for addressing the dual issue of an alien insect pest and projected climate change. As more is learned from experiments and observations through time, it is appropriate to use this approach as part of an adaptive management approach. We believe there is value in taking a proactive approach in this regard: if we use the available information to begin to consider and promote suitable native species replacements, we may help to maintain ecosystem function across a small but carefully selected portion of the threatened landscape, especially when the replacement species are underplanted in newly or imminently invaded black ash stands. Managers, policy makers, and landowners may use our results to assist in prioritizing sites for treatment based on the risk of infestation by EAB identified by this study combined with numerous other factors (ecosystem attributes, site accessibility, management goals, budget, and so on). Our results will also provide managers with useful information on a large suite of potential species for underplanting, replanting, and diversification efforts to mitigate the effects of EAB in black ash-dominated ecosystems with little natural regeneration of non-ash species. Specific planting methods, including timing of planting, choice of containerized stock vs. bare root stock vs. direct seeding, and deer protection, will depend on many site-specific factors (including existing vegetation, flooding regimes, site accessibility, deer density, management goals, and budget). Both the actual selection of lands for planting and the methods used for planting are beyond the scope of this study.

In the short term, because of the known rapid spread of EAB in OH, MI, and elsewhere, and because of the risk of EAB spread in MN as we have modeled (Figure 9), we believe that the impact of the EAB invasion on ash will overwhelm longer-term impacts of climate change in MN and adjoining areas. Very cold (< −30 °C) or large temperature swings in winter may slow EAB spread in northern MN (DeSantis and others 2013a, b), but this is not likely to have a long-term effect on eventual EAB distributions (Sobek-Swant and others 2012). In addition, this constraint may diminish if winter temperatures continue to increase as in the past (Figure 1) and into the future as predicted (IPCC 2014; Handler and others 2014). With the weight of evidence accumulating on how EAB infestations are shaping the forests of MI and OH (for example, Klooster and others 2014) and the prospect for continued advance in MN, it is vital we begin to experiment with tree species that can be potential replacements for black ash. In doing so, it may also be shortsighted not to consider our understanding of how tree species are and may be affected by climate change in these deliberations if our goal is to maintain productive, functioning forests (Lunt and others 2013). Therefore, we believe it appropriate to use the EAB risk maps of MN to develop priority areas where replacement species should be considered in the near-term. These would be places near the currently occupied zones and along major travel ways emanating from those zones as shown in Figure 9. Though underplanting in current live black ash stands has some risk of inhibition due to canopy shading, they are likely to survive better underplanted in live stands than in completely dead black ash stands; Looney and others (2015) have found that of the 12 species they planted, all survived better over 3 years in control, uncut plots as compared to clearcuts, and 7 of 12 species did as well or better in controls relative to girdled or group selection cuts. Underplanting before ash death also promotes tree establishment before the extra light promotes grass and shrub competition (Anthony D'Amato, personal communication).

By coupling plot-level (FIA) information with the overall trends in suitable habitat for co-occurring species, we provide new analyses on the possible future composition, perhaps with the assistance of humans (Williams and Dumroese 2013), of 'former' black ash ecosystems. For example, species that currently co-occur with black ash in MN might be assumed to be the most promising replacements, at least initially, especially if they are well adapted to the predicted future climate (Class A/A* species). Less suitable but still worthy of testing are those species that currently co-occur with black ash but that are not as well adapted to climate change nor predicted to gain much suitable habitat in MN into the future (Class B). Perhaps an even better set of species, possible replacements if movement were assisted to expand their known presence within MN, would be those that do not currently co-occur with black ash in MN but are present there, mostly in low numbers, and presumably able to grow as potential black ash replacements because they do co-occur with black ash in plots located 250–900 km farther south in MI/OH (Class C). Finally, there are those species that currently co-occur with ash in OH or lower MI, but not in MN. These species could also be relocated, via assisted range expansion by humans (Pedlar and others 2012), into areas where the climate is likely to be suitable in coming decades, such as into northern MN (Class D). If managers and researchers decide to apply assisted migration tools, precautions would need to be taken (Schwartz and others 2012), but tree species have been planted beyond their current range for centuries (Pedlar and others 2012), and several species mentioned above may be highly successful even when the models show limited suitable habitat there currently. Black ash ecosystems exhibit great variety in MN and elsewhere. Black ash occurs in several forest community types in mesic forest, floodplain forest, wet forest, forested rich peatland, and river shore systems (MDNR 2003). Very subtle variations in moisture and flooding regimes, topography, soils, and genetics can greatly influence which species may be appropriate, and transplant experiments may provide an approach for assessing this ''match.'' Due to this micro-variation across landscapes in concert with our broad-scale modeling assessment, some species we list as possible replacements will ultimately prove to be inappropriate, even as the climate changes. However, in the face of uncertainty regarding the magnitude of future climate change, it may be premature to exclude these species from further analysis and testing.

We have not included all factors to consider in addressing possible species replacements. As mentioned above, a key variable is the very wet moisture regime in much of the current black ash-dominated region, and Slesak and others (2014) have shown that the loss of black ash leads to a rise in water table in these systems. The flood tolerance of potential replacement species, therefore, must also be considered. Many black ash systems in MN have standing water into July and saturated soil conditions in the upper 100 cm through early August. Few species can tolerate that level of flooding year in and year out. Another issue is herbivory, especially deer, in establishing trees in MN and beyond. For example, northern white-cedar could be considered as a replacement species in habitat, but it could almost be ruled out because of heavy deer browsing and potentially large negative impacts from climate change (D'Amato, personal communication).

Proposing tree replacements for black ash comes with the implicit assumption that black ash sites will remain forest when stressed by future climate or EAB infestation. In MN this assumption is challenged by the fact that several shrubs and graminoids in black ash forests have importance values subordinate to black ash but higher than most of the suggested replacement trees. Rough alder (*Alnus incana* subsp. *rugosa*), red-osier dogwood (*Cornus sericea*), mountain maple (*Acer spicatum*), bluejoint (*Calamagrostis canadensis*), fowl manna grass (*Glyceria striata*), and lake sedge (*Carex lacustris*) are a set of species capable of site dominance and with higher importance in ash swamps than trees except for black ash. Unfortunately, the invasive glossy buckthorn (*Frangula alnus*) and reed canarygrass (*Phalaris arundinacea*) inhabit some MN ash swamps, and could dominate these sites if EAB kills the ash canopy (Minnesota Department of Natural Resources 2003).

In a study ongoing in the Chippewa National Forest in MN (Slesak and others 2014; Looney and others 2015), where in many places 90% of the overstory tree volume is black ash, experimentation has begun to better understand the changes in forest composition likely to occur in the wake of EAB. In this study, several species are being planted to test their viability as replacements for black ash. The planting list includes local wetland species such as tamarack, black spruce (*Picea mariana*), American elm, cottonwood, balsam poplar, red maple, yellow birch, quaking aspen, and northern white-cedar; species native to more southerly locations in MN, including hackberry (*Celtis occidentalis*) and swamp white oak (*Q. bicolor*); and the EAB-resistant Manchurian ash (*Fraxinus mandshurica*) as a temporary check (D'Amato, personal communication, Table 2). Among these species are ones from each of the primary classes listed in Table 2, as well as northern species to test whether they will be limited by warming temperatures. Red maple and American elm represent the Class A species that currently co-exist with black ash in MN. Tamarack represents the Class B group, with a little less capacity and suitable habitat under climate change scenarios. Hackberry represents the Class C species that are predicted by the models to increase habitat in northern MN. Class D species, which are represented by swamp white oak, are currently minimally present in MN and absent from northern MN, but could potentially have suitable habitat move north into that region in coming decades. Indeed, 3-year data from the experiment have shown that southern white oak (Class D) and hackberry (Class C), not presently occupying the region and, therefore, representing an 'assisted range expansion' of those species, are provisionally surviving better than many of the northern species (Looney and others 2015). As this experiment is followed further, growth and survival in the 2010s and beyond can be compared to the model forecasts for the 2040, 2070, and 2100 periods. In addition to the species tested in this experiment, our study suggests that several others may be promising species to test. For example, despite the only rare co-occurrence of silver maple (*A. saccharinum*) with black ash on FIA subplots in MN, this Class C species may be a promising one to test, due to its abundance in southern black ash ecosystems, its adaptation to very wet conditions, and the rapid growth rates in response to ash mortality seen in other studies (Flower and others 2013; K.C. Costilow, US Forest Service, unpublished data). As experimental and observational data accumulate, more discussion as to the role of assisted range expansion in moving suitable 'replacement' species into threatened ecosystems is warranted.

Conclusions

The convergence of multiple global change pressures on forests and the individual stressors on species that inhabit them requires us to consider these stressors in concert. This study illustrates the intersection of the two pervasive challenges of climate change and insect pest invasion facing black ash in the Northwoods of Minnesota, Wisconsin, and Michigan (USA), and southern Ontario (Canada). Emerald ash borer continues to spread in North America and the climate continues to warm and become more variable. We have modeled the near-term risk of EAB and the long-term risk of climate change on the forests of northern Minnesota. Projected effects of both threats do not bode well for the continued existence of black ash in the Northwoods. Hence, it makes practical sense to evaluate tree species that may be suitable replacements for black ash in these habitats, either through natural regeneration and migration, or via planting. Further, because humans will likely facilitate the connectivity of EAB, as modeled here (Figure 9), to the zones of high black ash abundance across the Northwoods, there is great urgency to consider the reality of a rapidly changing ecosystem (as has been witnessed in OH and MI riparian forests just since 2002). This study aims to narrow the range of possibilities based on modeling, observations from monitoring plots, and species traits. Table 2 provides such a list from which to start. In addition, the D'Amato/Palik study already underway (Looney and others 2015) can be used as a field experiment to test these forecasts, among other objectives.

Meanwhile, the fight to slow the spread of EAB in MN is being waged by many agencies, nongovernmental organizations, businesses, other organizations, and individuals. Though this process is demonstrated to simultaneously address the dual threats facing black ash in Minnesota, the elements to be considered and modeled would be similar for any other location and species which carries a serious pest or pathogen threat. It is our hope that the work presented here can serve as a mechanism and inspiration for further research aimed at addressing multiple global change issues, and most importantly, as guidance for managers in planning for these forests 'in peril.'

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