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Managing forest habitat for conservation-reliant species in a changing climate: The case of the endangered Kirtland's Warbler

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ABSTRACT

Conservation and recovery of species of concern necessitates evaluating forest habitat conditions under changing climate conditions, especially in the early stages of the delisting process. Managers must weigh implications of near-term habitat management activities within the context of changing environmental conditions and a species' biological traits that may influence their vulnerability to changing conditions. Here we applied established population-habitat relationships based on decades of monitoring and research-management collaborations for the Kirtland's Warbler (*Setophaga kirtlandii*) to project potential impacts of changing environmental conditions to breeding habitat distribution, quantity, and quality in the near future. Kirtland's warblers are habitat-specialists that nest exclusively within dense jack pine (*Pinus banksiana*) forests between ca. 5–20 years of age. Using Random Forests to predict changes in distribution and growth rate of jack pine under future scenarios, results indicate the projected distribution of jack pine will contract considerably (ca. 75%) throughout the Lake States region, U.S.A. in response to projected environmental conditions in 2099 under RCP 4.5 and 8.5 climate scenarios regardless of climate model. Reduced suitability for jack pine regeneration across the Lake States may constrain management options, especially for creating high stem-density plantations nesting habitat. However, conditions remain suitable for jack pine regeneration within their historical and current core breeding range in northern Lower Michigan and several satellite breeding areas. Projected changes in jack pine growth rates varied within the core breeding area, but altered growth rates did not greatly alter the duration that habitat remained suitable for nesting by the Kirtland's Warblers. These findings contribute to Kirtland's Warbler conservation by informing habitat spatial planning of plantation management to provide a constant supply of nesting habitat based on the spatial variability of potential loss or gain of lands environmentally suitable for regenerating jack pine in the long-term.

1. Introduction

Conservation and recovery of wildlife species requires knowledge about how changing environmental conditions may impact designated essential habitat in the short- and long-term, especially if future listing or down-listing under the Endangered Species Act is being considered. This information is especially important for species that depend on management activities for all aspects of their recovery (conservation-reliant), such as the endangered Kirtland's Warbler (*Setophaga kirtlandii*; Goble et al., 2012; Bocetti et al., 2012). The Kirtland's Warbler male population continues to increase after attaining the recovery goal of 1000 singing males targeted under the 1976 Recovery Plan (Byelich et al., 1976). Since 2012, the population estimate has remained above 2000 males (Bocetti et al., 2014). A critical factor in this recovery is the large-scale jack pine (*Pinus banksiana*) reforestation efforts within designated essential breeding habitat (Kirtland's Warbler Management Areas [KWMAs]) in the northern Lower Peninsula of Michigan, which represents the warblers' core breeding area (Bocetti, 1994; Byelich et al., 1976; Probst, 1986; Probst et al., 2003). As a result of management efforts and subsequent recovery of the species, the Kirtland's

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Warbler is being considered for delisting (Federal Register, 2018; USFWS, 2012). However, a critical step in future adaptive planning and conservation management is assessing impacts of changing environmental conditions on the future distribution, amount, and quality of the warblers' preferred breeding habitat.

Kirtland's Warblers breed almost exclusively within young (ca. 5–20 year old), dense (generally > 3000 stems ha^{-1}) jack pine dominated forests growing on coarse sands (mostly Grayling series) within KWMAs (Probst and Weinrich 1993). Historically, large stand-replacing wildfires in jack pine habitat of northern Lower Michigan regenerated this nesting habitat creating a patchy distribution with a shifting mosaic of age classes across the landscape (Donner et al., 2008). Because wildfire suppression reduces the area of natural regeneration of jack pine, the U.S. Forest Service (USFS) and Michigan Department of Natural Resources (MDNR) augment natural wildfire-created habitat using high stem-density jack pine plantations, which contain small openings to mimic wildfire-regenerated habitat (Kepler et al., 1996). Eighty percent of existing young jack pine forest (0–20 years) within KWMA counties originated from plantation regeneration (USDA Forest Service). These plantations are established on a rotation basis to ensure at least 12,000 ha of suitable breeding habitat in various age cohorts is available for nesting annually into the future (Kepler et al., 1996).

A major concern for long-term conservation of the Kirtland's Warbler is whether future environmental conditions will result in unsuitable environments for jack pine to survive and grow thereby influencing the ability to regenerate these jack pine plantations in the foreseeable future (MDNR, 2015; USFWS, 2012). Over 95% of the Kirtland's Warbler breeding population is found within these jack pine plantations (Brown et al., 2017; Federal Register, 2018). Being a habitat specialist, the Kirtland's Warbler's biogeography and population size (i.e., carrying capacity) is closely linked to the distribution and amount of jack pine-dominated breeding habitat within the core breeding area (Donner et al., 2008; Probst, 1986; Probst, 1988; Probst and Weinrich, 1993). This relationship is believed to influence the establishment of warbler breeding populations outside the historical core breeding area (Probst et al., 2003). Nesting was first recorded in Michigan's Upper Peninsula in 1994 on the Hiawatha National Forest (Levine et al., 2007) and in 2007 in Adams County, Wisconsin (Anich et al., 2011); both nesting events coincided with periods of rapid Kirtland's Warbler population growth in relation to the amount of suitable breeding habitat in the core breeding area (Donner et al., 2008; Probst, 1986). Changes in the ability to regenerate jack pine, therefore, can influence biogeography of the Kirtland's Warblers that will be important for long-term conservation planning.

Another consideration is how jack pine growth patterns will influence habitat quality and the number of years habitat is suitable for Kirtland's Warbler nesting. Temporal patterns of habitat use by warblers is related to the height of jack pine, which influences canopy cover. Warblers begin using habitat when it is 3–5 years old. Warbler numbers rapidly increase for the first 3–5 years after colonization, then stabilize over the next 4–7 years, and rapidly decline the following 3–5 years in response to aging habitat and increasing canopy cover (Bocetti, 1994; Probst, 1986). The period of greatest Kirtland's Warbler density is when jack pine is 1.7–3.3 m in height, which is considered optimal habitat conditions (Bocetti, 1994; Brown et al., 2017; Probst, 1986). Changing jack pine growth rates will influence the timing of habitat colonization and abandonment (i.e., duration of use by Kirtand'sWarbler) and ultimately, the amount of suitable habitat required on the landscape to maintain desired population goals (Donner et al., 2010). Thus, the relationship of male density to growth of jack pine (age) varies in response to site factors as well as regional warbler-habitat use patterns (Donner et al., 2009, 2010). Although growth and yield models for jack pine plantations account for site productivity, they typically do not incorporate climate variables (Sharma et al., 2015).

Changes in environmental conditions that influence jack pine – warbler relationships will have implications tor future management and conservation of Kirtland's Warblers. For example, if environmental conditions become unsuitable for jack pine occupancy within designated KWMAS on public lands, habitat management options to artificially regenerate jack pine may become limited. Alternatively, if conditions remain conducive for jack pine occupancy but tree growth rates vary significantly in response to predicted precipitation and temperature changes, duration of use by Kirtland's Warblers could be altered enough to impact the required landbase in which to establish enough breeding habitat as well as habitat creation rates. Botkin et al. (1991) investigated these relationships by simulating forest growth of individual trees in response to rainfall and temperature in northern Lower Michigan, and projected that jack pine growth would decrease while growth of other native tree species would increase, thereby shifting the system towards an open woodland dominated by aspen (*Populus* spp.) and oak (*Quercus* spp.) due to competition. However, competition by other tree species is not as relevant within the intensively managed jack pine plantations used today to create warbler habitat.

Recent climate change modeling studies using mechanistic-modeling approaches (e.g., LANDIS-II) also project a decrease in jack pine abundance in terms of aboveground biomass on the landscape. However, the spatial extent of these studies only covered the northern upper Lake States (e.g., Gustafson and Sturtevant, 2013; Handler et al., 2014a; Handler et al., 2014b, Janowiak et al., 2014), or were ecosystem-centric to barrens (e.g., Scheller and Mladenoff, 2008; Duveneck et al., 2014). Changes in above-ground biomass estimates as a response are difficult to translate into Kirtland's Warbler habitat management planning that targets siting, acreage, and rotation of young, dense jack pine forests on the landscape to incorporate the warbler's biological requirements and sustain population goals. The Climate Change Tree Atlas project (Iverson et al., 2008), which uses a climate envelop approach (i.e., niche-based modeling) to identify distributional changes of tree species to climate change also shows a contraction in jack pine distribution, but the coarse-scale across the region can be difficult to translate to Kirtland's Warbler management and does not consider growth .

The purpose of this study was to assess jack pine distribution and growth under changing climate scenarios within the context of future habitat management and conservation of the Kirtland's Warbler. Specific objectives were to (1) determine jack pine distribution (i.e., occupancy) and growth under current and future (2099) temperature and precipitation conditions across the Lakes States region, U.S.A., (2) assess change in jack pine occupancy between current and future environmental conditions to evaluate potential distribution shifts of the Kirtland's Warbler population in response, and (3) assess change in duration habitat is highly suitable based on modeled jack pine growth on lands predicted to be occupied by jack pine from objective 2 within current and historical nesting areas, specifically focusing on KWMAs in northern Lower Michigan. Our results can be incorporated into future habitat management plans to adjust conservation actions such as designated essential habitat land base, annual jack pine regeneration goals, and harvest rotation schedules to ensure that adequate breeding habitat is maintained on the landscape to sustain population goals.

2. Methods

2.1. Study area

To assess jack pine occupancy, we focused on the states of Michigan, Minnesota, and Wisconsin, USA (hereafter, the Lake States region), which encompass the southern border of the jack pine distribution as

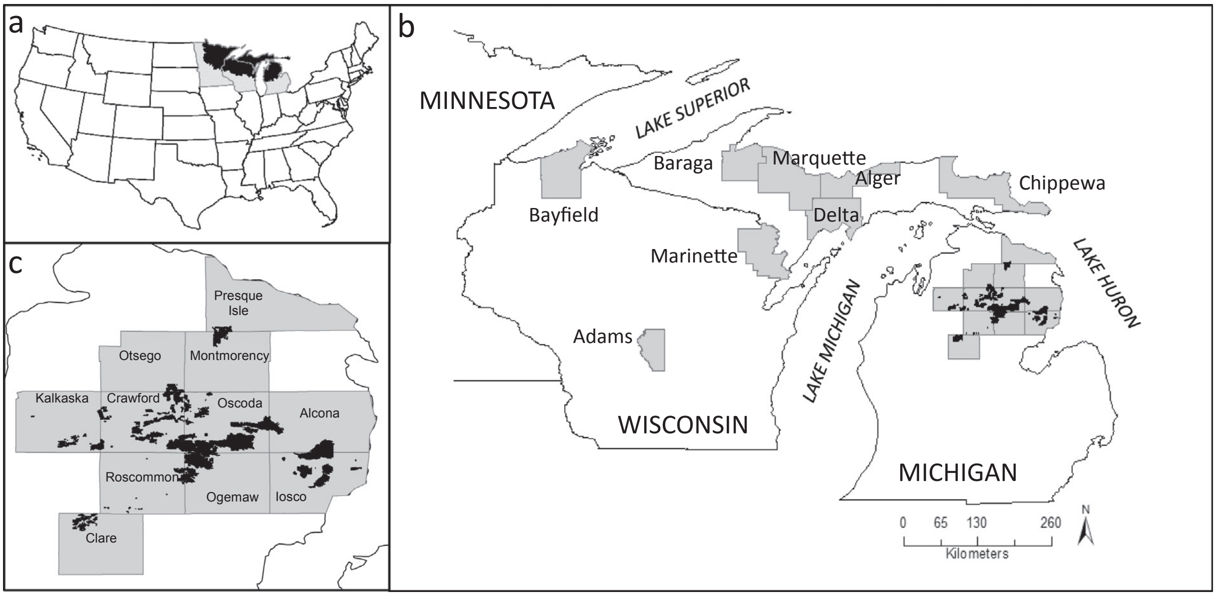

Fig. 1. Map of the study area showing (a) Lake States region in the United States in which jack pine occupancy modeled (black indicates Upper Lake States region - Mixed Laurentian Forest), (b) 19 counties with historical or current Kirtland's Warbler nesting activity (gray) within Michigan and Wisconsin in which jack pine occupancy and growth modeled, and (c) Kirtland's Warbler Management Areas (black) located within 11 counties in northern Lower Michigan.

well as the recorded geographical breeding range of the Kirtland's Warbler within the United States (Fig. 1a) (Bocetti et al., 2014; Rudolph and Laidly, 1990). Jack pine is a common component of outwash plain landscapes found throughout the Lake States region, and extensive tracts of jack pine forests are found throughout the outwash plains in northern Lower Michigan. The majority of Kirtland's Warbler breeding habitat falls within the Laurentian Mixed Forest Province (Cleland et al., 2007; ECOMAP, 1993) (Fig. 1a). Climate is characterized by moderately long winters with mean annual temperatures ranging from 2 to 8 °C and mean annual precipitation ranging from 51 to 94 cm with maximum precipitation during summer months (Cleland et al., 2007). Growing season is short, and the frost-free season lasts from 100 to 140 days, but midsummer frosts are common in low-elevation landforms (Kashian et al., 2003). Vegetation is considered transitional between northern boreal forest and southern broadleaf deciduous forest zones. Lakes Superior and Michigan can influence nearshore climates by lowering temperatures in the summer and increasing temperatures in winter compared to the interior areas (Albert, 1995). The southern breeding habitat in Wisconsin (Adams County) is located within the northernmost area of the Eastern Broadleaf Forest Province, which has an average annual temperature of 4 °C and an average precipitation of 51 cm with most precipitation occurring during the growing season (Cleland et al., 2007).

To assess how the duration of highly suitable habitat may be altered because of changes in jack pine growth, we focused on 19 counties (Fig. 1b) with current or documented historical nesting activities on glacial outwash landscapes within the last 15 years. Glacial outwash ecosystems are dominated by excessively drained sandy soils with low available water capacity, and dry jack pine and scrub-oak forests are common (WDNR 2015). We focused on changes in habitat suitability within 11 counties of northern Lower Michigan that include designated essential breeding habitat among 23 KWMAs (Fig. 1c). The KWMAs are dispersed across a 137 km × 130 km area, and vary in size from 5 to 120 km^2 (total 71,610 ha) (Byelich et al., 1976). These counties are considered the core breeding area because nearly the entire population nests within the KWMAs. Soils in these areas are composed of well-washed coarse sands with less than 5% silt plus clay, generally lack weatherable minerals, and are well-drained. Jack pine dominates these low nutrient soils and a mixture of low shrubs (e.g., blueberry [*Vaccinium angustifolium*], Juneberry [*Amelanchier* spp.], sweetfern [*Comptonia peregrine]*), grasses, sedges, and forbs provide forage and nesting cover for Kirtland's Warblers (Bocetti, 1994; Kashian et al., 2003; Probst and Donnerwright, 2003; Walkinshaw, 1983).

2.2. General modeling approach

We created a spatial grid (ca. 12 km^2 cells) across the Lake States region using prediction data derived from General Circulation Models (GCM) developed for the fifth Coupled Model Inter-comparison Project (CMIP5), which corresponds to Assessment Report 5 of the Intergovernmental Panel on Climate Change (IPCC; IPCC, 2013). We obtained contemporary and projected future climate data for 9 environmental variables (Table 1) from the CMIP3 and CMIP5 Climate and Hydrology Projection archive ((http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/), which included statistically downscaled GCM data to the 12 km^2 cells using a quantile mapping approach (Maurer et al., 2007). We used median ensemble values derived from 31 GCMs. The IPCC recommends using GCM ensembles to project climate changes because ensemble averages buffer against unusually low or high estimates from a single model relative to other models (IPCC 2010). However, we explored the influence of extreme precipitation and temperature by modeling jack pine occupancy and growth using a GCM model that represents high extremes (GFDL-ESM2M) and a GCM that represents low extremes (INM-CM4) (Hamann, 2016; Wang et al., 2016). Contemporary climate normals were estimated using extrapolations from observed meteorological data and land surface characteristics, and then normalized based on annual monthly means from 1970 to 1999. This time period also encompasses the period when much of the Kirtland's Warbler habitat relationships were developed and reflects the conditions the Kirtland's Warblers are experiencing.

We modeled jack pine occupancy using each cell's corresponding environmental data to spatially project contemporary climate conditions (1970–1999) as well as future climate conditions in 2099 under Representative Concentration Pathways (RCP) 4.5 and 8.5 scenarios. The RCP 4.5 scenario represents a potential future pathway where CO_2 emissions stabilize and then decrease over the next century, and the RCP 8.5 scenario represents a potential future pathway where CO_2 emissions continue to increase over the next century (Moss et al., 2010). We modeled jack pine growth only within the cells that were predicted to be occupied by jack pine within the 19 counties with current or

Table 1
Environmental variables used to predict jack pine (*Pinus banksiana*) occupancy and growth rate across the Lake States region, USA, based on significant relationships found in previous research on jack pine-climate relationships across the distributional range or expert opinion. Environmental variables included in the final models are shown in bold.

Environmental variables	Relationship	Location	Study information	Reference
Entisol (%)	±	Range-wide	Literature synthesis	Rudolph and Laidly (1990)
	±	Eastern and Central USA	Habitat suitability model	Prasad et al. (2007-ongoing)
Annual mean daily temperature[a]	±	Ontario, Canada	Seed-transfer experiment	Savva et al. (2007)
Annual maximum daily temperature	±	Ontario, Canada	Seed-transfer experiment	Savva et al. (2007)
Growing season daily temperature	±	Manitoba, Saskatchewan, and Quebec, Canada	Temporal variability in radial growth	Brooks et al. (1998); Genries et al. (2012)
	±	Michigan, USA	Spatial variability in height growth	Kashian and Barnes (2000)
	±	Michigan, USA	Spatial variability in height growth	Kashian et al. (2003)
	±	Ontario and Quebec, Canada	Spatial variability in radial growth	Huang et al. (2010); Genries et al. (2012)
	±	Manitoba and Saskatchewan, Canada	Temporal variability in radial growth	Metsaranta and Kurz (2012)
	±	Ontario, Canada	Spatial variability in radial growth	Subedi and Sharma (2013)
	±	Ontario, Canada	Spatial variability in height growth	Sharma et al. (2015)
July daily temperature	–	Eastern and Central USA	Habitat suitability model	Prasad et al. (2007-ongoing)
October daily temperature	±	Upper Lake States Region	Personal communication	M. Kubiske, U.S. Forest Service
Annual precipitation	–	Ontario, Canada	Seed-transfer experiment	Savva et al. (2007)
	–	Saskatchewan, Canada	Spatial variability in radial growth	Bouriaud et al. (2014)
	±	Saskatchewan, Canada	Temporal variability in radial growth	Bouriaud et al. (2014)
Growing season precipitation	±	Manitoba and Saskatchewan, Canada	Temporal variability in radial growth	Brooks et al. (1998)
	–	Eastern and Central USA	Habitat suitability model	Prasad et al. (2007-ongoing)
	±	Ontario, Canada	Temporal survival analysis	Longpré and Morris (2012)
	–	Ontario, Canada	Spatial variability in radial growth	Subedi and Sharma (2013)
	–	Ontario, Canada	Plantation stands tree height	Sharma et al. (2015)
Non-growing season precipitation	–	Manitoba, Quebec, and Saskatchewan, Canada	Temporal variability in radial growth	Brooks et al. (1998); Genries et al. (2012)
Snow-water-equivalent	–	Quebec, Canada	Spatial variability in snowpack and tree damage	Tremblay and Bégin (2005)
Annual soil moisture	–	Saskatchewan, Canada	Spatial variability in radial growth	Bouriaud et al. (2014)
Growing season soil moisture	±	Ontario, Canada	Survivorship of planted seedling trees	Grossnickle and Heikurinen (1989)

Mean annual predictors were included because growing season for conifers is positively related to winter snowpack (Hu et al., 2010) and conifers complete photosynthesis if autumn and winter days are warm enough (Kubiske et al., 2006).

documented historical nesting activities. Although models of jack pine growth were not explicitly linked with occupancy, projected future growth was assumed to apply to the geographic extent of projected future jack pine occupancy. To assess potential shifts in jack pine distribution, and changes in habitat amount and suitability for warbler nesting, we compared future projections to modeled contemporary conditions.

2.3. Jack pine occupancy

To determine the relationship of contemporary jack pine occupancy to environmental variables, we used US Forest Service Forest Inventory & Analysis (Forest Inventory and Analysis 2014; FIA) forested (> 50% forest) plot data across the study area (n = 15,137) to create a dataset and spatial map of jack pine occupancy across the Lake States region (Fig. 2a). FIA conducts the national forest inventory of the United States by collecting tree and condition data across all ownership classes based on a probability sample of permanent plots with fixed radius circular subplots. Trees and conditions are remeasured every 5–7 years, providing data for estimating tree growth, mortality, and removals. A FIA plot was considered occupied (presence) if jack pine was detected at any life stage, which resulted in 9% of plots being occupied by jack pine and used for the model (n = 1385; Fig. 2b). Field-measured forested plots with no recorded detection of jack pine were considered 'absence' plots, resulting in a jack pine presence/absence dataset. Publicly available FIA plot location coordinates have random error added due to a legal requirement for the FIA program to protect landowner privacy and to maintain ecological integrity of plot conditions. These coordinates fall within 1.6 km of the true plot location (most within 0.8 km; FIA 2014), resulting in assignment of most plots to the correct 12 km^2 cell. Effects of imprecise coordinate locations on resulting analyses were assumed to be minimal (McRoberts et al., 2005).

We used 4 precipitation and 5 temperature predictor variables based on previous research into jack pine-climate relationships (Table 1). We also included annual and growing season (May-September) soil moisture predictors that are influenced by climate (Maurer et al., 2002; Iverson et al., 2008; Yu et al., 2014), and are known to influence growth rates (i.e., site index; Rudolph and Laidly, 1990; Kashian et al., 2003) (Table 1). Growth improves on well drained loamy sands with greater water-holding capacity in the upper 30 cm due to an increase in fine sand and silt and clay (Rudolph and Laidly, 1990). We also included a static soil variable, % entisol, which was found to be the strongest predictor of jack pine habitat suitability in the Climate Change Tree Atlas (Prasad et al., 2007-ongoing). Entisols are mineral soils with little differentiation among horizons below the A horizon (i.e., weakly-developed soils) often associated with glacial outwash. We obtained % entisol from the Soil Geographic Database (STATSGO).

Because our objective was to project potential changes in jack pine distribution to guide future siting of plantations across a region, we used a niche-based modeling approach, Random Forest (RF; Breiman 2001) classification trees, to model the relationship between contemporary jack pine occupancy and the environmental variables. We then used these relationships to project potential future jack pine occupancy. Environmental niche modelling (or bioclimate envelope models) based on abiotic factors is suitable for predicting future distributional ranges of plants at a regional-scale because the approach incorporates the environmental conditions in which a species can survive and grow (see review by Pearson and Dawson, 2003). Random Forests is an ensemble-learning approach to quantify predictor-response variable relationships (Breiman 2001, Evans et al., 2010). In RF, classification (occupancy) trees are created using a random subset of both the response data set (i.e., FIA plots) and the environmental

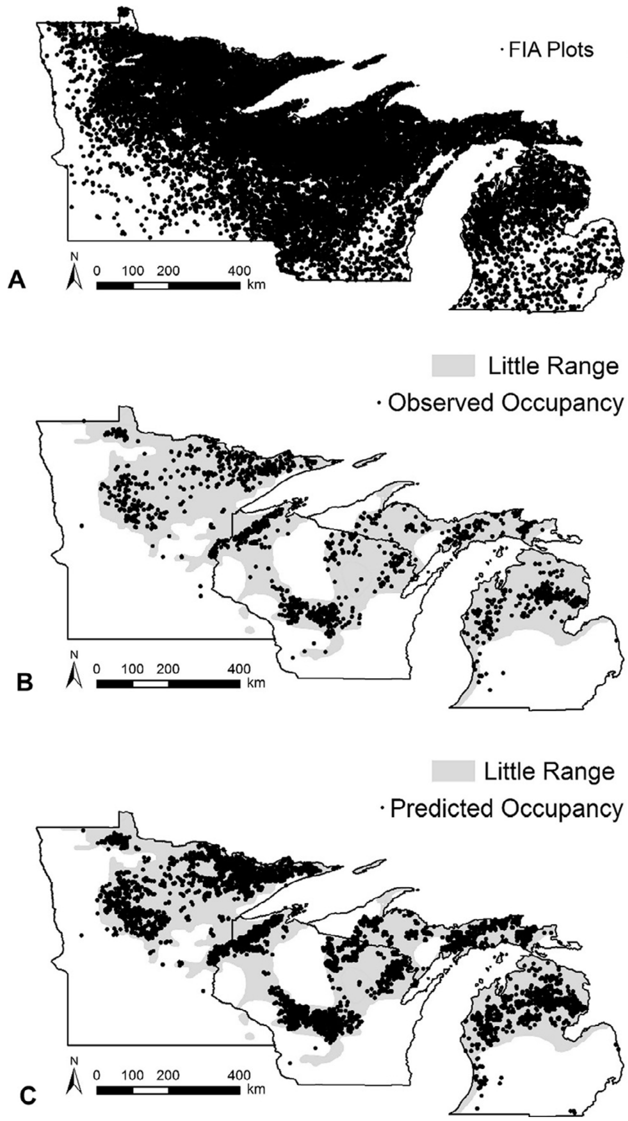

Fig. 2. Maps of (a) distribution of Forest Inventory and Analysis (FIA) plots across Lake States region, (b) plots occupied by jack pine in relation to jack pine geographic distribution (light gray; Little, 1971), and (c) plots predicted to occupied by jack pine using a Random Forests (RF) classification model with 5 environmental predictors in relation to jack pine geographic distribution (light gray; Little, 1971; Prasad and Iverson, 2003).

predictors (which differentiates RF from Bagging Trees; Prasad et al., 2006). The analysis is bootstrapped to quantify relationships and determine importance of predictors. Random Forest models are capable of handling correlated predictors and non-linear relationships, and have good predictive performance because they do not overfit the data (Prasad et al., 2006), and are a commonly used method for projecting changes in species distributions (e.g., Rehfeldt et al., 2006; Iverson et al., 2008; Ledig et al., 2010).

We created a preliminary RF model using all 12 environmental predictors, and assessed model performance by using "out-of-bag" (OOB) samples (i.e., unused portion of the dataset representing approximately a third of randomly selected observations for each iteration) to estimate predictive accuracy of the model and determine importance of individual predictors in which to build final models. The preliminary model showed a large imbalance towards absence locations that resulted in the model being fit primarily to minimize false absences. Thus, we implemented down-sampling for each iteration at a 1:1 ratio between presence and absence data to give presence locations adequate model weight (Kuhn and Johnson, 2013). In addition, removing redundant and uninformative predictors can improve performance of RF models (Murphy et al., 2010). We identified and removed 5 redundant predictors using QR decomposition ($P < 0.05$; Eldén, 2007), which had almost no effect on occupancy model accuracy (OOB error increased by 0.18%). Next, we ranked predictor variables by importance and removed one additional uninformative variable (OOB error increased by 0.23% after this variable was removed).

The final RF model included 5 variables: annual soil moisture, daily mean growing season precipitation, daily mean annual precipitation, % entisol, and mean annual temperature. We used 1500 bootstrap replications (> 1500 replications did not improve model performance). We assessed performance of the final model by (1) using OOB samples to estimate predictive accuracy, and (2) visually comparing the model's predicted presence/absence in FIA plots to actual presence/absence in FIA plot dataset. We conducted RF analyses using the packages randomForest (version 4.6–12) and rfUtilities (version2.0–0) in the program R (version 3.2.4).

We used the final RF model to map contemporary and future jack pine occupancy using the cell-specific climate variables (described above), omitting % entisol from future occupancy models under an assumption that this soil variable will remain static within the future modeling framework. We overlaid predicted future jack pine occupancy onto predicted contemporary occupancy geospatial datasets for the Lakes States region to assess changes in distribution and amount. We calculated percent change in jack pine occupancy for counties with current or documented historical Kirtland's Warbler nesting, and also within designated KWMAs.

2.4. Jack pine growth

We used FIA jack pine site tree records within the study area ($n = 666$) to create a jack pine growth dataset. FIA site trees are a sample of trees that provide a measure of site productivity on a forested condition, expressed by the height to age relationship of dominant and codominant trees of a given species, for a base or reference age (50 years for jack pine), and based on one of several published methods. FIA's site index values are based on models from a broader geographic extent than addressed in our study, and are less representative of jack tree ages suitable for warbler habitat (5–20 years). To obtain more spatially and temporally explicit jack pine site index scores we modeled site index from repeated measurements of FIA site trees. We extracted estimated tree height and age at-breast-height (ABH), and added 4 years to ABH based on the jack pine growth literature to estimate true age (Longpré et al., 1994, Béland and Bergeron 1996). Next, we conducted a regression-based point change analysis using the package "segmented" in Program R (version 3.3.2; Muggeo, 2003) to determine the age range where the growth rate was approximately linear given the non-linear cumulative tree growth curves during early and late ages. Based on this analysis, we restricted the growth data set to trees ≤ 53 years old ($n = 464$; range 12–53; 11% ≤20 years old), a threshold below which tree growth rate is approximately linear. Restricting model projections to trees ≤ 53 years old was adequate for our study objective because jack pine is only suitable as Kirtland's warbler breeding habitat from ca. 5–20 years old (Probst and Weinrich, 1993; Donner et al., 2010) under current climate. Site index curves developed for jack pine plantations within Wisconsin showed a linear relationship from 10 to 20 years old (Wilde et al., 1965). Site index curves using breast height age developed for jack pine in north central Ontario also showed linear relationships from 0 to 24 years old with only slight differences between plantations and natural stands (Guo and Wang, 2006). We divided height by age to obtain mean annual height growth.

We used RF regression trees to model the relationship between jack pine height growth and environmental variables following the same approach as for jack pine occupancy (see above). We applied the final model to cells predicted to be occupied by jack pine currently within the 19 counties with current or historical nesting activities. To assess temporal habitat suitability dynamics in response to projected changes in jack pine growth, we estimated the change in the number of years that jack pine would be suitable for nesting as well as the number of years that habitat would function as highly suitable based on the estimated growth rate for each cell between current and future climate conditions. We defined suitable nesting habitat as 1.3–5.0 m in jack pine height, and high suitability habitat as heights between 1.7 and 3.3 m (Brown et al., 2017). If jack pine growth rate declines under future conditions, the initial tree age at which suitability is attained may be delayed, but the total number of years that jack pine would function as suitable breeding habitat would increase (i.e., remain within height criteria) and presumably the duration of use by Kirtland's Warblers would be extended.

3. Results

3.1. Jack pine occupancy and growth models

The final jack pine occupancy model included, in order of importance, annual soil moisture, mean monthly growing season precipitation, mean daily annual precipitation, % entisol, and mean daily annual temperature. The overall OOB error was 18.54%, with an OOB error of 18.26% and 21.23% for false absences and presences, respectively. In general, the predicted occupied and unoccupied FIA plots closely matched the current jack pine distribution (Fig. 2c). Therefore, both model performance measures indicated the 5 environmental variables were sufficient to delineate the jack pine distribution across the study extent. In general, the suitability for jack pine occupancy increased in areas with lower annual soil moisture (i.e., drier), intermediate daily precipitation, greater growing season precipitation and percentage of entisol in soil as well as lower annual temperatures (Appendix A).

The final jack pine growth model included the same variables, but the order of importance was mean growing season precipitation, annual soil moisture, mean annual temperature, mean annual precipitation, and % entisol. Variance explained by the model was 13.25%. In general, jack pine growth increased in areas with greater growing season precipitation, annual soil moisture (i.e., wetter), and lower percentage of entisol in the soil (Appendix A).

Across the study area, mean conditions became hotter under all model scenarios as well as wetter during both the growing season and annually except for INM-CM4 RCP 4.5, which became drier (Appendix B). Soil moisture became drier except under both RCP 8.6 extreme climate scenarios. However, there was considerable spatial variability across the study area (Appendix C).

3.2. Change in jack pine occupancy

For contemporary climate conditions using the GCM ensemble median, 14.7% of the cells within the Lakes States region were modeled as suitable for jack pine occupancy (Fig. 3a). In 2099, projected jack pine occupancy declined to 3.8% and 3.4% of cells (RCP 4.5 and 8.5, respectively), an approximately 75% decline under both climate scenarios. Much of this decline in jack pine occupancy occurred throughout Minnesota, northern Wisconsin, and the Upper Peninsula of Michigan (Fig. 3b, c). Projected 2099 jack pine distribution was primarily a subset of the contemporary climate distribution (i.e., contraction of current distribution) except for a minor distribution shift into southeastern Lower Michigan (Fig. 3b, c). In southeastern Lower Michigan, annual soil moisture, which was the most important variable in the model, was projected to decline under both GCM ensemble models while average growing season precipitation (second most important variable) generally increased under both RCP climate scenarios.

Only 24.6% of cells in the five Michigan Upper Peninsula counties with current or historical nesting activity were modeled as suitable for jack pine occupancy under contemporary climate conditions. Jack pine occupancy was projected to decline by over 80% under future GCM ensemble climate scenarios (Table 2). Much of this decrease occurred in Alger, Baraga, and Chippewa counties, while no jack pine cells were suitable under RCP 4.5 and just a few cells were suitable for jack pine under RCP 8.5 (Table 2). In the three Wisconsin counties, 39.0% of cells were predicted to be suitable for jack pine occupancy under contemporary climate conditions. Under future conditions, Adams County was projected to remain relatively unchanged, while areas within Bayfield County became unsuitable and Marinette County had a 70–90% decrease in occupied jack pine area (Table 2). In the eleven counties containing KWMAS in northern Lower Michigan, 45.3% of the cells were modeled as suitable for jack pine occupancy under contemporary climate conditions, but this area was projected to decline by 44.2% and 22. 1% under RCP 4.5 and 8.5 climate scenarios, respectively (Table 2). Under RCP 4.5, the decline occurred primarily in Kalkaska, Presque Isle, and Clare counties, which contain periphery KWMAs (Fig. 3c). For the centrally located KWMAs, jack pine occupancy was predicted to decline by 64.5% and 72.4% under RCP 4.5 and 8.5 climate scenarios, respectively, but increase in Oscoda County under RCP 8.5 (Table 1).

Specifically, 90.7% of the cells containing KWMAs were modeled as suitable for jack pine occupancy under contemporary climate conditions, which encompassed 94.2% of historical observed Kirtland's warbler locations recorded from 2000 to 2013 during the official census (n = 21,512; Probst et al., 2005). Under the RCP 4.5 and 8.5 GCM ensemble median scenarios, only 70.4% and 54.7% of cells within the KWMAs, respectively, were modeled as suitable for jack pine occupancy. In particular, projected jack pine occupancy shifted out of the western KWMAs under both future climate scenarios (see Fig. 4b, c).

For the high temperature and precipitation extreme model (GFDL-ESM2M), 8.3% and 4.1% of the study cells were modeled as suitable for jack pine occupancy (RCP 4. 5 and 8.5, respectively), while for the low extreme model (INM-CM4), 2.1% and 3. 8%, respectively were modeled as suitable for jack pine occupancy (Appendix D). Only the RCP 4.5 climate scenario for both extreme models resulted in greater percentage (GFDL-ESM2M) or lower percentage (INM-CM4) of jack pine occupancy than the GCM ensemble medians. More cells were suitable for jack pine occupancy in northern Wisconsin and western Upper Peninsula Michigan under the high extreme model (GFDL-ESM2M; Appendix D).

3.3. Change in jack pine growth

Modeled annual tree height growth rates under contemporary climate conditions ranged from 0.23 to 0.41 m per year with the slowest growth rates occurring in northern Lower Michigan and fastest rates in central Wisconsin and north-central Minnesota. Projected annual growth rates generally increased under RCP 4. 5 and 8.5 GCM ensemble medians within the 11 counties in northern Lower Michigan, but declined in Upper Peninsula Michigan counties (Table 2). In Wisconsin, jack pine growth rates were projected to slow in Adams County, but increase in Marinette County under both climate scenarios (Table 2).

Based on these projected changes in growth rates, the duration that jack pine was suitable habitat for Kirtland's Warbler in northern Lower Michigan averaged 14.1 years (SD = 1.3, range = 11–18 years) under contemporary climate, but declined slightly to 12.6 and 11.7 years (SD = 0.5, range = 11–14 years and 10–13 years) under GCM ensemble RCP 4.5 and 8.5, respectively. Mean duration of high habitat suitability (optimal) under contemporary climate conditions was 5.6 years (SD = 0.8, range = 4–7 years) (Fig. 4a). Mean duration of high suitability under RCP 4.5 and 8.5 climate scenario was 5.3 and 5.9 (SD 0.5 for both, range = 4–6 years and 5–7 years), respectively. Duration

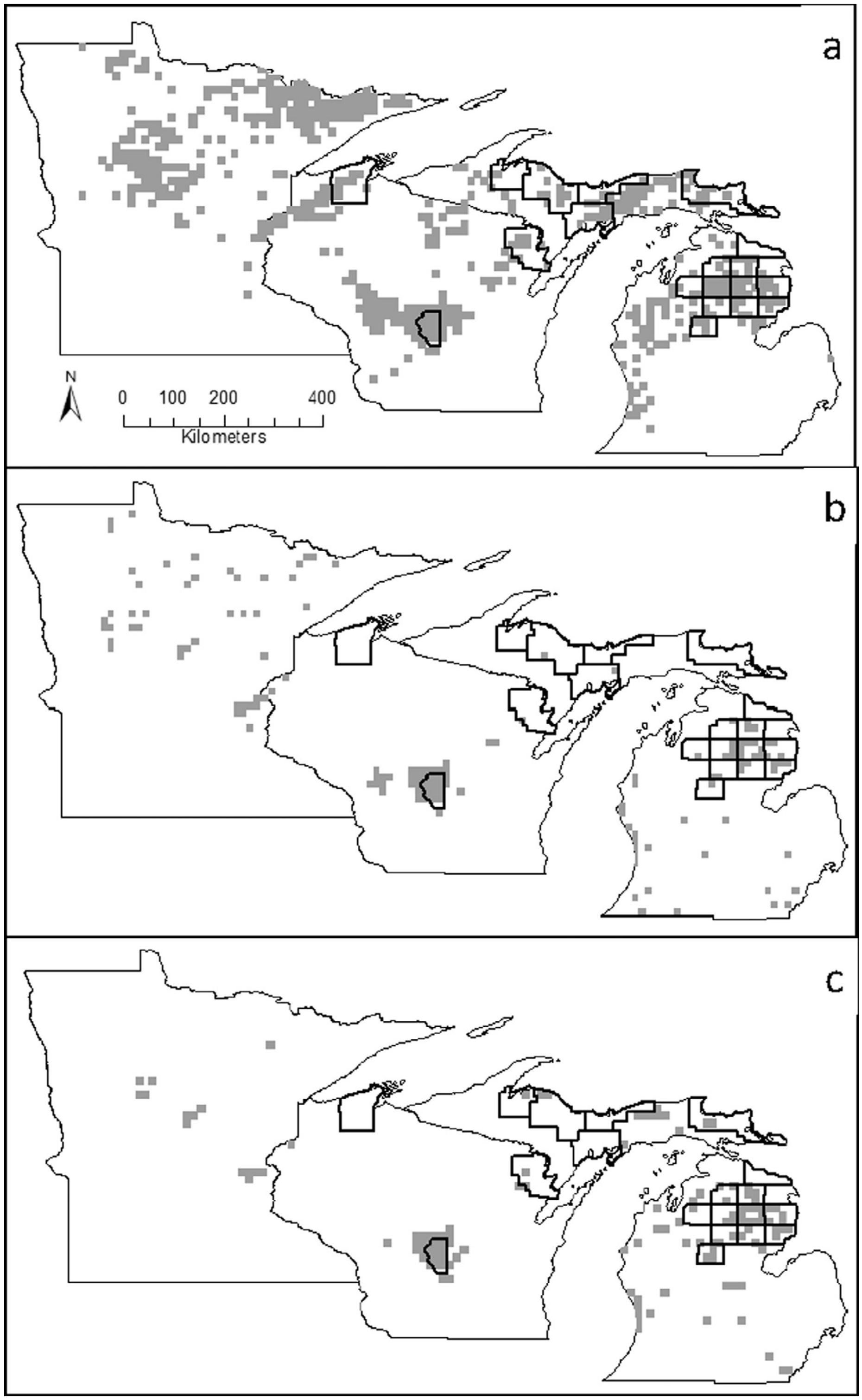

Fig. 3. Maps showing predicted jack pine occupancy (gray) using a Random Forest model with 5 environmental predictors for (a) contemporary climate conditions, and (b) projected jack pine occupancy in 2099 based on median Global Climate Model (GCM) ensemble values and Representative Concentration Pathways 4.5 and (c) 8.5. Bold lines represent borders of 19 counties with current or historical nesting activities by the Kirtland's Warbler.

varied spatially, with increases and decreases of only 1–2 years under both RCP scenarios (Fig. 4b, c). Under RCP 4. 5, duration declined by an average of 0.5 years, while under RCP 8.5, duration increased by an average of 0.2 years. In Adams County, WI, the average duration of highly suitable habitat was 3.9 years (SD = 0.7) under contemporary climate, and increased to 4.3 (SD = 0.5) and 5.5 (SD = 0.5) years under RCP 4.5 and 8.5, respectively.

For the high climate threshold model, average annual growth under contemporary condition was 0.36 m (SD = 0.05; 0.23–0.46) compared to 0.37 m (SD = 0.03, 0.30–0.43; SD = 0.04, 0.28–0.44) for GFDL-ESM2M 4.5 and 8.5, respectively. For the low threshold model, average annual growth under contemporary condition was 0.35 m (SD = 0.05, 0.23–0.45) compared to 0.36 m (SD = 0.05; 0.23–0.45) for INM-CM4 4.5 and 8.5.

Table 2
Predicted jack pine occupancy and growth under contemporary climate conditions and future climate scenarios RCP 4.5 and 8.5 in 2099 for the 19 counties with current or historical Kirtland's Warbler nesting activity.

		Percent occupied (% change)			Mean annual height (m)		
COUNTY	Area (km^2)	Contemporary climate	RCP 4.5	RCP 8.5	Contemporary climate	RCP 4.5	RCP 8.5
CORE BREEDING AREA, NORTHERN LOWER MICHIGAN							
Alcona	1800.4	50.9	28.7 (−43.7)	37.0 (−27.3)	0.28	0.31 (9.9)	0.31 (10.6)
Clare	1490.0	41.9	14.7 (−65.0)	35.4 (−15.5)	0.29	0.30 (3.9)	0.34 (16.5)
Crawford	1458.9	100.0	35.5 (−64.5)	27.6 (−72.4)	0.32	0.31 (−1.0)	0.37 (15.9)
Iosco	1467.9	48.7	39.4 (−19.2)	39.4 (−19.2)	0.29	0.31 (6.3)	0.31 (9.4)
Kalkaska	1471.0	28.7	8.6 (−70.2)	8.1 (−71.7)	0.29	0.30 (3.2)	0.37 (29.4)
Montmorency	1457.9	53.9	28.7 (−46.7)	39.4 (−26.9)	0.28	0.29 (3.6)	0.30 (7.2)
Ogemaw	1489.9	41.9	28.8 (−31.3)	27.0 (−35.5)	0.32	0.31 (−1.9)	0.35 (10.8)
Oscoda	1481.1	75.8	65.6 (−13.5)	81.4 (7.3)	0.28	0.30 (8.8)	0.32 (16.3)
Otsego	2718.6	32.1	19.5 (−39.2)	55.6 (73.0)	0.32	0.30 (−6.3)	0.35 (9.37)
Presque Isle	1774.2	9.3	3.1 (−66.9)	3.1 (−66.9)	0.27	0.30 (10.5)	0.31 (13.1)
Roscommon	1502.4	32.6	14.3 (−56.2)	23.1 (−29.1)	0.28	0.31 (10.3)	0.35 (24.3)
Total	18112.3	45.3	25.3 (−44.2)	35.3 (−22.1)	0.29	0.30 (5.2)	0.33 (15.3)
UPPER PENINSULA OF MICHIGAN							
Alger	2426.0	21.5	0.0 (−100.0)	0.4 (−98.0)	0.36	–	0.37 (2.7)
Baraga	2374.8	9.5	0.0 (−100.0)	5.5 (−42.2)	0.36	–	0.33 (−7.4)
Chippewa	4089.8	32.3	0.0 (−100.0)	6.5 (−79.7)	0.34	–	0.32 (−7.0)
Delta	3047.1	32.5	4.4 (−86.4)	0.5 (−98.3)	0.35	0.30 (−12.4)	0.34 (−0.9)
Marquette	4838.1	22.1	2.8 (−87.5)	5.4 (−75.6)	0.36	0.37 (1.5)	0.34 (−7.2)
Total	16775.8	24.6	1.6 (−93.5)	4.1 (−83.4)	0.36	0.34 (−5.4)	0.31 (−12.4)
WISCONSIN							
Adams	1781.3	88.3	84.9 (−3.8)	84.9 (−3.8)	0.39	0.37 (−5.4)	0.36 (−7.7)
Bayfield	3921.1	28.7	0.0 (−100.0)	0.0 (−100.0)	0.41	–	–
Marinette	3680.4	26.2	2.6 (−90.0)	7.0 (−73.3)	0.35	0.36 (4.8)	0.36 (4.8)
Total	9382.8	39.0	17.1 (−56.1)	18.9 (−51.7)	0.38	0.38 (−4.1)	0.36 (−5.4)

4. Discussion

Our results indicate that the projected distribution of jack pine may contract throughout the study area in response to projected environmental conditions in 2099 under RCP 4.5 and 8.5 climate scenarios. This would result in less area suitable for siting jack pine plantation habitat that will survive and grow within the Lakes States region, and thus, less potential for Kirtland's Warbler habitat on the landscape in the future. Plantations are the primary regeneration method used to meet target levels of suitable breeding habitat area on the landscape to supplement the amount of dense jack pine regenerated naturally following timber harvests or wildfires (Byelich, 1976; Kepler et al., 1996; MDNR, 2015). This management approach is expected to continue as wildfire suppression efforts in Michigan have reduced acreages burned and increased the average fire return interval to 775 years in the same landscape (Cleland et al., 2004; MDNR, 2015). Even with the potential limited expansion of habitat in southeastern Lower Michigan, the amount of land projected to become suitable for jack pine occupancy was minimal and would not offset losses elsewhere.

One of the primary questions of our study was whether environmental conditions would remain suitable within the Kirtland's Warblers primary breeding range (northern Lower Michigan) and whether altered jack pine growth rates would impact the duration that habitat was suitable. Conditions were projected to remain suitable for jack pine occupancy within northern Lower Michigan, and although projected jack pine growth rates varied in this area, such changes did not greatly

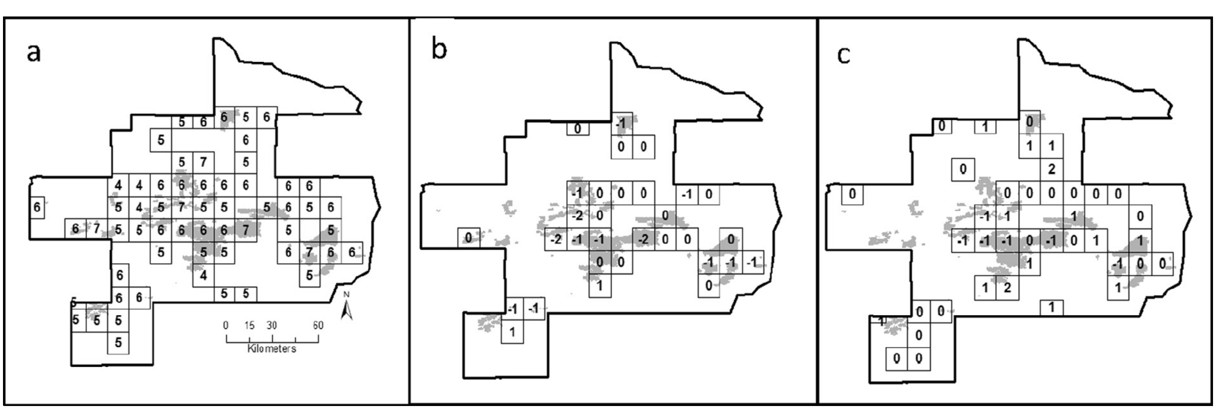

Fig. 4. Maps showing (a) the number of years jack pine is considered highly suitable habitat for Kirtland's Warblers based on jack pine growth model under contemporary conditions for cells modeled as occupied by jack pine within the 11 counties of northern Lower Michigan (see Fig. 3), and (b) change in number of years of high suitability in 2099 from contemporary conditions based on jack pine growth models under RCP 4.5 and (c) RCP 8.5 climate scenarios. Gray indicates of Kirtland's Warbler Management Areas.

alter the duration of habitat suitability nor the number of years in which habitat was highly suitable for nesting Kirtland's Warblers. In addition, conditions in peripheral nesting habitat in Adams County, WI, was predicted to remain suitable for jack pine occupancy with reduced jack pine growth rates that may extend the duration jack pine habitat could be used for nesting Kirtland's Warblers. However, many of the areas with current or historical nesting activity in the Upper Peninsula of Michigan became unsuitable, with the exception of the high threshold RCP 8.5 scenario.

Our projected contraction in jack pine distribution and general decline across the Lake States was also predicted by others that modelled forest community changes using above ground biomass across smaller spatial extents than our study. Scheller and Mladenoff (2008) simulated multiple scenarios of disturbance and climatic change using a mechanistic model (i.e, LANDIS-II) across a forested landscape (607,028 ha) in northwestern Wisconsin and projected a reduction in aboveground jack pine live biomass on the landscape. Gustafson and Sturtevant (2013) investigated drought stress from climate change in the Upper Lake States using LANDIS-II, and found pine (including jack pine) biomass was projected to decline, but it remained on the landscape. In climate vulnerability assessments for northern Wisconsin, and northern Michigan, distribution models also using LANDIS-II projected jack pine biomass to decrease across the landscape over the next 100 years in response to predicted hotter and wetter conditions (Handler et al., 2014a, b; Janowiak et al., 2014). This decline in biomass may be offset to some degree by other interacting natural ecosystem processes such as fire regime and harvesting disturbances as well as the capacity of jack pine to adapt to climate change (e.g., drought) or out-compete other species that may modify our projected future distribution and amount of naturally-regenerated jack pine on the landscape (Blois et al., 2013; Gustafson and Sturtevant, 2013; Longpré et al., 1994; Matthews et al., 2011; Rothstein and Spaulding, 2010).

Niche-based modeling is often viewed as a first approximation to species' distribution under changing environmental conditions within a multiscale hierarchical framework (Pearson and Dawson, 2003). Our study should be considered a first approximation to begin guiding future jack pine plantation management for creating Kirtland's Warbler habitat. Using niche-based modeling approaches, however, does not incorporate biotic interactions, adaptive genetic variation, and dispersal limitations explicitly (see Hampe, 2004 and response by Pearson and Dawson, 2004). But planting pure, dense jack pine stands is a human-mediated dispersal rather than natural dispersal, and competition from other species as well as adaptive genetic variability factors are not likely to influence our results because of the use of container stock seedlings that provide a competitive advantage during the establishment years (Greco, pers. communication) and the relatively short timeframe of our study. Moreover, niche-modeling techniques that use presence and absence data to project future distributions such as we did have been shown to provide a better fit for current distributions and subsequent projections of future distributions than techniques using presence-only data (Pearson et al., 2006).

The loss of area suitable for jack pine occupancy may be offset to some degree if annual jack pine growth declines enough to increase the number of years Kirtland's Warblers would use the habitat. However, our results indicate the change in jack pine growth will likely be minimal within the Kirtland's Warbler core nesting area, and most likely not enough to mitigate the loss of area suitable for jack pine occupancy. However, the low explanatory power of our growth model is a limitation of our results, and is most likely due to our niche-based modeling approach that does not incorporate local, biotic interactions (e.g., inter-species competition) explicitly. We parameterized our model based on growth relationships from naturally occurring jack pine forests, which introduced considerable variability due to local interactions. A future consideration for jack pine plantations is the influence different stocking densities may have on growth, and thus, Kirtland's warbler temporal use. The proposed nontraditional plantations (i.e., less dense) on 25% of required habitat (MDNR, 2015) may increase growth rates that, in turn, may result in fewer years used by the Kirtland's Warbler and the need to create more habitat on the landscape to offset the shorter duration of use. We encourage more research and mechanistic-based modeling at local and landscape scales to reduce the uncertainties associated with the complexity of interacting abiotic and biotic processes, changes to the fire regime, and population processes that may influence jack pine growth.

The spatial variability in growth across northern Lower Michigan counties seen in our projections, however, is consistent with previous research that found jack pine growth rates differed latitudinally and longitudinally in response to biotic and edaphic conditions, or site productivity (Carmean et al., 1989; Carmean and Lenthall, 1989; Béland and Bergeron, 1996; Kashian et al., 2003). In addition, the minimal differences in simulated jack pine growth in relation to climate variables may be related to the short period of time we used (i.e., age range for which Kirtland's Warblers use jack pine forests for nesting). Sharma et al. (2015) found jack pine height growth in plantations was less affected by climate than other tree species, and growth was not significantly affected by climate variables until the age of 15, which is nearing the age that jack pine begins declining in suitability for the Kirtland's Warbler. Another source of variability that may influence our results is the general lack of information on height growth rates for younger stand ages (i.e., < 5 years). Differential height growth rates may alter initial age jack pine becomes suitable or duration habitat is suitable if growth became nonlinear before 20 years of age, but we were projecting net change in years associated with projected changes in climate, which were minor. In addition, site-index curves have been found unreliable for juvenile pine plantations (Avery and Burkhart, 1994; Guo and Wang, 2006).

Given jack pine plantations will continue to be the primary regeneration method for creating Kirtland's Warbler nesting habitat, further studies on climate events that may increase mortality of seedlings is warranted to better assess the success and economics of a long-term plantation program. Climate was found to influence natural recruitment (i.e., seedling) patterns of the Scots pine (*Pinus sylvestris*) at its southern most distribution limit in the Mediterranean Basin that differed from northern forests (Castro et al., 2004; Benavides et al., 2013). Within the upper Lake States region, winter processes are expected to change temperature and precipitation dynamics that will influence the amount and timing of precipitation, duration of soil frost periods, and soil moisture (Handler et al., 2014a, b; Janowiak et al., 2014). These factors may impact seedling mortality, or growth at finer-scales. Preliminary analysis of a plantation program in Michigan found snow water equivalent (or amount of snow) may have an impact on seedling mortality (unpublished data, Tim Greco). Our predicted jack pine occupancy distribution could provide a template for investigating seedling mortality across a wide range of environmental conditions to explore this topic in more depth and results could be used to extend jack pine habitat (i.e., plantations) in areas outside our predicted geographical range.

5. Conclusion

Managing conservation-reliant species in the face of climate change is difficult because of uncertainty and limited resources. Threats for these species can be managed, but not eliminated (Goble et al., 2012). For the Kirtland's Warbler, habitat restoration activities since the 1980s reduced one of the major threats to the population (i.e., lack of suitable habitat), but it is uncertain if these gains can be maintained under future climate conditions. Our study suggests that most of the core breeding range of the Kirtland's Warbler range may be resilient to changing climate, but that some peripheral and newly established populations may be at risk. For example, the historical core breeding range in Lower Peninsula of MI and Adams County, WI remained suitable for Jack pine in the long-term future, but the Upper Peninsula of Michigan, which is currently viewed as a highly viable area in which to encourage population expansion, may have less long-term viability. Continuing the jack pine plantation program in northern Lower Michigan seems reasonable given conditions are projected to remain suitable for jack pine occupancy into the near future. Moreover, the expansion of suitability for jack pine in southeastern Michigan may represent potential new areas for creating jack pine habitat in the future. We assumed that the range of past and current conditions can reliably predict future relationships, but this may not be the case under novel conditions, which is a limitation of our results and should be considered. However, managers of Kirtland's Warbler habitat must use the best available current information to evaluate consequences of proposed management activities and assess the trade-offs required when financial resources and decision space (e.g., public versus private lands) are limited. The results of this study complement existing information from other types of models thereby adding to the knowledge base that can be used to inform short- and long-term habitat management planning within the context of the Kirtland's Warbler vulnerability to climate change.

Acknowledgments

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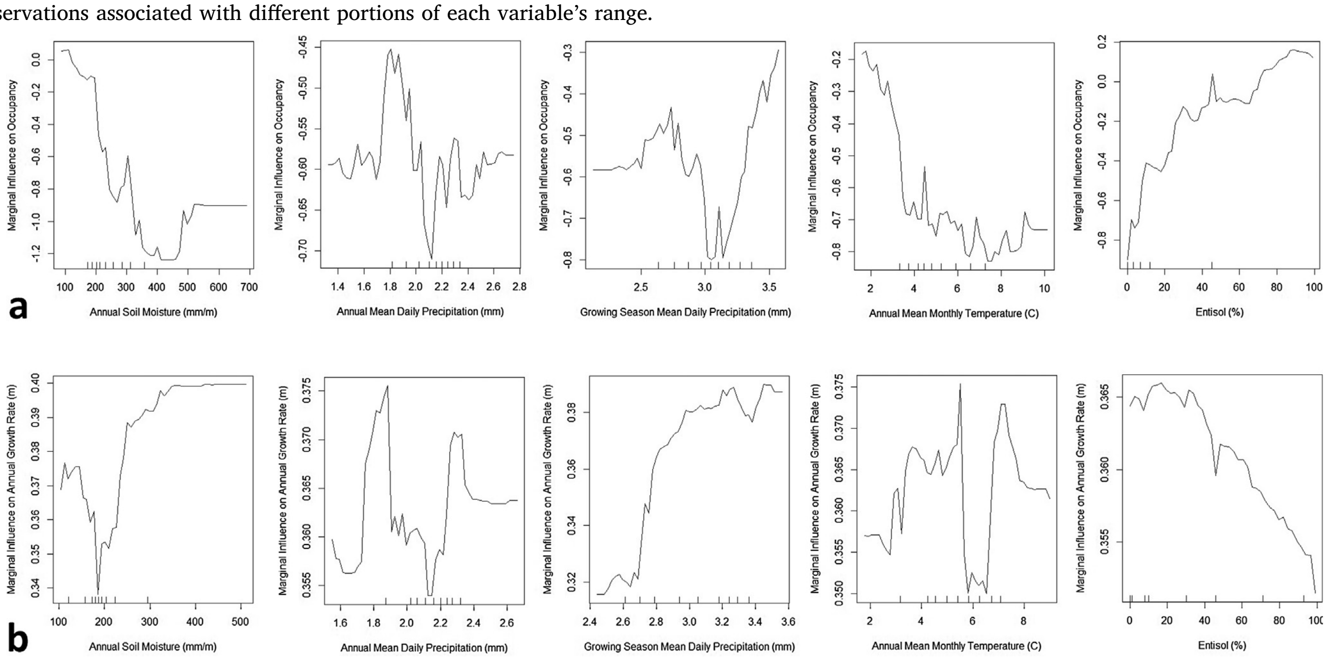
Appendix A

Partial dependence plots showing the marginal influence of each environmental variables on (a) occupancy and (b) annual growth rate of jack pine (*Pinus banksiana*) across Michigan, Minnesota, and Wisconsin, USA, after partialing out the influence of the other environmental variables in Random Forest models. Jack pine data were obtained (occupancy) or derived (growth rate) from the US Forest Service Forest Inventory & Analysis (FIA) database. Contemporary climate normals were obtained from the CMIP3 and CMIP5 Climate and Hydrology Projection archive, with a resolution of ca. 12 km^2. The observation data deciles are delineated by hash marks in each partial dependence plot, indicating the relative amount of observations associated with different portions of each variable's range.



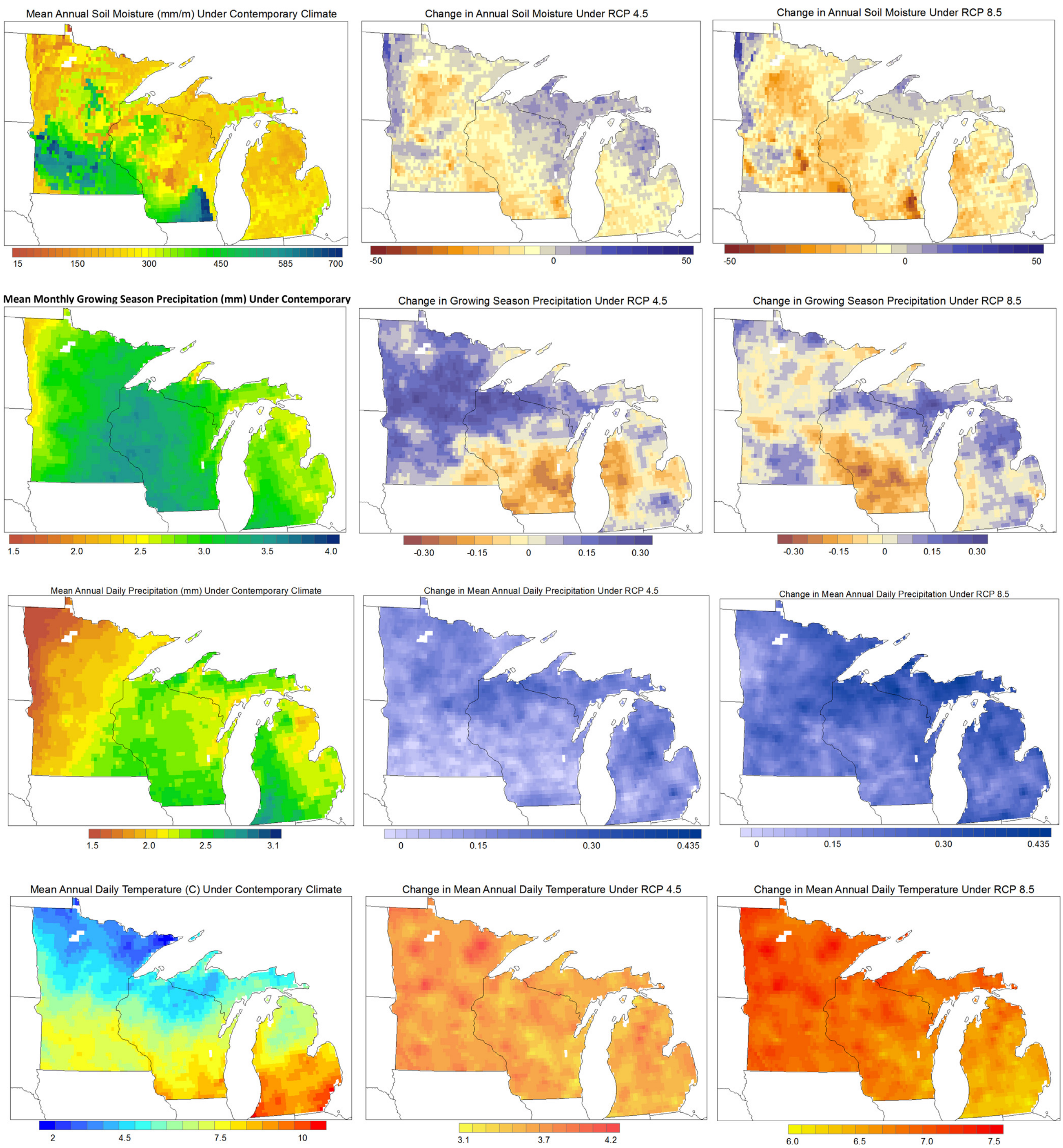
Appendix B

Model comparison of the four climate variables that entered into final Random Forest jack pine *(PInus banksiana)* occupancy and growth models under Global Climate Models (GCM) ensembles, and under high and low temperature and precipitation extreme models (GFDL-ELM2M and INM-CM4, respectively for contemporary climate and in 2099 under RCP 4. 5 and 8.5 climate scenarios across Michigan, Minnesota, and Wisconsin, USA.

Environmental variable	Model	Future climate condition	Mean	Std Dev	Min	Max
Annual daily precipitation (mm/day)	Contemporary	NA	2.09	0.26	1.32	2.75
	GCM	RCP 4.5	2.21	0.26	1.45	2.90
	GCM	RCP 8.5	2.30	0.28	1.48	3.04
	GFDL-ESM2M	RCP 4.5	2.24	0.40	1.25	3.31
	GFDL-ESM2M	RCP 8.5	2.57	0.49	1.32	4.25
	INM-CM4	RCP 4.5	1.93	0.35	1.15	3.24
	INM-CM4	RCP 8.5	2.38	0.33	1.45	3.52
Growing season daily precipitation (mm/day)	Contemporary	NA	2.96	0.30	2.12	3.57
	GCM	RCP 4.5	2.97	0.31	2.13	3.69
	GCM	RCP 8.5	2.93	0.27	2.08	3.56
	GFDL-ESM2M	RCP 4.5	3.03	0.37	1.95	4.14
	GFDL-ESM2M	RCP 8.5	3.58	0.67	2.29	5.35
	INM-CM4	RCP 4.5	2.55	0.38	1.74	3.65
	INM-CM4	RCP 8.5	3.05	0.45	1.73	4.42
Annual soil moisture (mm/m)	Contemporary	NA	283.46	113.52	0.00	689.14
	GCM	RCP 4.5	282.91	111.02	0.00	674.24
	GCM	RCP 8.5	277.12	110.96	0.00	662.98
	GFDL-ESM2M	RCP 4.5	273.55	122.22	56.35	724.55
	GFDL-ESM2M	RCP 8.5	304.46	117.42	91.82	720.94
	INM-CM4	RCP 4.5	271.64	113.73	54.14	693.39
	INM-CM4	RCP 8.5	291.85	120.70	74.64	724.59
Annual monthly temperature (C)	Contemporary	NA	5.88	1.73	1.60	10.13
	GCM	RCP 4.5	9.44	1.68	5.04	13.46
	GCM	RCP 8.5	12.62	1.58	8.44	16.37
	GFDL-ESM2M	RCP 4.5	8.11	2.62	2.49	12.61
	GFDL-ESM2M	RCP 8.5	10.69	3.00	4.48	16.31
	INM-CM4	RCP 4.5	8.25	2.93	2.16	13.63
	INM-CM4	RCP 8.5	11.56	2.63	6.66	16.54

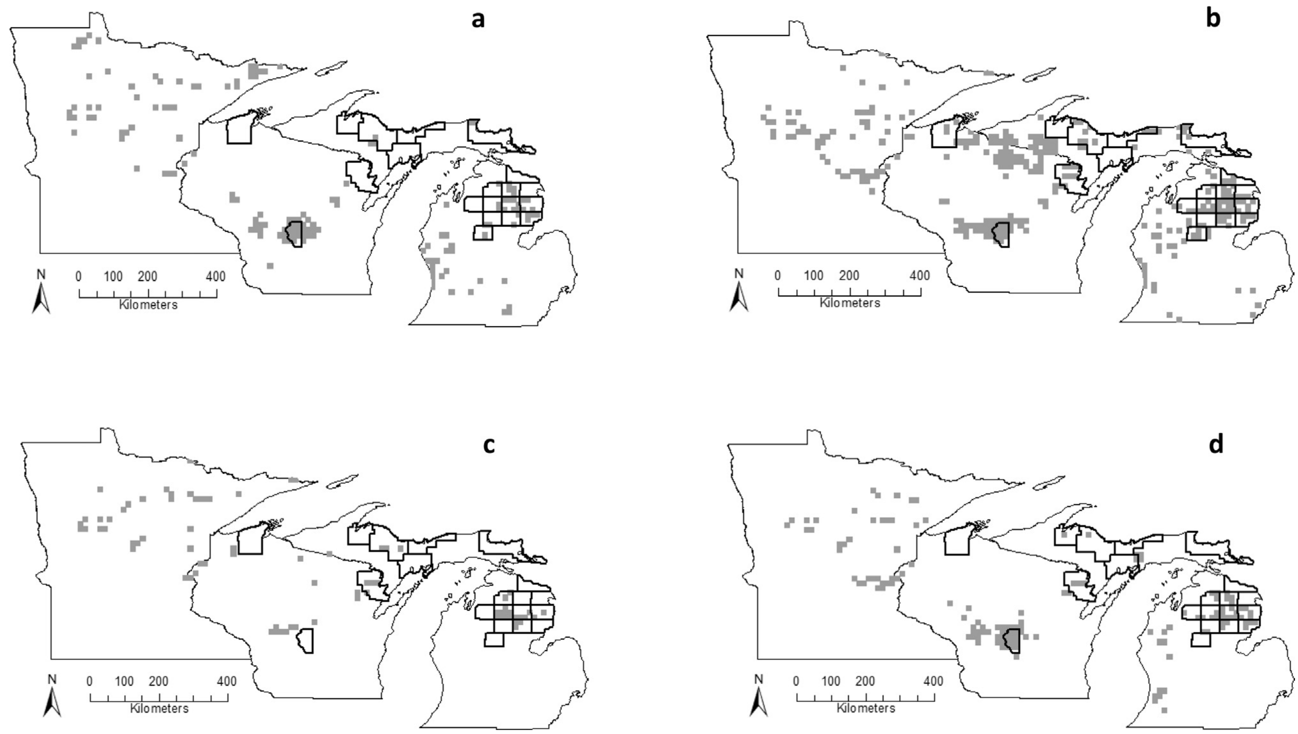
Appendix C

Maps showing spatial variability in climate variables under Global Climate Models (GCM) ensembles for contemporary climate, and in 2099 under RCP 4. 5 and 8.5 climate scenarios used to predict jack pine (*Pinus banksiana*) occupancy and growth across Michigan, Minnesota, and Wisconsin, USA. Annual soil moisture and growing season precipitation were the most influential predictor variables of jack pine occupancy and annual growth rate, respectively. These variables are projected to increase within much of the current distribution of jack pine. However, the increases do not exceed contemporary conditions in portions of the study area, which were used to model the species-environmental relationships.



Appendix D

Maps showing predicted jack pine (*PInus banksiana*) occupancy (gray) in 2099 using a Random Forest model with 5 environmental predictors for (a) high temperature and precipitation extreme model (GFDL-ELM2M under Representative Concentration Pathways (RCP) 4.5 and (b) RCP 8.5, and low temperature and precipitation extreme model (INM-CM4) under RCP (c) 4. 5 and (d) 8.5. Bold lines represent borders of 19 counties with current or historical nesting activities by the Kirtland's Warbler (*Setophaga kirtlandii*).



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