In an era of rapid climate and land transformation, it is increasingly important to understand how future changes impact natural systems. Scenario studies can offer the structure and perspective needed to understand the impacts of change and help inform management and conservation decisions. We implemented a scenario-based approach to assess how two high impact drivers of landscape change influence the distributions of managed wildlife species ($n = 10$) in the New England region of the northeastern United States. We used expert derived species distribution models (SDMs) and scenarios developed by the New England Landscape Futures Project (NELFP) to estimate how species distributions change under various trajectories ($n = 5$) of landscape change. The NELFP scenarios were built around two primary drivers – Socio-Economic Connectedness (SEC) and Natural Resource Planning and Innovation (NRPI) – and provide plausible alternatives for how the New England region may change over 50 years (2010–2060). Our models generally resulted in species occurrence and richness declines by 2060. The majority of species (7 of 10) experienced declines in regional occurrence for all NELFP scenarios, and one species experienced a projected increase in mean regional occurrence for all scenarios. Our models generally resulted in species occurrence and richness declines by 2060. The majority of species (7 of 10) experienced declines in regional occurrence for all NELFP scenarios, and one species experienced a projected increase in mean regional occurrence for all scenarios. Our results indicate that the NRPI and SEC drivers strongly influenced projected distribution changes compared to baseline projections. NRPI had a greater impact on distribution change for five species (coyote, moose, striped skunk, white-tailed deer, and wild turkey), while SEC had a greater impact on four species (American black bear, bobcat, raccoon, and red fox); one species (gray fox) was equally influenced by both NRPI and SEC. These results emphasize the importance of integrating both natural resource planning and socio-economic factors when addressing issues of distribution change and offer insights that can inform proactive management and conservation planning.
INTRODUCTION

Humans are a dominant driver of landscape change (Vitousek et al., 1997; Diaz et al., 2019). Historical alterations in land use, primarily the conversion of undisturbed forest to other forms of land use like agriculture and urban development, have resulted in the modification of landscapes at a global scale (Foley et al., 2005; Diaz et al., 2019). The rate of landscape modification is accelerating as human-dominated land use continues to expand worldwide (Klein Goldewijk et al., 2011; Seto et al., 2012). More than 30% of the world's land area is already under some degree of development and over 70% of the all forests are in close proximity (<1 km) to a non-forest edge (Foley et al., 2005; Haddad et al., 2015). With less than 15% of the world's terrestrial land under protection, natural ecosystems are highly susceptible to modification (UNEP-WCMC and IUCN, 2016).

Natural ecosystems are also exposed to the escalating pressures of shifting climatic conditions due to human activities (Walther et al., 2002; IPCC, 2014). With a global temperature increase of ca. 1°C over the past century and rates of warming nearly doubling over the latter quarter of the century, natural landscapes are subject to climate-induced changes at accelerating rates (IPCC, 2014; Hayhoe et al., 2018). The last three decades alone experienced global surface temperatures that were warmer than any preceding decade since 1850 and collectively represent the warmest 30-year period in the past 1,500 years (IPCC, 2014; Hayhoe et al., 2018).

Land use and climatic shifts can have substantial impacts on wildlife globally (Root et al., 2003; Thomas et al., 2004; Chen et al., 2011; Diaz et al., 2019). Changes in land use and climate can alter the quality and distribution of habitat (e.g., shifting the composition, structure, and configuration of plant communities), availability of food, prevalence of parasites and diseases, and frequency and intensity of physiological stress from heat or drought (Rustad et al., 2012; Diaz et al., 2019). While these changes can have considerable consequences for wildlife, information gaps and uncertainty around climate and land use trajectories currently limit our understanding of how future changes may impact wildlife species.

In the New England region of the northeastern United States (US), which covers six states and nearly 200,000 km², the recent and historic effects of climatic change and land use are evident for some species. For example, Canada lynx (Lynx canadensis) has experienced a distribution shift toward higher latitude and elevation in response to landscape change and warming conditions (Laliberte and Ripple, 2004; Koen et al., 2014). Similarly, warming climate conditions have benefited parasites like winter tick (Dermacentor albipictus) that have impacted moose (Alces alces) populations by reducing fitness and causing periodic epizootics (>50% die-offs) in some regions (Murray et al., 2006; Jones et al., 2019). With the continued pressures of human population expansion, urban development and sprawl, and warming climate trends, New England's natural landscapes are expected to experience rapid modification over the next half-century (White et al., 2009; Ololoson et al., 2016; Thompson et al., 2017; Dupigny-Giroux et al., 2018; Duveneck and Thompson, 2019).

Rapidly changing environments present considerable management challenges for federal and state agencies charged with maintaining viable wildlife populations. Across the New England region, wildlife management largely occurs at the state-level, and is characterized by different strategies for different species, which creates challenges for broader-scale conservation planning (Aycrigg et al., 2016; McBride et al., 2017). Scenario-based planning offers an approach to better understand the larger-scale impacts of change that can lead to more effective and proactive decision-making for species (Carpenter and Folke, 2006; Thompson et al., 2016). In New England, studies have been initiated to improve understanding and anticipate future trajectories of land-use and natural infrastructure (McBridge et al., 2017; McGarigal et al., 2017; Thompson et al., 2017; Duveneck and Thompson, 2019). For example, the Designing Sustainable Landscapes project developed a Landscape Change, Assessment and Design model to simulate current trends scenarios for landscape change in the northeastern US and assess the associated ecological impacts (McGarigal et al., 2017).

Another study, the New England Landscape Futures Project (NELFP), developed five scenarios that simulate different landscape futures for the New England region. Led by the Harvard Forest Long-Term Ecological Research program and the Scenarios, Services, and Society Research Coordination Network, this study simulated future conditions based on recent trends (Thompson et al., 2017; Duveneck and Thompson, 2019), and four alternative scenarios of landscape change (Thompson et al., 2019). The alternative scenarios were built around two uncertain, yet highly influential drivers of landscape change: Natural Resource Planning and Innovation (NRPI) and Socio-Economic Connectedness (SEC). The alternative scenarios were built around two uncertain, yet highly influential drivers of landscape change: Natural Resource Planning and Innovation (NRPI) and Socio-Economic Connectedness (SEC). The NRPI driver provides the extent to which the government and private sector invest in proactive land-use planning, ecosystem services, and technological advances for resource use, primarily land, energy, and water. The SEC driver provides the extent of local or global connectivity in population migration, culture, economic markets, trade policy, goods and services, and climate policy. These drivers form the basis for the four alternative scenarios to the continuation of recent trends (i.e., the “Business-As-Usual” scenario): “Connected Communities,” “Yankee Cosmopolitan,” “Go It Alone,” and “Growing Global.” The NELFP scenarios were collaboratively designed by stakeholders, simulation modelers, and researchers throughout New England and provide plausible trajectories of landscape change that incorporate informed simulations of climate, development, and agriculture, as well as forest structure and composition. However, wildlife species have not been assessed in the context of these scenarios.

Given the recent rates of landscape change in the New England region, combined with extensive evidence that changing climate, human expansion, and land transformation can have negative consequences for many wildlife species, decision-makers are faced with two crucial and unresolved questions: (1) How will changing climate and landscape conditions impact the future viability and distribution of the region’s wildlife species? (2) How do social drivers, such as NRPI or SEC, influence species distribution change in a future New England landscape? With
uncertainty around natural resource planning, innovation and socio-economic factors, we need a systematic approach that addresses these questions and advances our understanding of the complex, dynamic systems that affect wildlife. Approaching these questions proactively may (1) lead to more efficient, cost effective and sustainable conservation and management practices, (2) improve the state of biodiversity and natural systems, and (3) help protect iconic species and the benefits they offer to humans and society (Güneralp et al., 2013). By considering forecasted shifts in species distributions, wildlife agencies can plan for long-term conservation at multiple spatial and temporal scales.

We addressed these questions by evaluating how climate change and different trajectories of land-use may influence a group of commonly managed wildlife species in the New England region. We used expert-derived species distribution models (SDMs) developed by Pearman-Gillman et al. (2020) and the NELFP scenarios to: (1) estimate and map the future distributions of 10 focal wildlife species under five alternative scenarios, and assess regional species richness patterns, (2) quantify changes in species distributions under each scenario, and (3) compare distribution change across scenarios to quantify the impacts of SEC and NRPI, and identify the drivers with the greatest potential influence on individual and multi-species change.

**MATERIALS AND METHODS**

**Study Area**

The study area encompassed the six New England states (Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine) in the northeastern US (Figure 1). The region spans 186,458 km² with topography ranging from coastal plains to mountain peaks reaching nearly 2,000 m above sea level. Climatic conditions vary by season and geographic location throughout the region. Long-term climate records indicate an average annual precipitation of 104 cm (range: 79–255 cm) and a mean regional temperature ranging from 6°C (January) to 19°C (July) (Huntington et al., 2009).

The New England region supports a growing human population (14,845,063 in 2019) with three-quarters of the population concentrated in the regions major metropolitan areas (U.S. Census Bureau, 2019). The uneven distribution of people contributes to regional variability in land use patterns and intensities with large population centers in the south and more rural undeveloped landscapes in the north. Currently, approximately 80% of the region is covered by forest (Foster et al., 2010). Forested regions are ecologically diverse with areas dominated by northern hardwood, spruce-fir, oak-hickory, and pitch pine forest types (Brooks et al., 1992; Duveneck et al., 2015). Development (9.3%), agriculture (5.9%), and water (12.3%) also cover large portions of the New England landscape (Homer et al., 2015).

**Focal Species**

We focused our analysis on harvested wildlife species (n = 10) that occur widely throughout the region. This group includes nine mammals: American black bear (*Ursus americanus*), Bobcat (*Lynx rufus*), Coyote (*Canis latrans*), Gray fox (*Urocyon cinereoargenteus*), Moose (*Alces alces*), Raccoon (*Procyon lotor*), Red fox (*Vulpes vulpes*), Striped skunk (*Mephitis mephitis*), and White-tailed deer (*Odocoileus virginianus*); and one bird species: Wild turkey (*Meleagris gallopavo*). We selected these species because they are largely the emphasis of wildlife management at the state-level. Game species are important economically and culturally as they are harvested and often sought by wildlife watchers. Several of these species also exert large ecological effects on ecosystems, such as moose and deer (Jones et al., 1994; Pastor et al., 1998; Horsley et al., 2003).

**Objective 1 – Map Species Future Distributions**

**Distribution Models**

We used SDMs developed by Pearman-Gillman et al. (2020) to estimate and map distributions of the focal species. SDMs are often developed using presence-only data (e.g., animal locations) and relate environmental conditions to a measure of occurrence. For example, programs such as Maxent and BIOCLIM use presence-only data to model occurrence and map distribution across a landscape (Phillips et al., 2006; Franklin, 2010; Booth et al., 2014). Here, we used an alternative method that developed models from probability of occurrence data obtained through expert elicitation techniques, as outlined by James et al. (2010). Expert opinion based models have been used to estimate occupancy and map distribution for a variety of species and contexts (e.g., Pearce et al., 2001; Yamada et al., 2003; Mouton et al., 2009; Murray et al., 2009; Aylward et al., 2018). Developing SDMs from expert opinion data (occurrence estimates) can help overcome some of the limitations of presence-only modeling approaches, and yield models that capture the influence of climate and land use on regional wildlife dynamics (e.g., Pearce et al., 2001; Murray et al., 2008). For details about the expert elicitation model development for this study, see Pearman-Gillman et al. (2020). Briefly, we used the online survey tool, AMSurvey¹, to elicit expert opinion data on the probability of occurrence of each focal species throughout the New England region. We then used mixed-model methods and stepwise model selection (Zar, 1999; Burnham and Anderson, 2002; Bates et al., 2014) to develop a model for each species that predicted probability of occurrence as a function of landscape and climate variables (Table 1). Models included random effects that accounted for expert-to-expert variation in responses, and fixed effects that were identified in the literature, selected by experts, or were highly correlated with perceived occurrence (Tables 2, 3). Validation tests using independent data indicated that the models performed well at predicting species occurrence across the New England region (Pearman-Gillman et al., 2020).

**Scenario Simulations**

To estimate species distributions under projected conditions, we applied each SDM to the Recent Trends scenario and the four NELFP scenarios (McBride et al., 2017; Thompson et al., 2019), each defined by their degree of Natural Resource Planning and

¹https://code.usgs.gov/vtcfwru/amsurvey
FIGURE 1 | Map of the study region located in the northeastern United States. The study region included the six New England states: Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, and Vermont.

Innovation (NRPI) and Socio-Economic Connectedness (SEC). For details about the NELFP scenario development process, detailed scenario descriptions, and scenario figures, see McBride et al. (2017) and Thompson et al. (2019). A summary of each scenario is described below:

(1) **Recent Trends (Business-As-Usual).** This scenario represents a baseline projection extended from the region’s contemporary circumstances. It depicts the linear continuation of New England’s recent trends in the rate and spatial patterns of landscape change. This scenario offers a baseline for evaluating the other scenarios of change.

(2) **Connected Communities (High NRPI and Local SEC).** In this scenario, the New England population has slowly increased over the past 50 years and communities are coping with climate change by anchoring in place, making local culture and the protection of local resources important government and community priorities. Concerns about global unrest and the environmental impacts of global trade led New England communities toward a more community-focused lifestyle. Strengthened local relations and advances in local green energy contribute to more self-reliant communities. Heightened community interest and public policies protected wildlands, strengthened local economies and fueled growing local markets (primarily local food, wood, and recreation).
TABLE 1 | Species distribution models (SDMs) used to map distributions for 10 wildlife species and estimate changes in distribution across the New England region of the northeastern United States.

| Species                      | Model formula                                                                                                                                 |
|------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------|
| American black bear         | Mean \sim \text{prop}_\text{mature}_\text{forest} + \text{prop}_\text{all}_\text{roads} + \text{prop}_\text{forest}_5\text{k} + \text{mean}_\text{annual}_\text{precip}_\text{mm}_5\text{k} + \text{prop}_\text{fagugran}_5\text{k} + (1 \mid \text{State}) + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Bobcat                      | Mean \sim \text{prop}_\text{developed} + \text{prop}_\text{forest}_\text{edge} + \text{prop}_\text{agriculture} + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Coyote                      | Mean \sim \text{prop}_\text{waterbodies} + \text{prop}_\text{forest}_\text{edge} + \text{prop}_\text{major}_\text{roads}_3\text{k} + \text{prop}_\text{wetland}_3\text{k} + \text{prop}_\text{agriculture} + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Gray fox                    | Mean \sim \text{prop}_\text{forest}_\text{edge} + \text{prop}_\text{agriculture}_3\text{k} + \text{mean}_\text{DEM}_\text{km} + (1 \mid \text{State}) + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Moose                       | Mean \sim \text{prop}_\text{young}_\text{forest} + \text{prop}_\text{developed} + \text{prop}_\text{shrubland} + \text{mean}_\text{fall}_\text{tmax}_\text{degC} + \text{prop}_\text{forest}_5\text{k} + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Raccoon                     | Mean \sim \text{prop}_\text{agriculture}_5\text{km} + \text{prop}_\text{mature}_\text{forest}_5\text{km} + \text{mean}_\text{DEM}_\text{km}_5\text{km} + \text{prop}_\text{oak}_5\text{km} + \text{prop}_\text{developed}_5\text{km} + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Red fox                     | Mean \sim \text{prop}_\text{agriculture} + \text{prop}_\text{high}_\text{dev} + \text{mean}_\text{winter}_\text{precip}_\text{mm}_3\text{k} + \text{prop}_\text{shrubland}_3\text{k} + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Striped skunk               | Mean \sim \text{prop}_\text{agriculture}_5\text{km} + \text{prop}_\text{mature}_\text{forest}_5\text{km} + \text{prop}_\text{agriculture}_5\text{km} + \text{prop}_\text{forest}_\text{edge}_5\text{km} + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| White-tailed deer           | Mean \sim \text{prop}_\text{agriculture} + \text{prop}_\text{high}_\text{dev} + \text{prop}_\text{mature}_\text{forest} + \text{prop}_\text{hemlock}_\text{tamarack}_\text{cedar}_3\text{k} + (1 \mid \text{EcoRegion}) + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |
| Wild turkey                 | Mean \sim \text{prop}_\text{decid}_\text{forest} + \text{prop}_\text{forest}_\text{edge} + \text{prop}_\text{riparian} + \text{prop}_\text{grassland}_3\text{k} + (1 \mid \text{EcoRegion}) + (1 \mid \text{Expert}) + (1 \mid \text{Site}) |

Models were developed using expert-opinion data and generalized linear mixed modeling. Models include random-effects, noted in parentheses, and scaled fixed-effect variables. See Table 2 for descriptions of model variables. For details on model development and parameter estimates, see Pearman-Gillman et al. (2020).}

(3) **Yankee Cosmopolitan (High NRPI and Global SEC).** This scenario describes a future in which New England remains relatively resilient to climate change, has become a leader in research and technology, and subsequently experienced substantial population growth. The region’s population has largely grown due to an influx of international migrants seeking areas less vulnerable to the effects of climate change (e.g., heat, drought, sea-level rise). As a world leader in biotech and engineering, New England has a large demand for a skilled labor work force and established itself as a major center of economic and population growth within the U.S. Most development has occurred in urban areas with sprawl occurring as populations grow faster than the infrastructure can support. In a globally connected world, the region relies on imports for most food products. With a global shift toward sustainability, New England has invested in land protection, ecosystem services, and its carbon storing forests.

(4) **Growing Global (Low NRPI and Global SEC).** In this scenario, New England has remained relatively sheltered from the effects of climate change and has become a desirable location for migrants seeking more environmentally stable areas. This has led to population and development increases that have outpaced local planning efforts and contributed to city sprawl, haphazard expansion of development, poor transportation infrastructure and inefficient energy use. Underprepared government entities have struggled to support the region’s growing population leading to higher levels of privatized municipal services, limited natural resource planning and sharp declines in land protection. With trade barriers lifted, global trade has amplified and the U.S. has experienced a surge in the production and export of commodity crops. Increased agriculture, development and growing biofuel markets have increased the degradation and conversion of New England’s forested land. Globalization and increased transportation demands have strengthened a global reliance on conventional and cheap energy sources (fossil fuels). With little innovation and no global commitment to climate action, the world remains divided on issues of climate change and renewable energy.

(5) **Go It Alone (Low NRPI and Local SEC).** This scenario describes a New England with fairly low economic opportunity, population growth, and land development. A lack of global economic connectivity, tightened national borders, and reductions in national budgets have limited the nation’s ability to deal with unemployment, demographic change, and climate resilience. Global efforts at climate adaptation have failed and conventional energy sources still dominate. In New England, the lack of regulation decreased natural resources protection, technological innovation and availability of goods and municipal services. With reduced access to global energy markets, failure to launch new energy development projects and the degradation of conventional energy infrastructure, the price of energy has continued to rise. Increased energy and export expenses have reduced timber harvesting and commercial agriculture contributing to economic collapse. New residential developments lack appropriate planning and most public authorities lack the funds to maintain critical infrastructure such as roads and sewers. High energy costs, poor infrastructure planning and failure to fund climate change adaption has left communities isolated and heavily reliant on local resources. Poor planning and extractive use have significantly degraded the region’s ecosystem services and considerably decreased quality of life.

Each scenario narrative was translated into spatial patterns of change using methods described by Thompson et al. (2017, 2019) and Duveneck and Thompson (2019). Briefly, these simulations were developed in two stages: first using a spatially explicit cellular land change model, Dinamica Environment for Geoprocessing Objects (Dinamica EGO 2.4.1; Soares-Filho et al., 2009) and second using a forest landscape succession model, LANDIS-II v6.2 (Scheller et al., 2007). Dinamica was used to simulate 50 years (2010–2060) of forest loss, land-use change, and land protection relative to the underlying narrative of each
### TABLE 2
Variables and associated spatial (raster) layers used in the development of wildlife species distribution models and maps across the New England region of the northeastern United States.

| Variable                  | Category                | Covariate name                | Description                                                                 | Measurement | Scale(s) |
|---------------------------|-------------------------|-------------------------------|-----------------------------------------------------------------------------|-------------|----------|
| Annual Precipitation      | Climate                 | mean_annual_precip_mm         | Average annual precipitation during the years 2010–2012.                    | Meters      | 5k       |
| Average Daily High Temperature (Fall) | Climate | mean_fall_tmax_degC | Average daily high temperature observed during the months of September, October, and November during 2010–2012. | Degrees Celsius | 1k       |
| Total Winter Precipitation | Climate                 | mean_winter_precip_mm         | Average cumulative winter (December–February) precipitation during the years 2010–2012. This measure includes all types of precipitation, not just snowfall. | Meters      | 3k       |
| American Beech            | Forest Composition      | prop_fagugran                 | Forested land that is occupied by American beech (*Fagus grandifolia*).       | Proportion   | 5k       |
| Hemlock-Tamarack-Cedar Forest | Forest Composition | prop_hemlock_tamarack_cedar  | Forested land where AGB (above ground biomass) is dominated by eastern hemlock (*Tsuga canadensis*), native tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*). | Proportion   | 3k       |
| Mature Forest             | Forest Composition      | prop_mature_forest            | Forested land that is classified by tree cohorts between 40 and 100 years old. | Proportion   | 500 m, 1k |
| Oak Forest                | Forest Composition      | prop_oak                      | Forested land where AGB is dominated by white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), and black oak (*Q. velutina*). | Proportion   | 500 m    |
| Young Forest              | Forest Composition      | prop_young_forest             | Forested land that is classified by tree cohorts between 20 and 39 years old. | Proportion   | 1k       |
| Agriculture               | Land Cover              | prop_agriculture              | Area where land cover is classified as pasture, hay, and cultivated crops.   | Proportion   | 500 m, 1k, 3k |
| Deciduous Forest          | Land Cover              | prop_decid_forest             | Area where land cover is classified as deciduous forest.                     | Proportion   | 1k       |
| Developed                 | Land Cover              | prop_developed                | Area where land cover is classified as developed open space, low intensity, medium intensity, and high intensity development. | Proportion   | 500 m, 1k |
| Highly Developed          | Land Cover              | prop_high_dev                 | Area where land cover is classified as medium or high intensity development.  | Proportion   | 1k       |
| Forest                    | Land Cover              | prop_forest                   | Area where land cover is classified as deciduous, evergreen, and mixed forest. | Proportion   | 5k       |

(Continued)
| Variable          | Category    | Covariate name     | Description                                                                 | Measurement | Scale(s) | Current Source                                                                 | Source          |
|-------------------|-------------|--------------------|------------------------------------------------------------------------------|-------------|----------|--------------------------------------------------------------------------------|-----------------|
| Forest Edge       | Land Cover  | prop_forest_edge   | Area classified as forest that is within 300 m of non-forest land cover.     | Proportion  | 500m, 1k | NLCD 2011                                                                       | Thompson et al., 2019 |
| Grassland         | Land Cover  | prop_grassland     | Area where land cover is classified as grassland, herbaceous, pasture, or hay.| Proportion  | 3k       | NLCD 2011                                                                       | Thompson et al., 2019 |
| Major Roads       | Land Cover  | prop_major_roads   | Area where land cover is classified as a major road (controlled access highways, secondary highways, or major connecting roads and ramps). | Proportion  | 3k       | National Transportation Database (NTD 2016; U.S. Geological Survey, 2016)       | NTD 2016        |
| Roads             | Land Cover  | prop_all_roads     | Area where land cover is classified as major roads (controlled access highways, secondary highways, or major connecting roads, ramps) or local roads (local roads, 4WD roads, private driveways). | Proportion  | 1k       | NTD 2016                                                                        | NTD 2016        |
| Riparian          | Land Cover  | prop_riparian      | Area where vegetation is classified as riparian.                             | Proportion  | 1k       | LANDFIRE 2012 (U.S. Department of the Interior and U.S. Geological Survey, 2012) | LANDFIRE 2012; Thompson et al., 2019 |
| Shrubland         | Land Cover  | prop_shrubland     | Area where land cover is classified as shrub/scrub.                          | Proportion  | 1k, 3k   | NLCD 2011                                                                       | Thompson et al., 2019 |
| Water             | Land Cover  | prop_waterbodies   | Area occupied by waterbodies; lakes, ponds, reservoirs, estuaries, swamps, and marshes. | Proportion  | 1k       | NLCD 2011                                                                       | Thompson et al., 2019 |
| Wetland           | Land Cover  | prop_wetland       | Area classified as woody wetlands or emergent herbaceous wetlands.            | Proportion  | 3k       | NLCD 2011                                                                       | Thompson et al., 2019 |
| State             | Random Effect| State             | Area classified by USA state boundaries.                                     | –           | –        | MassGIS, 2018                                                                   | MassGIS, 2018   |
| Eco-Region        | Random Effect| EcoRegion         | Area classified by terrestrial Eco Regions.                                  | –           | –        | The Nature Conservancy, 2009                                                   | The Nature Conservancy, 2009 |
| Elevation         | Topography  | mean_DEM_km        | Height above sea level.                                                      | Kilometers  | 500 m, 1k | Digital Elevation Model (DEM, 2017; U.S. Geological Survey, 2017)               | DEM 2017        |

A total of 22 fixed-effect variables and 4 random-effect variables were included in map development. The fixed-effects included 3 climate variables, 5 forest composition variables, 13 land cover variables, and 1 topographic variable. The random-effects included 2 variables (site and expert) that were included in all models and 2 candidate variables (state and eco-region). Fixed-effect variables were included at the site scale (1 km) or a generalized home range scale (500 m, 3 km, or 5 km). Spatial layers were developed for current (2010) conditions and five future (2060) scenarios: Recent Trends, Community Connectedness, Yankee Cosmopolitan, Go It Alone, and Growing Global.

NELFP scenario. This process produced scenario specific land cover spatial layers (30 × 30 m) for forest, agriculture, high density development, and low density development (Thompson et al., 2017, 2019). Using these land cover spatial layers, a LANDIS-II forest simulation was run on all forest pixels for each scenario from 2010 to 2060 to simulate the growth, dispersal, and mortality of 32 individual tree species (Duveneck and Thompson, 2019). Climate change was incorporated into each scenario using climate projections (i.e., monthly maximum temperature, minimum temperature, and precipitation) based on the assumptions of the Representative Concentration Pathway (RCP) 8.5 emission scenario (IPCC, 2013) as simulated by the Hadley Global Environment Model v.2-Earth System (HADGE) Global Circulation Model (GCM). This climate future includes an increase in temperature and slight increase in precipitation in New England by 2060. Much larger changes in climate are expected beyond 2060 (IPCC, 2014). Indeed, the effects of climate in these simulations were largely outweighed by the effects of land use (Duveneck and Thompson, 2019). The LANDIS-II simulations included changes in forest composition relative...
to a warming climate, development, and harvest patterns for the Recent Trends (RT) scenario (Duvenec and Thompson, 2019) and each alternative NELFP scenario. The resulting above-ground biomass layers by tree species were used for modeling wildlife distributions (see below). Additional spatial layers utilized came from the HADGE GCMD simulated climate data, Dinamica land cover outputs, and recent conditions land cover data (see Table 2).

Mapping Projected Species Distributions
We applied the SDMs to the simulated spatial layers generated for each NELFP scenario (Table 2) to map the future distributions of each species in New England. Species distribution maps were generated for each scenario by (1) multiplying the scenario’s covariate rasters by the corresponding SDM coefficients for a given species, then (2) summing the resulting raster layers to obtain logit scores for every pixel, and (3) transforming the logits to create a raster of occurrence probabilities. This process generated species-specific distribution maps for each scenario (n = 5). We also created species richness maps by stacking the 10 individual species rasters and summing the values in each pixel to generate an index of species richness for each future scenario (Sauer et al., 2013). Richness values could potentially vary from 0 (no species present) to 10 (all species present). We developed distribution maps and species richness maps using the raster package (Hijmans, 2016) in the statistical computing software, R (R Core Team, 2019).

Objective 2 – Quantify Scenario-Specific Distribution Change
Scenario-specific distribution maps were compared against current distribution maps to estimate shifts (i.e., recession or expansion) in regional distributions. We compared each species’ current distribution (Pearman-Gillman et al., 2020) to each scenario’s projected distribution. Current distribution map pixels were subtracted from superimposed projected distribution map pixels to calculate values of projected change. Pixels with negative distribution change values represented locations of declining species occurrence and pixels with positive values represented locations of increasing occurrence.

Objective 3 – Compare the Impacts of NRPI and SEC on Wildlife Species
Isolating Driver Impacts
Each NELFP scenario was built around two directional drivers of land use change: NRPI (high or low) and SEC (global or local). For each species, we combined (averaged) distribution change information across scenarios with a common directional driver, marginalizing the influence of the second driver. For example, to obtain a distribution shift under the High NRPI driver, we averaged the two High NRPI scenarios (Yankee Cosmopolitan and Connected Communities), marginalizing over the directional SEC drivers. As a second example, to obtain a distribution shift for each species under the Local SEC driver, we averaged the two Local SEC scenarios (Go It Alone and Connected Communities), marginalizing over the directional NRPI drivers. We used this process to provide comparative baselines for NELFPs two primary drivers of land use change. Next, we subtracted the RT values from the isolated driver maps to account for forecasted baseline changes over the 50-year period, effectively removing the external factors of change that were not a product of shifts produced by the NRPI or SEC drivers. The resulting maps depict the potential influence of each driver on species occurrence and identify areas where species benefited from high or low investment in innovation and natural resources, or were most vulnerable to globalized or localized growth.

RESULTS
Objective 1 and 2 – Future Distributions and Projected Distribution Change
The projected distribution maps varied among species and the five scenarios. For all species but one (red fox), average regional occurrence likelihoods were projected to decline under nearly all scenarios by 2060 (see Supplementary Figure S1, for individual species maps). The locations and overall extent of distribution decline varied among species and scenarios. Generally, focal species distributions shifted away from areas of potential development expansion (largely in the southern New England states), and remained relatively stable in the northern and central regions of New England where less development was projected and timber harvest, forest management, and agriculture were largely driving landscape change (Supplementary Figure S1).

Projected declines in species occurrence probabilities were accompanied by declines in focal species richness. A regional average focal species richness ($\mu_s$) of 7.16 was estimated for the New England landscape in 2010 representing current conditions (Figure 2A). All future scenarios at 2060 projected lower focal species richness than was estimated for current conditions (Figures 2B–F). Of the future scenarios, average regional focal species richness was lowest under the Yankee Cosmopolitan (YC; $\mu_s = 6.44$, a 10.1% decline) and RT ($\mu_s = 6.54$, an 8.7% decline) scenarios (Figure 2). The Growing Global (GG) scenario had the highest average regional focal species richness ($\mu_s = 6.84$, a 4.4% decline), followed by Go It Alone (GA; $\mu_s = 6.72$, a 6.2% decline) and Connected Communities (CC; $\mu_s = 6.64$, a 7.2% decline; Figure 2).
For individual species, the greatest distribution declines across scenarios were projected for American black bear, gray fox, moose, and wild turkey (Figure 3). Considerably lower levels of decline were observed for bobcat, raccoon, and striped skunk, and minimal declines in mean regional occurrence were projected for coyote and white-tailed deer (Figure 3). An increase in regional occurrence was projected for red fox across all scenarios (Figure 3G).

Objective 3 – Impacts of NRPI and SEC on Wildlife Species

Eight of the focal species (American black bear, bobcat, coyote, gray fox, moose, raccoon, striped skunk, and wild turkey) simulated distribution declines under the RT scenario and all four of the driver-specific assessments (Figure 4A). For white-tailed deer, distribution increased slightly under RT and
declined under the four driver-specific assessments (although declines were generally lower than the declines for other species), and red fox distribution increased under all simulations (Figure 4A). Generally, the driver-specific simulations projected higher regional occurrence for the focal species than the 2060 RT simulations (Figure 4B).

SEC had a greater impact on distribution change than NRPI for four species, including American black bear, bobcat, raccoon and red fox (Table 4). For **American black bear**, Local SEC was the only driver that simulated higher regional occurrence than the 2060 RT projection, while both High NRPI and Low NRPI drivers led to distribution loss similar to the RT baseline. Of the directional drivers, Local SEC simulated the highest regional occurrence for American black bear, while Global SEC simulated the lowest regional occurrence (Table 3, Figure 4B, and see Supplementary Figure S2, for species-specific maps of driver isolated distribution change). For **bobcat**, Local SEC simulated the highest regional occurrence while Global SEC simulated the lowest regional occurrence. Both High NRPI and Low NRPI drivers led to distribution loss similar to the 2060 RT projection, and Global SEC was the only driver that projected lower regional occurrence than the RT baseline (Table 3, Figure 4B, and Supplementary Figure S2). The Global SEC driver simulated the highest regional occurrence for **raccoon**, while Local SEC simulated the lowest regional occurrence. Both High NRPI and Local SEC simulated slightly lower regional occurrence than the 2060 RT projection, and Low NRPI and Global SEC projected higher regional occurrence for raccoon than RT (Table 3, Figure 4B, and Supplementary Figure S2). For **red fox**, all four drivers led to distribution gain similar to the 2060 RT projection. Global SEC simulated the highest regional occurrence for red fox, while Local SEC was the only driver that simulated lower regional occurrence than the RT baseline (Table 3, Figure 4B, and Supplementary Figure S2).
NRPI had a greater impact on distribution change than SEC for five species, including coyote, moose, striped skunk, white-tailed deer, and wild turkey (Table 4). For coyote, the Low NRPI driver simulated the highest regional occurrence and the High NRPI driver simulated the lowest regional occurrence (Table 3, Figure 4B, and Supplementary Figure S2). Low NRPI simulated the highest regional occurrence for moose, while High NRPI simulated the lowest regional occurrence. High NRPI was also the only driver that simulated lower regional occurrence for moose than the 2060 RT projection, and Local SEC simulated considerably higher mean regional occurrence than expected under RT (Table 3, Figure 4B, and Supplementary Figure S2). For striped skunk, Low NRPI simulated the highest regional occurrence; Global SEC driver had a similar impact as Low NRPI, leading to higher mean regional occurrence than expected under RT (Table 3, Figure 4B, and Supplementary Figure S2). For white-tailed deer, Low NRPI simulated the lowest regional occurrence and had the largest impact on distribution change, while High NRPI had the smallest impact on distribution change (Table 3, Figure 4B, and Supplementary Figure S2). Low NRPI simulated the highest regional occurrence for wild turkey, and both Low NRPI and Global SEC projected higher regional occurrence than High NRPI and Local SEC (Table 3, Figure 4B, and Supplementary Figure S2).

For one species, gray fox, SEC and NRPI had an equal influence on distribution change (Table 4). Of the directional drivers, Low NRPI simulated the highest regional occurrence for gray fox (Table 3, Figure 4B, and Supplementary Figure S2). Low NRPI and Global SEC also projected considerably higher regional occurrence than High NRPI and Local SEC (Figure 4B).

Generally, Low NRPI and Global SEC were the most influential directional drivers of distribution change (Figure 5). Low NRPI had the largest impact on regional distribution change for six of the species (coyote, gray fox, moose, striped skunk, white-tailed deer, and wild turkey), while Global SEC had the largest impact for two species (raccoon and red fox) and
had a relatively large influence on distribution change for the remainder of the focal group. Of the four drivers, High NRPI had the smallest impact on distribution change for nearly all species, and Local SEC had a large impact for a few species but was otherwise less influential than the Low NRPI and Global SEC drivers (Figure 5). When comparing the difference between High
vs. Low NRPI and Local vs. Global SEC, we found a nearly 50/50 split in the focal group for which the primary driver had a greater impact on distribution change (Table 4).

**DISCUSSION**

The New England region is a large landscape that covers six US states and includes some of the largest expanses of hardwood forest and metropolitan areas in the country. Climate change and the pace of urban development has increased substantially in recent years, and the impacts of these changes on wildlife are largely unknown (Seto et al., 2012; Hayhoe et al., 2018). Our analysis suggests that a continuation of current trends will result in declines in the distribution of harvested species, which are important ecologically, socially, and economically in the region (U.S. Department of the Interior et al., 2016). For example, in Vermont, hunting, trapping, and shooting are important activities to residents, major contributors to the state’s economy, and are largely focused on species that exert strong ecological impacts on forest ecosystems like moose, deer, and bear (Pastor et al., 1998; Horsley et al., 2003; U.S. Department of the Interior et al., 2016; U.S. Bureau of Economic Analysis, 2019).

Species distributions are predicted to decline for most of the focal species if current climate and land use trends continue. The RT scenario – which simulated climate trends following the RCP 8.5 emission scenario and a continuation of recent trends in land use – resulted in 4.36% less forest cover by 2060 (Duveneck and Thompson, 2019) due to increases in development and agricultural land cover (37% and <5% more, respectively; Thompson et al., 2019). Under this scenario, eight of the ten focal species demonstrated a decrease in regional occurrence. Red fox and white-tailed deer were the only species that experienced an increase in regional occurrence (29.6 and 0.5%, respectively). The red fox is the widest ranging member of the Carnivora order and is capable of living in a variety of environments, including deserts, forests, tundra, and urban environments largely due to its physiology and behavioral plasticity (Voigt, 1987; Tesky, 1995; Lariviere and Pasitschniak-Arts, 1996). Similarly, white-tailed deer often occur at the interface between natural and developed areas and occupy a variety of habitat types (Swihart et al., 1993). Increases in these species distributions probably reflects their ability to adapt to the current trends of environmental change.

Among the species expected to decline if recent trends continue, four showed low to moderate declines in regional occurrence, including bobcat, coyote, raccoon, and striped skunk (ranging between a 3.0 and 6.6% decline by 2060). By comparison, American black bear, gray fox, moose, and wild turkey experienced relatively large reductions in distribution and average regional occurrence (ranging between 15.7 and 51.7% decline). These species are generally more sensitive to development and climate shifts, which may explain the projected negative impacts on distribution (Renecker and Hudson, 1986; Roberts and Porter, 1998; Rustad et al., 2012; COSEWIC, 2015; Evans, 2016; Lavoie et al., 2017; Environment and Climate Change Canada, 2018; Johnson et al., 2018). High levels of decline are concerning, especially for moose and gray fox, which have been identified as Species of Greatest Conservation Need by one or more of the New England states (Maine Dept. of Inland Fisheries and Wildlife, 2015; Massachusetts Division of Fisheries and Wildlife, 2015; New Hampshire Fish and Game Department, 2015; Rhode Island Department of Environmental Management Division on Fish and Wildlife, 2015; Vermont Fish and Wildlife Department, 2015). Additional assessments have also indicated recent population and distribution declines for moose in New England (Wattles and DeStefano, 2011; Timmermann and Rodgers, 2017) and many other regions in North America (Murray et al., 2006; Lenarz et al., 2010; Broders et al., 2012).

The RT scenario presents one plausible future, but we also explored the effects of other alternative futures on wildlife. The NELFP scenarios provided a set of alternative futures, influenced by climate change, yet based mainly on two social drivers of land use change – NRPI and SEC. These scenarios accounted for future climate impacts and allowed us to assess how patterns of wildlife occurrence and species richness were influenced by different drivers and trajectories of land use change. Of the four alternative scenarios, Growing Global (GG), Go It Alone (GA), and Connected Communities (CC) all led to higher species richness than RT; Yankee Cosmopolitan (YC) led to lower richness. Similarly, our assessment of the social drivers of change indicated that a low investment in NRPI and a global approach to SEC were most influential on distribution change and species richness.

In terms of land cover change, a low investment in NRPI led to increased rates of timber harvest in the NELFP scenarios. The GA and GG scenarios were built around the Low NRPI driver and simulated the highest timber harvest rates of all the scenarios (i.e., 135 and 110% increase in harvest rate compared to RT, respectively) and the highest species richness of all the scenarios. Timber harvest can benefit some species, including some in the focal group (Monthey, 1984; Hunter and Schmiegelow, 2011) by generating important habitats (e.g., early successional forest) and increasing heterogeneity in forest structure and composition (Hansen et al., 1991; Hunter and Schmiegelow, 2011). Moose,
gray fox, and wild turkey are all species that appear to benefit from increased forest heterogeneity driven by Low NRPI. For example, moose distribution was greatest under the GA and GG scenarios; probably because these scenarios resulted in high levels of timber harvest and larger amounts of young forest, which benefit moose (Monthey, 1984; Innes, 2010; Wattles and DeStefano, 2011). However, it is important to recognize that a continuation of Low NRPI actions and disregard for both innovation and more extensive natural resource planning activities will probably have less favorable long-term consequences for many other wildlife species. Climate impacts on forest composition may also have greater long-term consequences for wildlife. For this analysis we simulated climate and land use change 50 years into the future, however, the effects of climate change on forest composition are projected to increase dramatically beyond 50 years (Duveneck and Thompson, 2017; Janowiak et al., 2018). With larger shifts occurring in the second half of the 21st century, wildlife species may experience less favorable conditions over time. Economic development activities like urban expansion and the conversion of forest to agriculture can also have considerable impacts on species richness by reducing the availability and

FIGURE 5 | Radar plot showing species-specific (n = 10) distribution changes associated with each directional driver — i.e., high or low Natural Resource Planning and Innovation (NRPI), and global or local Socio-Economic Connectedness (SEC). The NRPI and SEC axes display how each driver impacted distribution change (i.e., change in mean regional occurrence likelihood) in the New England region of the northeastern United States between 2010 and 2060. All values were derived from species distribution models and provide a measure of how each driver shifted species regional occurrence likelihood relative to the occurrence likelihood simulated for Recent Trends. The overlay of all species shows driver associated trends within the focal group.
quality of habitat in the region (Murphy and Romanuk, 2014; Newbold et al., 2015). In the NELFP simulations, the CC and GA scenarios were built around the Local SEC driver and led to lower rates of development (i.e., 75 and 25% decrease in development rate, respectively) and higher species richness than the RT projection. By comparison, the GG and YC scenarios were built around the Global SEC driver and simulated high rates of development (i.e., 180 and 40% increase in development rate compared to RT, respectively). These two scenarios resulted in the highest (GG) and lowest (YC) species richness, showing that increased development rates can negatively influence species occurrence, but may not directly translate to lower richness. Rather, other factors including the pattern and intensity of development may be more influential than rate alone. Both Global and Local SEC drivers altered development patterns and subsequently influenced distribution change – drawing attention to the considerable influence that social and economic factors can have on natural systems and emphasizing the importance of including these factors in regional planning efforts.

The scenario assessments provide measures of the response of multiple wildlife species to future natural, social, and economic changes in New England. The results provide species information that can aid in landscape decision-making around management and conservation problems (Peterson et al., 2003). For a given problem, decision-makers can set objectives, then use the models to assess the consequences associated with each scenario, evaluate trade-offs among scenarios, and identify the trajectory that most successfully meets their objectives. As a simple example, a group interested in maximizing black bear populations in New England could compare occurrence probabilities across the scenarios to evaluate the trade-offs of each type of future scenario; in this case, choosing the GA scenario may be best as it projects the highest regional occurrence for black bear. Information about the GA scenario could then be used to help guide policy and management actions.

The scenarios could also be used in more complex decision-making problems that account for trade-offs across multiple objectives and multiple spatial and temporal scales. For example, the state of Vermont has set a goal of meeting 90% of the state's energy needs through renewable sources (e.g., solar, wind, forest-derived bioenergy) by the year 2050 (Vermont Department of Public Service, 2016). Considering this objective, Vermont may change following a trajectory similar to the CC scenario – in which advances in local green energy support a more self-reliant community – or the GA scenario – in which poor planning and extractive use significantly degrades the region's ecosystem services. However, the state also has objectives related to the sustainability of harvested species, other natural resources, and climate change. Decision-making frameworks following principles of Structured Decision Making (Gregory et al., 2012) could be used to evaluate possible impacts of climate change and the trade-offs of each future scenario on renewable energy production, and the sustainability of harvested species and other natural resources, which can inform policy actions.

Our assessments of landscape change on wildlife species accounted for several social, ecological, and economic factors based on information from models, expert opinion, and consensus from a consortium of scientists, managers, and community members (i.e., the Scenarios, Services, and Society Research Coordination Network that developed the NELFP scenarios). However, any future scenario projections involve uncertainties. Uncertainty in the SDM parameters has been estimated, which provides a measure of confidence in the occurrence estimates. Other factors not considered in the modeling process, such as species interactions or variable trajectories of climate change, may impact distribution patterns and induce additional uncertainty in the outcome for species (Royle and Dorazio, 2008). For example, coyotes are dominant competitors and have been shown to shape the distribution of other sympatric carnivore species (Johnson et al., 1996; Fedriani et al., 2000); changes in their occurrence over time may have impacts on red foxes and gray foxes through competition (Johnson et al., 1996; Fedriani et al., 2000; Levi and Wilmers, 2012), and even game birds like wild turkey through altered predation risk (Guthrey, 1995). Accounting for the behavioral and ecological complexities of species interactions is challenging, and would require additional (and currently unavailable) data to be integrated into future scenario modeling. Future climate conditions are also largely uncertain and species future distributions may vary considerably under different trajectories of climate change. Here, we simulated future climate conditions based on a single high emissions scenario to aide interpretability and offer distribution projections that account for both climate and land-use change. Considering additional climate scenarios and climate-related factors could provide further insight on species future distribution patterns.

We also used probability of occurrence at a 30 m pixel level as a measure for evaluating the effects of landscape change on a species. Occurrence probability reflects habitat quality, which we assumed also relates to the number of individuals, an important measure for harvest management (e.g., setting harvest quotas or bag limits). A positive relationship between occupancy probability and abundance has been shown for several wildlife species (Blackburn et al., 2006; Zuckerberg et al., 2009). However, this relationship is not always consistent and linear (Blackburn et al., 2006). For example, recent trends suggest that gray foxes are expanding in range in the northeastern US and eastern Canada (COSEWIC, 2015; Environment and Climate Change Canada, 2018). However, our projection for gray fox shows a decline in occurrence under the RT scenario. Here, it is important to distinguish range expansion from population growth and increased species occurrence – while the range of gray fox may be expanding, localized shifts in habitat can lead to lower abundance. It is also important to recognize that current trends may not continue into the future. While current conditions appear to facilitate range expansion for gray fox, changes to New England's climate and land use may decrease gray fox occurrence in the future. Brown et al. (2018) also showed that small declines in regional occurrence probability of bird species in New England can result in large declines in the actual number of territories that a region can support. This is an important consideration, as seemingly small changes in occurrence probability may translate to much larger shifts in a species actual abundance.
Resilience of wildlife communities to change is a conservation priority for the New England region (Anderson et al., 2016). Our study focused on harvested wildlife species and provides a foundation for evaluating areas of high and low resilience under regimes of change for this group of ecologically, socially, and economically important species. Many resilience studies have focused on identifying resilient areas for broader biodiversity using focal taxa (e.g., birds) or groups (e.g., rare species). For example, Anderson et al. (2014) estimated resilience to climate change in northeastern North America using locations of rare species populations and representative natural communities as measures of biodiversity. Our study complements this and other assessments in the region (e.g., Staying Connected Initiative; Smith et al., 2012) by providing fine-scale information on harvested wildlife species that have been largely excluded in regional analyses.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available through the FEMC Data Archive and can be found at https://www.uvm.edu/femc/data/archive/project/wildlife_future_scenarios/dataset.

AUTHOR CONTRIBUTIONS

SP-G and TD contributed to the concept and design of the project. SP-G conducted the analyses and drafted the manuscript. MD provided the forest change simulations. All authors participated in revising and editing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00164/full#supplementary-material

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