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Watershed forest cover and habitat restoration can offset some negative impacts of climate change on freshwater fishes and mussels

Jennifer B. Rogers[1¤a*], **Graziella V. DiRenzo**[2], **Allison H. Roy**[2], **Jason Carmignani**[3], **Rebecca S. M. O'Brien**[1¤b], **Rebecca M. Quiñones**[3], **Todd Richards**[3]

1 Massachusetts Cooperative Fish and Wildlife Research Unit, Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, United States of America, **2** U.S. Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit, Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, United States of America, **3** Massachusetts Division of Fisheries and Wildlife, Westborough, Massachusetts, United States of America

¤a Current address: Narragansett Bay Estuary Program, Roger Williams University, Bristol, Rhode Island, United States of America
¤b Current address: Department of Ecosystem Science and Management, Pennsylvania State University, University Park, Pennsylvania, United States of America
* jrogers@nbep.org

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Abstract

Many species of freshwater fishes and freshwater mussels have experienced population declines over the past century due to threats including habitat degradation, over-exploitation, species invasion, and climate change. Management actions may offset climate-related changes to biodiversity, although identifying appropriate strategies is challenging. Our goal was to identify the impacts of climate change on freshwater biota (i.e., fish and mussel) distribution and management actions that may offset the climate change impacts across the northeastern United States. We used land use, geography, stream temperature, and streamflow variables to predict species distribution in a baseline scenario, climate change scenario, and several climate change plus land use management scenarios. We found climate change negatively impacted (i.e., reduced the probability of occurrence of) coldwater fishes and reduced the relative occurrence probability of fluvial specialist and coolwater fishes compared to other species. Increasing watershed forest cover best offset these negative impacts and minimized the predicted transition from coldwater fish dominance to warmwater fish dominance in coldwater habitats; however, no intervention fully offset the negative impacts of climate change on vulnerable fish groups (i.e., coldwater and fluvial specialist fishes). Climate change negatively impacted all vulnerable groups of mussels (e.g., lotic species, drying intolerant) and mussel species richness. Combining multiple management interventions (e.g., increase forest cover, dam removal, etc.) had the greatest potential to offset the negative impacts of climate change for freshwater mussels and fishes. This study provides managers a comparison of management

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interventions across a landscape to combat the impacts of climate change on biota in streams and rivers.

1. Introduction

Freshwater ecosystems are under tremendous stress in the Anthropocene [1,2]. Compounding threats such as habitat degradation, overexploitation, and species invasion, among others, have caused dramatic declines of many species [3,4]. Layered on these threats is climate change. Global average air temperatures are expected to increase by approximately 3.2°C by 2100 [5], and precipitation patterns are projected to be more variable from their historical baseline. The predicted novel and extreme weather events and altered precipitation patterns directly impact streamflow patterns leading to extreme flooding [6–8], prolonged and more intense droughts [7,8], and altered timing of peak spring streamflow [9,10]. Additionally, increases in air temperature will increase stream temperatures [11,12].

Changing stream conditions may impact freshwater biota, including fishes and mussels. For example, increasing stream temperatures and responsive decreases in dissolved oxygen concentrations could impact habitat suitability for fish species that are adapted to high-oxygen environments [13]. Similarly, changing streamflow can influence fish reproductive success, with the magnitude and direction of the effect varying depending on spawn timing and extent of deviation from typical flows [14]. Overall, climate change is predicted to lower the functional diversity of freshwater fish [15]. Freshwater mussels are perhaps even more vulnerable to changing stream temperatures and flow regimes than fishes because of their sessile nature as adults. Extreme low flows have the potential to expose mussels to desiccation, predation, and deoxygenation, whereas high flows can flush mussels downstream or into the floodplain [16]. Because freshwater mussels depend on host fish for metamorphosis and dispersal, changes in fish species distribution due to climate change will likely also negatively impact mussel distribution [17,18].

Freshwater ecosystem management commonly focuses on improving water quality and restoration of riparian vegetation, instream habitat, and fish passage [19]; however, it is not known if these actions will lessen the impacts of climate change on freshwater biota. Effective management actions that reduce the effects of climate change or provide ecosystem resiliency can be challenging to identify. For example, dam removal has the potential to increase climate resilience [20], but linking changes in temperatures [21] to fish assemblage shifts is challenging. Knowledge of biotic responses to climate change is rapidly developing, with few case studies assessing predicted responses to management (e.g., [22,23]). Additionally, any effects of climate change are compounded by or confounded with other threats to freshwater systems [3,24]. Given these complexities, modeling with large datasets offers a promising method to disentangle climate-driven impacts on biota and evaluate effective management strategies for freshwater systems [25].

Modeling to estimate impacts of climate change and management intervention on freshwater species often follows two approaches: mechanistic modeling and statistical modeling. Mechanistic models use understanding of species physiology to estimate impacts; however, these models are often limited to a local scale, are applied to a single species of interest, and require extensive life history and physiological knowledge of that species [26]. Conversely, statistical models use statistical relationships between species occurrence and environmental conditions to identify impacts of a stressor and can be applied to large regions for many species (such as [27,28]). However, limitations of statistical models include the lack of consideration of microhabitats, dispersal ability, or biotic interactions [29,30]. Despite these limitations, statistical modeling can be used to identify effects of land use on stream conditions [31,32] and thus provide evidence for the effectiveness of certain types of management. For example, statistical models have been used to improve reserve planning for freshwater conservation [33,34] and to rank river restoration options [35]. The utility of statistical models for management decisions makes them a valuable tool, especially when decisions are time-sensitive, affect many species, and occur at large spatial scales.

Here, we used statistical models to quantify impacts of climate change on freshwater fishes and mussels in streams and rivers in the northeastern United States (U.S.) and identify management actions that can help mitigate these impacts. To do this, we adapted freshwater fish models and fish biodiversity groups from [36] and developed freshwater mussel models and mussel species groups based on data in [37] to make projections of distributions of these groups in baseline conditions. Then, we used these models to forecast the species' group distributions using 1) projected changes to streamflow and stream temperature with climate change, and 2) with climate change plus management interventions (i.e., increased riparian vegetation cover, increased watershed forest cover, decreased riparian impervious cover, and dam removal). These projections were used to identify which management interventions can offset the effects of climate change for each species grouping. We used the fish projections as covariates in the mussel species models to identify if host fishes negatively impacted by climate change (new absence or decreases in abundance) can further cause decreases in freshwater mussel populations or range beyond the direct impacts of climate change. Ultimately, these results can be used to inform climate-adaptive conservation and restoration by identifying the most vulnerable freshwater fishes and mussels and identifying effective interventions across the landscape.

2. Methods

2.1 Study region

This study focused on the northeastern-most states in the United States, which include Maine (ME), New Hampshire (NH), Vermont (VT), Massachusetts (MA), Connecticut (CT), and Rhode Island (RI, Fig 1). The area has five Level III ecoregions including mainly the Northeastern Highlands, Northeastern Coastal Zone, and the Acadian Plains and Hills, and small areas of Eastern Great Lakes Lowlands, and the Atlantic Coastal Pine Barrens [40]. The Appalachian Mountain range runs through a large portion of the study region including western CT and MA, almost all of VT and NH, and the northwestern portion of ME. The eastern portions of CT, MA, ME and the entire state of RI lie in the New England Seaboard lowlands. This creates a network of steep mountain streams running to the alluvial coastal plains before entering the Atlantic Ocean. Cape Cod, Nantucket, and Martha's Vineyard lie in the Atlantic Coastal Plain, which is a flat sandy region with extensive wetlands. The region has more than 50% forest cover, and the three northern states (VT, NH, and ME) have extensive forest cover approaching or greater than 80% [41]. Summer temperatures are relatively cool compared to much of the United States, and winters tend to be cold and snowy with an average annual snowfall of 154.82 cm [42]. The mountainous topography, relatively high latitude, and snowpack create conditions favorable to cool stream temperatures; the average July/August stream temperature in our study area is 18.59°C [43,44].

The region has experienced historical anthropogenic impacts that continue to affect streams and stream inhabitants. There are approximately 14,000 dams across the area's streams and rivers [45], including old mill dams, recreational dams, and flood control dams. Major cities and dense urban development in the southern three states have left streams

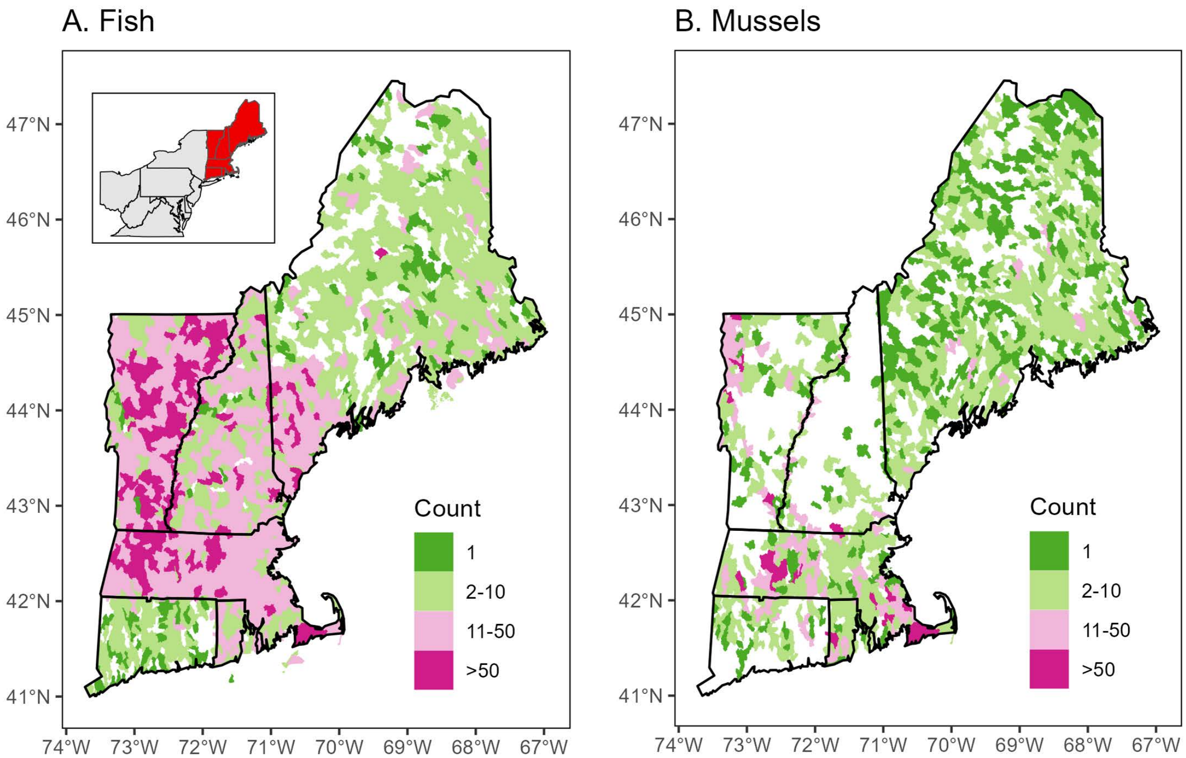

Fig 1. The number of A) freshwater fish surveys and B) freshwater mussel surveys per Hydrologic Unit Code 12 (HUC12) watershed. The inset map in the upper left of panel A) shows the study area (red) of the six northeastern states in the United States: Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and Rhode Island. White space indicates that no surveys from those watersheds were included in the analysis. (U.S. states reprinted from U.S. Census Bureau [38] and HUC12 boundary outlines reprinted from the U.S. Geological Survey (USGS) national hydrography dataset (NHD, [39])).

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in these areas channelized and modified. In the northern portion of the range, logging and gravel and sand mining impact the rivers and streams.

2.2 Data sources

All data analysis was done in R version 4.2.2 (2022-10-31 ucrt) using RStudio [46]. Data and software are provided in [47,48], respectively.

2.2.1 Fish species data. Fish species occurrence data were compiled from eight state fish and wildlife agencies (Table 1). Full methods for data compilation and standardization are described in [36]. Briefly, over 30,000 fish surveys were compiled with over 92% of surveys occurring since 1985 (range = 1949–2021). We limited records to surveys that included all observed species (as opposed to a few target species) and that were conducted in lotic habitats with backpack electrofishing methods. We excluded fish species that are predominantly marine, estuarine (except White Perch (*Morone americana*)), or diadromous (except American Eel (*Anguilla rostrata*)) because electrofishing did not adequately sample these species. Additionally, fish species that were too rare to be modeled successfully were not included in this analysis. In total, we modeled 53 freshwater fish species. To create the fish presence/absence dataset, we assumed that species were absent if not detected during a survey. If species count data were available (24,553 surveys), the relative abundance of individual species was calculated as the total count of individuals within a species divided by the total count of all individuals counted across all species in a survey.

Table 1. Description of the fish and mussel data used in this analysis. Only live occurrences of freshwater mussel species were included. Data are available from [47]. Agency abbreviations are as follows: MassWildlife: Massachusetts Division of Fisheries & Wildlife; CT DEEP: Connecticut Department of Energy & Environmental Protection; VT DEC: Vermont Department of Environmental Conservation; VFWD: Vermont Fish & Wildlife Department; RI DEM: Rhode Island Department of Environmental Management; NH DFG: New Hampshire Department of Fish and Game; NH DES: New Hampshire Department of Environmental Services; ME IFW Maine Department of Inland Fisheries and Wildlife. *Note that 17 freshwater mussel species are found in Vermont, but eight are excluded from this analysis as explained in [37]. NA = Not Applicable, no data were provided.

	Fish			Mussel		
Agency	Lotic surveys (#)	Date range	Species (#)	Lotic surveys (#)	Date range	Species (#)
MassWildlife	6,032	1994–2021	45	2,389	1866–2020	12
CT DEEP	313	2016–2021	35	289	1995–2021	12
VT DEC	2,031	1984–2021	47	901	1905–2022	9*
VT DFW	7,294	1949–2021	24	*NA*	*NA*	*NA*
RI DEM	442	1992–2020	34	227	2006–2020	8
NH DFG	2,865	1983–2021	48	169	1940–2019	8
NH DES	706	1996–2021	48	*NA*	*NA*	*NA*
ME IFW	4,821	1957–2018	38	1,189	1985–2009	10

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2.2.2 Mussel species data. Mussel species occurrence data were compiled from six state fish and wildlife agencies (Table 1) and are described in [37]. Briefly, a total of 6,390 mussel surveys were compiled from 1866 to 2022, with over 95% of surveys occurring since 1985. In contrast to [37], we only included samples taken from lotic habitats (5,627 surveys) and removed 763 samples from lentic habitats (though some 'unknown' habitats were included here). We included surveys that used different survey methods (e.g., snorkel, scuba, view buckets, etc.) and different levels of effort (e.g., full quantitative surveys and rapid visual surveys). Unlike [37] who included shell occurrences, we only included 'live occurrence' observations in our analysis. Our final dataset included 12 freshwater mussel species. To create the mussel presence/absence dataset, we assumed that species were absent if not detected during a survey. We did not calculate proportional abundance metrics because many surveys reported occurrence only.

2.2.3 Hydrography. The U.S. Geological Survey (USGS) medium resolution National Hydrography Dataset (NHD) Plus Version 2 [39] was used to link biotic data with watersheds at the stream reach (fishes) or Hydrologic Unit Code 12 (HUC12) scale (mussels). For fishes, every survey event was spatially joined to the nearest stream or river 'flowline' using the package 'sf' [49] in RStudio [46,50]. We calculated the distance of the georeferenced survey event to the nearest flowline and omitted samples that had a distance greater than 500 m due to the potential for erroneous location information. For mussels, many samples were greater than 500 m from a flowline (28% of the mussel surveys or 1,530 out of 5,416 surveys) possibly due to the omission of small streams from the NHD spatial dataset or errors in recording survey coordinates. Because of uncertainty in specific locations, we spatially joined mussel survey events to the HUC12 watershed using the package 'sf' [49], allowing all mussel surveys to be retained at the HUC12 scale.

2.2.4 Covariates. We used predictor variables (Table 2) from previously calibrated and validated freshwater fish models [36] and freshwater mussel models [37]. Variables were in five categories: geographic, climate, land use, connectivity, and host fishes. Variables for fishes were calculated for stream reaches, and variables for mussels were averaged within the HUC12 boundary. A few variables differed from previously published models so the predictor variables could be directly linked to management actions, and we describe those differences here. Here, we added the following variables in the fish models that were not in [36]: watershed forest, natural buffer, and impervious buffer, all of which were used as management intervention variables. We also removed certain variables that were included in the fish models in [36] to simplify the models given the added variables: summer flow, water table depth, watershed impervious, catchment open water, road crossings, and dam count. Land cover variables (e.g., forest, natural buffer) were calculated using data from the National Land Cover Database [60], which is based on 30-m resolution satellite imagery; thus, detailed

Table 2. Summary of covariates used in fish and mussel models. We report variable category (geographic, climate, land use, connectivity, and host fishes), variable, units, spatial scale, definition, which taxa the covariate was used for, and the source of the data. Catchment = the portion of land that drains directly to a National Hydrography Dataset stream segment, excluding upstream contributions [51]; Watershed = all upstream catchments that flow to the NHD stream segment [51]; Stream reach = Contiguous section of stream between upstream and down-stream tributaries [51]; NLCD = national land cover database; HUC12 = 12-digit hydrologic unit code; NHDv2 = National Hydrography Dataset version 2. Note that the variables derived from NLCD have a 30-m pixel resolution. *State dam database citations as follows: [52–57].

Category	Variable	Units	Spatial scale	Definition	Taxa	Source
Geographic	Latitude	Decimal degrees	Point	Reported latitude of the fish survey event	Fish & Mussel	[47]
Geographic	Longitude	Decimal degrees	Point	Reported longitude of the fish survey event	Fish & Mussel	[47]
Geographic	Elevation	Meter	Catchment	Mean elevation	Fish & Mussel	[51]
Geographic	Watershed area	Km^2	Watershed	Watershed area at NHDv2 stream segment outlet, log transformed	Fish & Mussel	[51]
Geographic	Calcium oxide	Percent	Watershed	Mean lithological calcium oxide (CaO) content in surface or near surface geology	Mussel	[51]
Climate	Annual mean summer temp	°C	HUC12	Mean summer stream temperature (June 1 - August 31) for the year the fish survey occurred	Fish & Mussel	[43,44]
Climate	Winter flood Frequency	Count	Stream reach	Average number of daily flows between December 1 and March 31 that exceed the 95th percentile of daily flows across the entire year aligned to each fish survey. Note some watersheds may experience the highest flows in the spring, and those will not be represented here.	Fish & Mussel	[58,59]
Climate	Low Flow Date	Day of cal-endar year	Stream reach	Average date of the center of the lowest seven-day flow of the year aligned to each fish survey	Fish & Mussel	[58,59]
Climate	Baseflow Index	unitless	Stream reach	Ratio of the average daily flow during the lowest seven-day flow of the year to the average daily flow during the year overall. Estimates proportion of streamflow from groundwater versus precipitation aligned to each fish survey	Fish & Mussel	[58,59]
Climate	Baseflow Index	Unitless	Watershed	Mean baseflow index	Fish	[51]
Land use	Open water	Percent	Watershed	Area classified as open water. Derived from the 2001, 2011, or 2019 NLCD landscape raster [60]	Fish	[51]
Land use	Forest	Percent	Watershed	Area classified as deciduous (class 41), evergreen (class 42), or mixed forest (class 43). Derived from the 2001, 2011, or 2019 NLCD landscape raster [60]	Fish & Mussel	[51]
Land use	Agriculture	Percent	Watershed	Area classified as pasture/hay (class 81) or cultivated crops (class 82). Derived from the 2001, 2011, or 2019 landscape raster [60]	Fish & Mussel	[51]
Land use	Wetland	Percent	Catchment	Area classified as woody wetland (class 90) and emergent herba-ceous wetland (class 95). Derived from the 2001, 2011, or 2019 NLCD landscape raster [60]	Fish & Mussel	[51]
Land use	Natural buffer	Percent	Stream reach	100-m (on each side of the stream) riparian buffer that is classified decid-uous, evergreen and mixed forest, (classes 41, 42, 43), shrub/scrub (52), and grassland/herbaceous (71). Derived from the 2001, 2011, or 2019 NLCD landscape raster. Longitudinal length of stream reaches vary.	Fish & Mussel	[60]
Land use	Impervious buffer	Percent	Watershed	Impervious land cover in the 100-m (on each side of the stream) riparian buffer. Derived from the 2001, 2004, 2006, 2008, 2010, 2011, 2013, 2016, or 2019 NLCD landscape raster	Fish & Mussel	[51]
Land use	Soil erodibility	Unitless	Watershed	Mean soil erodibility (Kf) factor of soils. The Kf factor is used in the Universal Soil Loss Equation and represents a relative index of sus-ceptibility of bare, cultivated soil to particle detachment and transport by rainfall	Mussel	[51]
Connec-tivity	Dam density	$Dams/km^2$	HUC12	The number of dams divided by the area of the HUC12	Fish & Mussel	State dam data-bases*
Host Fish	See Table 3 for host fish variables					

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microhabitats are not represented. We added the following variables in the mussel models that were not included in the mussel models in [37]: latitude, longitude, elevation, calcium oxide, baseflow index (reach and watershed), and natural buffer. Some variables from [37] were excluded in this paper to simplify models and remove correlated variables given the added variables: tidal influence, slope, waterbody volume, and occurrence of the mussel species within a HUC8. The mussel model covariates included occurrence or relative abundance of host fishes within the HUC12 watershed, based on the outcome of the freshwater fish models. From these predictions, three host fish variables were calculated (Table 3): 1) summed probability of occurrence of all fish species was used in all twelve mussel models; 2) summed predicted relative abundance of host fish was used in host specialist mussel models; and 3) raw fish occurrence data were used in host specialist mussel models only if those fish species distributions had not been modeled in previous analyses (host fish references provided in Table A in S1 Text).

2.3 Analysis

All models, analyses, and data visualizations were developed using R version 4.2.2 (2022-10-31 ucrt) using RStudio [46].

2.3.1 Model calibration and validation. ***Fish distribution model***: We modified previously calibrated and validated freshwater fish models [36] to model the distribution of freshwater fishes in our study region. Individual zero-inflated beta distribution regression models (one for each fish species) were used to simultaneously model the probability of species occurrence and the predicted relative abundance of each fish species at the NHD Version 2 stream reach scale. Each fish model included all covariates (Table 2). We fit each model using 80% of the species data and withheld 20% of the data for model validation. Because we modified the model covariates slightly from [36], we provide validation methods and metrics in the S1 Text and Table B in S1 Text. Briefly, we compared the predicted probability of occurrence to the known presence or absence observation using the remaining 20% of the data for each species with the presence.absence.accuracy function from the ‘PresentAbsence’ package [61] in R. Because the model returns the probability that the species occurrence equals 0 (as opposed to a binary presence/absence), we used a threshold that maximizes the sensitivity plus specificity by species (Table B in S1 Text) that would identify the cutoff of when a probability should represent a predicted species occurrence or absence.

Mussel distribution model: To model the probability of occurrence of 12 freshwater mussel species, we randomly selected 80% of the data as the training set and reserved the remaining 20% as the testing dataset. We fit 12 logistic regression models (one for each species) using the glm function in the ‘stats’ package and the family of models set to ‘binomial’ [50]. All species-specific models included the same set of geographic, climate, land use, and connectivity variables (Table 2); however, the models differed in the host fish distribution covariates depending on each mussel’s biology (Table 3). The eight models used for host fish generalist species had the same set of covariates. Models for the remaining five mussel species considered to be host fish specialist species (Eastern pearlshell (*Margaritifera margaritifera*), Tidewater mucket (*Atlanticoncha ochracea*), Eastern pondmussel (*Sagittunio nasutus*), Yellow lampmussel (*Lampsilis cariosa*), and Alewife floater (*Utterbackiana implicata*)) included the same covariates as the generalist species in addition to the host fish occurrence metrics that are specific to each species (Table 3). The models were validated using the remaining 20% of data in the same way as described above for the fish species models (see method details in the S1 Text and see Table C in S1 Text for the mussel validation metrics by species).

Prediction Scenarios: To project fish species and mussel species occurrence under climate change across the study region, we used both fish and mussel models in combination with the projected end-of-century (year 2100) stream temperature and streamflow variable predictions. The end-of-century stream temperature data were predicted by adding +4°C to baseline air temperatures. The end-of-century streamflow metrics (averaged across 2077–2099) were predicted using Representative Concentration Pathway (RCP) 8.5 and an ensemble of five climate models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) including the cnrm-cm5, hadgem2-es, ipsl-cm5a-mr, mri-cgcm3, and noresm1-m models [58,59]. The results were downscaled to approximately 12 km. Then, to assess impacts of management

Table 3. Host fish variables used in mussel species models. The first variable was used for all mussel species, and additional variables were used for mussel species that had a specific host fish that could be modelled (5 species) or where we had some data on raw fish occurrence (2 species). HUC12 = 12-digit hydrologic unit code, POC = probability of occurrence.

Mussel species	Host Fish	Variable Definition
All	All 41 fish species modeled in this analysis	Summed predicted POC by stream reach, then averaged across HUC12
Tidewater Mucket (*Atlanticoncha ochracea*)	White Perch (*Morone americana)* Banded Killifish (*Fundulus diaphanus*)	Summed predicted relative abundance stream reach, then averaged across HUC12
Yellow Lampmussel (*Lampsilis cariosa*)	Yellow Perch (*Perca flavescens*) and White Perch (*Morone americana)*	
Eastern Pearlshell (*Margaritifera margaritifera*)	Brown Trout (*Salmo trutta*), Brook Trout (*Salvelinus fontinalis*), Atlantic Salmon (*Salmo salar*), Rainbow Trout (*Oncorhynchus mykiss*)	
Eastern Pondmussel (*Sagittunio nasutus*)	Yellow Perch (*Perca flavescens*), Largemouth Bass (*Micropterus salmoides*), Bluegill (*Lepomis macrochirus*), Pumpkinseed (*Lepomis gibbosus*), Redbreast Sunfish (*Lepomis auritus*)	
Alewife floater (*Utterbackiana implicata*)	White Perch (*Morone americana),* Pumpkinseed (*Lepomis gibbosus*), White Sucker (*Catostomus commersonii*)	
Yellow Lampmussel (*Lampsilis cariosa*)	Striped Bass (*Morone saxatilis*)	Raw fish occurrence (0/1) data at the HUC12 scale
Eastern Pondmussel (*Sagittunio nasutus*)	3-, 4-, and 9-spined Sticklebacks (*Gasterosteus aculeatus*, *Apeltes quadracus*, *Pungitius pungitius,* respectively)	

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intervention, we applied the fish and mussel models using both the projected end-of-century stream temperature and streamflow variables plus a series of manipulated covariates that represented different scenarios. Overall, we evaluated seven scenarios (Table 4): 1) baseline, 2) climate change, 3) climate change plus removal of all dams (dams), 4) climate change plus removal of all impervious surfaces in the 100-m riparian area in the watershed (impervious), 5) climate change plus 100% natural land in the riparian area (natural), 6) climate change plus 100% watershed forest (forest), and 7) climate change plus all individual management scenarios (combined). Note that these management scenarios are extreme and unrealistic in a human-dominated landscape, but they provide a means to see the potential for restoration. We also acknowledge that climate change will impact land cover (e.g., increased temperature and frequency of extreme droughts may reduce forest cover [62]), and that the land cover may impact the climate change variables (e.g., decreased

Table 4. Prediction scenarios for each species' probability of occurrence: baseline, climate change, and the five management scenarios. The management scenarios included the combined impacts of each individual management action and climate change. The stream temperature and streamflow data columns for all climate change impacted rows show both the climate change scenario used to model the stream temperature or streamflow followed by the mean ± standard deviation impacts to each climate variable across the study region. See Table 2 for variable definitions. NLCD = national land cover database, HUC12 = 12-digit hydrologic unit code, BFI = baseflow index, riparian = 100 m on both sides of the stream line.

Scenario	Land cover data	Stream temperature data	Streamflow data
Baseline	2019 NLCD	Average of the water temperature predictions 2000– 2020	Average of the streamflow predictions from 1977–2006
Climate Change	2019 NLCD	Scenario: Air temperature +4°C: Mean stream temperature change of 3.60°C ± 0.50°C	Scenario: average of the End-of-century streamflow (2070–2099) Mean flood frequency change of 6.41 ± 2.90 Mean low flow date change of 9.12 days ± 7.71 Mean BFI change of (negative) -0.04 ± 0.01
Dams	Reduced dam density (HUC12 scale) to 0		
Impervious	Reduced riparian impervious within the entire upstream watershed to 0%		
Natural	Increased riparian 'natural' land cover to 100% (within a stream reach for fish or all riparian areas within a HUC12 for mussels)		
Forest	Increased upstream watershed scale forested land cover to 100%		
Combined	A combination of the above four rows		

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forest cover increases annual streamflow [63]); however, these indirect effects and feedback loops are excluded from this analysis for simplicity. A future analysis could aim to incorporate these interactions into predictions.

2.3.2 Biodiversity assessment and visualization. The species-specific probability of occurrence predictions for freshwater fishes (n = 53) and mussels (n = 12) for each HUC12 watershed were combined across biodiversity groups. Species were grouped in ways that are commonly used in management (e.g., native or listed species) or that are expected to be particularly vulnerable to climate change. For fishes, groups included origin category (native or introduced), a habitat group (fluvial specialist, fluvial dependent, or macrohabitat generalist), and a temperature group (warm, cool, or cold). Fish species characterizations are the same as those in [36]. Using information from the literature (Table D in S1 Text) together with partner feedback, each mussel species was grouped based on: host fish category (generalist or specialist), a habitat group (lotic or generalist), a drying event tolerance group (semi-tolerant or intolerant), and conservation status (based on the northeast Regional Species of Greatest Conservation Need (RSGCN); here, we combined low and moderate, and, high and very high, Table 5).

To spatially visualize the impacts of each scenario on each biodiversity group for both fishes and mussels, we summed the species-specific probability of occurrence across each biodiversity group by HUC12 in each of the seven scenarios. Additionally, to show possible community assemblage shifts under each scenario, we calculated proportions of biodiversity groups (e.g., cold/cold+cool+warm) using the summed probabilities of occurrence for each biodiversity group, and we compared the different management scenarios to the baseline values. These proportions were calculated for the region as a whole and for high (>181 m) and low (< 181 m) elevation stream reaches separately because the species assemblages at different elevations can vary substantially. The elevation groups are separated based on the median stream catchment elevation of 181 m [51]. Finally, using this proportion, we calculated the percentage of watersheds where a group's proportion was greater than 0.5, suggesting it may be the dominant group within that watershed.

We also predicted mussel species richness in each scenario. To calculate species richness, we used the projected probability of occurrence, combined with the thresholds identified during model validation that maximize specificity plus sensitivity (Table C in S1 Text). Each species has a probability of occurrence threshold above which we assigned that species a 'present' value. We summed the number of 'present' species within each HUC12 watershed to calculate the species richness.

Table 5. Freshwater mussel species common name, scientific name, and the characterizations for each of the biodiversity group assignments: Regional Species of Greatest Conservation Need (RSGCN) priority, host fish specificity (generalist or specialist), habitat (lotic or generalist), and drying event tolerance (semi-tolerant or intolerant).

Common name	Scientific name	RSGCN priority	Host fish specificity	Habitat	Drying event tolerance
Eastern Elliptio	*Elliptio complanata*	not listed	generalist	generalist	semi-tolerant
Eastern Lampmussel	*Lampsilis radiata*	not listed	specialist	generalist	semi-tolerant
Eastern Pearlshell	*Margaritifera margaritifera*	moderate	specialist	lotic	semi-tolerant
Yellow Lampmussel	*Lampsilis cariosa*	high	specialist	generalist	semi-tolerant
Eastern Floater	*Pyganodon cataracta*	not listed	generalist	generalist	semi-tolerant
Creeper	*Strophitus undulatus*	not listed	generalist	lotic	intolerant
Tidewater Mucket	*Atlanticoncha ochracea*	high	specialist	generalist	intolerant
Alewife Floater	*Utterbackiana implicata*	not listed	specialist	generalist	intolerant
Eastern Pondmussel	*Sagittunio nasutus*	high	specialist	generalist	intolerant
Triangle Floater	*Alasmidonta undulata*	moderate	generalist	lotic	intolerant
Dwarf Wedgemussel	*Prolasmidonta heterodon*	very high	generalist	lotic	intolerant
Brook Floater	*Alasmidonta varicosa*	very high	generalist	lotic	intolerant

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3. Results

3.1 Model performance

Model accuracy for zero-inflated beta models for the 53 fish species ranged from 0.6 to 1.0 (Fig A in S1 Text). Models also ranged in sensitivity (0 to 1.0), specificity (0.59 to 1.0), Cohen's Kappa coefficient (0 to 0.56), and area under the curve (AUC, 0.70 to 1.0). Of the 53 species, only 41 were used in subsequent analyses: we removed four species that had sensitivity less than 0.2, seven species for model convergence problems, and one species for inability to calculate validation metrics. Model accuracy for logistic regression models for freshwater mussels ranged from 0.60 to 0.93 (Fig B in S1 Text). Models also ranged in sensitivity (0.25 to 0.90), specificity (0.56 to 0.94), Cohen's Kappa coefficient (0.10 to 0.47) and AUC (0.56 to 0.94). The full set of fish and mussel validation statistics by species are available in Table B in S1 Text and Table C in S1 Text, respectively.

3.2 Biodiversity assessment

3.2.1 Freshwater fishes: Climate change impacts. Our model predictions indicate that climate change will have negative impacts on coldwater fishes (Fig 2A and Table 6). In the baseline scenario, the average (across HUC12

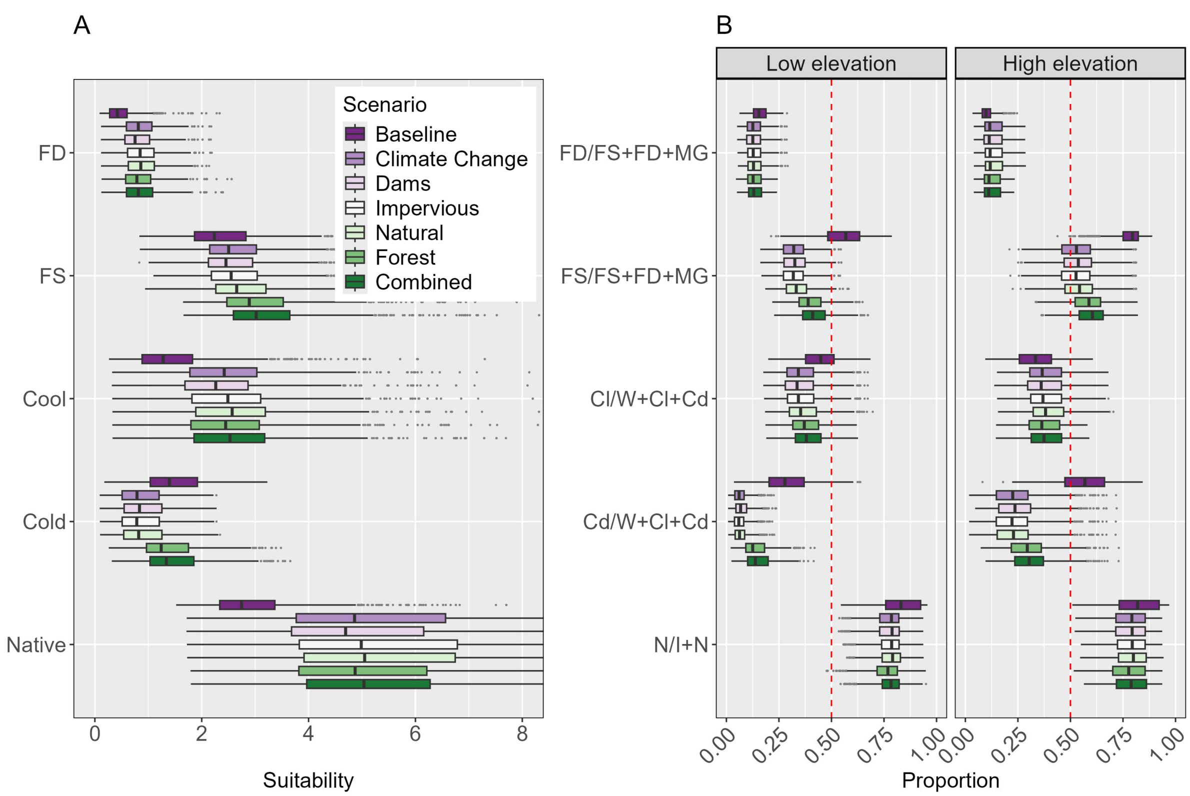

Fig 2. A) Projected suitability (summed probabilities of occurrence by group) for five freshwater fish biodiversity groups and each scenario. B) Projected habitat suitability proportions of freshwater fish groups under the seven different scenarios (Table 4) for low and high elevation watersheds (high elevation is average catchment elevation greater than 181m). The vertical red dotted line is at X = 0.50; values to the right indicate that the majority of species in the watershed belong to that particular biodiversity group, and values to the left indicate that fewer than half of the species in the watershed belong to the biodiversity group. The lower and upper horizontal lines of each 'box' correspond to the 25th and 75th percentiles. The whiskers extend to the largest value no further than 1.5 times the inter-quartile range from the edge of the box. Outliers are plotted individually as grey dots. FD = Fluvial dependent, FS = fluvial specialist, MG = Macrohabitat generalist, Cl = cool, Cd = cold, W = warm, N = native, I = Introduced.

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Table 6. Minimum (min), mean and standard deviation (SD), and maximum (max) summed probability of occurrence (POC) across hydrologic Unit Code 12 (HUC12) watersheds for each freshwater fish biodiversity group and scenario. Summary statistics are also included for the proportional POC for that group relative to the summed POC of all fish species. The last column on the right is the percent of HUC12s where that group has a higher POC compared to the other groups (e.g., the percent of HUC12s where the summed POC of coldwater species divided by the summed POC of cold-, cool-, and warmwater species is greater than 0.50).

	Summed POC				Summed POC proportion				
Scenario	**Min**	**Mean**	**SD**	**Max**	**Min**	**Mean**	**SD**	**Max**	**% higher**
Introduced									
Baseline	0.14	0.75	0.68	6.11	0.03	0.18	0.11	0.49	0
Climate change	0.17	1.66	1.06	7.75	0.06	0.23	0.09	0.48	0
Forest	0.18	1.71	1.09	8.30	0.05	0.24	0.09	0.52	0
Natural	0.17	1.62	1.01	7.37	0.06	0.22	0.08	0.45	0
Impervious	0.17	1.66	1.04	7.75	0.06	0.22	0.08	0.45	0
Dams	0.17	1.58	1.00	7.72	0.06	0.23	0.09	0.48	0
Combined	0.18	1.59	0.97	7.91	0.05	0.22	0.08	0.46	0
Native									
Baseline	1.53	2.95	0.87	8.53	0.51	0.82	0.11	0.97	100
Climate change	1.72	5.24	1.77	11.72	0.52	0.77	0.09	0.94	100
Forest	1.79	5.08	1.52	10.77	0.48	0.76	0.09	0.95	100
Natural	1.73	5.41	1.79	11.80	0.55	0.78	0.08	0.94	100
Impervious	1.73	5.41	1.89	12.83	0.55	0.78	0.08	0.94	100
Dams	1.72	5.02	1.61	11.57	0.52	0.77	0.09	0.94	100
Combined	1.80	5.21	1.52	11.99	0.54	0.78	0.08	0.95	100
Warm									
Baseline	0.22	0.74	0.76	4.98	0.05	0.18	0.12	0.64	3
Climate change	0.24	3.52	2.14	11.47	0.10	0.47	0.15	0.78	43
Forest	0.24	2.87	1.67	8.96	0.09	0.39	0.13	0.70	26
Natural	0.24	3.47	2.12	11.39	0.10	0.45	0.15	0.76	40
Impervious	0.24	3.62	2.26	12.04	0.10	0.47	0.15	0.77	43
Dams	0.24	3.31	1.95	11.31	0.10	0.46	0.15	0.78	41
Combined	0.24	2.70	1.56	9.60	0.09	0.37	0.13	0.68	20
Cool									
Baseline	0.26	1.46	0.83	7.24	0.09	0.38	0.11	0.69	16
Climate change	0.33	2.50	0.98	8.10	0.15	0.37	0.09	0.68	9
Forest	0.33	2.54	1.03	8.24	0.15	0.37	0.09	0.62	8
Natural	0.33	2.64	1.01	8.29	0.16	0.38	0.10	0.71	13
Impervious	0.33	2.57	1.00	8.17	0.15	0.37	0.09	0.68	9
Dams	0.32	2.37	0.94	8.07	0.14	0.37	0.10	0.68	9
Combined	0.33	2.62	1.06	8.49	0.14	0.39	0.09	0.63	11
Cold									
Baseline	0.18	1.50	0.60	3.22	0.04	0.44	0.19	0.84	41
Climate change	0.09	0.88	0.46	2.26	0.01	0.16	0.12	0.72	2
Forest	0.26	1.38	0.55	3.53	0.02	0.23	0.12	0.73	3
Natural	0.10	0.92	0.48	2.34	0.01	0.16	0.12	0.71	2
Impervious	0.09	0.88	0.46	2.27	0.01	0.16	0.12	0.71	2
Dams	0.09	0.92	0.46	2.27	0.01	0.17	0.12	0.72	2
Combined	0.32	1.48	0.58	3.72	0.02	0.24	0.12	0.73	3

(Continued)

Table 6. (Continued)

	Summed POC				Summed POC proportion				
Scenario	Min	Mean	SD	Max	Min	Mean	SD	Max	% higher
Macrohabitat generalist									
Baseline	0.23	0.80	0.78	5.84	0.06	0.2	0.12	0.67	4
Climate change	0.25	3.17	2.03	10.83	0.11	0.43	0.15	0.77	36
Forest	0.25	2.64	1.61	8.72	0.11	0.37	0.13	0.68	21
Natural	0.25	3.13	1.99	10.78	0.11	0.42	0.14	0.74	33
Impervious	0.25	3.24	2.12	11.19	0.11	0.43	0.14	0.75	36
Dams	0.25	2.99	1.85	10.74	0.11	0.43	0.14	0.77	34
Combined	0.25	2.50	1.52	9.19	0.10	0.35	0.13	0.65	15
Fluvial dependent									
Baseline	0.09	0.47	0.27	2.28	0.03	0.13	0.05	0.29	0
Climate change	0.12	0.86	0.33	2.15	0.04	0.13	0.05	0.29	0
Forest	0.13	0.83	0.33	2.48	0.04	0.13	0.04	0.24	0
Natural	0.12	0.89	0.34	2.12	0.04	0.14	0.05	0.29	0
Impervious	0.12	0.88	0.34	2.16	0.04	0.14	0.05	0.29	0
Dams	0.12	0.82	0.33	2.14	0.04	0.13	0.05	0.29	0
Combined	0.12	0.85	0.34	2.34	0.04	0.13	0.04	0.24	0
Fluvial specialist									
Baseline	0.83	2.39	0.74	6.75	0.21	0.68	0.14	0.89	87
Climate change	0.85	2.65	0.69	6.46	0.16	0.43	0.13	0.81	35
Forest	1.65	3.10	0.87	7.92	0.22	0.50	0.12	0.82	51
Natural	0.95	2.80	0.73	6.95	0.18	0.45	0.13	0.81	38
Impervious	1.08	2.67	0.68	6.49	0.17	0.43	0.13	0.81	35
Dams	0.84	2.59	0.66	6.45	0.16	0.44	0.13	0.81	37
Combined	1.66	3.25	0.91	8.35	0.23	0.52	0.12	0.82	55

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watersheds) of the summed probability of occurrence of coldwater group was 1.50 ± 0.60 (mean ± standard deviation) compared to 0.88 ± 0.46 in the climate change scenario (Fig 2A and Table 6). Accordingly, the proportion of coldwater fishes decreased from 0.44 ± 0.19 (baseline) to 0.16 ± 0.12 (climate change, Table 6). In baseline conditions, the proportion of coldwater fish was higher than the proportions of cool- and warmwater fish in 41% of all watersheds (Table 6), specifically in 69% of the high elevation watersheds and in 6% of low elevation watersheds (Fig 2B). In climate change, the probabilities of coldwater fish occurrence were higher than warm- and coolwater fish in just 2% of all watersheds (Table 6), specifically in 3% of high elevation watersheds and in 1% of low elevation watersheds (Fig 2B). For coolwater fishes, the summed probabilities of occurrence increased from 1.46 ± 0.83 (baseline) to 2.50 ± 0.98 (climate change; Fig 2A and Table 6); however, within low elevation watersheds, the proportion of coolwater fishes (compared to cold- and warmwater fishes) decreased from 0.45 ± 0.09 (baseline) to 0.36 ± 0.09 (climate change; Fig 2B). For warmwater fishes, the summed probability of occurrence increased from 0.74 ± 0.76 (baseline) to 3.52 ± 2.14 (climate change, Table 6) – this increase was observed both at high and low elevation, but the effect was greater at low elevations (results not shown).

At the species level, we observed reduced number of watersheds projected to have species present in climate change compared to baseline for many of the coldwater fish species (Fig 3), such as Atlantic Salmon (*Salmo salar*) and Brook Trout (*Salvelinus fontinalis*). Alternatively, we saw a higher number of watersheds projected to have species present in climate change compared to baseline for many of the warmwater fish species, such as Creek Chubsucker (*Erimyzon oblongus*) and Bluegill (*Lepomis macrochirus*).

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Fig 3. The total number of Hydrologic Unit Code 12 (HUC12) watersheds across the northeastern United States projected to have the fish species present in each of the different management scenarios (see Table 4). Probability of occurrence thresholds that designate a fish species occurrence were chosen based on the threshold that maximized the sensitivity and specificity in the validation data (Table B in S1 Text). Refer to Table B in S1 Text for the fish species scientific names.

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Fluvial dependent, fluvial specialist, and native species showed a positive response to future climate change overall (Fig 2A); however, the proportion of fluvial specialist species (relative to all fish species) decreased from 0.68 ± 0.14 (baseline) to 0.43 ± 0.13 (climate change, Table 6). Within high elevation watersheds, the proportion of fluvial specialists decreased from 0.78 ± 0.07 (baseline) to 0.52 ± 0.10 (climate change) and within low elevation watersheds, this proportion decreased from 0.55 ± 0.11 (baseline) to 0.32 ± 0.07 (climate change, Fig 2B). In high elevation watersheds, 100% of streams had higher proportions of fluvial specialist species compared to fluvial dependent and macrohabitat generalist species under baseline conditions, but this decreased to 62% of streams in climate change (Fig 2B). In low elevation watersheds, 71% of streams had higher proportions of fluvial specialist species compared to fluvial dependent and macrohabitat generalist species under baseline conditions, but this decreased to 2% of streams in climate change (Fig 2B). The proportion of watersheds projected to have higher probabilities of occurrence for native (versus introduced) species decreased slightly from 0.82 ± 0.11 in the baseline to 0.77 ± 0.09 in the climate change scenario (Table 6), but native species were projected to continue to be dominant at both high and low elevations (Fig 2B).

3.2.2 Freshwater fishes: Management impacts. The combined and the forest management scenarios had the largest potential to restore habitat suitability back to the baseline condition for the coldwater fish group (Fig 2A and Table 6); however, neither were able to reverse the expected transition from coldwater fish dominance to warmwater fish dominance at either high or low elevations (Fig 2B). Similarly, for the proportion of fluvial specialists, the combined and the forest management scenarios had the largest ability to offset climate change and bring the system back to baseline conditions; however, these management interventions were not able to fully offset the impacts of climate change (Fig 2B). None of the management scenarios could recreate identical species assemblages to baseline (Fig 2B). The management scenarios had no meaningful effect on fluvial dependent, coolwater, and native fishes groups (Fig 2).

3.2.3 Freshwater mussels: Climate change impacts. Climate change is predicted to have negative impacts on many of the freshwater mussel groups across the region (Fig 4A and Table 7). Across all watersheds, mean (averaged across HUC12 watersheds) summed probability of occurrence (by group) dropped from 0.68 ± 0.49 (baseline) to 0.38 ± 0.44 (climate change) for host fish specialists, 0.99 ± 0.43 (baseline) to 0.61 ± 0.30 (climate change) for lotic species, 0.93 ± 0.44 (baseline) to 0.66 ± 0.34 (climate change) for RSGCN listed species, and 0.98 ± 0.49 (Baseline) to 0.75 ± 0.43 (climate change) for drying intolerant species (Fig 4A and Table 7).

In addition to the decrease in summed probabilities of occurrence for each of the four mussel groups discussed above, the proportion of freshwater mussels projected to be lotic, host specialist species, drying intolerant, and RSGCN listed species is projected to be lower with climate change compared to baseline conditions (Fig 4B). For example, at high elevation, 49% of the watersheds are projected to have a higher proportion of the summed probabilities of occurrence for lotic species (compared to macrohabitat generalist species) in the baseline compared to just 1% of watersheds in the climate change scenario (Fig 4B – the data to the right of the vertical dashed line). A similar observation, though of lesser magnitude was projected for low elevation watersheds, where 12% of watersheds were projected to have a higher summed probabilities of occurrence proportion for lotic species (compared to lentic species) in the baseline conditions, compared to 1% in the climate change condition (Fig 4B). Similar projections were observed for host fish specialist species (compared to host fish generalist species), drying intolerant group (compared to drying semi-tolerant group), and RSGCN listed species (compared to RSGCN not listed species).

Mussel species richness was projected to decrease throughout the region from a mean of 3.49 ± 2.49 (baseline) to 3.0 ± 1.47 (climate change, Fig 5A). In the baseline, species richness was highest in low elevation watersheds in the southern portion of the study area and along the coast from Massachusetts to the horn of Maine (Fig 5). In the baseline, mussel species richness ranged from 0 to 10 (mean = 5.32 ± 2.0) at low elevations and from 0 to 7 (mean = 2.0 ± 1.72) at high elevations (Fig 5B). In the climate change scenario, mussel species richness was projected to decrease in the low elevation watersheds to a mean of 3.60 ± 1.62, which is an average decrease of 2 species per

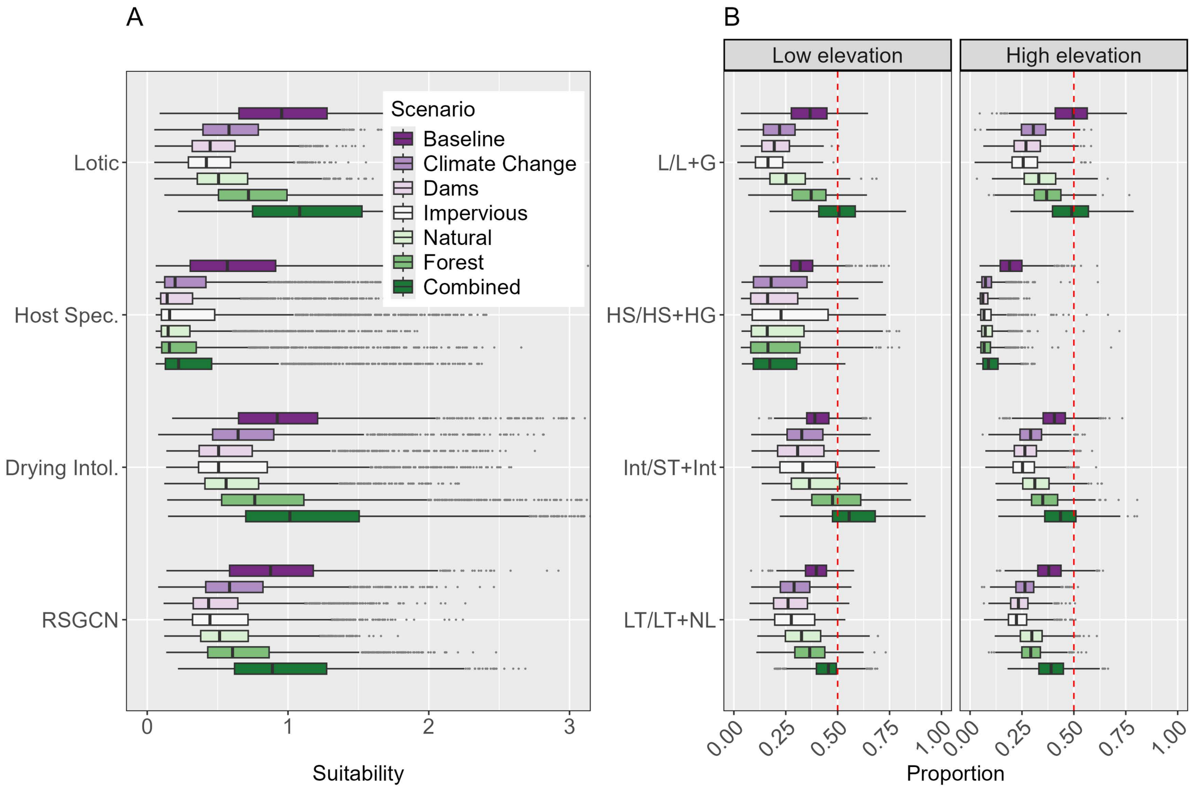

Fig 4. A) Projected suitability (summed probabilities of occurrence by group) for four freshwater mussel biodiversity groups and each scenario. B) Projected habitat suitability proportion of freshwater mussel groups under the seven different scenarios (Table 4) for low and high elevation watersheds (high elevation is average catchment elevation greater than 181m). The vertical dashed line is at X = 0.50; values to the right indicate that the majority of species in the watershed belong to that particular biodiversity group, and values to the left indicate that fewer than half of the species in the watershed belong to the biodiversity group. The lower and upper horizontal lines of each 'box' correspond to the 25th and 75th percentiles. The whiskers extend to the largest value no further than 1.5 times the inter-quartile range from the edge of the box. Outliers are plotted individually as grey dots. Host Spec. = Host Specialist; Drying Intol. = Drying Intolerant; RSGCN = RSGCN listed species. L = lotic; G = generalist; HS = Host Specialist; HG = Host Generalist; Int = Drying Intolerant; ST = Drying Semi-Tolerant; LT = RSGCN listed, NL = Not Listed by RSGCN.

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watershed compared to the baseline. In contrast, average species richness in the high elevation watersheds remained like baseline in the climate change scenario (mean = 2.60 ± 1.2). Maine (Fig 5A) has high species richness in the southeastern portion and low species richness in the northwestern portion in the baseline, but in climate change much of northern Maine has similar richness values projected (i.e., the range of richness values decreases). The individual occurrence projections by species predicted that the distribution of suitable habitat for some species (Eastern Floater (*Pyganodon cataracta*), Eastern Elliptio (*Elliptio complanata*), and Brook Floater (*Alasmidonta varicosa*)) would increase in climate change compared to baseline (Fig 6). All other species were projected to occur in fewer watersheds in climate change compared to baseline.

The direction of change for the host fish specialist mussels did not necessarily follow the direction of change for their host fish (Fig 7, Table E in S1 Text). Eastern Pearlshell was the only host fish specialist freshwater mussel species that had a significant and positive relationship with its host fish (a relationship we expected to see for all species). Eastern Pearlshell host fishes (i.e., Brook Trout, Brown Trout (*Salmo trutta*), Atlantic Salmon, Rainbow Trout (*Oncorhynchus mykiss*)) are all coldwater and fluvial specialist group species that were negatively affected by climate change (Figs 3 and 7). Most other host fishes for freshwater mussel specialist species (see Table 3) were predicted

Table 7. Minimum (min), mean and standard deviation (SD), and maximum (max) summed probability of occurrence (POC) across hydrologic Unit Code 12 (HUC12) watersheds for each freshwater mussel biodiversity group and scenario. Summary statistics are also included for the proportional POC for that group relative to the summed POC of all mussel species. The last column on the right is the percent of HUC12s where that group has a higher POC compared to the other groups (e.g., the percent of HUC12s where the summed POC of lotic species divided by the summed POC of lotic and macrohabitat generalist species is greater than 0.50).

	Summed POC				Summed POC Proportion				
Scenario	Min	Mean	SD	Max	Min	Mean	SD	Max	% higher
Drying intolerant									
Baseline	0.18	0.98	0.49	3.11	0.12	0.41	0.09	0.73	16
Climate change	0.08	0.75	0.43	2.82	0.06	0.32	0.10	0.66	7
Forest	0.14	0.91	0.54	3.22	0.13	0.42	0.14	0.85	24
Natural	0.12	0.65	0.36	2.21	0.12	0.35	0.12	0.84	14
Impervious	0.13	0.69	0.48	2.59	0.07	0.30	0.12	0.68	11
Dams	0.14	0.63	0.42	2.75	0.07	0.30	0.12	0.70	8
Combined	0.15	1.21	0.70	3.86	0.14	0.49	0.14	0.92	46
Drying semi-tolerant									
Baseline	0.34	1.37	0.47	2.93	0.27	0.59	0.09	0.88	84
Climate change	0.41	1.50	0.29	2.59	0.34	0.68	0.10	0.94	93
Forest	0.24	1.14	0.27	2.04	0.15	0.58	0.14	0.87	76
Natural	0.23	1.12	0.27	2.05	0.16	0.65	0.12	0.88	86
Impervious	0.63	1.40	0.27	2.53	0.32	0.70	0.12	0.93	89
Dams	0.62	1.36	0.25	2.26	0.30	0.70	0.12	0.93	92
Combined	0.14	1.09	0.25	2.20	0.08	0.51	0.14	0.86	54
Macrohabitat generalist									
Baseline	0.27	1.36	0.64	4.60	0.24	0.57	0.13	0.97	68
Climate change	0.5	1.64	0.48	3.80	0.42	0.73	0.10	0.98	99
Forest	0.38	1.27	0.39	3.28	0.23	0.63	0.10	0.93	91
Natural	0.36	1.22	0.34	2.69	0.31	0.69	0.12	0.98	94
Impervious	0.66	1.63	0.57	3.64	0.42	0.77	0.10	0.98	100
Dams	0.66	1.50	0.42	3.47	0.42	0.75	0.10	0.97	99
Combined	0.33	1.14	0.42	3.11	0.17	0.51	0.12	0.83	52
Host generalist									
Baseline	0.46	1.68	0.47	3.21	0.25	0.74	0.11	0.95	97
Climate change	0.53	1.86	0.40	3.05	0.28	0.85	0.13	0.97	97
Forest	0.43	1.71	0.41	3.15	0.20	0.86	0.13	0.97	97
Natural	0.42	1.48	0.37	2.58	0.20	0.85	0.14	0.97	96
Impervious	0.72	1.66	0.31	2.66	0.27	0.83	0.16	0.97	93
Dams	0.69	1.69	0.31	2.60	0.40	0.87	0.12	0.97	98
Combined	0.77	1.91	0.45	3.23	0.46	0.85	0.11	0.97	99
Host specialist									
Baseline	0.06	0.68	0.49	3.53	0.05	0.26	0.11	0.75	3
Climate change	0.06	0.38	0.44	2.52	0.03	0.15	0.13	0.72	3
Forest	0.06	0.33	0.41	2.66	0.03	0.14	0.13	0.80	3
Natural	0.06	0.28	0.33	1.92	0.03	0.15	0.14	0.80	4
Impervious	0.06	0.43	0.54	2.41	0.03	0.17	0.16	0.73	7
Dams	0.06	0.31	0.37	2.12	0.03	0.13	0.12	0.60	2
Combined	0.06	0.40	0.45	2.38	0.03	0.15	0.11	0.54	1

(Continued)

Table 7. (Continued)

	Summed POC				Summed POC Proportion				
Scenario	Min	Mean	SD	Max	Min	Mean	SD	Max	% higher
Lotic									
Baseline	0.09	0.99	0.43	2.51	0.03	0.43	0.13	0.76	32
Climate change	0.05	0.61	0.30	2.02	0.02	0.27	0.10	0.58	1
Forest	0.12	0.77	0.34	2.27	0.07	0.37	0.10	0.77	9
Natural	0.05	0.55	0.27	2.06	0.02	0.31	0.12	0.69	6
Impervious	0.05	0.46	0.23	1.82	0.02	0.23	0.10	0.58	0
Dams	0.05	0.49	0.24	1.78	0.03	0.25	0.10	0.58	1
Combined	0.22	1.16	0.51	2.87	0.17	0.49	0.12	0.83	48
Not RSGCN									
Baseline	0.32	1.42	0.48	2.92	0.36	0.61	0.08	0.92	92
Climate change	0.51	1.59	0.33	2.90	0.43	0.72	0.08	0.94	99
Forest	0.33	1.35	0.30	2.37	0.27	0.67	0.09	0.91	97
Natural	0.45	1.19	0.26	2.25	0.31	0.68	0.09	0.89	96
Impervious	0.67	1.52	0.32	3.04	0.46	0.74	0.09	0.93	99
Dams	0.63	1.46	0.28	2.66	0.44	0.74	0.09	0.93	99
Combined	0.56	1.30	0.36	2.72	0.31	0.58	0.09	0.82	84
RSGCN listed									
Baseline	0.14	0.93	0.44	2.92	0.08	0.39	0.08	0.64	8
Climate change	0.08	0.66	0.34	2.46	0.06	0.28	0.08	0.57	1
Forest	0.14	0.70	0.37	2.48	0.09	0.33	0.09	0.73	3
Natural	0.12	0.58	0.28	1.78	0.11	0.32	0.09	0.69	4
Impervious	0.12	0.58	0.36	2.24	0.07	0.26	0.09	0.54	1
Dams	0.12	0.54	0.32	2.26	0.07	0.26	0.09	0.56	1
Combined	0.22	1.00	0.47	2.69	0.18	0.42	0.09	0.69	16

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to increase in distribution (i.e., the number of watersheds that they are predicted to occupy expanded) under climate change (Figs 3 and 7) and one species, Banded Killifish (*Fundulus diaphanus*), showed very little change in response to climate change. Most of these host fishes are part of the warmwater and macrohabitat generalist fish groups, except for White Sucker (*Catostomus commersonii*), which is a coolwater, fluvial dependent species. Note that we did not model the well documented host fish for Tidewater Mucket (White Perch) or for Alewife Floater (Alewife, *Alosa pseudoharengus*) due to data limitations.

3.2.4 Freshwater mussels: Management scenarios. The combined management scenario had the greatest potential to restore habitat suitability for the different freshwater mussel biodiversity groups (Fig 4), species richness (Fig 5B), and for Eastern Pearlshell host fish (Figs 3 and 7). For lotic, drying intolerant, and RSGCN listed species, the combination of all management interventions showed a similar distribution of summed probability of occurrence values as the baseline scenario, despite also incorporating the impacts of climate change (Fig 4). The positive impact of the combined intervention is driven by the large positive impacts of the forest intervention; however, forest cover alone does not fully restore the distribution to baseline values for lotic, drying intolerant, and RSGCN listed species without the addition of the other management scenario. Host fish specialists and overall species richness similarly show the greatest benefit from the combined scenario (Figs 4 and 5); however, it does not result in values as high as the baseline.

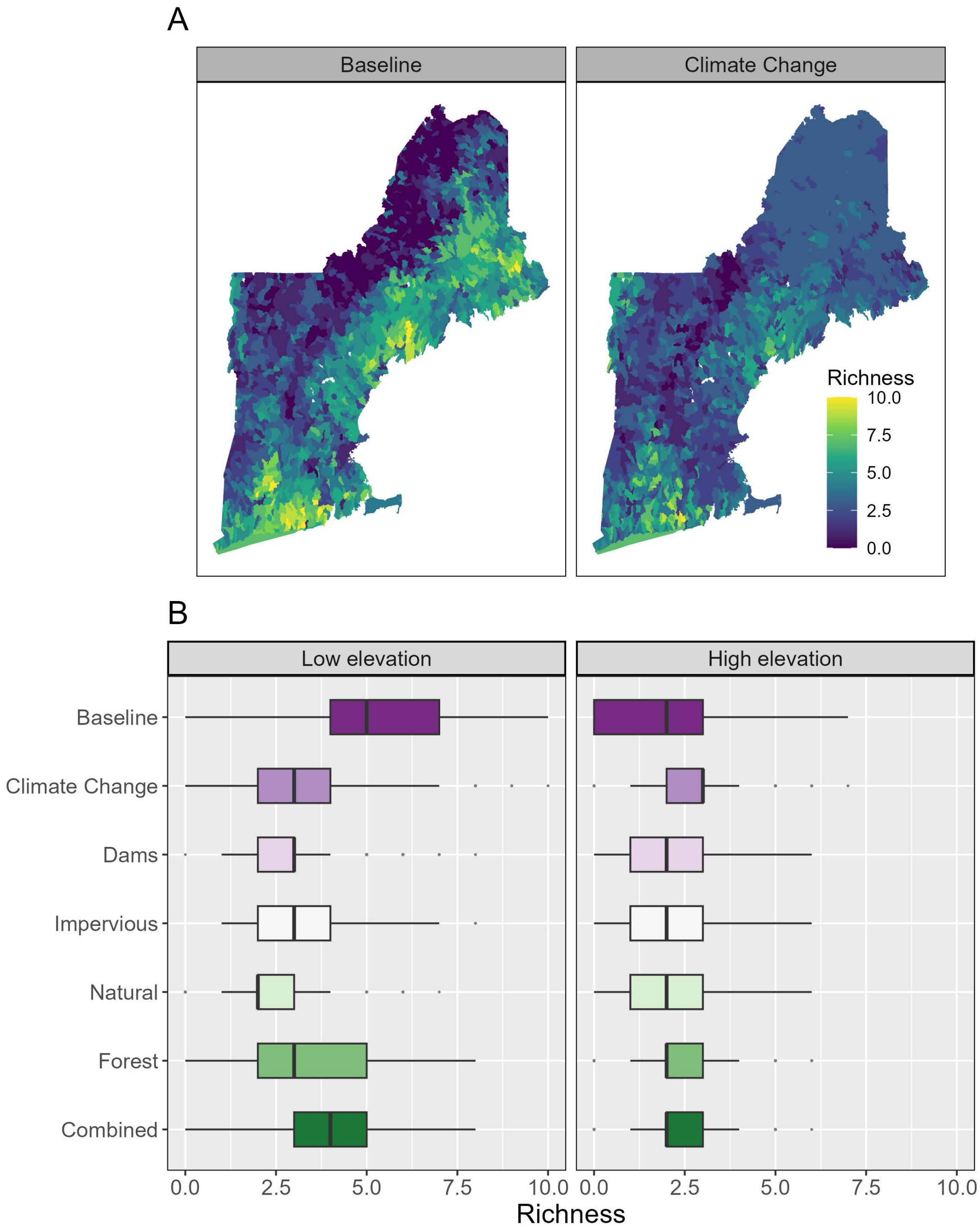

Fig 5. A) The projected mussel species richness in the baseline condition and the climate change scenario across the northeastern United States. (U.S. states outline reprinted from U.S. Census Bureau [38] and HUC12 boundary outlines reprinted from the U.S. Geological Survey (USGS) national hydrography dataset (NHD, [39])). **B)** The distribution of species richness values by different management scenario (Table 4), with panels indicating elevation (low versus high: high elevation is average catchment elevation greater than 181m). The lower and upper horizontal lines of each 'box' correspond to the 25th and 75th percentiles. The whiskers extend to the largest value no further than 1.5 times the inter-quartile range from the edge of the box. Outliers are plotted individually as grey dots.

https://doi.org/10.1371/journal.pclm.0000742.g005

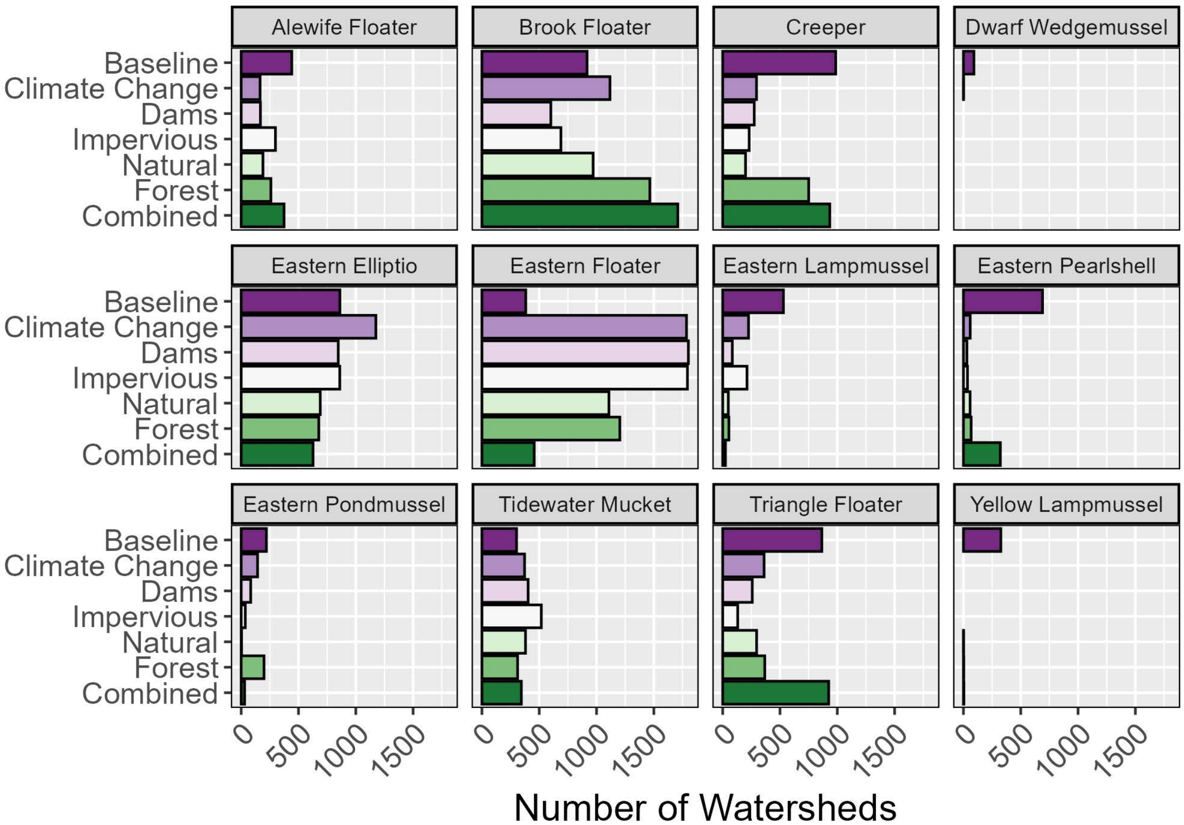

Fig 6. The total number of Hydrologic Unit Code 12 (HUC12) watersheds across the northeastern United States that are projected to have each mussel species present in each of the different management scenarios (see Table 4). Probability of occurrence thresholds that designate a mussel species occurrence were chosen based on the threshold that maximized the sensitivity and specificity in the validation data. Mussel species scientific names are in Table 5.

https://doi.org/10.1371/journal.pclm.0000742.g006

4. Discussion

4.1 Climate change impacts on species groups

Using statistical models developed with a data-rich, regional dataset, we predicted changes in the distribution and prevalence of stream fish and freshwater mussel biodiversity with climate change. Specifically, we found that increases in stream temperature, more frequent winter storm flows, a later low flow date, and lower baseflows [44,58,59] caused substantial shifts in fish community dominance, such that the currently dominant groups (e.g., fluvial specialist and coldwater fishes) may become the sub-dominant groups. Additionally, these projected impacts of climate change may alter habitat in a way that directly harms the coldwater fish group. High stream temperatures are known to negatively impact coldwater fishes [36,64–66]. Fish assemblages are largely shaped by streamflow regimes [67], although the impacts of flow alteration on fishes are less clear (compared to stream temperatures) due to multiple mechanisms of impact on the different life history phases and traits that interact with flows in different ways [14]. However, there are many examples in the literature of flow alteration harming fish species, such as impacts through altered flow magnitudes [68,69], storm flows [70], or low flow frequency and duration [71]. While some freshwater fishes may be able to respond to climate change through dispersal, these shifts are not able to offset the negative impacts entirely [72].

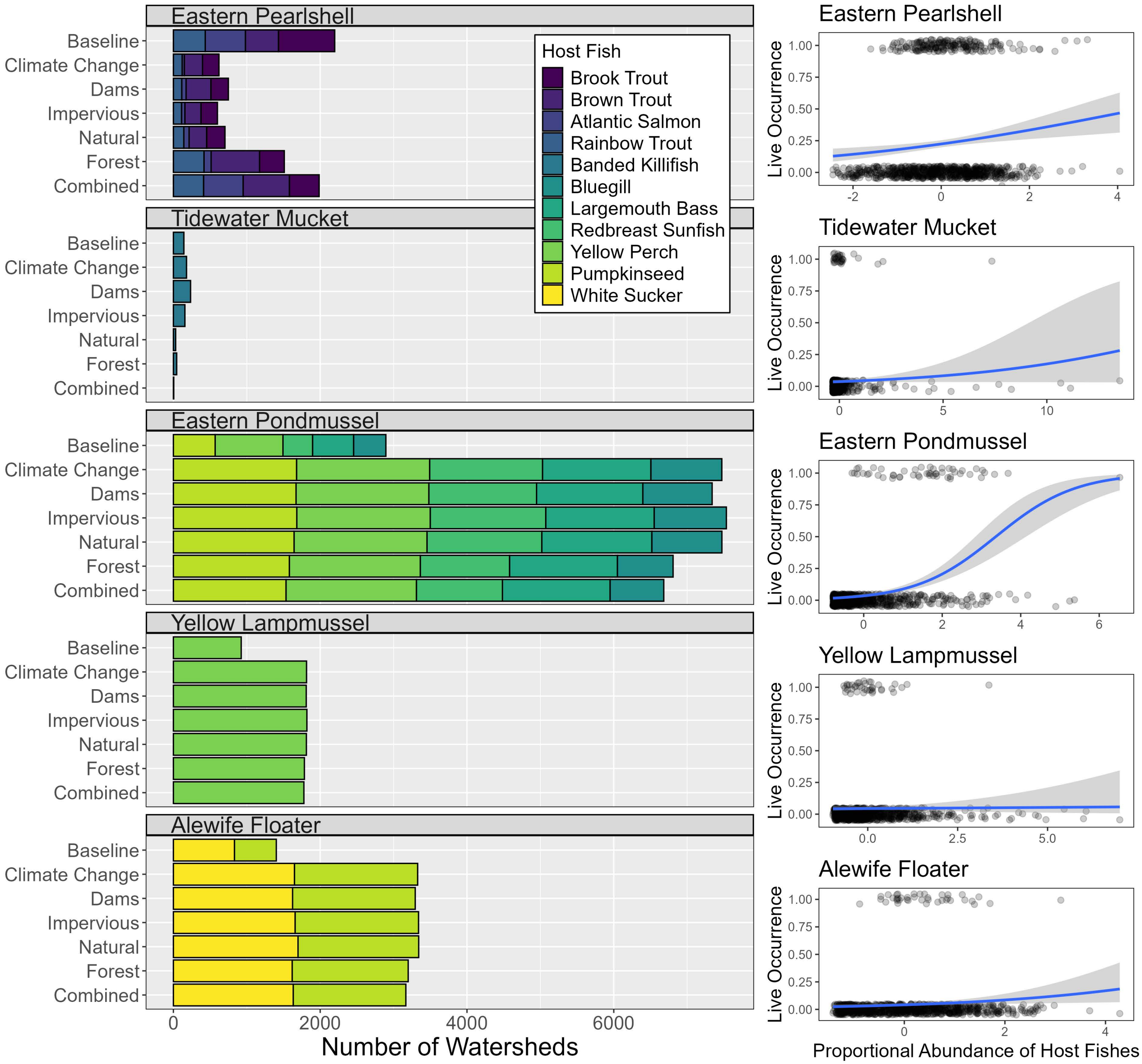

Fig 7. Left:The number of watersheds that each host fish (color) is projected to occur in the seven different scenarios (Table 4) for each of the host fish specialist mussels: Eastern Pearlshell (*Margaritifera margaritifera*), Tidewater Mucket (*Atlanticoncha ochracea*), Eastern Pondmussel (*Sagittunio nasutus*), Yellow Lampmussel (*Lampsilis cariosa*), and Alewife Floater (*Utterbackiana implicata*). Right: The relationship between the mussel occurrence (by Hydrologic Unit Code 12 (HUC12) watershed) and the predicted proportional abundance of the host fish within the HUC12 watershed. Blue fitted line shows a generalized linear model with a binomial link function, with the standard error shown in grey shading. Points represent the observed mussel data, where 1 is species detection and 0 is species non-detection. Points are semi-transparent and jittered to help show the density of points.

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For freshwater mussels, we found that the projected impacts of climate change on water temperature and streamflow may alter habitat in a way that directly harms all four vulnerable groups of mussels (lotic, host-fish specialist, drying intolerant, and RSGCN listed species). Additionally, we found that these four groups of species, which are sub-dominant groups in the baseline, became even less common relative to the dominant group in the face of climate change. High stream temperatures may negatively impact freshwater mussels through a decrease or complete prevention of lure display [73], which some species use to attract host fishes, a decrease in energy production and reserves [74], or by causing mortality at 35°C [74]. Low flows and drought also impact freshwater mussel fitness (individual mussel through community level assemblages) in numerous ways (reviewed by [75]). For example, drought can cause direct mortality of freshwater mussels due to dewatering and indirect mortality by altering dissolved oxygen, temperature, and biological oxygen demand [76]. High flows and high shear stress can also be harmful to freshwater mussels, limiting mussel recruitment [77], juvenile settlement [78], and survival [79].

With the exception of Eastern Pearlshell, mussel species were not significantly, positively related to their host fishes. For a few mussel species, we did not have projections of the preferred host fish (e.g., Alewife for Alewife Floater, White Perch for Tidewater Mucket) because we did not have modeled distributions for anadromous or estuarine species, which may explain the lack of observed relationships. Eastern Pondmussel have several host fishes (See Table A in S1 Text), which could have also prevented a clear signal between the mussels and their host fishes. Given that many of the mussel species' host fishes were warmwater and macrohabitat generalist species that are widespread, their distributions may not limit mussel distributions. The only host fish specialist mussel in this study that relied on coldwater, fluvial specialist fishes was the Eastern Pearlshell. The negative impacts of climate change on coldwater fishes identified in this study reduced the projected future distributions of Eastern Pearlshell, which has also been observed in Europe [18]. Future analyses could develop mechanistic models for host fish specialist species and determine if ranges of the host fish currently limit the mussel range.

The limited effect of climate change on habitat suitability for fluvial specialist and coolwater species combined with the large positive impact on habitat suitability for macrohabitat generalist and warmwater species manifested as a decrease in the proportion of fluvial specialist and coolwater species under climate change. Future studies could evaluate potential biotic interactions (competition for resources or predation) that may confirm these results. Some studies have incorporated biotic interactions in addition to the impacts of climate change on an individual group or species. For example, opportunistic expansions have been observed in rocky intertidal [80] and plant species where contractions in certain species lead to expansions in previously subdominant species [81]. While our work did not mechanistically model biotic interactions such as competition or predation along with habitat suitability, follow up work could explore interactions among species to determine if species with high habitat suitability under climate change might also have other competitive advantages.

4.2 Response to management interventions

Forest cover at the watershed scale can partially offset the negative impacts of climate change on freshwater fishes and mussels. Fluvial specialist and coldwater fish groups as well as lotic, drying intolerant and RSGCN listed mussel groups were all projected to be negatively impacted by climate change, but these negatives impacts were offset partially or fully by the forest scenario. By combining the forest scenario with the other restoration approaches (i.e., riparian impervious removal and riparian natural vegetation restoration), negative impacts to the freshwater mussel groups could be almost entirely offset. Other studies have shown the importance of maintaining or restoring forested areas in watersheds. For example, forest cover was found to be the most important variable in predicting sensitive macroinvertebrate taxa (i.e., mayflies (order: Ephemeroptera), stoneflies (order: Plecoptera), caddisflies (order: Trichoptera) and functional groups [82], and watershed-scale forested land cover can have a strong effect on habitat quality and fish biotic integrity [83,84]. Forested and vegetated habitat supports the three critical components of stream health: the natural streamflow regime

[85,86], stream temperature regime [87], and sediment regime [88]. Furthermore, forested habitat reduces watershed sediment runoff to the stream [89], maintains cooler water temperatures by reducing sunlight exposure to surface water runoff [90], and reduces stream flashiness levels [70] by reducing runoff [89] and increasing infiltration [89]. It is important to acknowledge, however, that the forest management scenario, which increased percent forest cover in the watershed to 100%, is impossible to be realized if people are living in a watershed. Moreover, the forest cover data used in this analysis from the National Land Cover Database is coarse in scale (30 m pixels) and does not distinguish different forest types, forest management approaches, or small microhabitats such as pocket meadows within a forest —simply having forest cover (vs. impervious or agriculture) is valuable.

Despite the extreme nature of these scenarios, the importance of preserving or restoring forest cover in the Northeast is evident. While many laws apply just to wetlands and riparian lands [91,92], this study shows that land cover throughout the watershed can influence riverine species distributions. Forest cover is shown here to benefit the full suite of vulnerable groups in both taxonomic groups at the regional scale, and conserving undeveloped areas or restoring areas with agriculture or urban land covers may be the best methods for promoting freshwater biodiversity conservation. Watershed imperviousness was highly negatively correlated with the watershed forest variable (shown in Fig S1 of [36]), and thus we did not use watershed imperviousness as a variable in our models. However, based on the relationship between the two variables, we suggest that removing impervious land cover to allow forest or other natural land restoration can promote freshwater biodiversity. Although we found forest land cover to be the most impactful variable for offsetting negative climate change impacts to freshwater fish and mussel biodiversity, many taxonomic groups require non-forest habitat, such as bogs, marshes, and grasslands for all or part of their life history. Increasing forest cover in areas that were historically forested (rather than in other natural habitats) can help maintain critical non-forest habitat. Furthermore, planting trees to increase tree density will not increase forest cover; rather, removing impervious or unused agricultural land may be needed to increase forest cover in developed landscapes.

Riparian buffer conservation or restoration is a common management action to improve water quality, quantity, and habitat [93] and is perhaps most often used for removing pollutants from runoff [94]. Surprisingly, we found that changes to riparian land cover (increased natural riparian land cover at the local scale, decreased riparian impervious cover throughout the watershed) did not show large potential to combat the impacts of climate change in isolation, though they did further contribute to species assemblage restoration when used alongside the other management scenarios. Encouragingly, many vulnerable species had a positive relationship with natural riparian vegetation and a negative relationship with riparian imperviousness (results not shown); however, the magnitudes of those relationships were less than the positive relationship with the watershed-wide forest variable. While high natural land cover and lower impervious cover within the riparian area have been found to be related to biotic integrity [95], studies that have compared land cover scales have found that larger (i.e., watershed) scales have stronger relationships with biota than local land cover [84,96]. Studies have found that benefits of riparian buffer vary based on the type of buffer, the desired goals, and the surrounding watershed [93,97]. For example, wooded and wetland buffers were found to have some of the greatest benefits towards water quality and habitat ecosystem services compared to grass buffers [97]. Our results combined with other findings in the literature point to the importance of carefully designing a riparian restoration, rather than implementing a 'one-size-fits-all' approach, and combining it with watershed wide management.

The large scale of our analysis may have prevented a strong signal from being observed from the impervious scenario in isolation. An overwhelming majority of the riparian % impervious values were less than 5%, so in most watersheds in our study, setting this value to zero would not have changed the outcome dramatically. Large changes may have been observed in a few highly urbanized watersheds; however, at the regional scale, a change in the probability of occurrence outcome for a few watersheds out of thousands would not have made an appreciable difference in the results. A follow up analysis could apply our models to urban watersheds specifically to test whether restoring riparian impervious cover to natural vegetation in urban areas could result in greater impacts to biota than shown here.

Dam removal is increasingly employed throughout the northeastern United States for restoring stream ecosystems [45], although studies documenting biotic responses remain limited [98]. Dam removals restore longitudinal stream connectivity, which has been shown to benefit migratory (e.g., [99,100]) and non-migratory (e.g., [101]) fishes, along with freshwater mussels that rely on these host fishes [102]. Dam removal can also restore water quality (e.g., reduced temperatures) and habitat (transitioning from lentic to lotic habitat), indirectly benefitting certain biota (e.g., lotic taxa; [101]), although there can be mixed responses depending on the species and timeframe [103]. Surprisingly, we found that reducing dam densities had little impact in isolation on any of the fish or mussel biodiversity groups. Our analysis likely missed positive impacts of dam removal due to the focus on the full fish assemblage such that the species that benefit most from dam removal were evaluated along with other species that benefit or are less harmed by dams. Additionally, we did not evaluate many of the diadromous species in the Northeast most harmed by dams (and thus with the greatest potential to benefit from their removal), such as river herring (Alewife and Blueback Herring (*Alosa aestivalis*)) or American Shad (*Alosa sapidissima*). At the regional scale, consideration of diadromous species may have been needed to show a positive impact of dam removal, whereas local impacts of dam removal to the resident fishes analyzed here may be missed these benefits. While increased connectivity can potentially improve mussel dispersal via host fishes [104], dam removal can also unintentionally harm freshwater mussels due to the upstream dewatering of the impoundment, loss of flow refugia downstream, and increased sedimentation downstream [105–107]. Thus, it is possible that the positive and negative effects of dam removal can offset each other and limit regional scale responses. Another important consideration is that in this study, an increase in probability of occurrence could reflect improvement in a species' current habitat, or it could represent an increase in stream habitat suitability in watersheds where that species is rare. In the latter case, future studies could evaluate the likelihood of species being able to disperse into watersheds based on connectivity and species-specific mobility following dam removal.

The combination of management scenarios restored freshwater mussel groups to baseline levels and provided additional restoration to the coldwater and fluvial specialist fish groups, although they did not recover fully to baseline levels. Incorporating multiple management actions can together benefit the full suite of vulnerable species. The management actions considered here may also impact biotic assemblages indirectly through their impacts to water quality (e.g., [108]), quantity (e.g., [109]), and temperature [110] —yet we did not incorporate these interactions in our models—suggesting the land-cover-based management scenarios may have more ability to offset climate change impacts than shown here. Future studies could build upon our framework by considering other management interventions such as groundwater pumping and stormwater management. Additionally, future studies may focus on small regions and select management actions that are location specific (i.e., impervious removal in urban areas). Finally, future studies may investigate the impacts of these management interventions on individual species, rather than on species guilds to identify species-specific differences and the value of each intervention on certain fish or mussel species.

5. Conclusion

Climate change is projected to exacerbate the stresses on already vulnerable groups of freshwater fishes [111] and mussels [75]. While climate driven impacts to streamflow and temperature regimes are beyond the control of habitat managers, we show that land-use-based habitat restoration or conservation decisions can help offset some of the negative impacts of climate change. In particular, we found that in isolation, increasing watershed-wide forest cover had the most potential to offset climate change impacts at large scales, more so than dam removal and riparian (floodplain) restoration, two common habitat restoration techniques. Overall, the combined scenario - restoration of forest cover where appropriate throughout watersheds together with local restoration techniques, including dam removal and riparian restoration, may offer the best opportunity to offset adverse climate change impacts to freshwater mussel and fish biodiversity. Managers can use the findings of this study to inform efforts for land conservation and habitat restoration in addition to the traditional riparian restoration projects.

Supporting information

S1 Text. Supplemental text, figures, and tables for the manuscript watershed forest cover and habitat restoration can offset some negative impacts of climate change on freshwater fishes and mussels. This appendix provides additional description, data, and results on the modeling validation methods, model performance, mussel host fish citations, mussel group assignment citations, and the mussel model results.
(DOCX)

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Author contributions

Conceptualization: Jennifer B. Rogers, Graziella V. DiRenzo, Allison H. Roy, Jason Carmignani, Rebecca M. Quiñones, Todd Richards.

Data curation: Jennifer B. Rogers.

Formal analysis: Jennifer B. Rogers.

Funding acquisition: Graziella V. DiRenzo, Allison H. Roy, Rebecca M. Quiñones.

Methodology: Jennifer B. Rogers, Graziella V. DiRenzo, Allison H. Roy, Jason Carmignani, Rebecca M. Quiñones.

Project administration: Graziella V. DiRenzo, Allison H. Roy.

Software: Jennifer B. Rogers.

Supervision: Graziella V. DiRenzo, Allison H. Roy, Rebecca M. Quiñones.

Visualization: Jennifer B. Rogers.

Writing – original draft: Jennifer B. Rogers, Rebecca S.M. O'Brien.

Writing – review & editing: Jennifer B. Rogers, Graziella V. DiRenzo, Allison H. Roy, Jason Carmignani, Rebecca S.M. O'Brien, Rebecca M. Quiñones, Todd Richards.

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