Double trouble for native species under climate change: Habitat loss and increased environmental overlap with non-native species

Running title: Climate Change Amplifies Native Species' Risk

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Abstract.

Climate change and biological invasions are affecting natural ecosystems globally. The effects of these stressors on native species' biogeography have been studied separately, but their combined effects remain overlooked. Here, we develop a framework to assess how climate change influences both the range and niche overlap of native and non-native species using ecological niche models. We hypothesize that species with similar niches will experience both range reductions and increased niche overlap under future climates. We evaluate this using the invasion of smallmouth bass (*Micropterus dolomieu*) and northern pike (*Esox lucius*), and the native salmonids redband trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) in western North America. Future climate conditions will reduce habitat suitability for native and non-native species, but an increased niche overlap might exacerbate negative effects on native fish. Our framework offers a tool to predict potential species distribution and interactions under climate change, informing adaptive management globally.

Keywords: Biological invasions, salmonids, stream networks, ecological niche, rivers, Smallmouth bass, Northern pike, Trout.

Introduction

Global freshwater biodiversity has been disproportionately threatened by climate change and the introduction of non-native species (Parmesan & Yohe, 2003; Sala et al., 2000). Yet, many uncertainties hinge on complex interactions between climate change and biological invasions (Simberloff et al., 2013), particularly when the ecological niches of native and non-native species overlap (García et al., 2020). Ecological niche is defined as an n-dimensional hypervolume that describes the environmental conditions required for a species to thrive (Hutchinson, 1957). Ecological niche models based on the concept of Hutchinson's duality have been used extensively for predicting risks of invasion and climate change by quantifying niches based on the relationships between species distributions and environmental factors (Escobar et al., 2016). Climate change influences the invasion risks and opportunities for non-native species across ecosystems **(Fig. 1)**. It also affects native species and their habitats via climate-induced niche shifts and range expansions (Atwater et al., 2017; Cunze et al., 2018; Liu et al., 2023a; Manzoor et al., 2020; Sadir & Marske, 2023). It is still unclear how climate-induced changes may influence the overlap of environmental niches for native and non-native species (Strubbe et al., 2015). These changes in environmental niche overlap could also be expressed as shifts in geographic distributions and thus affect potential ecological interactions between native and non-native species.

Elucidating species dynamics in environmental and geographic spaces is crucial for predicting potential invasion outcomes and the conservation of native biodiversity under climate change. Geographic space refers to the spatial representation of physical habitats that species inhabit, whereas the environmental space corresponds to a set of environmental variables representing the ecological niche of a species (Peterson et al., 2011). Environmental space (a.k.a. niche space) can be estimated using ecological niche models (ENMs) that associate environmental variables with observed species occurrences (Cooper & Soberón, 2017). Non-native species often have spatial overlap in their geographic distribution with native species(Escoriza et al., 2021; Freed & Cann, 2009; Guo et al., 2012; Jan et al., 2023) which often leads to the intersection of their ecological niches, indicating potential species interactions (Bradley et al., 2014; Jan et al., 2024.). Over time, the evolving niche dynamics can lead to antagonistic relationships between native and non-native species such as competition or predation that can result in population declines and ultimately, the local extirpation of native species (Haubrock et al., 2020).

Factors such as invasion history, dispersal barriers, and species interactions have long influenced the geographic distribution of non-native species (Rato et al., 2024). However, with the forecasted rapid changes in the global climate, these species may also experience shifts in their environmental niches, i.e., the range of conditions and resources they can utilize. As climate change continues to alter these environmental conditions and biotic interactions, species may expand, contract, or shift their realized niches (Escobar et al., 2016; Liu et al., 2023b) (**Fig. 2**). Understanding how climate change affects these environmental niches and, consequently, the geographic distribution of species, is crucial for predicting future ecological interactions between native and non-native species (Rejas et al., 2023).

Here, we use a simple framework (**Fig. 2**) to evaluate how climate-induced changes might differentially affect the niche overlap between native and non-native species under climate change and provide insights on predicting ecosystem vulnerability to biological invasions. In this study, we use the term 'environmental niche' as a proxy for the multidimensional representation of environmental attributes influencing species distributions. While not encompassing the full complexity of the true ecological niche, this approach provides a practical framework for projecting potential distributional changes under future conditions. We illustrate our framework using the ongoing invasion of smallmouth bass (*Micropterus dolomieu*) and northern pike (*Esox lucius*) on the native habitats of redband trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) in western North America. These non-native species are top predators in their native ranges and have negatively affected native salmonids in invaded systems (Jalbert et al., 2021a;

Rubenson & Olden, 2020). First, we examine and contrast the environmental niche overlap among these native and non-native species at present and under a future scenario (2070; SSP2-Shared Socioeconomic Pathway 2-4.5) of climate change. Then, we explore how climate-induced shifts in environmental niches are expressed as geographic distributions and overlap among these native and non-native species.

We hypothesized that species with similar environmental niches will exhibit differential geographic overlap in the future. This is because non-climatic environmental factors, such as geophysical templates, may act as additional filters, restricting the use of novel habitats in stream networks. For example, climate change could not only reduce geographic habitat overlap in downstream areas by diminishing habitat suitability (e.g., warmer streams), but also drive both native and non-native species towards similar upstream cold-water refuges potentially increasing species interactions. Climate change, therefore, poses a dual challenge for native species including the increasing risk of losing habitat suitability as well as, increasing the risk of negative interactions with non-native species (e.g., predation and competition). Effective freshwater conservation necessitates targeted policy considerations to achieve biodiversity conservation goals and support ecosystem services that communities worldwide rely upon (Flitcroft et al., 2023). This comprehensive analysis of geographic and environmental dynamics offers critical insights for anticipating and adapting management strategies to the shifting interactions between native and non-native species.

Material and Methods

Occurrence data for native and non-native species

We aggregated presence records for both native and non-native species from diverse datasets. Specifically, for smallmouth bass and northern pike, we acquired presence records from the

Global Biodiversity Information Facility (GBIF) within their native ranges from regions such as the Great Lakes, Ohio, and Upper Mississippi basins (HUC 2-digit watersheds; regions 4, 5, and 7) to calibrate our models. The occurrence data from portions of the native range effectively captured the ecological niches of the species, as evidenced by the Gaussian responses observed for all environmental variables. These responses included clear lower and upper limits, as well as optima for each variable, consistent with the theoretical expectations of niche representation (Peterson et al., 2011). Subsequently, we used data from the Pacific Northwest Region (PNW) region (HUC 2-digit watershed; region 17) for model validation. Occurrence data for redband trout and bull trout were sourced from the Oregon Department of Fisheries and Wildlife, Pacific States Marine Fisheries Commission, and GBIF within the Columbia River basin in the PNW. To ensure data quality, we screened all occurrences for potential errors related to any unknown or assumed datum, duplicates, and ambiguous references. Records with geographic uncertainty exceeding 100 m were excluded from our analyses. Please, see the data availability section for more information. URLs of the occurrence data for all species can be accessed at https://doi.org/10.5061/dryad.w0vt4b935.

Environmental variables

Recent literature advocates for the integration of landscape-scale network and climatic variables with spatially continuous reach-scale topographic stream variables for robust ecological niche modeling within stream networks (Jan et al., 2023). We integrated a suite of climatic, topographic, and network variables identified as key determinants of fish distribution at the basin scale (**Fig. 6**). Stream networks were extracted from the foundational layers of the national hydrography dataset (NHDPlus High Resolution), whereas current and projected climatic variables sourced from the WorldClim Version 2 database(Fick & Hijmans, 2017) at 30 seconds (~1 km2) spatial resolution, were augmented with topographic and network variables at reach scale. We filtered the base hydrography layer from the NHDPlus High Resolution dataset to include only natural flowing water bodies (e.g., stream/river; FCode 33400). Additionally, we applied a flow threshold to retain only streams with a minimum discharge of 0.1 $m^3 s^{-1}$, ensuring the analysis focused on ecologically relevant flow conditions. A detailed methodology of stream network delineation using ArcGIS Pro has been published elsewhere (Jan et al., 2023). Selection of candidate variables was guided by their ecological significance, inter-variable correlations, and their influence on principal components and model performance upon multiple iterations. Variables exhibiting Pearson's correlation coefficients exceeding 0.7 were excluded from the analysis, following recommendations by Dormann et al. (2013). All environmental parameters were assigned to spatially continuous 1-km stream segments using ArcGIS Pro version (3.2.2).

For the future environmental variables in 2070, we assumed that topographic and network variables will remain constant, whereas climatic variables were obtained from future climate projections. Our models used the MRI-ESM2-0 (Meteorological Research Institute Earth System Model version 2.0) General Circulation Model (GCM) within the moderate climate change scenario SSP2-4.5 (Shared Socioeconomic Pathway 2-4.5) to develop our final models. The SSP2-4.5 scenario portrays a future scenario where global society adopts measures to combat climate change through the implementation of emission reduction policies, transitioning towards cleaner energy sources, and embracing sustainable practices. The selection of the MRI-ESM2-0 GCM was predicated on its superior spatial resolution compared to alternative GCMs, providing enhanced capabilities for evaluating regional climate attributes and implications. Moreover, this GCM closely aligned with the average temperature and precipitation projections for the Pacific Northwest (PNW) region as outlined in the sixth IPCC report (Roger and Mauger, 2021).

Extraction of stream networks: Modelling approach

Geographic space

Our model selection approach was informed by recent research that evaluated various model types based on their performance metrics, with the top-performing model identified as an ensemble of tuned individual models (Valavi et al., 2021). Notably, down-sampled Random Forest (RF), tuned Maximum Entropy (MaxEnt), and Boosted Regression Trees (BRT) emerged as the top performers in our analysis. In this investigation, we employed an ensemble comprising tuned MaxEnt, BRT, and down-sampled RF models to forecast potential habitat suitability for both native and non-native species. By aggregating suitability scores from MaxEnt, BRT, and RF models based on their Area Under the Curve (AUC) scores, we aimed to enhance predictive accuracy. Given that smallmouth bass and northern pike are non-native species in the PNW, our models were calibrated using data from part of their native ranges before being spatially transferred to the western North America (HUC- region 17) and temporally projected to the future (2070). This enabled us to capture the ecological breadth of non-native species and mitigate the risk of underestimating habitats vulnerable to invasion in western North America. For redband trout and bull trout, models were developed using data in their native ranges and subsequently interpolated to the entire region for both current and future scenarios. To define potentially suitable areas, we applied a threshold to the model output, retaining weight-averaged suitability values above the lower quartile. This thresholding can be thought of as the 25% training percentile in MaxEnt, accounting for a 25% margin of error in occurrence records. This assumption posits that 25% of occurrence records within the least suitable habitats may not represent regions representative of the species' overall habitat. R scripts for ensemble distribution models of all species can be accessed at https://doi.org/10.5061/dryad.w0vt4b935.

Environmental (Niche) space

To evaluate the overlap between native and non-native species, we utilized the Ellipsenm R package, which quantifies niche overlap in environmental spaces as ellipsoids using the Jaccard index. Modelling ecological niches as ellipsoids in multidimensional space is an approach supported by physiological data. The Jaccard index (J) measures the similarity between two sets by calculating the ratio of their intersection to their union. In the context of ecological niche modeling, this translates to the ratio of the intersection to the union of two environmental niches. The Jaccard index ranges from 0, indicating no overlap, to 1, indicating complete overlap. In this study, we assessed the overlap of environmental niches between native and non-native fish species within their respective environmental spaces. Specifically, we estimated the ecological niches for smallmouth bass and northern pike using occurrence data from both their native habitats and invaded ranges, offering a comprehensive view of their ecological breadth. Conversely, the niche estimation for redband trout and bull trout was based solely on occurrence records from their native ranges under the assumption that these species have likely reached their ecological and geographic limits in their native environments.

To estimate the environmental niches of both native and non-native species, we used environmental variables associated to 1000 stream reaches with the highest suitability scores. The robust performance of our ensemble models, as indicated by high Area Under the Curve (AUC) scores, instilled confidence in our niche estimations using variables associated with the top 1000 highly suitable stream reaches. Comparing the niche estimated from species presence data with that derived from the 1000 stream reaches with the highest suitability scores revealed no significant disparities. In projecting niche estimations for the future, we adopted a similar methodology by using the variables associated with the first 1000 stream reaches with the highest suitability scores. Our rationale for this approach was that even under adverse climatic scenarios induced by climate change, if the species were to persist, these 1000 stream reaches would present the highest likelihood of occupancy. During niche estimation within the environmental space, we excluded the lower quartile, representing the 25% least suitable niche space, to enhance the reliability of using environmental conditions that accurately reflected species preferences. This refinement aimed to improve niche estimation by focusing on stream reaches with the highest probability of occupancy in the future.

Our approach to estimating future distribution of species was grounded in the environmental associations of their current distribution, operating under the assumption of niche conservatism. However, it is important to note that the environmental niche derived from future distributions should not be interpreted as a definitive 'future niche', rather a multidimensional representation of the environmental attributes associated with future distribution. The primary objective of our study was to develop environmental spaces from the variables linked to both present and projected future distribution of species (**Fig. 6**) and to examine the degree of overlap between the environmental spaces for native and non-native species. The focus was on understanding how climate-induced changes in these overlaps might influence ecological interactions between native and non-native species, rather than asserting absolute predictions of the future niche or contributing to the already inconsistent use of terminologies in the field (Peterson & Soberón, 2012; Warren, 2012). R scripts for niche overlap analysis can be accessed at https://doi.org/10.5061/dryad.w0vt4b935.

Results

Environmental niches of native and non-native species

The niche overlap between native and non-native fishes **(Fig. 3)** will change under a future projected moderate climate scenario (SSP2-4.5, i.e., Shared Socioeconomic Pathway 2-4.5) compared to present conditions. In all our native/non-native species paired comparisons, except for non-native smallmouth bass and native bull trout, the niche overlap increased. Elevation, slope, flow velocity, and temperature variables (e.g., maximum temperature of the warmest month and minimum temperature of the coldest month) were important determinants of niche size for these species (**Figs. S2 and S3**). The niche dynamics analysis showed varying niche sizes among species in the future (**Tab. S1**). Specifically, the niche size of the native bull trout is expected to shrink whereas it will increase for the native redband trout. Temporal changes in niche size occurred despite the overall contraction of the geographic ranges for these native species (**Figs. 4 and 5**). The predicted future reduction of the bull trout's niche is attributed to its confinement to higher elevations. In contrast, redband trout will face a net loss of suitable habitats, but its future distribution is expected to encompass greater environmental heterogeneity compared to current conditions, explaining the anticipated increase in its niche size. Additionally, the niche sizes of smallmouth bass and northern pike will increase slightly in the future, facilitating the expansion and further spread of suitable habitats across our study region (**Figs. 4 and 5**).

Geographic distribution of suitable habitats for native and non-native species

Our analyses indicate a substantial range overlap between native and non-native fishes with shifts toward higher elevations in the future (**Figs. 4 and 5**). All species are expected to experience reductions in habitat suitability over time, except for smallmouth bass. The future projected distribution of suitable habitats showed a notable shift towards higher elevation areas with colder stream temperatures for northern pike and, to a lesser degree, for smallmouth bass. This altitudinal range expansion may increase the risk of sympatry with native salmonids. Streams with similar topographic and climatic attributes therefore will potentially represent convergence zones, likely increasing the risk of ecological interactions between these species.

For native redband trout and bull trout, as well as non-native northern pike, habitat suitability will decline, particularly at lower elevations (**Figs. 4 and 5**). In contrast, habitat suitability for non-native smallmouth bass at lower elevations is expected to remain unchanged and may even improve at higher elevations. This shift in habitat suitability for these native and non-native fishes explains the observed decrease in niche overlap between bull trout and smallmouth bass. Further, the increase in environmental heterogeneity associated with the future distribution of redband trout will increase its niche overlap with smallmouth bass and northern pike. Statistically significant differences in niche overlap, when compared to null distributions, underscore that habitat ranges will vary according to species-specific preferences (Figures S4 and S5 in the supplementary material).

Every major basin in our study region contained suitable habitats for the non-native smallmouth bass (**Fig. 4**). Under the future climate scenario, a substantial gain in habitat suitability for this non-native species will occur in middle and higher order streams (**Fig. S6.6**) including the upper Columbia, Puget Sound, Southern Oregon coast, Upper Snake, and Pend Oreille. A slight decline in habitat suitability for smallmouth bass is predicted for the Willamette

River basin. Presently, the range overlap between smallmouth bass and redband trout occurred mainly in the Upper Columbia, Spokane region, Lower Snake, Clearwater, Deschutes, and John Day sub-basins. However, climate change will significantly reduce this overlap, primarily remaining in the Middle Snake and Pend Oreille areas. Similarly, the present range overlap between smallmouth bass and bull trout occurred primarily in Pend Oreille, Spokane region, Kootenai, and Upper Columbia sub-basins; but it is projected to shift in the future limited to the Upper Columbia and Kootenai sub-basins. The range overlap between smallmouth bass and redband trout will decrease by 55% in the future, with a shift southward and eastward to higher elevations (average increase of 200 m). The range overlap between smallmouth bass and bull trout will also decrease by 73% in the future, shifting northward and eastward to higher elevations (average increase of 98 m).

The present range of the non-native northern pike was located primarily in eastern Washington and Oregon and northwestern Idaho and Montana (**Fig. 5**). Contrary to general expectations for invasive species, there will be a reduction in future habitat suitability for this species, especially in middle and higher order streams (**Fig. S6.6**). Lower order streams in the upper Columbia, Kootenai, Pend Oreille, Spokane, Clearwater rivers, and the mainstem of the Snake River sub-basin will maintain suitable habitats in the future (**Fig. 5**). Conversely, in the northern regions of the upper Columbia and upper Kootenai sub-basins there will be an increase in habitat suitability. Currently, range overlap between northern pike and redband trout occurred in the Upper Columbia, Pend Oreille, Spokane, Lower Snake, John Day, and Deschutes sub-basins. This overlap is expected to persist in the future, albeit with fewer streams supporting both species. Several areas at higher elevations in Kootenai, Upper Columbia, and Pend Oreille sub-basins were projected to become suitable for both species in the future. Similarly, range overlap between northern pike and bull trout occurred mainly in the Upper Columbia, Kootenai, Pend Oreille, and Spokane sub-basins, with some scattered areas in the Clearwater and Salmon basins. This overlap is expected to be restricted to the northern portions of the Upper Columbia and Kootenai basins in the future, primarily due to the reductions in habitat suitability for bull trout in other basins. The range overlap between northern pike and redband trout will decrease by 79% in the future, with a shift northward and westward to higher elevations (average increase of 102 m). The range overlap with bull trout will also decrease by 83%, shifting northward and eastward to higher elevations (average increase of 112 m).

Discussion

We demonstrate that climate change can lead to the expansion or contraction of ecological niches, affecting the availability and quality of suitable habitats for both native and non-native fishes. Our framework contextualizes observed shifts in environmental niches showing increases and decreases in range overlap among species which could result in unexpected outcomes for native species. Changes in ecological niches due to climate change have been observed across ecosystems (Walther et al., 2002) with consequences for niche overlap between native and non-native species (Bradley et al., 2014; Sorte et al., 2010). One possible outcome of decreasing habitat suitability due to climate change is to push species to occupy the habitats that will remain suitable for them in smaller geographic areas resulting in an increased environmental overlap. These climate-induced changes to niche overlap between native and non-native species will likely result in altered ecological interactions (Alexander et al., 2016).

Our model projections indicate a decline in habitat suitability for native salmonids. These species are particularly vulnerable to habitat loss due to rising river temperature and altered flow regimes (Beechie et al., 2013), but see (Armstrong et al., 2021). The habitat ranges of cold-water-dependent salmonids are anticipated to shrink drastically in the future (Isaak et al., 2012). Although suitable habitats for the non-native northern pike will be reduced too, mainly in mainstems and major tributaries, adequate habitats are expected to persist in some areas of the upper Columbia. Additionally, an increase in habitat suitability is foreseen in the northern regions of the upper Columbia and upper Kootenai sub-basins. Given the warm water tolerance of smallmouth bass their geographic range is expected to expand under anticipated climate change scenarios as shown in other studies (Carey et al., 2011; Rubenson & Olden, 2020; Winkowski et al., 2024). These changes threaten the viability of native salmonid populations and point to the pressing need for conservation efforts that take into consideration the evolving habitat dynamics between native and non-native species.

The geographic distribution of suitable habitats for native redband trout and bull trout, and non-native smallmouth bass and northern pike will undergo reductions under future climatic conditions, and this will be accompanied by an upward elevation shift. The resulting reduction in range overlap is primarily due to the loss of suitable habitats at low elevations and the convergence of species into colder areas upstream. These findings align with the broader literature that emphasizes the dynamic nature of species distributions in response to climate change (Carim et al., 2022; Rubenson & Olden, 2020), underscoring the importance of considering elevation shifts in conservation planning.

Climate change could pose a dual threat to native species by declining their habitat suitability and intensifying predation pressure from non-native species. Cold-water refuges in upstream areas will serve as converging zones for both native and non-native fishes, hence facilitating biotic interactions between them. Predatory interactions toward salmonids have been documented for smallmouth bass and northern pike in basins where these species are in sympatry (Carim et al., 2019; Jalbert et al., 2021b; Rubenson & Olden, 2020). The presence of smallmouth bass and northern pike in our study region represents year-round predation and competition pressures during the early life-history stages of salmonids. This increased interaction could lead to local extinctions of native salmonids similar to patterns observed in southcentral Alaska (Jalbert et al., 2021b). Thus, the dynamics between native and non-native fishes extend beyond mere habitat gain or loss due to climate change and highlights the need for integrated management strategies that address both direct and indirect effects of interactions among species.

We acknowledge the inherent limitations and assumptions associated with using ecological niche models to infer implications for species interactions stemming from future quality habitat redistribution. First, our models assume that ecological niches are ellipsoidal; an assumption that finds some support in physiological data (Cobos et al., 2020). Second, the habitat distribution maps generated by our models do not account for dispersal barriers or in the case of non-native species, any suppression or control program. These maps identify areas that could potentially offer suitable habitats for the species, contingent upon their access to them. Nonetheless, our results can inform suppression and eradication programs for non-native species by mapping their suitable habitats. Given the expansive range of these species and the limited management resources, identifying the spatial distribution of available habitats is a critical initial step in predicting the future impacts their potential geographic extent of non-native species (Jan et al., 2023). Our approach is simple and cost-effective for prioritizing habitats for the early detection and monitoring of invasive species and their potential future impacts on native species.

In conclusion, our study underscores the intricate and multifaceted impacts of climate change on the interactions between native and non-native species. By employing an ensemble of species distribution models, we demonstrated that predicted changes in climate not only degrade habitat suitability for native species, but also facilitate increased niche overlap with invasive species in some areas. This dual threat - declining habitat suitability and heightened predation pressure - poses significant challenges for the conservation of native species. Local extinctions of native species may happen not just by their inability to adapt to the predicted warming climate, but more so by heightened predation pressure from non-native species (Carim et al., 2022; Crane et al., 2015; Monroe, 2012). Our findings highlight the necessity for adaptive management strategies that account for these complex dynamics, ensuring the protection of vulnerable native species. This framework, adaptable across taxa and ecosystems, provides a robust tool for predicting and mitigating the future impacts of climate change and biological invasions on biodiversity.

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Figure 1. Map depicting species examined for ecological or climatic niche overlap to evaluate temporal distribution patterns, niche dynamics, and invasion potential. Understanding these dynamics is vital for forecasting the impacts of climate change and biological invasions on future species distributions. (a) *Pusa hispida* (b) *Phengaris arion* (c) *Hypsugo savii* (d) *Perca fluviatilis* (e) *Panthera uncia* (f) *Emberiza schoeniclus* (g) *Amazilia yucatanensis* (h) *Azolla filiculoides** (i) *Bombus ruderatus** (j) *Loxodonta africana* (k) *Ochotona sikimaria* (l) *Litoria caerulea*. More information about the systematic literature review informing this figure, which depicts the influence of climate-induced niche dynamics on future species distributions and potential interactions, is available in the Supplementary Material. Asterisks denote invasive species. All images are licensed under CC BY 4.0. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Figure 2. Conceptual framework illustrating the ‘double trouble’ for native species under future climate change. (a) In environmental space, native species' niches are predicted to contract while non-native niches expand, potentially increasing niche overlap. (b) In geographic space, native species are expected to lose high-quality habitat (red) and shift upstream, reducing overlap (yellow) with expanding non-native species (orange) at higher elevations. Alternative hypotheses, such as native expansion, non-native contraction, or increased overlap, are not shown. This figure highlights the interplay between niche contraction, habitat degradation, and distribution shifts, emphasizing the challenges native species face from both increased competition and reduced habitat availability.

Figure 3. Differential environmental niche overlap (J = Jaccard index) between native and non-native species under the present and future (2070) climatic scenarios. (a) future increase in niche overlap between redband trout and both smallmouth bass and northern pike. (b) future decrease in niche overlap between bull trout and smallmouth bass, and future increase in niche overlap between bull trout and northern pike. Except for the smallmouth bass - bull trout, increase in niche overlaps between other native/non-native pairs support our hypothesis of increased niche overlaps in future between native and non-native species.

Figure 4. Projected changes in the distribution of suitable habitats and habitat overlap for non-native smallmouth bass, and native redband trout and bull trout under present and a moderate climatic scenario in the future (2070). Panels (a), (b), and (c) depict the changes in the distribution of suitable habitats for redband trout, smallmouth bass, and bull trout, respectively, between present and future including areas that increased suitability (gain = blue), decreased suitability (loss = orange), and did not change habitat quality (unchanged = yellow). Changes in overlap of suitable habitats between present and future are shown between smallmouth bass and redband (d) and between smallmouth bass and bull trout (e). Density of overlapped suitable habitats under present and future climatic scenarios are shown between smallmouth bass and redband trout (f), and between small mouth bass and bull trout (g). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Figure 5. Projected changes in the distribution of suitable habitats and habitat overlap for non-native northern pike, and native redband trout and bull trout under present and a moderate climatic scenario in the future (2070). Panels (a), (b), and (c) depict the changes in the distribution of suitable habitats for redband trout, northern pike, and bull trout, respectively, between present and future including areas that increased suitability (gain = blue), decreased suitability (loss = orange), and did not change habitat quality (unchanged = yellow). Changes in overlap of suitable habitats between present and future are shown between northern pike and redband (d) and between northern pike and bull trout (e). Density of overlapped suitable habitats under present and future climatic scenarios are shown between northern pike and redband trout (f), and between northern pike bass and bull trout (g). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Figure 6. (a) List of variables used in ensemble distribution models and niche overlap analysis. (b) Map illustrating the study area's 2-digit hydrological units, displaying parts of the native range of smallmouth bass and Northen pike on the right and the invaded range on the left. Species occurrence data are indicated by dots, with blue dots representing Northen pike and yellow representing smallmouth bass. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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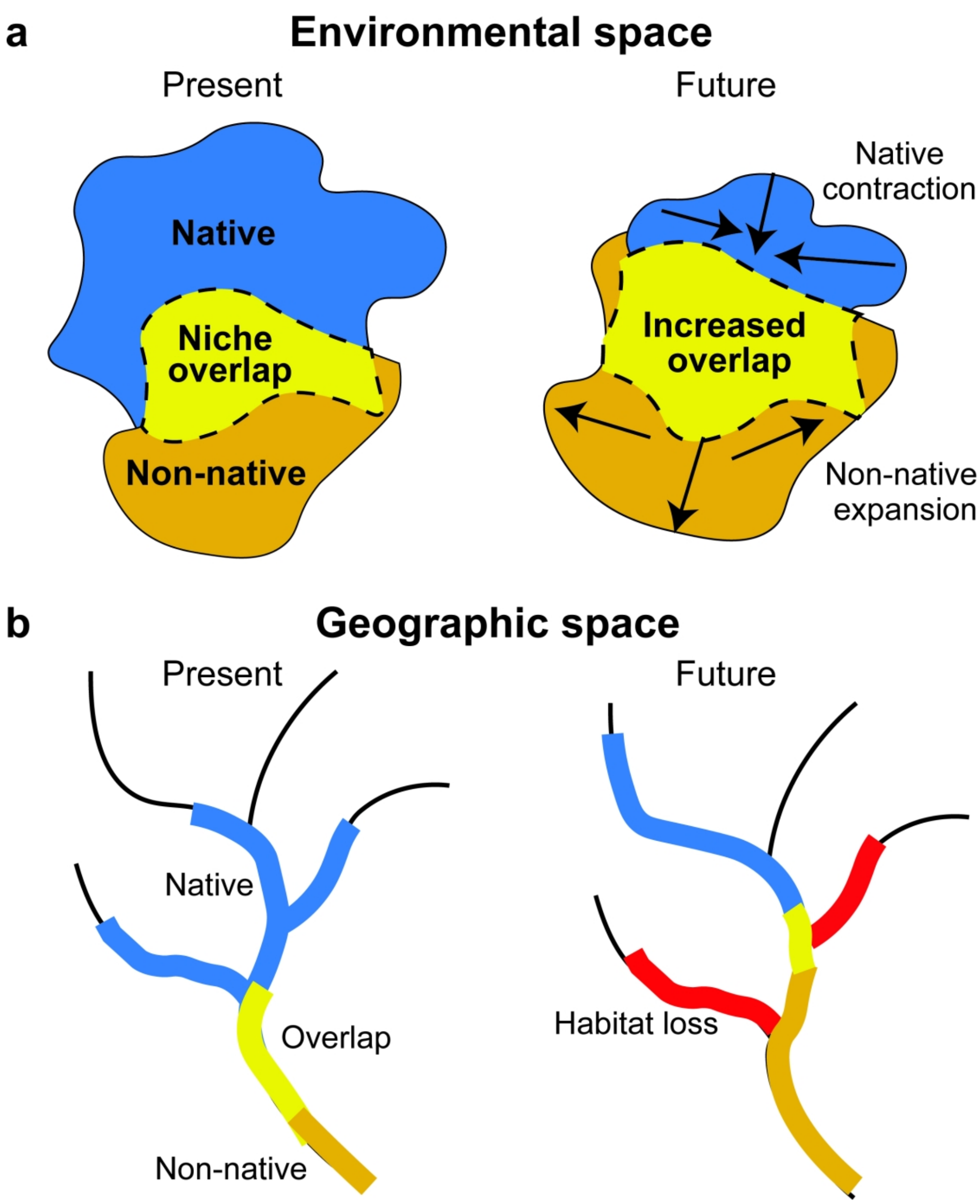

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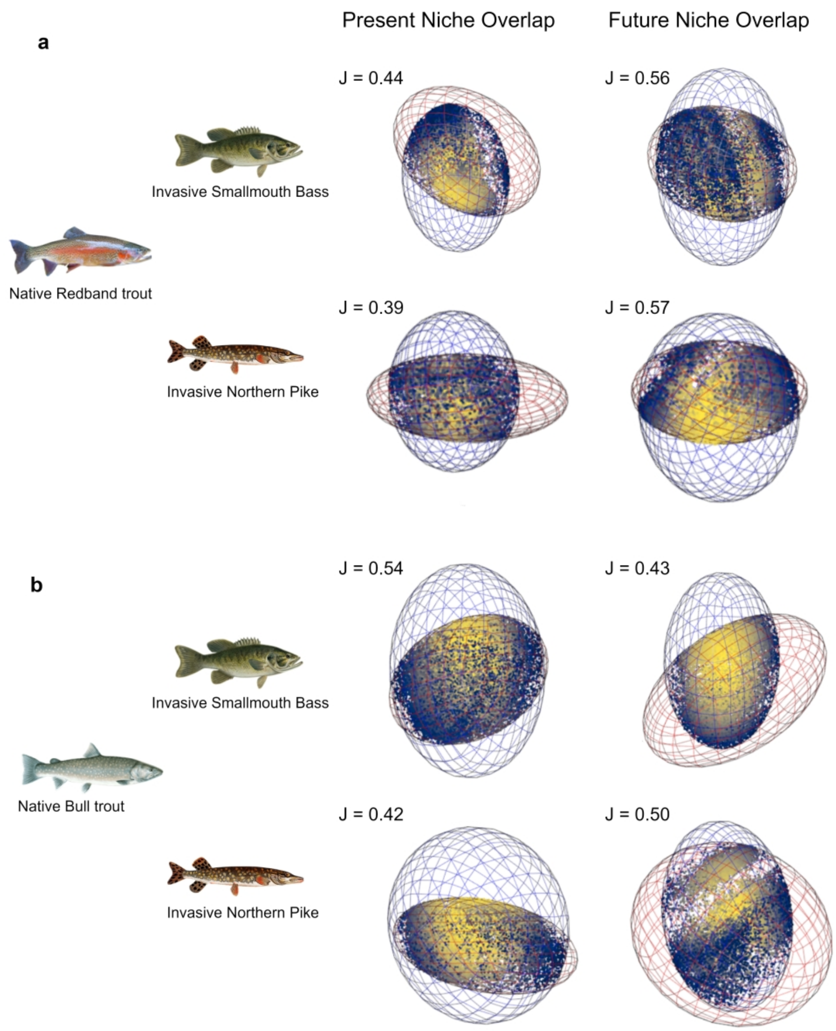

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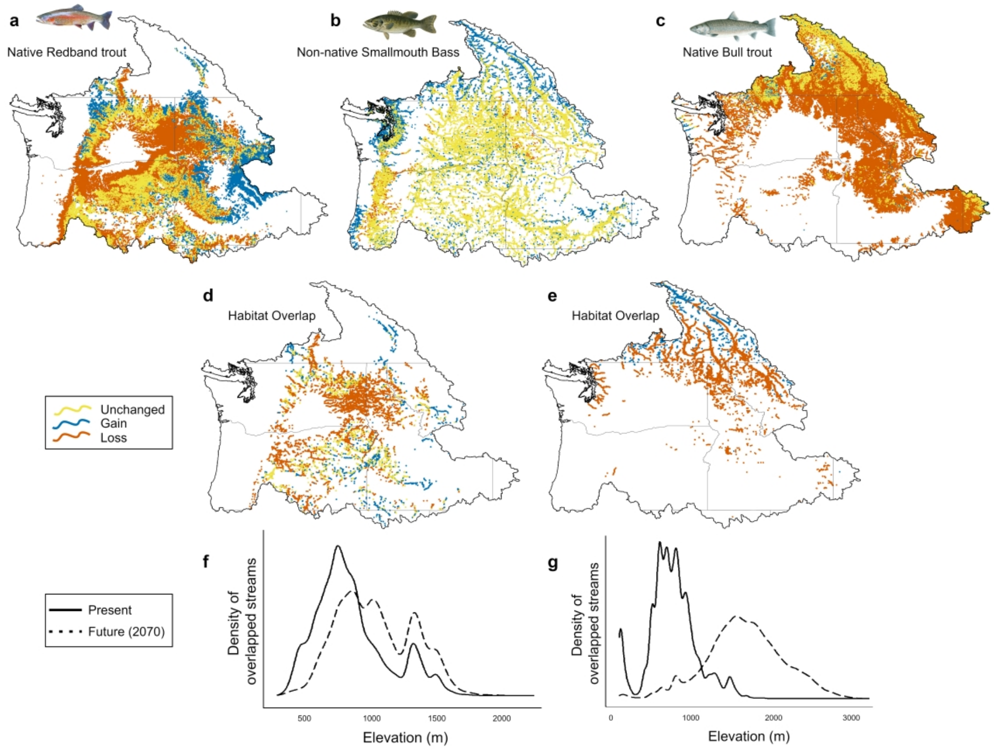

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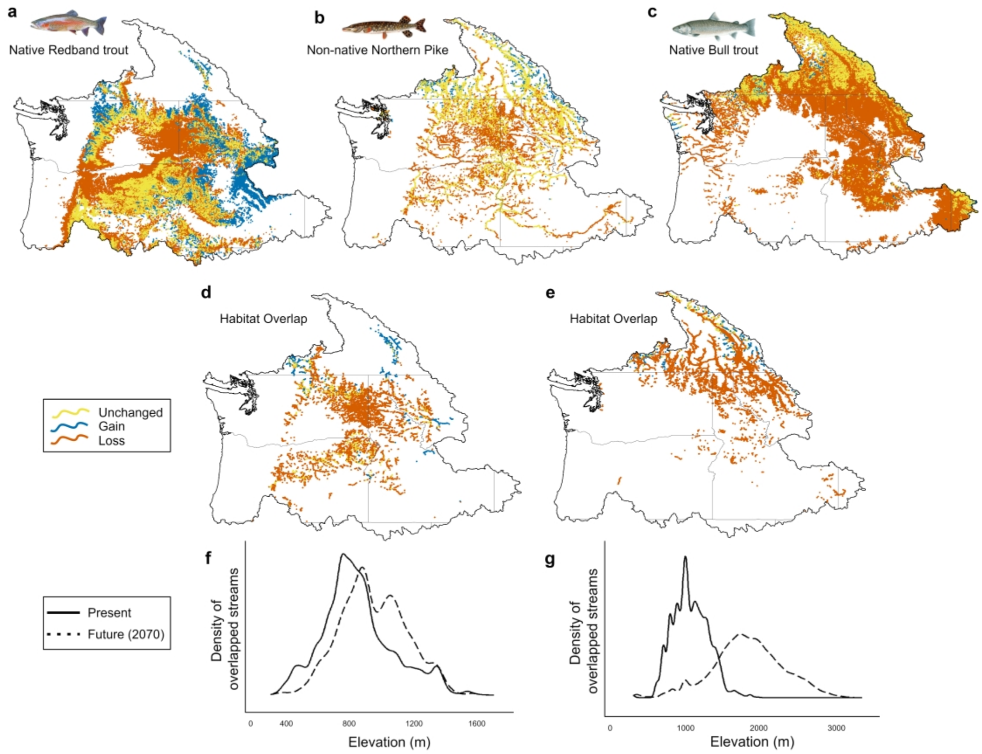

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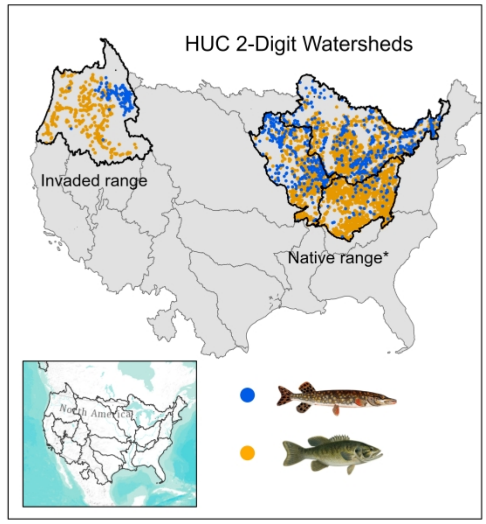
710x548mm (236 x 236 DPI)

a

Climatic	Maximum Temperature of Warmest Month
	Minimum Temperature of Coldest Month
	Precipitation of Wettest Month
	Precipitation of Driest Month
Topographic	Elevation
	Reach Slope
	Velocity
	Upstream drainage area
Stream Network	Stream Order
	Stream Level
	Headwater (Yes/No)
	Stream Terminus (Yes/No)

b



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