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

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Introduction

Global freshwater biodiversity is increasingly threatened by climate change and the introduction of non-native species (Dudgeon 2019). However, the intricate dynamics between climate change and biological invasions remain poorly understood, leading to significant uncertainties (García et al. 2020). Climate change alters the risks and opportunities for non-native species invasions and affects native species through climate-induced niche shifts and range expansions (**Fig.1**). The impact of climate change on environmental niche overlaps between native and non-native species, and the resulting geographic distribution shifts, are not fully understood. These shifts can affect ecological interactions, leading to competition or predation, and potentially result in the population decline or local extirpation of native species.

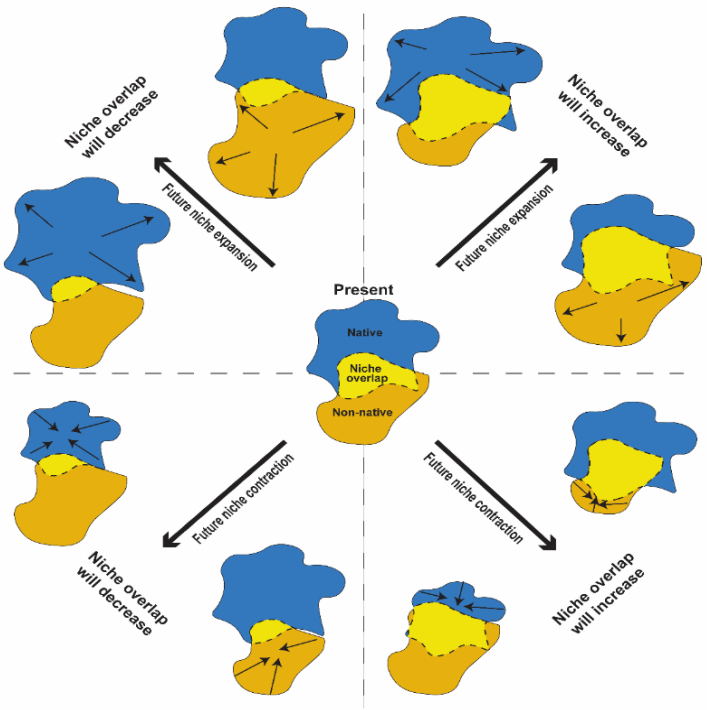

Figure 1 Conceptual diagram illustrating hypothesized changes in environmental niches and the resulting overlaps between native and non-native species in response to climate change.

Understanding species dynamics in both environmental (niche) space and geographic space is crucial for predicting invasion outcomes and conserving native biodiversity under climate change (Peterson et al. 2011). Non-native species often share geographic distribution and ecological niches with native species, indicating potential interactions (Jan et al. 2023). Over time, these interactions can lead to antagonistic relationships such as competition or predation. Climate change can cause species to expand, contract, or shift their realized niches, influenced by biotic interactions, invasion history, dispersal barriers, and other factors (Peterson et al. 2011). Forecasting how climate change will alter species' environmental niches and geographic distributions is essential for anticipating future ecological interactions.

Here we evaluate how climate-induced changes might affect the niche overlap between native and non-native species using our framework (**Fig. 1**) applied to the ongoing invasion of smallmouth bass (*Micropterus dolomieu*) and northern pike (*Esox lucius*), and the native redband trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) in western North America. By contrasting the environmental niche overlap at present and under a future climate scenario, we explore how shifts in environmental niches translate into geographic distribution and habitat overlap. We hypothesize that climate change could reduce downstream habitat quality and drive species towards similar upstream cold-water refuges, increasing interactions. This presents a dual challenge for native species, as they may encounter both habitat loss and heightened predation. Our framework can be adapted to gain critical insights for developing adaptive management strategies to address the evolving dynamics between native and non-native species.

Methods: Species occurrence data were compiled from various sources. All data were screened for errors and geographic uncertainty exceeding 100 m was excluded. Spatially continuous instream geomorphological variables were extracted for each 1km stream reach and were appended with climatic and network variables. Ensemble ecological niche models (ENMs) were used to predict the distribution of suitable habitats for native and those vulnerable to invasion by non-native species. We employed the Ellipsenm R package (Cobos et al., 2020) to evaluate environmental niche overlaps in 3D between native and non-native species, assuming ecological niches can be represented as ellipses in multidimensional space.

Results:

Niches overlap: Niche overlaps between native and non-native species **(Fig. 2)** will increase and decrease under a projected moderate future climate scenario (SSP2-4.5, i.e., Shared Socioeconomic Pathway 2-4.5) compared to present conditions. In all native/non-native paired comparisons, except for smallmouth bass and bull trout, the niche overlap increased in the future. Consequently, the risk of sympatry among these four species will increase. Streams with similar topographic and climatic attributes therefore will serve as convergence zones, likely intensifying ecological interactions between these native and non-native fishes in future.

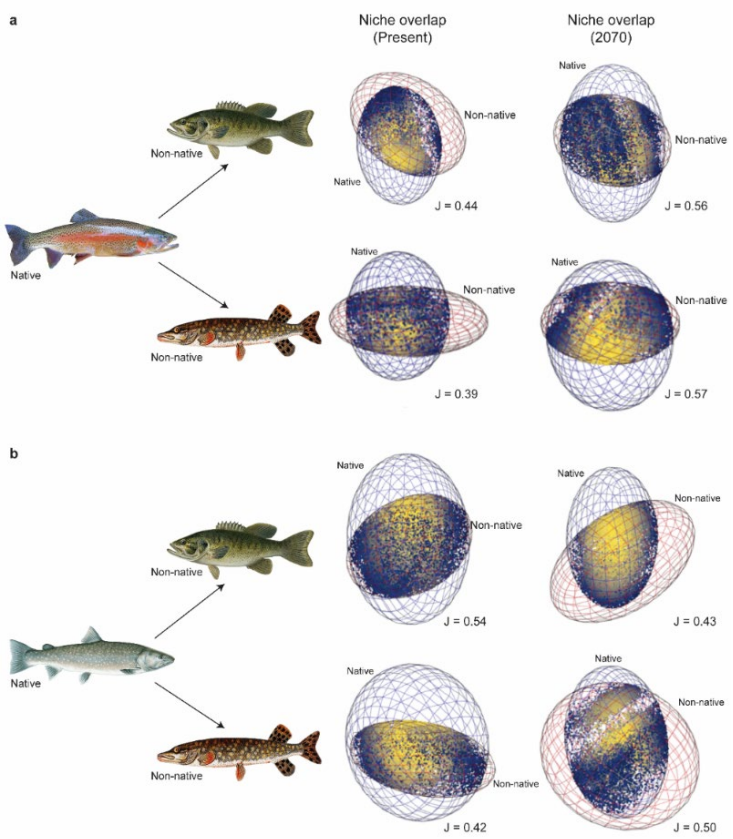

Figure 2 Environmental niche overlap (J = Jaccard index) between native and non-native species under the present and future (2070) climatic scenarios.

Smallmouth bass: Smallmouth bass will find suitable habitats in every watershed across the PNW, at least in part, and in streams of different orders. Under the moderate climate change scenario, our models predict a substantial overall gain in habitat quality for smallmouth bass in the PNW. The projected gain in habitat quality for this species is in the upper Columbia, Puget sound, Southern Oregon coast, Upper Snake and Pend Oreille. The overlap in suitable stream reaches of smallmouth bass with redband and bull trout will decrease by 55% and 73%, respectively, under future climate change scenarios. Future projections indicate an upward shift in suitable habitats, with mean elevations of streams shared by smallmouth bass and redband trout increasing from 707 meter (m) to 805 m, and with bull trout from 779 m to 980 m above mean sea level.

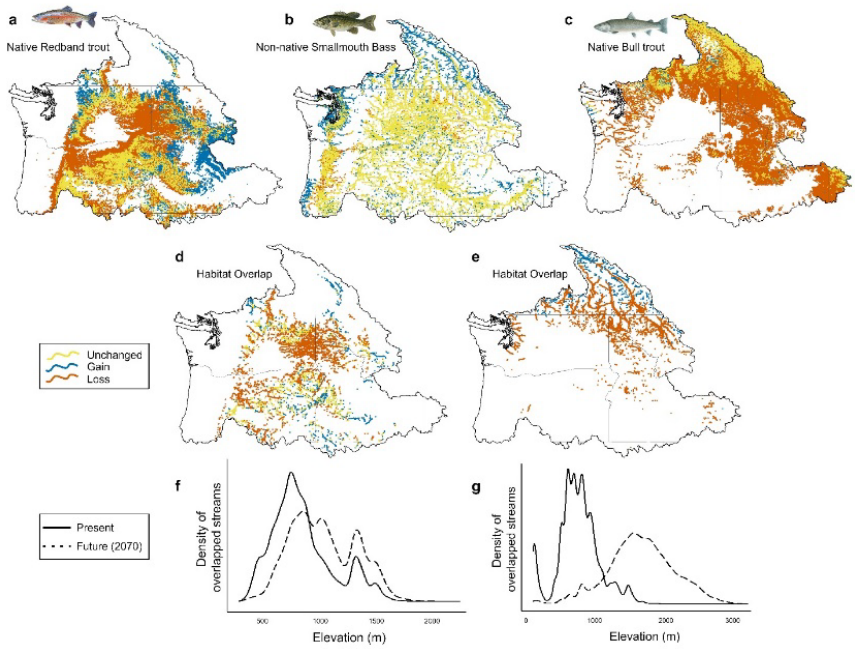

Figure 3 Projected changes in the distribution of suitable habitats and habitat overlap for smallmouth bass, and native trout.

Northern pike: Northern pike presently finds suitable habitats mostly in northeastern Washington and northern Idaho and Montana, i.e., less widely distributed compared to smallmouth bass. Contrary to general expectations for invasive species, northern pike will experience a decrease in habitat quality with climate change with most of this decline in habitat quality in the middle and higher order streams. However, the spatial overlap of northern pike with native species mirrors the overlap patterns observed between smallmouth bass and native species. The overlap in suitable stream reaches of northern pike with redband and bull trout will decrease by 79% and 83%, respectively, under moderate climate change scenario. Future projections indicate an upward shift in suitable habitats, with mean elevations of streams shared by northern pike and redband trout increasing from 762 m to 864 m, and with bull trout from 845 m to 957 m above mean sea level.

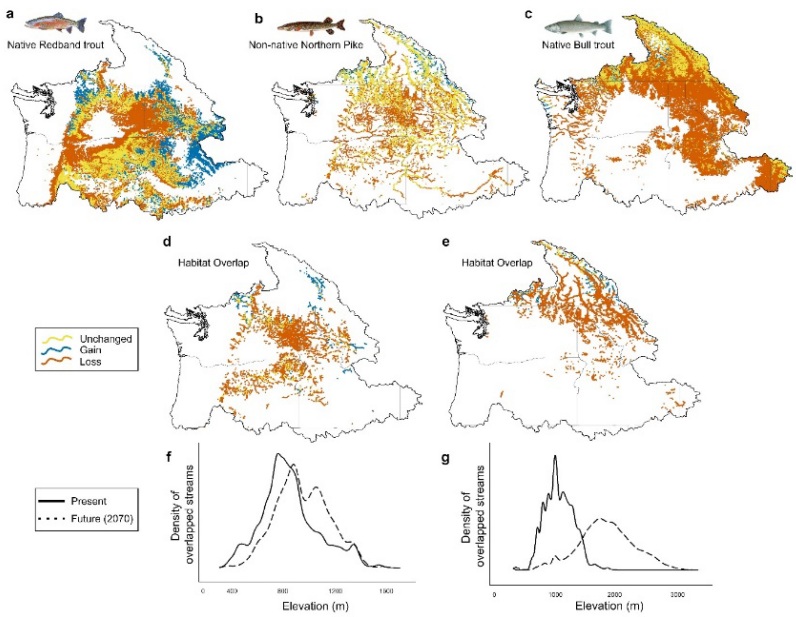

Figure 4 Projected changes in the distribution of suitable habitats and habitat overlap for northern pike and native trout.

Discussion: Presence of smallmouth bass and northern pike is a year-round predation and competition pressure during a sensitive life-history stage for salmonids. Our results indicate decreasing geographic overlap but an increasing niche overlap between native and non-native species, except for the case of smallmouth bass and bull trout. This trend suggests that the reduction of cold-water refuges due to climate warming may intensify interactions between native and non-native species. Consequently, there is likely to be a heightened predation pressure on native salmonids from these non-native predators. Climate change, therefore, in addition to exerting a direct adverse effect on native salmonids it is anticipated to increase their sympatry with non-native fishes. This increased interaction could lead to local extinctions of native salmonids in the PNW, similar to patterns observed in southcentral Alaska (Jalbert et al. 2021). Local extinctions of native salmonids may happen not just by their inability to adapt to warming temperatures due to climate change, but more so by heightened predation pressure from non-native species like smallmouth bass and northern pike. Thus, the dynamics between native and non-native fishes extend beyond mere habitat gain or loss due to climate change. Despite the loss of habitat quality for all species in this study, except for smallmouth bass, the altered and contracted distributions predicted under climate change will likely result in the severe decline of native salmonids mainly through predation by smallmouth bass and northern pike.

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Key words: Biological invasion, climate change, smallmouth bass, Northen pike, salmonids

Preference: Oral presentation (PowerPoint and projector required)