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Unveiling climatic niches for deeper insights into invasion potential and enhanced distribution models of freshwater fishes

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Abstract

Introduced species may exhibit variations in their preferred climatic niches between their native and introduced ranges, which can have important implications for the transferability of distribution models. In the Himalayan ecoregion, little is known about the geographic distribution and climatic niche overlap between native and introduced cold-water species. Here, we used the COUE (centroid shift, overlap, unfilling, and expansion) framework to explore the invasive potential of rainbow (*Oncorhynchus mykiss*) and brown (*Salmo trutta fario*) trout and corresponding climatic niche overlap with native snow trout (*Schizothorax plagiostomus* and *Schizothorax richardsonii*) in the Indus and Ganges River basins. Although we found more stability in the climatic niche for *O. mykiss* (93%) than *S. trutta* (58%), both species do not conserve their climatic niches in this region ($p > 0.05$). *S. trutta* has expanded more toward new environmental conditions (42%) compared to *O. mykiss* (7%). However, there are still available environmental gaps that *O. mykiss* and *S. trutta* can potentially occupy in the future. There was a higher overlap in climatic niches between *S. plagiostomus* and *O. mykiss* and between *S. richardsonii* and *S. trutta*. Observed shifts in climatic niches of these introduced species can negatively affect the transferability of distribution models, which may underestimate the assessments of habitat suitability for introduced trout in the Himalayas. Our study demonstrates that the information on climatic niche dynamics can inform the model-building process and improve the transferability and predictive performance to better assess vulnerability of sensitive habitats to introduced species in the Himalayas and elsewhere.

KEYWORDS
brown trout, invasion, MaxEnt, niche overlap, rainbow trout, snow trout

1 | INTRODUCTION

It is estimated that 20%–30% of freshwater fish species may face extinction in the near future due to habitat change and biological invasions (Simberloff & Rejmánek, 2011). While our understanding of invasions largely stems from successful invaders (Arismendi et al., 2014), we possess limited knowledge about failed invasions and species that have not yet become invasive. This gap in understanding likely exists, in part, due to the inherent complexity and multifaceted nature of the invasion process. For example, some introduced

species occupy different climatic niches (range of climatic conditions in which a species can thrive and reproduce) in their native compared with their introduced ranges, affecting the performance of predictive distribution models and making risk assessment difficult (Escobar et al., 2016). Understanding the niche dynamics of introduced species can offer valuable insights into their future expansion and invasion potential. Such knowledge is instrumental in proactive detection and the development of effective, long-term mitigation strategies. The absence of such information contributes to the lack of well-defined policies for managing introduced species across the globe, especially in complex mountainous areas such as the Himalayas.

The cryosphere of the Himalayas, often referred to as "the third pole," sustains extensive river networks with extraordinary fish diversity and high levels of endemism (Goettsch Mittermeier et al., 2004). Two of the most successful salmonid invaders, rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta fario*), have been introduced to this ecoregion (Olson & Dinerstein, 2002) for commercial and recreational purposes. Brown trout was introduced as early as 1928 (Ali et al., 1980; Akhtar, 1991; Peter, 1999; Sehgal, 1999; Yaqoob, 2002); on the other hand, rainbow trout was introduced in 1973 from Japan, and subsequently in 1980 from the United States (Edwards, 1991). Introduced trout species compete for space and resources with native cold-water cyprinids (Jan et al., 2023) of the genus *Schizothorax* (commonly named snow trout, which is taxonomically incorrect). They are called snow "trout" probably because both taxonomic groups have produced species complexes independently via convergent evolution with resident nature and similar ecological roles and requirements in their native ranges (Keeley et al., 2019; Regmi et al., 2020, 2021). Two vulnerable snow trout species (*S. plagiostomus* and *S. richardsonii*) appear to have a substantial spatial overlap with introduced trout in the northern parts of the Indus and Ganges River Basins (Jan et al., 2023). Nonetheless, introduced trout propagation via hatchery programmes is still ongoing in this region.

The headwater streams of Indus River have naturalised self-sustaining populations of *O. mykiss* in some watersheds such as the upper reaches of the River Panjkora and the River Swat (Jan, 2019), both tributaries of the Indus River. *S. trutta* have also become invasive in some portions of the Ganges Basin such as Asiganga, Tirthan, and Parwati (Johal et al., 2021; Sharma et al., 2021). Under the hatchery programmes in Pakistan and India, introduced trout have been stocked into streams with little regard to their impact on native species. *O. mykiss* necessitates a consistent flow of at least 25% of the base flow annually and a low gradient to establish naturalised populations. The Himalayan streams, such as those in the Kumrat Valley of the Indus Basin, with their high propagule pressure and combination of low gradient and high elevation, therefore, offer optimal habitat for the naturalisation of introduced trout. It is conceivable that introduced trout could be passing through their lag-phase before they cause an "ecological surprise," as they have already been reported to have profound impacts as invasives on native snow trout in some parts of the Himalayas (Johal et al., 2021, Sharma et al., 2021, Jan & Daniels, 2022). However, little is known about their invasion ecology, making it difficult to forecast future expansion, and decide on the best management strategies in the Himalayas.

Prevention has been argued to be the best approach to reduce the impacts of introduced species on native systems (Simberloff, 2009). Knowledge of the environmental characteristics of the native habitats, as well as those of the novel habitats, is essential to limit the negative impact of introduced species (Latombe et al., 2017). For example, ecological niche models (ENMs) can be developed in the native ranges of *O. mykiss* and *S. trutta* and transferred to the Himalayas for predicting the availability and spatial distribution of suitable habitats for these two invasive species (Jan et al., 2023). ENMs rely on the assumptions of "distributional equilibrium" and "niche conservatism," which posit that the introduced species is in environmental and geographic equilibrium in its introduced range, and that the species maintains its niche requirements across space and time (Peterson et al., 2011). However, the extent to which these assumptions are held in practice remains a topic of debate.

ENMs are based on the concept of Hutchinson's duality framework, and have been used extensively for predicting potential invasion risks by quantifying species niches based on the relationships of species distributions and environmental predictors (Escobar et al., 2016). In the process of colonising new habitats, introduced species either maintain, expand, or contract their climatic niche. Change in the climatic niche, however, does not suggest evolutionary adaptation, rather expansion of species to part of fundamental niche that currently may not be available in the native range (Guisan et al., 2014). A number of statistical tools have been used for testing niche dynamics (Broennimann et al., 2012), assumptions about niche conservation (Peterson, 2011; Warren et al., 2008), and chances of success and failure of species in introduced ranges (Escobar et al., 2016; Martínez-Meyer et al., 2013). Although no specific tool is considered ideal in all contexts, the COUE framework (a unified terminology referring to centroid shift, overlap, unfilling, and expansion) developed by Broennimann et al. (2012) and improved by Petitpierre et al. (2012) has become the recommended approach to address inquiries related to niche conservation and its spatial and temporal dynamics (Liu et al., 2020).

The success of some invasive species can partially be attributed to their ability to occupy a distinct range of environmental conditions in the introduced than its native range (Gallagher et al., 2010). Although many introduced species occupy environmental conditions that are similar to those in their native ranges (Petitpierre et al., 2012), for some species, occupancy of a distinct range of environments in the introduced range leads to greater dominance within communities (Callaway & Ridenour, 2004), colonisation of new types of habitats (Agrawal, 2001), or growth under novel climates (Broennimann et al., 2007). The gap between the climatic conditions occupied in native range versus in the introduced range makes risk assessment challenging because, in that case, ENMs may underestimate the range of habitats that the species can occupy in the introduced range.

Here, we aim to explore whether there is any shift in the climatic niches of *O. mykiss* and *S. trutta* in the Himalayas, and if so, how does that influence the estimation of spatial distribution of suitable habitats and their overlap with native snow trout habitats. Our main objectives are to determine: (a) whether *O. mykiss* and *S. trutta* have potential for future expansion and invasion in the Himalayas; and (b) whether the climatic niches of *O. mykiss* and *S. trutta* overlap with climatic niches of native snow trout species. We expected both introduced trout to occupy distinct set of environmental conditions given the differences in climate and riverscapes conditions between Himalayas and their native ranges. We also anticipated a substantial overlap in the climatic niches of snow trout and introduced trout given that both taxa have similar ecological requirements (Jan et al., 2023; Regmi et al., 2021). Examining climatic niche dynamics can provide insights into the stage of invasion and potential for future expansion, which is crucial for effective management. Knowledge of climatic niche dynamics can also inform the model-building process and improve the transferability and predictive performance of distribution models to better assess vulnerability of sensitive habitats to introduced species in the Himalayas and elsewhere.

2 | MATERIALS AND METHODS

2.1 | Datasets of species occurrences

In northern Pakistan, Hindu Kush Himalayas (Figure 1), we collected occurrence data ($n = 255$) for the snow trout *S. plagiostomus* and introduced *O. mykiss* ($n = 98$) and *S. trutta* ($n = 82$) through field sampling using scoop and cast nets every summer from 2017 to 2019. For the snow trout *S. richardsonii*, we found occurrence data ($n = 244$) in the published literature (Sharma et al., 2021), and the Global Biodiversity Information Facility (https://doi.org/10.15468/dl.m3xxse). We obtained occurrence data ($n = 1801$) for *O. mykiss* in its native range from the Oregon Department of Fish and Wildlife (https://nrimp.dfw.state.or.us/FHD_FPB_Viewer/index.html), and the Pacific States Marine Fisheries Commission (https://maps.

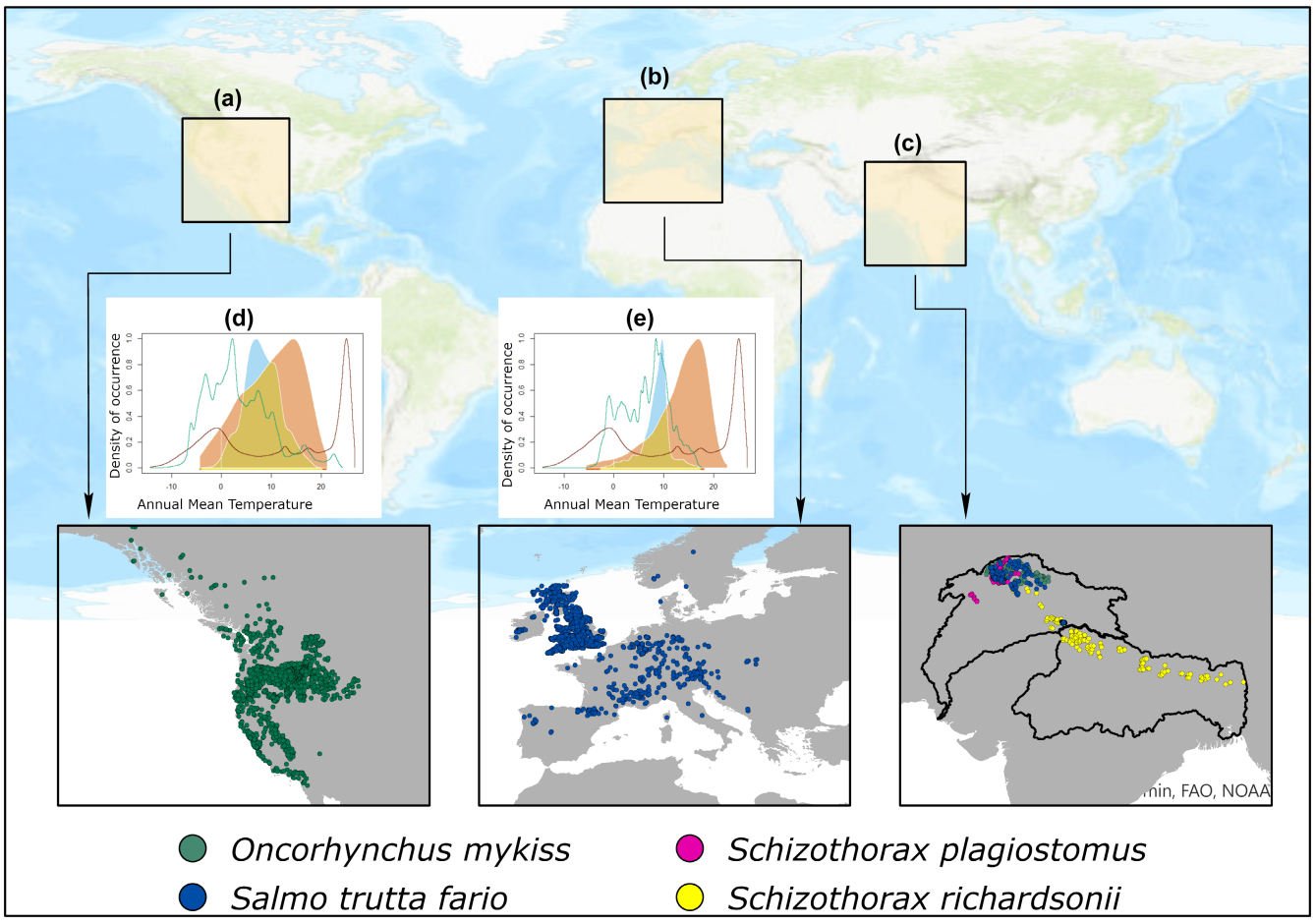

FIGURE 1 Study area map for all four species showing native and introduced ranges with species occurrences. Native ranges of *O. mykiss* and *S. trutta* are shown in panels (a,b), respectively. The native range of snow trout species and introduced range of *O. mykiss* and *S. trutta* is shown in panel (c). The Indus River Basin is situated on the left, while the Ganges River Basin is on the right. (d,e) represent the distribution of mean annual temperatures in the unfilled (blue), stability (yellow), and expansion (orange) portions of the climatic niche for *O. mykiss* and *S. trutta*, respectively.

psmfc.org/server/rest/services). Lastly, for *S. trutta*, we obtained occurrence data ($n = 2279$) in its native range from the National Biodiversity Network of the United Kingdom (https://nbnatlas.org/). We filtered occurrence data for all species to minimise potential errors associated to unknown/assumed data, duplicates, and fuzzy references (Shen et al., 2023) and discarded occurrences with geographic uncertainty >100 m.

2.2 | Bioclimatic variables

The climate has been considered an important aspect of the realised niche of species (Escobar et al., 2016; Tsai et al., 2020), but some climatic variables can have a differential sensitivity to the ordination approaches that define environmental niche spaces (Lo Parrino et al., 2023). Here, we describe PCA environmental spaces using climatic variables obtained consistently across our study regions (native ranges of *O. mykiss* and *S. trutta* and the Indus and Ganges River basins). We extracted bioclimatic variable from WorldClim database version 2 (Fick & Hijmans 2017, http://www.worldclim.org) at a resolution of 30 arc seconds (~1 km^2).

We selected bioclimatic layers based on correlations among variables ($r < .75$; Guisan et al., 2017), and their contribution to the first two components of the principal component analysis (PCA). We checked Pearson's correlation matrices among climatic variables at each ecoregion for consistency of positive or negative directions in the associations between ranges (e.g., native range of *O. mykiss* vs. introduced range in the Himalayan mountains). To select among available bioclimatic layers, we included an additional criterion to account for ecological relevance. Specifically, a year-round perspective of thermal regimes (Arismendi et al., 2013) can influence species distributions (Chesson, 2000; McMeans et al., 2020; Shimadzu et al., 2013). To account for this seasonality across temporal scales, in addition to the mean annual average of temperature (bio1), we included mean diurnal range (bio2), isothermality (quantifies how large the day-to-night temperatures oscillate relative to the annual summer-to-winter temperatures) (bio3), and temperature seasonality (annual temperature variation) (bio4) (e.g., Guo et al., 2015, Manjarrés-Hernández et al., 2018). Mean temperature of the wettest quarter (bio8) may also affect species seasonal distributions and spawning success. Quarterly extremes of precipitation and precipitation variability are important predictors in determining the establishment of introduced fishes, and in delineating fish distributions in general (Bear et al., 2007). For instance, *O. mykiss* requires minimum baseflows of not less than 25% of average annual daily flow for establishing natural populations (Wesche, 1980). Therefore, we used precipitation of the wettest (bio16) and driest (bio17) quarters, precipitation of coldest quarter, and precipitation seasonality (bio15). In summary, we selected nine bioclimatic layers that were not only ecologically relevant and weakly correlated ($r < .75$), but also, they substantially contributed (76% in the first two principal components) to define multivariate environmental spaces of our studied species (Figures S1–S3).

2.3 | Climatic niches of introduced *O. mykiss* and *S. trutta*

The COUE framework (Guisan et al., 2014) is one of the most widely used methods for niche related inquiries. This framework overcomes biases introduced by spatial resolution and sampling efforts through kernel density estimations. We first constructed a 2D environmental space from two synthetic axes associated with all environmental variables using a PCA. In the PCA environment, we stacked the native and introduced climatic niches for *O. mykiss* and *S. trutta*, which allows us to estimate stability (*S*), expansion (*E*), and unfilling (*U*). Stability estimates the proportion of realised niches shared between two regions (Petitpierre et al., 2012). In our case, these were represented by the introduced range (Himalayas) and each one of the two native regions of *O. mykiss* and brow trout, respectively. Expansion estimates the proportion of climatic conditions in the introduced range that do not overlap with the climatic conditions in the native range niche; and unfilling estimates the proportion of the native niche that is not yet occupied in the introduced niche (Petitpierre et al., 2012). The magnitudes of *S* and *E* are weighted by the occurrence density in the introduced range, whereas the magnitude of *U* is weighted by the occurrence density in the native range (Guisan et al., 2014).

The COUE framework not only provides information about the continuous process or magnitude of niche shift, but also tests the binary pattern of whether there is niche conservatism/divergence or lack thereof. Using the PCA environmental space, we performed tests of niche equivalency and niche similarity (Warren et al., 2008) to examine whether *O. mykiss* and *S. trutta* conserve their native climatic niches when introduced in the Himalayas. Niche equivalency tests assess if native and introduced niches are significantly equivalent to each other by randomly reallocating species occurrences between both ranges. Also, niche similarity tests assess whether native and introduced niches are more similar to each other than expected by chance through randomly reallocating species occurrences in the introduced range only (Di Cola et al., 2017; Warren et al., 2008). To perform these tests we used functions in the "ecospat" package in R (Di Cola et al., 2017). For niche similarity, we used the *overlap.alternative* test in both ways (i.e., "greater" and "lower" to see any significant "conservatism" and "divergence," respectively). For niche similarity and niche divergence tests of introduced trout, we kept the native niche as reference (i.e., shifting only the invasive niche *random.type* = 2).

We measured niche shifts only within the PCA environmental space shared (intersection) between the native and introduced range. This is important to determine whether introduced trout shifted their climatic niches to analogous or non-analogous environmental spaces. We restricted our analyses to analogous climatic conditions only, which is a more rigorous approach to assess niche expansion (Guisan et al., 2014). Expansions observed in the analogous environmental space could be caused by biotic interactions and dispersal limitation in the native range. We standardised the environmental space in which we assessed niche dynamics

by the density of pooled occurrences between the native and introduced ranges (i.e., "correction = True" in the *ecospat.plot.niche* function in R).

2.4 | Climatic niche overlaps between native and introduced trout

We quantified climatic niche overlaps between native snow trout species and introduced *O. mykiss* and *S. trutta* using functions available in the *ecospat* package in R (Di Cola et al., 2017). For native-introduced pair analyses, we kept the "*rand.type = 1*" option in the package *ecospat* in R (Di Cola et al., 2017) making no assumptions about reference niche (i.e., both niches were simultaneously shifted). We used the Schoener's D index of similarity measured using occurrence data in the environmental space depicted by the two first components of the PCA environmental space (Warren et al., 2008). Schoener's D indicates the overall match between two niches and varies between 0 (no overlap at all) and 1 (complete overlap). Niche occupancy corresponds to species density corrected by the environmental availability (Broennimann et al., 2012). Thus, we tested whether niche overlap between snow trout and non-native trout was higher compared to a random niche overlap. We accounted for environmental availability by comparing the observed overlap in suitable conditions to the expected overlap based on the background distribution of suitability values in each pixel of the PCA environmental space estimated using kernel density. This allows for an accurate assessment of niche overlap that considers the relative availability or scarcity of suitable habitats in the PCA environmental space for each species (Guisan et al., 2014). We pooled occurrences from native and introduced ranges for non-native trout to capture the full breadth of their climatic niche (Broennimann et al., 2007), and then, we estimated their overlap with native snow trout.

2.5 | Implication of niche shifts on the transferability of distribution models

We compared the performance of maximum entropy (MaxEnt, version 3.4.4) models when significant disparities of occupied climatic conditions occurred in the native and introduced ranges. MaxEnt is a widely used machine learning algorithm that predicts the presence and distribution of suitable habitats for a species (Phillips et al., 2006). MaxEnt has been extensively adopted when presence-only data are available producing consistently competitive and ecologically meaningful predictions based on georeferenced occurrence data coupled to bioclimatic variables (Elith et al., 2011).

Here, we hypothesised that the transferability of MaxEnt models can be affected when significant shifts (i.e., unfilling and expansion) occurred in climatic niches between native and introduced ranges. We tested this hypothesis by developing MaxEnt models with species information from different scenarios including only native range (native model), only introduced range (introduced model), and native and introduced ranges (global model). Then, we compared the predictive performance of MaxEnt models under these different scenarios using independent dataset from the Himalayas and the omission rate as the performance index (i.e., model's inability to correctly identify areas where the species is known to occur). We built MaxEnt models based on the climatic layers we used to define the PCA environmental spaces above.

3 | RESULTS

3.1 | Climatic niches of *O. mykiss* and *S. trutta* in the Himalayas

The climatic niche indices (unfilling, expansion, and stability) for *O. mykiss* and *S. trutta* provided insights about their differential invasive potential in the Himalayas (Figure 2). For *O. mykiss*, there was a higher climatic niche overlap between the Himalayas and their native range (S = 93%) compared to *S. trutta* (S = 58%). The climatic niche expansion of *O. mykiss* in the Himalayas was smaller (E = 7%) compared to *S. trutta* (E = 42%). Yet, there were potential climatic conditions available in the Himalayas that both introduced trout may colonise in the future. This is shown by the smaller "unfilling" space for *O. mykiss* (U = 30%) compared to *S. trutta* (U = 85%) trout.

There was a higher overlap in Schoener's D between native and introduced niches for *O. mykiss* (D = 0.25) than for *S. trutta* (D = 0.07). These findings showed not enough evidence to qualify for significant niche conservatism (Figure 2). *O. mykiss* and *S. trutta* did not significantly diverge their climatic niches in the Himalayas either (*overlap.alternative = "lower"*) as shown by the divergence tests for *O. mykiss* and *S. trutta* (Table 1) despite the observed expansion and "unfilling" (Figure 2). The observed overlaps between native and introduced climatic niches for both *O. mykiss* and *S. trutta* were as random as one would expect between two different species.

3.2 | Climatic niche overlaps between native snow trout and introduced trout species

We found a higher overlap between the climatic niches of *O. mykiss* and *S. plagiostomus* (D = 0.32) than between *O. mykiss* and *S. richardsonii* (D = 0.14) (Figure 3). The difference in overlap between *O. mykiss* and both native snow trout species may be due to their different relationships with elevation. *S. plagiostomus* occupied a wide range of elevations and overlapped more with *O. mykiss*, whereas *S. richardsonii* mostly occupied relatively lower elevations. Similarity tests of climatic niche provided moderate evidence ($p < .05$) of climatic similarity in *O. mykiss* and *S. plagiostomus*. However, we did not find any significant ($p > .05$) climatic similarity between *O. mykiss* and *S. richardsonii*. On

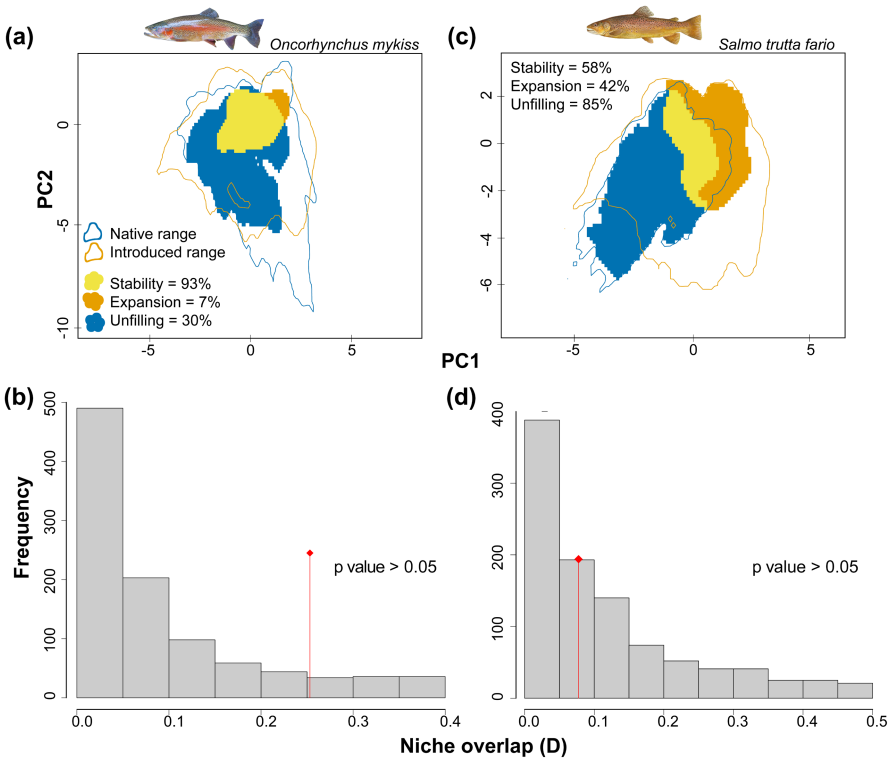

FIGURE 2 Overlap between native and introduced niches shows gaps in the climatic niche space that *O. mykiss* and *S. trutta* could use in the future. Niche dynamics (a) show that *O. mykiss* do not significantly conserve its climatic niche (b). Similarly, niche dynamics of *S. trutta* (c) also show no significant climatic niche conservation (d) in the Himalayan ecoregion. The red lines represent observed value of D.

TABLE 1 Niche dynamics indices and significance tests for niche similarity and equivalency among native snow trout species and introduced trout species.

Comparison		Niche shift metrics				Equivalency test	Similarity test
Niche 1	Niche 2	D	S	E	U	Alternative hypothesis	Alternative hypothesis
Native OM	Introduce OM	0.25	0.93	0.30	0.30	Greater**	Greater Lower
Native ST	Introduced ST	0.07	0.58	0.42	0.85	Greater**	Greater Lower
Global OM	Native SP	0.32	0.60	0.40	0.01	Greater**	Greater*
Global OM	Native SR	0.14	0.26	0.73	0.40	Greater**	Greater
Global ST	Native SP	0.22	0.39	0.61	0.33	Greater**	Greater
Global ST	Native SR	0.42	0.80	0.20	0.07	Greater**	Greater*

Abbreviations: D, Schoener's overlap; E, Expansion; OM, *O. mykiss*; S, Stability; SP, *S. plagiostomus*; SR, *S. richardsonii*; ST, *Salmo trutta*; U, Unfilling.
$^{**}p < .01$, $^{*}p < .05$.

the other hand, the observed Schoener's D values in both cases rejected the null hypothesis ($p < .05$) of niche equivalency (Table 1) with any of the native snow trout species. Rejecting niche equivalency suggested that *O. mykiss* did not occupy the same types of climatic conditions as often as we would have expected if their habitat preferences were random. Lack of niche equivalency was not unexpected since we measured niche overlap among different species (*O. mykiss* & *S. plagiostomus* and *O. mykiss* & *S. richardsonii*), as opposed to niche overlap between native and introduced population of a single species.

S. trutta can withstand relatively higher temperatures at lower elevations, as a result we found its climatic niche overlaps to a greater extent with *S. richardsonii* (D = 0.42) than with *S. plagiostomus* (D = 0.22) (Figure 4). We found significant ($p < .05$) climatic niche similarity between *S. trutta* and *S. richardsonii*. This compares with the extent of climatic niche similarity between *S. trutta* and *S. plagiostomus* that did not qualify as statistically significant, despite the broad elevational range of *S. plagiostomus*. The observed overlap in climatic niches found between *S. trutta* and *S. plagiostomus* was more than expected by chance; whereas the observed overlap in climatic niches found between *S. trutta* and *S. richardsonii* was less than expected by chance. For niche equivalency tests, the observed values of D in both cases rejected the null hypothesis (Table 1) that both niches were equivalent ($p < .01$). As in the case of *O. mykiss*, lack of niche equivalency between *S. trutta* and *S. plagiostomus*, and *S. trutta* and *S. richardsonii* was expected since we measured niche overlap between two different species.

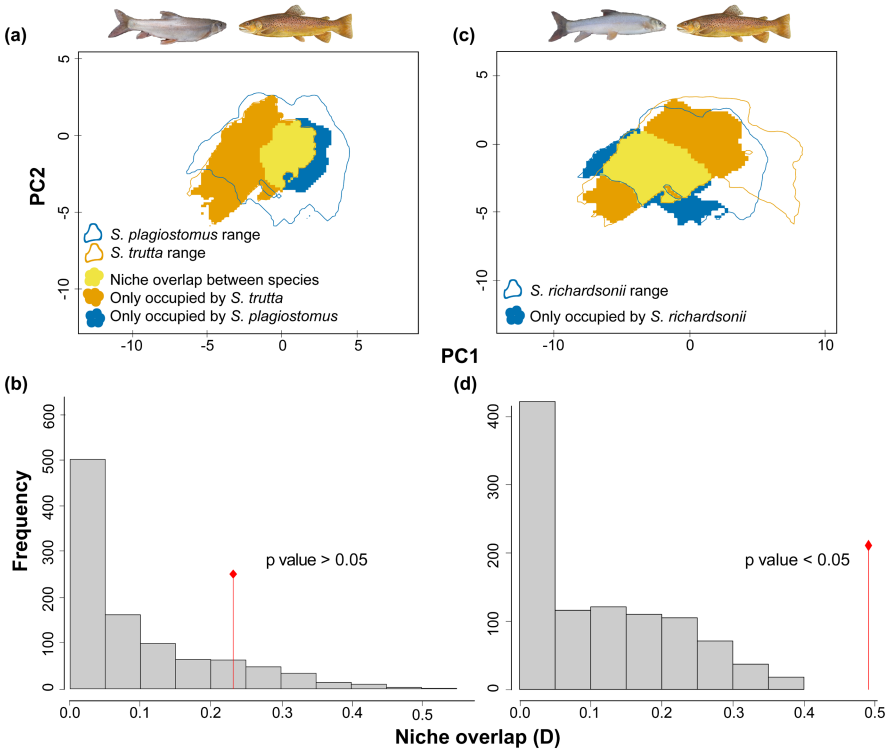

FIGURE 3 *O. mykiss* has more climatic similarity with *S. plagiostomus* than with *S. richardsonii*. Overlap in climatic niches between *O. mykiss* and *S. plagiostomus* (a) shows a significant ($p < .05$) climatic similarity (b). Whereas overlap in climatic niches between *O. mykiss* and *S. richardsonii* (c) shows a non-significant ($p > .05$) climatic similarity (d). The red lines represent observed value of D.

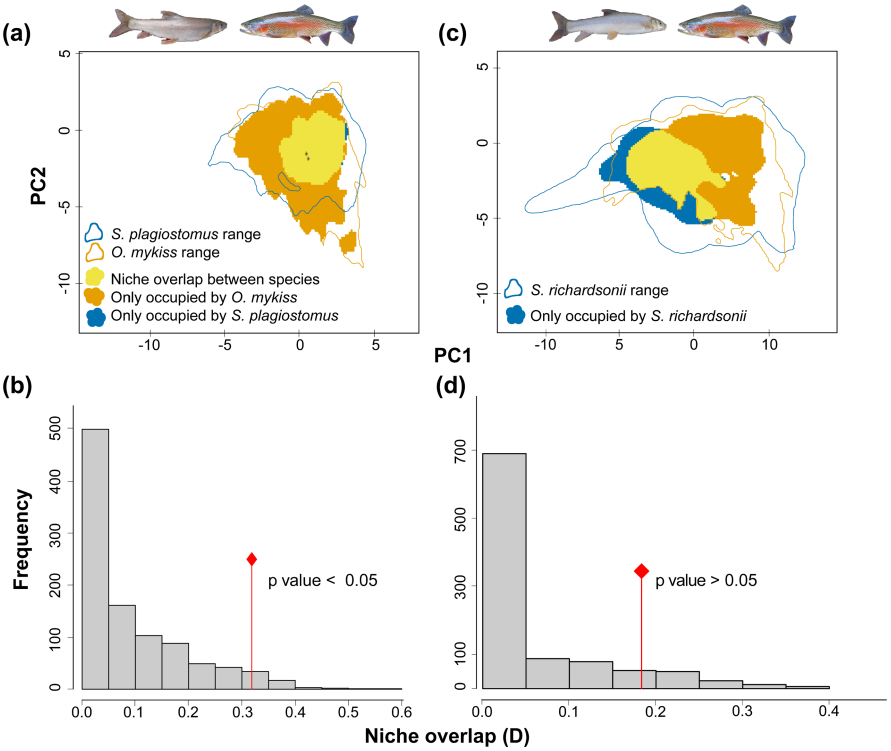

FIGURE 4 *S. trutta* has more climatic similarity with *S. richardsonii* than with *S. plagiostomus*. Overlap in climatic niches between *S. trutta* and *S. plagiostomus* (a) shows a non-significant ($p > .1$) climatic similarity (b). Whereas overlap in climatic niches between *S. trutta* and *S. richardsonii* (c) shows a significant ($p < .01$) climatic similarity (d). The red lines represent observed value of D.

3.3 | Climatic niche shifts negatively affect transferability of MaxEnt models

Comparing native, introduce, and global models showed that there was a positive association between the extent of climatic niche shift and omission rate in MaxEnt models (Table 2). We noticed that in case of climatic niche shifts in the introduced range, global models that incorporated data from a wide range of geographic locations should be preferred over native and introduced models. Native MaxEnt models developed for *O. mykiss* had a 3% omission rate on introduced populations in the Himalayas, whereas they showed a 2% omission rate on independent occurrence data from the Himalayan range. We did not find much difference in omission rate in the native and global model due to a very slight shift

TABLE 2 MaxEnt model predictive performance using omission rates for validation and independent datasets.

	O. mykiss			*S. trutta*		
Omission rates on dataset types	**Native**	**Introduced**	**Global**	**Native**	**Introduced**	**Global**
Validation dataset from the native range	0.03	0.03	0.00	0.01	0.00	0.06
Introduced dataset from the Himalayan range	0.02	0.01	0.02	0.33	0.01	0.08
Independent dataset from the Himalayan range	0.02	0.01	0.01	0.42	0.01	0.11

in climatic niche centroid for *O. mykiss* in the Himalayas. For the same reason, even introduced models had only a 1% omission rate. However, we demonstrated potential future expansion of *O. mykiss* (Figure 2) suggesting that introduced models for these species were not appropriate. Native models for *S. trutta* had up to 42% omission rate on independent occurrence data from the Himalayan range. This clearly showed the inability of native models to be transferred for predicting distribution of suitable habitats, which can be explained by the shift in the climatic niche of *S. trutta* in the Himalayas. However, when we used the global model for *S. trutta*, the omission rate dropped to 11% on the independent occurrence data from the Himalayan range. The introduced model for *S. trutta* had the lowest omission rate of 1%. *S. trutta* had a substantial part of native niche yet unoccupied (U) in the Himalayas and in case of future expansion, introduced models can underestimate habitat suitability resulting in high omission rates.

4 | DISCUSSION

O. mykiss and *S. trutta* were introduced into the Himalayas during the last century (Sehgal, 1999; Yaqoob, 2002). The building of multiple cold-water hatcheries in the region starting in the 1960s has contributed to the propagation of introduced trout. This has been done with little regard for their impacts on native species and ecosystems (Jan et al., 2023). Collectively, these introductions have produced complex niche dynamics that are suitable for testing hypotheses about biological invasions and their impacts on receiving ecosystems. The climatic niche of native *S. plagiostomus* overlaps more with introduced *O. mykiss* whereas climatic niche of native *S. richardsonii* overlaps more with introduced *S. trutta*. Our findings show that the magnitude of "unfilling" niches for introduced trout might lead to increases in niche overlap with native species in the future. Expansion to currently unoccupied portions of the fundamental niche of trout are likely due to dispersal barriers, biotic interactions, or simply because those environments do not exist in their native range (Guisan & Thuiller, 2005) but do in the Himalayas. The rapid spread and extensive growth of introduced trout in some parts of the Indus and Ganges basins (Jan et al., 2023; Johal et al., 2021; Sharma et al., 2021) show that environmental conditions within Himalayan riverscapes constitute highly suitable habitat for them. In addition, *S. trutta* has expanded more than *O. mykiss* into novel climatic conditions found in the Himalayas. Considering the suite of environmental conditions that characterise their native ranges are not fully occupied in the Himalayas, we would anticipate a future spread of these species beyond their current distribution.

We found different magnitudes of expansions to novel habitats for *O. mykiss* and *S. trutta*. Expansion to habitats with novel climatic conditions is particularly striking in the case of *S. trutta* (E = 42%), which can be attributed to its early introduction in 1928 into streams in the northern areas of Pakistan (Petr & Swar, 2002). Early introduction of *S. trutta* gave them more time to adapt to environmental conditions in the Himalayas. Furthermore, the remarkable phenotypic plasticity (Keeley et al., 2019) and more competitive behaviour of *S. trutta* than of snow trout (Sharma et al., 2021) favour them to gain control of suitable habitat patches. These behavioural and ecological traits may have helped *S. trutta* expand its realised niche into novel climatic conditions in the Himalayas. On the other hand, *O. mykiss* was introduced more recently in 1973 from Japan and subsequently in 1980 from United States (Edwards, 1991). As of now, *O. mykiss* has expanded only slightly (E = 7%) into novel climatic conditions. This is probably because *O. mykiss* requires a stable flow, that is, at least 25% of the base flow, throughout the year in order to establish naturalised populations (Raleigh, 1984). Several watersheds in the Himalayas have steep slopes with faster flows to allow for successful *O. mykiss* spawning. Finally, substantial variations and unpredictable discharge patterns in Himalayan streams (Liu et al., 2018) present challenges for the successful establishment of *O. mykiss* in certain regions of the Indus and Ganges basins, as their ideal spawning conditions are stable, slow, and predictable flows (Raleigh, 1984).

To develop cost-effective strategies on managing invasions, conservation efforts should be focused on those areas within the Indus and Ganges basins that have climatic characteristics analogous to those in the native ranges of the introduced trout species, but that are not yet occupied. Our estimates of niche dynamics and niche overlap comes from the analogous environmental space only; complementary experimental approaches therefore are needed to determine whether, for instance, expansions in non-analogous conditions may represent a change of the fundamental niche (Warren et al., 2008). Colonisation of non-analogous climates in the introduced range may be a challenge to consider from a management perspective, calling for separate ENM projections in both analogous and non-analogous climates in the introduced range, that is, through fitting ENMs with pooled data from the native and introduced ranges (e.g., Jan et al., 2023). Figures S4 and S5 provide details on the distribution of individual climatic variables in the in the unfilling, stability, and expansion regions for brown and rainbow trout, respectively.

4.1 | Implications of climatic niche shifts on the transferability of MaxEnt models

The assumption that a species can occur in other locations where environmental conditions are similar to the ones in its native range (Peterson et al., 2011) is foundational to correlative distribution models. However, in this study we do not find any significant climatic niche conservatism for *O. mykiss* and *S. trutta* in the Himalayas. Rather, we show that global models calibrated with data from both ranges better represent introduced environments (Jan et al., 2023). Global models are developed with information from a wide range of environmental conditions and reduce the reliance on assumptions based solely on the species' native range. This avoids underestimation of potentially suitable habitats. A shift in the realised niches for introduced species negatively affects the predictive performance of distribution models, and therefore should be validated with independent test data and/or experts' evaluations when possible (Jan et al., 2023).

The stability (S) value in the global climatic niche indicates the accuracy of the model in predicting the distribution of a species or populations under current environmental conditions. A high stability value indicates that the model is accurate in its species distribution predictions. We show a high stability (93%) for *O. mykiss*, which explains low omission error for native models. In the case of *S. trutta*, we found lower stability (58%) compared to *O. mykiss*, which results in high omission error. We recommend exploring niche dynamics of native and introduced populations before transferring MaxEnt models to the introduced range.

It is important to acknowledge that our study relies exclusively on climatic variables, thus providing partial information on the invasion process. Only climatic variables were used because ordination analyses are sensitive to the combination of different sets of variables and methodological choices (Lo Parrino et al., 2023). Additionally, at basin scale, climatic variables are more influential than other classes of variables in demarcating species ranges (Fournier et al., 2017). For geographically explicit fish distribution models, MaxEnt was also supplied with other variables that delimit fish distribution at riverscape scale, for example, geomorphic, landcover, and river networks (Bizama et al., 2023; Jan et al., 2023). Our analyses only highlight climatic niche dynamics; other factors (e.g., anthropogenic disturbances, game fishing intensity, and management strategies) could also determine the success and further spread of introduced trout. Finally, more studies on biotic interactions between introduced trout and snow trout can improve our understanding of this invasion process in the Himalayas.

This study provides baseline information on the stages of invasion and future potential for expansion of introduced trout. Our findings underscore the potential ramifications of continued trout stocking, particularly in the context of their expanding distribution and overlap with native snow trout. The introduced trout species have the capacity to propagate and disperse beyond their initial stocking sites, which in turn raises serious concerns regarding the ecological well-being of snow trout. For instance, the introduction of Rainbow trout from hatcheries in 2016 led to a significant viral outbreak of haemorrhagic septicaemia, resulting in mortality among numerous populations of *S. plagiostomus* in the Swat, Dir, and Chitral districts of Pakistan.

Therefore, it is of utmost importance that fisheries managers consider a reevaluation of trout stocking policies in the Himalayas, with a focus on balancing the need for recreational fisheries with the conservation of snow trout. Our study demonstrates that the information on climatic niche dynamics can inform model-building process and improve the transferability and predictive performance to better assess vulnerability of sensitive habitats to introduced species in the Himalayas and elsewhere. Our research illustrates that insights into climatic niche dynamics can inform the process of model construction, enhancing transferability and predictive accuracy. This approach enables the assessment of vulnerable habitats to introduced species in the Himalayas and elsewhere.

AUTHOR CONTRIBUTIONS

AJ conceived and designed the study, ran the analyses and wrote the manuscript taking input from all authors. IA and GG constantly supervised the project. All authors including RF helped with reviewing and editing the manuscript, discussed the results and implications and commented on the manuscript at all stages.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All datasets used R codes for the analyses will be uploaded to a repository in case of publication of this manuscript.

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