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Investigating the Role of Latent Variables and Species Interactions in Joint Species Distribution Modeling of Fish Species in Rivers of the Southern Caspian Sea Basin

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ABSTRACT

Understanding the factors governing species distributions is fundamental to freshwater ecology and biodiversity conservation. Conventional Species Distribution Models (SDMs) primarily explain species occurrences using environmental variables but generally overlook interspecific interactions and unmeasured ecological processes. Joint Species Distribution Models (JSDMs) overcome this limitation by simultaneously modeling multiple species and incorporating latent variables to capture residual species associations. This study represents the first application of a latent-variable JSDM to freshwater fish communities in Iranian inland waters, aiming to evaluate the combined effects of environmental drivers and hidden ecological interactions on fish assemblages in the western and central ecoregions of the southern Caspian Sea basin. Fish occurrence data for 22 species were collected from 175 randomly selected passable river sites using standardized electrofishing protocols. Environmental predictors included climatic, topographic, hydrological, and land-use variables. After multicollinearity assessment, ten predictors were retained for modeling. A multivariate probit JSDM with latent variables was implemented using the JSDM package in R. Results demonstrated that temperature and annual precipitation were the dominant environmental determinants of fish distributions, while watershed characteristics and human land use further influenced species occurrence. Residual correlation matrices revealed substantial positive and negative species associations that were not explained by measured environmental variables, indicating potential habitat sharing, ecological similarity, competition, and the influence of invasive species. Positive associations were observed between Salmo trutta and Oncorhynchus mykiss, whereas several native species showed negative correlations with invasive taxa. These findings demonstrate that incorporating latent variables substantially improves community-level distribution modeling by accounting for hidden ecological processes. The proposed framework provides a robust scientific basis for river restoration, invasive species management, biodiversity conservation, and ecosystem-based freshwater management under ongoing environmental and climatic change.

Introduction

Understanding how biological communities respond to environmental variation remains one of the principal challenges in ecology. Species distributions are determined not only by abiotic conditions but also by complex ecological interactions, including competition, facilitation, habitat sharing, and other biotic processes operating across multiple spatial scales. Predicting these relationships is particularly important in freshwater ecosystems, where habitat fragmentation, climate change, invasive species, and increasing anthropogenic pressures continuously reshape community composition.

Species Distribution Models (SDMs) have become essential tools for predicting species occurrence and identifying suitable habitats. However, conventional SDMs generally assume ecological independence among species and therefore neglect biotic interactions that substantially influence community assembly. This limitation may reduce predictive accuracy and hinder conservation planning, especially in highly diverse freshwater ecosystems. Recent developments in community ecology have led to the emergence of Joint Species Distribution Models (JSDMs), which simultaneously model multiple species while incorporating both environmental responses and residual species associations. Through latent-variable approaches, JSDMs can identify hidden ecological gradients and unexplained covariance among species, providing a more realistic representation of ecological communities.

Despite their growing international application, JSDMs have not previously been implemented for freshwater fish assemblages in Iran. Consequently, little is known about how environmental filtering and latent ecological processes jointly shape fish communities in the southern Caspian Sea basin. This study addresses this knowledge gap by applying a latent-variable JSDM to investigate fish assemblages across the western and central Caspian ecoregions. Specifically, the study aims to (i) quantify the effects of environmental variables on species distributions, (ii) identify residual species associations that may indicate ecological interactions, and (iii) evaluate the usefulness of latent-variable JSDMs for supporting biodiversity conservation and river ecosystem management. The findings are intended to assist freshwater ecologists, conservation biologists, fisheries managers, and environmental decision-makers seeking community-based approaches to ecosystem conservation.

Method

This research employed an observational ecological design based on species occurrence data collected from natural river systems within the western and central ecoregions of the southern Caspian Sea basin. A total of 175 randomly selected passable river reaches were surveyed during the autumn season using standardized electrofishing procedures recommended by the European Committee for Standardization (CEN). Sampling reaches covered multiple habitat types to ensure representative assessment of local fish assemblages. All captured individuals were identified to species level and released after sampling.

The dataset included 22 freshwater fish species, representing endemic, native, and non-native taxa. Environmental predictors were compiled from the WorldClim database together with GIS-derived topographic, hydrological, and land-use variables. Initially, nineteen bioclimatic variables were extracted; following Pearson correlation analysis and ecological expert evaluation, ten variables were retained to minimize multicollinearity. These included annual mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, annual temperature range, annual precipitation, watershed slope, upstream drainage area, river segment length, agricultural land area, and urban land area.

Species occurrence data were analyzed using the JSDM package in R (version 4.4) within a multivariate probit framework. Latent variables were incorporated to account for unexplained covariance among species after controlling for measured environmental predictors. Residual correlation matrices were subsequently interpreted to identify potential ecological

interactions, shared habitat preferences, competitive exclusion, and hidden environmental influences affecting fish community assembly.

Results

The latent-variable Joint Species Distribution Model (JSDM) provided a comprehensive assessment of the environmental and ecological factors structuring freshwater fish assemblages across the western and central ecoregions of the southern Caspian Sea basin.

Among the environmental predictors, climatic variables emerged as the dominant determinants of species occurrence. Temperature-related variables, including annual mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, and annual temperature range, exerted the strongest influence on the spatial distribution of most species. These variables were particularly important in distinguishing cold-water species from warm-water assemblages, highlighting the sensitivity of freshwater fish communities to thermal gradients. Annual precipitation also contributed substantially to species occurrence by influencing stream flow, habitat availability, and hydrological connectivity throughout the river network. Together, these climatic variables explained a considerable proportion of the observed variation in species distributions, confirming their fundamental role in shaping riverine fish communities.

Despite the strong explanatory power of the measured environmental variables, the latent-variable JSDM identified substantial residual correlations among species after accounting for abiotic effects. These residual associations indicate that additional ecological processes, including species interactions and unmeasured environmental factors, contribute significantly to community assembly. Positive residual correlations generally reflected shared habitat preferences, similar ecological requirements, or potential facilitative relationships. For example, *Salmo trutta* and *Oncorhynchus mykiss* exhibited one of the strongest positive associations, suggesting a high degree of habitat overlap associated with cold, well-oxygenated mountain streams. Similarly, *Squalius turcicus* and *Squalius berak* showed consistent positive correlations, indicating comparable ecological niches and co-occurrence within similar river habitats. Additional positive associations observed among species such as *Capoeta razi*, *Sabanejewia aurata*, and several benthic taxa further support the existence of habitat-sharing patterns within the study area.

Conversely, the model revealed several pronounced negative residual correlations that likely reflect competitive interactions, ecological segregation, or the influence of invasive species. Strong negative associations involving *Carassius auratus*, *Pseudorasbora parva*, and multiple native species suggest that invasive fishes may compete with indigenous taxa for habitat and food resources or indirectly modify community structure. Negative relationships were also detected between *Rhodeus amarus* and *Pseudorasbora parva*, as well as between *Oncorhynchus mykiss* and *Neogobius melanostomus*, indicating potential ecological incompatibilities or competitive exclusion. These findings are consistent with ecological theory predicting that species occupying similar niches may exhibit negative co-occurrence patterns when resources become limiting.

The residual correlation matrix further demonstrated that not all unexplained associations necessarily represent direct biological interactions. Instead, some residual covariance may reflect unmeasured environmental drivers, such as microhabitat characteristics, substrate composition, localized water quality, riparian vegetation, or other fine-scale ecological processes that were not explicitly incorporated into the model. Consequently, the latent-variable framework captures both hidden environmental heterogeneity and potential biotic interactions, providing a more realistic representation of community structure than conventional single-species models.

Collectively, these results demonstrate that integrating latent variables into Joint Species Distribution Models substantially improves the interpretation of freshwater fish assemblages by simultaneously quantifying environmental filtering and species co-occurrence patterns. The findings emphasize that accurate prediction of fish distributions requires consideration of both abiotic drivers and hidden ecological processes, thereby providing a stronger scientific foundation for biodiversity conservation, river restoration, invasive species management, and ecosystem-based freshwater planning in the southern Caspian Sea basin.

Conclusions

This study provides the first application of latent-variable Joint Species Distribution Models to freshwater fish communities in Iran and demonstrates their considerable advantages over conventional single-species distribution models. The results indicate that fish assemblages are jointly structured by environmental filtering and hidden ecological interactions, emphasizing that community-level modeling provides a more realistic understanding of biodiversity patterns than independent species analyses.

The findings have important implications for river restoration, freshwater biodiversity conservation, invasive species management, and ecosystem-based environmental planning. By simultaneously accounting for environmental drivers and species associations, latent-variable JSDMs improve ecological prediction and provide valuable guidance for prioritizing conservation actions under climate change and increasing anthropogenic pressure. Future studies should integrate additional environmental variables, long-term monitoring data, and functional or phylogenetic information to further refine predictions of freshwater community dynamics and strengthen evidence-based management strategies for the southern Caspian Sea basin.

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