Title	Multidimensional assessment of structural dynamics in native fish assemblages in lentic habitats and identification of potential conservation areas
Author(s)	戴, 秉国
Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	甲第16070号
Issue Date	2024-09-25
DOI	https://doi.org/10.14943/doctoral.k16070
Doc URL	https://hdl.handle.net/2115/96075
Type	doctoral thesis
File Information	DAI_Bingguo.pdf

Multidimensional assessment of structural dynamics in native fish assemblages in lentic habitats and identification of potential conservation areas
（止水域における在来魚類群集構造動態の多面的解析および潜在的保全地域の特定）

北海道大学大学院環境科学院

戴　秉国
DAI Bingguo

北海道大学
HOKKAIDO UNIVERSITY

Multidimensional assessment of structural dynamics in native fish assemblages in lentic habitats and identification of potential conservation areas

A Dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy

in the field of

Environmental Science Development

by

DAI Bingguo

2024

This dissertation comes from
Course in Human and Ecological Systems
Graduate School of Environmental Science, Hokkaido University
N10W5 Sapporo Hokkaido 060-0810 Japan

Printed in Sapporo

ABSTRACT

Global biodiversity in freshwater ecosystems is declining rapidly, with freshwater fish species facing extinction at concerning rates. Despite substantial investments in conservation efforts, these have largely not met their goals. A potential cause for this shortfall is the overemphasis on taxonomic changes in fish species, overlooking their evolutionary histories and ecological functions. This dissertation examines the spatial and temporal diversity patterns of freshwater fish in Japan, using a multifaceted approach combining taxonomic, phylogenetic, and functional diversity metrics. Specifically, this study analyses native fish assemblages in 39 lakes across the Japanese archipelago and 28 oxbow lakes along the Ishikari River in Hokkaido. Additionally, this research proposes a computational framework for a cumulative diversity index that integrates multifaceted diversity measures into a concise metric. Temporal multifaceted diversity analysis indicates a nationwide continuation of native fish species loss, especially among endemic species, leading to increased homogenization of fish compositions. Such native loss and homogenization in three facets, i.e., taxonomic, phylogenetic, and functional, are all expected to be continued in the future if the endangered species remain at risk. Meanwhile, although the native fish in the Ishikari oxbow lakes have maintained their richness over the studied decade, this study revealed a significant loss of native functions as well as the phylogenetic and functional redundancy. Moreover, national spatial multifaceted diversity analysis reveals a correlation between fish assemblage cumulative diversity and lake location, with the northernmost (Hokkaido) and southernmost (Kyushu) islands exhibiting low native fish richness but high uniqueness, marking them as high-priority conservation areas. Regionally, in the Ishikari River basin, the upper oxbow lakes host a greater richness and are exposed to lesser impact from non-native expansion, thereby have greater potential as native fish conservation areas. Additionally, this research shows that spatial patterns primarily influenced by dispersal constraints are hard to shift along the time, while that spatial patterns mainly shaped by ecological competition are alterable. To summarize, this dissertation deepened the understanding of the structural dynamic processes of native fish communities inhabiting the lentic habitats in Japan from taxonomic, phylogenetic and functional facets. Also, this dissertation validates the applicability of the proposed cumulative diversity index and evaluation framework in pinpointing potential native fish conservation areas.

Keywords: fish conservation, homogenization, invasion, phylogenetic and functional diversity

要旨

世界の淡水生態系における生物多様性は急速に減少しており、淡水魚種は深刻な速度で絶滅の危機に直面している。保全活動への多額の投資にもかかわらず、その目標は効率的に達成されていないと考えられる。この不足の潜在的な原因は、魚類種の分類学的変化を過度に重視し、その進化史や生態学的機能を見落としたことにあると見受けられる。本論文では、分類的、系統的、機能的多様性指数を組み合わせた多面的アプローチを用いて、日本の淡水魚の空間的と時間的多様性パターンの変化を検討する。具体的には、日本列島全域の 39 の湖沼と北海道の石狩川沿いの 28 の河跡湖における在来魚類群集を分析する。さらに、本研究では、多面的な多様性指数を簡潔な指数に統合する累積多様性指数の計算フレームワークを提案する。時系列的な多面的多様性分析から、全国的に在来魚種の減少が続いており、特に固有種の間で魚類組成の均質化が進んでいることが示された。分類学的、系統学的、機能的という 3 つの観点から、このような在来種の減少と均質化は、絶滅危惧種が効率的に保護されないままであれば、今後も続くと予想される。一方、石狩川沿いの河跡湖の在来魚は、2000 年代から 2010 年代にかけて 10 年間で種の豊かさを維持しているものの、外来種と競争により、在来種の生態的機能が著しく失われ、系統的・機能的な冗長性も失われていることが明らかになった。さらに、全国的な空間的多様性分析により、魚類群集の累積多様性と湖沼の位置との相関関係が明らかになり、最北端（北海道）と最南端（九州）の島嶼は在来魚の豊かさは低いが、独自性は高く、優先度の高い保全地域であることが示された。石狩川流域では、上流域の河跡湖の方が在来魚の多様性が豊富であり、外来魚の移入による影響も少ないことから、魚類保全区としての可能性が高い。また、本研究は、主に分散制約に影響される空間パターンは時間的に変化しにくいこと、一方、主に生態学的競合によって形成される空間パターンは時間的に変化可能であることを示した。以上のように、本論文は、日本の止水域に生息する在来魚類群集の構造的動態プロセスについて、分類的、系統的、機能的観点から理解を深めた。また、本論文により、提案した累積多様性指標と評価フレームワークの在来魚保護潜在域の特定への適用性が検証された。

キーワード：魚類保全、均質化、外来種移入、系統的・機能的多様性

ACKNOWLEDGEMENT

During my thousand-day journey in Japan as an international doctoral student, I found myself immersed in a vibrant tapestry of experiences. This academic and cultural odyssey was made possible by the generous support of the Ministry of Education, Culture, Sports, Science and Technology (MEXT) of Japan and the China Scholarship Council (CSC). I am grateful to either of them.

I would like to extend my heartfelt thanks to the members of my dissertation committee for their invaluable feedback on my work. Besides, my sincerest gratitude also goes to my supervisor, Assoc. Prof. Dr. NEGISHI Junjiro, whose insightful guidance was instrumental in the completion of my research over the past three years. The fieldwork we conducted together throughout Hokkaido was deeply inspiring, and his passion for nature continues to motivate me in my future careers. I am also grateful for the support from Dr. MATSUZAKI Shin-Ichiro of the National Institute for Environmental Studies, Japan; Assoc. Prof. Dr. JIANG Zhongguan of Anhui University; and Dr. CHENG Lei of Huainan Normal University

I am thankful to the members of our Watershed Conservation & Management Laboratory, including Dr. HIROMI Uno, Dr. MIURA Aya, Dr. Md. Khorshed Alam, Mr. Mc Jervis Soltura Villaruel, Mrs. Janine Mihara, Mr. LIU Shanmu, Mr. GAO Haizhou, Mr. OKAZAKI Koya, Ms. YAO Shuyu, and Ms. WU Junyi, among others, for making my doctoral journey fulfilling and memorable. Additionally, I would like to thank my dear friends Ms. OSADA Sachiko, Ms. MAO Yuting, Ms. ZHANG Zelan, Mr. MASHIMA Yoshitaka, Mr. MITSUI Mei, Mr. Chalermpan Tantara, Mr. Aleksandr Nogovitcyn, Mr. CHEN Xiaodong, Mr. WU Yiyan, Mr. MA Shiwen, Mr. LIANG Chao, Mr. ZHONG Zhaocheng, Mr. ZHOU Jian, Dr. YANG Jun, Mr. WANG Shaobo, Mr. WANG Ziwei, and Mr. WANG Tianyu, among others, for their invaluable assistance and support. I deeply appreciate my parents' unwavering support.

I am fortunate to have participated in international exchanges that broadened my horizons across different cultures. I would like to thank Prof. David Bastviken at Linköping University, Sweden, as well as Dr. Chainarong Rattanakreetakul and Dr. Pongsivapai P. Nack at Kasetsart University, Thailand. My gratitude also goes to the OGGs Central Office and the Environmental Science Alumni Association for their financial support of some of my international travels.

In closing, but by no means less important, I extend my heartfelt gratitude and exclusive favour to Mr. Ric TSUI Hon Fai for his exceptional companionship.

On the flight departing from Tung Chung
June 2024

戴秉冈

VITA

2017	Bachelor of Science in Biological Science, Huaibei Normal University
2020	Master of Science in Ecology, Anhui University
2024	Doctor of Philosophy in Environmental Science Development, Hokkaido University

Publications

1. Dai, B., Matsuzaki, S.S., Negishi, J.N., Xia, Z., Alam, M.K., Jiang, Z. (2024) Native fish assemblages in natural lakes across Japan: Endemism deterioration lasting centuries. *Diversity and Distributions*, 30, e13850.
2. Dai, B., Chen, S., Wang, C., Jiang, Z. (2024) Functional zeta diversity can better reveal fish metacommunity assembly process in a transitional floodplain. *Ecological Indicators*, 160, 111792.
3. Dai, B., Negishi, J.N., Fujii, K., Alam, M.K., Jiang, Z. (2023) Non-native fish species expand tacitly but rapidly toward upstream oxbow lakes along the longitudinal gradient. *NeoBiota*, 85, 101–123.
4. Xie, C., Dai, B., Wu, J., Liu, Y., Jiang, Z. (2022) Initial recovery of fish faunas following the implementation of pen-culture and fishing bans in floodplain lakes along the Yangtze River. *Journal of Environmental Management*, 319, 115743.
5. Dai, B., Wang, C., Jiang, Z. (2021). Beta diversity dynamics of fish communities inhabiting typical floodplain habitats driven by water level variation. *Journal of Hydroecology*, 42(6), 85–91. (in Chinese with English abstract).
6. Jiang, Z., Dai, B., Wang, C., Xiong, W. (2020). Multifaceted biodiversity measurements reveal incongruent conservation priorities for rivers in the upper reach and lakes in the middle-lower reach of the largest river-floodplain ecosystem in China. *Science of the Total Environment*, 739, 140380.
7. Dai, B., Jiang, Z., Wang, C., Matsuzaki, S.S., & Zhou, L. (2020). Abundance-based dissimilarity measurements reveal higher heterogeneity of fish communities in the lotic habitats of the Yangtze-Caizi transitional floodplain. *Ecological Indicators*, 112, 106122.

Conference Presentations

Oral, The 6th International EcoSummit Congress. Gold Coast, Australia. 2023.
Poster, ELR 2022. Tsukuba, Japan. 2022

Research Grant

River Fund of The River Foundation, Japan. 600,000.00 JPY. 2023–202

TABLE OF CONTENTS

ABSTRACT I

要旨 II

ACKNOWLEDGEMENT III

VITA IV

TABLE OF CONTENTS V

LIST OF FIGURES VIII

LIST OF TABLES IX

LIST OF ABBREVIATIONS X

CHAPTER 1 GENERAL INTRODUCTION 1

1.1 BACKGROUND 1

Freshwater biodiversity facing threats 1
Freshwater fish: Crucial biota of freshwater ecosystems 2
Native fish assemblages needing conservation 3
Neglected phylogenetic and functional evidence in native conservation 4
Lentic habitats: An ideal conservation area candidate 5
Species assembly process: A hint to native fish conservation 5

1.2 STUDY GAP 7

1.3 OBJECTIVE 8

1.4 STRUCTURE OF THE DISSERTATION 8

CHAPTER 2 ASSESSMENT APPROACHES FOR MULTIDIMENSIONAL FRESHWATER FISH DIVERSITY 10

2.1 TAXONOMIC, PHYLOGENETIC, AND FUNCTIONAL DIVERSITY 10

Taxonomic diversity 10
Phylogenetic diversity 11
Functional diversity 12

2.2 ALPHA DIVERSITY 13

2.3 BETA DIVERSITY 14

2.4 LOCAL CONTRIBUTION TO BETA DIVERSITY 18

2.5 GAMMA DIVERSITY 19

2.6 ALGORITHMIC RESOURCES UTILIZED FOR DIVERSITY ASSESSMENTS 19

CHAPTER 3 NATIVE FISH ASSEMBLAGES IN NATURAL LAKES ACROSS JAPAN: ENDEMISM DETERIORATION LASTING CENTURIES 21

3.1 INTRODUCTION 21

3.2 METHODS 25

Data collection and collation 25
Phylogenetic and functional dendrogram construction 29
Multifaceted biodiversity assessment 30
Statistical analysis 31
3.3 RESULTS 32

Temporal changes in multidimensional alpha diversity 32
Temporal changes in multidimensional beta diversity 33
Lakes with unique fish assemblages 34
3.4 DISCUSSION 37

CHAPTER 4 NATIVE FISH SPECIES CONFINED TO UPSTREAM OXBOW LAKES ALONG THE LONGITUDINAL GRADIENT 41

4.1 INTRODUCTION 41

4.2 METHODS 43

Study areas and fish datasets 43
Calculation of diversity metrics 45
Statistical analysis 46
4.3 RESULTS 47

Temporal change in fish richness 47
Temporal change in regional dissimilarity and local contributions 47
Regional patterns corresponding to dissimilarity changes 50
4.4 DISCUSSION 51

CHAPTER 5 LONGITUDINAL DISPARITIES IN NATIVE FISH RESPONSES TO HOMOGENIZED NON-NATIVE INVASIONS: CONTRASTING PHYLOGENETIC AND FUNCTIONAL SPATIAL PATTERNS 56

5.1 INTRODUCTION 56

5.2 METHODS 58

Data arrangement and dendrogram generation 58
Phylogenetic and functional diversity measurement 58
Statistical analysis 58

5.3 RESULTS 59
Alpha diversity variations 59
Beta diversity changes 59
Relationships between changes in phylogenetic and functional beta diversity 61
Changes in phylogenetic and functional LCBD 63
5.4 DISCUSSION 63
CHAPTER 6 SPATIAL PATTERNS OF FISH CUMULATIVE DIVERSITY DRIVEN BY STOCHASTIC AND DETERMINISTIC PROCESSES 68
6.1 INTRODUCTION 68
6.2 METHODS 71
Proposed assessment framework for cumulative diversity 71
Statistical Analysis 71
6.3 RESULTS 73
Spatial patterns of fish diversity driven by stochastic processes 73
Spatial patterns of fish diversity driven by deterministic processes 78
Relationships between 2D- and 3D-cDI 80
6.4 DISCUSSION 83
CHAPTER 7 SUMMARY AND GENERAL DISCUSSION 87
7.1 SUMMARY OF THE STUDY 87
7.2 URGENT CONSERVATION NEEDS FOR FRESHWATER FISH IN JAPAN 89
7.3 NECESSITY OF INTEGRATING MULTI-FACETED DIVERSITY ASSESSING 90
7.4 APPLICATION OF THE CUMULATIVE DIVERSITY INDEX 91
7.5 FISH DISTRIBUTIONAL PATTERNS INDICATE CONSERVATION AREAS 92
7.6 EXAMPLES OF FOCAL LAKES AND SPECIES 93
7.7 LIMITATIONS OF THE STUDY 94
REFERENCES 95

LIST OF FIGURES

Figure 3.1 Map showing location of the 39 studied lakes across Japanese archipelago.......41
Figure 3.2 Associations between the phylogenetic and functional dendrogram.................46
Figure 3.3 Boxplots showing taxonomic alpha diversity (Richness), two phylogenetic alpha diversity: mean phylogenetic distance (MPD) and mean nearest phylogenetic distance (MNPD), and two functional alpha diversity: mean functional distance (MFD) and mean nearest functional distance (MNFD) for freshwater fish across historical, current, future I, and future II period...47
Figure 3.4 Triangular plots depict the beta diversity of freshwater fish populations during the historical, current, future I, and future II periods..48
Figure 3.5 Three-dimensional scatter plots demonstrate the LCBD values for individual lakes during the historical, current, future I, and future II periods 49
Figure 4.1 Location of the studied oxbow lakes along the Ishikari River...........................59
Figure 4.2 Distribution of simulated multiple-site dissimilarity metric values for overall, native, and non-native fish assemblages in the 2000s and the 2010s......................64
Figure 4.3 Local contributions to regional dissimilarity (LCBD) of overall, native, and non-native fish faunas inhabiting each lake in the periods of the 2000s and 2010 64
Figure 4.4 Linear regression relationships between temporal change in beta diversity metrics of overall, native, and non-native fish assemblages in each oxbow lake and their distances from the river sources...65
Figure 4.5 Linear regressions between the distance from the river source (DRS) and temporal change in LCBD values (ΔLCBD) of the 28 oxbow lakes for overall, native, and non-native fish assemblage 65
Figure 5.1 Phylogenetic (MPD and MNPD) and functional (MFD and MNFD) alpha diversity of native and non-native fish assemblages in upper and lower lakes...........75
Figure 5.2 Phylogenetic dissimilarity, turnover, and estedness, as well as the functional counterparts of native and non-native fish assemblages in upper and lower lake.......76
Figure 5.3 Linear regression between change in phylogenetic beta diversity metrics and changes in their functional counterpart...77
Figure 6.1 Schematic illustration of the cumulative diversity calculation framework 87
Figure 6.2 Points on the map of Japan denote each lake's cumulative diversity, with point size reflecting the diversity index value..89
Figure 6.3 Linear regression plots of cumulative diversity indices (cAlpha, cBeta, cLCBD) of native and non-native fish assemblages in oxbow lakes of the Ishikari River basin versus the latitude at which the lakes are located for the 2000s and 2010 94

LIST OF TABLES

Table 2.1 Summary of the primary diversity indices used in this study........................35
Table 3.1 Location and basic information on the studied lakes 42
Table 3.2 Table presenting a list of freshwater fish recorded in the Japanese archipelago, along with their respective extinction risk 43
Table 3.3 Functional traits used for functional diversity measurements 45
Table 3.4 Statistic results of one-way PERMANOVA comparing significance of differences across five alpha diversity indices over four time periods.....................50
Table 3.5 Statistic results of one-way PERMANOVA analysis comparing significance of differences across beta diversity indices over four time periods 51
Table 4.1 DRS and fish incidence of the studied oxbow lakes....................................63
Table 4.2 Multi-site dissimilarities of overall, native, and non-native fish faunas..........64
Table 5.1 The proportion of phylogenetic and functional p_{turn} values for native and non-native fish assemblages in upper and lower lakes across two periods.............75
Table 5.2 Changes in pLCBD and fLCBD values of native and non-native fishes 75
Table 6.1 Results of quadratic polynomial regression between the alpha diversity indexes of native fishes in lakes across Japan and the latitude at which the lakes are located at which the lakes are located 90
Table 6.2 Results of quadratic polynomial regression between the beta diversity indexes of native fishes in lakes across Japan and their latitudes...............................91
Table 6.3 Results of quadratic polynomial regression between the LCBD indexes of native fishes in lakes across Japan and their latitudes.......................................92
Table 6.4 Results of linear regression between the alpha indices of native and non-native fish assemblages in oxbow lakes along the Ishikari River and their latitudes...95
Table 6.5 Results of linear regression between the beta indexes of native and non-native fish assemblages in oxbow lakes along the Ishikari River and their latitudes...96
Table 6.6 Results of linear regression between the LCBD indices of native and non-native fish assemblages in oxbow lakes along the Ishikari River and their latitudes 96
Table 6.7 Correlations between 2D cumulative diversity indices and 3D diversity indices calculated using only two diversity combinations in the national case 97
Table 6.8 Correlations between 2D cumulative diversity indices and 3D diversity indices calculated using only two diversity combinations in the Ishikari case 97

LIST OF ABBREVIATIONS

cAlpha	Cumulative alpha diversity
cBeta	Cumulative beta diversity
cDI	Cumulative diversity index
cLCBD	Cumulative local contribution to beta diversity
CR	Critically endangered
DRS	Distance from the Ishikari River source
EN	Endangered
FD	Functional diversity
fLCBD	Local contribution to functional beta diversity
$\mathrm{f}p_{turn}$	Proportion of functional turnover to functional dissimilarity
fβ	Functional beta diversity
$\mathrm{f}\beta_{\mathrm{sim}}$	Pairwise functional turnover (Simpson dissimilarity index)
$\mathrm{f}\beta_{\mathrm{sne}}$	Pairwise functional nestedness
$\mathrm{f}\beta_{\text{sør}}$	Pairwise functional Sørensen dissimilarity index
LCBD	Local contribution to beta diversity
LP	Endangered local population
MFD	Mean functional distance
MNFD	Mean nearest functional distance
MNPD	Mean nearest phylogenetic distance
MPD	Mean phylogenetic distance
NE	Not evaluated
NFCA	Native fish conservation area
NT	Near threatened
PD	Phylogenetic diversity
pLCBD	Local contribution to phylogenetic beta diversity
$\mathrm{p}p_{turn}$	Proportion of phylogenetic turnover to phylogenetic dissimilarity
pβ	Phylogenetic beta diversity
$\mathrm{p}\beta_{\mathrm{sim}}$	Pairwise phylogenetic turnover (Simpson dissimilarity index)
$\mathrm{p}\beta_{\mathrm{sne}}$	Pairwise phylogenetic nestedness
$\mathrm{p}\beta_{\text{sør}}$	Pairwise phylogenetic Sørensen dissimilarity index
S	Species richness
TD	Taxonomic diversity
tLCBD	Local contribution to taxonomic beta diversity
$\mathrm{t}p_{turn}$	Proportion of taxonomic turnover to taxonomic dissimilarity
tβ	Taxonomic beta diversity
$\mathrm{t}\beta_{\mathrm{sim}}$	Pairwise taxonomic turnover (Simpson dissimilarity index)
$\mathrm{t}\beta_{\mathrm{SIM}}$	Multi-site taxonomic turnover (Simpson dissimilarity index)
$\mathrm{t}\beta_{\mathrm{sne}}$	Pairwise taxonomic nestedness
$\mathrm{t}\beta_{\mathrm{SNE}}$	Multi-site taxonomic nestedness
$\mathrm{t}\beta_{\text{sør}}$	Pairwise taxonomic Sørensen dissimilarity index
$\mathrm{t}\beta_{\text{SØR}}$	Multi-site taxonomic Sørensen dissimilarity index
VU	Vulnerable

Chapter 1

General introduction

1.1 Background

Freshwater biodiversity facing threats

Freshwater habitats cover less than 1% of Earth's surface, yet they boast a remarkable biodiversity (Balian et al., 2008; Gleick, 1996). These indispensable freshwater habitats are home to 18,675 freshwater fish species, constituting approximately 40% of global fish species (Allen & Pavelsky, 2018; Fricke et al., 2024). Additionally, the fresh-water habitats support a diverse range of species including amphibians like frogs and salamanders, aquatic reptiles such as turtles and crocodiles, mammals including porpoises, otters, and platypuses. Overall, as many as one-third of all vertebrate species are confined to freshwater habitats (Dudgeon et al., 2006). Furthermore, a wide variety of organisms including plankton, algae, aquatic plants, wetland plants, aquatic macroinvertebrates, waterfowls, and even bears, rhinos, and elephants rely on freshwater habitats for their survival and are integral components of freshwater ecosystems (Smit & Ferreira, 2010; Ward et al., 2002). These diverse species contribute as a whole to the structure and stability of freshwater ecosystems through complex networks established by inter- and intraspecific relationship and interactions between species and habitat environments, allowing the implementation of material transfer, information exchange, and energy flow. Such disproportionate richness of freshwater species compared to the confined availability of freshwater habitats makes the freshwater ecosystem, and the biodiversity it supports, highly vulnerable to environmental changes (Dudgeon et al., 2006). A recent global assessment revealed that since the 1970s, populations of freshwater species have declined by over 80% on average, a rate far exceeding the declines seen in terrestrial and marine ecosystems (Grooten & Almond, 2018).

Undeniably, human activities are the principal trigger behind the drastic loss of biodiversity in freshwater ecosystems. Freshwater is a vital and irreplaceable resource for human life. Over thousands of years, human use of natural freshwater sources has often altered the physical, chemical, and biological properties of freshwater ecosystems (Carpenter et al., 2011). These changes have resulted in five primary threats to freshwater biodiversity: water pollution, flow modification, habitat destruction, overexploitation, and non-native invasion. These factors do not operate independently; rather, they interact and collectively exacerbate damage to freshwater biodiversity. Additionally, broader global changes driven by human activities, such as global warming, alterations in precipitation and evaporation patterns, and increased nitrogen deposition, compound these five threats (Dudgeon et al., 2006; Fenoglio et al., 2010). Despite the increasing calls and public awareness for the protection of freshwater ecosystems, the actions taken so far are still far from adequate (Sills et al., 2018).

Freshwater fish: Crucial biota of freshwater ecosystems

Freshwater fish play a crucial role in maintaining the stability and functionality of freshwater ecosystems by offering fundamental ecosystem services (Holmlund & Hammer, 1999; Villéger et al., 2017). Two types of fundamental ecosystem services were generated by fish populations: regulating services and linking services (Holmlund & Hammer, 1999). Regulating services involve the regulation of trophic structures through organism consumptions by fish, thereby dynamically regulating the stability, resilience, and food webs of freshwater ecosystems. Specifically, fish at higher trophic levels, including carnivorous and planktivorous species, significantly influence the dynamics of food webs and trophic balance by strong top-down controls (Carpenter et al., 1985). Additionally, the physical disturbance of sediments by some fish during their feeding and spawning activities, such as digging holes, is also classified under regulating services (Montgomery et al., 1996). Lastly, the process of influencing carbon-fixing capacity in the habitats and thus regulating carbon fluxes between the water and the atmosphere further exemplifies their regulating services (Schindler et al., 1997). Most linking services generated by fish are associated to their movement. Active links, such as the migration between foraging and resting areas or between fattening and spawning sites, are usually accompanied by material exchange (e.g., released carbon, nitrogen, phosphorus, and other organic matter by excreta, spermatophores, and dead individuals) across regions (Havn et al., 2017; Kashem et al., 2023). Correspondingly, passive links are established when fish are consumed by predators from aquatic, aerial, and terrestrial ecosystems (Sparholt, 1994).

Additionally, fish population are vital to human welfare, serving as ecological indicators, food sources and supporting recreational and cultural activities which are considered as the demand-derived ecosystem services (Holmlund & Hammer, 1999). Specifically, due to their large size, rapid growth, and high position in the food chain, fish are particularly sensitive to anomalous physicochemical properties the freshwater habitats, making them effective early warning for ecosystem stability and indicators of ecosystem resistance and resilience (Schindler, 1990). Furthermore, fish populations preserve traces of historic climate changes. Fish also generate optional values, act as a repository of genetic resources for potential future applications in medicine and aquaculture, spark human fascination with nature, and offer aesthetic and recreational benefits (Arlinghaus et al., 2019; Dudgeon et al., 2006).

However, the diversity of global freshwater fish is undergoing significant alterations through the homogenization process, which is directly caused by the loss of native species and the introduction of non-native species (Hoffmann, 1996; Su et al., 2021). Particularly, more than 25% of freshwater fish species are now at risk of extinction, particularly acute for native and endemic fish species (IUCN, 2023; Tickner et al., 2020).

Native fish assemblages needing conservation

Native freshwater fishes are vulnerable in this context and are among the groups experiencing the most dramatic declines in diversity (Mandrak & Cudmore, 2010; Williams et al., 2013). This vulnerability primarily stems from the extensive evolutionary adaptations of native fish to specific ecological conditions. The limited geographic ranges and specialized survival strategies of these native species have made it difficult for them to adapt to environmental changes, leading to their continued decline (Primack, 1995; Tabata et al., 2016). Such specializations render them susceptible when environmental factors like water quality, food resources, and predator presence undergo changes, as they struggle to adapt swiftly. Moreover, the introduced non-native fish often bring with them diseases and parasites lethal to native species and demonstrate superior resource competitiveness, intensifying survival challenges for native fish (Dominguez Almela et al., 2021; Kang et al., 2023). Genetic integrity is also at risk due to hybridization with non-native species, which can dilute the distinctive genetic traits and adaptive strengths of native populations. Concurrently, other human actions such as overfishing, pollution, and habitat destruction continue to indirectly pose significant threats to these native species (Pereira et al., 2010; Su et al., 2021).

Efforts to reverse the decline of native fish diversity have led to the planning and establishment of fish conservation areas specifically for threatened and endangered freshwater species (Kang et al., 2023). These conservation initiatives align with global conservation goals, such as the Kunming-Montreal Global Biodiversity Framework (UN Convention on Biological Diversity, 2022), national legislation such as the Steens Mountain Cooperative Management and Protection Act of 2000 that established the Donner und Blitzen Redband Trout Reserve in Oregon, US (Williams et al., 2011), and regional protection practice like the National Nature Reserve for Rare and Endemic Fishes in the Upper Yangtze River Basin in China (He et al., 2011). However, despite significant financial investments by agencies and conservation organizations, relatively few initiatives have been successfully realized (Williams et al., 2011). It has been reported that more than 40% of attempts to reintroduce native fish to their habitats have failed (Cochran-Biederman et al., 2015), and that most fish ex situ conservations are declared a failure an average of 9.2 years after translocation, when it is evaluated that they could not conclude successful reproductions or establishment of long-term viable populations (Bubac et al., 2019).

Neglected phylogenetic and functional evidence in native conservation

The focus on preserving the taxonomic number of fish species (Myers et al., 2000), while neglecting their diverse evolutionary histories and ecological roles, is often cited as a key reason for the ineffectiveness of traditional conservation efforts (Presley et al., 2018; Véron et al., 2019). Phylogenetic diversity sheds light on the evolutionary history of community species and their genetic relationships, potentially indicating the adaptive capacity of fish assemblages to environmental changes (Webb et al., 2002). Functional diversity analyses traits linked to species' roles in ecosystems, reflecting interactions among fish species and their utilization of environmental resources (Petchey et al., 2007; Violle et al., 2017). Recent research increasingly supports the use of these approaches from different perspectives to assess biodiversity expecting for effective conservation strategies (Jiang et al., 2020; Willig et al., 2023).

The inherent association between phylogenetic and functional diversity metrics is currently a subject of vigorous debate. Some research argues that phylogenetic diversity, which reflects a comprehensive representation of species' intrinsic and extrinsic characteristics, should be prioritized over functional diversity (Jiang et al., 2019; Owen et al., 2019). Whilst others contend that maximizing phylogenetic diversity does not reliably reflect the ecosystem functions, and therefore, functional diversity should take precedence in conservation efforts (Mazel et al., 2018). This debate is detailed in the next chapter. It is important to note that increasing research confirms a strong positive correlation between phylogenetic and functional diversity across biotas and different spatial scales. Besides, both types independently convey exclusive biodiversity information (Jiang et al., 2020; Xu et al., 2022). Consequently, more studies are moving away from advocating exclusively for one metric over the other. Instead, they are calculating both phylogenetic and functional diversity simultaneously, using them complementarily to guide conservation strategies (Li et al., 2021; Purschke et al., 2013; Swenson, 2011).

Lentic habitats: An ideal conservation area candidate

Establishment of Native Fish Conservation Areas (NFCA) requires consideration of the characteristics of different freshwater habitats, as well as understanding the ecological processes that could pose threats to biodiversity (Linke et al., 2012). The basic categories of freshwater habitats are lentic, lotic, and wetlands (Vaccari et al., 2005). Lentic habitats are characterized by slow-moving water, commonly found in lakes, that accumulate significant amounts of freshwater. Lotic habitats comprise speedily flowing waters, such as rivers and streams. Wetlands are areas where the soil is either permanently or intermittently saturated or inundated. These habitats are naturally interconnected through water flows, creating an extensive network that supports a diverse array of life forms within the ecosystem (Bracken & Croke, 2007). Among these, lentic habitats (taking lakes as an example) offer more stable hydrological conditions and richer nutrients compared to lotic and wetland habitats, hence supporting a greater diversity of fish species (Wang et al., 2019). Usually, lakes that are isolated or have limited connectivity within the same watershed often have distinct fish communities, much like aquatic islands (Rahel, 2007), each lake fostering unique freshwater fish community structures under varying environmental conditions (Amarasinghe & Welcomme, 2002; Ding et al., 2017). Besides, the clear and stable boundaries of lakes, along with their distinctive names, facilitate long-term research, the establishment of protected areas, and public involvement in conservation efforts (Jacobson et al., 2016). Therefore, analysing fish diversity patterns in lakes and establishing NFCAs centred on these lakes is a prevalent strategy for protecting native fish species. Such lake-based conservation efforts have been implemented in Minnesota, US (Minnesota Department of Natural Resources, 2013), as well as in the oxbow lakes of the Amazon freshwater systems in Madre de Dios, Peru (Barocas et al., 2021). Similar initiatives have also been proposed for lakes in the lower Yangtze River basin in China (Liu & Wang, 2010).

Species assembly process: A hint to native fish conservation

Studying how species form local communities is a core question in community ecology that could facilitate efforts in biodiversity conservation (Pettersen et al., 2022). The reassembly of ecological communities is primarily determined by two principal processes: stochastic processes and deterministic processes (Dai et al., 2024; Dini-Andreote et al., 2015). The neutral theory based on stochastic process assumes the community structures are primarily shaped by unpredictable events, such as dispersal limitation, drifts, or birth, death, colonization, speciation, and extinction (Chave, 2004; Deng et al., 2022; Ge et al., 2021). Meanwhile, another theory suggests that deterministic processes, such as environmental filtering and niche-related interspecific interactions, shape community structures (Chase & Myers, 2011; Yuan et al., 2019). In practical cases, by assessing the relative impacts of these two processes on the changes in native fish community structures, targeted conservation strategies for native fish can be developed (Ohira et al., 2015). Specifically, for communities primarily affected by stochastic processes such as dispersal limitation, the locations where dispersal limitation occurs could be considered as the ecological boundaries of potential conservation areas with appropriate spatial coverage, whereas for communities primarily affected by deterministic processes like niche competition, conservation usually involves measures such as the targeted provision of habitat conditions required by species of concern (Dai et al., 2024; Viana & Chase, 2019).

Freshwater fishes, confined to freshwater habitats, are particularly susceptible to topographic barriers compared to terrestrial and aerial species (Kuiper et al., 2023). It is widely acknowledged that watersheds act as natural boundaries; fish in lakes separated by different watersheds rarely intermingle, leading to the development of distinct community structures (Ding et al., 2017). Taking lakes on the Japanese archipelago as an example, due to the presence of the strait, it is nearly impossible for freshwater fish species inhabiting certain lakes to naturally expand their range to watersheds on other islands. In this context of the stochastic process represented by dispersal limitation, species composition and spatial distribution patterns of freshwater fish in lakes across Japanese archipelago provide an opportunity to explore the relative uniqueness of fish communities on the different islands separated by the strait, and thus implicitly the need for different conservation strategies on either side of the strait. Compared to inter-island dispersal at the national scale in Japan, the structure and distribution of fish communities within the same watershed face fewer dispersal constraints and are therefore primarily influenced by deterministic processes such as local environmental filtration and interspecific competition with non-native species. The Ishikari River basin, the largest on Hokkaido Island, features abundant oxbow lakes along the river maintaining similar lateral connectivity with the Ishikari River main channel. It is worth noting that non-native fish species have been recorded in oxbow lakes of the Ishikari River basin over the past century, predominantly originating from the southern islands of Japan (Hayashida et al., 2010). The introduction of these non-native fishes could plausibly have changed the assemblage structure and spatial distribution of the native fish communities. Moreover, since the early 21st century, this area has not undergone significant changes in land use, urban expansion, industrial pollution, or another extensive introduction wave of non-native fish species. This stability offers a prime setting to investigate the fish community structure dynamics predominantly driven by deterministic processes specifically the interactions between native and non-native fish fauna.

1.2 Study gap

Despite a bulk of studies on freshwater fish diversity across the Japanese archipelago (Matsuzaki et al., 2013, 2016; Watanabe et al., 2017), there is a notable lack of comprehensive research that simultaneously explores the diversity of native freshwater fishes from the taxonomic, phylogenetic, and functional perspectives. This gap in knowledge, particularly in phylogenetic and functional data, could undermine conservation efforts by missing critical aspects of fish protection. Moreover, there are few reports on simulating and projecting future trends in the diversity and distribution of fishes across Japan using a multifaceted approach to diversity. Undertaking such comprehensive studies could offer clear guidance for the conservation of Japanese native fishes and help make precise conservation strategies.

Additionally, the oxbow lakes in the Ishikari River basin offers a valuable opportunity to explore changes in the diversity and distribution of native fishes along a longitudinal river spatial gradient in a real-world setting. This area is predominantly influenced by the introduction of non-native fishes since the 21st century. In contrast, most other studies on fish diversity in floodplain oxbow lakes lack adequate samples to account for spatial longitudinal variations allied to river flow, or they cannot eliminate factors like the ongoing deterioration of biotic and abiotic environmental conditions during the study period (Ding et al., 2017; Wan & Zhong, 2014; Winemiller et al., 2000). Consequently, the research conducted in the Ishikari River basin can provide dependable insights into the diversity changes principally driven by interactions between native and non-native fishes.

Finally, while an increasing number of studies are now simultaneously employing taxonomic, phylogenetic, and functional diversity indices to analyse alpha, beta, gamma, and correlation indices of communities, the complexity and profusion of these metrics can complicate the generation of comprehensive conclusions. Consequently, there is a growing need for a new framework that consolidates these three perspectives to calculate diversity indices, which could enhance ecological research and bolster biodiversity conservation efforts.

1.3 Objective

This dissertation examined the spatiotemporal changes in the taxonomic, phylogenetic, and functional diversity of native freshwater fish assemblies in lakes across Japan over centuries (Chapters 3 and 6), and in oxbow lakes along the Ishikari River over a decade (Chapters 4–6), respectively. Spanning national and regional scales, and encompassing time frames from centuries to a decade, this study was conducted to address the study gaps mentioned above, with the specific objective outlined below.

- To analyse changes in the diversity of native fishes in the lakes across the Japanese archipelago from the historical to the present periods, using taxonomic, phylogenetic, and functional perspectives. Simulate the extinction scenarios of these fishes to predict future trends and identify key areas requiring urgent conservation efforts.
- To assess the impact of non-native fish expansion on the community structure of native fishes in the Ishikari River oxbow lakes from the 2000s to the 2010s, from taxonomic, phylogenetic, and functional perspectives. Identify potential refuges for native fishes that should be prioritized for conservation.
- To develop a new framework for calculating diversity indices that integrates taxonomic, phylogenetic, and functional diversities. This framework will be used to investigate and validate temporal changes in fish community structures at both national and regional cases.

1.4 Structure of the dissertation

Chapter 1: The current chapter. General introduction on background related to native freshwater fish diversity change and its conservation.

Chapter 2: This chapter outlines the methodology employed in this dissertation to assess multidimensional biodiversity. It provides an overview of the definitions, calculation methods, and ecological significance of taxonomic, phylogenetic, and functional biodiversity. The methods for calculating multidimensional alpha diversity, beta diversity, and the LCBD index are also detailed.

Chapter 3: This chapter quantifies changes in the taxonomic, phylogenetic, and functional alpha and beta diversity, as well as the LCBD of native fishes in 39 lakes across Japan from historical to current period. It also simulated future trends for native fishes in these lakes based on two scenarios. Additionally, lakes that require prioritized attention to prevent further loss of native fish species are identified.

Chapter 4: This chapter examines the changes in taxonomic diversity of native and non-native fishes in oxbow lakes along the Ishikari River from the 2000s to the 2010s. It specifically investigates whether species composition changes align with the longitudinal gradient from upstream to downstream along the river.

Chapter 5: This chapter builds on the findings of Chapter 4, delving deeper into the shifts in phylogenetic and functional diversity in relation to the diversity and distribution changes of native and non-native fishes in the oxbow lakes of the Ishikari River basin.

Chapter 6: This chapter proposes a new framework for calculating a cumulative diversity index that integrates taxonomic, phylogenetic, and functional diversity information. This index is applied to fish assemblages in lakes across Japan and in the Ishikari oxbow lakes. The analysis investigates whether the cumulative diversity index of fish communities in each lake correlates with their geographical location, aiding in the identification of priority areas for fish diversity conservation.

Chapter 7: This concluding chapter amalgamates the main findings of the dissertation in relation to the research objectives. It explores the theoretical implications of the discovered diversity patterns for the conservation of native Japanese fish and evaluates the potential application of the newly proposed cumulative diversity index to other biotas and regions.

Chapter 2

Assessment Approaches for Multidimensional Freshwater Fish Diversity

2.1 Taxonomic, phylogenetic, and functional diversity

Taxonomic diversity

Taxonomic diversity, which focuses on the count of species and their spatial distribution, is a fundamental indicator for describing biodiversity (Magurran, 1988). The taxonomic metrics offer a structured approach for evaluating the ecological variety within specific habitats or across broader ecological zones, enabling a systematic understanding of biological richness (He & Legendre, 2002; McGill, 2011). Historically, this species-level taxonomic perspective has dominated both ecological research and efforts to conserve biodiversity (Cannon et al., 1998; Myers et al., 2000). Maximizing taxonomic diversity has emerged as the explicit or implicit primary objective of current conservation policies (May, 1988). To quantify taxonomic diversity, abundant diversity indices have been developed, and the correlations among these indices continue to be explored (Chao & Chiu, 2016). Undoubtedly, these intuitive and accessible measurement methods have significantly advanced global biodiversity research, enhanced public awareness of conservation issues, and facilitated the establishment of conservation goals and actions (Leadley et al., 2022).

However, increasing studies suggest that traditional taxonomic diversity assessments might be overly simplistic, occasionally overlooking or misrepresenting critical ecological information (Biswas & Mallik, 2011; Dai et al., 2024; Jiang et al., 2020; Su et al., 2021). When measuring traditional taxonomic diversity, it is typically assumed that all species within a community hold equal value, focusing primarily on quantifying the dynamics of species numbers while neglecting the evolutionary history and survival strategies of each species (Devictor et al., 2010). In reality, even if two communities have the same taxonomic diversity, they might be composed of species with different phylogenetic backgrounds. Similarly, in regions where environmental filtering is strong, only species with certain functional traits may be able to get resources to survive, even though species richness may vary between different locations within the region. Therefore, in addition to traditional taxonomic diversity, considering both the phylogenetic diversity and the functional diversity of species is crucial for a deep understanding of the composition, structure, and dynamics of communities (Maherali & Klironomos, 2007; Xia et al., 2022). It is believed that such a comprehensive approach could be instrumental in guiding effective biodiversity conservation strategies.

Phylogenetic diversity

Phylogenetic diversity, reflecting the evolutionary history and complexity of species relationships within a community, is increasingly utilized in ecological studies (Owen et al., 2019; Srivastava et al., 2012). The phylogenetic structure of communities is often shaped over a long term by the environmental conditions of their habitats. These conditions and available resources continue to shape the phylogenetic structure of the communities, with this process being more pronounced in communities of native species (Ackerly et al., 2006; Jiang et al., 2019). Additionally, the phylogenetic diversity of a community could indicate its potential pre-adaptation to future environmental changes (Qian & Sandel, 2022; Ricciardi & Mottiar, 2006). Communities with high phylogenetic diversity may possess greater evolutionary potential because they encompass a broader array of genetic information. Furthermore, protecting phylogenetic diversity maintains the option value, such as the potential cure for future disease, preserving the potential for future ecological, medical, and technological benefits derived from the Earth's evolutionary legacy (Faith, 2018; Tucker et al., 2019).

Phylogenetic diversity calculations typically rely on phylogenetic trees, which represent the evolutionary relationships among species by measuring their relative distances and positions within a tree (Owen et al., 2019). Traditional methods involve extracting and comparing genetic information from all target species samples to construct these trees, offering a detailed molecular-level view of species affinities (Hugenholtz & Pace, 1996; Luebert & Scherson, 2024; Xu et al., 2022). However, this approach is costly, labour-intensive, and less feasible for extinct or rare species with limited sample availability. Alternatively, some studies use global species phylogenetic trees, matching local species lists against a global database to extrapolate the necessary branches for their specific phylogenetic tree (Rabosky et al., 2018; Xia et al., 2023). This method's effectiveness depends heavily on the database's comprehensiveness and its update frequency, which can pose challenges for accurately representing endemic species or those with recently changed scientific names. Consequently, many macroecological studies have shifted towards using Linnaean taxonomy classification as a proxy to circumvent the challenges of gathering genetic data and provide sufficiently reliable phylogenetic diversity insights (Cai et al., 2018; Heino & Tolonen, 2017; Jiang et al., 2020; Winter et al., 2013). Following this approach, in the present study, phylogenetic trees were constructed using the seven Linnaean taxonomic levels of fish species (subclass, subphylum, superorder, order, family, genus and species). Then, the phylogenetic diversity of the fish community was calculated based on such phylogenetic trees.

Functional diversity

The functional diversity assessment uses functional traits, defined as measurable biological characteristics of an individual that impact organism performance and fitness (Villéger et al., 2017; Violle et al., 2007). These traits are crucial for understanding how species respond to environmental changes and contribute to ecosystem functions. For instance, in fish communities, functional diversity is demonstrated through traits that influence ecosystem processes like food web dynamics, habitat modification, and nutrient cycling (Holmlund & Hammer, 1999). Additionally, functional traits help to distinguish species based on their functional redundancy or uniqueness, independent of their phylogenetic affiliation (Mouillot et al., 2014). Theoretically, in a community where multiple species share similar functional traits—indicating high functional redundancy—there tends to be greater resistance to environmental changes (Pimiento et al., 2020). Meanwhile, the loss of species with unique functional traits may indicate severe environmental alterations and have more obvious consequences than the extinction of species with redundant traits (Mouillot et al., 2013; Violle et al., 2017). Therefore, assessing functional diversity enables the generalization of species' functional contributions to ecosystems and allows considering the potential ecological impacts of their introductions and extirpations (Jiang et al., 2015).

The selection of appropriate functional traits is a prerequisite for measuring functional diversity. For fish species, the traits selected in the present study fall into all five primary functional categories: food acquisition, mobility, nutrient strategy, reproduction ability, and predation resistance (Villéger et al., 2017). One method to measure the functional diversity of a community involves establishing a multidimensional space with functional traits serving as axes and then observing how species are distributed within this space (Mammola et al., 2021). Two common techniques are the convex hull-based binary hypervolume (Villéger et al., 2013) and the density-based probabilistic hypervolume (Mammola & Cardoso, 2020). Another widely used method involves creating a distance dendrogram that represents distances between species based on functional traits and quantifying these distances on the functional distance dendrogram to gauge community functional diversity (Petchey & Gaston, 2002). This approach parallels the calculation of phylogenetic diversity, using tree-based distance calculations that facilitate the comparison and analysis of both phylogenetic and functional diversity. Hence, the present study utilized functional dendrograms to assess the functional diversity.

2.2 Alpha diversity

Alpha diversity is a fundamental concept in ecology that quantifies the species variety within a specific local area or ecosystem, providing insights into its biological complexity and ecological health (Whittaker, 1960). By measuring alpha diversity, ecologists can evaluate the overall size of the regional species pool and resilience of ecosystems to disturbances. This metric is essential for effective conservation planning, helping to highlight local hotspots and inform the placement of protected areas (Gering et al., 2003).

Taxonomic richness, a widely used alpha diversity index, plays a fundamental role in biodiversity conservation as it serves as a key indicator of alpha diversity. This metric quantifies the total number of different species within a specific area, aiding in the identification of biodiversity hotspots (Reid, 1998). In this study, we have compiled a comprehensive list of fish species. Each species' scientific name was meticulously verified using the latest versions of the online databases FishBase (Froese & Pauly, 2024) and Eschmeyer's Catalog of Fishes (Fricke et al., 2024). Additionally, we developed a binary fish incidence distribution matrix $\mathbf{Y} = [y_{ij}]$, which records the presence (1) or absence (0) of p fish species (represented as column vectors $\mathbf{y}_1, \mathbf{y}_2, \ldots, \mathbf{y}_p$ in $\mathbf{Y}$) observed across n lakes (represented as row vectors $\mathbf{x}_1, \mathbf{x}_2, \ldots, \mathbf{x}_n$ in $\mathbf{Y}$); y_{ij} represents the fish species i in lake j. This binary incidence distribution matrix helps mitigate biases arising from varying sampling intensities and enables consistent comparison of data collected by different teams and at different times. Accordingly, the sum of species recorded in a certain lake j, row $\mathbf{y}_j$ in $\mathbf{Y}$, is the taxonomic richness of that lake (S_j).

Phylogenetic richness quantifies the diversity of evolutionary lineages within a community, encapsulating the collective, unique evolutionary trajectories that have culminated in the current composition of species (Graham & Fine, 2008; Webb et al., 2002). This measure is critical for elucidating the depth and breadth of biodiversity, encompassing not merely the count of species present but also the evolutionary distances separating them (Jiang et al., 2019). In addition to phylogenetic richness, the concept of phylogenetic evenness is employed to evaluate the distribution of evolutionary heritage among the species in a community. This metric offers insights into the ecological equilibrium of habitats, revealing whether the community's structure is influenced by the predominance of closely related species or a more balanced dispersion of evolutionary lineages (Safi et al., 2011). In this research, we employed the Mean Phylogenetic Distance (MPD) and the Mean Nearest Phylogenetic Distance (MNPD) as the metrics for phylogenetic richness and evenness, respectively. Based on the generated phylogenetic dendrogram, the MPD metric calculates the mean phylogenetic distance between pairs of species randomly selected from a given fish assemblage in lake. On the other hand, the MNPD metric performs a similar calculation, but the distance between species pairs is measured only to their closest non-conspecific relative (Pinto-Ledezma et al., 2020; Vamosi et al., 2009; Zu et al., 2019).

Parallelly, functional richness and evenness can be assessed based on the functional trait distance dendrogram (Swenson, 2014). Functional richness reflects the range of ecological roles and traits present, indicating the breadth of ecological strategies and adaptations in a community. Functional evenness, on the other hand, measures how uniformly these traits are distributed among species, which can indicate the balance of ecological functions and resource usage (Mammola et al., 2021). To calculate functional diversity, we employed two indices—Mean Functional Distance (MFD) and Mean Nearest Functional Distance (MNFD)—derived from methods from the aforementioned phylogenetic alpha diversity indices (Xu et al., 2022). This adaptation allows the indices to reflect the spread and clustering of functional traits within a community, thus providing a clear picture of how traits influence ecological dynamics.

2.3 Beta diversity

Beta diversity is measured by calculating the relative composition dissimilarity between communities, which describes the heterogeneity of community structure (Whittaker, 1960). This calculation reveals the assembling processes within a specific spatial range and reflects the fundamental principles that maintain the structure and diversity patterns of the regional communities (Socolar et al., 2016). Increasingly, research across fields such as ecology, evolutionary biology, biogeography, and conservation biology is exploring the importance of community beta diversity. More and more researchers use beta diversity patterns to simulate the spatial distribution of communities, define biogeographic boundaries, and predict the evolutionary processes of virous biotas (Dai et al., 2020; Ding et al., 2017; Graham et al., 2006; Moritz et al., 2001). In the field of conservation biology, quantitative analysis of community beta diversity helps in the selection of conservation areas, planning of spatial extents, and selection of key species by providing theoretical support, as it can accurately reflect the differences in species composition between different areas and their patterns of species exchange (Jiang et al., 2020; Su et al., 2021).

To further investigate the species/phylogeny/traits (for the sake of simplicity, these will be referred to as species hereafter) dynamics that shape community beta diversity patterns, researchers have studied the patterns of species differences among communities (Jiang et al., 2019; Jiang et al., 2020; Si et al., 2016). They propose that community beta diversity patterns are formed by two processes: mutual replacement and unidirectional flow of species between communities (Baselga, 2007; Harrison et al., 1992). These processes are conceptualized as *turnover* and *nestedness*, two additive components for overall beta diversity, respectively (Baselga, 2010). Turnover refers to the replacement of some species by others from another community, usually resulting from environmental sorting or spatial and historical constraints (Qian et al., 2005). Nestedness indicates the continuous loss or gain of species in communities, leading communities to become subsets of larger communities or amalgamations of smaller ones, reflecting a non-random species removal process during community disassembly (Gaston & Blackburn, 2000). For example, in areas of high beta diversity, high community beta diversity patterns can arise from the mutual replacement of different species between communities (where turnover is the primary component); alternatively, they can emerge from significant differences in species richness between two communities, where one community encompasses the species of smaller communities (where nestedness is the primary component). It is important to emphasize that while many matrix configurations are possible (Almeida-Neto et al., 2008), all scenarios where communities differ can be characterized by just two main patterns—turnover and nestedness—or their combinations (Baselga, 2010). These patterns suffice to account for all possible community configurations through the processes of species replacement and species loss or gain. It must be pointed out that the term species loss (or gain) is used here simply to denote the absence of certain species from specific communities, irrespective of the underlying reasons, such as extinction or differential dispersal capabilities. (Ulrich et al., 2009). To properly understand biodiversity patterns and their underlying causes—patterns that may indicate different processes—distinguishing between the two components is necessary (Williams et al., 1999). In this context, the two processes, turnover and nestedness, that form the basis of beta diversity measurements are not just distinct; they are contradictory (Williams, 1996).

To measure the taxonomic beta diversity between communities, the Sørensen dissimilarity index ($t\beta_{sør}$) is frequently utilized (Si et al., 2017). Considering the extensive geographic range of this study, which encompasses three major islands of Japan and the Ishikari River basin, respectively, and given that the fish data are incidence-based, the Sørensen index is deemed the most appropriate diversity index (Dai et al., 2020). The Sørensen index spans from 0 to 1, where a value of 0 signifies that the species composition of the two communities is the same, and a value of 1 indicates completely distinct community compositions. At this juncture, the Simpson dissimilarity index ($t\beta_{sim}$) is used to further quantify the taxonomic turnover pattern between communities (Lennon et al., 2001). Based on the mathematical concept of beta diversity partitioning, $\beta_{sør} \equiv \beta_{sim} + \beta_{sne}$, the difference between the Sørensen and Simpson indices reflects the extent of taxonomic nestedness ($t\beta_{sne}$) between communities (Baselga, 2010). The indices $t\beta_{sør}$, $t\beta_{sim}$, and $t\beta_{sne}$ are formulated as:

$$t\beta_{sør} = \frac{b+c}{2a+b+c} \tag{2.3}$$

$$t\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)} \tag{2.4}$$

$$t\beta_{sne} = \frac{\max(b,c)-\min(b,c)}{2a+\min(b,c)+\max(b,c)} \times \frac{a}{a+\min(b,c)} \tag{2.5}$$

where a represents the number of species shared by both sites, b is the number of species found only at the first site, and c is the number of species present only at the second site.

A phylogenetic tree that represents the evolutionary relationships of all species in a region is fundamental for measuring regional phylogenetic beta diversity between communities. Typically, the phylogenetic tree of a single community's species composition is a subset of the regional phylogenetic tree. Quantifying phylogenetic beta diversity involves comparing the distribution of species from different communities on the regional tree. This approach is analogous to taxonomic beta diversity, which examines the shared and distinct species between communities, but phylogenetic diversity calculations focus on the shared or distinct branches of the phylogenetic trees among communities. Mathematically, replacing the variables that denote the number of species, a, b, and c, in Equation 2.3 with variables that reflect the lengths of the phylogenetic branches allows for similar computational methods to be used to measure phylogenetic beta diversity. Similarly, metrics for phylogenetic diversity turnover and nesting can be calculated using comparable methods. Specifically, consider a tree T composed of all species within a region,

with each branch *t* having a branch length w_t. The phylogenetic diversity of the trees T_j and T_k, representing
communities j and k respectively, can be denoted by $PD_j = \sum_{T_j} w_j$ and $PD_k = \sum_{T_k} w_k$. The branch length of the phylogenetic tree constructed by the specie shared by both communities *j* and *k* (still a subset of the regional tree) is represented as

$PD_{Tol} = \sum_{T_j \cup T_k} w_t$ (Leprieur et al., 2012). Henceforward, the phylogenetic beta

diversity ($\mathrm{p\beta_{sør}}$), including its turnover ($\mathrm{p\beta_{sim}}$) and nestedness ($\mathrm{p\beta_{sne}}$) components, can be calculated using the following equations.

$$\mathrm{p\beta_{sør}} = \frac{PD_{Tot} - PD_j + PD_{Tot} - PD_k}{2(PD_j + PD_k - PD_{Tot}) + PD_{Tot} - PD_j + PD_{Tot} - PD_k}$$

$$= \frac{2PD_{Tot} - PD_k - PD_j}{PD_k + PD_j} \qquad 2.6$$

$$\mathrm{p\beta_{sim}} = \frac{\min(PD_{Tot} - PD_j, PD_{Tot} - PD_k)}{PD_j + PD_k - PD_{Tot} + \min(PD_{Tot} - PD_j, PD_{Tot} - PD_k)} \qquad 2.7$$

$$\mathrm{p\beta_{sne}} = \mathrm{p\beta_{sør}} - \mathrm{p\beta_{sim}} \qquad 2.8$$

Likewise, functional beta diversity ($\mathrm{f\beta_{sør}}$), along with functional turnover ($\mathrm{f\beta_{sim}}$) and nestedness ($\mathrm{f\beta_{sne}}$), can be computed using the same method, but by substituting the phylogenetic tree with a dendrogram that represents distances based on functional traits.

Additionally, to determine whether turnover or nestedness predominantly influences the overall beta diversity pattern among communities, the p_{turn} index is commonly evaluated (Jiang et al., 2020; Si et al., 2016). This index measures the contribution of the turnover component to the overall beta diversity. A p_{turn} index above 0.5 suggests that turnover is the primary driver of community differences, whereas a value below 0.5 indicates that nestedness primarily dictates inter-community dependency. The p_{turn} index is calculated from taxonomic ($\mathrm{t}p_{turn}$), phylogenetic ($\mathrm{p}p_{turn}$), and functional ($\mathrm{f}p_{turn}$) perspectives:

$$\mathrm{t}p_{turn} = \frac{\mathrm{t\beta_{sim}}}{\mathrm{t\beta_{sør}}} \qquad 2.9$$

$$\mathrm{p}p_{turn} = \frac{\mathrm{p\beta_{sim}}}{\mathrm{p\beta_{sør}}} \qquad 2.10$$

$$\mathrm{f}p_{turn} = \frac{\mathrm{f\beta_{sim}}}{\mathrm{f\beta_{sør}}} \qquad 2.11$$

2.4 Local Contribution to Beta Diversity

The Local Contribution to Beta Diversity (LCBD) index has been introduced to quantitatively assess the relative importance of fish communities within individual lakes in shaping regional fish beta diversity patterns (Legendre & De Cáceres, 2013), which is becoming widely utilized in ecological studies (da Silva et al., 2018; Dai et al., 2020; De et al., 2023; Hill et al., 2021). In the context of matrix **Y**, the LCBD values are assessed as the proportion of the sum of squares corresponding to the *j*th lake (SS_j) in the total sum of squares of matrix **Y** (SS_{total}). For lake j, the LCBD$_j$ could be calculated following the equation below (Legendre & De Cáceres, 2013). The notations of components in the following equation are consistent with what was introduced in Section 2.2 in the current chapter.

$$tLCBD_j = \frac{SS_j}{SS_{total}} = \frac{\sum_{j=1}^{n}\left(y_{ij} - \bar{y}_j\right)^2}{\sum_{i=1}^{p}\sum_{j=1}^{n}\left(y_{ij} - \bar{y}_j\right)^2} \qquad 2.12$$

It is worth noting that this calculation was designed for a taxonomic species matrix and does not take into account phylogenetic and functional information. Therefore, the prefix *t-* is used here to differentiate it from the phylogenetic (pLCBD) and functional (fLCBD) LCBD assessment discussed below.

Shooner et al. (2018) proposed a method to calculate pLCBD using a matrix of phylogenetic distance. Subsequently, Nakamura et al. (2020) refined the approach and extended it to the calculation of fLCBD. Both pLCBD and fLCBD calculations are based on the fish incidence distribution matrix **Y**, but it must be redescribed to include information on the distribution of clades and traits among communities. This step involves constructing resemblance matrices for phylogeny and functional traits, $\mathbf{S_p}$ and $\mathbf{S_f}$, with each element comprising similarities between a species pair. The phylogenetic matrix $\mathbf{S_p}$ is obtained by calculating the total branch length connecting any two species nodes on the phylogenetic tree and then converting these distances into similarities. Analogously, the functional matrix $\mathbf{S_f}$ can be generated by calculating trait distances between species pairs and transforming them into similarities, as described above. These matrices, $\mathbf{S_p}$ and $\mathbf{S_f}$, are then standardized by their respective column totals and multiplied by the transposition of **Y** to produce new matrices **P** and **F**, representing the phylogenetic and functional compositions of fish assemblages across lakes, respectively. In short, through the intermediation of the phylogenetic and functional resemblance matrices $\mathbf{S_p}$ and $\mathbf{S_f}$, the original taxonomic matrix **Y** is reweighted by phylogenetic and functional relationships, allowing the newly formed phylogenetic matrix **P** and functional matrix **F** to assess the contributions of fish assemblages in specific lakes from phylogenetic and functional perspectives by measuring the proportion that each lake accounts for of the total variation presented in **P** and **F**, respectively.

Overall, the LCBD index provides a straightforward method to evaluate the relative distinctiveness of fish assemblages in particular lakes. The multidimensional LCBD is particularly useful for conservation, as it helps identify sites that warrant special attention due to their unique species composition, evolutionary history, and functional traits (Nakamura et al., 2020). Generally, higher LCBD values indicate that a lake may have a unique combination of species/phylogeny/traits, suggesting significant conservation value or urgent necessities for conservation actions (Legendre & De Cáceres, 2013).

2.5 Gamma diversity

Gamma diversity represents the total species diversity within a large geographic region or landscape, encompassing multiple ecosystems and habitats. It integrates both alpha and beta diversity, highlighting the complexity and richness of biodiversity at a broader scale (Crist et al., 2003). In this research, the focus is primarily on alpha and beta diversity to provide a detailed and nuanced understanding of biodiversity patterns within and between specific ecosystems. While gamma diversity offers valuable insights at a broader regional scale (Jost et al., 2010; Zhang et al., 2014), the decision to concentrate on alpha and beta diversity allows for a more precise examination of native fish richness and compositional changes at finer spatial scales. This targeted approach ensures a thorough investigation of biodiversity dynamics, which is critical for localized conservation strategies and ecological management practices. Future studies may build upon these findings by incorporating gamma diversity to extend the scope of biodiversity assessments to larger landscapes.

2.6 Algorithmic resources utilized for diversity assessments

The phylogenetic and functional dendrograms were generated in R (R Core Team, 2024) using a combination of functions from various packages, including VEGAN (Oksanen et al., 2022) and APE (Paradis & Schliep, 2019). Taxonomic richness of fish assemblages in each lake was obtained with the aid of the software PRIMER (Clarke & Gorley, 2015). The calculations of phylogenetic (MPD, MNPD) and functional (MFD, MNFD) alpha diversity were performed in R using the package PICANTE (Kembel et al., 2010). Taxonomic ($t\beta_{\text{sør}}$), phylogenetic ($p\beta_{\text{sør}}$), and functional ($f\beta_{\text{sør}}$) beta diversities, as well as their respective turnover ($t\beta_{\text{sim}}$, $p\beta_{\text{sim}}$, $f\beta_{\text{sim}}$) and nestedness ($t\beta_{\text{sne}}$, $p\beta_{\text{sne}}$, $f\beta_{\text{sne}}$) components, of fish assemblages were calculated with the aiding of the package BETAPART (Baselga et al., 2022) in R. Taxonomic LCBD (tLCBD) index was assessed by utilizing the R package ADESPATIAL (Dray et al., 2022), whilst the phylogenetic (pLCBD) and functional (fLCBD) ones were calculated with the help of the R function `Beta.div_adapt()` developed by Nakamura et al. (2020). It should be noted that the calculation of all diversity indices throughout this study (Table 2.1) follows the methods and approaches outlined in this chapter, even though the fish incidence matrixes utilized in subsequent chapters vary.

Table 2.1 Summary of the primary diversity indices used in this study.

	Taxonomic	Phylogenetic	Functional
Alpha	**S**: species richness	**MPD**: mean phylogenetic distance between species pairs **MNPD**: mean nearest phylogenetic distance between species pairs	**MFD**: mean functional distance between species pairs **MNFD**: mean nearest functional distance between species pairs
Beta	$\mathbf{t\beta}_{\text{sør}}$: overall species dissimilarity $\mathbf{t\beta}_{\text{sim}}$: species turnover $\mathbf{t\beta}_{\text{sne}}$: species nestedness	$\mathbf{p\beta}_{\text{sør}}$: overall phylogenetic dissimilarity $\mathbf{p\beta}_{\text{sim}}$: phylogenetic turnover $\mathbf{p\beta}_{\text{sne}}$: phylogenetic nestedness	$\mathbf{f\beta}_{\text{sør}}$: overall functional dissimilarity $\mathbf{f\beta}_{\text{sim}}$: functional turnover $\mathbf{f\beta}_{\text{sne}}$: functional nnestedness
LCBD	**tLCBD**: local contribution of one lake to regional taxonomic beta diversity	**pLCBD**: local contribution of one lake to regional phylogenetic beta diversity	**fLCBD**: local contribution of one lake to regional functional beta diversity

Chapter 3

Native fish assemblages in natural lakes across Japan: Endemism deterioration lasting centuries

3.1 Introduction

The global biodiversity crisis, an alarming decline in the variety of life on Earth, has put nearly one million species at risk of extinction (Díaz et al., 2019; Sills et al., 2018; Singh, 2002). With its roots in anthropogenic activities, the crisis has accelerated since the mid-20th century (Steffen et al., 2015), when pollution, habitat destruction and fragmentation, invasive species, overexploitation, and climate change became more pronounced (Dirzo et al., 2014; Foley et al., 2005; Haddad et al., 2015; Noyes et al., 2009; Pecl et al., 2017). Freshwater ecosystems undergo a significant rate of biodiversity loss, nearly four times higher than that of terrestrial ecosystems (Albert et al., 2021; Turak et al., 2017). Freshwater fishes rank as the second most endangered group of vertebrates, surpassed only by amphibians in terms of threat levels (Arthington et al., 2016; Darwall & Freyhof, 2015). The list of extinct fish continues to grow with new extinction records worldwide (Reid et al., 2019). Nonetheless, this silent crisis, concealed below water, has not received adequate public, political, or scientific attention (Cooke et al., 2016). Hence, it is urgent to propose appropriate conservation strategies for freshwater fish assemblages towards the post-2020 goals and targets negotiated at the 15th meeting of the Conference of the Parties to the United Nations Convention on Biological Diversity (COP15).

Amidst the global biodiversity crisis, native fishes, especially those endemic to specific regions, are considered the most affected group within aquatic systems, accounting for a significant proportion of the overall loss of freshwater species (Dudgeon et al., 2006). Endemic fish species developed morphological, physiological, reproductive, feeding, and behavioural adaptations during long-term evolutionary processes, enabling them to thrive under specific ecological conditions of their local habitat context (Braaten & Guy, 2002; Chapman et al., 2011; Schulte, 2001; Wainwright & Richard, 1995; Werner & Hall, 1988). In addition, some endemic fish species with narrow distributional ranges could be attributed to historical geographic events, such as tectonic movements and volcanic activity (Crandall et al., 2010; Salzburger et al., 2014). However, disturbance or destruction to ecosystems often poses a challenge for endemic species, making it difficult for them to adapt to the altered environment and leading to declines in their populations and, in some instances, extinction. The loss of endemic fish species can disrupt local ecosystems, leading to nutrient cycling and food web imbalances while impacting local economies and cultural practices that depend on these species (Ding et al., 2023; Reis et al., 2015). Protecting endemic fish populations through diverse conservation measures has become one of the utmost priorities at the present moment.

Re-establishing essential ecological processes is a practical approach to fish conservation, necessitating an integrated and efficient framework for understanding assembling processes of fish assemblages (Jiang et al., 2020; Radinger et al., 2023). A growing consensus among ecologists has come to acknowledge that, alongside traditional taxonomic diversity, phylogenetic relatedness and functional composition offer valuable insights into the community assembling mechanisms. Phylogenetic distances among species reflect their evolutionary histories and can reveal ecological differences (Webb et al., 2002). Native species extinctions are not random occurrences within hierarchical phylogenetic trees; instead, they expose the life history responses of these species to environmental changes (Fréville et al., 2007; Winter et al., 2009). Extinctions disproportionally impact native or endemic fish species, often originating from families with lower species richness and representing unique components of their biotas (Gaston, 1998; Vamosi & Wilson, 2008). Functional diversity assessments consider the functional traits of fish species, enabling direct inferences about ecological responses to environmental alterations. For example, by examining morpho- anatomical traits related to food acquisition, researchers can assess the effects of fish on other aquatic organisms through trophic interactions (Villéger et al., 2017). Although the importance of phylogenetic and functional diversity indicators for conservation is widely acknowledged, prioritizing one over the other remains a debated issue (Mazel et al., 2018; Owen et al., 2019). Concurrently, numerous phylogenetic and functional diversity indices and computational approaches have emerged in the past decades, proposing various perspectives on ecosystem functions and services. However, these metrics' intricacy presents challenges to researchers and policymakers involved in native fish conservation (Tuomisto, 2010). Pursuing a concise and comprehensive index that integrates taxonomic, phylogenetic, and functional information is thus a pressing concern in practical conservation biology.

Native conservation necessitates understanding biodiversity organization from local to regional spatial scales, thereby aiding conservation planning (Gardner et al., 2013; Socolar et al., 2016). Alpha and beta diversity of community serve as vital tools for analysing species assembling within local sites and among distinct locations, respectively (Veech et al., 2002). Measuring the multifaceted alpha diversity can identify local biodiversity hotspots and guide the establishment of protected areas (Jiang et al., 2020). Meanwhile, assessing the multifaceted beta diversity, including its turnover and nestedness components, can guide decisions on the numbers and locations of conservation sites from a broader scale (Gering et al., 2003; Simberloff & Abele, 1976). Spatial turnover quantifies the extent to which species are exchanged between communities, while nestedness reflects unidirectional concentration of species among communities (Baselga, 2010). If the turnover pattern is the primary driver of beta diversity, conservation measures should prioritize protecting several locations with unique species; while if the nestedness pattern is more important, the conservation approach targeting areas that exhibit high alpha diversity would be adequate (Jiang et al., 2019; Tscharntke et al., 2002; Tuomisto et al., 2003). Furthermore, the recently widely utilized LCBD index holds significant value in conservation studies (Legendre & De Cáceres, 2013). It measures the uniqueness of a community at each study site within a larger region. High LCBD values, which represent unique species composition, help prioritize specific locations for conservation efforts and assess the effectiveness of these strategies over time (Dai et al., 2023). Hence, by employing concurrent measurements of alpha and beta diversity, as well as related metrics, conservation-related insights can be gained comprehensively, supporting efforts to prevent additional loss of biodiversity at both local and regional scales (Jiang et al., 2020; Montaño-Centellas et al., 2020).

The Japanese archipelago, stretching about 2,000 km in a northeast-southwest direction, is an ideal natural laboratory to study spatial patterns of freshwater fishes. During the Plio-Pleistocene (about five million years ago), the archipelago was frequently connected and disconnected from continental Asia, thereby leading to a unique freshwater fish fauna (Lindberg, 1972; Watanabe et al., 2017). Stemmed from continental Asia, freshwater fishes established themselves in the Japanese archipelago through two main pathways: the Siberian route and the Chinese route (Aoyagi, 1957). The Siberian route involved predominantly cold-water fishes spreading from the Heilongjiang River (aka the Amur River) to the waters in Hokkaido, the northernmost island of present-day Japan (Kai, 2022). The Chinese route witnessed a fish fauna primarily composed of temperate species originating from the ancient Yellow River basin, relocating to Kyushu, the southernmost main island of Japan (Tabata, 2022). Subsequently, fishes from Hokkaido and Kyushu made their way to Honshu, Japan's largest island in the middle (see Figure 1 for island locations), yielding a unique spatial pattern of freshwater compositions across the Japanese archipelago. According to previous research, native freshwater fishes in the Japanese archipelago experienced alterations due to escalating environmental and artificial pressures, as evidenced by a decline in species richness and significant shifts in functional group composition from roughly two centuries ago (Matsuzaki et al., 2013, 2016). However, these studies did not consider phylogenetic information and regional beta diversity patterns of native fishes across the nation. Phylogenetic information reflects the historical and ecological uniqueness of fish species and suggests the foundation for adapting to environmental changes. Failure to measure phylogenetic diversity could result in gaps within comprehensive fish conservation initiatives. Additionally, without depicting regional fish dissimilarity patterns among the studied lakes using beta diversity they did not provide direct evidence for identifying specific areas for practical conservation measures. What's more, previous studies have only examined alterations in fish diversity spanning from the historical to the current period, yet without conducting quantitative analyses to anticipate potential future trends. Considering that the fish species lost during this transition are primarily threatened species identified as at risk of extinction by the Japanese Red List, simulating future native extinctions based on the fish species in the current period and their categories in the Red List is deemed a viable approach to address this gap.

In this context, the chapter emphasizes regional fish beta diversity and spatial distribution patterns, supplemented with phylogenetic information of native freshwater fishes in lakes across Japan. Specifically, this chapter analyses and compares the changes over time in the multifaceted alpha and beta diversity of native fishes in Japanese lakes from the past to the present and anticipates future trends. In addition, by utilizing multidimensional LCBD framework, this chapter attempted to pinpoint the specific lakes that possess greater conservation priority. Ultimately, this chapter will provide direct theoretical support for restoring and conserving freshwater ecosystems in Japan amidst the ongoing biodiversity crisis.

3.2 Methods

Data collection and collation

This chapter utilized the native freshwater fish assemblage data in 39 Japanese lakes (Figure 3.1, Table 3.1) from the previous research (Matsuzaki et al., 2013; 2016). These lakes, situated between 30° and 45° north latitude, broadly scatter across the majority of eco-regions for freshwater fish fauna in Japan (Watanabe, 2012), with areas ranging from less than 1 km^2 to approximately 670 km^2, and their average depths differ by over 51 m. Additionally, lakes with various trophic statuses are encompassed, including oligotrophic, mesotrophic, and eutrophic lakes. Covering such a wide range of latitude, eco-region, area, depth and trophic status, the studied lakes are considered representative of Japanese lakes in general. The native fish dataset was compiled by reviewing over 300 references and over 1 000 museum specimens, as described by Matsuzaki et al. (2016). To avoid redundancy, these sources are not reiterated here. This chapter, however, focuses on a different lake than the one examined by Matsuzaki et al. (2016) Specifically, high-altitude lakes around Mt. Fuji were excluded from this study due to their relative isolation and low native fish diversity. Moreover, the methodology and time periods used in this study, particularly the historical and current periods, closely adhere to the setup of Matsuzaki et al. (2016) to ensure consistent data comparability across different periods. Although the sampling methods of fish collection in the referenced literature varied among lakes, fish records from all studied lakes were cross corroborated by at least three different sources to ensure the validity of the fish species records in the lakes. In addition, only fish incidence (presence/absence) rather than abundance data was used in this study, further excluding biased results that may have been caused by different sampling intensities (Dai et al., 2023). This chapter specifically targeted strict freshwater fish species (i.e., fish that remain their entire life cycles in freshwaters) that inhabit lakes and those that migrate between lakes and surrounding drainage basins. As previously described by Matsuzaki et al. (2016), distributional records of the strict freshwater fish in both “historical” and “current” periods were obtained. The historical period refers to the native fish fauna of the past, specifically before massive anthropogenic extirpation, and roughly corresponds to the pre-Meiji Era, a period characterized by rapid industrialization and modernization in Japan. Thus, the historical period fish dataset contains the greatest number of native freshwater fish species. The current dataset indicates that some species are becoming locally unrecorded, reflecting changes in the distribution patterns of native fish species since the 21st century.

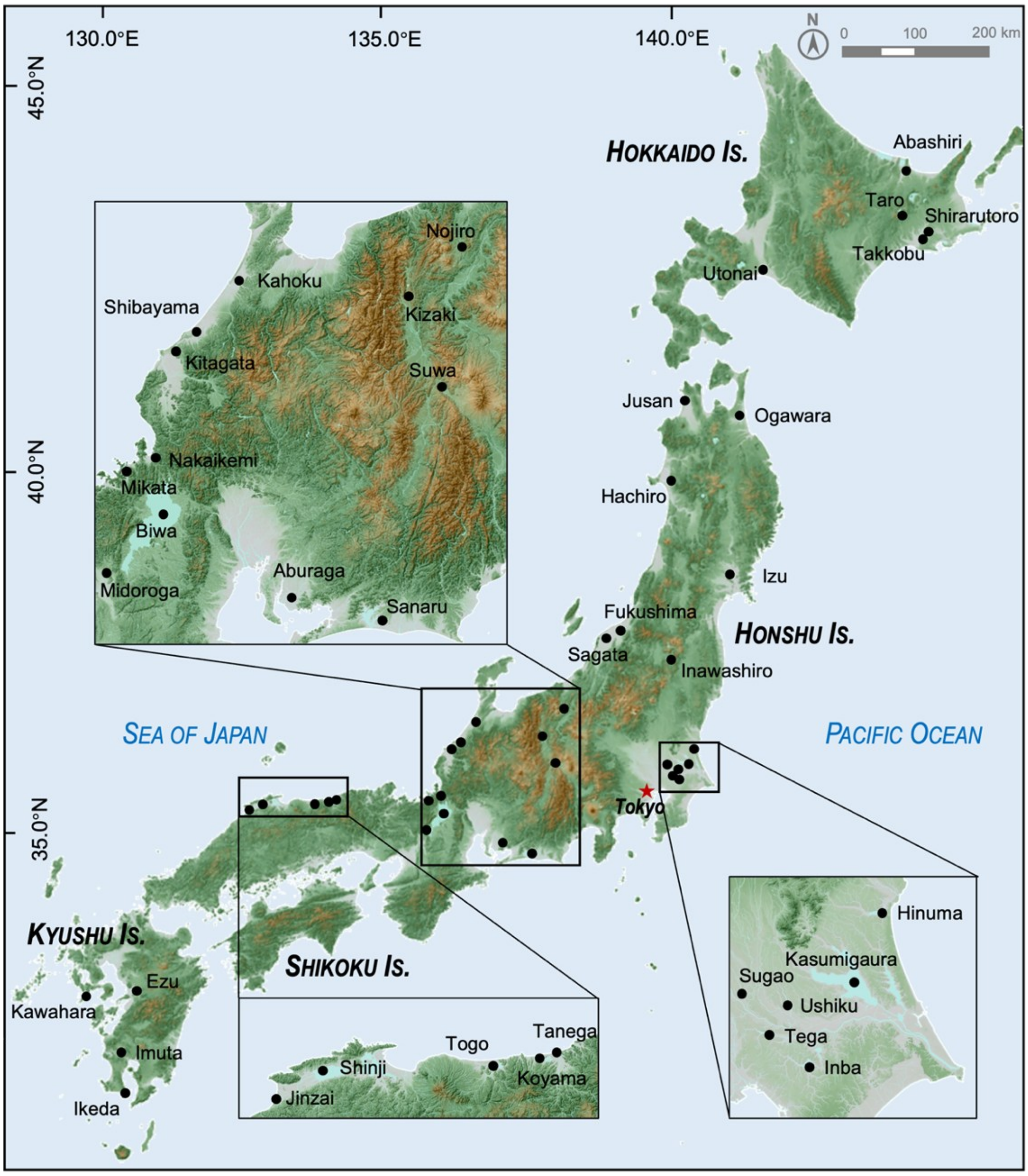


Figure 3.1 Map showing the location of 39 studied lakes across the Japanese archipelago. Derived based on Takemura (2015).

Considering that ninety percent of the unrecorded fish species from past to present were designated as threatened, either critically endangered (CR), endangered, (EN) or vulnerable (VU) (Table 3.2), according to the Japanese Red List (Ministry of the Environment, 2020), this research emulated two extinction scenarios based on the current-period fish datasets following Pimiento et al. (2020). The first scenario, dubbed "future I", involved categorizing species as extinct or extant according to the associated extinction probability of their respective red list category. According to the results of Davis et al. (2018), which estimated the probability of extinction for species across different categories over a 100-year period under the current conservation status, fish species were excluded from the records of all lakes based on respective probabilities for different categories.

Table 3.1 Location and basic information on the studied lakes.

Lake	Latitude (°N)	Longitude (°E)	Prefecture	Area (km^2)	Max.depth (m)	Volume (km^3)
Abashiri	43.967	144.167	Hokkaido	33.000	16.10	0.233
Shirarutoro	43.433	144.141	Hokkaido	1.720	2.30	0.003
Toro	43.179	144.502	Hokkaido	6.270	7.00	0.020
Takkobu	43.105	144.484	Hokkaido	1.310	3.00	0.003
Utonai	42.699	141.711	Hokkaido	2.100	1.50	0.002
Ogawara	41.033	140.342	Aomori	61.980	25.00	0.714
Jusan	40.783	141.333	Aomori	17.810	3.00	-
Hachiro	39.917	140.017	Akita	27.750	12.00	-
Izu	38.719	141.101	Miyagi	3.320	1.30	-
Inawashiro	37.910	139.247	Fukushima	103.240	94.60	5.400
Fukushima	37.817	138.875	Nigata	1.930	0.60	-
Sagata	37.483	140.100	Nigata	0.436	-	-
Hinuma	36.825	138.222	Ibaraki	9.300	6.50	0.020
Ushiku	36.649	136.675	Ibaraki	3.550	3.00	-
Sugao	36.558	137.838	Ibaraki	2.300	1.20	-
Kasumigaura	36.351	136.377	Ibaraki	220.000	7.10	0.850
Tega	36.275	140.500	Chiba	4.020	3.80	0.006
Inba	36.272	136.242	Chiba	9.430	2.50	0.003
Kizaki	36.058	136.768	Nagano	1.690	29.50	0.025
Suwa	36.049	138.085	Nagano	12.810	7.20	0.063
Nojiri	36.035	140.391	Nagano	4.450	38.50	0.096
Shibayama	36.029	139.914	Ishikawa	1.920	4.90	4.600
Kahoku	35.946	140.130	Ishikawa	4.200	6.50	14.700
Kitagata	35.857	140.032	Fukui	2.160	4.00	0.006
Mikata	35.748	140.191	Fukui	3.580	5.80	0.005
Nakaikemi	35.660	136.088	Fukui	0.250	-	-
Sanaru	35.566	135.884	Shizuoka	1.130	2.50	0.002
Aburaga	35.535	134.238	Aichi	0.640	5.00	0.002
Biwa	35.508	134.151	Shiga	669.260	103.58	27.500
Midoroga	35.476	133.894	Kyoto	0.090	3.50	-
Koyama	35.450	132.958	Tottori	6.990	7.50	0.020
Togo	35.329	136.161	Tottori	4.050	3.60	0.006
Tanega	35.327	132.682	Tottori	0.020	15.10	0.001
Shinji	34.905	137.013	Tottori	79.250	6.40	0.340
Jinzai	34.711	137.690	Tottori	1.140	10.00	
Ezu	32.774	130.742	Kumamoto	0.490	5.00	0.001
Imuta	32.624	129.832	Kagoshima	0.630	2.70	0.001
Ikeda	31.817	130.472	Kagoshima	10.910	233.00	1.380
Kawahara	31.233	130.567	Nagasaki	0.120	9.00	-

Table 3.2 Table presenting a list of freshwater fish species recorded in the Japanese archipelago, along with their respective extinction risk category (Cat.) evaluated by the Japanese Red List 2020. CR: Critically endangered, EN: Endangered, VU: Vulnerable, NT: Near threatened, LP: Endangered local population, NE: Not evaluated. The presence or absence of a species is denoted by "○" and "×" for the historical (H) and current (C) periods, indicating whether the species was recorded or not during those periods. For the future II (F) period, "○" represents the retention of the species, while "×" indicates exclusion during the extinction simulation. (*For the native *Cyprinus carpio* population in Lake Biwa, which was assessed as LP, only the records in Lake Biwa were removed in the extinction simulation.)

Species	Cat.	H	C	F	Species	Cat.	H	C	F
Cyprinus carpio	LP	○	○	○*	*Pungtungia herzi*	NE	○	○	○
Carassius cuvieri	EN	○	○	×	*Gnathopogon elongatus*	EX	○	○	×
Carassius auratus	NE	○	○	○	*Gnathopogon caerulescens*	CR	○	○	×
Tanakia tanago	CR	○	×	×	*Biwia zezera*	VU	○	○	×
Tanakia lanceolata	NT	○	○	○	*Pseudogobio esocinus*	NE	○	○	○
Tanakia limbata	NT	○	○	○	*Hemibarbus longirostris*	NE	○	×	×
Acheilognathus melanogaster	EN	○	○	×	*Hemibarbus labeo*	NE	○	○	○
Acheilognathus tabira	EN	○	○	×	*Squalidus gracilis*	NE	○	○	○
Acheilognathus rhombeus	NE	○	○	○	*Squalidus japonicus*	VU	○	○	×
Acheilognathus cyanostigma	CR	○	○	×	*Squalidus chankaensis*	VU	○	○	×
Acheilognathus longipinnis	CR	○	×	×	*Parabotia curtus*	CR	○	×	×
Acheilognathus typus	CR	○	×	×	*Misgurnus anguillicaudatus*	NT	○	○	○
Rhodeus ocellatus	CR	○	×	×	*Cobitis biwae*	NE	○	○	×
Rhodeus atremius	CR	○	○	×	*Cobitis matsubarae*	VU	○	○	×
Ischikauia steenackeri	CR	○	○	×	*Cobitis striata*	VU	○	○	×
Hemigrammocypris neglectus	EN	○	○	×	*Barbatula barbatula*	NE	○	○	○
Opsariichthys uncirostris	VU	○	○	×	*Lefua nikkonis*	EN	○	○	×
Zacco platypus	NE	○	○	○	*Lefua echigonia*	EN	○	○	×
Nipponocypris temminckii	NE	○	○	○	*Tachysurus nudiceps*	NE	○	○	○
Nipponocypris sieboldii	NE	○	○	○	*Tachysurus tokiensis*	VU	○	○	×
Rhynchocypris sachalinensis	NT	○	○	○	*Tachysurus aurantiacus*	VU	○	×	×
Rhynchocypris lagowskii	NE	○	○	○	*Silurus lithophilus*	NT	○	○	○
Rhynchocypris oxycephalus	NE	○	○	○	*Silurus biwaensis*	NE	○	○	○
Pseudorasbora parva	NE	○	○	○	*Silurus asotus*	NE	○	○	○
Pseudorasbora pumila	CR	○	×	×	*Liobagrus reini*	VU	○	×	×
Pseudorasbora pugnax	CR	○	×	×	*Oryzias latipes*	VU	○	○	×
Sarcocheilichthys biwaensis	CR	○	○	×	*Odontobutis obscura*	NE	○	○	○
Sarcocheilichthys variegatus	NT	○	○	○					

However, it should be noted that Davis et al. (2018) simplifies changes in species populations to an exponential model. These extinction probabilities are likely to be optimistically conservative, as the number of species predicted to go extinct is typically smaller than the actual observed values. For instance, species categorized as VU were assigned a minimum extinction probability of 0.1 over the next century (Kindvall & Gärdenfors, 2003; Mooers et al., 2008; Redding & Mooers, 2006). Specifically, during one round of simulation, this research simultaneously and randomly excluded 99.90%, 67.23%, and 10.00% of fish species from each of the CR, EN, and VU categories, respectively. This process resulted in a new fish distribution table, which served as a subset of the fish distribution dataset for the current period. Diversity indices based on the pruned fish distribution matrix were then calculated. After completing both the species removal and diversity calculations, we reintroduced the excluded species for a new round of simulations and calculations. This entire sequence of steps was repeated 1 000 times to ensure statistical robustness. The average of the 1,000-time diversity index calculations was subsequently recorded as the measure of diversity among native fishes in lakes across Japan for the "future I" period. The second scenario, termed "future II", assumes the extinction of all currently threatened fish species (Barnosky et al., 2011; Smiley et al., 2020). This scenario aimed to illustrate the potentially dire consequences of threatened native fish loss if no conservation measures are implemented and emphasize the collective contribution of these species to fish biodiversity assemblages (Toussaint et al., 2016).

Phylogenetic and functional dendrogram construction

The Linnaean classifications of all recorded native fishes were arranged in a phylogenetic dendrogram across seven levels: subclass, subphylum, superorder, order, family, genus, and species. The classification information was subjected to a double comparison between Fishes of the World (Nelson et al., 2016) and Eschmeyer's Catalog of Fishes (Fricke et al., 2023). If there were any conflicting classifications, the latest version was adopted. Following Matsuzaki et al. (2016), this chapter opted to employ 16 functional traits (maximum total body length, body shape, trophic guild, dietary components, diet breadth, foraging period, vertical position, temperature preference, flow preference, substrate preference, age at maturation, parental protection, egg diameter, longevity, fecundity, and spawning substrate) that reflecting these crucial ecological functions to construct a functional dendrogram (Table 3.3). Furthermore, a Mantel test was conducted, performed in r with the vegan package, to evaluate the correlation between the two dendrograms,

Table 3.3 Functional traits used for functional diversity measurements. Traits data were obtained from Matsuzaki et al. (2016).

Functional trait	Type	Unit/Category/Describe
Maximum total body length	Numeric	cm
Body shape	Categorical	Compressed, fusiform, cylindrical, dorso-ventrally flattened
Trophic guild	Categorical	Omnivore, herbivore, detritivore, invertivore, piscivores
Dietary components	Categorical	Plant/algae/detritus, zoobenthos, plankton, aquatic and terrestrial insect, fish/egg, amphibian/mammals/bird
Diet breadth	Integral	Total number of major diet items
Foraging period	Binary	Diurnal, nocturnal
Vertical position	Categorical	Demersal, benthopelagic, pelagic
Temperature preference	Binary	Warm, cool
Flow preference	Categorical	Fast, moderate, slow
Substrate preference	Categorical	General, silt/mud, sand, rubble
Age at maturation	Numeric	a
Parental protection	Binary	Care, no care
Egg diameter	Categorical	0-1.5, 1.5-3.0, >3.0 mm
Longevity	Categorical	≦1, 2-4, 5-9, ≧10 a
Fecundity	Categorical	0-1000, 1000-100 000, >100 000 eggs
Spawning substrate	Categorical	Vegetation, mussels, mineral, pelagic, various

with the aim of determining whether there were significant overlaps between the two trees (Figure 3.2). The Mantel test produced a relatively low coefficient value, suggesting that only a limited amount of functional information was found to overlap with phylogenetic signals (Xu et al., 2022). Consequently, in the subsequent assessments of native fish diversity, two dendrograms were separately evaluated.

Multifaceted biodiversity assessment

This chapter assesses the multifaceted native fish diversity of 39 Japanese lakes across different four periods using respective fish incidence distribution matrices: historical, current, and two simulated futures, Future I and Future II. Building on the methods introduced in Chapter 2, this analysis includes alpha diversity measures in taxonomic (S), phylogenetic (MPD, MNPD), and functional (MFD, MNFD) diversity. Additionally, this chapter examines beta diversity in these same categories ($t\beta_{sør}$, $p\beta_{sør}$, $f\beta_{sør}$), along with the components of turnover ($t\beta_{sim}$, $p\beta_{sim}$, fβ_{sim}) and nestedness (tβ_{sne}, pβ_{sne}, fβ_{sne}), respectively. This chapter also quantifies the proportion of turnover patterns within the total beta diversity framework. Lastly, this chapter evaluates the relative importance of the native fish assemblages in each lake from taxonomic (tLCBD), phylogenetic (pLCBD), and functional (fLCBD) perspectives regarding their contribution to the national beta diversity patterns during these four periods.

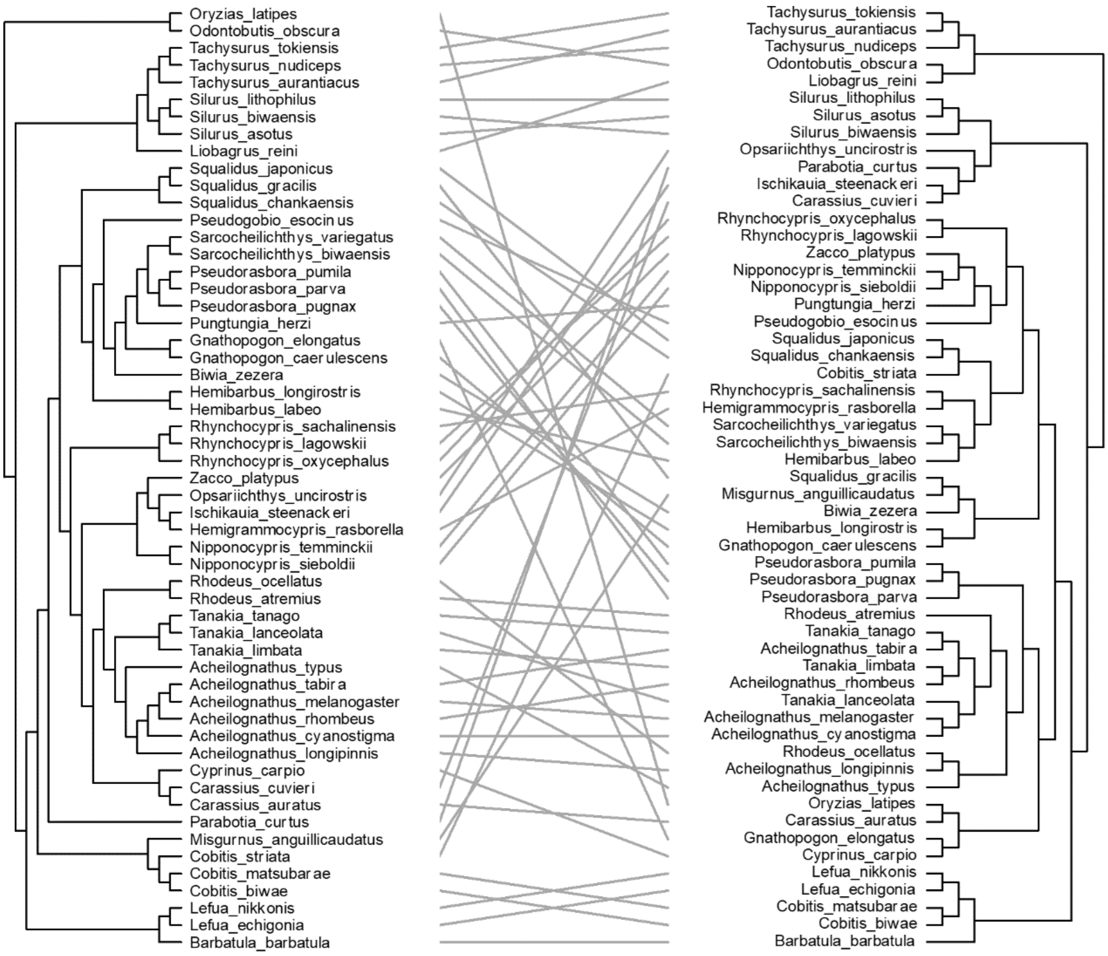


Figure 3.2 Associations between the phylogenetic (left) and functional (right) dendrogram. The coefficient of the correlations between two dendrograms are 0.412 (Mantel test, $p < 0.001$). The branch lengths in the figure are standardized to reflect their topological structures. The same species on two dendrograms are connected by grey lines.

Statistical analysis

First, a comparative analysis of the discrepancies in the values of each measured alpha and beta diversity index and related metrics across the four temporal periods was conducted to discern the temporal trends in the diversity of native fish assemblages within the Japanese lakes. This was accomplished by utilizing the one-way permutational multivariate analysis of variance with 9,999 permutations to assess the differences among four datasets, which comprised the diversity indices of fish fauna in all studied lakes during the historical, current, future I, and future II periods, respectively. Then, a three-dimensional spatial coordinate system was constructed, utilizing the taxonomic, phylogenetic, and functional LCBD indices as the three respective axes. Lakes exhibiting relatively greater ecological uniqueness were identified according to the positions within this three-dimensional space. In this context, lakes with greater relative importance (ecological uniqueness of species composition) refer to those with LCBD index values surpassing the mean values of the corresponding indices (Duarte et al., 2022; Sor et al., 2018).

3.3 Results

Temporal changes in multidimensional alpha diversity

In the studied lakes across Japan, an enumeration of 55 freshwater fish species, categorized into 29 genera and 13 families, was recorded in the historical period,

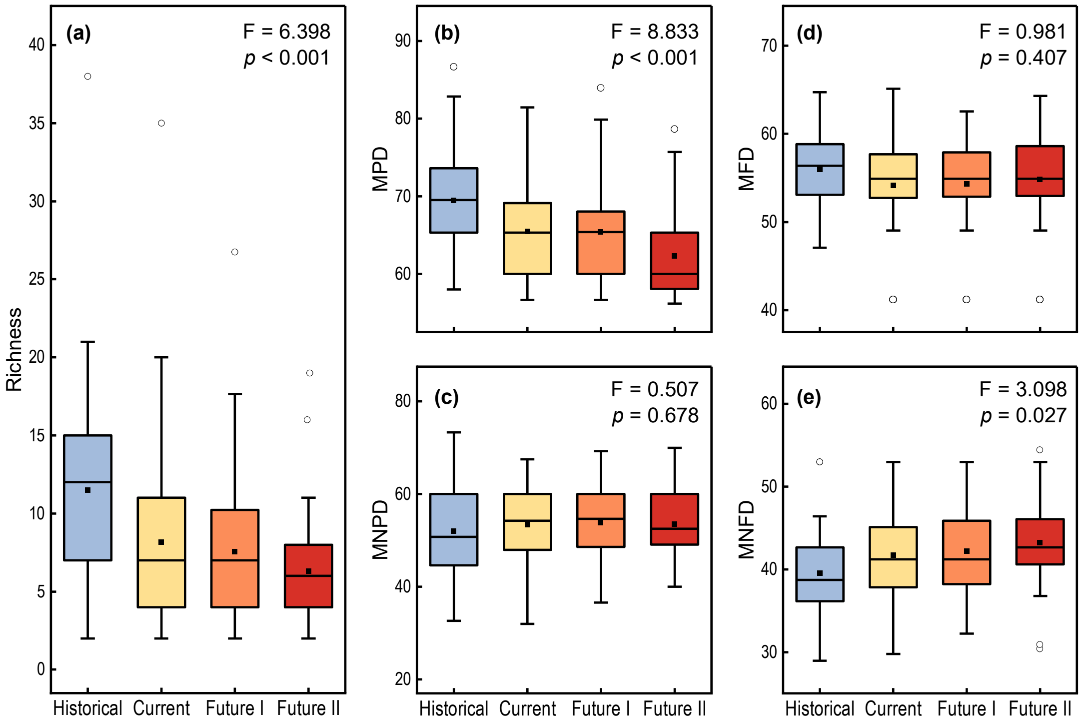


Figure 3.3 Boxplots showing taxonomic alpha diversity (Richness, a), two phylogenetic alpha diversity: mean phylogenetic distance (MPD, b) and mean nearest phylogenetic distance (MNPD, c), and two functional alpha diversity: mean functional distance (MFD, d) and mean nearest functional distance (MNFD, e) for freshwater fish across historical (blue), current (yellow), future I (orange), and future II (red) periods.

of which 30 species were designated as threatened, according to their present, not historical, conservation status. In the current period, after the 21st century, a total of 45 native freshwater fish species were recorded, of which nine out of the ten extirpated species were classified as threatened. In the two scenarios of extinction simulations, 35 species were preserved for future I and 23 for future II period. The PERMANOVA results demonstrate that native fish richness is significantly decreased from the historical to current period (F = 5.252, $p = 0.019$). However, the phylogenetic and functional alpha diversity exhibited divergent trends. A substantial decline in the MPD index from the historical period to future (F = 8.833, $p < 0.001$) was observed, while simultaneously, the alterations in MNPD values remained insignificant across all periods ($p = 0.678$). Contrarily, for functional diversity indices, little changes were observed in MFD values throughout the time ($p > 0.407$), but MNFD values consistently and significantly rose across four periods (F = 3.098, $p = 0.027$).

Temporal changes in multidimensional beta diversity

Unlike the monotonic alterations in alpha diversity across all periods, the changes in beta diversity over time exhibited significant hump-shaped trends ($p < 0.019$, Figure 3.4; Table 3.5). During the historical periods, the average tβ, pβ, and

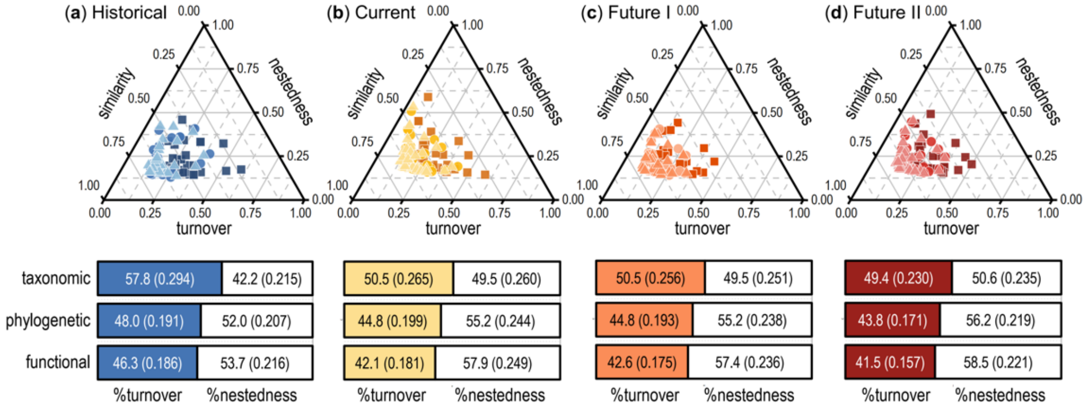
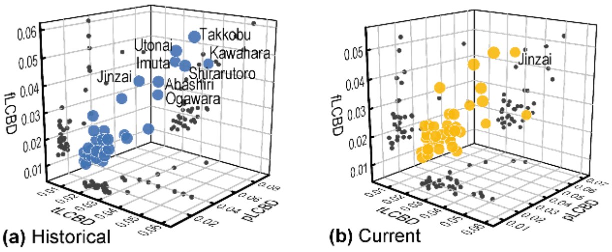


Figure 3.4 Triangular plots depict the beta diversity of freshwater fish populations during the historical (blue, a), current (yellow, b), future I (orange, c), and future II (red, d) periods. The three axes, ranging from zero to one, denote similarity and two aspects of beta diversity (turnover and nestedness). Individual points on the plots represent beta diversity in a specific lake, each from a different measurement: taxonomic (square), phylogenetic (circle), and functional (triangle). Bar charts beneath each triangular plot, from top to bottom, illustrate the proportions of taxonomic, phylogenetic, and functional turnover (coloured) and nestedness (white) to the overall beta diversity, respectively. Proportional values of turnover metrics are accompanied by their mean values in parentheses.

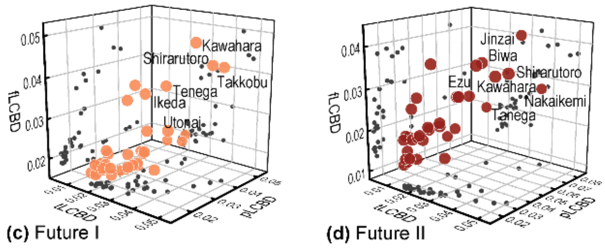
fβ values were 0.059 ± 0.096, 0.398 ± 0.092, and 0.402 ± 0.087 (mean ± SD), respectively. These beta diversity indices then experienced an increase till the current periods to 0.525 ± 0.081, 0.443 ± 0.065, and 0.430 ± 0.068. However, as for the simulated results, in the future I period, there was a decrease in these beta diversity values, which continued to fall in the future II period to 0.465 ± 0.086, 0.390 ± 0.067, and 0.377 ± 0.069, respectively. Meanwhile, a steady decline was noted in the proportion of turnover patterns. While taxonomic turnover was the primary factor influencing species beta diversity in the historical period (contributing to 57.8% of overall dissimilarity, Figure 3.4a), its dominance began to equalize with the nestedness pattern during both the current and future I period (accounting for 50.5%, Figure 3b,c). This dominance eventually lessened in the future II period, with its proportion falling below 50% (Figure 3.4d). However, the influence of phylogenetic and functional turnovers consistently remained lower than that of nestedness and continued diminishing over time (Figure 3.4; Table S4).

Lakes with unique fish assemblages

By positioning the studied lakes in a three-dimensional coordinate space based on their tLCBD, pLCBD, and fLCBD values, the lakes whose indices exceeded the corresponding mean in all three dimensions were pinpointed, as labelled in Figure 3.5. These particular lakes were indicated to possess the most unique native fish compositions. During the historical period, eight lakes were identified with the most unique species composition. These lakes displayed tLCBD, pLCBD, and fLCBD values exceeding their respective average values simultaneously. Notably, the lakes with the highest LCBD values were concentrated in the northernmost (Hokkaido) and southernmost (Kyushu) islands. However, in the simulated future I and II, the number of unique lakes increased to six and seven, respectively, and the majority of them were located in central and western Honshu rather than Hokkaido or Kyushu.



(a) Historical (b) Current



(c) Future I (d) Future II

Figure 3.5 The three-dimensional plots demonstrate LCBD values for studied lakes during the historical (a), current (b), future I (c), and future II (d) periods. Each axis represents a different aspect of LCBD: tLCBD, pLCBD, and fLCBD. Lakes with all three LCBD values exceeding their respective means are labelled by their names.

Table 3.4 Statistic results of one-way PERMANOVA (with 9,999 permutations) comparing significance of differences across five alpha diversity indices over four time periods. Results include summary of overall measures and detailed pairwise comparisons. *P* values below 0.05 are highlighted in bold, while those between 0.05 and 0.1 are in italics.

Metric	Comparison		F	*p*
Richness	Summary		6.398	**< 0.001**
	Pairwise	Historical vs Current	5.252	**0.019**
		Historical vs Future I	8.747	**0.003**
		Historical vs Future II	17.990	**< 0.001**
		Current vs Future I	0.243	0.638
		Current vs Future II	2.707	0.107
		Future I vs Future II	1.624	0.211
MPD	Summary		8.833	**< 0.001**
	Pairwise	Historical vs Current	7.571	**0.008**
		Historical vs Future I	7.821	**0.006**
		Historical vs Future II	27.370	**< 0.001**
		Current vs Future I	0.002	0.971
		Current vs Future II	5.555	**0.023**
		Future I vs Future II	5.388	**0.023**
MNPD	Summary		0.507	0.678
	Pairwise	Historical vs Current	0.628	0.430
		Historical vs Future I	1.094	0.300
		Historical vs Future II	0.742	0.400
		Current vs Future I	0.075	0.785
		Current vs Future II	0.003	0.953
		Future I vs Future II	0.053	0.824
MFD	Summary		0.981	0.407
	Pairwise	Historical vs Current	2.922	*0.091*
		Historical vs Future I	2.261	0.138
		Historical vs Future II	1.068	0.310
		Current vs Future I	0.033	0.858
		Current vs Future II	0.308	0.580
		Future I vs Future II	0.143	0.713
MNFD	Summary		3.098	**0.027**
	Pairwise	Historical vs Current	3.070	*0.085*
		Historical vs Future I	4.797	**0.031**
		Historical vs Future II	9.424	**0.003**
		Current vs Future I	0.119	0.733
		Current vs Future II	1.337	0.252
		Future I vs Future II	0.704	0.405

Table 3.5 Statistic results of one-way PERMANOVA analysis (with 9,999 permutations) comparing significance of differences across beta diversity indices over four time periods. Results include summary of overall measures and detailed pairwise comparisons. *P* values below 0.05 are highlighted in bold, while those between 0.05 and 0.1 are in italics.

Comparison		Taxonomic		Phylogenetic		Functional	
		F	*p*	F	*p*	F	*p*
Dissimilarity							
Summary		3.467	**0.018**	4.745	**0.003**	3.463	**0.018**
Pairwise	Historical vs Current	0.594	0.444	6.380	**0.014**	2.431	0.127
	Historical vs Future I	0.008	0.935	3.274	*0.070*	0.244	0.620
	Historical vs Future II	4.574	**0.034**	0.159	0.689	2.042	0.155
	Current vs Future I	0.907	0.346	0.824	0.364	1.447	0.239
	Current vs Future II	10.000	**0.003**	12.610	**< 0.001**	11.610	**0.001**
	Future I vs Future II	5.122	**0.028**	7.264	**0.010**	4.741	**0.030**
Turnover							
Summary		2.804	**0.040**	1.036	0.378	1.349	0.253
Pairwise	Historical vs Current	1.650	0.209	0.226	0.637	0.097	0.761
	Historical vs Future I	3.214	*0.073*	0.012	0.913	0.528	0.463
	Historical vs Future II	9.414	**0.003**	1.700	0.193	4.251	**0.041**
	Current vs Future I	0.141	0.713	0.118	0.740	0.122	0.715
	Current vs Future II	2.244	0.138	2.448	0.116	2.237	0.139
	Future I vs Future II	1.412	0.237	1.652	0.200	1.432	0.228
Nestedness							
Summary		1.911	0.131	1.808	0.141	1.267	0.284
Pairwise	Historical vs Current	4.628	**0.033**	4.002	**0.043**	2.747	*0.097*
	Historical vs Future I	3.509	*0.065*	2.896	*0.092*	1.167	0.287
	Historical vs Future II	1.221	0.282	0.552	0.454	0.060	0.802
	Current vs Future I	0.146	0.708	0.133	0.717	0.410	0.533
	Current vs Future II	1.381	0.246	1.941	0.175	2.170	0.146
	Future I vs Future II	0.687	0.404	1.113	0.296	0.756	0.395

3.4 Discussion

This chapter demonstrated the deterioration process of native fishes across the Japanese lakes. As the decline of native fish species continues, species that are functionally close are particularly vulnerable to the threat of local extinction. These species, often ranked as threatened in the Japanese Red List (Ministry of the Environment, 2020), are the first to vanish from the lakes, leading to a nationwide homogenous distributional pattern. Besides, this chapter pinpointed that the lakes situated in Hokkaido and Kyushu islands have pronouncedly lost their fish endemism. The findings of this chapter suggested that the decline of native fish species, along with the fish homogenization and endemism loss, is an ongoing process that will exacerbate without immediate, specific conservation actions, especially for threatened fish species. Large-scale, ongoing processes such as climate change and urbanization, driven primarily by human activities, have been identified as key factors contributing to the decline in global freshwater fish diversity over the past few centuries, significantly altering environmental conditions in freshwater ecosystems (Closs et al. 2016; Strayer & Dudgeon, 2010). For instance, rising temperatures and altered precipitation patterns disrupt aquatic ecosystems, affecting fish physiology and migration patterns. Extreme weather events, such as floods and droughts, further degrade habitats. Urbanization exacerbates these effects by destroying natural habitats through construction, deforestation, and pollution. Runoff from urban areas introduces harmful chemicals and waste into water bodies, while dams and water diversions fragment habitats, impeding fish movement.

The results of the decline of native fish alpha diversity revealed that the shrinking of phylogenetic and functional dendrograms was not synchronized. The incongruent findings reported in this study are consistent with those of previous research (Devictor et al., 2010; Jiang et al., 2020; Purschke et al., 2013; Xu et al., 2022), suggesting that examining changes in community diversities using either perspective alone might lead to biased conclusions. This chapter observed that the branches lost in the phylogenetic tree tended to be more distant and isolated, while species with closer phylogenetic associations were retained, resulting in decreasing MPD values while the MNPD values remained unchanged. In contrast, the degradation of functional dendrograms showed a preferential loss of species from groups with high functional similarity, while keeping the basic skeleton of functional tree intact, leading to stable MFD values accompanied by increasing MNFD values. The contrasting degradation of phylogenetic and functional alpha diversity can be explained by the complementary nature of phylogenetic and functional information (Galland et al., 2019). Phylogenetic relations generally reflect internal preadaptation to novel environments, whereas functional similarity suggests phenotypic characteristics related to interspecific resource competitions (Xu et al., 2022). Phylogenetic diversity reveals species'' abilities adapted to local environmental conditions over long periods of evolution, especially physiological traits such as heat tolerance and low oxygen tolerance (Collins et al., 2013; Comte & Olden, 2017; Karabanov et al., 2021). The result of conserved phylogenetic shrinking lends support to the theory that disturbances tend to select assemblages of phylogenetically close species, as these species are more likely to share similar resistance abilities (Helmus et al., 2010). Given that the majority of the fish species that were the first to be lost in this research were predominantly endemic or rare fish with restricted habitats, their early disappearance indicates the limited inherent resilience and heightened susceptibility to environmental shifts of endemic fishes. The vanishing of these imperilled species correlates with a reduction in phylogenetic dendrogram branch (evidenced by decreased MPD values), underscoring the urgent need for heightened conservation efforts and closer scrutiny of these unique and scarce species. Meanwhile, the findings of this study reveal a clear trend of decreased functional redundancy in native fish assemblages, indicating that species with similar traits have similar resource utilization patterns and, thus, high levels of competition, ultimately leading to a greater risk of local extinction. This finding also highlights the importance of functional redundancy in ecosystem stability, which provides insurance against species loss (Chua et al., 2019; Oliver et al., 2015; Xu et al., 2022).

Homogenization is a significant issue in global freshwater biodiversity (Su et al., 2021). This study also revealed a clear homogenization trend in the Japanese archipelago lakes. Beta diversity is crucial for biodiversity conservation since it reveals the variations in species composition and distribution across different habitats or regions, enabling targeted conservation strategies and the preservation of diverse ecological communities (Socolar et al., 2016). The findings of this chapter suggest that the loss of native fish species in Japanese lakes was independent, resulting in an initial increase and a subsequent drastic decrease in fish composition dissimilarity. Although high beta diversity can reflect high habitat heterogeneity and ecological resistance in some cases with abundant and stable species pools, this study highlights the need for caution when interpreting beta diversity results, particularly in the context of shrinking species pools. As an empirical demonstration of the conceptual trajectory proposed by Socolar et al. (2016), illustrating the typical patterns of beta diversity change in response to anthropogenic disturbances, this study corroborates the transient increase in beta diversity at the early onset of ongoing biodiversity degradation processes at a long temporal scale. Accordingly, a comprehensive assessment and detection of species diversity patterns, in combination with within-site richness and among-site dissimilarity, is a prerequisite for effective conservation efforts. Moreover, during the historical period, the high beta diversity pattern of native fishes throughout Japan was dominated by species turnover, indicating the presence of unique endemic fishes in scattered lakes. However, with species loss, especially when species with high extinction risk were excluded, the dominant patterns of overall beta diversity shifted to nestedness patterns. This means that, during fish homogenization, more fish assemblages become subsets of certain species-rich lakes, such as Lake Biwa. Moreover, the proportions of turnover patterns in taxonomic, phylogenetic, and functional aspects are consistently decreasing over time, while there is a rising trend in nestedness across all three perspectives. It's worth highlighting that, during the historical period, the percentage of taxonomic turnover sites (tp_{turn}) remained approximately 60%. This value consistently exceeded 50% until Future II, where it declined to 49.4%. In contrast, the contributions of phylogenetic (pp_{turn}) and functional (fp_{turn}) turnover were consistently below 50%, demonstrating a steady decline alongside decreasing species richness. The persistently higher taxonomic turnover compared to phylogenetic and functional turnover proportions may be attributed to the heightened sensitivity of phylogenetic and functional diversity indicators.

The LCBD results pronouncedly highlight the endemism degeneration of fish species in Hokkaido and Kyushu. Within the historical period, eight lakes were identified with high ecological uniqueness. These lakes encompassed 80% of the investigated lakes on Hokkaido Island and half on Kyushu Island. This observation posits that barring anthropogenic interference, lakes on the northernmost (Hokkaido) and southernmost (Kyushu) islands harbour exceedingly unique fish fauna. Moreover, most native fish species found on these two islands are not shared, underlining the paramount role of these distant lakes in fostering respective endemic species. This historical pattern of distinctiveness resonates with the function of Hokkaido and Kyushu as the northern and southern gateways for the dispersion of freshwater fish from continental Asia to the Japanese archipelago (Aoyagi, 1957; Watanabe et al., 2017). However, the lakes making the most significant contributions to the national beta diversity patterns of fish are shifting from those in Hokkaido and Kyushu to certain lakes on Honshu Island. These Honshu lakes typically exhibit higher levels of species richness, phylogenetic diversity, and functional richness. As unique endemic fish species progressively vanish, especially from lakes in Hokkaido and Kyushu, the importance of these species-rich lakes in Honshu becomes more pronounced. This trend is corroborated by an increasing presence of nestedness patterns in beta diversity partitioning.

By comparing fish records from historical and current periods, this study found that species of the bitterling group (Family Acheilognathidae) accounted for about 40 percent of the species that have not been recorded in the current period. The number of bitterling species native to Japan is relatively small, and their distribution range is narrow. Bitterling species has a short lifespan, specialized reproduction methods (highly relying on freshwater mussels), and a relatively small number of eggs laid in a single spawning event (Smith et al., 2004). Additionally, non-native Bitterling species introduced from China and the Korean Peninsula are encroaching on the already narrow niche due to their high ornamental value (Iitsuka et al., 2024). Together, these factors threaten the survival of native bitterling species in Japan. Most of the surviving bitterling species are evaluated as EN or even CR according to Japan Red List.

The findings of this chapter on the multifaceted diversity of native fish species in lakes within the Japanese archipelago offer valuable insights for the native conservation management. Temporally, this chapter demonstrated a continuous decline of native fish, particularly those endemic species with unique evolutionary histories and ecological functions. This decline is accelerating the irreversible homogenization of native fish fauna across Japan's lakes. Regarding spatial considerations, it is crucial to prioritize conservation efforts in the northernmost (Hokkaido) and the southernmost island (Kyushu), as their greater uniqueness. These areas require immediate attention to safeguard the remaining endemic fish species unique to each region. While conservation priorities on Honshu Island should focus on lakes with a higher number of species, as they can serve as important dispersal centres for native species. Furthermore, the results of this chapter emphasized that particular attention should be given to threatened species, especially endemic ones, as their unique status and restricted distribution make them particularly vulnerable. Prioritizing actions such as re-establishing native habitats and minimizing both biotic and abiotic negative impacts is crucial for effective native conservation efforts. The former provides environments that closely resemble the preferred habitats of the threatened species, thereby providing them with suitable conditions for survival and reproduction, while the latter creates more favourable conditions for the recovery and population growth of the threatened species.

Chapter 4

Native fish species confined to upstream oxbow lakes along the longitudinal gradient

4.1 Introduction

Native fishes are particularly vulnerable to non-native species invasions, which are among the most pervasive drivers of biodiversity losses in most freshwater ecosystems (Dudgeon et al., 2006; Leprieur et al., 2008). In recent decades, non-native fish species have been intentionally relocated across watersheds, countries, and continents for economic, biological control, recreational, and ornamental purposes (Gozlan et al., 2010; Xiong et al., 2015). Non-native fish introductions also occur due to unintentional actions like aquaculture escapes, canal or waterway connections, and ballast water discharges from vessels (Hulme et al., 2008; Musil et al., 2010). The combination of intentional and unintentional introductions of non-native species has led to significant declines in local native fish species in various regions around the world (Moi et al., 2021; Sleezer et al., 2021; Angulo-Valencia et al., 2022; Kang et al., 2022; Zhang et al., 2022). The need to mitigate diversity loss and enforce conservation intervention for native fish species has been widely acknowledged (Fensham et al., 2011; Xing et al., 2016).

The concept of native fish conservation areas (NFCAs) has been developed with the aim of protecting endemism from non-native species invasion (Williams et al., 2011). One major challenge in demarcating NFCAs is the expansive spatial region encompassed by interconnecting drainage systems. Focusing only on partial areas within a drainage region without considering the integrity of the drainage systems (Abell et al., 2007) can lead to inconsistent protection efforts within subregions and can hinder the conservation of the entire system (Williams et al., 1989). Furthermore, the spatiotemporally dynamic utilization of heterogeneous aquatic habitats by aquatic organisms, particularly fish species that rely on movement across diverse habitats to complete their life cycles (Roni, 2019), necessitates the inclusion of essential habitats for native species to manifest all crucial life cycle stages, as well as critical areas for migration, spawning, and rearing within the basin (Olden et al., 2010; Williams et al., 2011). The protection of native fish cannot be ensured through the sole consideration of limited, specific locations. Therefore, it is recommended that when selecting NFCAs, a comprehensive assessment of all accessible water bodies in the watershed be conducted, followed by the identification of waters with high conservation values.

NFCAs are often established covering shallow lakes or floodplain oxbow lakes along the river mainstem because of the stable hydrological environments, providing ideal habitat and sustenance, facilitate the interconnectivity of fish species interactions (Barocas et al., 2021; Dai et al., 2020). Abundant studies have ascertained the nomination of floodplain lakes as prospective candidates for NFCAs by assessing the lateral connectivity between lakes and the main channels, which might elevate groundwater levels, offering additional habitats (Miranda, 2005; Pander et al., 2018; Wang et al., 2020). Nevertheless, in addition to lateral connectivity, the longitudinal gradient of the physiochemical properties of the aquatic habitats from upstream to downstream (Vannote et al., 1980; Doretto et al., 2020) prompts us to anticipate diverse roles and functions of floodplain lakes along the longitudinal river gradient, which are frequently overlooked. Hence, this chapter suggests that it is a valuable chance to explore fish metacommunity variations in the Ishikari floodplain lakes along longitudinal gradients to highlight the prioritization of oxbow lakes for NFCAs in river-floodplains.

Longitudinal upstream-downstream gradients in river-floodplain ecosystems are characterized by continuous environmental gradients in climate, hydrological regime, and sediments (Suvarnaraksha et al., 2012; Oberdorff et al., 2019). However, river landscape gradients have been modified intensively in the Anthropocene, with pristine natural environments in the upper reaches and disturbed urbanized areas in the lower reaches (Wan & Zhong, 2014; Wang et al., 2017; Xiao et al., 2021). Such longitudinal variations in hydrological features and landscapes have also been frequently observed in shallow lakes and oxbow lakes along the main river (Pongsivapai et al., 2021). The downstream urban area in floodplain systems usually provides habitats favoured by introduced non-native species and substitution for native fish niches (Olden et al., 2006; Pingram et al., 2021). Native species that are sensitive to environmental conditions may prefer lakes located in upstream areas with minor anthropogenic disturbance (Shochat et al., 2010; Goetz et al., 2015; Ishiyama et al., 2020; Zhang et al., 2022). This study believes that such spatial longitudinal variations must also be considered when establishing oxbow lake-based NFCAs for more efficient and targeted native conservation in these lakes.

The Ishikari River basin (the second largest in Japan) is characterized by a substantial presence of oxbow lakes, which exhibit a significant longitudinal distribution pattern along the river. The Ishikari basin underwent considerable urban transformation throughout the last century, predominantly within its downstream regions, which have now become subject to the highest population density in Hokkaido. Despite the intense anthropogenic activities have substantially decelerated in the 21st century, it is recognized that preceding alterations to the watershed environments, attributable to industrialization, contamination, and other factors, have already exerted deleterious impacts on the river-floodplain ecosystems. In the early 2000s, Hayashida et al. (2010) conducted research on the fish species community composition in the oxbow lakes and evidenced the presence of non-native fish invasion in the Ishikari River basin. A subsequent study by Fujii et al. (2019) about a decade later further reported fish species composition of these oxbow lakes based on both traditional and molecular approaches. However, neither study considered the potential link between the fish community of individual lakes and their longitudinal spatial distribution along the river. This chapter, building upon the findings of two prior research, seeks to analyse the taxonomic interactions between native and non-native fish assemblages in oxbow lakes during the period from 2003 to 2016, a period with minimal external environmental changes. Additionally, the study aims to discern whether any observed changes in these interactions present a longitudinal pattern, shifting from upstream to downstream considering the spatial distribution of these oxbow lakes along the Ishikari River. This analysis will further inform the identification of critical locations for NFCA. The hypotheses of this chapter posit that (1) Temporally, native fish will be sporadically distributed in specific lakes and result in a decline in native richness but an increase in regional dissimilarity. On the other hand, the introduction and expansion of non-native fish will result in an increase in non-native richness and temporal similarity; (2) Spatially, this study hypothesize that both native and non-native fish species will exhibit longitudinal patterns in metacommunity changes. This is because non-native species, with their high environmental adaptability, are likely to be more prominent in downstream areas, while native fish prefer upstream lakes that offer diverse conditions resembling their natural habitat.

4.2 Methods

Study areas and fish datasets

The Ishikari River in Japan drains 14,330 km^2, flowing from its source on Mt. Ishikari to the Sea of Japan (Figure 4.1). Oxbow lakes formed in great numbers longitudinally along the middle-lower Ishikari River mainstem. This study selected a total of 28 oxbow lakes along the Ishikari River as sampling sites (Table 4.1). These lakes are situated 90 to 140 kilometres away from the river source. These lakes are currently being maintained with similarly low to moderate lateral connectivity to the Ishikari mainstream because of the presence of flood dikes and sluice gates on outflow channels. Notably, during the studied period (2003–2016), negligible land use change occurred (Pongsivapai et al., 2021) and no extensive fish introductions were conducted in the Ishikari River basin. Based on sampling methods detailly described in Hayashida et al. (2010) and Fujii et al. (2019), fish collections were conducted once at each lake in each of two periods: 2003/2004/2005 (the 2000s for abbreviation) and 2016 (the 2010s), respectively. Although the personnels conducting fish collection in two periods were not identical the personnels and instruments conducting fish collection in two periods were not identical, the

Figure 4.1 Location of the studied oxbow lakes along the Ishikari River.

fish surveys were conducted during the summer months, and the common electrofishing method was used in both cases. To avoid biased results due to differences in sampling intensity and equipment, this study extracted the fish incidence rather than abundance for further statistical analysis. Despite the lack of abundance information, the use of incidence data ensured comparability of fish diversity results between the two periods without generating contradictory outcomes when compared to abundance-based results (Dai et al., 2020; Xia et al., 2022). Fish datasets are also partially extracted from Hayashida et al. (2010) and Fujii et al. (2019). This study then identified the native and non-native fish species, compiling the distributional matrix for native and non-native fish assemblages, respectively.

Calculation of diversity metrics

In this chapter, the taxonomic diversity of overall, native, and non-native fish assemblages in 28 oxbow lakes along the Ishikari River during the 2000s and 2010s was measured respectively. Aligning with the methodology outlined in Chapter 2, for each lake, the diversity assessments included species richness, dissimilarity of fish species composition ($t\beta_{sør}$), and the dynamics of species turnover ($t\beta_{sim}$) and nestedness ($t\beta_{sne}$) patterns. Additionally, the respective contribution of fish compositions in individual lakes on the overall pattern of regional beta diversity within the basin (tLCBD) for each period was calculated. It is important to note that this chapter also calculates pairwise species variability ($t\beta_{sør}$), but with a different focus than the previous chapter. Instead of comparing fish species composition between different lakes in the same time period, this chapter compares changes in the species composition of the same lake between the 2000s and 2010s. Consequently, the $t\beta_{sør}$ here, as well as $t\beta_{sim}$ and $t\beta_{sim}$, reflects the extent of species change within individual lakes over approximately a decade.

Besides, this chapter assessed the multi-site community dissimilarity. Unlike the classical pairwise beta diversity measurement described in Chapter 2, the multi-site community dissimilarity assessment implies regional species co-occurrence patterns among multiple lakes. Hence, it is usually considered superior to the traditional comparisons between independent community pairs (Baselga, 2013). Importantly, this index facilitates the subsequent conduct of a resampling beta diversity measures. Consequently, we calculated multiple-site Sørensen dissimilarity indices to evaluate regional dissimilarities ($\beta_{SØR}$) of fish assemblages among all 28 oxbow lakes for each period (Baselga, 2013). Two independent species distribution patterns, turnover (β_{SIM}) and nestedness (β_{NES}), were further assessed. The multi-site dissimilarity calculations follow the equations below.

$$\beta_{\text{SØR}} = \frac{\left[\sum_{j<k} \min(b_{jk}, b_{kj})\right] + \left[\sum_{j<k} \max(b_{jk}, b_{kj})\right]}{2\left[\sum_j S_j - S_{\text{T}}\right] + \left[\sum_{j<k} \min(b_{jk}, b_{kj})\right] + \left[\sum_{j<k} \max(b_{jk}, b_{kj})\right]} \qquad 4.1$$

$$\beta_{\text{SIM}} = \frac{\left[\sum_{j<k} \min(b_{jk}, b_{kj})\right]}{\left[\sum_j S_j - S_{\text{T}}\right] + \left[\sum_{j<k} \min(b_{jk}, b_{kj})\right]} \qquad 4.2$$

$$\beta_{\text{NES}} = \frac{\left[\sum_{j<k} \max(b_{jk}, b_{kj})\right] - \left[\sum_{j<k} \min(b_{jk}, b_{kj})\right]}{2\left[\sum_j S_j - S_{\text{T}}\right] + \left[\sum_{j<k} \min(b_{jk}, b_{kj})\right] + \left[\sum_{j<k} \max(b_{jk}, b_{kj})\right]} \times \frac{\sum_j S_j - S_{\text{T}}}{\left[\sum_j S_j - S_{\text{T}}\right] + \left[\sum_{j<k} \min(b_{jk}, b_{kj})\right]} \qquad 4.3$$

where b_{jk} and b_{kj} are the fish species numbers exclusive to lake j and k, respectively, S_j is the richness of fish species in lake j, S_{T} is the regional fish richness including all studied lakes (Baselga, 2010). The multi-site dissimilarity metrics were obtained using the R package BETAPART.

Statistical analysis

First, the respective temporal changes in average overall, native, and non-native fish richness across 28 oxbow lakes during two time periods were assessed. Next, the multiple-site dissimilarity of fish assemblages was measured, and then decoupled it into turnover and nestedness based on the observed data in two periods, respectively. Further, following the same equations, 100 simulated multiple-site dissimilarity indices by randomly sampling seven sites from the observed fish matrixes were computed (Jiang et al., 2019). PERMANOVA tests with 9,999 permutations (Anderson, 2001) were then utilized to test the statistical significance of the differences in the average values of the 100 simulated indices between the two periods, acting as the proxy of statistical significance of observed temporal changes in multi-site dissimilarity metrics. Subsequently, after estimating the degree of temporal changes in the fish composition of individual lakes over the decade (pairwise beta diversity), linear regressions between pairwise metrics of each lake and their distance from the river source (DRS) were performed to explore whether temporal changes in fish composition were associated with the longitudinal river gradient. Afterwards, this study estimated the temporal change of local contributions to regional dissimilarity ($\Delta\text{LCBD} = \text{LCBD}_{2010\text{s}} - \text{LCBD}_{2000\text{s}}$). The oxbow lakes with significantly changed contribution values could be identified. Linear regressions were again applied to test whether the ΔLCBD of the oxbow lake also occurred in response to the longitudinal river gradient. Calculations for multi-site or pairwise dissimilarity indices, and LCBD values were concurrently computed for overall, native, and non-native fish assemblages respectively in R; PERMANOVA tests and linear regression analyses were performed in software PAST (Hammer et al., 2001).

4.3 Results

Temporal change in fish richness

A total of 27 fish species were documented, of which 18 were classified as native and 9 as non-native (as presented in Table 4.1). There were 15 oxbow lakes with increased overall fish richness from the 2000s to the 2010s. Specifically for native and non-native fish assemblages, the proportion of non-native fish increased in 19 lakes, while native fish increased in only 3 of the 28 studied lakes. Regarding regional average, overall fish richness and non-native richness increased significantly during the studied decade, with insignificant changes in native fish richness (Table 4.1).

Temporal change in regional dissimilarity and local contributions

While there was a minor increase in multi-site dissimilarity for the overall fish species, a significant decrease in species turnover and an increase in nestedness over ten-year periods was found. Nevertheless, inconsistent temporal trends were found when native and non-native fish species were examined separately. For the native fish species, dissimilarity and turnover increased significantly between the two periods. But for the non-native assemblages, both dissimilarity and turnover decreased, and only nestedness increased from the 2000s to the 2010s (Table 4.2, Figure 4.2).

In terms of the overall fish community, the contribution of oxbow lakes to regional dissimilarity was relatively homogeneous in the 2000s (Figure 4.3). However, the difference in local contribution to regional dissimilarity changed remarkably after a decade, with decreased contributions of upstream lakes and increased downstream contribution. Specifically for native fish faunas, relatively unique fish assemblages were found in the upper lakes in the 2000s. In contrast, the uniqueness of native fishes inhabiting these lakes declined remarkably in the 2010s. In general, the distribution patterns of LCBD for overall fish assemblages in the 2000s were similar to those of native fish faunas at that time, suggesting that the distribution of native fish dominated the community structure and spatial distribution of overall fish assemblages. Nevertheless, this dominance was surpassed by non-native fish in the 2010s, reflecting a spatial pattern of LCBD for overall fish assemblages that were similar to non-natives.

Table 4.1 Distances of the 28 oxbow lakes studied from the Ishikari River Source (DRS.). The number of native and non-native species, with their proportions indicated in parentheses are also enumerated. An increase in the fish richness in a particular lake from the 2000s to the 2010s is marked with a superscript [+]. Statistically significant average increases in regional fish richness are highlighted in bold ($p < 0.05$, determined using PERMANOVA tests with 9,999 permutations.)

Oxbow lake	DRS (km)	2000s			2010s		
		Overall	Native	Non-native	Overall	Native	Non-native
Tanba	92.56	9	8 (88.9)	1 (11.1)	11 [+]	7 (63.6)	4 (36.4) [+]
Ikenomae	92.70	14	8 (57.1)	6 (42.9)	14	8 (57.1)	6 (42.9)
Takonokubi	92.93	11	7 (63.6)	4 (36.4)	12 [+]	7 (58.3)	5 (41.7) [+]
Shisun	94.82	11	4 (36.4)	7 (63.6)	14 [+]	7 (50.0) [+]	7 (50.0)
Fukuroji	95.87	10	5 (50.0)	5 (50.0)	15 [+]	7 (46.7)	8 (53.3) [+]
Shimotoppu	97.04	12	6 (50.0)	6 (50.0)	17 [+]	9 (52.9) [+]	8 (47.1)
Mizuho	99.38	14	9 (64.3)	5 (35.7)	10	6 (60.0)	4 (40.0) [+]
Pira	99.95	12	7 (58.3)	5 (41.7)	11	6 (54.5)	5 (45.5) [+]
Toi	101.26	10	5 (50.0)	5 (50.0)	15 [+]	7 (46.7)	8 (53.3) [+]
Urausu	102.82	8	5 (62.5)	3 (37.5)	13 [+]	6 (46.2)	7 (53.8) [+]
Shin	104.91	15	9 (60.0)	6 (40.0)	18 [+]	10 (55.6)	8 (44.4) [+]
Higashi	106.35	13	7 (53.8)	6 (46.2)	15 [+]	8 (53.3)	7 (46.7) [+]
Sakura	106.71	7	6 (85.7)	1 (14.3)	11 [+]	6 (54.5)	5 (45.5) [+]
Nishi	107.10	12	6 (50.0)	6 (50.0)	13 [+]	5 (38.5)	8 (61.5) [+]
Hishi	107.51	8	4 (50.0)	4 (50.0)	13 [+]	6 (46.2)	7 (53.8) [+]
Ito	108.61	10	5 (50.0)	5 (50.0)	13 [+]	6 (46.2)	7 (53.8) [+]
Miyajima	114.22	12	6 (50.0)	6 (50.0)	8	4 (50.0)	4 (50.0)
Sankaku	114.49	4	4 (100)	0 (0.0)	4	3 (75.5)	1 (25.0) [+]
Omagari	115.66	12	5 (41.7)	7 (58.3)	12	6 (50.0) [+]	6 (50.0)
Kagami	119.10	6	5 (83.3)	1 (16.7)	3	3 (100)	0 (0)
Bibai	120.21	11	6 (54.5)	5 (45.5)	11	4 (36.4)	7 (63.6) [+]
Tsukio	121.94	13	8 (61.5)	5 (38.5)	8	6 (75.5)	2 (25.5)
Onuma	122.23	7	4 (57.1)	3 (42.9)	8 [+]	6 (75.0)	2 (25.0)
Tsukiko	122.71	9	6 (66.7)	3 (33.3)	14 [+]	9 (64.3)	5 (35.7) [+]
Tomoenojyo	127.77	10	5 (50.0)	5 (50.0)	10	4 (40.0)	6 (60.0) [+]
Echigo	132.68	8	6 (75.0)	2 (25.0)	8	6 (75.0)	2 (25.0)
Shinotsugawa	136.70	9	5 (55.6)	4 (44.4)	9	3 (33.3)	6 (66.7) [+]
Kyutoyohira	138.06	10	4 (40.0)	6 (60.0)	7	2 (28.6)	5 (71.4) [+]
Average		10.3	5.9 (59.5)	4.4 (40.5)	**11.3**[+]	6.0 (54.7)	**5.4 (45.3)**[+]

Table 4.2 Regional multi-site dissimilarities of overall, native, and non-native fish faunas in the 2000s and 2010s, respectively. Multi-site turnover and nestedness patterns were assessed either. Based on dissimilarity metrics generated by multiple-site resampling simulations (n = 7, N = 100), statistical significance of differences in all dissimilarity metrics between two periods were tested by PERMANOVA (based on Euclidean distance index with 9,999 permutations). Differences that were statistically significant ($p < 0.05$) were marked as bold p values.

Metric	Overall			Native			Non-native		
	2000s	2010s	p	2000s	2010s	p	2000s	2010s	p
$\beta_{\text{SØR}}$	0.842	0.846	0.693	0.844	0.867	**0.001**	0.841	0.814	**0.001**
β_{SIM}	0.763	0.741	**0.002**	0.766	0.791	**0.027**	0.636	0.487	**0.001**
β_{SNE}	0.079	0.105	**0.001**	0.078	0.076	0.215	0.205	0.327	**0.003**

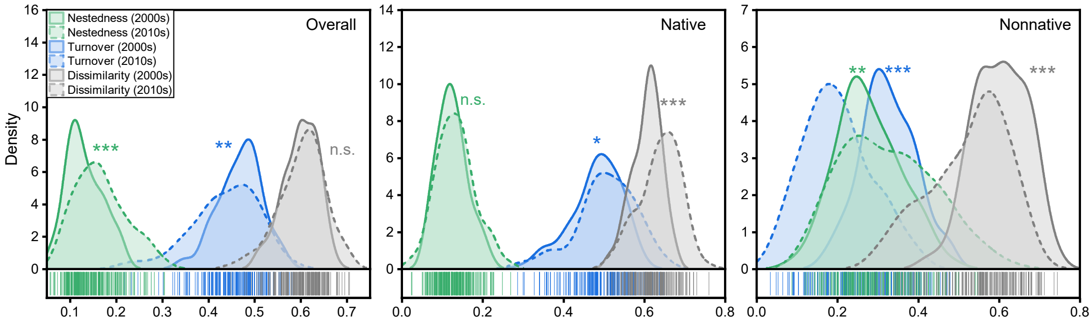


Figure 4.2 Distribution of simulated multiple-site dissimilarity metric values for overall, native, and non-native fish assemblages in the 2000s (solid lines) and the 2010s (dash lines). Overall dissimilarities (grey), as well as turnover (blue) and nestedness (green) components, were demonstrated in different colours. Frequency distributions were estimated by bootstrapping procedure (N = 100, with replacement) of seven sites per permutation to calculate multiple-site dissimilarities. Denotes: ***: $p < 0.001$; **: $0.001 \leqslant p < 0.01$; *: $0.01 \leqslant p < 0.05$; n.s. = no significance: $p \geqslant 0.05$, based on PERMANOVA tests with 9,999 permutations.

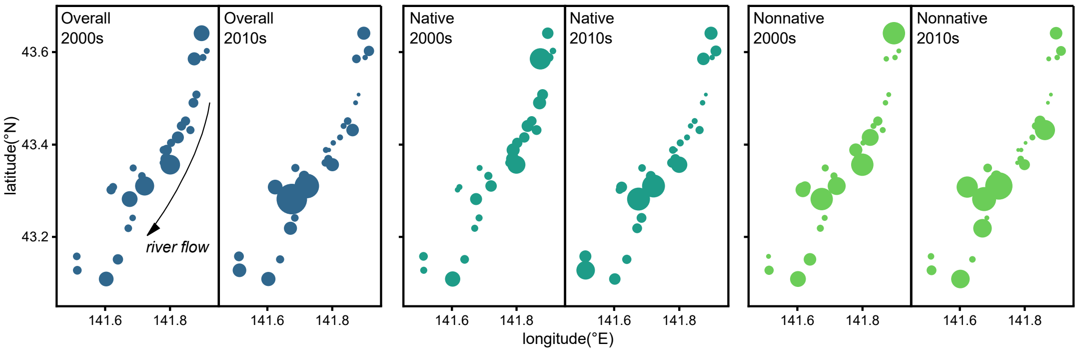


Figure 4.3 Local contributions to regional dissimilarity (LCBD) of overall (blue), native (green), and non-native (light green) fish faunas inhabiting each lake in the periods of the 2000s and 2010s, respectively. The dots represent the 28 oxbow lakes along the Ishikari River, and the dot size is proportional to the LCBD values of each lake.

Regional patterns corresponding to dissimilarity changes

Significant positive correlations were discovered between the lake location and the temporal changes in species dissimilarity and turnover for both overall and native fish assemblages in each lake (Figure 4.4). The findings indicate that oxbow lakes in the downstream region have undergone more significant temporal shifts in species composition, particularly in native species turnover. However, the dissimilarity changes of non-native species did not show a significant correlation.

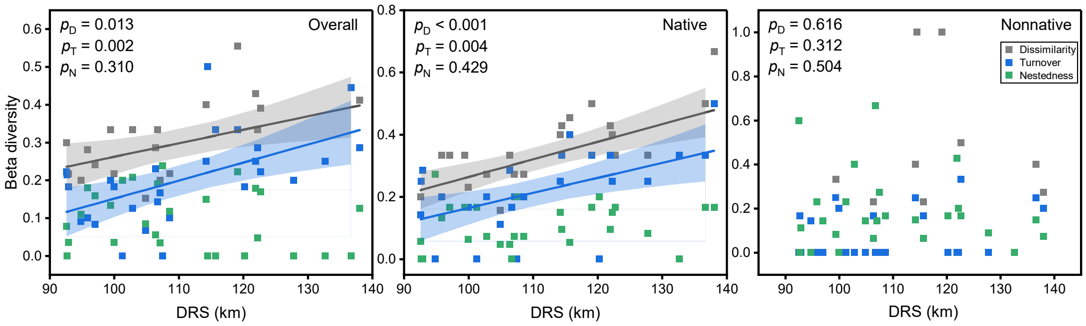


Figure 4.4 Linear regression relationships between temporal change in beta diversity (dissimilarity in grey, turnover in blue, and nestedness in green, y-axis) of overall, native, and non-native fish assemblages in each oxbow lake and their location, i.e., distances from the river sources (DRS, x-axis). The p value for each correlation pair is given. Only correlations with statistical significance ($p < 0.05$) are presented in solid line.

Significant correlations between the temporal change in LCBD values of oxbow lakes and their locations were found (Figure 4.5). While the LCBD values for overall and non-native fish assemblages were positively correlated with increasing distance of the lakes from the source of Ishikari River, the association was negative for native fish populations. Interestingly, regression analysis revealed that the location with the least LCBD value change is 110 km afar from the river source.

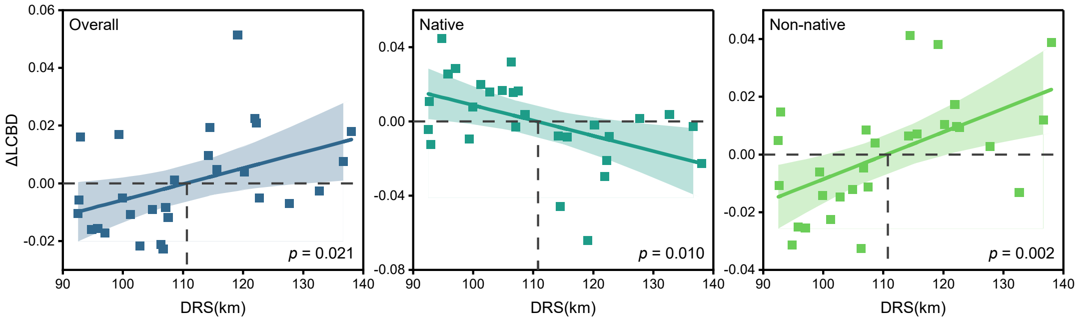


Figure 4.5 Linear regressions between the distance from the river source (DRS) and temporal change in LCBD values (ΔLCBD) of the 28 oxbow lakes for overall (blue), native (green), and non-native (light green) fish assemblages. The intersection of the fitted line with the horizontal dashed line indicates the theoretical location of the oxbow lake where there is no temporal change in the LCBD values (ΔLCBD = 0.)

4.4 Discussion

Anthropogenic activities, including non-native fish introductions, have made the freshwater fish homogenization an intractable issue around the world (Villéger et al., 2011; Su et al., 2021). This homogenization results in a reduction of the global species pool, a loss of phylogenetic diversity, and ultimately threatens ecosystem services and stability. Like many well-known hotspots for freshwater ecology research, such as the Great Lakes region in North America (Campbell & Mandrak, 2019), the Yangtze River basin in Asia (Kang et al., 2018), and the Amazon region in South America (Arantes et al., 2018), etc., the far east high-latitude island represented by this study, is no exception to this trend. We found that introducing non-native fishes enriched the overall fish richness in oxbow lakes along the Ishikari River but altered the regional dissimilarity patterns significantly: reduced turnover accompanied by higher nestedness. Such homogenization patterns were dominated by non-native species diversity patterns, demonstrating the most significant reduction in species turnover. The aggressive invasion of non-native species likely intensified interspecific competition and niche shifts in fish assemblages (Lauzeral et al., 2011; Ishiyama et al., 2020; Liu et al., 2020). As a result, native fish species were forced to occur in specific habitable oxbow lakes, leading to an increase in regional species turnover. The observed increase in native turnover reinforces the theory proposed by Socolar et al. (2016), which suggests that high community dissimilarity can serve as evidence of ongoing biodiversity degradation processes. In this scenario, a brief increase in community dissimilarity is then followed by a dramatic decrease, culminating in a homogenous species composition in the region. Hence, it is essential to interpret the community dissimilarity results with caution.

This chapter found that the daunting change in fish composition of Ishikari River basin is tacit but rapid. Although the Ishikari River watershed is subject to a high population density and intense urbanization in Hokkaido, there were no apparent new major anthropogenic drivers or landscape alterations in the Ishikari basins during the study periods (from 2003 to 2016). The differences in environmental conditions and land use between the upper and lower reaches were already in place before this study began (mainly formed in the last century). The relatively stagnant urbanization and land development during the study periods do not suggest that the non-native expansion was accelerated as the increased intensity of anthropogenic activities like other studies reported (Anas & Mandrak, 2021; Głowacki et al., 2021). In this context of little external environmental alteration, non-native fishes were still tacitly remodifying the fish community structures in the basin, suggesting the strong competitiveness of these non-native fish during inter-specific competitions with natives (Alves et al., 2017; Zhang et al., 2022). In addition, a recent study by Haubrock et al. (2021) reported shifts in fish communities over the last two centuries in the Arno River, Italy. Their results indicated an increase in non-native fish richness, with six new established non-native species reported during the 1950s-2000s, a period marked by intensive industrial development. Afterwards, a decrease of two non-native species was observed by 2015 (Haubrock et al., 2021), concurrent with a deceleration in anthropogenic modifications to the environment. When compared to the long-term time frame (decades even hundreds of years) of the case study in Italy, the results from the present study in Ishikari watersheds in Japan demonstrate an expeditious expansion of non-native fishes over about only one decade, despite relatively little-changed environmental conditions during the study periods. While intermittent initiatives like fish stocking, fish ladder construction, and habitat restoration were in place in certain areas of the Ishikari watershed, this study advocates for the exploration of more comprehensive conservation strategies. The intent is to modify the status quo of native fish assemblages aiming towards the enhancement of their population size.

Identification of spatial distribution patterns of native fish is the cornerstone for establishing NFCAs to preserve endemism from invasions (Dauwalter et al., 2011; Williams et al., 2011). For many years, the within-site (alpha) diversity has been a cornerstone in the development of conservation strategies and policies. For instance, regions with high alpha diversity are often accorded elevated conservation priority due to their likelihood of hosting a wide array of species, including endangered and endemic ones, thereby assuring enhanced levels of ecosystem services. However, recent studies have begun to highlight the importance of incorporating the between-site (beta) diversity into management decisions. Beta diversity, which takes into account not only the species richness, but also the dissimilarities between different communities, provides a more comprehensive understanding of diversity loss processes (Baselga, 2010). This information generated by dissimilarity analysis is crucial for accurately defining protected areas and ensuring their effectiveness in conserving biodiversity (Socolar et al., 2016; Dai et al., 2020; Jiang et al., 2020). In the present study, the temporal variation in fish assemblage dissimilarities along a longitudinal river gradient was analysed, revealing significant longitudinal differences. Specifically, greater changes in fish species composition were observed in the downstream lakes, while upstream changes were relatively lower. These habitat occupancy patterns were reflected in the temporal variation of LCBD across the longitudinal lakes. A stark contrast was observed in the changes of native and non-native fish species, with the upstream lakes becoming increasingly important for native fish fauna, and the downstream lakes for non-native fish assemblages.

Remarkably, a point of equal change was identified at 110 km from the river source, where the upstream lakes still maintained a higher degree of uniqueness for native species, but non-native species dominated the downstream lakes. These results suggest that the displacement of native fish by non-native species progresses from downstream to upstream, with the dominance of non-native species extending up to 110 km from the river source after a decade. Based on these findings, it can be concluded that the conservation of native fish should be given priority in upstream lakes located less than 110 km from the source of the Ishikari River when establishing NFCAs (Walls, 2018). It is important to note, however, that pressures such as anthropogenic activities on the Ishikari River in this study show a unidirectional longitudinal gradient in line with the river flow, which does not always occur in other river basins. In many cases, especially in large river basins, factors like population density, dam construction, flow regulation, and pollutant discharges tend to occur without a clear longitudinal gradient of change (Walling, 2006; Maavara et al., 2020). This implies that observing changes in fish diversity in more complex river systems is essential to fully understand the intensity and spatial distribution of local environmental pressures and to analyse the response of the spatial distribution pattern of fish to different environmental pressures throughout the river basin.

The variations in the external environmental conditions that these oxbow lakes, situated from up- to downstream watersheds, encounter offer a viewpoint to understand the fish community remodifications along the longitudinal gradient of the Ishikari River. The downstream oxbow lakes lie in Hokkaido's most extensive urban area (Duan et al., 2015). The impact of human activities, such as landscape alterations, hydrological and industrial facilities, agriculture activities, etc., could be considered triggers for the loss of native presences (Zhang et al., 2019; Boys et al., 2021; Pingram et al., 2021; Su et al., 2021). In the present context, it is noteworthy that certain non-native fish species, exemplified by the topmouth gudgeon (*Pseudorasbora parva*), exhibit robust adaptability and possess aggressive traits. Particularly, the topmouth gudgeon has displayed a remarkable capacity to tolerate and adapt to varying levels of COD in water, which serves as a widely accepted indicator of organic pollution resulting from domestic and industrial waste (Zhang et al., 2022). The high adaptability has facilitated their successful colonization, especially in lakes characterized by eutrophic conditions. Consequently, these non-native fish species have been able to complement and, in some cases, even outcompete native species within their ecological niches (Yamamoto et al., 2001; Zhang et al., 2022). Correspondingly, receiving minor disturbances from anthropogenic activities, the upper oxbow lakes provided heterogeneous shelters for fish assemblages, e.g., sufficient littoral shades and for sheltering, root mats and submerged woods for habitability, and less contaminated water quality for surviving, etc. (Lucas & Baras, 2008; Garrett-Walker et al., 2020; Ishiyama et al., 2020; Pingram et al., 2021), thus maintaining relatively stable fish community compositions. Simultaneously, the results also demonstrated that the upstream lakes offered refuge for some non-native species that are less competitive in interspecific interactions. Nevertheless, it is imperative to remain vigilant to the potential that these non-native fish species, seeking refuge in the upstream oxbow lakes, may perpetuate the reduction of the ecological niche occupied by native fish species, presenting a continued danger to their survival.

The findings of this study confirm that there was a significant longitudinal gradient in the species composition alteration of native and non-native fish communities. On this basis, we propose utilizing the temporal change in the contribution of lakes to the regional dissimilarity (LCBD) as an indicator of potential protected areas for fish assemblages, which would reflect the competition between native and non-native fish species along the longitudinal river gradient. Despite the heterogeneous and fragmented administrative divisions within the basin typically making it challenging to the development of comprehensive conservation strategies that encompass the entire watersheds (Abell et al., 2007; Olden et al., 2010), this study provides a framework for determining the spatial range of these areas, which is the frontier point of the contest between importance of native and non-native fishes. The proposed framework involves identifying waters that have increased in relative importance for native fish species as potential protected areas, and then measuring along the longitudinal river gradient until waters that have not changed in importance are found. The position of these unchanged waters would then delimit the potential boundary of the protected region. Regular recalculation of the importance change can be used to monitor whether the position with no importance change has moved upstream or downstream. An upstream shift would suggest that the expansion of non-native fish species is ongoing, while a downstream shift would indicate the effectiveness of conservation and environmental efforts for native fish species. While we acknowledge the limitations of this framework in its simplicity and crudeness, we anticipate that through further validation and application in additional river basins, it has the potential to assist in the identification of priority areas for the conservation of native fish species within the basin.

However, it must be acknowledged that this research lacks quantitative data on the water environmental variables or the intensity of human activities during the fish sampling periods in the 2000s and 2010s. This limitation hinders the ability to statistically quantify and verify the relationship between the observed spatial differences in fish community structure and human activities. In this thesis, explanations for this phenomenon rely on indirect references to relevant literature. For example, it is noted that the nutrient levels in the oxbow lakes downstream in the Ishikari River basin are higher than those in the upstream lakes (Pongsivapai et al., 2021). Considering that there were no large-scale urban development or industrial pollution events in the Ishikari River basin during the study period (2000s to 2010s), it is assumed that the spatial differences in eutrophication levels between upper and lower lakes remained constant throughout the study period. Thus, this consistency is used to explain the spatial differences in the diversity changes of native and non-native fish species observed in this study.

This chapter investigated the changes in the fish assemblage structures in 28 oxbow lakes in the Ishikari watershed in Japan spanning a decade. Results revealed a trend towards regional homogenization of fish assemblages, primarily driven by the rapid spread of non-native fish species, which resulted in an increase in nestedness patterns. Meanwhile, the sporadic occurrence of native fish species in specific lakes led to increased turnover patterns. Additionally, the changes in fish composition showed a significant association with longitudinal river gradients. The most significant changes were observed in downstream lakes close to urban areas, whereas the alterations in fish species in upstream lakes were relatively modest. The LCBD index assessments revealed that downstream lakes were more susceptible to non-native invasions, leading to a homogeneous fish composition dominated by non-native species. This dominance was observed to be expanding upstream along the longitudinal river gradient, extending up to a point 110 km from the river source. In contrast, upstream lakes were found to be more natural and provided favourable habitats for native fish species. This chapter therefore suggests that the NFCAs in the Ishikari River basin should be established in the oxbow lakes within the upper reaches range 110 km from the river source as a priority. The findings provide an example of using alterations of species and location contribution to regional metacommunity dissimilarities to guide the delineation of conservation areas and can be applied in other riverine basins with significant longitudinal river gradients.

Chapter 5

Longitudinal disparities in native fish responses to homogenized non-native invasions: Contrasting phylogenetic and functional spatial patterns

5.1 Introduction

Large rivers and their flow directions play a central role in freshwater ecosystems (Döll & Zhang, 2010; Thorp et al., 2006). On the one hand, large rivers and neighbouring water bodies (e.g., oxbow lakes, ponds, streams, etc.) are intertwined to form a water network that provides diverse habitats, breeding sites, and food sources for freshwater fishes (Woolnough et al., 2009). On the other hand, the river continuum concept sheds light on the ecological transitions and productivity variations from the headwaters to the mouths of the river systems, revealing that downstream areas tend to exhibit higher productivity than their upstream counterparts (Bayley, 1991; Oberdorff et al., 2019; Suvarnaraksha et al., 2012). This variance in productivity is not merely a manifestation of natural ecological dynamics; it also mirrors the extensive history of interaction between human societies and freshwater systems. The fertile soils and copious water supplies of river lower reaches have historically attracted agricultural development and dense human settlements (Dai et al., 2023; Wan & Zhong, 2014; Xiao et al., 2021). Yet, such intensive human footprint has exerted significant pressures and challenges on the freshwater ecosystems downstream and their adjacent waters (Jiang et al., 2020; Venter et al., 2016). Alterations in the rivers' natural flows due to extensive hydraulic constructions, coupled with severe pollution from nutrients and contaminants such as heavy metals and persistent organic pollutants stemming from agriculture and industry, have wreaked havoc on aquatic habitats in the lower reaches (Tockner et al., 2008). These disturbances have jeopardized the well-being of fish and cast a long shadow over the biodiversity and functional integrity of the ecosystems (Su et al., 2021).

Biogeographical realms across the world have observed the introduction and establishment of non-native fish species, leading to irreversible alterations in local fish diversity patterns and emerging as a critical concern in global biodiversity conservation efforts (Bernery et al., 2022; Gozlan, 2008; Leprieur et al., 2008). The presence of non-native fishes frequently escalates niche competition with native species, vying for essential resources such as food and habitat (Crooks, 2002; Dominguez Almela et al., 2021). This competition can lead to a redistribution of resources, impacting the survival and reproductive success of fish species and thus altering community structures. The potential for interbreeding between non-native and native fish species further risks genetic assimilation, diluting the genetic integrity and adaptability of native populations (Jiang et al., 2019). Fish species that are broadly introduced and established in new habitats often possess a competitive edge over native fishes due to their broad diets, robust reproductive strategies, and tolerance to adverse environmental conditions, hastening the decline of native species, particularly those that are endemic (Bernery et al., 2024). Such interplay between native and non-native fish species not only foster the alteration of taxonomic, phylogenetic, and functional structures of fish faunas globally but also diminish the complexity and stability of freshwater ecosystems, thereby constituting a grave threat to biodiversity. The comprehensive assessments could deepen the understanding of the composition and assembly rules of local communities, offering critical insights for the conservation of biodiversity, particularly for the protection of native species.

As introduced in Chapter 4, the Ishikari River basin serves as an ideal study area for examining changes in fish community structure across space and time within its oxbow lake groups (Fujii et al., 2019; Hayashida et al., 2010). The last chapter has shown that, from the 2000s to the 2010s, there were significant shifts in fish distribution patterns across the basin. These changes were driven by the expansion of non-native species, leading to noticeable species turnover in downstream areas and an enrichment of species upstream. Chapter 4 also identified a critical spatial threshold, located approximately 110 km from the river source. Oxbow lakes upstream of this point harbour a greater uniqueness of native fish assemblages, whereas downstream of this site, non-native fish assemblages show greater dominance in the fish communities. Despite these insights, the last chapter have only focused on taxonomic richness, without considering the phylogenetic and ecological traits of the fish species. Building on these findings of Chapter 4, the current research delineates the basin into upper and lower zones, demarcated by the 110 km marker from the river source. By incorporating data on phylogenetic relationships and functional traits, this chapter delve into the impacts of non-native species expansions on the spatiotemporal patterns of fish assemblages' phylogenetic and functional diversity in the oxbow lakes of the Ishikari River basin from the 2000s to the 2010s. This investigation aims to unravel the underlying mechanisms driving these species changes from a phylogenetic and functional standpoint, thereby enhancing conservation strategies for fish diversity.

5.2 Methods

Data arrangement and dendrogram generation

Fish datasets used in this chapter were collected from 16 upper and 12 lower oxbow lakes along the Ishikari River during the 2000s and 2010s (Fujii et al., 2019; Hayashida et al., 2010). Following the data collation methods described in detail in the last chapter, this study examines temporal and spatial variations in the phylogenetic and functional diversity of both native and non-native fish while ensuring the consistency and comparability of the datasets. As outlined in Chapter 2, phylogenetic and functional diversities were assessed by measuring species distances on phylogenetic trees and functional trait dendrograms (Xu et al., 2022). The functional trait dendrograms considered nine functional traits of the species (age at sexual maturity, body length at sexual maturity, body shape, diet patterns, expected longevity, growth rate, habitat preference, maximum body length, and trophic level) in this chapter.

Phylogenetic and functional diversity measurement

Phylogenetic and functional alpha diversity for native and non-native fish assemblages during the two periods were calculated using the indices MPD, MNPD, MFD, and MNFD, as outlined in Chapter 2. Phylogenetic ($p\beta_{sør}$) and functional ($f\beta_{sør}$) beta diversity for each lake were determined by comparing its species distribution on the dendrograms with those of other lakes and averaging these comparisons. Additionally, the respective turnover ($p\beta_{sim}$, $f\beta_{sim}$) and nestedness ($p\beta_{sne}$, $f\beta_{sne}$) components, along with turnover proportions (pp_{turn}, fp_{turn}), were calculated following the protocols from Chapter 2. This chapter also evaluates the phylogenetic (pLCBD) and functional (fLCBD) local contribution to beta diversity of native and non-native fish assemblages in each lake across the two periods.

Statistical analysis

The two-way PERMANOVA to evaluate differences in alpha and beta diversity indices for phylogenetic and functional structures among native and non-native fish assemblages across periods (2000s versus 2010s) and locations (upper versus lower) were performed. Furthermore, the temporal changes (Δ) in beta diversity indices for native and non-native fish assemblages in upstream and downstream lakes were measured. This chapter explored whether temporal changes in the phylogenetic structures of fish assemblages corresponded with changes in functional patterns—either in parallel or opposite directions—by performing linear regressions on the differences (Δ values) in phylogenetic and functional diversity, using Pearson's index to assess correlation. The two-way PERMANOVA tests and linear regressions were performed in R (R Core Team, 2024). Additionally, this chapter assessed the changes in pLCBD and fLCBD from 2000s to 2010s (ΔpLCBD and ΔfLCBD) of native and non-native fish assemblages in upper and lower lakes, respectively

5.3 Results

Alpha diversity variations

For native fish assemblages, the two-way PERMANOVA test revealed that the phylogenetic alpha diversity indices, including MPD and MNPD, remained stable over periods and locations. The functional alpha diversity index, however, reflects a slight downward trend from the 2000s to the 2010s. This was demonstrated by significantly decreased MFD and MNFD indices in the 2010s compared to the 2000s, with a particularly significant reduction in functional richness observed in lower lakes over the decade. In contrast, non-native fish species exhibited no substantial spatiotemporal changes in either phylogenetic or functional alpha diversity indices, with the sole exception being a slight spatial difference in MPD indices (Figure 5.1).

Beta diversity changes

Contrasting trends in beta diversity over time between native and non-native fish assemblages were found (Figure 5.2). From the 2000s to the 2010s, native fishes experienced a significant increase in phylogenetic and functional differentiation (increased bet diversity) across different lakes. In contrast, non-native fish species presented a significant trend towards phylogenetic and functional homogenization (decreased beta diversity) during the same timeframe. These findings emphasize a notable temporal increase in beta diversity among native fish assemblages in lower lakes over the past decade. This rise was accompanied by an upsurge in the turnover pattern's magnitude and proportion, establishing it as the predominant component (Table 5.1). On the other hand, the beta diversity of non-native fish species showed significant spatial differences between upper and lower lakes during the 2010s. During this period, this study also witnessed a significant increase in the value and ratio of the nestedness pattern, making it the critical contributor to the overall beta diversity (Table 5.1), contrasting to the 2000s when such spatial distinctions were absent.

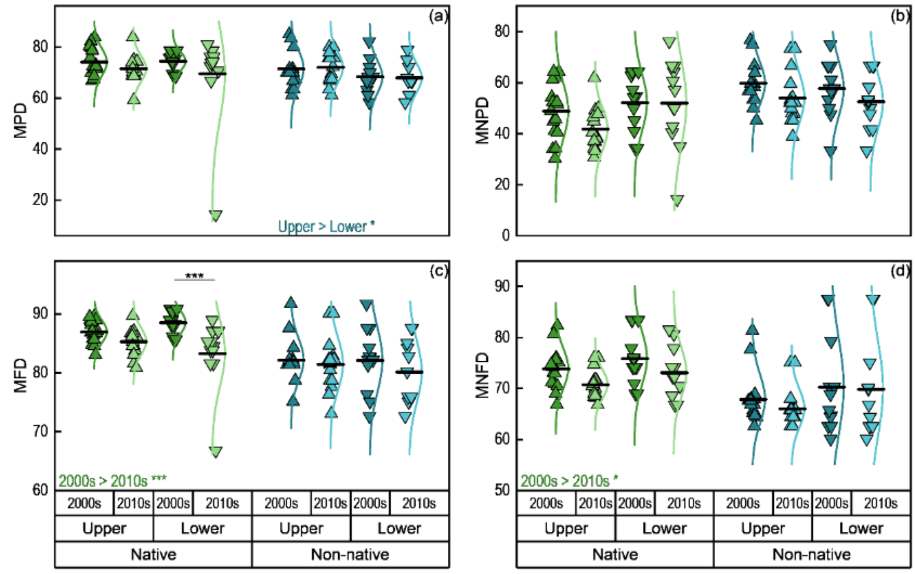


Figure 5.1 Phylogenetic, MPD (a) and MNPD (b), and functional, MFD (c) and MNFD (d), alpha diversity of native (green) and non-native (blue) fish assemblages in upper (regular triangles) and lower (inverted triangles) lakes. Two periods, the 2000s and 2010s, are shown in dark and light colours, respectively. Triangles represent studied lakes. Horizontal lines among triangles indicate average values, and curves adjacent to the triangles show the data's normal distribution. The results are based on two-way PERMANOVA tests, focusing on the main factors of periods (2000s vs. 2010s) and location (upper vs. lower lakes). When significant interactions between periods and location were detected, multiple comparisons were conducted, and the results are indicated by asterisks (***: $p < 0.001$, **: $0.001 \leqslant p < 0.01$, *: $0.01 \leqslant p < 0.05$.)

Table 5.1 The proportion of phylogenetic and functional turnover components to their respective overall dissimilarities (p_{turn}) for native and non-native fish assemblages in upper and lower lakes in two periods.

		Upper lakes		Lower lakes	
		2000s	2010s	2000s	2010s
Native	pp_{turn}	0.644 ± 0.029	0.667 ± 0.045	0.505 ± 0.040	0.549 ± 0.047
	fp_{turn}	0.677 ± 0.021	0.712 ± 0.038	0.622 ± 0.051	0.690 ± 0.039
Non-native	pp_{turn}	0.375 ± 0.039	0.346 ± 0.049	0.321 ± 0.041	0.161 ± 0.020
	fp_{turn}	0.381 ± 0.040	0.324 ± 0.046	0.388 ± 0.044	0.152 ± 0.018

Table 5.2 Changes in phylogenetic and functional LCBD values of native and non-native fish assemblages in upper and lower lakes. The statistically significant changes (one-way PERMANOVA test, $\alpha = 0.05$) are denoted by asterisks (***: $p < 0.001$, **: $0.001 \leqslant p < 0.01$, *: $0.01 \leqslant p < 0.05$).

		Upper lakes	Lower lakes	
Native	pLCBD	-0.018 ± 0.022	0.024 ± 0.012	
	fLCBD	-0.016 ± 0.005	0.021 ± 0.010	**
Non-native	pLCBD	-0.007 ± 0.006	0.010 ± 0.024	
	fLCBD	-0.011 ± 0.009	0.015 ± 0.017	

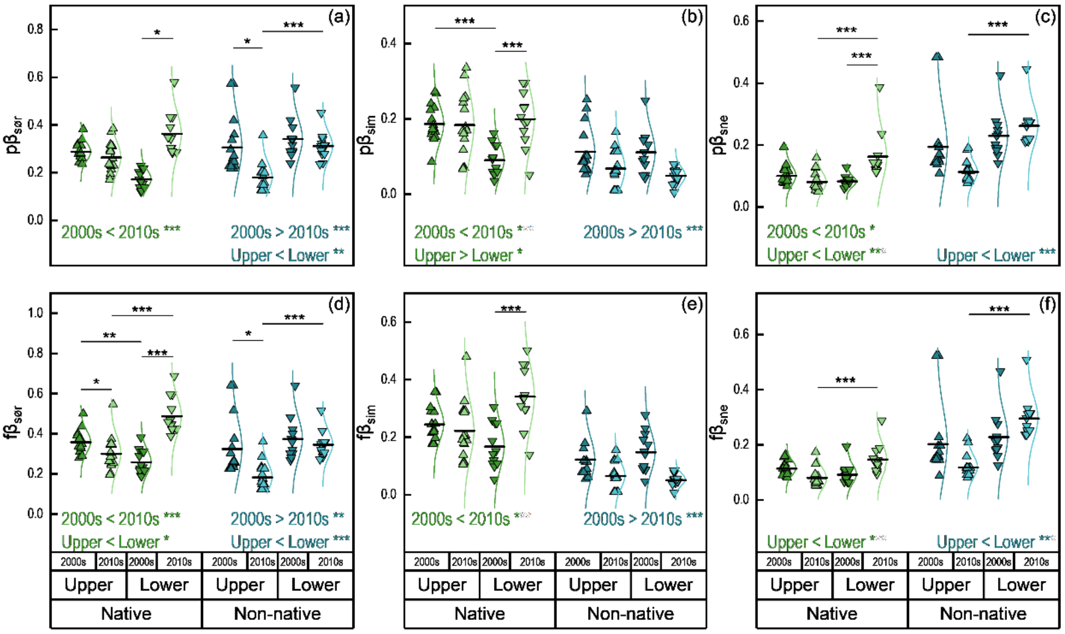


Figure 5.2 Phylogenetic beta diversity ($p\beta_{\text{sør}}$, a), phylogenetic turnover ($p\beta_{\text{sim}}$, b), and phylogenetic nestedness ($p\beta_{\text{sne}}$, c), as well as the functional counterparts—$f\beta_{\text{sør}}$ (d), $f\beta_{\text{sim}}$ (e), and $f\beta_{\text{sne}}$ (f)—of native (green) and non-native (blue) fish assemblages in upper (regular triangles) and lower (inverted triangles) lakes. Two periods, 2000s and 2010s, are differentiated in dark and light colours, respectively. Each triangle represents a studied lake. Horizontal short lines among triangles indicate the average values, while curves adjacent to the triangles depict the normal distribution of the data. The results are based on two-way PERMANOVA tests, focusing on the main factors of periods (2000s vs. 2010s) and location (upper vs. lower lakes). When significant interactions between periods and location were detected, multiple comparisons were conducted, and the results are indicated by asterisks (***: $p < 0.001$, **: $0.001 \leqslant p < 0.01$, *: $0.01 \leqslant p < 0.05$).

Relationships between changes in phylogenetic and functional beta diversity

Linear regression analyses demonstrated significant positive correlations between the changes in phylogenetic and functional beta diversity indices for both native and non-native fish communities (Figure 5.3). However, the correlation was significantly weaker for native fish communities ($p = 0.003$) compared to non-native species. Further examination of the results, particularly the distribution of data points across the quadrants of Figure 5.3, indicated that native fish in upper lakes trended towards greater phylogenetic and functional homogenization over the decade. Conversely, native fish in lower lakes demonstrated a pronounced shift towards increased heterogeneity. Meanwhile, non-native fish assemblages, maintained a consistent trend of phylogenetical and functional homogeneity across all lakes of the watershed.

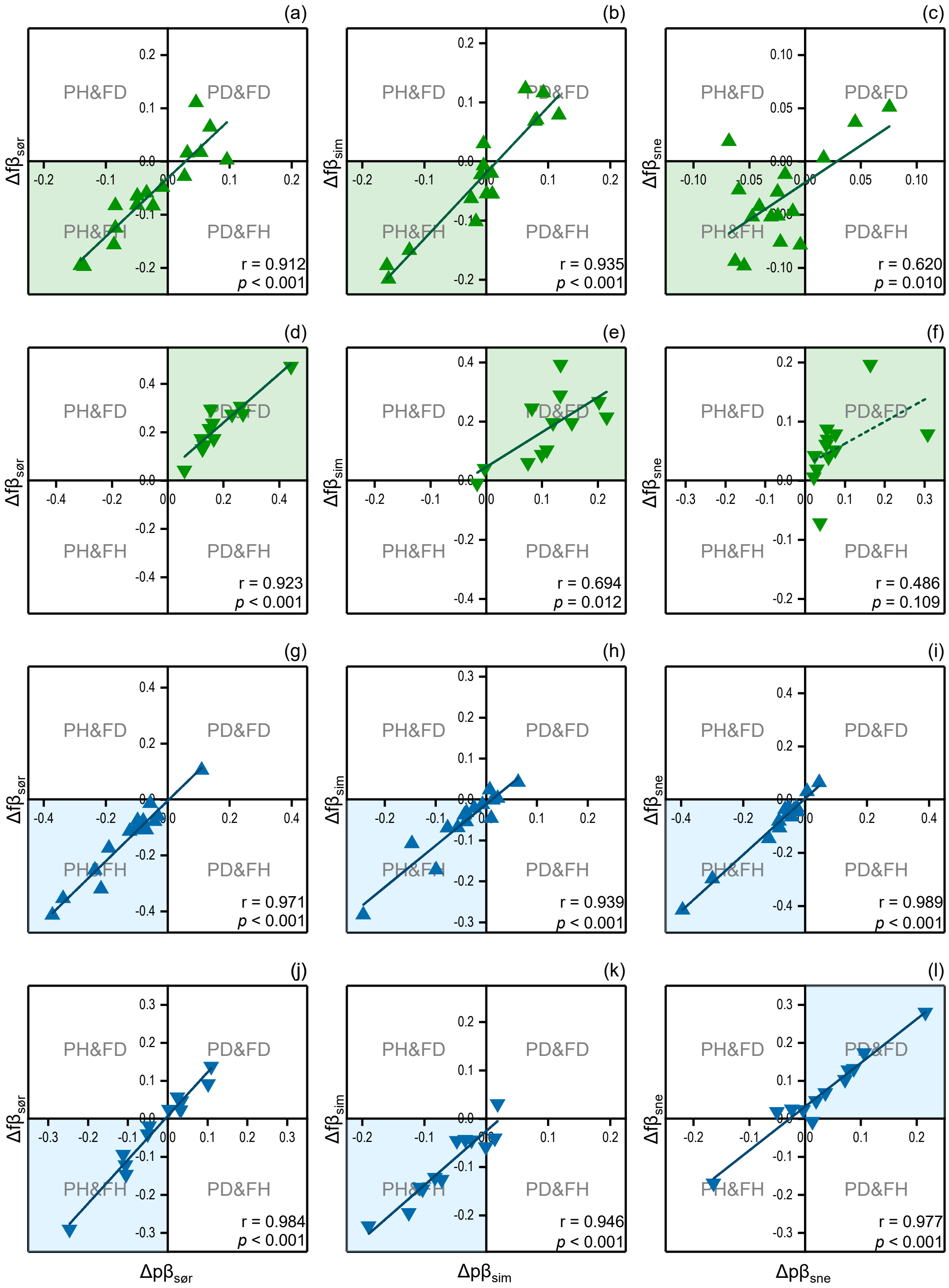


Figure 5.3 Linear regression between change in phylogenetic beta diversity metrics and changes in their functional counterparts: $\Delta\beta_{\text{sør}}$ (a, d, g, j), $\Delta\beta_{\text{sim}}$ (b, e, h, k), and $\Delta\beta_{\text{sne}}$ (c, f, i, l). Each regular triangle represents a studied upper lake, while inverted ones are the lower lakes. Green and blue triangles indicate native and non-native fish assemblages, respectively. The Pearson correlation (r) and significance (*p* values) are denoted. The coloured quadrants indicate where the majority (more than half) of lakes are concentrated. PH = phylogenetic homogenization, PD = phylogenetic differentiation, FH = functional homogenization, FD = functional differentiation.

Changes in phylogenetic and functional LCBD

Temporal changes in lake LCBD values revealed notable spatial distinctions between upper and lower lakes, despite observing similar trends in phylogenetic and functional LCBD alterations (Table 5.2). The relative uniqueness of fish assemblages in upper lakes continued to reduce over the studied periods (indicated by negative ΔLCBD values), whereas uniqueness in lower lakes escalated (indicated by positive ΔLCBD values). Notably, this spatial contrast was more accentuated in terms of functional compositions of native fish assemblages.

5.4 Discussion

The previous chapter has demonstrated an increase in taxonomic richness of non-native fishes in the oxbow lakes of the Ishikari River basin over the span of a decade, from the 2000s to the 2010s. However, the present study reveals that this rise in species richness did not lead to a significant increase in phylogenetic or functional diversity; instead, a relatively stable level was maintained across periods and locations. These findings suggest intense fish competition in the region, with successful introduction and establishment of non-native species possessing specific phylogenetic associations or ecological functions (Jiang et al., 2019), alongside persistent invasive pressure throughout the study period from non-native on native fish species in terms of phylogenetic information and ecological functions. However, this persistent invasion pressure varied among lakes. High heterogeneity in the phylogenetic structure and ecological function of non-native fishes across lakes in the 2000s significantly decreased by the 2010s, accompanied by significant reductions in the turnover patterns. Nonetheless, the results of this chapter indicate that regardless of the period and location, the nestedness pattern consistently dominated dissimilarity among lakes, contributing 62.5–83.9% and 61.2–84.8% to the phylogenetic and the functional dissimilarity, respectively. Altogether, the dominance of nestedness patterns and the reduction of turnover patterns signify a significant loss of phylogenetic information and ecological function in certain scattered lakes, favouring a broadly distributed pattern of characteristically monopolized phylogenetic and ecological functional structures. For instance, the representative species of non-native fishes, the topmouth gudgeon, belonging to Cypriniformes, expanded into all studied lakes within a decade (Dai et al., 2023). Its establishment and expansion in non-native habitats were facilitated by its wide-ranging diet and high environmental tolerance (Bernery et al., 2024; Zhang et al., 2022). In general, the reduced dissimilarity in non-native fish species across the basin, determined by nestedness patterns, suggests a clear trend towards homogenization. Fish species with specific phylogenetic relativeness and functional traits have expanded their presence across more lakes, thereby dominating the structures of non-native fish assemblages.

The dynamic interplay of non-native invasive species has profoundly altered the phylogenetic and functional structures of native fish communities in the oxbow lakes. This chapter underscores a notable shrink in the functional diversity of native fish from the 2000s to the 2010s. This decline correlates with the disappearance of species situating at the distant and isolated branches of the functional dendrogram. It implies a non-random process of native loss (Jiang et al., 2020; Si et al., 2016), where those possessing unique and isolated functional traits face heightened vulnerability under invasive pressures, while functions shared by multiple species endure temporarily. Supporting this, the beta diversity results reveal a significant increase in dissimilarity in both phylogenetic and functional structure from the 2000s to the 2010s. This coincides with a growing dominance of turnover patterns in phylogenetic and functional structure, indicating a shift towards less shared species among lakes over time. Initially, diverse phylogenetic backgrounds and ecological functions characterized the native fish communities in the 2000s. However, prolonged competition with non-native species has progressively restricted certain native fishes with unique functions, reducing the probability of observing similar functions across lakes (Cilleros et al., 2016) and, then further, exacerbating the turnover patterns. While some studies suggest that heightened turnover signifies greater habitat diversity and less shared function (Carvalho et al., 2021; Myers et al., 2021), the findings of this chapter paint a different picture. Elevated turnover patterns may serve as an early alarm of significant species loss rather than a positive sign of enriched biodiversity. Hence, this chapter believes that analysing turnover pattern changes requires careful consideration of various factors, including non-native invasions, over extended time frames. Moreover, this study aligns with the conceptual model of community homogenization proposed by Socolar et al. (2016), wherein beta diversity initially rises before sharply declining.

Spatially, such selective loss of native fish assemblages in oxbow lakes within the lower Ishikari basin is of particular concern. This is evident from the significant decrease in MFD values and the increase in other metrics such as $p\beta_{\text{sør}}$, $p\beta_{\text{sim}}$, $p\beta_{\text{sne}}$, $f\beta_{\text{sør}}$, and $f\beta_{\text{sim}}$ for native fish assemblages inhabiting these lower lakes from the 2000s to the 2010s. Despite no significant deterioration in external environmental conditions, like land use changes or massive sewage discharge, occurring in the lower Ishikari basin during the study period, this area stands out as the most densely populated and industrialized region within the watershed and even across

Hokkaido Island. Oxbow lakes here face considerable disturbance from human activities, including frequent river diversions, water withdrawals for domestic and agricultural purposes, and worsening water quality due to eutrophication. These factors have likely facilitated the introduction and establishment of non-native fish species with strong adaptive capacities in these lakes. Additionally, these factors have exacerbated the nestedness pattern of phylogenetic and functional structures among non-native fish species as they spread across multiple lakes, leading to a trend of spatial homogenization dominated by a few robust phylogenies and functional traits in lower lakes. Meanwhile, native fish assemblages, under pressure from both external environmental limitations and non-native invasions, have endured relatively independently in different lakes, resulting in a process of spatial heterogenization in both phylogenetic and functional structures. Furthermore, the relative importance of both native and non-native fish species in terms of phylogenetic and functional structures within lower lakes has increased from the 2000s to the 2010s, reflecting significant changes in fish community patterns as species distributions have intensively shifted. Notably, native fish species have exhibited a doubling in both phylogenetic and functional uniqueness relative to non-native species. This highlights their diminished competitive standing against non-native fish and the amplified rise in relative uniqueness due to their forced sporadic distribution.

In contrast to the highly competitive lower oxbow lakes, the oxbow lakes situated in the upper reach of the Ishikari River basin serve as shelters for native fish assemblages. Over the span of the 2000s to the 2010s, both native and non-native fish assemblages in the upper lakes experienced a decrease in their relative uniqueness, indicating a trend toward greater similarity in terms of both evolutionary history and ecological functions. However, in comparison to lower lakes, the native fish assemblages in the upper lakes exhibited a more heterogeneous evolutionary lineage (higher turnover and lower nestedness), although their functional roles showed less dissimilarity. This suggests that upper lakes still collectively shelter the functional diversity of native fishes, despite distant distribution of native species on the phylogenetic tree. This chapter found less dissimilarity in phylogenetic and functional structures of non-native fishes successfully established in upper lakes than in downstream lakes, suggesting that non-native fishes that spread upstream were more homogenous in their evolutionary history and ecological function (showing a significant nestedness pattern). However, as the invasion of non-native species persisted, the influence of this nestedness pattern on the overall diversity of fish species in the upper lakes diminished, reflecting the continued introduction of non-native species with a wider range of evolutionary history and ecological functions. This ongoing invasion is mirrored by an increase in the turnover proportions of native fish in the upper lakes. This spatial disparity between upstream and downstream lakes can potentially be attributed to the lower levels of human influence experienced by upper lakes along the Ishikari River, which have maintained more favourable environmental conditions, thus providing a conducive environment for both native and non-native fish populations to thrive.

Like previous research focusing on the diversity of fish faunas in terms of their phylogenetic and functional aspects, this study also found that changes over time in the phylogenetic dissimilarity of fish assemblages were closely correlated to changes in their functional dissimilarity. When focusing on changes in phylogenetic and functional nestedness, both native and non-native fish showed significant spatial differences between upper and lower lakes. More phylogenetically and functionally nestedness patterns appeared in the lower lakes, implying that fish with relatively distinctive phylogenetic and functional traits were lost in the Ishikari downstream area. Consequently, phylogenetic structures and functional traits tended to become more similar between lower lakes, demonstrating a typical pattern of homogenization (Jiang et al., 2019). This indicates that both the phylogenetic and functional compositions of fish assemblages respond to interactions between native and non-native species. Although this positive coupling between changes in evolutionary history and functional traits was observed in both native and non-native fish, this study noticed some subtle differences in the strength of this relationship. Non-native fish assemblages exhibited a particularly strong correlation between changes in their evolutionary history and functional traits, suggesting that as the ecological functions of non-native fish became more similar, their evolutionary diversity also simultaneously became more homogeneous. Such variations in consistency also reflect the weaker phylogenetic affinities and relatively independent ecological functions among non-native fishes, hinting at the randomness and variety of their origins. However, while the phylogenetic structure of native fish assemblages changed over time, the corresponding changes in their functional traits were relatively modest. This suggests that certain native species, despite having different evolutionary histories, fulfil similar ecological functions. This current chapter propose that this functional redundancy among native fish serves as a proactive resistance against environmental variations and ecological invasions. Despite the direct influence of competition for ecological niches and interactions among species based on functional traits on community composition, the presence of functional redundancy among native fish enables the maintenance of functional diversity even in the absence of certain species. Moreover, it preserves the potential for restoring the ecological functional structure of the community by drawing from a wider range of phylogenetic sources.

In conclusion, this chapter investigates the changes in phylogenetic and functional structure of native fish assemblages under invasive pressure over about ten-year period and the spatial upstream and downstream differences in this process, using fish data from the oxbow lakes along the Ishikari River. The findings of this chapter reveal a persistent influence of non-native species on both the evolutionary and functional aspects of the native fish communities, with a prevailing trend towards homogenization primarily driven by nestedness structures. As non-native species continued to infiltrate, certain native fish phylogenies and functions became confined to sporadic lakes, leading to heightened turnover patterns. Despite observing functional redundancy among native fish in response to environmental shifts and competition for resources, this redundancy appeared less effective in mitigating pressures in the lower lakes, where environmental conditions and invasive species impacts were more pronounced. Consequently, a significant loss of native evolutionary diversity and functional traits was foreseen in these regions. In contrast, the upper lakes emerged as potential sanctuaries for native fish, capable of accommodating species with diverse evolutionary backgrounds and ecological traits not found in the lower lakes. Thus, this chapter underscore the importance of prioritizing conservation efforts in the upstream oxbow lakes of the Ishikari River. Despite the presence of non-native species in upper regions, they still retain a higher degree of native fish diversity, preserving unique evolutionary information and ecological functions compared to their downstream counterparts.

Chapter 6

Spatial patterns of fish cumulative diversity driven by stochastic and deterministic processes

6.1 Introduction

Exploring how species assemble into local communities is a fundamental question in community ecology which could pave the way for aiding biodiversity conservation (Clements, 1916; Gleason, 1927; Pettersen et al., 2022). Community assembly, defined as the dynamics of local communities linked by the dispersal of potentially interacting species (Leibold et al., 2004), has been extensively studied to generate a widely accepted framework in depicting ecological process (Alberti & Wang, 2022; Iwamoto et al., 2022). In terms of community, theoretical and empirical ecologists have identified four assembly paradigms, i.e., patch-dynamic, species-sorting, mass-effect, and neutral models. The patch-dynamic model focuses on spatial heterogeneity and the role of habitat patches in species colonization and persistence; the species-sorting model emphasizes environmental heterogeneity and niche differentiation, where local conditions determine species presence; the mass-effect model highlights the importance of connectivity and dispersal, with species persisting in less suitable habitats due to immigration from other areas; and the neutral model posits that species are ecologically equivalent, with community composition driven by random processes rather than niche differentiation (Leibold et al., 2004). Given the non-mutual independence and the ease of measurement of these paradigms (Brown et al., 2018), recent ecologists suggest examining the stochastic and deterministic processes in metacommunity assembling (Chase & Myers, 2011; Ning et al., 2019). The neutral theory based stochastic process posits that communities were randomly assembled by unpredictable events (e.g., passive dispersal, unpredictable disturbances, random extinction). In contrast, deterministic process assume that niche-related interspecies interactions and environmental filtering can result in selected communities (Chase & Myers, 2011; Stegen et al., 2012). Benefitting from resolving the metacommunity assembly process, tailored and targeted biodiversity conservation strategies could be implemented (Ohira et al., 2015), with conservation efforts prioritizing increasing ecosystem resilience to damage from random events and sustaining desired habitat properties in deterministic process. In consequence, it is of great importance to distinguish the ecological process underpinning meta-community assembly (Viana & Chase, 2019).

While an increasing number of studies are examining the relative influence of stochastic and deterministic processes on community structure, most research still predominantly focuses on changes in species composition at the taxonomic level (Dai et al., 2024; Stegen et al., 2012). Typically, these studies use simulations to compare theoretical species compositions against actual observed data, by simulating stochastic and deterministic processes separately as a prerequisite qualification, such as the recently proposed dispersal-niche continuum index (Vilmi et al., 2021) and the traditional elements of metacommunity structure framework (Presley et al., 2010). This approach presents two significant issues: first, it often overlooks the crucial phylogeny background and ecological functions that underpin different species assemblies; second, it overly relies on virtual simulations, which can obscure the individual impact of either process on community formation in practical cases. This chapter aims to offer new perspectives and methodologies to address these challenges, enhancing the understanding of community dynamics beyond the traditional scope.

The objective of simplifying complex ecological changes into concise metrics has been a longstanding aim in quantitative ecological research and is crucial for biodiversity conservation practices. As discussed in Chapter 2, the methods for describing biodiversity are diverse, and the wide array of available diversity indices can be bewildering for practitioners in diversity conservation who lack specific training (Lyashevska & Farnsworth, 2012). These indices include taxonomic diversity indices, which primarily count species and their variance; phylogenetic diversity indices, which consider the genetic relationships and lineage proximity among species; and functional diversity indices, which assess species abilities to adapt to their environment and utilize resources (Fusco et al., 2021; Su et al., 2021; Xu et al., 2024). While each index captures a unique aspect of species diversity within a community, they only represent a fragment of the full spectrum of biodiversity (Castro et al., 2020), reminiscent of the parable of the blind men and the elephant. In this context, this chapter explores the possibility of mathematically synthesizing these multidimensional diversity indices into a single, more comprehensive, and informative metric. Although there have been efforts to integrate these indices (Chao et al., 2021; Jiang et al., 2015), a unified and scalable computational framework applicable across different taxa and spatial scales is still missing. To address this gap, this chapter introduces a novel computational concept and develops a framework to amalgamate biodiversity information from multiple dimensions, detailed in the following Methods section, termed the cumulative diversity index. This index aims to encompass a broader range of diversity aspects while maintaining simplicity in its application and interpretation.

The Japanese archipelago is composed of numerous islands aligned from northeast to southwest, with the largest islands being Hokkaido, Honshu, Shikoku, and Kyushu, arranged in a north-to-south sequence. These islands are divided by significant natural barriers, including the Tsugaru Strait, the Kanmon Straits, and the Seto Inland Sea, which severely limit the natural dispersal of many species (Watanabe et al., 2017). This geographic isolation is particularly impactful for freshwater fish, which are restricted to rivers and lakes and thus find cross-island movement almost impossible (Ponce de León et al., 2014; Šlechtová et al., 2004). Thus, on a national scale, this dispersal limitation is believed the primary factor influencing the spatial distribution of fish diversity across Japanese archipelago. The configuration of the Japanese islands provides a unique environment to discuss the location where dispersal limitation occurs, i.e., the straits in this case, could indicate potential boundaries of NFCAs.

Although industrialization and urbanization in the Ishikari basin concluded in the last century, the area has been relatively free from significant anthropogenic disturbances like water pollution, dam construction, and the massive introduction of invasive species since the beginning of this century (Fukushima et al., 2007). Nevertheless, it is important to recognize that some non-native species have established since the last century and now compete with native fish populations, impacting their survival and distribution (Hayashida et al., 2010). Given these conditions, this chapter posits that the fish communities in oxbow lakes along the Ishikari River are primarily shaped by deterministic processes, especially through interactions between native and invasive species, rather the dispersal limitation comparing to the lakes across the Japanese archipelago by straits. Thus, these oxbow lakes in Ishikari River basin serves as an exemplary case study for examining how deterministic processes influence the spatial distribution of fish community.

Using a framework developed for calculating the cumulative diversity index and utilizing fish data from previous chapters, this chapter differentiates between fish community structures mainly shaped by the stochastic and the deterministic processes, respectively. Given the constant presence of straits, the spatial diversity pattern, such as the national case, principally shaped by stochastic processes generally remains. In contrast, interspecies competition, which is highly sensitive to temporal changes, means that diversity patterns influenced by deterministic processes can shift over relatively short periods of time, such as the Ishikari case. The hypotheses tested are twofold: First, it is proposed that the cumulative diversity of native fish assemblages in lakes across the Japanese archipelago exhibits a distinct and stable spatial pattern over time, with each island displaying a unique diversity profile. Second, the fish in the oxbow lakes of the Ishikari River basin show varied patterns of cumulative diversity between upstream and downstream area.

6.2 Methods

Proposed assessment framework for cumulative diversity

The previous chapter examines various diversity indices from multiple perspectives (taxonomic, phylogenetic, and functional) at different levels (alpha, beta, LCBD), which are collectively encapsulate various facets of a fish community diversity. Building on this, the chapter introduces a computational framework designed to integrate these diversity indices from multiple perspectives into a unified measure, which is termed the cumulative diversity index. The cumulative diversity index is calculated by taking the arithmetic mean of logarithmically transformed values of the taxonomic, phylogenetic and functional indices of the same type. The equation for cumulative diversity calculation of assemblage *j* can be expressed succinctly as:

$$\left[\sum_{d=1}^{x} \log_{10}\left(\mathrm{DI}_{jd} + 1\right)\right] / x \qquad 6.1$$

where x is the number of diversity indices integrated into the assessment, and DI_{jd} represents the value of diversity index d of the assemblage j (Figure 6.1). For instance, in this chapter, when employing the equation to compute the cumulative LCBD (cLCBD) values, d denotes an element of the set encompassing all the LCBD indices ascertained in previous steps, i.e., $d \in \{\text{tLCBD, pLCBD, fLCBD}\}$, subsequently assigning a value of three to x. Similarly, the cumulative alpha (cAlpha) and beta (cBeta) diversity were computed for each studied native fish assemblage, respectively.

Statistical Analysis

To evaluate the practicality of the computational framework for the newly proposed cumulative diversity index, this chapter utilizes two fish community datasets from lakes at distinct spatial scales: nationally across Japan (discussed in Chapter 3) and within the Ishikari River basin (covered in Chapters 4 and 5). This chapter employs the same testing settings as those in Chapter 3, which examined all four time periods for native fishes across Japan, and Chapter 4, which studied both native and non-native fishes in oxbow lakes along the Ishikari River during the 2000s and 2010s, respectively. First, regression analyses were conducted to determine if a correlation exists between the fish diversity, as indicated by traditional diversity indices at each lake, and their spatial locations. This chapter then assessed whether the cumulative diversity indices could accurately mirror the spatial patterns observed with traditional indices at both spatial scales. The findings of Chapter 3 suggested that lakes in the northernmost (highest latitude) and the southernmost (lowest latitude) islands of Japan exhibit unique fish compositions, leading to the hypothesis of a quadratic polynomial relationship between diversity indices of each lake and its latitude in the nationwide analysis. Whereas the results of Chapter 4 illustrated that changes in fish species in the oxbow lake along the Ishikari River showed up- to downstream spatial differences in linear changes, this chapter continues to focus on the spatial pattern of fish diversity in the Ishikari oxbow lakes based on linear regression models. Furthermore, it is worthy to recognize the geographical orientation of the Ishikari River, which predominantly flows from north to south, particularly in regions where oxbow lakes are concentrated. Consequently, the distance from the river source (DRS, discussed in Chapter 4) of these oxbow lakes showed a significant negative correlation with latitude (Person's $r = -0.96$, $p < 0.001$), that is to say lakes at higher latitudes are nearer to the river source. For consistency, in this chapter, latitude was employed as the variable representing spatial positioning of lakes at both national and watershed spatial scales.

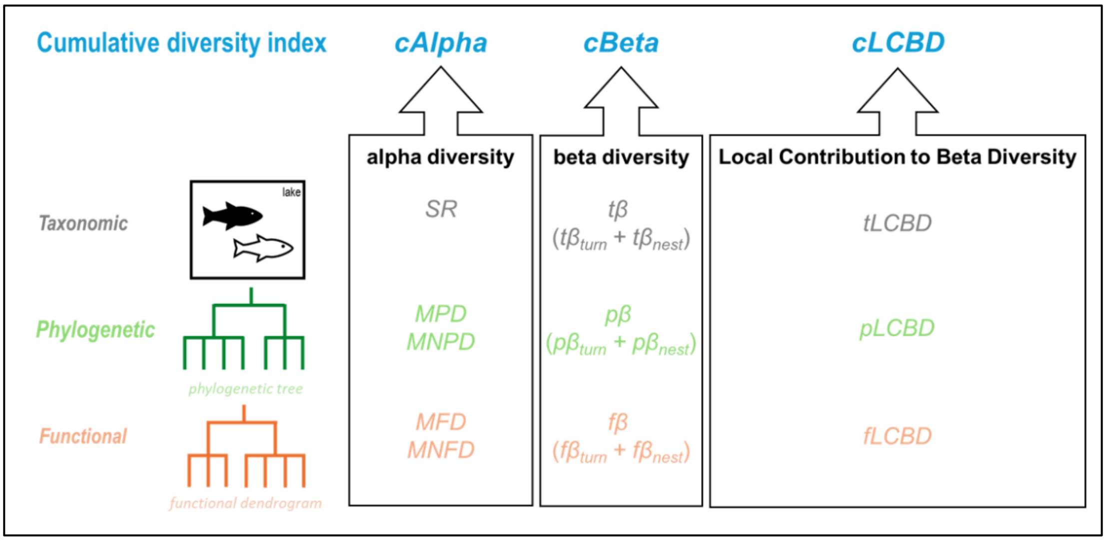


Figure 6.1 Schematic representation of the cumulative diversity calculation framework. The meaning of the variables in the cumulative diversity calculation equation in the figure, as well as the abbreviations for diversity indices, is consistent with the narrative in the text.

To further discuss the robustness of the cumulative diversity results and their correlation with individual components, this section additionally calculated the two-dimensional cumulative diversity index (2D-cDI) using pairs of diversity perspectives (i.e., any two of taxonomic (TD), phylogenetic (PD), and functional (FD) diversity indices). These 2D-cDI values were then correlated with the cumulative diversity calculated in the previous section (3D-cDI). For national lakes, the 2D- and 3D-cDI of native fishes was quantified for each of four time periods. For oxbow lakes along the Ishikari River, the correlation between the 2D- and 3D-cDI of native and non-native fishes was calculated for the 2000s and 2010s, respectively.

6.3 Results

Spatial patterns of fish diversity driven by stochastic processes

The spatial pattern of fish diversity in national lakes based on traditional diversity indices was significant. At the alpha diversity level, apart from the MPD index for the Future II period, all other indices demonstrated significant quadratic diversity relationships with lake latitude across all periods ($p < 0.044$; Table 6.1). Specifically, species richness and MFD exhibited negative correlations with latitude during all four periods, whereas MFND consistently showed a positive correlation. At the beta diversity level, all indices revealed strong positive correlations with lake latitude ($p < 0.001$; Table 6.2), indicating a consistent pattern across all periods. Similarly, strong positive correlations were observed with both taxonomic and functional LCBD indices in relation to lake locations ($p < 0.001$; Table 6.3). However, a few phylogenetic diversity indices did not show significant correlations with lake latitude during certain periods.

The proposed cumulative diversity allows to visualize changes in the diversity and distribution patterns of native fish assemblages in Japanese lakes (Figure 6.2). The cumulative alpha diversity (cAlpha), revealing hump-shaped associations with the latitude ($p < 0.001$; Figure 6.2b), suggested that the richness of native fishes was comparatively low on Hokkaido (the northernmost) and Kyushu (the southernmost). Instead, lakes in the Honshu demonstrated high levels of species richness. This spatial distribution pattern of cAlpha was consistently observed across all temporal periods, despite a continuous decline in the average index values (F = 6.521, $p = 0.001$, Figure 6.2a). Conversely, this research observed higher cumulative beta diversity (cBeta) values in the lakes of Hokkaido and Kyushu, resulting in a U-shaped curve along the latitudinal gradient ($p < 0.001$, Figure 6.2d). These spatial patterns were similarly observed across all three temporal periods, but with an inc-

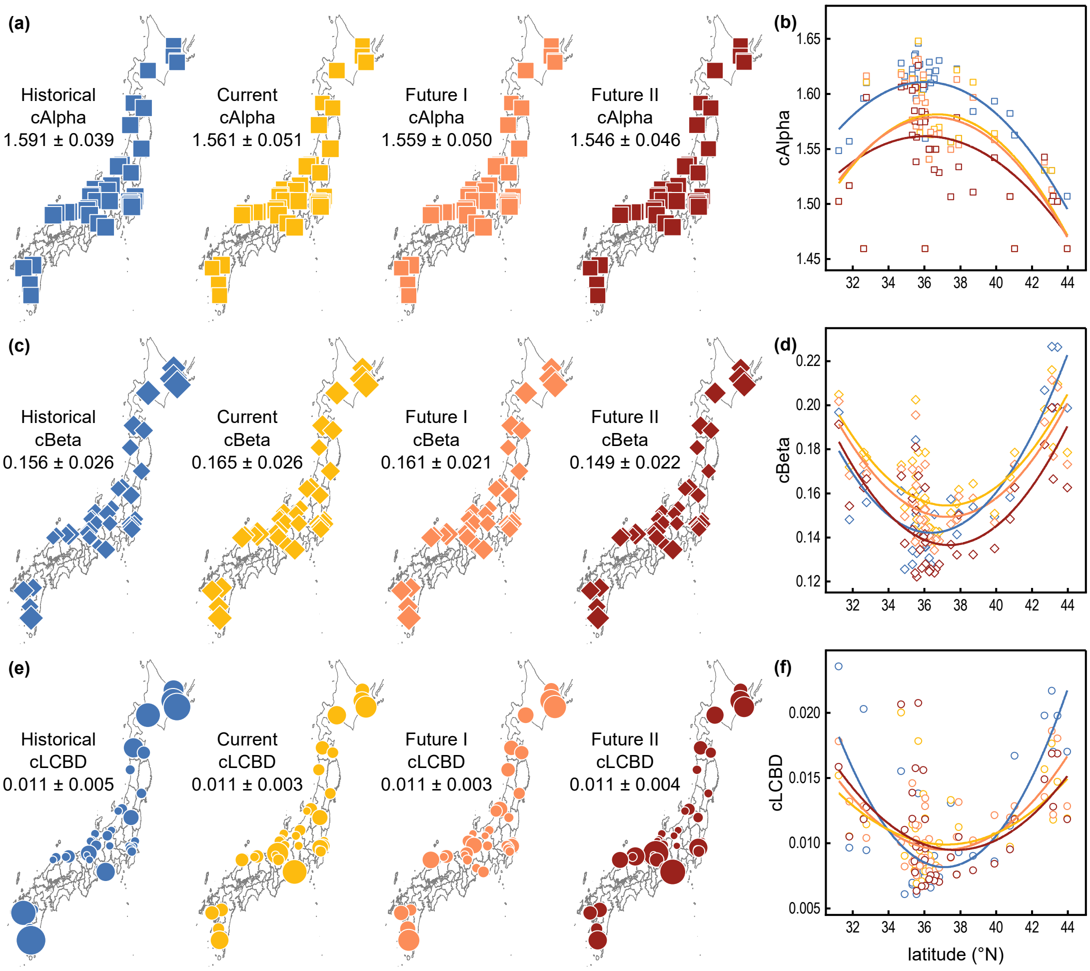


Figure 6.2 Points on the map of Japan denote each lake's cumulative diversity, with point size reflecting the diversity index value. Squares symbolize cumulative alpha diversity (cAlpha, a), diamonds represent cumulative beta diversity (cBeta, c), and circles indicate each lake's cumulative location contribution to beta diversity (cLCBD, e). Average values with a standard deviation of cumulative diversity are presented in the corresponding panels. On the right side, three scatter plots display the spatial correlation between each lake's cAlpha (b), cBeta (d), cLCBD (f) and its latitude, respectively. Colour codes distinguish between the four periods: blue for the historical period, yellow for the current period, and orange and red for the future I and II periods, respectively.

rease in cBeta values from 0.156 in the historical period to 0.165 in the current period, followed by a decrease to 0.149 in the simulative future II period (F = 3.879, $p = 0.012$, Figure 6.2c). Finally, a significant spatiotemporal pattern shift in cumulative LCBD values was identified throughout the Japan archipelago. During the historical period, the lakes located in the northernmost and southernmost islands exhibited the most out-standing contribution to nationwide fish beta diversity (highest cLCBD values), resulting in significant U-shaped curves along the latitude ($R^2 = 0.647$, $p < 0.001$). However, in the following periods, this curve was flattened, indicating the homogeneous relative contribution of individual lakes (Figure 6.2f).

Table 6.1 Results of quadratic polynomial regression (equation: y=B1x+B2x^2+Intercept) between the alpha diversity indexes of native fishes in lakes across Japan and the latitude at which the lakes are located. *P* values less than 0.05 are bolded.

Metric	Period	B1	S.E.	B2	S.E.	Intercept	S.E.	r^2	F	*p*
S	Historical	16.149	5.612	-0.224	0.073	-277.141	106.593	0.327	10.225	**< 0.001**
	Current	10.215	5.733	-0.142	0.075	-173.368	108.900	0.151	4.369	**0.020**
	Future I	9.518	4.489	-0.133	0.059	-161.888	85.265	0.208	5.979	**0.006**
	Future II	6.194	3.338	-0.088	0.044	-101.778	63.395	0.227	6.571	**0.004**
MPD	Historical	-2.611	5.760	0.019	0.075	139.384	109.411	0.262	7.729	**0.002**
	Current	16.270	5.817	-0.219	0.076	-234.341	110.497	0.185	5.325	**0.009**
	Future I	14.938	5.853	-0.202	0.077	-208.617	111.178	0.167	4.817	**0.014**
	Future II	2.442	5.514	-0.038	0.072	24.777	104.739	0.033	1.643	0.208
MNPD	Historical	-24.344	8.225	0.328	0.108	500.014	156.231	0.211	6.091	**0.005**
	Current	-7.838	6.550	0.113	0.086	188.302	124.417	0.113	3.412	**0.044**
	Future I	-9.356	5.903	0.132	0.077	218.004	112.132	0.150	4.345	**0.020**
	Future II	-12.953	5.749	0.178	0.075	286.701	109.193	0.189	5.423	**0.009**
MFD	Historical	11.885	3.311	-0.162	0.043	-160.857	62.886	0.336	10.618	**< 0.001**
	Current	9.424	5.187	-0.131	0.068	-113.883	98.527	0.147	4.287	**0.021**
	Future I	9.883	5.111	-0.138	0.067	-121.789	97.083	0.170	4.892	**0.013**
	Future II	11.438	5.226	-0.159	0.068	-149.886	99.266	0.201	5.772	**0.007**
MNFD	Historical	-8.138	3.855	0.120	0.050	174.722	73.232	0.462	17.290	**< 0.001**
	Current	-12.594	5.617	0.170	0.074	272.763	106.682	0.125	3.711	**0.034**
	Future I	-12.724	5.161	0.172	0.068	275.977	98.037	0.150	4.345	**0.020**
	Future II	-8.150	5.283	0.113	0.069	189.181	100.343	0.087	2.811	**0.073**

Table 6.2 Results of quadratic polynomial regression (equation: y=B1x+B2x^2+Intercept) between the beta diversity indexes of native fishes in lakes across Japan and the latitude at which the lakes are located. *P* values less than 0.05 are bolded.

Metric	Period	B1	S.E.	B2	S.E.	Intercept	S.E.	r^2	F	*p*
tβ	Historical	-0.355	0.055	0.005	0.001	6.918	1.052	0.686	42.480	**< 0.001**
	Current	-0.327	0.060	0.004	0.001	6.588	1.144	0.470	17.874	**< 0.001**
	Future I	-0.276	0.064	0.004	0.001	5.591	1.220	0.381	12.675	**< 0.001**
	Future II	-0.363	0.063	0.005	0.001	7.223	1.195	0.492	19.426	**< 0.001**
pβ	Historical	-0.355	0.043	0.005	0.001	6.790	0.817	0.794	74.187	**< 0.001**
	Current	-0.276	0.045	0.004	0.001	5.552	0.859	0.537	23.022	**< 0.001**
	Future I	-0.230	0.049	0.003	0.001	4.664	0.934	0.427	15.160	**< 0.001**
	Future II	-0.279	0.050	0.004	0.001	5.589	0.947	0.470	17.865	**< 0.001**
fβ	Historical	-0.340	0.047	0.005	0.001	6.560	0.888	0.724	50.723	**< 0.001**
	Current	-0.265	0.049	0.004	0.001	5.310	0.940	0.496	19.711	**< 0.001**
	Future I	-0.242	0.053	0.003	0.001	4.834	1.003	0.449	16.509	**< 0.001**
	Future II	-0.282	0.047	0.004	0.001	5.560	0.901	0.551	24.311	**< 0.001**

Table 6.3 Results of quadratic polynomial regression (equation: y=B1x+B2x^2+Intercept) between the LCBD indexes of native fishes in lakes across Japan and the latitude at which they are located. *P* values less than 0.05 are bolded.

Metric	Period	B1	S.E.	B2	S.E.	Intercept	S.E.	r^2	F	p
tLCBD	Historical	-0.028	0.006	3.96E-04	8.14E-05	0.514	0.117	0.634	33.025	**<0.001**
	Current	-0.023	0.007	3.16E-04	8.84E-05	0.438	0.127	0.350	10.940	**<0.001**
	Future I	-0.024	0.007	3.30E-04	8.67E-05	0.458	0.124	0.374	12.037	**<0.001**
	Future II	-0.031	0.008	4.23E-04	1.02E-04	0.586	0.146	0.389	12.776	**<0.001**
pLCBD	Historical	-0.047	0.011	6.35E-04	1.46E-04	0.876	0.209	0.388	12.718	**<0.001**
	Current	0.000	0.014	-2.60E-06	1.90E-04	0.046	0.273	-0.033	0.402	0.672
	Future I	-0.003	0.009	5.53E-05	1.17E-04	0.070	0.167	0.063	2.237	0.122
	Future II	-0.018	0.017	2.23E-04	2.29E-04	0.372	0.328	-0.007	0.877	0.425
fLCBD	Historical	-0.048	0.008	6.67E-04	1.12E-04	0.895	0.160	0.617	30.863	**<0.001**
	Current	-0.035	0.008	4.81E-04	1.06E-04	0.666	0.151	0.432	15.043	**<0.001**
	Future I	-0.032	0.007	4.43E-04	8.56E-05	0.611	0.123	0.508	20.138	**<0.001**
	Future II	-0.031	0.007	4.19E-04	9.63E-05	0.593	0.138	0.367	11.720	**<0.001**

Upon the removal of all threatened species in the future simulations, lakes located in southern Honshu, such as Lake Biwa, experienced a significant increase in cLCBD values, establishing them as the lakes with the more important contribution to nationwide native fish dissimilarity patterns (Figure 6.2e).

Spatial patterns of fish diversity driven by deterministic processes

The diversity patterns of fish communities in the oxbow lakes along the Ishikari River showed spatial variations along latitude for only a few indices. Alpha diversity of non-native fish species across all lakes revealed no significant correlation with geographical location (Table 6.4). Among native fish, only species richness demonstrated significant positive correlations with the lakes' latitude during both the 2000s ($p = 0.049$) and 2010s ($p = 0.005$). Additionally, no significant spatial patterns along latitude were observed for phylogenetic and functional alpha diversity indices. Beta diversity of both native and non-native fish species in the oxbow lakes showed no significant correlation with the lake latitude (Table 6.5). However, consistent spatial patterns were noted in phylogenetic and functional beta diversity. For native fish, the phylogenetic and functional beta diversity increased with latitude during the 2000s ($p < 0.013$), but this positive correlation changed to a significant negative correlation in the 2010s ($p < 0.022$). Conversely, the phylogenetic and functional beta diversity of non-native fish negatively correlated with lake latitude during the 2010s only ($p = 0.007$). Additionally, aside from the statistically significant negative correlation of functional LCBD indices for native fishes with latitude in the 2010s ($p = 0.047$), all other LCBD indices for both native and non-native fish, across all time periods, showed no spatial patterns related to latitude (Table 6.6).

Overall, the cumulative diversity index successfully mirrored the latitudinal spatial patterns of fish assemblages in the oxbow lakes in the Ishikari River basin, similar to those shown by the traditional diversity indices (Figure 6.3). For native fishes, the cBeta index also indicated a positive correlation with latitude during the 2000s ($p = 0.004$), which shifted to a negative correlation in the 2010s ($p = 0.007$). Furthermore, the cLCBD index in the 2010s revealed a negative correlation ($p = 0.042$), indicating that the uniqueness of native fishes in these lakes decreased as latitude increased. For non-native fish, a negative correlation between cumulative Beta diversity and latitude was also observed in the 2010s ($p = 0.044$). However, it is worth noting that the spatial pattern of taxonomic richness of native fishes across latitudes was not captured by the cumulative diversity index.

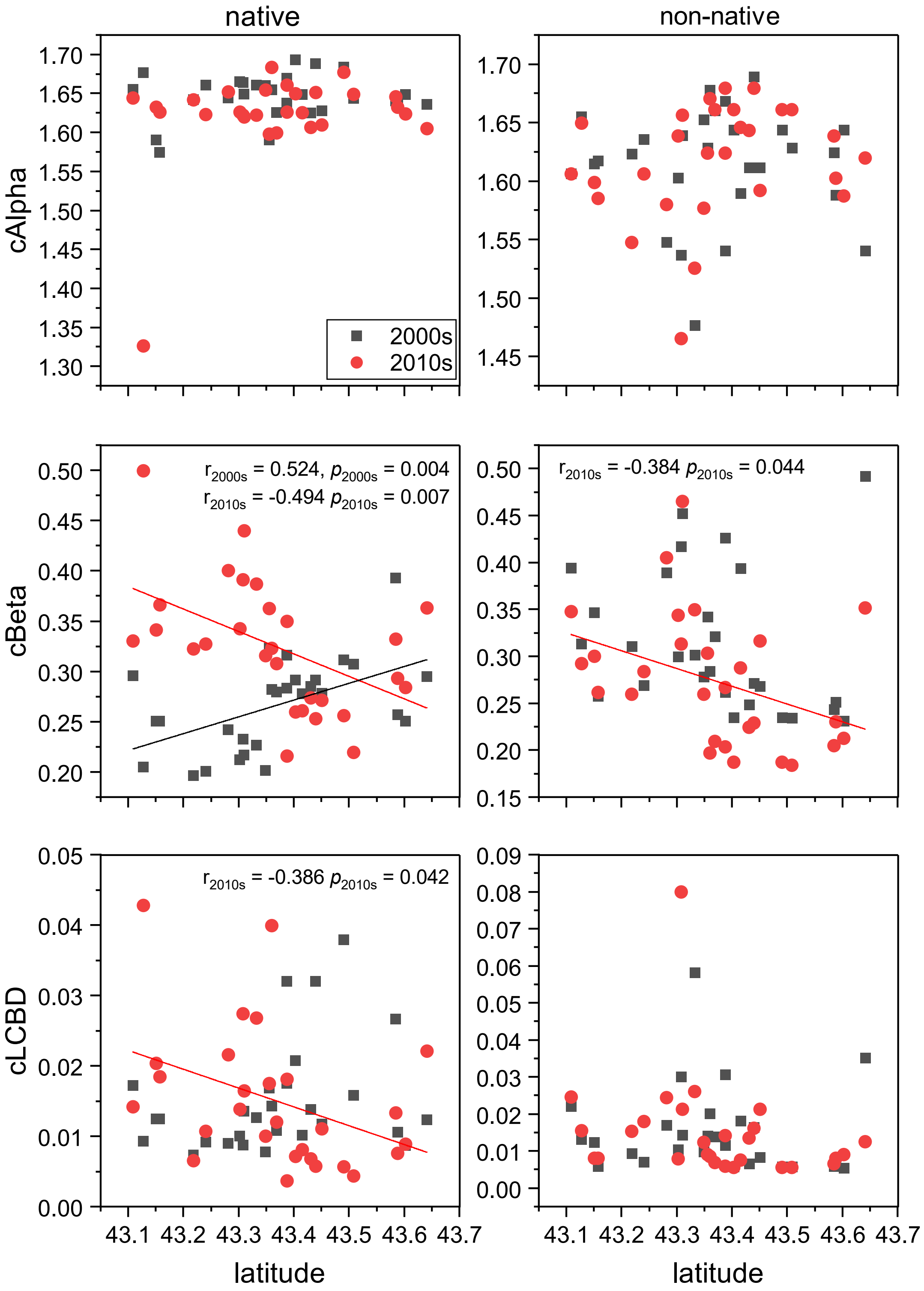


Figure 6.3 Linear regression plots of cumulative diversity indices (cAlpha, cBeta, cLCBD) of native (panels on the left) and non-native (panels on the right) fish assemblages in oxbow lakes of the Ishikari River basin versus the latitude at which the lakes are located for the 2000s (black squares) and 2010s (red dots). Only statistically significant regression lines (*p* values less than 0.05) are printed.

Relationships between 2D- and 3D-cDI

Overall, the 2D-cDI showed a higher correlation with the 3D-cDI values (Table 6.7). However, for the national case, the correlation between the 2D-cAlpha and 3D-cAlpha was not statistically significant when the taxonomic alpha diversity index (species richness) was excluded. Meanwhile, the correlation coefficient between any 2D-cBeta and 2D-cBeta index was only around 0.5 in the Future I simulation. In the Ishikari River oxbow lakes, the correlation coefficients of 3D-cAlpha and 2D-cAlpha (excluding phylogenetic information) were less than 0.6 for both the 2000s and 2010s (Table 6.8).

Table 6.4 Results of linear regression between the alpha indexes of native and non-native fish assemblages in oxbow lakes along the Ishikari River and the latitude at which the lakes are located. *P* values less than 0.05 are bolded.

		Slope	se	Intercept	se	r	*p*
Richness							
native	2000s	3.912	1.900	-163.760	82.383	0.374	**0.049**
	2010s	7.085	2.279	-301.300	98.813	0.521	**0.005**
non-native	2000s	1.828	2.611	-74.918	113.240	0.136	0.490
	2010s	4.913	2.964	-207.700	128.540	0.309	0.109
MPD							
native	2000s	-2.780	6.339	194.760	274.900	-0.086	0.665
	2010s	11.500	16.201	-428.120	702.620	0.138	0.484
non-native	2000s	0.105	9.396	65.546	407.470	0.002	0.991
	2010s	3.402	8.157	-77.289	353.750	0.082	0.680
MNPD							
native	2000s	-4.413	15.051	241.660	652.720	-0.057	0.772
	2010s	-23.512	17.853	1065.800	774.230	-0.250	0.199
non-native	2000s	-12.152	12.578	585.870	545.460	-0.186	0.343
	2010s	3.270	13.679	-88.421	593.250	0.047	0.813
MFD							
native	2000s	-3.962	2.717	259.430	117.840	-0.275	0.157
	2010s	8.273	5.371	-274.360	232.930	0.289	0.136
non-native	2000s	-4.247	5.965	266.280	258.670	-0.138	0.483
	2010s	-1.013	6.480	124.790	281.020	-0.031	0.877
MNFD							
native	2000s	-4.440	6.184	267.260	268.190	-0.139	0.479
	2010s	-4.246	5.292	255.860	229.500	-0.155	0.430
non-native	2000s	-15.569	9.290	744.050	402.880	-0.312	0.106
	2010s	-17.389	8.711	821.800	377.780	-0.365	0.056

Table 6.5 Results of linear regression between the beta indexes of native and non-native fish assemblages in oxbow lakes along the Ishikari River and the latitude at which the lakes are located. *P* values less than 0.05 are bolded.

		Slope	Error	Intercept	Error	r	*p*
tβ							
native	2000s	0.114	0.086	-4.589	3.736	0.252	0.196
	2010s	-0.288	0.142	12.966	6.154	-0.370	0.052
non-native	2000s	-0.142	0.219	6.599	9.510	-0.126	0.522
	2010s	-0.142	0.219	6.599	9.510	-0.126	0.522
pβ							
native	2000s	0.297	0.074	-12.641	3.215	0.618	**<0.001**
	2010s	-0.266	0.109	11.848	4.729	-0.432	**0.022**
non-native	2000s	-0.119	0.142	5.486	6.160	-0.162	0.409
	2010s	-0.295	0.104	13.040	4.517	-0.486	**0.009**
fβ							
native	2000s	0.245	0.091	-10.297	3.960	0.465	**0.013**
	2010s	-0.515	0.141	22.695	6.132	-0.581	**0.001**
non-native	2000s	-0.145	0.173	6.618	7.498	-0.162	0.410
	2010s	-0.363	0.125	15.993	5.403	-0.496	**0.007**

Table 6.6 Results of linear regression between the LCBD indexes of native and non-native fish assemblages in oxbow lakes along the Ishikari River and the latitude at which they are located. *P* values less than 0.05 are bolded.

		Slope	Error	Intercept	Error	r	*p*
tLCBD							
native	2000s	0.022	0.017	-0.925	0.756	0.242	0.215
	2010s	-0.041	0.022	1.835	0.969	-0.342	0.075
non-native	2000s	-0.021	0.028	0.949	1.205	-0.147	0.455
	2010s	-0.044	0.031	1.965	1.339	-0.272	0.162
pLCBD							
native	2000s	0.085	0.059	-3.650	2.577	0.270	0.165
	2010s	-0.077	0.066	3.361	2.845	-0.223	0.253
non-native	2000s	-0.016	0.059	0.744	2.571	-0.054	0.785
	2010s	-0.056	0.065	2.450	2.820	-0.166	0.400
fLCBD							
native	2000s	0.009	0.022	-0.337	0.960	0.076	0.701
	2010s	-0.077	0.037	3.360	1.597	-0.378	**0.047**
non-native	2000s	-0.005	0.062	0.253	2.688	-0.016	0.936
	2010s	-0.075	0.069	3.272	3.008	-0.206	0.292

Table 6.7 Correlations between 2D cumulative diversity indices and 3D diversity indices calculated using only two diversity combinations in the national case. Statistically significant ($p < 0.05$) Pearson correlation coefficients are bolded.

	Historical	Current	Future I	Future II
cAlpha				
TD+PD	**0.960**	**0.950**	**0.955**	**0.945**
TD+FD	**0.906**	**0.959**	**0.965**	**0.954**
PD+FD	-0.103	0.234	0.283	0.370
cBeta				
TD+PD	**0.998**	**0.996**	**0.489**	**0.994**
TD+FD	**0.998**	**0.999**	**0.503**	**0.998**
PD+FD	**0.998**	**0.997**	**0.511**	**0.997**
cLCBD				
TD+PD	**0.984**	**0.945**	**0.936**	**0.966**
TD+FD	**0.945**	**0.818**	**0.931**	**0.854**
PD+FD	**0.985**	**0.948**	**0.960**	**0.964**

Table 6.8 Correlations between 2D cumulative diversity indices and 3D diversity indices calculated using only two diversity combinations in the Ishikari case. Statistically significant ($p < 0.05$) Pearson correlation coefficients are bolded.

	Native		Non-native	
	2000s	2010s	2000s	2010s
cAlpha				
TD+PD	**0.975**	**0.996**	**0.966**	**0.970**
TD+FD	**0.511**	**0.587**	**0.900**	**0.908**
PD+FD	**0.794**	**0.899**	**0.450**	**0.443**
cBeta				
TD+PD	**0.977**	**0.965**	**0.963**	**0.961**
TD+FD	**0.977**	**0.987**	**0.975**	**0.975**
PD+FD	**0.958**	**0.954**	**0.897**	**0.883**
cLCBD				
TD+PD	**0.966**	**0.933**	**0.953**	**0.976**
TD+FD	**0.710**	**0.812**	**0.922**	**0.977**
PD+FD	**0.977**	**0.973**	**0.970**	**0.977**

6.4 Discussion

Upon integrating taxonomic, phylogenetic and functional data, the cumulative diversity elucidated similar temporal fluctuations in native fish diversity, characterized by a consistent de-crease in cAlpha and an initial increase in cBeta followed by a precipitous decline. By incorporating the latitude of individual lakes into the analysis, the cumulative diversity effectively dis-closed the spatial distribution pattern of integrated native fish diversity. Notably, the cAlpha and cBeta of native fish residing within lakes across the Japanese archipelago exhibited highly significant correlations, albeit inverse, with the latitudinal gradient at any period. Specifically, islands situated at the northern- and southernmost of the Japanese archipelago (Hokkaido at higher lati-tudes and Kyushu at lower latitudes) displayed pronounced dissimilarities in native fish compositions, despite their low species richness. This observation suggests the presence of distinct endemic fishes on these two geographically distant islands. In contrast, the larger Honshu Island, located centrally, harbours a substantial number of native fish species, with lakes exhibiting simi-lar species compositions. The geographical isolation of Hokkaido and Kyushu from Honshu by the Tsugaru Strait and Kanmon Strait, respectively, represents a significant barrier to the dispersion and exchange of freshwater fish among these regions. Hence, the fish species are only able to within freshwater habitats on their respective islands and have facilitated the emergence of fish community structures distinct from those on other islands. Although this study does not explicitly quantify the contribution of geographical isolation imposed by the two straits on the fish com-munity structures of the distinct islands through mathematical modelling, the highly significant latitudinal distribution patterns identified by the cumulative diversity results provide compelling evidence in favour of limitation hypothesis, which posits that geographic isolation and limited dispersal are key factors, the stochastic processes, in maintaining species distribution patterns (da Silva et al., 2018; de Oliveira et al., 2020). The significant U-shaped curve between cLCBD values and the latitudinal position of the lakes also signifies the high endemism of Hokkaido and Kyushu fishes. The spatial patterns between cumulative diversity indices and lakes latitudes have been wobbled over time, yet the overarching spatial patterns with latitudes have remained consistent, further highlighting the long-term influence of stochastic processes, such as ongoing dispersal constraints, on the patterns of fish diversity at a broader scale. The significant correlation between cDI and latitude offers a basis for investigating the mediating influences on the spatial distribution patterns of fish diversity. Other environmental factors exhibiting a latitudinal gradient across the Japanese archipelago could also be considered as potential influences. One such factor is the human footprint (Su et al., 2021). Human activities are less intense on the northern-most and southernmost islands compared to Honshu, resulting in a lower threat to native fish species and a higher likelihood of survival for some unique species. Additionally, Honshu's larger size compared to Kyushu and Hokkaido increases the probability of fish dispersal to more lakes within the island, which may contribute to the U-shaped beta-diversity curve that is concave at mid-latitudes.

The fish diversity in the oxbow lakes along the Ishikari River also exhibited spatial variations linked to latitude. Native fishes demonstrated higher species richness in the upper lakes, consistent with findings from Chapter 4, which indicated that these less anthropogenically disturbed upper lakes offer diverse microhabitats favourable to native species. Conversely, lower lakes, being closer to human settlements, face greater environmental disturbances, including the introduction of non-native fishes. The dataset, confined to a single watershed and comprising species with similar evolutionary histories and resource use, did not exhibit a clear upstream-downstream gradient in alpha diversity regarding phylogeny and function. However, both phylogenetic and functional beta diversity displayed strong correlations with latitude. Specifically, native fishes, initially widespread in many lower lakes and thus exhibiting low beta diversity, have progressively lost habitats there due to competition with non-native species. This competition reversed the original positive correlation with lake latitude into a negative one, leading to a marked increase in beta diversity downstream. This significant shift in the spatial diversity pattern was not captured by traditional taxonomic diversity indices, underscoring that phylogenetic relationships and ecological functions of species are more responsive to competitive pressures from non-native fishes. The cumulative beta diversity index, which integrates multiple dimensions of diversity, also revealed a significant spatial pattern in the distribution of native fish assemblages and their inversion under the influence of non-native species. In addition, while only the functional LCBD index for native fishes showed a significant negative correlation with lake location in the 2010s, this pattern was also detected by the cumulative LCBD index.

This chapter demonstrates that the newly proposed cumulative diversity index can successfully reflect the spatial pattern of community diversity and its variations at both the national scale and the regional scale of individual watersheds, at least not without contradictory results to the traditional diversity index, confirming its feasibility in a wider range of ecologically demanding cases. Notably, in the Ishikari River oxbow lakes, while phylogenetic and functional alpha diversity failed to mirror spatial patterns, the taxonomic richness of native fish inversely correlated with latitude, suggesting phylogenetic and functional redundancy among species in upper lakes. This type of redundancy, overlooked by taxonomic diversity measures, is aptly highlighted by the cumulative diversity index. Additionally, the chapter investigates how temporal shifts in the spatial patterns of fish diversity, influenced by two ecological processes, affirm the resilience of patterns formed under dispersal constraints until these constraints are removed. These spatial patterns remain stable despite other ecological pressures. In contrast, patterns formed due to inter-plays between native and non-native species show significant variability, even potentially reversing due to deterministic processes. This analysis confirms the robustness and adaptive capacity of the cumulative diversity index in diverse ecological frameworks.

The novel cumulative diversity index offers a comprehensive perspective on changes in community diversity patterns. Without requiring any additional data, the cumulative diversity index could be derived directly from existing metrics, making them easy to interpret and highly usable. Generally, greater cumulative diversity values indicate richer diversity information. How-ever, it should be pointed out that, as a limitation, the new index cannot directly reflect respective changes in taxonomic, phylogenetic or functional information from numerical differences in the cumulative diversity index. Additionally, in this study assigned equal weights to the taxonomic, phylogenetic and functional indices. The rational allocation of these weights remains a topic of ongoing ecological debate. Thus, this research also advocates for further exploration, involving more models or examples in future research, to validate the weighting of these components. It is believed that this framework assessing cumulative diversity supports macroecological studies and explorations with a focus on conserving biodiversity, especially valuable for forecasting shifts in species diversity, and for the strategic prioritization of regions and species. The cumulative diversity index is especially suitable in cases where the complexity of multiple diversity indices calculated from different perspectives necessitates a concise yet informative diversity measure to depict diversity patterns in the region. Although this study is cantered predominantly on freshwater ichthyofauna within the Japanese archipelago, what is envisaged that this methodological structure could serve as an invaluable resource for future conservation planning efforts concerning various biotas, regions and ecosystems. Instead of primarily focusing on particular facets of diversity (Devictor et al., 2010), this research champion safeguarding of ecological integrity in specific regions by conserving a broad scope of biodiversity (Jiang et al., 2020; Meynard et al., 2011). Nonetheless, it is acknowledged the imperative of interpreting the outcomes of diverse forms of diversity analysis with circumspection. Furthermore, the results emphasize the significance of considering the biodiversity–habitat relationships specific to each region when devising conservation strategies (de Carvalho & Tejerina-Garro, 2015).

Although the 2D- and 3D-cDI showed a relatively strong positive correlation, some non-significant and low correlation coefficients suggest that comprehensive diversity changes cannot be fully captured using only two types of diversity indices. The results indicate that taxonomic, phylogenetic, and functional diversity indices each provide unique information in assessing biodiversity. Therefore, it is recommended to measure and interpret diversity information from all three perspectives for efficient and accurate biodiversity research and conservation. Specifically, significant correlations between 2D- and 3D-cDI were lost when taxonomic alpha diversity was excluded, suggesting that species richness is a key component of cAlpha diversity pat-terns in natural lakes across Japan. Prioritizing the survival of native fish species, i.e., pursuing high native fish richness, should be a priority for maintaining high cAlpha diversity. In addition, the highest cBeta diversity values were observed during the future I period, a time of simulated sustained species loss, indicating that individual lakes were losing species, phylogenetic, and ecological characteristics, which increased their dissimilarity. However, the lower correlation co-efficient of 2D- with 3D-cBeta diversity showed that about 50% of the variation in beta diversity was consistently unexplained, regardless of the use of any of the 2D combinations, which, while demonstrating the importance of using all three types of diversity indices, reflects the fact that the loss of species in lakes at this time was accompanied by a dramatic loss of unique phylogeny and ecological functional characteristics.

Chapter 7

Summary and general discussion

7.1 Summary of the study

The Anthropocene has ushered in a severe decline in the biodiversity of freshwater ecosystems worldwide, with the endangered state of freshwater fish species being particularly alarming (Dudgeon et al., 2006; Newbold et al., 2020; Pimm et al., 2014). Conservation biology underscores the importance of identifying specific regions and shielding fish populations within these areas from human impact to prevent further loss of species (Cadotte & Tucker, 2018). Numerous indices have been developed to assess biodiversity status and aid in the conservation of fish diversity (Kunakh et al., 2023). However, recent research critiques traditional diversity indices for their limited ability to capture genetic relationships and adaptability to environmental changes (Jiang et al., 2020). Although phylogenetic diversity indices and functional diversity indices have been developed and have proved their validity and informativeness in freshwater fish diversity studies around the world (Alahuhta et al., 2019; Cilleros et al., 2016; Kuczynski et al., 2018; Lin et al., 2021; Pool et al., 2014), there are limited studies on freshwater fish diversity in Japan simultaneously using taxonomic, phylogenetic and functional diversity assessments. The present study aimed to fill this knowledge gap in Japanese lakes and to develop a new framework for calculating a cumulative diversity index that integrates multifaceted diversity information and based on the results of this cumulative diversity index, to identify inland lentic waters with high fish conservation priorities.

This dissertation focuses on Japanese freshwater fish diversity at two scales: nationally across Hokkaido, Honshu, and Kyushu, and regionally within Ishikari River basin in Hokkaido. This dual-scale approach facilitates a deeper understanding of the spatial and temporal variations in fish diversity and tests the new cumulative diversity index's applicability at different scales. In addition, the formation of temporal and spatial patterns of communities is influenced by both stochastic and deterministic processes (Chase & Myers, 2011; Ning et al., 2019). While previous studies have often struggled to exclusively explore the influence of a single process (Dai et al., 2024), the setup of the present study provides the possibility for such a study. Specifically, this study first investigated the changes in the spatial and temporal diversity patterns of native freshwater fish in 39 lakes across Japan, from Lake Abashiri in Hokkaido to Lake Ikeda in Kagoshima. It was believed that the diversity patterns in these geographically scattered lakes were predominantly shaped by stochastic processes such as dispersal limitations created by natural geographic barriers like straits. Subsequently, the research shifted focus to the spatio-temporal diversity variations in 28 interconnected oxbow lakes within the Ishikari River basin, the largest in Hokkaido. Here, deterministic processes, primarily interactions between native and invasive fish species, played a crucial role in defining the diversity patterns of the fish communities in these habitats.

The first part of this study (Chapter 3) examines the shifts in alpha and beta diversity among native freshwater fish assemblages across 39 lakes in Japan, spanning from the historical to current periods, and assesses the relative uniqueness of fish composition in each lake from taxonomic, phylogenetic, and functional perspectives. Additionally, this chapter projected the future trends in these diversity indices in light of the ongoing decline of native species, taking into account the extinction probabilities of different freshwater fish species according to the Japanese Red List (Ministry of the Environment, 2020). The findings indicate a consistent decrease in native fish richness over time, leading to a future projection of further losses. As species extinction continues, the functional redundancy within fish communities is reduced, meanwhile species with close phylogenetic background possess greater survival probabilities. Concurrent with the decrease in species numbers, there was an initial increase followed by a sharp decline in species dissimilarity among the lakes evidenced by all three perspectives, illustrating a nationwide trend towards homogenization of fish species (Socolar et al., 2016).

The second part of this study (Chapter 4) investigates the changes in richness and dissimilarity of both native and non-native fish species in 28 oxbow lakes along the Ishikari River, comparing data from the 2000s to the 2010s. Throughout this nearly decade-long period, there was a notable 22.73% average increase in non-native fish species per lake, while the richness of native fish remained stable on average. The analysis linked the changes in alpha and beta diversity to specific lake locations, revealing a distinct pattern of longitudinal gradient changes in fish assemblages from upstream to downstream. Upper lakes exhibited less species turnover but preserving a high level of native uniqueness. Conversely, lower lakes became hotspots for competition between native and non-native species, with native fish survival becoming increasingly restricted to isolated lakes amidst the growing presence of non-native species, which notably altered the pattern of species turnover. Using the LCBD index, the chapter traced the upward expansion of non-native fish dominance as far as 110 km from the river source by the 2010s, identifying lakes upstream of this point as potential crucial refuges for native fish populations.

The third section of this study (Chapter 5) categorizes the 28 oxbow lakes into two groups—upper and lower—based on their proximity to the river source, with the dividing line set at 110 km as concluded in Chapter 4. This chapter examines the changes in phylogenetic and functional diversity patterns of fish assemblages inhabiting these lakes during the non-native expansion process and analyses how the phylogeny and functional diversity of native fish have responded to these changes. Similar with the conclusion of the previous chapter, the findings highlighted the continuous and pervasive impact of non-native species on native fish communities, leading to a homogenization of phylogenetic and functional diversity, particularly in lower lakes areas; while upper lake maintain higher biodiversity and serve as refuges for native species, preserving unique ecological functions. Furthermore, this chapter reveals that while native fish in the lower lakes exhibited functional redundancy, this did not prevent the encroachment of their ecological niches by non-native species. Consequently, the phylogenetic and functional diversity of native fish in these downstream lakes is expected to continue declining.

The final section of this study (Chapter 6) outlines the proposal and application of the cumulative diversity index (cDI) to datasets from the national lakes and the Ishikari oxbow lakes. The cDI effectively mirrored the spatial and temporal variations in fish diversity detected in earlier chapters, affirming its effectiveness and relevance for analysing diversity patterns. Additionally, by correlating the cDI of fish assemblages in the lakes with their latitudes, this chapter visualized the spatial distribution of fish diversity at two spatial scales, emphasizing the high conservation priority of the lakes in Hokkaido and Kyushu on a national scale, and upper oxbow lakes in the Ishikari River basin. In addition, this chapter demonstrated that stochastic processes represented by dispersal constraints shaped the spatial pattern of fish assemblages that will be maintained until the removal of dispersal barriers, whereas the spatial pattern of fish assemblages dominated by deterministic processes represented by native-nonnative competition may be erased or even inverted due to the process of species interactions.

7.2 Urgent conservation needs for freshwater fish in Japan

The findings of this study highlight a significant reduction and constraint in the distribution of native freshwater fish species across Japan, evident at both national and regional scales, with a clear trend towards species homogenization. This aligns with the global biodiversity crisis (Sax & Gaines, 2003; Su et al., 2021; Thomas, 2013), confirming that freshwater fish diversity in Japan is never an exception (Hosoya, 2022; Katano & Matsuzaki, 2012). Chapter 2 reported that 18.2%

of native fish species have become unrecorded from the studied Japanese lakes from the historical to the current periods, with 90% of the remaining native species now at risk of extinction. The survived wide-spread native species are contributing to a nationwide homogenization of lake fish compositions, dominated by national nestedness patterns (Socolar et al., 2016). While the native fishes in the Ishikari oxbow lakes have not seen a steep decline in species richness over the studied decade, they are being progressively outcompeted by non-native fish species, reducing their survival in fewer lakes, and leading to their sporadic presence. The ongoing invasive pressures are expected to further erode the diversity of native fish, risking the loss of all viable habitats (Kang et al., 2022). This study conclusively shows the continuing crisis in the diversity of native freshwater fishes in Japan, observed across national and regional spatial scales and over both long- and short-time frames, with particular concern for the survival of narrowly distributed endemic species. The urgent need for effective and immediate conservation measures to prevent further loss of this native fish diversity is starkly emphasized.

7.3 Necessity of integrating multi-faceted diversity assessing

An increasing number of research suggests that traditional diversity assessments, which focus solely on taxonomic changes in species, struggle to capture complex ecological processes and subtle shifts in diversity patterns (Chao et al., 2021; Su et al., 2021; Villéger et al., 2017). This issue was evidenced in this study, which utilized taxonomic, phylogenetic, and functional diversity indices to analyse the diversity of Japanese freshwater fishes. For instance, Chapter 3 reported a decline in fish species numbers, while the functional diversity indices, MFD and MNFD, remained stable or increased. This indicates that species loss is not random (Si et al., 2016), but involves the selective extinction of species with overlapping functional traits due to competitive pressures. Additionally, Chapter 5 observed that the upper oxbow lakes in the Ishikari River basin hosted more native fish species than the lower lakes, yet this difference was not mirrored in the phylogenetic or functional diversity indices. This suggests that the upper lakes provide more suitable ecological niches, supporting a higher number of species despite their similar evolutionary histories and functional traits, leading to redundancy in these aspects. Ultimately, this study demonstrates that expanding biodiversity assessments to include phylogenetic and functional dimensions can better reveal the ecological processes and mechanisms behind diversity changes, supporting a more comprehensive approach to setting conservation priorities (Jiang et al., 2020).

Fish diversity in this study was assessed at two levels: within individual lakes (alpha diversity) and between different lakes (beta diversity). Alpha diversity indices effectively capture the variability and richness of fish species within lakes, while beta diversity is essential for identifying compositional differences between lakes. This dual approach allows for a comprehensive understanding of species diversity and distribution at specific spatial scales, which is crucial for setting targeted conservation priorities, especially when resources are limited. For instance, Chapter 2 highlighted that alpha diversity of fish assemblages in the lakes on Hokkaido Island was consistently low, suggesting it might not be a biodiversity hotspot by traditional conservation standards. However, the beta diversity analysis revealed significant differences between fish communities on Hokkaido and those in southern islands, emphasizing the ecological uniqueness and potentially endangered status of the fish species. This insight argues for a higher conservation priority for Hokkaido Island. Furthermore, Chapter 6 compared the alpha diversity of native fishes in the upper versus lower oxbow lakes of the Ishikari River basin during the 2000s and 2010s. While the upper lakes showed consistently higher alpha diversity, the beta diversity patterns shifted dramatically—from lower upstream and higher downstream in the 2000s to the opposite in the 2010s, likely driven by intense competition between native and invasive species. Hence, the integration of alpha and beta diversity ensures that subtle yet critical changes in spatial patterns of diversity, which might otherwise be overlooked, are considered in conservation planning.

7.4 Application of the cumulative diversity index

This study introduced a novel computational framework designed to integrate taxonomic, phylogenetic, and functional diversity indices into a unified metric, termed the cumulative diversity index. Its efficacy and adaptability were validated through case studies analysing the spatial and temporal diversity patterns of freshwater fish assemblages inhabiting Japanese lakes in this study. While this study focused on freshwater fishes, the framework is versatile enough to be applied to other biotas and potentially other fields, as it does not depend on specific species taxa. The individual components of the cumulative diversity index are independent and highly interchangeable, allowing future studies to substitute the diversity indices used in this study with alternatives that better suit specific case needs. For instance, the taxonomic richness could be replaced with the Shannon-Wiener index, and phylogenetic or functional indices could be swapped for metrics like phylogenetic distance, e.g., average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+), or functional diversity indices (e.g., functional richness (FRic), functional evenness (FEve), functional originality (FOri) (Jiang et al., 2020; Mammola & Cardoso, 2020; Villéger et al., 2017; Wang et al., 2019). The application of the cumulative diversity index in this study showed a strong consistency with the results obtained from its component metrics across alpha, beta, and LCBD levels, which bolsters the index's credibility. This index offers intuitive interpretations similar to traditional diversity metrics: a high cAlpha indicates rich community diversity, a high cBeta suggests significant structural dissimilarity among communities, and a high cLCBD reflects the uniqueness of a community compared to others. This straightforward interpretation aids conservationists in quickly assessing regional multi-faceted biodiversity, which is crucial for planning, implementing, and adjusting conservation strategies. However, calculating cumulative diversity requires additional steps beyond traditional diversity assessments. Developing a computer algorithm that automates these preliminary steps and directly provides cumulative diversity results could increase its adoption among researchers and conservationists, broadening the application scope of the proposed cumulative diversity index (Chao et al., 2021).

7.5 Fish distributional patterns indicate conservation areas

Chapter 6 highlighted a distinctive spatial distribution pattern of freshwater fishes across Japan. Notably, the northernmost island, Hokkaido, and the southernmost, Kyushu, host relatively few freshwater species. However, the composition of fish in lakes on these islands is significantly different compared to other regions, a disparity rooted in the historical migration of freshwater fishes into Japan from both northern and southern origins (Aoyagi, 1957). The LCBD results further emphasize the unique fish compositions of these islands, underscoring their high conservation value. Importantly, the distinct species common to both islands necessitate tailored conservation strategies rather than a uniform approach. Additionally, this study revealed a linear diversity pattern along the river flow direction in the Ishikari oxbow lakes, supporting the river continuum theory (Doretto et al., 2020; Vannote et al., 1980). The lower oxbow lakes, experiencing intense competition between native and invasive fishes, contrast with the upstream lakes which, subjected to less anthropogenic and invasive pressure, continue to support native fish assemblages, and are identified as potential conservation sites.

The findings exemplify how metacommunity structures in aquatic environments are shaped by both stochastic and deterministic processes (Chase, 2010; Lepori & Malmqvist, 2009; Stegen et al., 2012). The limited north-south dispersal of species, constrained by the geographic barrier of the straits, exemplifies a stochastic process influencing metacommunity assembly (Shipley et al., 2012). This geographic impediment consistently impacts the spatial distribution pattern relative to latitude, maintaining a stable pattern despite other ecological changes over time. In contrast, the Ishikari oxbow lakes demonstrate a metacommunity structure influenced by deterministic processes, notably competitive interactions between native and non-native (Ye et al., 2023), which create variable spatial patterns over shorter periods depending on the specific ecological pressures. These insights into the formation of fish assemblages through different processes are crucial for devising effective conservation strategies tailored to the unique ecological dynamics of each area (Leonov, 2023; Wang et al., 2020).

7.6 Examples of focal lakes and species

Lake Biwa, Japan's largest and oldest freshwater lake, has seen a significant decline in its native fish populations over the past two centuries (Nishino et al., 2011; Okuda et al., 2014). This decline is due to several factors: habitat destruction, pollution, and the introduction of non-native species. Urbanization and industrial activities have damaged crucial habitats and altered water flows, while pollution from agricultural runoff and industrial wastewater has reduced water quality, impacting fish survival (Gao et al., 2023). Non-native species have exacerbated these problems by increasing competition and predation pressures on native fish. Effective conservation efforts for native fish diversity inhabiting Lake Biwa require improving habitats, controlling non-native species, and protecting key species. The Lake Biwa Comprehensive Development Project, established in the 1970s, focuses on sustainable development and conservation, including measures to protect water quality and natural habitats (Nakamura, 1995). It features habitat restoration projects to revitalize spawning grounds and improve water flow, as well as targeted invasive species management. Additionally, implementing sustainable land-use practices and stricter fishing regulations is crucial to prevent further habitat destruction and overfishing. Increased monitoring and community involvement are essential for adaptive management, supported by ongoing research to safeguard native fish diversity. Efforts also include protecting and raising awareness about key species, such as the endangered biwa trout (*Oncorhynchus rhodurus*) and biwa catfish (*Silurus biwaensis*), through captive breeding programs. By integrating these strategies, it is expected to address the multifaceted threats facing Lake Biwa's unique native fish fauna and freshwater ecosystem. In the Ishikari oxbow case, the stone loach (*Lefua nikkonis*) was no longer recorded in all studied lakes during fish surveys conducted in the 2010s, compared to the 2000s. This species, endemic to Hokkaido, prefers cold water with slow currents and has a high COD requirement (Nagatsu et al., 2007). It is listed as EN on the Japanese Red List due to the loss of its natural habitat, attributed to increased water temperatures alongside the climate change.

7.7 Limitations of the study

This study explored the temporal and spatial variations in taxonomic, phylogenetic, and functional diversity of Japanese freshwater fishes, acknowledging certain limitations. Primarily, the fish datasets were derived from published investigations and diversity studies, collected by different teams with inconsistent survey intensities. While common data treating methods were applied to transform fish abundance into species incidence (presence-absence datasets), enhancing data comparability and minimizing biases (Belmaker & Jetz, 2015; Keil & Chase, 2019). However, this transformation possibly distorted the relative importance of dominant versus rare species within the fish communities, obscuring key structural features reflected by differences in species individual numbers (Dai et al., 2020). Additionally, inconsistencies in species identification across different datasets, due to subjective expertise variances and identification errors among researchers, could not be eliminated (He et al., 2020). Furthermore, the study concentrated exclusively on the patterns of change in freshwater fish diversity without quantitatively linking these changes to environmental factors such as total nitrogen, total phosphorus, temperature, conductivity, pH, and surrounding land use in the studied lakes, unlike other studies that included these elements (Almeida & Cetra, 2016; Bogdziewicz et al., 2019; Xia et al., 2022). This omission limits deeper understanding of the drivers behind these fish diversity patterns and restricts specific conservation guidance regarding aquatic environmental conditions. Moreover, in projecting the continued loss of native species in the future, there has not been any culling of species with low levels of concern or exclusion of species that have not yet been assessed due to insufficient data. As a result, such modelling results appear to be more conservative, potentially underestimating the actual number of species lost. Also, the created cumulative diversity index, combining various indices conservatively, assumed an equal contribution from each component. This approach, while common applied (Jiang et al., 2015; Su et al., 2021), neglects the debated connections and potential substitutability between phylogenetic and functional diversity (Mazel et al., 2018; Owen et al., 2019), suggesting that future research should consider varying weights for different indices depending on the context. Finaly, this thesis examined fish community patterns in separate groups of isolated natural lakes and floodplain oxbow lakes, but did not compare and discuss in depth the differences between the two lake types in terms of causes of formation, geographic location, and hydrological characteristics, etc. The lack of discussion of these differences may reduce the generalizability of the conclusions and impede its application to a wider range of cases.

REFERENCES

Abell, R., Allan, J.D., & Lehner, B. (2007). Unlocking the potential of protected areas for freshwaters. *Biological Conservation*, *134*, 48–63. https://doi.org/10.1016/j.biocon.2006.08.017pp

Ackerly, D. D., Schwilk, D. W., & Webb, C. O. (2006). Niche evolution and adaptive radiation: Testing the order of trait divergence. *Ecology*, *87*(sp7), S50–S61. https://doi.org/10.1890/0012-9658(2006)87[50:NEAART]2.0.CO;2

Alahuhta, J., Erős, T., Kärnä, O. M., Soininen, J., Wang, J., & Heino, J. (2019). Understanding environmental change through the lens of trait-based, functional, and phylogenetic biodiversity in freshwater ecosystems. *Environmental Reviews*, *27*(2), 263–273. https://doi.org/10.1139/er-2018-0071

Albert, J. S., Destouni, G., Duke-Sylvester, S. M., Magurran, A. E., Oberdorff, T., Reis, R. E., Winemiller, K. O., & Ripple, W. J. (2021). Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio*, *50*(1), 85–94. https://doi.org/10.1007/s13280-020-01318-8

Alberti, M., & Wang, T. (2022). Detecting patterns of vertebrate biodiversity across the multidimensional urban landscape. *Ecology Letters*, *25*(4), 1027–1045. https://doi.org/10.1111/ele.13969

Allen, G. H., & Pavelsky, T. M. (2018). Global extent of rivers and streams. *Science*, *361*(6402), 585–588. https://doi.org/10.1126/science.aat0636

Almeida, R. S., & Cetra, M. (2016). Longitudinal gradient effects on the stream fish metacommunity. *Natureza & Conservação*, *14*(2), 112–119. https://doi.org/10.1016/j.ncon.2016.10.001

Almeida-Neto, M., Guimarães, P., Guimarães Jr, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, *117*(8), 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Alves, G. H. Z, Figueiredo, B. R. S., Manetta, G. I., Sacramento, P. A., Tófoli, R. M., & Benedito, E. (2017). Trophic segregation underlies the coexistence of two piranha species after the removal of a geographic barrier. *Hydrobiologia*, *797*, 57–68. https://doi.org/10.1007/s10750-017-3159-6

Amarasinghe, U. S., & Welcomme, R. L. (2002). An Analysis of Fish Species Richness in Natural Lakes. *Environmental Biology of Fishes*, *65*(3), 327–339. https://doi.org/10.1023/A:1020558820327

Anas, M. U. M., & Mandrak, N. E. (2021). Drivers of native and non-native freshwater fish richness across North America: Disentangling the roles of environmental, historical and anthropogenic factors. *Global Ecology and Biogeography*, *30*, 1232–1244. https://doi.org/10.1111/geb.13298

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Angulo-Valencia, M. A., Dias, R. M., Alves, D. C., Winemiller, K. O., & Agostinho, A. A. (2022). Patterns of functional diversity of native and non-native fish species in a neotropical floodplain. *Freshwater Biology*, *67*, 1301–1315. https://doi.org/10.1111/fwb.13918

Aoyagi, H. (1957). *Nihon rettosan tansui gyorui sosetsu (General notes on the freshwater fishes of the Japanese Archipelago)*. Taishukan.

Arantes, C. C., Winemiller, K. O., Petrere, M., Castello, L., Hess, L. L., & Freitas, C. E. C. (2018). Relationships between forest cover and fish diversity in the Amazon River floodplain. *Journal of Applied Ecology*, *55*, 386–395. https://doi.org/10.1111/1365-2664.12967

Arlinghaus, R., Abbott, J. K., Fenichel, E. P., Carpenter, S. R., Hunt, L. M., Alós, J., Klefoth, T., Cooke, S. J., Hilborn, R., Jensen, O. P., Wilberg, M. J., Post, J. R., & Manfredo, M. J. (2019). Governing the recreational dimension of global fisheries. *Proceedings of the National Academy of Sciences*, *116*(12), 5209–5213. https://doi.org/10.1073/pnas.1902796116

Arthington, A. H., Dulvy, N. K., Gladstone, W., & Winfield, I. J. (2016). Fish conservation in freshwater and marine realms: Sstatus, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(5), 838–857. https://doi.org/10.1002/aqc.2712

Balian, E. V., Segers, H., Lévèque, C., & Martens, K. (2008). The Freshwater Animal Diversity Assessment: an overview of the results. *Hydrobiologia*, *595*(1), 627–637. https://doi.org/10.1007/s10750-007-9246-3

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived?. *Nature*, *471*(7336), 51–57. https://doi.org/10.1038/nature09678

Barocas, A., Araujo Flores, J., Alarcon Pardo, A., Macdonald, D. W., & Swaisgood, R. R. (2021). Reduced dry season fish biomass and depleted carnivorous fish assemblages in unprotected tropical oxbow lakes. *Biological Conservation*, *257*, 109090. https://doi.org/10.1016/j.biocon.2021.109090

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, *36*, 124–128. https://doi.org/10.1111/j.1600-0587.2012.00124.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., & Logez, M. (2022). betapart: Partitioning beta diversity into turnover and nestedness components. https://CRAN.R-project.org/package=betapart.

Baselga, A. (2007). Disentangling distance decay of similarity from richness gradients: response to Soininen et al. 2007. *Ecography*, *30*(6), 838–841. https://doi.org/10.1111/j.2007.0906-7590.05191.x

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Martinez-Santalla, S., Martin-Devasa, R., Gomez-Rodriguez, C., & Crujeiras, R. (2023). *betapart: partitioning beta diversity into turnover and nestedness components*. R package version 1.6. https://CRAN.R-project.org/package=betapart

Bayley, P. B. (1991). The flood pulse advantage and the restoration of river-floodplain systems. *Regulated Rivers: Research & Management*, *6*(2), 75–86. https://doi.org/10.1002/rrr.3450060203

Belmaker, J., & Jetz, W. (2015). Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters*, *18*(6), 563–571. https://doi.org/ 10.1111/ele.12438

Bernery, C., Bellard, C., Courchamp, F., Brosse, S., & Leroy, B. (2024). A global analysis of the introduction pathways and characteristics associated with non-native fish species introduction, establishment, and impacts. *Ecological Processes*, *13*(1), 22. https://doi.org/10.1186/s13717-024-00495-8

Bernery, C., Bellard, C., Courchamp, F., Brosse, S., Gozlan, R. E., Jarić, I., Teletchea, F., & Leroy, B. (2022). Freshwater Fish Invasions: A Comprehensive Review. *Annual Review of Ecology, Evolution and Systematics*, *53*, 427–456. https://doi.org/10.1146/annurev-ecolsys-032522-015551

Biswas, S. R., & Mallik, A. U. (2011). Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere*, *2*(4), art52. https://doi.org/10.1890/ES10-00206.1

Bogdziewicz, M., Szymkowiak, J., Fernández-Martínez, M., Peñuelas, J., & Espelta, J. M. (2019). The effects of local climate on the correlation between weather and seed production differ in two species with contrasting masting habit. *Agricultural and Forest Meteorology*, *268*, 109–115. https://doi.org/10.1016/j.agrformet.2019.01.016

Boys, C. A., Rayner, T. S., Baumgartner, L. J., & Doyle, K. E. (2021) Native fish losses due to water extraction in Australian rivers: Evidence, impacts and a solution in modern fish- and farm-friendly screens. *Ecological Management & Restoration*, *22*, 134–144. https://doi.org/10.1111/emr.12483

Braaten, P. J., & Guy, C. S. (2002). Life history attributes of fishes along the latitudinal gradient of the Missouri river. *Transactions of the American Fisheries Society*, *131*(5), 931–945. https://doi.org/10.1577/1548-8659(2002)131<0931:LHAOFA>2.0.CO;2

Bracken, L. J., & Croke, J. (2007). The concept of hydrological connectivity and its contribution to understanding runoff-dominated geomorphic systems. *Hydrological Processes*, *21*(13), 1749–1763. https://doi.org/10.1002/hyp.6313

Brown, L. E., Khamis, K., Wilkes, M., Blaen, P., Brittain, J. E., Carrivick, J. L., Fell, S., Friberg, N., Füreder, L., Gislason, G. M., Hainie, S., Hannah, D. M., James, W. H. M., Lencioni, V., Olafsson, J. S., Robinson, C. T., Saltveit, S. J., Thompson, C., & Milner, A. M. (2018). Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution*, *2*(2), 325–333. https://doi.org/10.1038/s41559-017-0426-x

Bubac, C. M., Johnson, A. C., Fox, J. A., & Cullingham, C. I. (2019). Conservation translocations and post-release monitoring: Identifying trends in failures, biases, and challenges from around the world. *Biological Conservation*, *238*, 108239. https://doi.org/10.1038/s41559-017-0426-x

Cadotte, M. W., & Tucker, C. M. (2018). Difficult decisions: Strategies for conservation prioritization when taxonomic, phylogenetic and functional diversity are not spatially congruent. *Biological Conservation*, *225*, 128–133. https://doi.org/10.1016/j.biocon.2018.06.014

Cai, Y., Zhang, M., Xu, J., & Heino, J. (2018). Geographical gradients in the biodiversity of Chinese freshwater molluscs: Implications for conservation. *Diversity and Distributions*, *24*(4), 485–496. https://doi.org/10.1111/ddi.12695

Campbell, S. E., & Mandrak, N. E. (2019) Temporal dynamics of taxonomic homogenization in the fish communities of the Laurentian Great Lakes. *Diversity and Distributions*, *25*, 1870–1878. https://doi.org/10.1111/ddi.12986

Cannon, C. H., Peart, D. R., & Leighton, M. (1998). Tree species diversity in commercially logged Bornean rainforest. *Science*, *281*(5381), 1366–1368. https://doi.org/10.1126/science.281.5381.1366

Carpenter, S. R., Kitchell, J. F., & Hodgson, J. R. (1985). Cascading trophic interactions and lake productivity. *BioScience*, *35*(10), 634–639.

Carpenter, S. R., Stanley, E. H., & Vander Zanden, M. J. (2011). State of the World's Freshwater Ecosystems: Physical, Chemical, and Biological Changes. *Annual Review of Environment and Resources*, *36*, 75–99. https://doi.org/10.1146/annurev-environ-021810-094524

Carvalho, R. A., Teresa, F. B., & Tejerina-Garro, F. L. (2021). The effect of riverine networks on fish β-diversity patterns in a Neotropical system. *Hydrobiologia*, *848*(2), 515–529. https://doi.org/10.1007/s10750-020-04459-9

Castro, F. S. d., Da Silva, P. G., Solar, R., Fernandes, G. W., & Neves, F. d. S. (2020). Environmental drivers of taxonomic and functional diversity of ant communities in a tropical mountain. *Insect Conservation and Diversity*, *13*(4), 393–403. https://doi.org/10.1111/icad.12415

Chao, A., & Chiu, C. H. (2016). Nonparametric estimation and comparison of species richness. In *Encyclopedia of Life Sciences* (pp. 1-11). Wiley. https://doi.org/10.1002/9780470015902.a0026329

Chao, A., Henderson, P. A., Chiu, C.-H., Moyes, F., Hu, K.-H., Dornelas, M., & Magurran, A. E. (2021). Measuring temporal change in alpha diversity: A framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization. *Methods in Ecology and Evolution*, *12*(10), 1926–1940. https://doi.org/10.1111/2041-210X.13682

Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-A., Nilsson, J.-Å., Brodersen, J., Anders Nilsson, P., Skov, C., & Brönmark, C. (2011). To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, *14*(9), 871–876. https://doi.org/10.1111/j.1461-0248.2011.01648.x

Chase, J. M. (2010). Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science*, *328*(5984), 1388–1391. https://doi.org/doi:10.1126/science.1187820

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2351–2363. https://doi.org/10.1098/rstb.2011.0063

Chua, K. W. J., Tan, H. H., & Yeo, D. C. J. (2019). Loss of endemic fish species drives impacts on functional richness, redundancy and vulnerability in freshwater ecoregions of Sundaland. *Biological Conservation*, *234*, 72–81. https://doi.org/10.1016/j.biocon.2019.03.019

Chave, J. (2004). Neutral theory and community ecology. *Ecology letters*, *7*(3), 241-253. https://doi.org/10.1111/j.1461-0248.2003.00566.x

Cilleros, K., Allard, L., Grenouillet, G., & Brosse, S. (2016). Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages. *Journal of Biogeography*, *43*(9), 1832–1843. https://doi.org/10.1111/jbi.12839

Clarke, K. R., & Gorley, R. N. (2015). *PRIMER v7: User Manual/Tutorial*. PRIMER-E.

Clements, F. E. (1916). *Plant succession: an analysis of the development of vegetation*. Carnegie institution of Washington.

Closs, G., Krkosek, M., & Olden, J. D. (Eds.). (2016). *Conservation of freshwater fishes* (No. 20).

Cambridge University Press. www.cambridge.org/9781107040113

Collins, G. M., Clark, T. D., Rummer, J. L., & Carton, A. G. (2013). Hypoxia tolerance is conserved across genetically distinct sub-populations of an iconic, tropical Australian teleost (*Lates calcarifer*). *Conservation Physiology*, *1*(1), cot029. https://doi.org/10.1093/conphys/cot029

Comte, L., & Olden, J. D. (2017). Evolutionary and environmental determinants of freshwater fish thermal tolerance and plasticity. *Global Change Biology*, *23*(2), 728–736. https://doi.org/10.1111/gcb.13427

Cooke, S. J., Allison, E. H., Beard, T. D., Arlinghaus, R., Arthington, A. H., Bartley, D. M., Cowx, I. G., Fuentevilla, C., Leonard, N. J., Lorenzen, K., Lynch, A. J., Nguyen, V. M., Youn, S.-J., Taylor, W. W., & Welcomme, R. L. (2016). On the sustainability of inland fisheries: Finding a future for the forgotten. *Ambio*, *45*(7), 753–764. https://doi.org/10.1007/s13280-016-0787-4

Crandall, E. D., Taffel, J. R., & Barber, P. H. (2010). High gene flow due to pelagic larval dispersal among South Pacific archipelagos in two amphidromous gastropods (Neritomorpha: Neritidae). *Heredity*, *104*(6), 563–572. https://doi.org/10.1038/hdy.2009.138

Crist, T. O., Veech, J. A., Gering, J. C., & Summerville, K. S. (2003). Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. *The American Naturalist*, *162*(6), 734–743. https://doi.org/10.1086/378901

Crooks, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, *97*(2), 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

da Silva, P. G., Hernández, M. I. M., & Heino, J. (2018). Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. *Diversity and Distributions*, *24*(11), 1674–1686. https://doi.org/10.1111/ddi.12785

Dai, B., Chen, S., Wang, C., & Jiang, Z. (2024). Functional zeta diversity can better reveal fish metacommunity assembly process in a transitional floodplain. *Ecological Indicators*, *160*, 111792. https://doi.org/10.1016/j.ecolind.2024.111792

Dai, B., Jiang, Z., Wang, C., Matsuzaki, S.-I. S., & Zhou, L. (2020). Abundance-based dissimilarity measurements reveal higher heterogeneity of fish communities in the lotic habitats of the Yangtze-Caizi transitional floodplain. *Ecological Indicators*, *112*, 106122. https://doi.org/10.1016/j.ecolind.2020.106122

Dai, B., Negishi, J. N., Fujii, K., Alam, M. K., & Jiang, Z. (2023). Non-native fish species expand tacitly but rapidly toward upstream oxbow lakes along the longitudinal gradient. *NeoBiota*, *85*, 101–123. https://doi.org/10.3897/neobiota.85.99296

Darwall, W., & Freyhof, J. (2015). Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity. In G. Closs, M. Krkosek, & J. Olden (Eds.), *Conservation of freshwater fishes* (Conservation biology, pp. 1–36). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139627085.002

Dauwalter, D. C., Sanderson, J. S., Williams, J. E., & Sedell, J. R. (2011). Identification and Implementation of Native Fish Conservation Areas in the Upper Colorado River Basin. *Fisheries*, *36*, 278–288. https://doi.org/10.1080/03632415.2011.582411

Davis, M., Faurby, S., & Svenning, J.C. (2018). Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences*, 115(44), 11262–11267. https://doi.org/10.1073/pnas.1804906115

de Carvalho, R. A., & Tejerina-Garro, F. L. (2015). Relationships between taxonomic and functional components of diversity: implications for conservation of tropical freshwater fishes. *Freshwater Biology*, *60*(9), 1854–1862. https://doi.org/10.1111/fwb.12616

de Oliveira, P. H. F., Machado, K. B., Teresa, F. B., Heino, J., & Nabout, J. C. (2020). Spatial processes determine planktonic diatom metacommunity structure of headwater streams. *Limnologica*, *84*, 125813. https://doi.org/10.1016/j.limno.2020.125813

De, K., Singh, A. P., Sarkar, A., Singh, K., Siliwal, M., Uniyal, V. P., & Hussain, S. A. (2023). Relationship between species richness, taxonomic distinctness, functional diversity, and local contribution to β diversity and effects of habitat disturbance in the riparian spider community of the Ganga River, India. *Ecological Processes*, *12*(1), 13. https://doi.org/10.1186/s13717-023-00421-4

Deng, Z., Zhao, J., Wang, Z., Li, R., Guo, Y., Luo, T., & Zhang, L. (2022). Stochastic processes drive plant community assembly in alpine grassland during the restoration period. *Diversity*, *14*(10), 832. https://doi.org/10.3390/d14100832

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, *13*(8), 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Dini-Andreote, F., Stegen, J. C., Van Elsas, J. D., & Salles, J. F. (2015). Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. *Proceedings of the National Academy of Sciences*, *112*(11), E1326–E1332. https://doi.org/10.1073/pnas.1414261112

Ding, C., Jiang, X., Xie, Z., & Brosse, S. (2017). Seventy-five years of biodiversity decline of fish assemblages in Chinese isolated plateau lakes: widespread introductions and extirpations of narrow endemics lead to regional loss of dissimilarity. *Diversity and Distributions*, *23*(2), 171–184. https://doi.org/10.1111/ddi.12507

Ding, C., Sun, J., Huang, M., Bond, N., Ding, L., & Tao, J. (2023). Flow and thermal regimes altered by a dam caused failure of fish recruitment in the upper Mekong River. *Freshwater Biology*, *68*, 1319-1329. https://doi.org/10.1111/fwb.14105

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401–406. https://doi.org/10.1126/science.1251817

Dominguez Almela, V., South, J., & Britton, J. R. (2021). Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species. *Journal of Animal Ecology*, *90*(11), 2651–2662. https://doi.org/10.1111/1365-2656.13571

Doretto, A., Piano, E., & Larson, C. E. (2020). The River Continuum Concept: lessons from the past and perspectives for the future. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(11), 1853–1864. https://doi.org/10.1139/cjfas-2020-0039

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guénard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., & Wagner, H. H. (2022). *adespatial: Multivariate Multiscale Spatial Analysis*. In https://CRAN.R-project.org/package=adespatial

Duan, W. L., He, B., Takara, K., Luo, P. P., Nover, D., & Hu, M. C. (2015). Modeling suspended sediment sources and transport in the Ishikari River basin, Japan, using SPARROW. *Hydrology and Earth System Sciences*, *19*, 1293–1306. https://doi.org/10.5194/hess-19-1293-2015

Duarte, C., Antão, L. H., Magurran, A. E., & de Deus, C. P. (2022). Shifts in fish community composition and structure linked to seasonality in a tropical river. *Freshwater Biology*, *67*(10), 1789–1800. https://doi.org 10.1111/fwb.13975

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., . . . Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Döll, P., & Zhang, J. (2010). Impact of climate change on freshwater ecosystems: a global-scale analysis of ecologically relevant river flow alterations. *Hydrology and Earth System Sciences*, *14*(5), 783–799. https://doi.org/10.5194/hess-14-783-2010

Faith, D. P. (2018). Biodiversity's option value: A comment on Maier (2018). *Ambio*, *47*(6), 735–736. https://doi.org/10.1007/s13280-018-1069-0

Fenoglio, S., Bo, T., Cucco, M., Mercalli, L., & Malacarne, G. (2010). Effects of global climate change on freshwater biota: A review with special emphasis on the Italian situation. *Italian Journal of Zoology*, *77*(4), 374–383. https://doi.org/10.1080/11250000903176497

Fensham, R. J., Silcock, J. L., Kerezsy, A., & Ponder, W. (2011). Four desert waters: Setting arid zone wetland conservation priorities through understanding patterns of endemism. *Biological Conservation*, *144*, 2459–2467. https://doi.org/10.1016/j.biocon.2011.06.024

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., & Snyder, P. K. (2005). Global consequences of land use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Fricke, R., Eschmeyer, W. N., & Fong, J. D. (2024). *Eschmeyer's catalog of fishes: genera, species, references*. California Academy of Sciences. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Froese, R., & Pauly, D. (2024). *FishBase* http://www.fishbase.org

Fréville, H., McConway, K., Dodd, M., & Silvertown, J. (2007). Prediction of extinction in plants: interaction of extrinsic threats and life history traits. *Ecology*, 88(10), 2662–2672. https://doi.org/10.1890/06-1453.1

Fujii, K., Doi, H., Matsuoka, S., Nagano, M., Sato, H., & Yamanaka, H. (2019). Environmental DNA metabarcoding for fish community analysis in backwater lakes: A comparison of capture methods. *PLOS ONE*, *14*(1), e0210357. https://doi.org/10.1371/journal.pone.0210357

Fukushima, M., Kameyama, S., Kaneko, M., Nakao, K., & Ashley Steel, E. (2007). Modelling the effects of dams on freshwater fish distributions in Hokkaido, Japan. *Freshwater Biology*, *52*(8), 1511–1524. https://doi.org/https://doi.org/10.1111/j.1365-2427.2007.01783.x

Fusco, J., Walker, E., Papaïx, J., Debolini, M., Bondeau, A., & Barnagaud, J. Y. (2021). Land use changes threaten bird taxonomic and functional diversity across the mediterranean basin: A spatial analysis to prioritize monitoring for conservation. *Frontiers in Ecology and Evolution*, *9*, 612356. https://doi.org/10.3389/fevo.2021.612356

Gao, B., Chen, M., Hao, H., Yamashiki, Y. A., Ishikawa, K., Jiao, C., ... & Ismail, S. (2023). Recent mechanisms of surface ecological changes driven by climate change and human activities in Lake Biwa, Japan. *Frontiers in Ecology and Evolution*, *11*, 1335990. https://doi.org/10.3389/fevo.2023.1335990

Galland, T., Adeux, G., Dvořáková, H., E-Vojtkó, A., Orbán, I., Lussu, M., Puy, J., Blažek, P., Lanta, V., Lepš, J., de Bello, F., Pérez Carmona, C., Valencia, E., & Götzenberger, L. (2019). Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology*, *107*(5), 2090–2104. https://doi.org/10.1111/1365-2745.13246

Gardner, T. A., Ferreira, J., Barlow, J., Lees, A. C., Parry, L., Vieira, I. C. G., Berenguer, E., Abramovay, R., Aleixo, A., Andretti, C., Aragão, L. E. O. C., Araújo, I., de Ávila, W. S., Bardgett, R. D., Batistella, M., Begotti, R. A., Beldini, T., de Blas, D. E., Braga, R. F., . . . Zuanon, J. (2013). A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1619), 20120166. https://doi.org/10.1098/rstb.2012.0166

Garrett-Walker, J., Collier, K. J., Daniel, A., Hicks, B. J., & Klee, D. (2020). Design features of constructed floodplain ponds influence waterbird and fish communities in northern New Zealand. *Freshwater Biology*, *65*, 2066–2080. https://doi.org/10.1111/fwb.13602

Gaston, K. J. (1998). Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1366), 219–230. https://doi.org/10.1098/rstb.1998.0204

Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and process in macroecology*. Blackwell Science. https://doi.org/10.1002/9780470999592

Ge, Y., Meng, X., Heino, J., García-Girón, J., Liu, Y., Li, Z., & Xie, Z. (2021). Stochasticity overrides deterministic processes in structuring macroinvertebrate communities in a plateau aquatic system. *Ecosphere*, *12*(7), e03675. https://doi.org/10.1002/ecs2.3675

Gering, J. C., Crist, T. O., & Veech, J. A. (2003). Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conservation Biology*, *17*(2), 488–499. https://doi.org/10.1046/j.1523-1739.2003.01465.x

Gleason, H. A. (1927). Further Views on the Succession-Concept. *Ecology*, *8*(3), 299–326. https://doi.org/10.2307/1929332

Gleick, P. H. (1996). Water resources. *Encyclopedia of climate, weather*, 817–823. https://cir.nii.ac.jp/crid/1574231875534157696

Goetz, D., Miranda, L. E., Kröger, R., & Andrews, C. (2015). The role of depth in regulating water quality and fish assemblages in oxbow lakes. *Environmental Biology of Fishes*, *98*, 951–959. https://doi.org/10.1007/s10641-014-0330-z

Gozlan, R. E., Andreou, D., Asaeda, T., Beyer, K., Bouhadad, R., Burnard, D., Caiola, N., Cakic, P., Djikanovic, V., Esmaeili, H. R., Falka, I., Golicher, D., Harka, A., Jeney, G., Kováč, V., Musil, J., Nocita, A., Povz, M., Poulet, N., Virbickas, T., Wolter, C., Serhan Tarkan, A., Tricarico, E., Trichkova, T., Verreycken, H., Witkowski, A., Guang Zhang, C., Zweimueller, I., & Robert Britton, J. (2010). Pan-continental invasion of *Pseudorasbora parva*: towards a better understanding of freshwater fish invasions. *Fish and Fisheries*, *11*, 315-340. https://doi.org/10.1111/j.1467-2979.2010.00361.x

Gozlan, R. E. (2008). Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries*, *9*(1), 106–115.https://doi.org/10.1111/j.1467-2979.2007.00267.x

Graham, C. H., & Fine, P. V. A. (2008). Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters*, *11*(12), 1265–1277. https://doi.org/10.1111/j.1461-0248.2008.01256.x

Griffin, J. N., Byrnes, J. E. K., & Cardinale, B. J. (2013). Effects of predator richness on prey suppression: a meta-analysis. *Ecology*, *94*(10), 2180–2187. https://doi.org/https://doi.org/10.1890/13-0179.1

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M. E., Meng, J., Mulligan, M., Nilsson, C., Olden, J. D., Opperman, J. J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R. J. P., Snider, J., Tan, F., Tockner, K., Valdujo, P. H., van Soesbergen, A., & Zarfl, C. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*, 215–221. https://doi.org/10.1038/s41586-019-1111-9

Grooten, M., & Almond, R. E. (2018). *Living planet report-2018: aiming higher*. WWF international.

Głowacki, Ł., Kruk, A., & Penczak, T. (2021). Advancing improvement in riverine water quality caused a non-native fish species invasion and native fish fauna recovery. *Scientific Reports*, *11*, 16493. https://doi.org/10.1038/s41598-021-93751-2

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., . . . Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electronica* 4: 9. https://www.nhm.uio.no/english/research/resources/past/.

Harrison, S., Ross, S. J., & Lawton, J. H. (1992). Beta Diversity on Geographic Gradients in Britain. *Journal of Animal Ecology*, *61*(1), 151–158. https://doi.org/10.2307/5518

Haubrock, P. J., Pilotto, F., Innocenti, G., Cianfanelli, S., & Haase, P. (2021). Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. *Global Change Biology*, *27*, 606–623. https://doi.org/10.1111/gcb.15442

Havn, T. B., Økland, F., Teichert, M. A. K., Heermann, L., Borcherding, J., Sæther, S. A., Tambets, M., Diserud, O. H., & Thorstad, E. B. (2017). Movements of dead fish in rivers. *Animal Biotelemetry*, *5*(1), 7. https://doi.org/10.1186/s40317-017-0122-2

Hayashida K, Hirayama A, Ueda H (2010) Changes in fish fauna in oxbow lakes on the Ishikari River and the influence of invasive fish species. *Annual Journal of Hydraulic Engineering*, 54, 1261–1266. http://library.jsce.or.jp/jsce/open/00028/2010/54-0211.pdf (in Japanese with English abstract)

He, D., Sui, X., Sun, H., Tao, J., Ding, C., Chen, Y., & Chen, Y. (2020). Diversity, pattern and ecological drivers of freshwater fish in China and adjacent areas. *Reviews in Fish Biology and Fisheries*, *30*(2), 387–404. https://doi.org/10.1007/s11160-020-09600-4

He, F., & Legendre, P. (2002). Species diversity patterns derived from species–area models. *Ecology*, *83*(5), 1185–1198. https://doi.org/10.1890/0012-

9658(2002)083[1185:SDPDFS]2.0.CO;2

He, Y., Wang, J., Lek, S., Cao, W., & Lek-Ang, S. (2011). Structure of endemic fish assemblages in the upper Yangtze River Basin. *River Research and Applications*, *27*(1), 59–75. https://doi.org/10.1002/rra.1339

Heino, J., & Tolonen, K. T. (2017). Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity. *Limnology and Oceanography*, *62*(6), 2431–2444. https://doi.org/10.1002/lno.10577

Helmus, M. R., Keller, W., Paterson, M. J., Yan, N. D., Cannon, C. H., & Rusak, J. A. (2010). Communities contain closely related species during ecosystem disturbance. *Ecology Letters*, *13*(2), 162–174. https://doi.org/10.1111/j.1461-0248.2009.01411.x

Hill, M. J., White, J. C., Biggs, J., Briers, R. A., Gledhill, D., Ledger, M. E., Thornhill, I., Wood, P. J., & Hassall, C. (2021). Local contributions to beta diversity in urban pond networks: Implications for biodiversity conservation and management. *Diversity and Distributions*, *27*(5), 887–900. https://doi.org/10.1111/ddi.13239

Hoffmann, R. C. (1996). Economic Development and Aquatic Ecosystems in Medieval Europe. *The American Historical Review*, *101*(3), 631–669. https://doi.org/10.2307/2169418

Holmlund, C. M., & Hammer, M. (1999). Ecosystem services generated by fish populations. *Ecological Economics*, *29*(2), 253-268. https://doi.org/10.1016/S0921-8009(99)00015-4

Hosoya, K. (2022). Conservation of Freshwater Fish Diversity in Japan. In Y. Kai, H. Motomura, & K. Matsuura (Eds.), *Fish Diversity of Japan: Evolution, Zoogeography, and Conservation* (pp. 395–408). Springer Nature Singapore. https://doi.org/10.1007/978-981-16-7427-3_23

Hugenholtz, P., & Pace, N. R. (1996). Identifying microbial diversity in the natural environment: A molecular phylogenetic approach. *Trends in Biotechnology*, *14*(6), 190–197. https://doi.org/10.1016/0167-7799(96)10025-1

Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W., & Vilà, M. (2008). Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology*, *45*, 403–414. https://doi.org/10.1111/j.1365-2664.2007.01442.x

Iitsuka, Y., Nishio, M., Kawakami, R., & Yamazaki, Y. (2024). Spatio-temporal genetic composition of rosy bitterling Rhodeus ocellatus subspecies in the Himi region, central Japan. *Ichthyological Research*, *71*(1), 193–199. https://doi.org/10.1007/s10228-023-00923-3

IUCN. (2023). *The IUCN red list of threatened species*. https://www.iucnredlist.org

Ishiyama, N., Miura, K., Yamanaka, S., Negishi, J. N., & Nakamura, F. (2020). Contribution of small isolated habitats in creating refuges from biological invasions along a geomorphological gradient of floodplain waterbodies. *Journal of Applied Ecology*, *57*, 548–558. https://doi.org/10.1111/1365-2664.13546

Iwamoto, H., Tahara, D., & Yoshida, T. (2022). Contrasting metacommunity patterns of fish and aquatic insects in drainage ditches of paddy fields. *Ecological Research*, *37*(5), 635–646. https://doi.org/10.1111/1440-1703.12334

Jacobson, P. C., Cross, T. K., Dustin, D. L., & Duval, M. (2016). A Fish Habitat Conservation Framework for Minnesota Lakes. *Fisheries*, *41*(6), 302–317. https://doi.org/10.1080/03632415.2016.1172482

Jiang, X., Ding, C., Brosse, S., Pan, B., Lu, Y., & Xie, Z. (2019). Local rise of phylogenetic diversity due to invasions and extirpations leads to a regional phylogenetic homogenization of fish fauna from Chinese isolated plateau lakes. *Ecological Indicators*, *101*, 388–398. https://doi.org/10.1016/j.ecolind.2019.01.041

Jiang, X., Ding, C., Brosse, S., Pan, B., Lu, Y., & Xie, Z. (2019). Local rise of phylogenetic diversity due to invasions and extirpations leads to a regional phylogenetic homogenization of fish fauna from Chinese isolated plateau lakes. *Ecological Indicators*, 101, 388–398. https://doi.org/10.1016/j.ecolind.2019.01.041

Jiang, X., Peng, D., Alahuhta, J., Heino, J., Li, Z., & Xie, Z. Eutrophication modifies the relationships between multiple facets of macroinvertebrate beta diversity and geographic distance in freshwater lakes. *Diversity and Distributions*, *30*(5), e13830. https://doi.org/10.1111/ddi.13830

Jiang, Z. G., Brosse, S., Jiang, X. M., & Zhang, E. (2015). Measuring ecosystem degradation through half a century of fish species introductions and extirpations in a large isolated lake. *Ecological Indicators*, *58*, 104–112. https://doi.org/10.1016/j.ecolind.2015.05.040

Jiang, Z., Dai, B., Wang, C., & Xiong, W. (2020). Multifaceted biodiversity measurements reveal incongruent conservation priorities for rivers in the upper reach and lakes in the middle-lower reach of the largest river-floodplain ecosystem in China. *Science of The Total Environment*, *739*, 140380. https://doi.org/10.1016/j.scitotenv.2020.140380

Jost, L., DeVries, P., Walla, T., Greeney, H., Chao, A., & Ricotta, C. (2010). Partitioning diversity for conservation analyses. *Diversity and Distributions*, *16*(1), 65–76. https://doi.org/10.1111/j.1472-4642.2009.00626.x

Kai, Y. (2022). Fish diversity of subarctic waters in Japan. In Y. Kai, M. Motomura, & K. Matsuura (Eds.), *Fish diversity of Japan: Evolution, zoogeography, and conservation* (pp. 111–124). Singapore: Springer Nature Singapore. https://doi.org/10.1007/978-981-16- 7427-3_7

Kang, B., Huang, X., Yan, Y., Yan, Y., & Lin, H. (2018). Continental-scale analysis of taxonomic and functional fish diversity in the Yangtze river. *Global Ecology and Conservation*, *15*, e00442. https://doi.org/10.1016/j.gecco.2018.e00442

Kang, B., Vitule, J. R. S., Li, S., Shuai, F., Huang, L., Huang, X., Fang, J., Shi, X., Zhu, Y., Xu, D., Yan, Y., & Lou, F. (2023). Introduction of non-native fish for aquaculture in China: A systematic review. *Reviews in Aquaculture*, *15*(2), 676–703. https://doi.org/10.1111/raq.12751

Karabanov, D. P., Kodukhova, Y. V., Pashkov, A. N., Reshetnikov, A. N., & Makhrov, A. A. (2021). "Journey to the west": three phylogenetic lineages contributed to the invasion of stone moroko, *Pseudorasbora parva* (Actinopterygii: Cyprinidae). *Russian Journal of Biological Invasions*, *12*(1), 67–78. https://doi.org/10.1134/S2075111721010070

Kashem, A. H. M., Das, P., Hawari, A. H., Mehariya, S., Thaher, M. I., Khan, S., Abduquadir, M., & Al-Jabri, H. (2023). Aquaculture from inland fish cultivation to wastewater treatment: a review. *Reviews in Environmental Science and Bio/Technology*, *22*(4), 969–1008. https://doi.org/10.1007/s11157-023-09672-1

Katano, O., & Matsuzaki, S. S. (2012). Biodiversity of Freshwater Fish in Japan in Relation to Inland Fisheries. In S.-i. Nakano, T. Yahara, & T. Nakashizuka (Eds.), *The Biodiversity Observation Network in the Asia-Pacific Region: Toward Further Development of Monitoring* (pp. 431-444). Springer Japan. https://doi.org/10.1007/978-4-431-54032-8_29

Keil, P., & Chase, J. M. (2019). Global patterns and drivers of tree diversity integrated across a continuum of spatial grains. *Nature Ecology & Evolution*, *3*(3), 390–399. https://doi.org/10.1038/s41559-019-0799-0

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kindvall, O., & Gärdenfors, U. (2003). Temporal Extrapolation of PVA Results in Relation to the IUCN Red List Criterion E. *Conservation Biology*, 17(1), 316–321. https://doi.org/10.1046/j.1523-1739.2003.01316.x

Kuczynski, L., Legendre, P., & Grenouillet, G. (2018). Concomitant impacts of climate change, fragmentation and non-native species have led to reorganization of fish communities since the 1980s. *Global Ecology and Biogeography*, *27*, 213–222. https://doi.org/10.1111/geb.12690

Kuiper, S. D., Coops, N. C., Hinch, S. G., & White, J. C. (2023). Advances in remote sensing of freshwater fish habitat: A systematic review to identify current approaches, strengths and challenges. *Fish and Fisheries*, *24*(5), 829–847. https://doi.org/10.1111/faf.12772

Kunakh, O., Volkova, A., Tutova, G., & Zhukov, O. (2023). Diversity of diversity indices: Which diversity measure is better?. *Biosystems Diversity*, *31*(2), 131–146. https://doi.org/10.15421/012314

Kärgenberg, E., Thorstad, E. B., Järvekülg, R., Sandlund, O. T., Saadre, E., Økland, F., Thalfeldt, M., & Tambets, M. (2020). Behaviour and mortality of downstream migrating Atlantic salmon smolts at a small power station with multiple migration routes. *Fisheries Management and Ecology*, *27*(1), 32–40. https://doi.org/10.1111/fme.12382

Lauzeral, C., Leprieur, F., Beauchard, O., Duron, Q., Oberdorf,f T., & Brosse, S. (2011). Identifying climatic niche shifts using coarse-grained occurrence data: a test with non-native freshwater fish. *Global Ecology and Biogeography*, *20*, 407–414. https://doi.org/10.1111/j.1466-8238.2010.00611.x

Leadley, P., Gonzalez, A., Obura, D., Krug, C. B., Londoño-Murcia, M. C., Millette, K. L., Radulovici, A., Rankovic, A., Shannon, L. J., Archer, E., Armah, F. A., Bax, N., Chaudhari, K., Costello, M. J., Dávalos, L. M., Roque, F. d. O., DeClerck, F., Dee, L. E., Essl, F., . . . Xu, J. (2022). Achieving global biodiversity goals by 2050 requires urgent and integrated actions. *One Earth*, *5*(6), 597–603. https://doi.org/10.1016/j.oneear.2022.05.009

Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, 16(8), 951–963. https://doi.org/10.1111/ele.12141

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lennon, J. J., Koleff, P., GreenwooD, J. J. D., & Gaston, K. J. (2001). The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, *70*(6), 966–979. https://doi.org/10.1046/j.0021-8790.2001.00563.x

Leonov, V. D. (2023). Stochastic and Deterministic Processes in the Establishment of Taxonomic, Functional and Phylogenetic Diversity of Ecological Communities: A Review of Modern Concepts. *Russian Journal of Ecology*, *54*(4), 251–265. https://doi.org/10.1134/S1067413623040057

Lepori, F., & Malmqvist, B. (2009). Deterministic control on community assembly peaks at intermediate levels of disturbance. *Oikos*, *118*(3), 471–479. https://doi.org/10.1111/j.1600-0706.2008.16989.x

Leprieur, F., Albouy, C., De Bortoli, J., Cowman, P. F., Bellwood, D. R., & Mouillot, D. (2012). Quantifying phylogenetic beta diversity: Distinguishing between 'true' turnover of lineages and phylogenetic diversity gradients. *PLOS ONE*, *7*(8), e42760. https://doi.org/10.1371/journal.pone.0042760

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T., Brosse, S. (2008). Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS biology* 6: e28–e28. https://doi.org/10.1371/journal.pbio.0060028

Li, F., Yan, Y., Zhang, J., Zhang, Q., & Niu, J. (2021). Taxonomic, functional, and phylogenetic beta diversity in the Inner Mongolia grassland. *Global Ecology and Conservation*, *28*, e01634. https://doi.org/10.1016/j.gecco.2021.e01634

Lin, L., Deng, W., Huang, X., & Kang, B. (2021). Fish taxonomic, functional, and phylogenetic diversity and their vulnerabilities in the largest river in southeastern China. *Ecology and Evolution*, *11*(16), 11533–11548. https://doi.org/10.1002/ece3.7945

Lindberg, G. (1972). *Large-scale fluctuations of sea level in the Quaternary period: hypothesis based on biogeographical evidence*. Tokai University Press.

Linke, S., Kennard, M. J., Hermoso, V., Olden, J. D., Stein, J., & Pusey, B. J. (2012). Merging connectivity rules and large-scale condition assessment improves conservation adequacy in river systems. *Journal of Applied Ecology*, *49*(5), 1036–1045. https://doi.org/10.1111/j.1365-2664.2012.02177.x

Liu, C., Wolter, C., Xian, W., & Jeschke, J. M. (2020). Most invasive species largely conserve their climatic niche. *Proceedings of the National Academy of Sciences*, *117*, 23643–23651. https://doi.org/10.1073/pnas.2004289117

Liu, X., & Wang, H. (2010). Estimation of minimum area requirement of river-connected lakes for fish diversity conservation in the Yangtze River floodplain. *Diversity and Distributions*, *16*(6), 932–940. https://doi.org/10.1111/j.1472-4642.2010.00706.x

Lucas, M., Baras, E. (2008). *Migration of freshwater fishes*. John Wiley & Sons. https://doi.org/10.1002/9780470999653

Luebert, F., & Scherson, R. A. (2024). Choice of molecular marker influences spatial patterns of phylogenetic diversity. *Biology Letters*, *20*(3), 20230581. https://doi.org/10.1098/rsbl.2023.0581

Lyashevska, O., & Farnsworth, K. D. (2012). How many dimensions of biodiversity do we need? *Ecological Indicators*, *18*, 485–492. https://doi.org/10.1016/j.ecolind.2011.12.016

Maavara, T., Chen, Q., Van Meter, K., Brown, L. E., Zhang, J., Ni, J., & Zarfl, C. (2020). River dam impacts on biogeochemical cycling. *Nature Reviews Earth & Environment*, *1*(2), 103–116. https://doi.org/10.1038/s43017-019-0019-0

Magurran, A. E. (1988). *Ecological diversity and its measurement*. Princeton University Press.

Maherali, H., & Klironomos, J. N. (2007). Influence of Phylogeny on Fungal Community Assembly and Ecosystem Functioning. *Science*, *316*(5832), 1746–1748. https://doi.org/10.1126/science.1143082

Mammola, S., & Cardoso, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods in Ecology and Evolution*, *11*(8), 986–995. https://doi.org/10.1111/2041-210X.13424

Mammola, S., Carmona, C. P., Guillerme, T., & Cardoso, P. (2021). Concepts and applications in functional diversity. *Functional Ecology*, *35*(9), 1869–1885.

https://doi.org/10.1111/1365-2435.13882

Mandrak, N. E., & Cudmore, B. (2010). The fall of Native Fishes and the rise of Non-native Fishes in the Great Lakes Basin. *Aquatic Ecosystem Health & Management*, *13*(3), 255–268. https://doi.org/10.1080/14634988.2010.507150

Matsuzaki, S. S., Sasaki, T., & Akasaka, M. (2013). Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Global Ecology and Biogeography*, *22*(9), 1071–1082. https://doi.org/10.1111/geb.12067

Matsuzaki, S. S., Sasaki, T., & Akasaka, M. (2016). Invasion of exotic piscivores causes losses of functional diversity and functionally unique species in Japanese lakes. *Freshwater Biology*, *61*(7), 1128–1142. https://doi.org/10.1111/fwb.12774

May, R. M. (1988). How many species are there on Earth? *Science*, *241*(4872), 1441–1449. https://doi.org/10.1126/science.241.4872.1441

Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso, M. V., Loyola, R., Diniz-Filho, J. A. F., Mouillot, D., & Thuiller, W. (2014). Multifaceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Global Ecology and Biogeography*, *23*(8), 836–847. https://doi.org/10.1111/geb.12158

Mazel, F., Pennell, M. W., Cadotte, M. W., Diaz, S., Dalla Riva, G. V., Grenyer, R., Leprieur, F., Mooers, A. O., Mouillot, D., Tucker, C. M., & Pearse, W. D. (2018). Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications*, *9*(1), 2888. https://doi.org/10.1038/s41467-018-05126-3

McGill, B. J. (2011). Linking biodiversity patterns by autocorrelated random sampling. *American Journal of Botany*, *98*(3), 481–502. https://doi.org/10.3732/ajb.1000509

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Meynard, C. N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., & Mouquet, N. (2011). Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecology and Biogeography*, *20*(6), 893–903. https://doi.org/10.1111/j.1466-8238.2010.00647.x

Ministry of the Environment. (2020). *Publication of the ministry of the environment red list 2020* https://www.env.go.jp/press/107905.html

Minnesota Department of Natural Resources. (2013). *Fish habitat plan: a strategic guidance document*. Minnesota Department of Natural Resources. https://www.dnr.state.mn.us/fisheries/habitat.html

Miranda, L. E. (2005). Fish assemblages in oxbow lakes relative to connectivity with the Mississippi River. *Transactions of the American Fisheries Society*, *134*, 1480-1489. https://doi.org/10.1577/T05-057.1

Moi, D. A., Alves, D. C., Figueiredo, B. R. S., Antiqueira, P. A. P., Teixeira de Mello, F., Jeppesen, E., Romero, G. Q., Mormul, R. P., Bonecker, C. C. (2021) Non-native fishes homogenize native fish communities and reduce ecosystem multifunctionality in tropical lakes over 16 years. *Science of The Total Environment*, *769*, 144524. https://doi.org/10.1016/j.scitotenv.2020.144524

Moi, D. A., Alves, D. C., Figueiredo, B. R. S., Antiqueira, P. A. P., Teixeira de Mello, F., Jeppesen, E., Romero, G. Q., Mormul, R. P., & Bonecker, C. C. (2021). Non-native fishes homogenize native fish communities and reduce ecosystem multifunctionality in tropical lakes over 16 years. *Science of The Total Environment*, *769*, 144524. https://doi.org/10.1016/j.scitotenv.2020.144524

Montaño-Centellas, F. A., McCain, C., & Loiselle, B. A. (2020). Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients. *Global Ecology and Biogeography*, *29*(2), 232–245. https://doi.org/10.1111/geb.13021

Montgomery, D. R., Buffington, J. M., Peterson, N. P., Schuett-Hames, D., & Quinn, T. P. (1996). Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(5), 1061–1070. https://doi.org/10.1139/f96-028

Mooers, A. Ø., Faith, D. P., & Maddison, W. P. (2008). Converting endangered species categories to probabilities of extinction for phylogenetic conservation prioritization. *PLOS ONE*, 3(11), e3700. https://doi.org/10.1371/journal.pone.0003700

Moritz, C., Richardson, K. S., Ferrier, S., Monteith, G. B., Stanisic, J., Williams, S. E., & Whiffin, T. (2001). Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1479), 1875–1881. https://doi.org/10.1098/rspb.2001.1713

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J., & Thuiller, W. (2013). Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS biology*, *11*(5), e1001569. https://doi.org/10.1371/journal.pbio.1001569

Musil J, Jurajda P, Adámek Z, Horký P, Slavík O (2010) Non-native fish introductions in the Czech Republic–species inventory, facts and future perspectives. *Journal of Applied Ichthyology*, *26*, 38–45. https://doi.org/10.1111/j.1439-0426.2010.01500.x

Myers, E. M. V., Eme, D., Liggins, L., Harvey, E. S., Roberts, C. D., & Anderson, M. J. (2021). Functional beta diversity of New Zealand fishes: Characterising morphological turnover along depth and latitude gradients, with derivation of functional bioregions. *Austral Ecology*, *46*(6), 965–981. https://doi.org/10.1111/aec.13078

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nakamura, G., Vicentin, W., Súarez, Y. R., & Duarte, L. (2020). A multifaceted approach to analyzing taxonomic, functional, and phylogenetic β diversity. *Ecology*, *101*(10), e03122. https://doi.org/10.1002/ecy.3122

Nakamura, M. (1995). Lake Biwa: Have sustainable development objectives been met?. *Lakes & Reservoirs: Research & Management*, *1*(1), 3–29. https://doi.org/10.1111/j.1440-1770.1995.tb00002.x

Nagatsu, M., Ohbayashi, K., Hodoki, Y., Ono, Y., & Murano, N. (2007). The distribution and habitat of the endangered 'ezo' eight-barbell loach, *Lefua nikkonis* (Jordan and Fowler), on Hokkaido Island, Japan. *Japanese Journal of Conservation Ecology*, *12*, 60–65. (in Japanese with English abstract). https://doi.org/10.18960/hozen.12.1_60

Nelson, J. S., Grande, T. C., & Wilson, M. V. (2016). *Fishes of the World*. John Wiley & Sons.

Newbold, T., Bentley, L. F., Hill, S. L. L., Edgar, M. J., Horton, M., Su, G., Şekercioğlu, Ç. H., Collen, B., & Purvis, A. (2020). Global effects of land use on biodiversity differ among functional groups. *Functional Ecology*, *34*(3), 684–693. https://doi.org/10.1111/1365-2435.13500

Ning, D., Deng, Y., Tiedje, J. M., & Zhou, J. (2019). A general framework for quantitatively assessing ecological stochasticity. *Proceedings of the National Academy of Sciences*, *116*(34), 16892–16898. https://doi.org/10.1073/pnas.1904623116

Nishino, M., Nishino, M., Azuma, Y., Tatsumi, M., Kaneko, Y., Tatsumi, M., ... & Nakajima, T. (2011). Ecological changes in lake Biwa. In *Lake Biwa: Interactions between nature and people* (pp. 155–238). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-007-1783-1_3

Noyes, P. D., McElwee, M. K., Miller, H. D., Clark, B. W., Van Tiem, L. A., Walcott, K. C., Erwin, K. N., & Levin, E. D. (2009). The toxicology of climate change: Environmental contaminants in a warming world. *Environment International*, *35*(6), 971–986. https://doi.org/10.1016/j.envint.2009.02.006

Oberdorff, T., Dias, M. S., Jézéquel, C., Albert, J. S., Arantes, C. C., Bigorne, R., Carvajal-Valleros, F. M., De Wever, A., Frederico, R. G., Hidalgo, M., Hugueny, B., Leprieur, F., Maldonado, M., Maldonado-Ocampo, J., Martens, K., Ortega, H., Sarmiento, J., Tedesco, P. A., Torrente-Vilara, G., . . . Zuanon, J. (2019). Unexpected fish diversity gradients in the Amazon basin. *Science Advances*, *5*(9), eaav8681. https://doi.org/doi:10.1126/sciadv.aav8681

Ohira, M., Tsunoda, H., Nishida, K., Mitsuo, Y., & Senga, Y. (2015). Niche processes and conservation implications of fish community assembly in a rice irrigation system. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*(3), 322–335. https://doi.org/10.1002/aqc.2558

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., . . . Weedon, J. (2022). *vegan: Community Ecology Package*. R package version 2.6-4. https://CRAN.R-project.org/package=vegan

Okuda, N., Watanabe, K., Fukumori, K., Nakano, S. I., & Nakazawa, T. (2014). *Biodiversity in aquatic systems and environments: Lake Biwa*. Springer Japan. https://link.springer.com/book/10.1007/978-4-431-54150-9

Olden, J. D., Poff, N. L., & McKinney, M. L. (2006). Forecasting faunal and floral homogenization associated with human population geography in North America. *Biological Conservation*, *127*(3), 261–271. https://doi.org/10.1016/j.biocon.2005.04.027

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A., & Bullock, J. M. (2015). Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, *30*(11), 673–684. https://doi.org/10.1016/j.tree.2015.08.009

Owen, N. R., Gumbs, R., Gray, C. L., & Faith, & D. P. (2019). Global conservation of phylogenetic diversity captures more than just functional diversity. *Nature Communications*, *10*(1), 859. https://doi.org/10.1038/s41467-019-08600-8

Pander, J., Mueller, M., & Geist, J. (2018). Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation*, *217*, 1–10. https://doi.org/10.1016/j.biocon.2017.10.024

Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., . . . Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., . . . Walpole, M. (2010). Scenarios for Global Biodiversity in the 21st Century. *Science*, *330*(6010), 1496–1501. https://doi.org/10.1126/science.1196624

Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, *5*(3), 402–411. https://doi.org/10.1046/j.1461-0248.2002.00339.x

Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, *76*(5), 977–985. https://doi.org/10.1111/j.1365-2656.2007.01271.x

Pettersen, A. K., Marzinelli, E. M., Steinberg, P. D., & Coleman, M. A. (2022). Impact of marine protected areas on temporal stability of fish species diversity. *Conservation Biology*, *36*(2), e13815.https://doi.org/10.1111/cobi.13815

Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J. S., Albouy, C., Rasher, D. B., Davis, M., Svenning, J. C., & Griffin, J. N. (2020). Functional diversity of marine megafauna in the Anthropocene. *Science Advances*, *6*(16), eaay7650. https://doi.org/10.1126/sciadv.aay7650

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

Pingram, M. A., Collier, K. J., Williams, A. K., David, B. O., Garrett-Walker, J., Górski, K., Özkundakci, D., & Ryan, E. F. (2021). Surviving invasion: Regaining native fish resilience following fish invasions in a modified floodplain landscape. *Water Resources Research*, *57*, e2020WR029513. https://doi.org/10.1029/2020WR029513

Pinto-Ledezma, J. N., Villalobos, F., Reich, P. B., Catford, J. A., Larkin, D. J., & Cavender-Bares, J. (2020). Testing Darwin's naturalization conundrum based on taxonomic, phylogenetic, and functional dimensions of vascular plants. *Ecological Monographs*, *90*(4), e01420. https://doi.org/10.1002/ecm.1420

Ponce de León, J. L., León, G., Rodríguez, R., Metcalfe, C. J., Hernández, D., Casane, D., & García-Machado, E. (2014). Phylogeography of Cuban Rivulus: Evidence for allopatric speciation and secondary dispersal across a marine barrier. *Molecular Phylogenetics and Evolution*, *79*, 404–414. https://doi.org/10.1016/j.ympev.2014.07.007

Pongsivapai, P., Negishi, J. N., Izumi, H., Garrido, P. A., & Kuramochi, K. (2021). Morphometry-Driven Divergence in Decadal Changes of Sediment Property in Floodplain Water Bodies. *Water*, *13*, 469. https://doi.org/10.3390/w13040469

Pool, T. K., Grenouillet, G., & Villéger, S. (2014). Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. *Diversity and Distributions*, *20*(11), 1235–1244. https://doi.org/10.1111/ddi.12231

Presley, S. J., Cisneros, L. M., Higgins, C. L., Klingbeil, B. T., Scheiner, S. M., & Willig, M. R. (2018). Phylogenetic and functional underdispersion in Neotropical phyllostomid bat communities. *Biotropica*, *50*(1), 135–145. https://doi.org/10.1111/btp.12501

Presley, S. J., Higgins, C. L., & Willig, M. R. (2010). A comprehensive framework for the evaluation of metacommunity structure. *Oikos*, *119*(6), 908–917. https://doi.org/10.1111/j.1600-0706.2010.18544.x

Primack, R. B. (1995). *A primer of conservation biology*. Sinauer Associates.

Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M., & Prentice, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology*, *101*(4), 857–866. https://doi.org/10.1111/1365-2745.12098

Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M., & Prentice, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology*, *101*(4), 857–866. https://doi.org/10.1111/1365-2745.12098

Qian, H., & Sandel, B. (2022). Darwin's preadaptation hypothesis and the phylogenetic structure of native and alien regional plant assemblages across North America. *Global Ecology and Biogeography*, *31*(3), 531–545. https://doi.org/10.1111/geb.13445

Qian, H., Ricklefs, R. E., & White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, *8*(1), 15–22. https://doi.org/10.1111/j.1461-0248.2004.00682.x

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T. J., Coll, M., & Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, *559*(7714), 392–395. https://doi.org/10.1038/s41586-018-0273-1

Radinger, J., Matern, S., Klefoth, T., Wolter, C., Feldhege, F., Monk, C. T., & Arlinghaus, R. (2023). Ecosystem-based management outperforms species-focused stocking for enhancing fish populations. *Science*, *379*(6635), 946—951. https://doi.org/10.1126/science.adf0895

Rahel, F. J. (2007). Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology*, *52*(4), 696–710. https://doi.org/10.1111/j.1365-2427.2006.01708.x

Redding, D. W., & Mooers, A. Ø. (2006). Incorporating evolutionary measures into conservation prioritization. *Conservation Biology*, *20*(6), 1670–1678. https://doi.org/10.1111/j.1523-1739.2006.00555.x

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*(3), 849–873. https://doi.org/10.1111/brv.12480

Reid, W. V. (1998). Biodiversity hotspots. *Trends in Ecology & Evolution*, *13*(7), 275–280.

https://doi.org/10.1016/S0169-5347(98)01363-9

Reis, I. C. d., Honório, N. A., Barros, F. S. M. d., Barcellos, C., Kitron, U., Camara, D. C. P., Pereira, G. R., Keppeler, E. C., da Silva-Nunes, M., & Codeço, C. T. (2015). Epidemic and endemic malaria transmission related to fish farming ponds in the Amazon frontier. *PLOS ONE*, *10*(9), e0137521. https://doi.org/10.1371/journal.pone.0137521

Ricciardi, A., & Mottiar, M. (2006). Does Darwin's naturalization hypothesis explain fish invasions? *Biological Invasions*, *8*, 1403–1407. https://doi.org/10.1007/s10530-006-0005-6

Roni, P. (2019). Does river restoration increase fish abundance and survival or concentrate fish? The effects of project scale, location, and fish life history. *Fisheries*, *44*, 7–19. https://doi.org/10.1002/fsh.10180

Safi, K., Cianciaruso, M. V., Loyola, R. D., Brito, D., Armour-Marshall, K., & Diniz-Filho, J. A. F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1577), 2536–2544. https://doi.org/10.1098/rstb.2011.0024

Salzburger, W., Van Bocxlaer, B., & Cohen, A. S. (2014). Ecology and evolution of the African Great Lakes and their faunas. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 519–545. https://doi.org/10.1146/annurev-ecolsys-120213-091804

Sax, D. F., & Gaines, S. D. (2003). Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution*, *18*(11), 561–566. https://doi.org/10.1016/S0169-5347(03)00224-6

Schindler, D. E., Carpenter, S. R., Cole, J. J., Kitchell, J. F., & Pace, M. L. (1997). Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science*, *277*(5323), 248–251. https://dio.org/ 10.1126/science.277.5323.248

Schindler, D. W. (1990). Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos*, *57*, 25–41. https://doi.org/10.2307/3565733

Schulte, P. M. (2001). Environmental adaptations as windows on molecular evolution. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 128(3), 597–611.https://doi.org/10.1016/S1096-4959(00)00357-2

Shipley, B., Paine, C. E. T., & Baraloto, C. (2012). Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. *Ecology*, *93*(4), 760–769. https://doi.org/10.1890/11-0944.1

Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., & Nilon, C. H. (2010). Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, *60*, 199–208. https://doi.org/10.1525/bio.2010.60.3.6

Shooner, S., Davies, T. J., Saikia, P., Deka, J., Bharali, S., Tripathi, O. P., Singha, L., Latif Khan, M., & Dayanandan, S. (2018). Phylogenetic diversity patterns in Himalayan forests reveal evidence for environmental filtering of distinct lineages. *Ecosphere*, *9*(5), e02157. https://doi.org/10.1002/ecs2.2157

Si, X., Baselga, A., Leprieur, F., Song, X., & Ding, P. (2016). Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. *Journal of Animal Ecology*, *85*(2), 409–418. https://doi.org/10.1111/1365-2656.12478

Si, X., Zhao, Y., Chen, C., Ren, P., Zeng, D., Wu, L., & Ding, P. (2017). Beta-diversity partitioning: methods, applications and perspectives. *Biodiversity Science*, *25*, 464–480. https://doi.org/10.17520/biods.2017024

Sills, J., Harrison, I., Abell, R., Darwall, W., Thieme, M. L., Tickner, D., & Timboe, I.

(2018). The freshwater biodiversity crisis. *Science*, *362*(6421), 1369–1369. https://doi.org/10.1126/science.aav9242

Simberloff, D. S., & Abele, L. G. (1976). Island biogeography theory and conservation practice. *Science*, *191*(4224), 285–286. https://doi.org/10.1126/science.191.4224.285

Singh, J. S. (2002). The biodiversity crisis: A multifaceted review. *Current Science*, *82*(6), 638–647. http://www.jstor.org/stable/24106689

Šlechtová, V., Bohlen, J., Freyhof, J., Persat, H., & Delmastro, G. B. (2004). The Alps as barrier to dispersal in cold-adapted freshwater fishes? Phylogeographic history and taxonomic status of the bullhead in the Adriatic freshwater drainage. *Molecular Phylogenetics and Evolution*, *33*(1), 225–239. https://doi.org/10.1016/j.ympev.2004.05.005

Sleezer, L. J., Angermeier, P. L., Frimpong, E. A., & Brown, B. L. (2021). A new composite abundance metric detects stream fish declines and community homogenization during six decades of invasions. *Diversity and Distributions*, *27*, 2136–2156. https://doi.org/10.1111/ddi.13393

Smiley, T. M., Title, P. O., Zelditch, M. L., & Terry, R. C. (2020). Multi-dimensional biodiversity hotspots and the future of taxonomic, ecological and phylogenetic diversity: A case study of North American rodents. *Global Ecology and Biogeography*, *29*(3), 516–533. https://doi.org/10.1111/geb.13050

Smit, I. P. J., & Ferreira, S. M. (2010). Management intervention affects river-bound spatial dynamics of elephants. *Biological Conservation*, *143*(9), 2172–2181. https://doi.org/10.1016/j.biocon.2010.06.001

Smith, C., Reichard, M., Jurajda, P., & Przybylski, M. (2004). The reproductive ecology of the European bitterling (*Rhodeus sericeus*). *Journal of Zoology*, *262*(2), 107–124. https://doi.org/10.1017/S0952836903004497

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation?. *Trends in Ecology & Evolution*, *31*(1), 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Sor, R., Legendre, P., & Lek, S. (2018). Uniqueness of sampling site contributions to the total variance of macroinvertebrate communities in the Lower Mekong Basin. *Ecological Indicators*, *84*, 425–432. https://doi.org/10.1016/j.ecolind.2017.08.038

Sparholt, H. (1994). Fish species interactions in the Baltic Sea. *Dana*, *10*, 131–162. https://www.aqua.dtu.dk/english/-/media/institutter/aqua/publikationer/dana/dana_vol_10_pp_131_162.pdf

Srivastava, D. S., Cadotte, M. W., MacDonald, A. A. M., Marushia, R. G., & Mirotchnick, N. (2012). Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters*, *15*(7), 637–648. https://doi.org/10.1111/j.1461-0248.2012.01795.x

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., & Ludwig, C. (2015). The trajectory of the Anthropocene: The great acceleration. *The Anthropocene Review*, 2(1), 81–98. https://doi.org/10.1177/2053019614564785

Stegen, J. C., Lin, X., Konopka, A. E., & Fredrickson, J. K. (2012). Stochastic and deterministic assembly processes in subsurface microbial communities. *The ISME Journal*, *6*(9), 1653–1664. https://doi.org/10.1038/ismej.2012.22

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, *29*(1), 344–358. https://doi.org/10.1899/08-171.1

Su, G., Logez, M., Xu, J., Tao, S., Villéger, S., & Brosse, S. (2021). Human impacts on global freshwater fish biodiversity. *Science*, *371*(6531), 835–838. https://doi.org/10.1126/science.abd3369

Suvarnaraksha, A., Lek, S., Lek-Ang, S., & Jutagate, T. (2012). Fish diversity and assemblage patterns along the longitudinal gradient of a tropical river in the Indo-Burma hotspot region (Ping-Wang River Basin, Thailand). *Hydrobiologia*, *694*(1), 153–169. https://doi.org/10.1007/s10750-012-1139-4

Swenson, N. G. (2011). The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *American Journal of Botany*, *98*(3), 472–480. https://doi.org/10.3732/ajb.1000289

Swenson, N. G. (2014). *Functional and phylogenetic ecology in R*. Springer. https://doi.org/10.1007/978-1-4614-9542-0

Tabata, R. (2022). Lake Biwa and the phylogeography of freshwater fishes in Japan. In Y. Kai, M. Motomura, & K. Matsuura (Eds.), *Fish diversity of Japan: Evolution, zoogeography, and conservation* (pp. 205–218). Singapore: Springer Nature Singapore. https://doi.org/10.1007/978-981-16-7427- 3_12

Takemura, K. (2015). Ground Interface. http://www.gridscapes.net/

Thomas, C. D. (2013). Local diversity stays about the same, regional diversity increases, and global diversity declines. *Proceedings of the National Academy of Sciences*, *110*(48), 19187–19188. https://doi.org/10.1073/pnas.1319304110

Thorp, J. H., Thoms, M. C., & Delong, M. D. (2006). The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications*, *22*(2), 123–147. https://doi.org/10.1002/rra.901

Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., Cooke, S. J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclère, D., Lynch, A. J., Leonard, P., McClain, M. E., Muruven, D., Olden, J. D., . . . Young, L. (2020). Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery Plan. *BioScience*, *70*(4), 330–342. https://doi.org/10.1093/biosci/biaa002

Tockner, K., Bunn, S. E., Gordon, C., Naiman, R. J., Quinn, G. P., & Stanford, J. A. (2008). *Flood plains: Critically threatened ecosystems in aquatic ecosystems: Trends and global prospects*. Cambridge University Press. http://dx.doi.org/10.1017/CBO9780511751790.006

Tornwall, B., Sokol, E., Skelton, J., & Brown, B. L. (2015). Trends in stream biodiversity research since the river continuum concept. *Diversity*, *7*(1), 16–35. https://www.mdpi.com/1424-2818/7/1/16

Toussaint, A., Charpin, N., Brosse, S., & Villéger, S. (2016). Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Scientific Reports*, *6*(1), 22125. https://doi.org/10.1038/srep22125

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., & Thies, C. (2002). Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research*, 17(2), 229–239. https://doi.org/10.1046/j.1440-1703.2002.00482.x

Tucker, C. M., Aze, T., Cadotte, M. W., Cantalapiedra, J. L., Chisholm, C., Díaz, S., Grenyer, R., Huang, D., Mazel, F., Pearse, W. D., Pennell, M. W., Winter, M., & Mooers, A. O. (2019). Assessing the utility of conserving evolutionary history. *Biological Reviews*, *94*(5), 1740–1760. https://doi.org/10.1111/brv.12526

Tuomisto, H. (2010). A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 33(1), 2–22. https://doi.org/10.1111/j.1600-0587.2009.05880.x

Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299(5604), 241–244. https://doi.org/10.1126/science.1078037

Turak, E., Harrison, I., Dudgeon, D., Abell, R., Bush, A., Darwall, W., Finlayson, C. M., Ferrier, S., Freyhof, J., Hermoso, V., Juffe-Bignoli, D., Linke, S., Nel, J., Patricio, H. C., Pittock, J., Raghavan, R., Revenga, C., Simaika, J. P., & De Wever, A. (2017). Essential biodiversity variables for measuring change in global freshwater biodiversity. *Biological Conservation*, 213, 272–279. https://doi.org/10.1016/j.biocon.2016.09.005

UN Convention on Biological Diversity. (2022). *Kunming-Montreal Global biodiversity framework*. https://www.unep.org/resources/report/kunming-montreal-global-biodiversity-framework

Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, *118*(1), 3–17. https://doi.org/10.1111/j.1600-0706.2008.17053.x

Vaccari, D. A., Strom, P. F., & Alleman, J. E. (2005). *Environmental biology for engineers and scientists*. John Wiley & Sons.

Vamosi, J. C., & Wilson, J. R. U. (2008). Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecology Letters*, 11(10), 1047–1053. https://doi.org/10.1111/j.1461-0248.2008.01215.x

Vamosi, S. M., Heard, S. B., Vamosi, J. C., & Webb, C. O. (2009). Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, *18*(4), 572–592. https://doi.org/10.1111/j.1365-294X.2008.04001.x

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Veech, J. A., Summerville, K. S., Crist, T. O., & Gering, J. C. (2002). The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, 99(1), 3–9. https://doi.org/10.1034/j.1600-0706.2002.990101.x

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016). Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific Data*, *3*(1), 160067. https://doi.org/10.1038/sdata.2016.67

Viana, D. S., & Chase, J. M. (2019). Spatial scale modulates the inference of metacommunity assembly processes. *Ecology*, *100*(2), e02576. /https://doi.org/10.1002/ecy.2576

Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T., & Brosse, S. (2011). Homogenization patterns of the world’s freshwater fish faunas. *Proceedings of the National Academy of Sciences*, *108*, 18003–18008. https://doi.org/10.1073/pnas.1107614108

Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., & Vanni, M. J. (2017). Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences*, *79*(4), 783–801. https://doi.org/10.1007/s00027-017-0546-z

Villéger, S., Grenouillet, G., & Brosse, S. (2013). Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, *22*(6), 671–681. https://doi.org/10.1111/geb.12021

Vilmi, A., Gibert, C., Escarguel, G., Happonen, K., Heino, J., Jamoneau, A., Passy, S. I., Picazo, F., Soininen, J., Tison-Rosebery, J., & Wang, J. (2021). Dispersal–niche continuum index: a new quantitative metric for assessing the relative importance of dispersal versus niche processes in community assembly. *Ecography*, *44*(3), 370–379. https://doi.org/10.1111/ecog.05356

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J. B., Cadotte, M. W., Livingstone, S. W., & Mouillot, D. (2017). Functional Rarity: The Ecology of Outliers. *Trends in Ecology & Evolution*, *32*(5), 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Véron, S., Saito, V., Padilla-García, N., Forest, F., & Bertheau, Y. (2019). The use of phylogenetic diversity in conservation biology and community ecology: A common base but different approaches. *The Quarterly Review of Biology*, *94*(2), 123–148. https://doi.org/10.1086/703580

Wainwright, P. C., & Richard, B. A. (1995). Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes*, 44(1), 97–113. https://doi.org/10.1007/BF00005909

Walling, D. E. (2006). Human impact on land–ocean sediment transfer by the world's rivers. *Geomorphology*, *79*(3-4), 192-216. https://doi.org/10.1016/j.geomorph.2006.06.019

Walls, S. C. (2018). Coping with constraints: Achieving effective conservation with limited resources. *Frontiers in Ecology and Evolution*, *6*, 24. https://doi.org/10.3389/fevo.2018.00024

Wan, H., & Zhong, Z. (2014). Ensemble simulations to investigate the impact of large-scale urbanization on precipitation in the lower reaches of Yangtze River Valley, China. *Quarterly Journal of the Royal Meteorological Society*, *140*(678), 258–266. https://doi.org/10.1002/qj.2125

Wang, D., Li, Z., Li, Z., Pan, B., Tian, S., & Nie, X. (2020). Environmental gradient relative to oxbow lake-meandering river connectivity in Zoige Basin of the Tibetan Plateau. *Ecological Engineering*, *156*, 105983. https://doi.org/10.1016/j.ecoleng.2020.105983

Wang, C., Jiang, Z., Zhou, L., Dai, B., & Song, Z. (2019). A functional group approach reveals important fish recruitments driven by flood pulses in floodplain ecosystem. *Ecological Indicators*, *99*, 130–139. https://doi.org/10.1016/j.ecolind.2018.12.024

Wang, J., Legendre, P., Soininen, J., Yeh, C.-F., Graham, E., Stegen, J., Casamayor, E. O., Zhou, J., Shen, J., & Pan, F. (2020). Temperature drives local contributions to beta diversity in mountain streams: Stochastic and deterministic processes. *Global Ecology and Biogeography*, *29*(3), 420–432. https://doi.org/10.1111/geb.13035

Ward, J. V., Tockner, K., Arscott, D. B., & Claret, C. (2002). Riverine landscape diversity. *Freshwater Biology*, *47*(4), 517-539. https://doi.org/10.1046/j.1365-2427.2002.00893.x

Watanabe, K. (2012). Faunal structure of Japanese freshwater fishes and its artificial disturbance. *Environmental Biology of Fishes*, 94, 533–547. https://doi.org/10.1007/s10641-010-9601-5

Watanabe, K., Tominaga, K., Nakajima, J., Kakioka, R., & Tabata, R. (2017). Japanese freshwater fishes: biogeography and cryptic diversity. In M. Motokawa & H. Kajihara (Eds.), *Species Diversity of Animals in Japan* (pp. 183-227). Springer Japan. https://doi.org/10.1007/978-4-431-56432-4_7

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and Community Ecology. *Annual Review of Ecology, Evolution and Systematics*, *33*, 475–505.

https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Werner, E. E., & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology*, 69(5), 1352-1366. https://doi.org/10.2307/1941633

Whittaker, R. H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338.

Williams, C. F., Britton, J. R. & Turnbull, J. F. (2013). A risk assessment for managing non-native parasites. *Biological Invasions*, 15, 1273–1286. https://doi.org/10.1007/s10530-012-0364-0

Williams, J. E., Johnson, J. E., Hendrickson, D. A., Contreras-Balderas, S., Williams, J. D., Navarro-Mendoza, M., McAllister, D. E., & Deacon, J. E. (1989). Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries*, *14*, 2–20. https://doi.org/10.1577/1548-8446(1989)014<0002:FONAET>2.0.CO;2

Williams, J. E., Williams, R. N., Thurow, R. F., Elwell, L., Philipp, D. P., Harris, F. A., Kershner, J. L., Martinez, P. J., Miller, D., Reeves, G. H., Frissell, C. A., & Sedell, J. R. (2011). Native Fish Conservation Areas: A Vision for Large-Scale Conservation of Native Fish Communities. *Fisheries*, *36*(6), 267–277. https://doi.org/10.1080/03632415.2011.582398

Williams, P. H. (1996). Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society B: Biological Sciences*, *263*(1370), 579–588. https://doi.org/10.1098/rspb.1996.0087

Williams, P. H., de Klerk, H. M., & Crowe, T. M. (1999). Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography*, *26*(3), 459–474. https://doi.org/10.1046/j.1365-2699.1999.00294.x

Willig, M. R., Presley, S. J., Klingbeil, B. T., Kosman, E., Zhang, T., & Scheiner, S. M. (2023). Protecting biodiversity via conservation networks: Taxonomic, functional, and phylogenetic considerations. *Biological Conservation*, *278*, 109876. https://doi.org/10.1016/j.biocon.2022.109876

Winemiller, K. O., Tarim, S., Shormann, D., & Cotner, J. B. (2000). Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. *Transactions of the American Fisheries Society*, *129*(2), 451–468. https://doi.org/10.1577/1548-8659(2000)129<0451:FASIRT>2.0.CO;2

Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution*, *28*(4), 199–204. https://doi.org/10.1016/j.tree.2012.10.015

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., Didžiulis, V., Hejda, M., Hulme, P. E., Lambdon, P. W., Pergl, J., Pyšek, P., Roy, D. B., & Kühn, I. (2009). Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences*, 106(51), 21721–21725. https://doi.org/10.1073/pnas.0907088106

Woolnough, D. A., Downing, J. A., & Newton, T. J. (2009). Fish movement and habitat use depends on water body size and shape. *Ecology of Freshwater Fish*, *18*(1), 83–91. https://doi.org/10.1111/j.1600-0633.2008.00326.x

Xia, Z., Heino, J., Liu, F., Yu, F., Xu, C., Hou, M., Zou, X., & Wang, J. (2022). Interspecific variations in fish occupancy and abundance are driven by niche characteristics in a monsoon climate river basin. *Journal of Biogeography*, *49*(12), 2231–2242.

https://doi.org/10.1111/jbi.14502

Xia, Z., Heino, J., Yu, F., He, Y., Liu, F., & Wang, J. (2022). Spatial patterns of site and species contributions to β diversity in riverine fish assemblages. *Ecological Indicators*, *145*, 109728. https://doi.org/10.1016/j.ecolind.2022.109728

Xia, Z., Heino, J., Yu, F., Xu, C., Lin, P., He, Y., Liu, F., & Wang, J. (2023). Local environmental and spatial factors are associated with multiple facets of riverine fish β-diversity across spatial scales and seasons. *Freshwater Biology*, *68*(12), 2197–2212. https://doi.org/10.1111/fwb.14187

Xiao, F., Zhu, B., & Zhu, T. (2021). Inconsistent urbanization effects on summer precipitation over the typical climate regions in central and eastern China. *Theoretical and Applied Climatology*, *143*(1), 73–85. https://doi.org/10.1007/s00704-020-03404-z

Xing, Y., Zhang, C., Fan, E., & Zhao, Y. (2016). Freshwater fishes of China: species richness, endemism, threatened species and conservation. *Diversity and Distributions*, *22*, 358–370. https://doi.org/10.1111/ddi.12399

Xiong, W., Sui, X., Liang, S., & Chen, Y. (2015). Non-native freshwater fish species in China. *Reviews in Fish Biology and Fisheries*, *25*, 651–687. https://doi.org/10.1007/s11160-015-9396-8

Xu, M., Li, S., Dick, J. T. A., Gu, D., Fang, M., Yang, Y., Hu, Y., & Mu, X. (2022). Exotic fishes that are phylogenetically close but functionally distant to native fishes are more likely to establish. *Global Change Biology*, 28(19), 5683–5694. https://doi.org/10.1111/gcb.16360

Xu, M., Li, S., Liu, C., Tedesco, P. A., Dick, J. T. A., Fang, M., Wei, H., Yu, F., Shu, L., Wang, X., Gu, D., & Mu, X. (2024). Global freshwater fish invasion linked to the presence of closely related species. *Nature Communications*, *15*(1), 1411. https://doi.org/10.1038/s41467-024-45736-8

Yamamoto, T., Nagasawa, T., Inoue, T., & Kusa, D. (2001). Evaluation of oxbow lakes in Ishikari River basin for its function of water quality conservation. *Journal of Rural Planning Association*, *20*, 49–54. (in Japanese with English abstract) https://doi.org/10.2750/arp.20.20-suppl_49

Ye, G., Chen, J., Yang, P., Hu, H.-W., He, Z.-Y., Wang, D., Cao, D., Zhang, W., Wu, B., Wu, Y., Wei, X., & Lin, Y. (2023). Non-native Plant Species Invasion Increases the Importance of Deterministic Processes in Fungal Community Assembly in a Coastal Wetland. *Microbial Ecology*, *86*(2), 1120–1131. https://doi.org/10.1007/s00248-022-02144-z

Yuan, H., Mei, R., Liao, J., & Liu, W.-T. (2019). Nexus of stochastic and deterministic processes on microbial community assembly in biological systems. *Frontiers in Microbiology*, *10*, 1536. https://doi.org/10.3389/fmicb.2019.01536

Yuma, M., Hosoya, K., & Nagata, Y. (1998). Distribution of the freshwater fishes of Japan: an historical overview. *Environmental Biology of Fishes*, *52*(1), 97–124. https://doi.org/10.1023/A:1007451417556

Zhang, C., Ding, C., Ding, L., Chen, L., Hu, J., Tao, J., & Jiang, X. (2019). Large-scale cascaded dam constructions drive taxonomic and phylogenetic differentiation of fish fauna in the Lancang River, China. *Reviews in Fish Biology and Fisheries*, *29*, 895–916. https://doi.org/10.1007/s11160-019-09580-0

Zhang, Q., Hou, X., Li, F. Y., Niu, J., Zhou, Y., Ding, Y., ... & Kang, S. (2014). Alpha, beta and gamma diversity differ in response to precipitation in the Inner Mongolia grassland. *PLoS One*, *9*(3), e93518. https://doi.org/10.1371/journal.pone.0093518

Zhang, S., Zheng, Y., Zhan, A., Dong, C., Zhao, J., & Yao, M. (2022). Environmental DNA captures native and non-native fish community variations across the lentic and lotic systems of a megacity. *Science Advances*, *8*, eabk0097. https://doi.org/10.1126/sciadv.abk0097

Zu, K., Luo, A., Shrestha, N., Liu, B., Wang, Z., & Zhu, X. (2019). Altitudinal biodiversity patterns of seed plants along Gongga Mountain in the southeastern Qinghai-Tibetan Plateau. *Ecology and Evolution*, *9*(17), 9586–9596. https://doi.org/10.1002/ece3.5483