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Spatiotemporal Patterns and Drivers of Fish Biodiversity on a Remote Freshwater Archipelago

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ABSTRACT

Aim: Fish communities are shaped by environmental filters operating across different spatiotemporal scales. While many recent studies focus on anthropogenic gradients, few can isolate the role of natural drivers in community assembly. Isle Royale's inland lakes offer a rare opportunity to explore long-term fish biodiversity dynamics with minimal confounding influences. We analysed fish communities in 23 lakes surveyed in the 1920s, 1990s, and 2020s to 1) assess temporal changes in richness and composition 2) identify lakes and species experiencing the greatest change, and 3) evaluate environmental drivers of community structure.

Location: Isle Royale National Park, USA.

Taxon: Freshwater fish.

Methods: We analysed historical and contemporary fish survey data using species-area curves, PERMANOVA, and multivariate dispersion tests to quantify changes in richness and composition, temporal beta diversity indices and similarity percentages (SIMPER) to identify lakes and species changing most, and non-metric multidimensional scaling (NMDS) to examine relationships with environmental factors.

Results: Mean richness and species-area curve slopes declined slightly but non-significantly over time. Community composition remained largely stable with no homogenization, although subtle shifts from cold-water to cool-water species were observed in larger lakes. Species gains and losses were associated with isostatic rebound rate. Fast-rebounding lakes tended to gain species, while slower-rebounding lakes tended to lose species. Richness and predator presence were structured along lake area and elevation gradients, respectively.

Main Conclusions: Fish biodiversity of Isle Royale's lakes has remained remarkably stable over the past century, reflecting minimal anthropogenic influence. Subtle shifts suggest continuous filtering by geological and environmental processes, however, and spatial gradients in composition highlight interactions between large- and small-scale filters. This study provides a valuable baseline reference for understanding the processes of community assembly and environmental change in more impacted ecosystems.

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1 | Introduction

Fish communities are products of several filters spanning multiple spatiotemporal scales (Tonn 1990; Jackson et al. 2001). Large-scale filters such as glaciation determine original species source pools with diverse life history strategies, while regional filters regulate biodiversity via climate, dispersal routes, and landscape geology, and local filters such as lake morphometry, physiochemical conditions, resource availability, and biotic interactions determine communities of individual lakes (Eadie et al. 1986; Tonn 1990). As environmental conditions change, community assembly can be challenging to predict given species-specific responses, temporal variability in conditions, and stochastic events. External lake features influence immigration, while within-lake features including complexity, productivity, and disturbance determine extinctions (Minns 1989; Rosenzweig 1995; Magnuson et al. 1998). Lakes with gradual stream connections, low elevation, and proximity to source pools host higher richness due to fewer dispersal barriers and increased immigration (Eadie et al. 1986; Kratz et al. 1997; Schlosser and Kallemeyn 2000; Hrabik et al. 2005). Richness increases with lake size and depth due to habitat variability and refuge (Barbour and Brown 1974; Eadie et al. 1986; Minns 1989). Other important factors include predation (Chapleau et al. 1997; Findlay et al. 2000), temperature (Magnuson et al. 1979), oxygen (Magnuson et al. 1998), and pH (Matuszek et al. 1990).

Common biodiversity measures include richness within individual lakes (alpha diversity), richness across a region (gamma diversity), and variation in composition (beta diversity) over space or time. Analysing composition provides more insight into mechanisms guiding community structure than richness alone (Cardinale et al. 2018). Heino et al. (2024) outlines four approaches to thoroughly examine spatiotemporal patterns of beta diversity. These include the following:

1. Spatial beta diversity along environmental gradients is examined with dissimilarity indices and multivariate methods (Anderson et al. 2011; Anderson and Walsh 2013).
2. Temporal variation in spatial beta diversity analyzes these patterns through time, revealing compositional change and homogenization (Rolls et al. 2023).
3. Temporal beta diversity quantifies the magnitude of change over time based on species gains and losses (Legendre 2019; Lindholm et al. 2021).
4. Spatial variation in temporal beta diversity examines how change over time varies among habitats.

These four analyses are essential to understanding mechanisms driving community assembly, but few have integrated all of these approaches. Recent studies emphasise anthropogenic impacts on fish communities, including land use change (Lawson et al. 2024; Liang et al. 2024), species introductions (Kuczyński et al. 2018; Cazelles et al. 2019), and combinations of stressors (Wu et al. 2024). However, most focus on gradients of anthropogenic impact and remain unable to isolate the role of natural filters governing community trends. Natural filters like elevation, connectivity, morphometry, chemistry,

and predation have been applied to infer immigration and extinction based on static patterns of richness, but studies exploring their importance in long-term assembly are limited. It is challenging to characterise how interacting filters impact community change, highlighting the need to explore this process in an isolated setting.

Isle Royale National Park is a remote archipelago of 99% federally-designated wilderness in northwestern Lake Superior (Figure 1), an ideal site for studies requiring isolation from anthropogenic impact. Comprehensive fish surveys of Isle Royale's inland lakes were conducted only in 1929 (Koelz 1929; Hubbs and Lagler 1949) and 1995–1997 (Kallemeyn 2000). Both rare and cold-water species including cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), lake trout (*Salvelinus namaycush*), and finescale dace (*Chrosomus neogaeus*) were documented, along with several highly-valued communities over several 1000 years old. Gorman et al. (2014) suggested suitable habitat in some lakes may be threatened by environmental shifts but also noted Lake Superior's climate may effectively buffer and preserve habitat. Since 1970, mean annual air temperature on Isle Royale has increased at a rate of 2.6°C per century, and precipitation has increased but remained highly variable (Climate Change Response Program 2024). Given environmental change and minimal confounding factors, these lakes present a unique opportunity to assess environmental effects on fish communities.

We used the natural isolation of Isle Royale to examine how multi-scale filters shape long-term fish community dynamics with minimal anthropogenic influences. Using surveys from 1929, 1995–1997, and 2023–2024 across 23 inland lakes, we addressed three questions: (1) How have species richness and composition changed in the past century? (2) Which lakes and species changed most? (3) Which environmental factors most strongly influence current communities? We hypothesized richness would decline and communities would homogenise, primarily driven by cold-water species losses and more limited gains of cool-water species. We expected greater compositional change in shallow lakes with historically rich communities due to losses of oxy-thermal habitat. We hypothesized that lake area, elevation, and predation would be key determinants of community structure. Surveys are hereafter addressed as their corresponding decade (1920s, 1990s, 2020s).

2 | Methods

2.1 | Study Site

Isle Royale consists of over 400 islands spanning 72 km in northwestern Lake Superior. Ridges and valleys comprise most topography, with boreal coniferous forest dominant near shorelines transitioning to northern hardwood forest further inland. Isle Royale became a United States national park in 1940 and federally-designated wilderness in 1976, preventing further development. While direct anthropogenic impact is not extensive currently, Isle Royale experienced historical human habitation and disturbances including commercial fisheries in Lake Superior and small-scale logging and mining investigations. Current direct impacts are

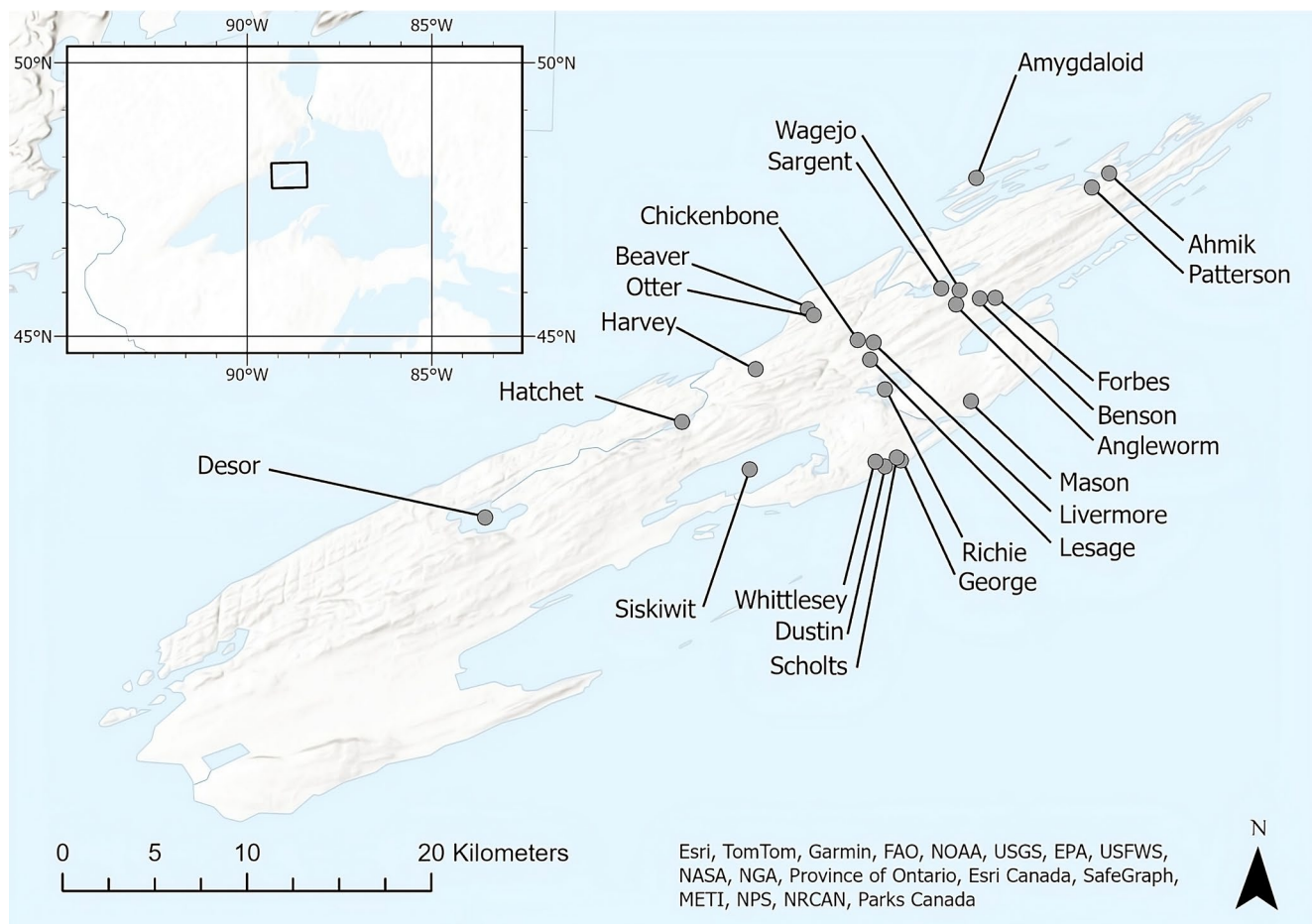


FIGURE 1 | Locations of 23 study lakes on Isle Royale, MI.

minimal but not absent as thousands of people visit each year. No aquatic invasive species have been documented in the inland lakes.

2.2 | Fish Sampling

The first comprehensive fisheries survey of 38 inland lakes occurred in the 1920s with gillnets, beach seines, angling, and stomach content analysis (Koelz 1929). The next occurred in the 1990s using gillnets, minnow traps, beach seines, angling, and stomach content analysis on 32 lakes (Kallemeyn 2000). Most recently, conventional methods were used in 23 inland lakes (Figure 1), which are the focus of this study and all subsequent analyses. Ten lakes were sampled in 2023, and 13 lakes were sampled in 2024. Sampling occurred between late May and August of both years. Lakes represented the fish biodiversity gradient found in previous surveys (Koelz 1929; Kallemeyn 2000), and lakes and species sampled are presented with abbreviations in Tables S1 and S2. Methods closely mirrored Kallemeyn (2000), with rare exceptions due to logistics, weather, or high catches. Conventional methods included nylon experimental gillnets, minnow traps, and a seine net. Gillnet dimensions were 76.2 × 1.8 m with five equal length panels of 19.1, 25.4, 31.8, 38.1, and 50.8 mm mesh sizes. In four lakes sampled in 2023, three 24.4 × 1.8 m monofilament gillnets with equivalent mesh sizes as the larger nets were used as substitutes for single nylon gillnets. Gee minnow traps were 419 mm long and

229 mm in diameter with a 3.2 mm wire mesh size. The seine was 1.2 × 6.1 m with 6 mm bar mesh. Gillnet sets in each lake were stratified by lake area (Table S3; Kallemeyn 2000). Gillnets were deployed strategically to sample a variety of depths in all lake basins. Trap sets varied with lake area with an average of 1.12 sets/ha (SD = 1.14) and depended on the number of sampling days (Table S3). Traps were baited with dry cat food and set in < 1 m depth around the lakeshore. Trap locations sampled all present habitats, including muck, rock, sand, macrophytes, and woody debris. All gillnets and traps were deployed via canoe. Seining was performed in a variety of habitats, but success was often limited near steep shorelines and woody debris. Seining effort increased with lake area, and at least three hauls were performed at multiple sites around each lake. Additionally, hook and line angling was performed in place of gillnets in Scholts Lake due to shallow depths (Kallemeyn 2000).

All adult and juvenile fish collected were identified and enumerated, and several individuals of each species in each lake were preserved in 70% ethanol to later confirm species identification. When species including trout, lake whitefish, northern pike (*Esox lucius*), walleye (*Sander vitreus*), or larger yellow perch (*Perca flavescens*) were captured, stomach contents of at least five individuals of each species in each lake were physically examined for species, such as sculpins (*Cottus* spp.), not effectively sampled with standard equipment due to low abundance or elusive behaviour. Fish that were alive after identification were released.

It is possible that surveys did not capture all species present while sampling. The terms “gain” and “loss” refer to new species detections or non-detections, respectively, although species may have been present, yet remained undetected due to low abundance or sampling efficiency. Different sampling locations and slight variability in effort among surveys may influence species detections. However, this was necessary given the limited number of surveys and logistics of remote sampling.

2.3 | Lake Characteristic Sampling

Limnological sampling was performed by canoe over the deepest point in each lake during mid-July or early August during 2022–2024. Temperature, dissolved oxygen (DO), pH, and conductivity profiles were measured at 0.5 m or 1 m intervals from surface to bottom using a Eureka MM774 sonde calibrated before each use. Water clarity was measured using a Secchi disk. Water for chlorophyll-*a* and chemistry analyses was collected in 2 L plastic bottles via hand-grab samples just below the surface or integrated samples from the surface down to two meters. Samples were stored on ice during transport to a lab and prepared for analysis within 24 h as follows.

Water was filtered through a 47 mm glass microfiber GF/C filter for chlorophyll-*a* analysis. The filter was frozen and processed via acetone extraction and spectrophotometry. Raw water was refrigerated for alkalinity, chloride, and sulphate analysis and frozen for total phosphorus and total nitrogen analyses. Water was filtered through a 47 mm pall filter and either preserved in sulfuric acid and refrigerated for dissolved organic carbon (DOC) analysis, preserved in nitric acid and refrigerated for silicate and cation analyses, or frozen for nitrate, nitrite, and ammonia analyses. Alkalinity, chloride, sulphate, DOC, silicate, and cations were analysed by CT Laboratories in Baraboo, Wisconsin. Chlorophyll-*a*, nitrogen, and phosphorous were analysed by the St. Croix Watershed Research Station in Marine on St. Croix, Minnesota. Chlorophyll-*a*, nitrate, nitrite, potassium, and chloride were each undetectable in at least one lake and excluded from analyses.

Morphometry data including lake surface area (hereafter area), maximum depth, watershed area, and shoreline development were taken from Kallemeyn (2000). Elevation and isostatic rebound rates were identified from Gorman et al. (2014). We estimated mean hypolimnion DO and temperature using profile data. We characterised the hypolimnion as all depths below the point where temperature declines by more than 1°C over a 1 m depth change. For unstratified lakes, we used values directly above the bottom as a proxy for hypolimnetic values. Five lakes sampled for water quality in 2023 lacked conductivity profiles, so we substituted values for those same lakes from mid-July in 2022. Lake characteristics are displayed in Tables S4 and S5.

2.4 | Objective 1—Temporal Variation in Alpha, Gamma, and Spatial Beta Diversity

For alpha diversity, we used a generalised linear mixed model with a Poisson distribution to evaluate differences in species richness among surveys, with lake as a random effect to account for repeated surveys. A likelihood ratio test was used to

compare this model to a null model including only the lake random effect. Species-area curves were assessed for differences in slope between surveys using linear regression with richness as a response variable and an area*survey interaction. To assess gamma diversity and sampling completeness across lakes, we generated lake-based species accumulation curves using the “iNEXT” package (Hsieh et al. 2016). Raw incidence data (species presence-absence across lakes) were used to calculate Chao2 asymptotic richness estimators and sample coverage for each survey year. Chao2 estimates total richness by incorporating the frequency of species detected in only one or two lakes to extrapolate beyond the observed samples and account for undetected species. Sample coverage is the proportion of the total community represented by observed incidences. Rarefaction and extrapolation were conducted using Hill numbers of order $q=0$ with 50 bootstrap replications to estimate 95% confidence intervals. For spatial beta diversity, presence-absence data were pooled into a matrix with species columns and rows for lake-survey observations, and pairwise Jaccard dissimilarity was calculated for all lake-survey pairs (Jaccard 1908). Non-metric multidimensional scaling (NMDS) was used to ordinate lake-survey observations into two dimensions, and Kruskal’s stress was used to assess fit. We used the metaMDS function in the R package “vegan” (Oksanen et al. 2024) for NMDS with 100 random starts, and convex hulls were plotted around survey groups to visually assess compositional change and homogenization. Convex hulls were also plotted around each lake to assess individual community responses. Species vectors were plotted using the envfit function in “vegan” with 1000 permutations to characterise community shifts. We used the adonis2 function in “vegan” to run PERMANOVA with survey and lake as predictors to determine whether average composition across lakes shifted over time (Anderson and Walsh 2013). If significant differences were detected, the pairwise.adonis2 function in “pairwiseAdonis” (Martinez Arbizu 2020) was used for multiple comparisons tests with Bonferroni corrections. We assessed homogenization using the betadisper function in “vegan” to test whether multivariate dispersion (mean distance to centroid) varied between surveys (Buckley et al. 2021). Spatial beta diversity analyses were repeated on the six largest lakes to explore more subtle shifts.

2.5 | Objective 2—Lake and Species Variation in Temporal Beta Diversity

To examine which of the 23 lakes experienced the greatest compositional change over time, we calculated temporal beta diversity indices (TBI; Legendre 2019) using the TBI function in “adespatial” (Dray et al. 2024). This approach calculates Jaccard dissimilarity between two surveys of a single lake and derives the contributions of losses and gains to TBI. These contributions were plotted as coordinates to visually assess the importance of gains and losses for each lake. Permutational *t*-tests were used to identify lakes showing exceptionally different communities between surveys. A paired permutational *t*-test revealed whether gains or losses dominated across all lakes (Legendre 2019), and results were displayed on TBI plots as lines with a slope of one running through the centroid of coordinates. We used Holm corrections for multiple testing in both analyses. We also explored whether lake factors were associated with TBI, contribution of gains, contribution of losses, or the difference between gain and

loss contributions (hereafter gain-loss difference, calculated as gain contribution minus loss contribution). Gain-loss difference represents a gradient from lakes in which losses caused the greatest TBI to lakes in which gains caused the greatest TBI. We used the `rpart` function in “`rpart`” (Therneau et al. 2025) to identify regression trees with each of these four variables as a response in separate models and lake factors as predictors. Because only 23 lakes were sampled, initial model parameters required 3 observations in each terminal node with at least 6 observations and 1% additional explained variability to allow a bifurcation. We used “leave one out” cross validation to assess model fit. We pruned each tree by selecting the simplest tree within one standard error of the split with the lowest cross-validation error, although more complicated trees were explored if errors were similar (De'ath and Fabricius 2000). We considered 21 lake characteristics including area, maximum depth, geometry ratio (fourth root of area/maximum depth), watershed area, area: watershed area, elevation, isostatic rebound rate, shoreline development, total phosphorus, total nitrogen, magnesium, sodium, sulphate, silicate, alkalinity, DOC, Secchi depth, mean hypolimnetic DO, mean hypolimnetic temperature, and mean water column pH and conductivity. Area, maximum depth, and watershed area were $\log_{10}$ -transformed.

We explored which species changed most using three approaches. We ran similarity percentage (SIMPER) analysis in “`vegan`” with Jaccard dissimilarity to determine which species contributed most to differences between surveys. We used the `tpaired.krandtest` function in the “`adespatial`” package for permutational paired *t*-tests with Holm corrections to assess for which species presence changed significantly between surveys. Finally, we quantified frequencies of gains and losses by species thermal guilds outlined in Gorman et al. (2014). Thermal guilds were based on species temperature preferences and distributions throughout North America. All TBI analyses were performed for each survey pair (1920s–1990s, 1990s–2020s, and 1920s–2020s).

2.6 | Objective 3—Environmental Drivers of Current Spatial Beta Diversity

To assess spatial variation in current community composition and explore environmental drivers, we used Jaccard dissimilarities from the 2020s survey to ordinate communities into two dimensions with NMDS. We plotted either species or environmental vectors over the ordination and assessed correlations using the `envfit` function in “`vegan`” with 1000 permutations. We eliminated seven correlated lake factors ($r > 0.70$) and standardised the 14 remaining prior to plotting environmental vectors. All analyses were performed in R version 4.4.2. Statistical tests were considered significant at $p < 0.05$.

3 | Results

3.1 | Objective 1—Temporal Variation in Alpha, Gamma, and Spatial Beta Diversity

Thirty fish species were detected across all surveys. Yellow perch and northern pike were the most widely distributed species, while 25 other species were detected in five or fewer lakes

in the 2020s. We captured 2684 individuals in gillnets and 1279 individuals in minnow traps across both years of the recent survey. We identified 8379 individuals from seining in 2024, while total counts were not recorded in 2023 due to time constraints. Nine individuals were angled in Scholts Lake. There were five incidences of species detected only via stomach content analysis across lakes, including pearl dace (*Margariscus nachtriebi*) from Lake Desor, spottail shiner (*Notropis hudsonius*) from Lake Whittlesey, slimy sculpin (*Cottus cognatus*) from Sargent Lake, and both cisco and slimy sculpin from Siskiwit Lake. The range of richness across lakes varied from 1 to 16 species in the 1920s to 2–13 species in the 2020s.

Alpha, gamma, and spatial beta diversity generally remained stable but showed subtle shifts in the last century. Mean species richness declined from 5.48 (SD = 3.76) species in both the 1920s and 1990s to 5.17 (SD = 3.05) species in the 2020s, although no significant differences were detected between surveys based on the likelihood ratio test ($\chi^2_{(df=2)} = 0.266$, $p = 0.876$). Species-area curves showed the interaction between area and survey was non-significant ($F_{2,63} = 0.362$, $p = 0.698$), although the slope declined slightly from 0.327 in the first survey to 0.263 more recently (Figure 2).

Observed gamma diversity remained relatively stable, as total species richness was 28 in the 1920s and 1990s and 27 in the 2020s. Spoonhead sculpin (*Cottus ricei*) was the only species detected the 1920s and 1990s that went undetected in the 2020s (Table 1). The 1990s survey failed to detect two species (brook trout (*Salvelinus fontinalis*), mottled sculpin (*Cottus bairdii*)) from the 1920s survey but found two additional species (blackchin shiner (*Notropis heterodon*), northern redbelly dace (*Chrosomus eos*)) (Table 1). Asymptotic richness estimates (with 95% confidence intervals) were 34.1 (28.0–49.6), 31.3 (28.0–41.5), and 30.4 (27.0–46.9) for the 1920s, 1990s, and 2020s

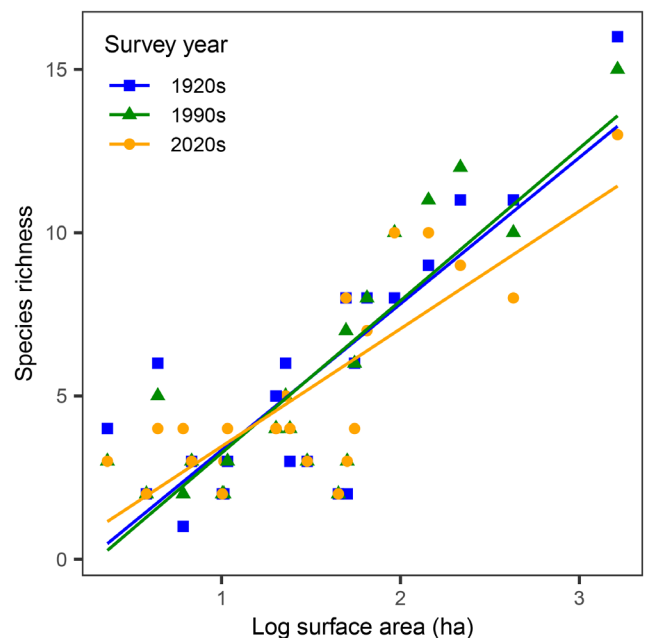


FIGURE 2 | Species-area curves for three fish surveys conducted on 23 inland lakes on Isle Royale, MI in the 1920s, 1990s and 2020s.

TABLE 1 | Fish species composition of 23 inland lakes sampled in the 1920s, 1990s and 2020s on Isle Royale, MI. Numbers indicate the survey(s) during which each species was detected (1920s = 1, 1990s = 2, 2020s = 3), and no change (NC) indicates the species was present in all three surveys. Lake codes are presented in Table S1.

Species	AHM	AMY	ANG	BEA	BEN	CHI	DES	DUS	FOR	GEO	HAR	HAT	LES	LIV	MAS	OTT	PAT	RIC	SAR	SCH	SIS	WAG	WHI
Cisco							NC											NC	NC		NC		
Lake whitefish							NC														NC		
Brook trout							1					1											
Lake trout																							
Northern pike	NC	NC	NC	NC		NC		NC		NC			NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	
Lake chub							NC																
Pearl dace							NC		NC		1/2	NC											
Golden shiner				NC		3									NC	1		NC	NC				
Emerald shiner																					NC		
Blackchin shiner						2/3													2/3			3	
Blacknose shiner				NC	NC	2/3		NC	NC		NC			NC	NC	NC		NC	NC	NC		2/3	
Spottail shiner		NC		1		NC		3								NC		NC	1/2		NC	NC	
Mimic shiner																		NC					
Northern redbelly dace						2/3	2					2/3											
Finescale dace					NC																		
Fathead minnow											NC	NC											
Creek chub												NC											
White sucker	3		2/3			1/2	NC	1/2			NC	NC						NC	NC	1	NC	NC	
Trout-perch							NC					NC						1/2			NC	1/2	
Burbot																					NC		
Brook stickleback					2/3		NC				1/2	NC						2			1		

(Continues)

TABLE 1 | (Continued)

Species	AHM	AMY	ANG	BEA	BEN	CHI	DES	DUS	FOR	GEO	HAR	HAT	LES	LIV	MAS	OTT	PAT	RIC	SAR	SCH	SIS	WAG	WHI
Ninespine stickleback							NC					1/3									1/2		
Pumpkinseed						2/3								NC				NC	2/3				3
Iowa darter		3				NC													NC				
Yellow perch	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	2/3	NC
Logperch								1															NC
Walleye						NC		1/2													NC		NC
Mottled sculpin						1																	NC
Slimy sculpin						1	1							1				1/2	NC		NC		
Spoonhead sculpin							1/2														1/2		1

surveys, respectively (Figure S1). Sample coverage ranged from 94.0% to 94.9% across surveys (Figure S1).

For spatial beta diversity, ordination of the three surveys (Kruskal's stress = 0.111) showed wide variability among all lakes and large overlap of survey convex hulls (Figure 3). No significant shifts in overall composition were detected between surveys when controlling for between-lake variability (Pseudo- $F_{2,44} = 1.488$, $p = 0.113$). No differences in dispersion were detected between surveys (betadisper, $F_{2,66} = 0.201$, $p = 0.819$). We repeated these analyses on the six largest lakes to detect more subtle community shifts. NMDS on this subset of lakes (Kruskal's stress = 0.071) showed a shift in the position of convex hulls between surveys (Figure 4A). Centroids shifted toward blackchin shiner, blacknose shiner (*Notropis heterolepis*), golden shiner (*Notemigonus crysoleucas*), and pumpkinseed (*Lepomis gibbosus*), which were all gained in at least one lake. Centroids shifted away from mottled sculpin, spoonhead sculpin, and trout-perch (*Percopsis omiscomaycus*), which were all lost from at least one lake (Table 1). PERMANOVA indicated differences in composition between surveys (Pseudo- $F_{2,10} = 3.090$, $p = 0.014$), and post hoc tests indicated significant differences between all three surveys after controlling for between-lake variability (all $p < 0.007$). Dispersion did not vary between surveys for these six lakes (betadisper, $F_{2,15} = 0.0963$, $p = 0.909$). Plotting convex hulls around lakes also showed relatively consistent directional shifts from cold-water species to cool-water species between surveys (Figure 4B).

3.2 | Objective 2—Lake and Species Variation in Temporal Beta Diversity

TBI analyses indicated three lakes experienced relatively greater change than others. Wagejo, Chickenbone, and Dustin lakes showed mean TBI values of 0.583, 0.432, and 0.413, respectively, while remaining TBIs ranged from zero in five lakes to 0.241 in Lake Desor across all time periods (Table S6). However, permutational t -tests indicated no lake experienced extreme change compared to others after correcting for multiple comparisons (all $p > 0.1$). Mean TBI was 0.161 from 1920s to 1990s, 0.131 from 1990s to 2020s, and 0.249 across the entire study. Neither gains nor losses were dominant during any period (all $p > 0.7$). The largest difference occurred from the 1920s to 1990s, where gains contributed 53.7% and losses contributed 46.3%. Regression trees detected few relationships among TBI, contributions of gains and losses, gain-loss difference, and lake factors. The strongest model for 1920s–2020s predicted gain-loss difference with a split in rebound rate (> 0.845 m/100 years). Fast-rebounding lakes tended to gain species, while slow-rebounding lakes tended to lose species (Figure 5A). Linear regression showed a moderately strong positive relationship between gain-loss difference and rebound rate ($R^2 = 0.320$, $p = 0.005$). Regression trees for 1920s to 1990s indicated null models were strongest, but predicting gain-loss difference with three splits resulted in similar cross-validation error to the corresponding null model (1.093 vs. 1.187) and explained a large portion of variability ($R^2 = 0.803$). An initial split occurred at a rebound rate (> 0.845 m/100 years), plus one split at watershed area (> 50.2 ha) in lakes with faster rebound

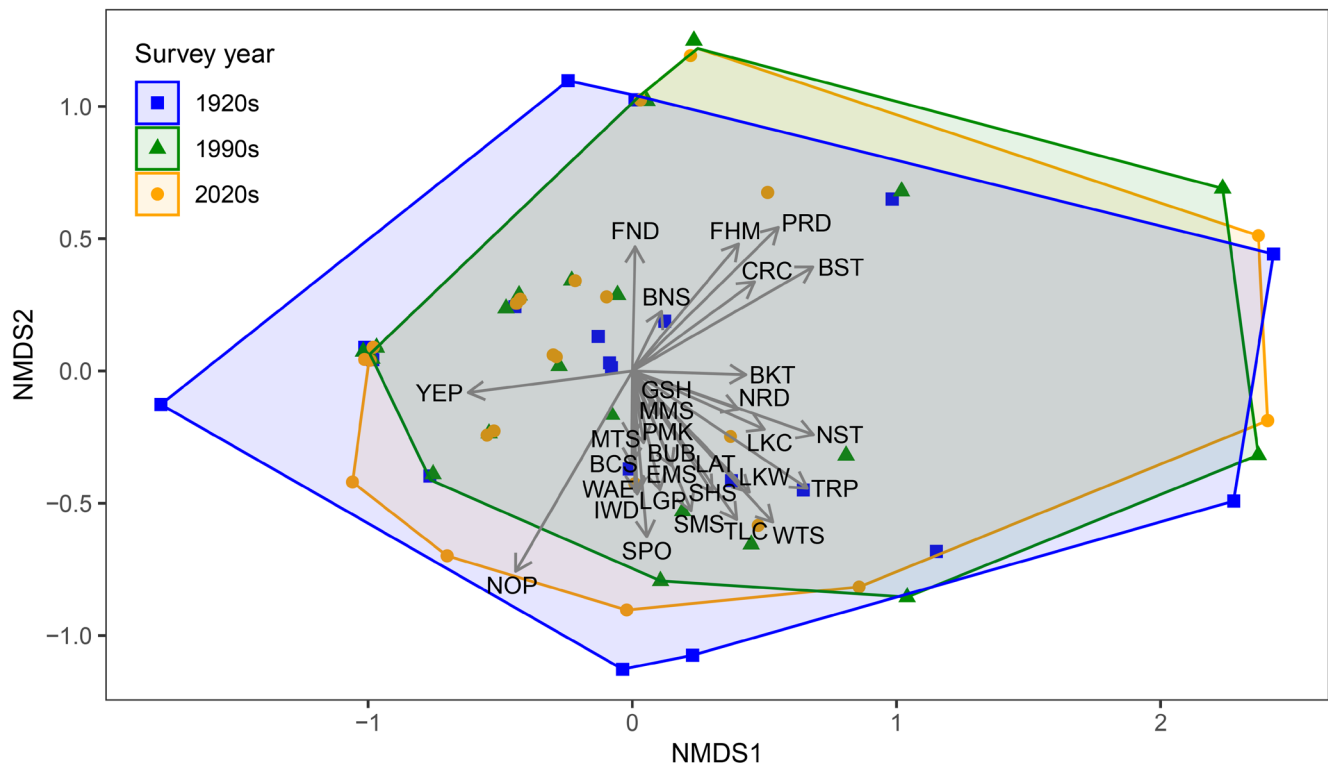


FIGURE 3 | NMDS ordination of fish species composition using Jaccard dissimilarity between 23 inland lakes sampled in the 1920s, 1990s and 2020s on Isle Royale, MI (Kruskal's stress=0.111). Convex hulls are plotted around all lakes for each survey. Species vectors are plotted over the convex hulls and species codes are presented in Table S2.

and one split at Secchi depth (> 2.45 m) in lakes with slower rebound (Figure 5B). Regression trees for 1990s–2020s revealed two relationships. Predicting gain-loss difference with one split by DOC (< 7.4 mg/L) was within 1 SE of the null model. Linear regression showed a positive relationship between DOC and gain-loss difference ($p=0.009$), indicating gains were more prevalent in high DOC lakes (Figure 5C). Predicting TBI with a split by shoreline development (> 1.75 units) showed lakes with less shoreline development had greater change during this period.

SIMPER indicated that species contributing most to differences between surveys in the six largest lakes were slimy sculpin, trout-perch, blacknose shiner, and pumpkinseed, although no species was dominant in its contribution (all $< 7\%$, Table S7). Permutational paired t -tests indicated that no species shifted significantly between any surveys, although slimy sculpin was the closest ($p=0.07$) between the 1920s and 2020s. Gains and losses varied by species thermal guild between the 1920s and 2020s (Table S8). On average, each cold-water species experienced 1.3 losses and 0.1 gains, each cool-water species experienced 0.6 losses and 1.5 gains, and each thermally-tolerant species experienced 0.8 losses and 0.3 gains.

3.3 | Objective 3—Environmental Drivers of Current Spatial Beta Diversity

NMDS of current communities showed several types of fish communities associated with environmental gradients

(Tables S9 and S10; Figure 6A,B). The simplest communities contained only northern pike and yellow perch (George, Lesage, Patterson), and occasionally one additional species like white sucker (*Catostomus commersonii*) (Ahmik, Angleworm) or blacknose shiner (Livermore, Scholts). Some lakes included at least two species in addition to northern pike and yellow perch, including blacknose shiner, blackchin shiner, spottail shiner, golden shiner, pumpkinseed, and Iowa darter (*Etheostoma exile*) (Amygdaloid, Beaver, Dustin, Mason, Otter, Wagejo). The most diverse lakes contained northern pike and yellow perch plus several minnows (Chickenbone, Whittlesey) and cold-water species including cisco or slimy sculpin (Siskiwit, Richie, Sargent). Lakes lacking northern pike but containing yellow perch and least one other species grouped together (Benson, Forbes, Harvey). However, lakes lacking both yellow perch and northern pike but hosting rare species like trout-perch, ninespine stickleback (*Pungitius pungitius*), lake chub (*Couesius plumbeus*), and creek chub (*Semotilus atromaculatus*) were the most extreme (Desor, Hatchet). Plotting environmental vectors showed several significant gradients (Table S10; Figure 6A). Communities with northern pike and yellow perch transitioned to those without both species along an increasing elevational gradient. Simple communities with fewer than five species transitioned to more diverse communities with up to 13 species with increasing area and decreasing hypolimnetic temperature and rebound rate.

4 | Discussion

Overall, this study highlights how fish communities relatively isolated from anthropogenic impacts have shifted over time in

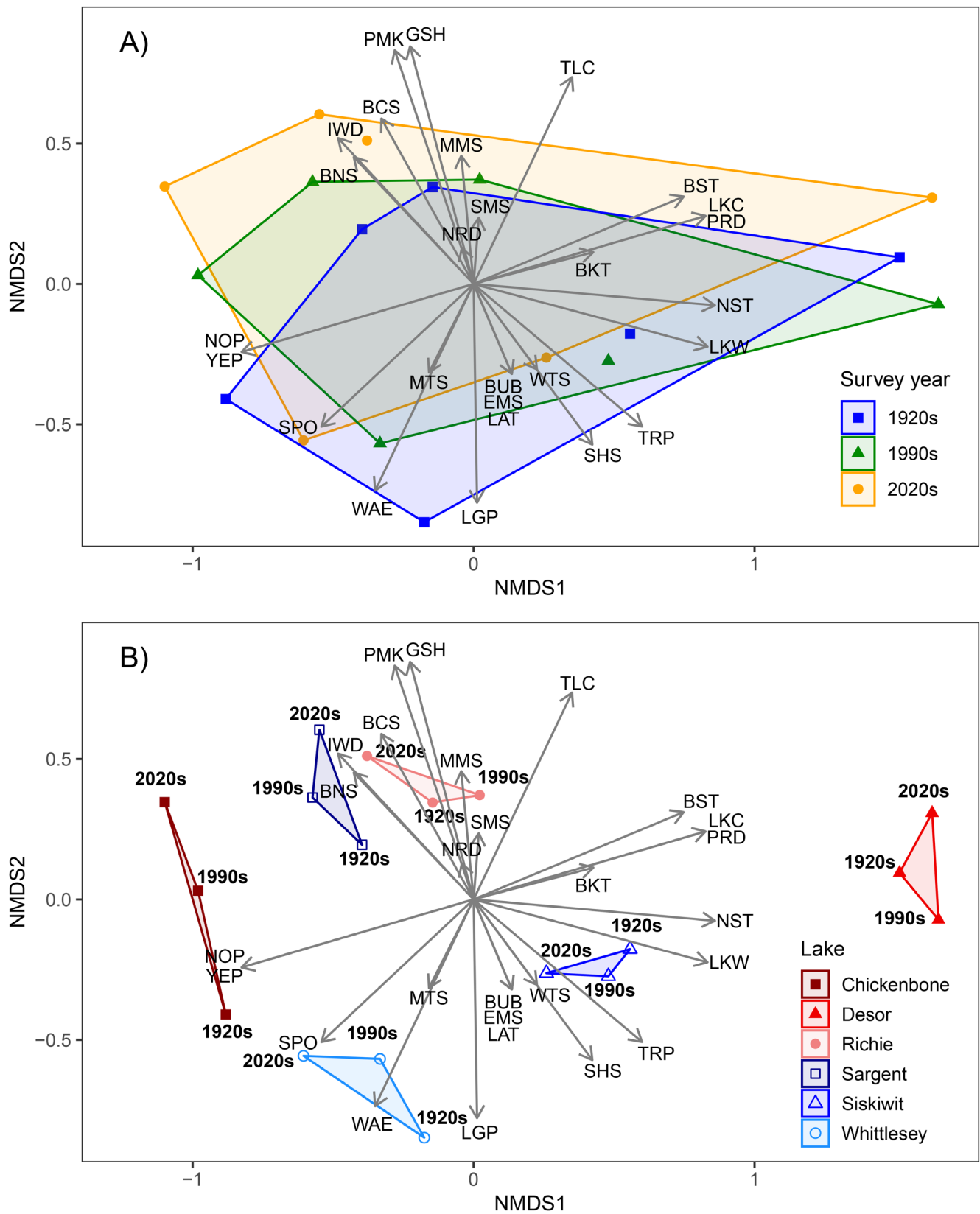


FIGURE 4 | NMDS ordination of fish species composition using Jaccard dissimilarity between the six largest lakes sampled in the 1920s, 1990s and 2020s on Isle Royale, MI (Kruskal's stress = 0.071). Convex hulls group communities by (A) survey showing shifts in average composition across all six lakes and (B) lakes showing directional change of each fish community over time with survey decades noted in bold. Species vectors are plotted over the convex hulls and species codes are presented in Table S2.

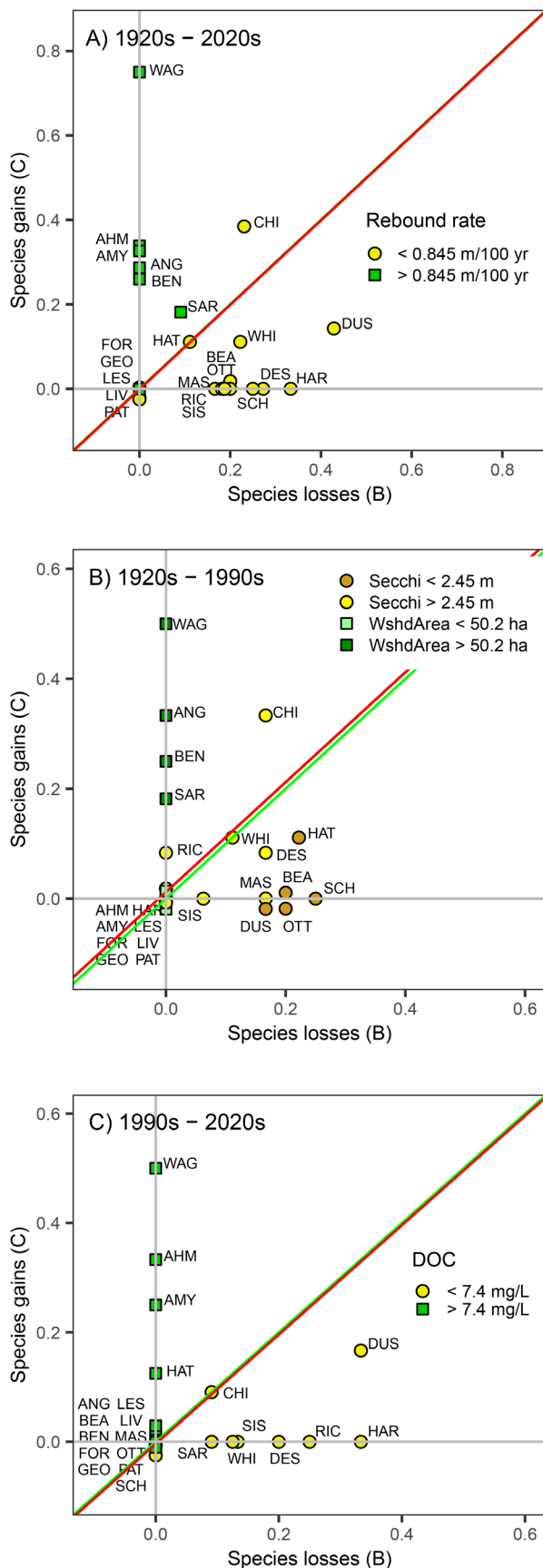


FIGURE 5 | Contribution of fish species gains and losses to temporal beta diversity in 23 inland lakes on Isle Royale, MI from (A) 1920s to 2020s (B) 1920s to 1990s and (C) 1990s to 2020s. Each point represents one lake and symbols represent lake groups based on top variables from regression tree results. For 1920s to 2020s isostatic rebound rate was the only split. For 1920s to 1990s lakes with isostatic rebound rates faster and slower than 0.845 m/100 years are shown as squares and circles respectively with subsequent splits by watershed area in lakes with fast rebound and by Secchi depth in lakes with slow rebound. For 1990s to 2020s dissolved organic carbon (DOC) was the only split. One to one lines are shown in green and the parallel red lines and run through the centroid of all points in each plot. Lake codes are presented in Table S1.

composition remained relatively stable, with non-significant declines in richness, shifts from cold-water to cool-water species in larger lakes, and no homogenization. TBI analyses indicated no lake or species changed exceptionally, although gains and losses were related to lake characteristics and thermal guild. Area and elevation explained gradients in richness and predator presence, respectively, while isostatic rebound informed gains and losses. These findings serve as a useful reference for spatial and temporal fish community trends in more impacted regions.

4.1 | Objective 1—Temporal Variation in Alpha, Gamma, and Spatial Beta Diversity

Gamma diversity remained mostly stable over the past century, and asymptotic richness estimates showed minor variability among surveys. This consistency, combined with high sample coverage, supports the reliability of richness estimates and suggests the observed trends more likely reflect long-term ecological patterns rather than sampling differences. Our hypothesis for declining richness was generally unsupported, as alpha diversity remained constant, and gamma diversity declined by one species across Isle Royale's inland lakes in the past century. This contrasts with Minnesota and Canadian lakes, where richness has generally increased in recent decades due to human-assisted migration (Radomski and Goeman 1995; Cazelles et al. 2019) and faster range expansions than contractions with lake warming (Wu et al. 2023). Our results suggest Isle Royale's lakes have maintained remarkably stable richness, likely due to buffered habitat and isolation. However, subtle declines in certain lakes may indicate early stages of change observed elsewhere. Species-area slopes declined slightly but non-significantly, providing marginal evidence that gains and losses were more common in small and large lakes, respectively. However, lack of colonisation by species new to Isle Royale and losses of three species in each of the two largest lakes likely contributed to the declining slope. Thermally-sensitive species are limited to the larger lakes, increasing the likelihood of losses relative to smaller lakes containing more tolerant species. The range of richness across lakes also contracted during the study, suggesting steady richness may be driven by variable shifts along a lake size gradient. Cazelles et al. (2019) found small lakes tend to gain more species than larger lakes, and our

response to lake characteristics, geological processes, and potential environmental change, all important steps for understanding broader biodiversity trends. We found richness and

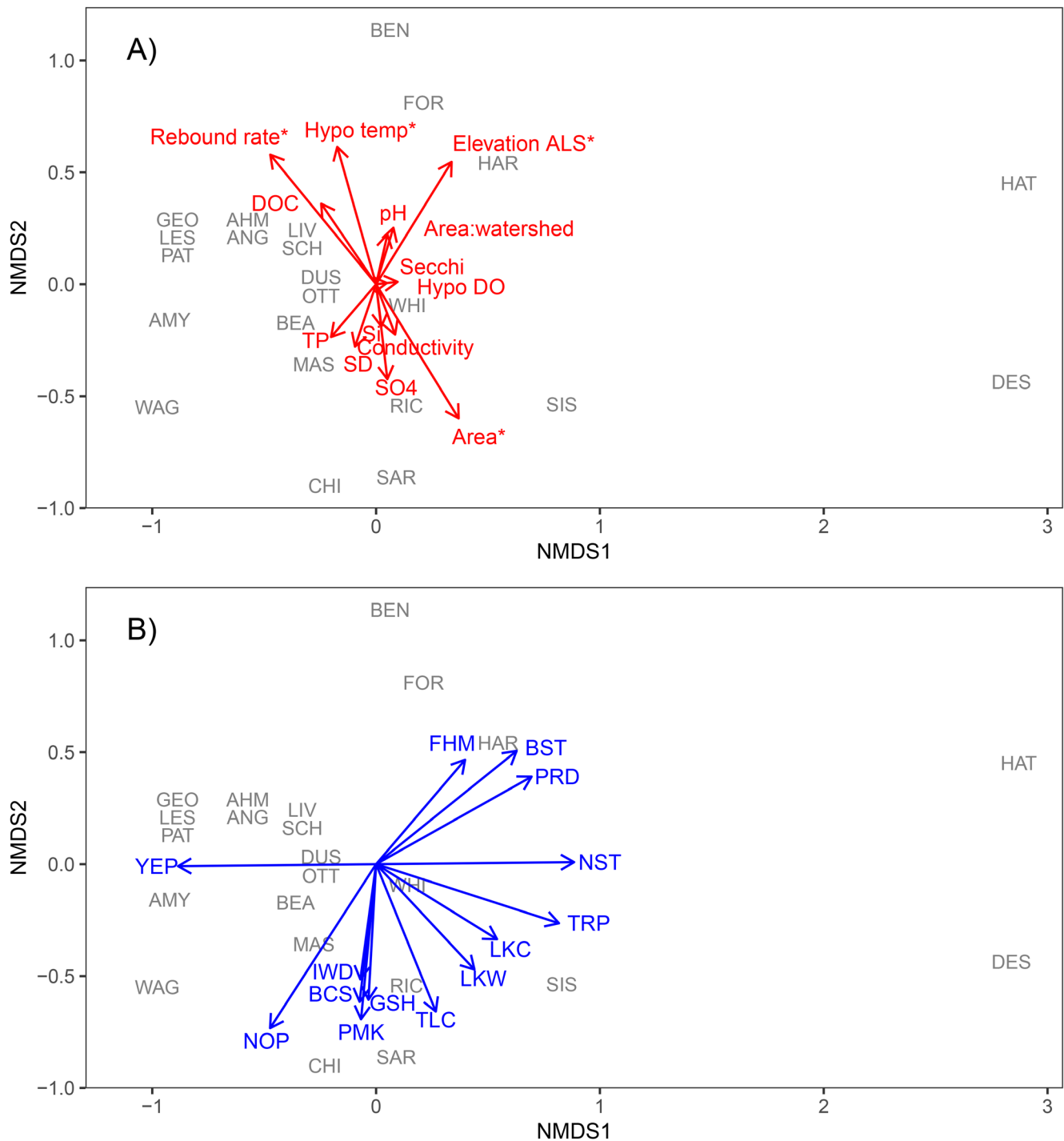


FIGURE 6 | NMDS ordination of fish species composition using Jaccard dissimilarity between 23 inland lakes on Isle Royale, MI based on the 2020s survey. (A) Environmental vectors include surface area to watershed ratio shoreline development (SD) rebound rate elevation above Lake Superior (ALS) dissolved organic carbon (DOC) total phosphorus (TP) sulphate (SO₄) silicate (Si) mean pH Secchi depth mean hypolimnetic dissolved oxygen (DO) mean hypolimnetic temperature and mean specific conductivity. Asterisks for environmental factors indicate a significant correlation with the overall ordination. (B) Species vectors show only those with a significant correlation with the ordination. Lake and species abbreviations are shown in Tables S1 and S2.

results may suggest a similar, although more subtle pattern, is occurring on Isle Royale.

Our hypotheses of shifts toward cool-water species and homogenization were mostly unsupported, as spatial beta diversity remained constant across all lakes, with no evidence for

compositional change or homogenization. Wide variability in composition and richness among lakes likely obscured patterns at this broader scale. Most lakes on Isle Royale are small and contain only cool-water or thermally tolerant species, which are less sensitive to environmental change than cold-water species (Kallameyn 2000). Historical communities of

small lakes were likely filtered down to their present structure before the study period, which may explain the lack of change we observed. However, analysing only the largest, most diverse lakes revealed shifts from cold-water to cool-water species in the past century. These findings indicate immigration and extinction altered the general composition of Isle Royale's larger lakes but not variability among them, lending partial support to our hypothesized shifts toward cool-water species. There are a few plausible explanations for these patterns. First, suitable oxy-thermal habitat is decreasing in some lakes that have historically hosted cold-water species (Damstra et al. 2014; Xu et al. 2024), likely causing extirpation for species including sculpins, trout-perch, ninespine stickleback, and brook trout. It is unclear whether losses were driven by lack of suitable habitat or sampling deficiency as other cold-water species including cisco, lake whitefish, and lake trout were detected in some lakes where losses occurred. However, extirpation is certainly reasonable given that mid-summer profiles usually indicate some level of stress in non-refuge lakes (Gorman et al. 2014). Second, cool-water habitat is expanding within the inland lakes of Isle Royale at the expense of cold-water habitat given warming water temperatures (Xu et al. 2024). Increased precipitation may create more persistent stream connections and facilitate immigration (Magnuson et al. 1998; Climate Change Response Program 2024), and losses of cold-water species could promote colonisation via reduced competition (Cornell and Lawton 1992). Gains from 1920s to 1990s could generally be attributed to stream dispersal (Kallemeyn 2000), and the same holds for the recent survey as gains occurred in lakes with close proximity to more diverse waterbodies, including both inland lakes and Lake Superior. Wide variability in gains among lakes likely prevented homogenization despite common losses of sculpin species. No species colonised more than two of the six largest lakes, and total gains varied from zero in Siskiwit to five in Chickenbone. Although both lakes have low elevation and direct stream outlets to Lake Superior, the Siskiwit outlet contains barrier falls limiting immigration, while the Chickenbone outlet is more gradual. Overall, these findings suggest that isolated fish communities can exhibit considerable stability with only subtle shifts over a century. This strongly contrasts with more disturbed regions, where homogenization and species turnover are more common (Cazelles et al. 2019; Haubrock et al. 2021; Liang et al. 2024).

4.2 | Objective 2—Lake and Species Variation in Temporal Beta Diversity

Analysis of species contributions over time further supported the pattern of compositional change without homogenization. No species was dominant in its contribution to change, implying the shift toward cool-water communities in larger lakes was driven by multiple species. Both cool-water and cold-water species were among those with the largest contributions, suggesting both thermal guilds drove compositional change. Cold-water species were most commonly lost, and cool-water species were most commonly gained across all lakes. These opposite but relatively balanced trends highlight how general community composition shifted but did not homogenise, providing additional support for our hypotheses of shifts toward cool-water species. These results align with past

research highlighting the general northward range expansions and contractions of cool-water and cold-water species, respectively (Comte et al. 2013).

Although we hypothesized losses would be the main driver of temporal beta diversity, we found a balance between gain and loss contributions, further supporting the lack of homogenization. Despite several gains and losses in multiple lakes, TBI showed no lake experienced significantly greater change than others. We hypothesized losses of oxy-thermal habitat would drive temporal beta diversity, but our results suggest high stream connectivity, disturbance events such as winter-kill, and reduced biotic interactions explain why three lakes showed noticeably higher magnitudes of change (Magnuson et al. 1998; Rolls et al. 2023). A stream connection to a more diverse waterbody is present in all three lakes, likely facilitating immigration. Given relatively shallow depths, winter-kill may reduce fish abundances and allow colonisation via reduced competition and predation (Henriksson et al. 2015). Low or declining northern pike, walleye, and yellow perch abundances were documented coinciding with colonisation by small-bodied species (data not shown). Two of these lakes also lost at least three species in the last century, suggesting opening of niche space may facilitate immigration (Cornell and Lawton 1992).

Several environmental factors explained spatial patterns in temporal beta diversity. Gains were more prevalent in lakes with faster isostatic rebound, while losses were more common with slower rebound. Previous research has addressed the role of isostatic rebound in determining historical species richness (Hubbs and Lagler 1949; Stephenson and Momot 1994), but no studies have found associations with recent community trends. Differences in species saturation is one explanation, as mean richness shifted from 3.1 to 4.1 and from 6.7 to 5.7 in lakes with fast and slow rebound rates, respectively. Lakes with slower rebound may have initially experienced more colonisation given longer exposure to the source pool during water decline and lake formation (Hinch et al. 1991; Stephenson and Momot 1994; Illyes et al. 2023). Higher richness may have subsequently limited future immigration success (Stachowicz and Byrnes 2006). Competition and predation are generally more intense in diverse communities (Cornell and Lawton 1992), which reduces available niche space and species establishment even with stream connections. Recent introductions to Lake Superior combined with stable or declining alpha diversity in our study lakes also provides evidence of saturation (Tonn et al. 1990), which may explain why extinction is dominant in lakes with slower rebound. In contrast, limited dispersal opportunity to lakes with faster isostatic rebound may have created historically species-poor communities. Low richness can indicate available niche space and facilitate establishment if dispersal becomes possible (Henriksson et al. 2015), explaining why gains were more common with faster isostatic rebound. However, there are several caveats to this explanation. We cannot explicitly quantify the degree of species saturation, available niche space, or specific filters limiting richness (Mateo et al. 2017; Olivares et al. 2018). Isle Royale's lakes are generally unproductive and host depauperate communities. Low connectivity, however, likely prevented recent introductions from Lake Superior to undersaturated

lakes (Gorman et al. 2014). The strength of biotic interactions is also unclear, although predatory northern pike are common and reduce colonisation success (Tonn et al. 1990; Henriksson et al. 2015). Niche opportunity also affects colonisation (Shea and Chesson 2002), which varies widely with habitat complexity. Consequently, although there is evidence that saturation differences are driving gains and losses, additional work is needed to explore these mechanisms.

Several lake characteristics were related to temporal beta diversity over shorter time scales. From the 1920s to 1990s, lakes with both faster rebound rates and larger watersheds experienced more gains. One possible explanation is larger watersheds have larger, more persistent stream outlets to facilitate fish movement, but we did not test this directly. For lakes with slower rebound rates, those with lower water clarity experienced more losses. Low water clarity is mainly driven by high DOC on Isle Royale, which can correspond to low primary production, pH, and macrophyte cover (Erlandsson et al. 2010; Stasko et al. 2012). These conditions may be intolerable for certain species, although Matuszek et al. (1990) found pH thresholds of lost species were well-below levels measured in our study lakes. Interestingly, the opposite pattern was detected between the 1990s and 2020s during which gains contributed more to TBI at higher DOC concentrations. One potential explanation is that pH-tolerant species were responsible for gains in high DOC lakes, while pH-sensitive species were responsible for losses, although this remains unclear. DOC indirectly affects thermal, oxygen, and optical habitat in many ways that may be both beneficial and harmful (Stasko et al. 2012), which likely contributes to the conflicting patterns we observed. We also observed a negative relationship between TBI and shoreline development from the 1990s to 2020s. Convolutioned shorelines may provide predation refuge and habitat variability that buffers environmental changes and biotic interactions, explaining why less change was detected in complex lakes.

4.3 | Objective 3—Environmental Drivers of Current Spatial Beta Diversity

Our results support our hypothesis that multiple environmental gradients drive current community structure. Lake area was positively associated with richness, and most species showed limited distributions to only the largest, deepest lakes with cold, oxygenated hypolimnions. These species included not only cold-water species such as cisco, lake whitefish, lake trout, and lake chub but also cool-water and thermally tolerant species such as pumpkinseed, blackchin shiner, and golden shiner. Greater complexity in larger lakes reduces extinction rates (Eadie et al. 1986; Minns 1989), particularly through more substrate types, macrophyte cover, and oxy-thermal habitat that reduces the intensity of biotic interactions. Predator presence also shifted with elevation. Five of the six highest lakes lacked northern pike, and two of these also lacked yellow perch. High elevation is a common dispersal barrier and indicates earlier lake formation (Minns 1989; Gorman et al. 2014; Illyes et al. 2023), suggesting northern pike and potentially yellow perch were absent from the initial pool of colonisers. Both species have cool-water preferences, and cold conditions may have prevented early dispersal

from glacial refuge through Lake Superior (Gorman et al. 2014). Some higher elevation lakes also hold cold-water species that were early migrants like ninespine stickleback, lake chub, and trout-perch, further indicating thermal tolerance precluded early colonisation by northern pike. These lakes also host rarer small-bodied species including pearl dace, brook stickleback (*Culaea inconstans*), and fathead minnow (*Pimephales promelas*) due to lack of predation (Jackson et al. 2001). Taken together, these spatial gradients demonstrate how large-scale filters driving immigration can ultimately determine the importance of small-scale filters driving extinction.

5 | Conclusion

Overall, this study highlights stability in the fish communities of Isle Royale's inland lakes over the past century, likely owing to isolation from direct anthropogenic pressures. Despite ongoing environmental change, richness remained relatively constant, and communities have not homogenised across lakes. However, subtle compositional changes including gains of cool-water species and losses of cold-water species in larger lakes suggest that environmental shifts and filtering are still impacting fish communities in measurable ways. These patterns were associated with natural environmental gradients such as lake area, elevation, and isostatic rebound, indicating that even with minimal anthropogenic influence, long-term geological and environmental processes continue to shape fish community trends. By documenting these patterns in a relatively pristine setting, this study provides a long-term baseline for understanding the mechanisms of natural fish community assembly, an important step for interpreting change in more impacted ecosystems.

Author Contributions

Conceptualization: D.J.G., M.C.R., J.D.G., S.A.M., T.R.H. Developing methods: D.J.G., M.C.R., J.D.G., S.A.M., T.R.H., C.E.L., D.K.B. Data analysis: D.J.G., T.R.H. Preparation of figures and tables: D.J.G., T.R.H. Conducting the research, data interpretation, writing: D.J.G., M.C.R., J.D.G., S.A.M., C.E.L., D.K.B., T.R.H.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.h44j0zpvz>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Lake names and abbreviations for 23 inland study lakes on Isle Royale, MI. **Table S2:** Common and scientific names with abbreviations for 30 fish species historically found in the inland lakes of Isle Royale, MI. **Table S3:** Gear effort with average deployment times (standard deviation) in hours during the 2020s survey of 23 inland lakes on Isle Royale, MI. One set indicates one night spent sampling. Effort was stratified based on lake area and nights spent at each lake. Asterisks for gillnets indicate reduced effort compared to Kallemeyn 2000. Four of 12 gillnets and 12 of 36 traps were deployed for two nights in Siskiwit Lake due to weather. Angling was used in place of gillnets in Scholts Lake, and NA indicates deployment times were not available. **Table S4:** Water quality variables for 23 inland lakes on Isle Royale, MI sampled between mid-July and early-August of 2023 or 2024. Asterisks indicate the value was below the level of quantification, and non-detections are listed as ND. **Table S5:** Characteristics of 23 inland lakes on Isle Royale, MI. Area, elevation above Lake Superior (ALS), isostatic rebound rate, watershed area, shoreline development (SD), depth, and geometry ratio (GR) are from Gorman et al. (2014). Epilimnion and hypolimnion temperature, dissolved oxygen (DO), mean water column pH, and specific conductivity (EC) were measured between mid-July and early-August of 2022, 2023, or 2024. **Table S6:** Temporal beta diversity of fish communities in 23 inland lakes between the 1920s, 1990s, and 2020s on Isle Royale, MI. Jaccard dissimilarity

was calculated between each pair of surveys for each lake. Zeros indicate no change in species composition between surveys, while values closer to one indicate greater dissimilarity. **Table S7:** Similarity percentage (SIMPER) results based on Jaccard dissimilarity showing the contribution of each fish species to differences in community composition of the six largest lakes on Isle Royale, MI between each pair of surveys. Species contributions for each survey pair are sorted in descending order. **Table S8:** Thermal classes of 30 fish species historically found in the inland lakes of Isle Royale, MI with total gains and losses based on surveys in the 1920s, 1990s, and 2020s. Classes are based on Gorman et al. (2014). Mottled sculpin was classified as a cool-warm species but included in the thermally tolerant group for analyses. **Table S9:** Global correlations (r) and p -values for each species with the NMDS ordination of 23 inland lakes on Isle Royale, MI based on the 2020s survey. Jaccard dissimilarities were calculated between all lake pairs using species presence data for the ordination. Values were calculated by the `envfit` function in the R package *vegan*. **Table S10:** Global correlations (r) and p -values for each lake characteristic with the NMDS ordination of 23 inland lakes on Isle Royale, MI based on the 2020s survey. Jaccard dissimilarities were calculated between all lake pairs using species presence data for the ordination. Values were calculated by the `envfit` function in the R package *vegan*. **Figure S1:** Species accumulation curves for fish surveys conducted in the 1920s, 1990s, and 2020s on Isle Royale, MI, showing (A) total species richness and (B) sample coverage as a function of the number of lakes sampled. Asymptotic richness estimates (with 95% confidence intervals) were 34.1 (28.0–49.6), 31.3 (28.0–41.5), and 30.4 (27.0–46.9) for the 1920s, 1990s, and 2020s surveys, respectively. Sample coverage ranged from 94.0% to 94.9% across surveys.