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Temporal Patterns and Drivers of Freshwater Fish Beta-Diversity of Gravel Pit Lakes

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ABSTRACT

Freshwater ecosystems are in the midst of a biodiversity crisis marked by non-random and often dramatic shifts in fish community composition. Yet, the patterns and underlying ecological drivers of these community dynamics within gravel pit lakes—widespread artificial lakes with significant socioeconomic and ecological value—remain understudied. This study examines patterns and drivers of beta-diversity of fish communities across 16 gravel pit lakes in southwestern France over 10 years. Our results unveiled strong shifts in fish community composition, with lake maturity (older and more productive) emerging as the main driver. Immature lakes experienced substantial species turnover over one decade, harbouring more unique fish communities, whereas mature lakes showed little change, contributing less to overall beta-diversity. Highly invaded lakes displayed higher levels of species nestedness than species turnover compared with uninvaded lakes. The contributions of native and non-native species to beta-diversity remained relatively constant on average over the study period, although with some notable exceptions. Non-native species such as common carp (*Cyprinus carpio*) and Wels catfish (*Silurus glanis*) had increasing contributions to beta-diversity, whereas native European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) were increasingly more common (i.e., widespread) despite declining biomass when present. A number of abiotic and biotic factors likely contributed to the diversity patterns observed. Eutrophication is associated with increasing turbidity and hypoxia/anoxia, promoting the dominance of more tolerant, largely non-native, fish species. The higher proportion of species nestedness in invaded communities may stem from reduced invasibility or local extinctions over time. Finally, European perch, a pioneer species, exhibited increasing homogenisation of its biomass across lakes over the 10-year period, resulting in similar small populations distributed throughout the study area. These findings highlight temporal changes in fish community composition within gravel pit lakes, revealing the complex interplay between lake maturity and non-native species dynamics as major drivers.

1 | Introduction

Freshwater ecosystems, including streams, lakes, and wetlands, support high levels of biodiversity and provide important services to human society (Reynaud and Lanzanova 2017). At the same time, they are among the most threatened ecosystems on the globe, facing increasing impacts from a wide array of anthropogenic stressors (Tickner et al. 2020; Easterling et al. 2000). Freshwater ecosystems now stand at the centre of the current biodiversity crisis (Harrison et al. 2018), experiencing non-random gains and losses of species (Thomas 2013; Dornelas et al. 2014) that have strongly reshuffled communities (Reid et al. 2019). Fish are exemplars of the strong changes in biodiversity being witnessed across the world (Danet et al. 2024).

Gravel pit lakes, created through aggregate extraction (Mollema and Antonellini 2016), are a common artificial freshwater ecosystem found across the world (Blanchette and Lund 2016; Søndergaard et al. 2018; Vucic et al. 2019). In France alone, over 220 new gravel pits are excavated annually. These systems are typically located in alluvial floodplains and fill with water naturally through seepage, resulting in permanent waterbodies that are hydrologically isolated from surrounding rivers and lakes (Deere et al. 2006; Mollema and Antonellini 2016). Initially created for industrial purposes (i.e., construction industry), gravel pit lakes are frequently managed for recreational uses once extraction ceases (e.g., angling; Meyerhoff et al. 2019; Nikolaus et al. 2021). Additionally, they provide refuges and substitutes for lost or degraded natural ecosystems, therefore promoting biodiversity (Santoul et al. 2004; Lenda et al. 2012). Although typically fishless at formation, gravel pit lakes rapidly develop fish communities shaped by both natural and human-mediated processes. Natural colonisation, primarily through avian zoochory, may contribute during the early stages of lake formation, especially for native species such as European perch (*Perca fluviatilis*) that spawn in late winter or early spring when aquatic bird activity peaks (Garcia et al. 2023). Later, human-mediated introductions, either intentional (e.g., recreational stocking; Gimenez et al. 2023) or unintentional (e.g., introduction of non-target species during stocking events; Paz-Vinas et al. 2021), remain the most probable vectors for the introduction of fish species, especially non-native species. Fish communities in gravel pit lakes often resemble those in natural lakes subject to similar anthropogenic pressures (Emmrich et al. 2014; Matern et al. 2022; Martinsen et al. 2023).

Beta-diversity, defined as community variation within a geographic area (Whittaker 1972), is a central component of biodiversity and its response to global change (Socolar et al. 2016). Examining beta-diversity across space and time can improve understanding of the mechanisms underlying community variation (Ruhí et al. 2017). Beta-diversity is a core dimension of biological diversity, including its vulnerability to global change (Socolar et al. 2016). For instance, biotic homogenisation, or the temporal decline in beta-diversity, is driven largely by environmental change, with major implications for ecosystem stability (Olden et al. 2004, 2018). Decomposing beta-diversity into contributions from species and localities reveals patterns of turnover (i.e., species replacement) and nestedness (i.e., species gain/loss) that structure community change (Anderson et al. 2011; Legendre 2014). This perspective aids in identifying drivers of biodiversity change and informing conservation strategies to enhance ecological resilience or manage ecosystem transitions (Socolar et al. 2016). For example, Rogosch and Olden (2019) highlighted that intermittent streams in the Colorado River basin (United States) support native species persistence and contribute to beta-diversity, making their protection important for regional biodiversity. Contributions of localities and species to beta-diversity may vary over time, especially under global change, emphasising the need to better understand the multifaceted nature of biodiversity (Mouton et al. 2020). Given their increasing number and spatial clustering, gravel pit lakes now constitute a significant component of freshwater landscapes in many regions and provide a relevant model for studying temporal patterns and drivers of beta-diversity.

In this study, we assess whether site and species contributions to beta-diversity in freshwater fish communities of gravel pit lakes have changed over time; we also identify their ecological drivers. We analysed 10-year changes in fish communities from 16 gravel pit lakes in southwestern France. Our findings seek to bring insights into the dynamics of fish communities in artificial lakes, which have key implications regarding their socio-economic and ecological values.

2 | Materials and Methods

2.1 | Study Sites

Haute-Garonne County is crossed by one of the biggest rivers of France, the Garonne River, which rises in the Pyrenees and flows into the Atlantic Ocean. Toulouse, located along the Garonne River, is France's fourth-largest city (512,000 inhabitants in the city and 1.51 M in the metro area as of 2022), and remains one of the fastest-growing urban areas in the country (+6.0% between 2016 and 2022). Consequently, since the 1960s, gravel extraction along the Garonne River has been a significant source of aggregates, meeting the construction industry's demands for the expansion of Toulouse metropolitan area. This study was performed in 16 gravel pit lakes located in the central part of the Garonne floodplain in southwestern France (Figure 1) that are disconnected from one another and from surrounding waterbodies (Zhao et al. 2016; Alp et al. 2016). These artificial lakes, all within a 55 km radius, were chosen to provide a gradient of local environmental conditions (Table 1). Their ages range from 16 to 49 years after excavation at the beginning of the study. Moreover, they also differ in shoreline perimeter (from 564 to 4934 m), surface area (from 1.89 to 27.14 ha) and maximum depth (from 2.0 to 6.9 m). In addition, their trophic status spans a gradient from mesotrophic to hypereutrophic. To quantify the temporal variation of beta-diversity contribution of each community, the lakes were studied twice, separated by 10 years (past period: 2012; and present period: 2022). For logistic reasons, three lakes (namely SOA, SOB and SOC) were sampled in 2013 and 2023 (Figure 1).

2.2 | Fish Community

Fish communities were sampled twice in each lake using the same protocol based on gill netting and electrofishing to cover all types of habitats (Zhao et al. 2016). In the morning (approx. 08:00 am), six to eight gill nets were deployed during 1.5 h (to minimise fish mortality) in both the pelagic zone of the deepest area ($n=2$ gill nets; mesh size: 20 and 50 mm) and the littoral zone ($n=4$ to 6 depending on lake size and habitat diversity; mesh size: 12, 20, 30 and 60 mm) to represent the different types of substrates and habitats. Therefore, the number of nets was scaled with lake size and habitat diversity, resulting in an average density of 0.89 ± 0.83 net.ha^{-1}. Electrofishing was performed using the point abundance sampling approach, which is

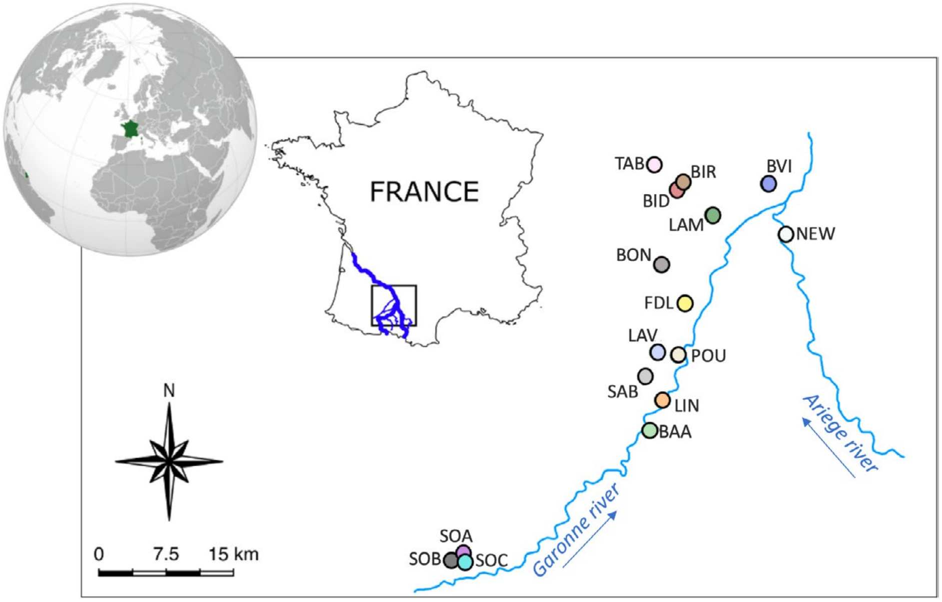

FIGURE 1 | Location of the 16 studied gravel pit lakes in the Garonne floodplain (Southwestern France). Coloured circles represent individual lake sites (lake codes; see Table 1 for full lake names). The blue lines indicate the Garonne River and its main tributary, the Ariege River. Arrows indicate the direction of river flow.

TABLE 1 | Table of environmental conditions of lakes studied.

Lake code	Excavation year	Age in 2012[a]	Surface (ha)	Perimeter (m)	Depth (m)	Trophic Status Index (TSI)[b]
BAA	1984	28	9.10	1617	4.4	55.37
BID	1993	19	15.18	2583	2.9	68.97
BIR	1992	20	20.36	2634	2.6	60.80
BON	1990	22	27.14	4934	5.6	61.80
BVI	1963	49	1.89	564	1.9	64.31
FDL	1980	32	18.77	3922	2.0	61.76
LAM1	1970	42	21.30	4139	3.0	68.55
LAV	1992	20	18.21	2485	3.7	53.36
LIN	1987	25	4.40	862	3.7	68.80
NEW	1966	46	8.33	2151	4.8	62.95
POU	1996	16	10.39	2199	4.3	48.04
SAB	1997	15	16.29	2113	5.1	51.79
SOA	1986	26	8.70	1220	5.9	27.88
SOB	1992	20	21.00	2070	6.9	18.35
SOC	1998	14	14.60	1679	7.0	33.77
TAB	1984	28	2.86	814.95	4.3	77.15

[a] Lake age was calculated as 2012 minus excavation year.
[b] TSI was calculated from total phosphorus concentration, chlorophyll-a concentration, and Secchi depth measured during the final sampling (Carlson 1977).

a cost-effective and non-destructive method to sample different species and life stages of fish communities in the littoral habitat of the lakes (Persat and Copp 1990). Following Copp and Garner (1995) regarding the number of individual PAS, an average of 31 ± 7 PAS (ranging from 25 to 50 depending on lake size and perimeter) were performed. Each captured fish was measured for fork length to the closest millimetre and identified to the species level, except for *Blicca bjoerkna* and *Abramis brama*—as earlier life stages could not be discriminated in the field—which were pooled and referred to as bream spp. (Zhao et al. 2016) (Table 2). Each species sampled was classified as native or non-native in the study area using literature (Keith et al. 2020). In total, 15,459 individuals belonging to 22 species were sampled during the study (Table 2). Individual biomass was estimated from fork length using species-specific length–weight relationships from the study area (Zhao et al. 2019) and used to calculate species biomass (BPUE, Biomass Per Unit Effort).

2.3 | Environmental Characteristics of the Lakes

Fishery management is a key factor influencing fish biodiversity in gravel pit lakes (Zhao et al. 2016). Although lakes may share the same fishery management, this may translate into contrasting practices, particularly in terms of fish stocking. For instance, Gimenez et al. (2023) showed that similarly managed lakes differed markedly in fish assemblages due to differences in stocking density (27.7 ± 239.1 $\mathrm{kg.year^{-1}.ha^{-1}}$ and ranged among lakes from 1.6 to 907 $\mathrm{kg.year^{-1}.ha^{-1}}$) and targeted species (e.g., percids vs. cyprinid-dominated stocking). To account for the ecological outcomes of such variation, we quantified two key metrics: the invasion level of fish communities and lake productivity. The invasion level of each lake (non-native dominance) was calculated using the proportion of non-native species biomass (BPUE) relative to the total biomass of the community. Productivity was assessed using the Trophic Status Index (TSI) (Carlson 1977) based on total phosphorus concentration (colorimetric analysis NF EN 6878, expressed in $\mu g \cdot L^{-1}$), chlorophyll-a concentration (measured with an AlgaeTorch, BBE Moldaenke) and water clarity (Secchi depth), following Jackson et al. (2017). To obtain a representative value for each lake, we used the average TSI measured during both the past and present sampling periods. This choice was supported by environmental monitoring conducted every 2 years on a subset of eight lakes, which revealed limited interannual variability and no significant temporal trends, indicating relatively stable trophic conditions throughout the study period.

In addition, we examined the influence of habitat alteration and ecosystem age on beta-diversity. Habitat complexity was estimated using the shoreline development index (i.e., ratio of the lake shore length to the circumference of a circle with lake area) calculated as $L / (2\pi^{0.5} \times A^{d/2})$, where L is the shoreline of the lake (measured via satellite imagery), A the area, and d the shoreline fractal dimension (here $d = 1.17$ and was obtained by regressing shoreline length by area for the 16 gravel pit lakes; see details in

TABLE 2 | List of fish species (common name, scientific name and code) collected during the study.

Common name	Scientific name	Code	Invasive status
Black bullhead	*Ameiurus melas*	*A. melas*	Non-native
Bream	*Abramis brama/Blicca bjoerkna*	*Bream* spp.[a]	Native
Chub	*Squalius cephalus*	*S. cephalus*	Native
Common carp	*Cyprinus carpio*	*C. carpio*	Non-native
European bitterling	*Rhodeus amarus*	*R. amarus*	Native
European eel	*Anguilla anguilla*	*A. anguilla*	Native
European perch	*Perca fluviatilis*	*P. fluviatilis*	Native
Grass carp	*Ctenopharyngodon idella*	*C. idella*	Non-native
Gudgeon	*Gobio occitaniae*	*G. occitaniae*	Native
Largemouth bass	*Micropterus nigricans*	*M. nigricans*	Non-native
Northern pike	*Esox lucius*	*E. lucius*	Native
Pikeperch	*Sander lucioperca*	*S. lucioperca*	Non-native
Prussian carp	*Carassius gibelio*	*C. gibelio*	Non-native
Pumpkinseed	*Lepomis gibbosus*	*L. gibbosus*	Non-native
Rainbow trout	*Oncorhynchus mykiss*	*O. mykiss*	Non-native
Roach	*Rutilus rutilus*	*R. rutilus*	Native
Rudd	*Scardinius erythrophthalmus*	*S. erythrophthalmus*	Native
Ruffe	*Gymnocephalus cernua*	*G. cernua*	Non-native
Silver carp	*Hypophthalmichthys molitrix*	*H. molitrix*	Non-native
Tench	*Tinca tinca*	*T. tinca*	Native
Wels catfish	*Silurus glanis*	*S. glanis*	Non-native
Western mosquitofish	*Gambusia affinis*	*G. affinis*	Non-native

[a] *Blicca bjoerkna* and *Abramis brama* earlier life stages could not be discriminated in the field; all individuals were pooled into Bream spp.

Seekell et al. 2022). Lake age was calculated as the number of years since excavation.

2.4 | Beta-Diversity Contribution Analysis

Beta-diversity, defined as the total variance in a regional community dataset, can be partitioned into the contributions of individual sites and species (Legendre and De Cáceres 2013). For both sampling periods, we calculated local contribution to beta-diversity (LCBD) and species contribution to beta-diversity (SCBD) using biomass per unit effort (BPUE) as input data. In our studied systems, we used biomass rather than abundance to limit the potential overrepresentation of numerically abundant young of the year of several non-native species during the sampling period, such as pumpkinseed (*Lepomis gibbosus*), black bullhead (*Ameiurus melas*) or Western mosquitofish (*Gambusia affinis*). Higher LCBD values indicate sites with more distinct species composition relative to other sites, while higher SCBD values identify species with greater influence (i.e., more unique species) on beta-diversity (Legendre and De Cáceres 2013; Heino and Grönroos 2017). We computed LCBD and SCBD using the *beta.div* function (adespatial package; Dray et al. 2019), applying a Hellinger transformation to species biomass data. This transformation reduces the influence of rare species and scales the total variance in community composition between 0 and 1, facilitating comparisons across datasets (Legendre and De Cáceres 2013). Finally, to quantify the variation of site and species contribution to beta-diversity, we calculated delta values of LCBD (ΔLCBD) and SCBD (ΔSCBD) as the difference between past and present values.

To evaluate the respective contributions of species turnover (replacement of species between sites, T) and species nestedness (species losses and gains that cause differences in richness between sites, N) to the changes in beta-diversity (ΔLCBD), we employed a Jaccard dissimilarity matrix based on presence/absence data. This approach, following Legendre (2014), allows partitioning beta-diversity into additive components of turnover (T) and nestedness (N), with their sum equalling 1. This decomposition was applied at two levels: regional comparison (i.e., all lakes between past and present period) and pairwise comparison (i.e., same lake between past and present period). Calculations were performed using the *betapart* package (Baselga and Orme 2012).

To investigate environmental drivers of variation in ΔLCBD, we performed a principal component analysis (PCA) on lake age, trophic status, habitat complexity, and invasion level. We also compared changes in species contribution to beta-diversity (ΔSCBD) between non-native and native species. All analyses were performed in the software program R (version 4.4.1717).

3 | Results

3.1 | Lake Contributions to Beta-Diversity

In 10 years, fish communities exhibited little change in both species richness (mean # species = 7.56 ± 2.99 and 7.06 ± 2.69; respectively) and overall beta-diversity (mean Jaccard dissimilarity = 0.617 ± 0.160 and 0.619 ± 0.158; respectively). Similarly, no major differences were observed in the components of beta-diversity: species turnover (T) (past = 0.78, present = 0.80) and nestedness (N) (past = 0.11, present = 0.09). In contrast, local contributions to beta-diversity varied substantially among lakes over time (mean ΔLCBD = 0.021 ± 0.012; Figure 2). For instance, some lakes became more unique in their fish community composition, leading to elevated beta-diversity (positive ΔLCBD; e.g., SOC and POU), whereas others became more similar to the regional pool, reducing beta-diversity (negative ΔLCBD; e.g., NEW and FDL; see Figure 2).

The association between changes in lakes' contribution to beta-diversity (ΔLCBD) and environmental characteristics of the lakes was assessed using a PCA (Figure 3). The first axis (49.4% of the total variance explained) was mainly associated with the trophic status index (i.e., primary productivity; loading on PC1: 0.86), as well as to a lesser extent lake age and habitat complexity (0.64 and 0.70, respectively; Figure 3 and Table S1). High scores along this axis reflect older and more productive lakes, whereas low scores correspond to younger and less productive systems. The second axis (22.8% of the total variance explained) was mainly associated with the dominance of non-native species in fish communities (loading on PC2: 0.75; Figure 3 and Table S1). Low scores along this axis correspond to lakes dominated by native species, whereas high scores represent communities dominated by non-native species.

Lakes with negative ΔLCBD (i.e., becoming less important in their contribution to beta-diversity) were generally older and more productive lakes (high scores on the first axis: mean PC1 score of 0.56 ± 0.58 SE), whereas lakes with positive ΔLCBD (i.e., becoming more unique in their composition and increasing their contribution to beta-diversity) were younger and less productive lakes (low scores on the first axis: mean PC1 score of −0.61 ± 0.44 SE) (Figure 3). This pattern was consistent with greater compositional shifts observed in younger and less productive lakes compared to the more stable communities of older and more productive lakes (Figure S1). Differences in non-native dominance between lakes with positive and negative ΔLCBD values were relatively small (mean PC2 score ± SE: −0.20 ± 0.55 vs. 0.13 ± 1.04), indicating only a modest influence of non-native species on lake-level changes in beta-diversity (Figure 3).

The partitioning of species turnover (T) and species nestedness (N) between past and present periods for each lake provided additional context into the temporal trends in beta-diversity. Lakes dominated by non-native fishes demonstrated greater changes in species nestedness ($N > T$), suggesting that species gains and losses over time played a more important role in shaping beta-diversity (Figure 3). In contrast, lakes dominated by native species showed higher turnover ($T > N$), suggesting replacement of species over time as the primary mechanism (Figure 3). No clear association was found between lake age and productivity and the contributions of turnover and nestedness to beta-diversity (Figure 3).

3.2 | Species Contribution to Beta-Diversity

The relative biomass of fish species within the study area exhibited notable changes over a decade (Figure 4). Several non-native

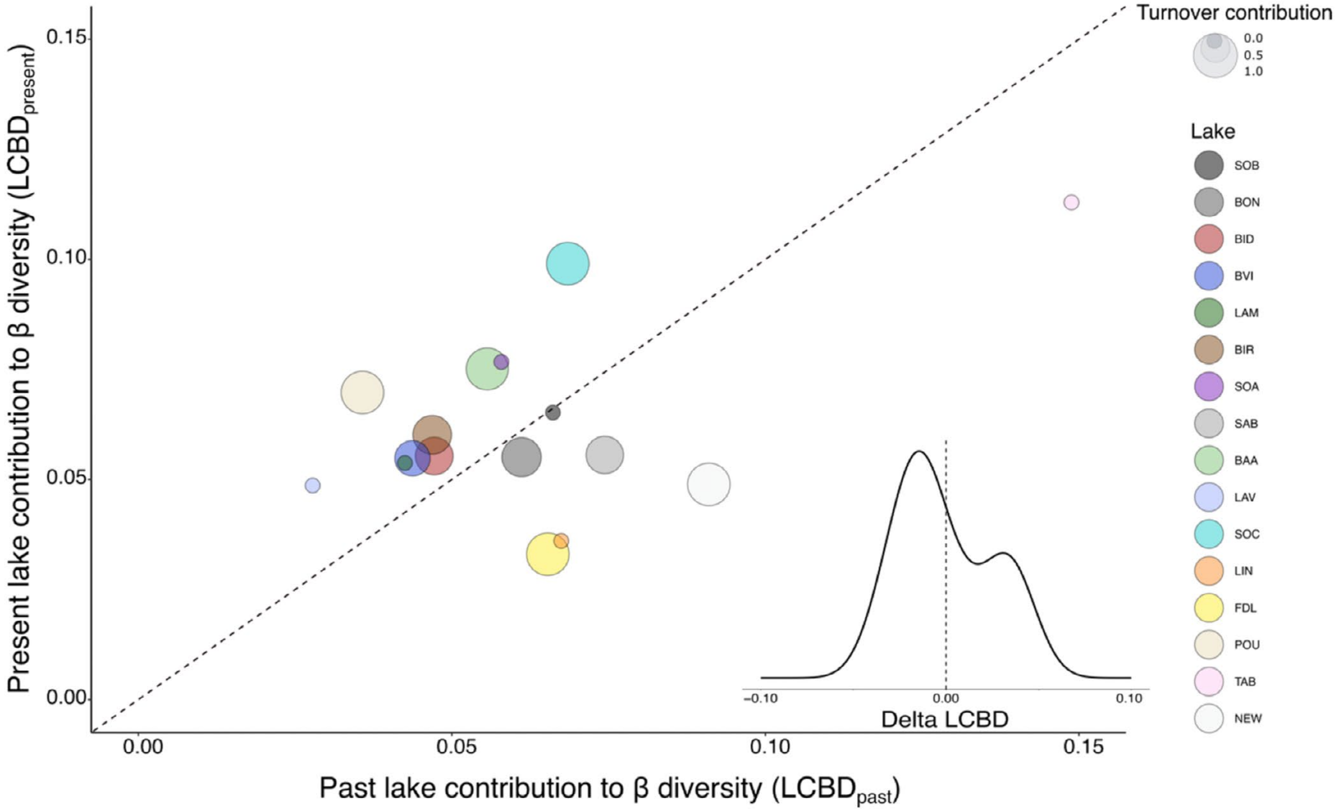

FIGURE 2 | Relationship between present lake contribution to beta-diversity ($LCBD_{present}$) and past lake contribution to beta-diversity ($LCBD_{past}$) in the 16 study lakes. The black dotted line indicates no change in LCBD between past and present. The size of the dots represents the relative contribution of species turnover to beta-diversity (turnover [T]). The accompanying histogram displays the difference between $LCBD_{present}$ and $LCBD_{past}$ (ΔLCBD).

species—such as common carp (*Cyprinus carpio*), pikeperch (*Sander lucioperca*), largemouth bass (*Micropterus nigricans*) and Wels catfish (*Silurus glanis*)—displayed notable increases in their relative biomass. In contrast, some native species, including some cyprinids (e.g., bream spp. or tench, *Tinca tinca*) and the European perch (*Perca fluviatilis*), experienced substantial declines in their relative biomass.

Fish species showed varying contributions to overall beta-diversity that, in some instances, changed over time (Figure 5). Species contributions to beta-diversity (ΔSCBD) did not differ according to invasive status, with a few notable exceptions (Figure 6). Roach (*Rutilus rutilus*) and European perch, two native species, contributed less to compositional differences among lakes over time, whereas the common carp and Wels catfish, two non-native species, were increasingly contributing to beta-diversity (Figures 5, 6). Other species showed little change in their contribution to beta-diversity in the study area, especially species with an initial low contribution to beta-diversity, such as the gudgeon (*Gobio occitaniae*), ruffe (*Gymnocephalus cernua*) or Western mosquitofish (Figures 5, 6).

4 | Discussion

This study showed that the relative contributions of individual lakes and species to fish alpha- and beta-diversity varied over time. Temporal changes in beta-diversity were primarily driven by species turnover (i.e., species replacement), as frequently observed in freshwater ecosystems (Soininen et al. 2018). In contrast, nestedness (i.e., species gain or loss) contributed less to beta-diversity in these gravel pit lakes, likely due to their isolation from other waterbodies (Mollema and Antonellini 2016), making them less prone to invasion and colonisation. This contrasts with more connected ecosystems, such as streams, where turnover and nestedness tend to contribute more equally (e.g., Rogosch and Olden 2019). The predominance of species turnover in our results suggests that observed changes in beta-diversity were mainly shaped by deterministic processes (i.e., local drivers; Anderson et al. 2011; Legendre 2014), such as eutrophication or agriculture (e.g., García-Navas et al. 2022; Menezes et al. 2023).

The main factor influencing changes in the contribution to beta-diversity among lakes was their maturity, as defined by lake productivity and age. This interpretation is directly supported by Colas et al. (2021), who identified a comparable maturity gradient in the same gravel pit lakes, related to chlorophyll-a, nutrient levels and lake age. Immature lakes exhibited higher species turnover over the 10-year period and supported more distinct fish communities; whereas mature lakes showed little change, contributing less to overall beta-diversity. Ecosystem maturity has functional implications for community composition and beta-diversity. Specifically, eutrophication occurring in mature lakes is known to promote biotic homogenisation across ecosystems and taxa (Donohue et al. 2009; De Schrijver et al. 2011),

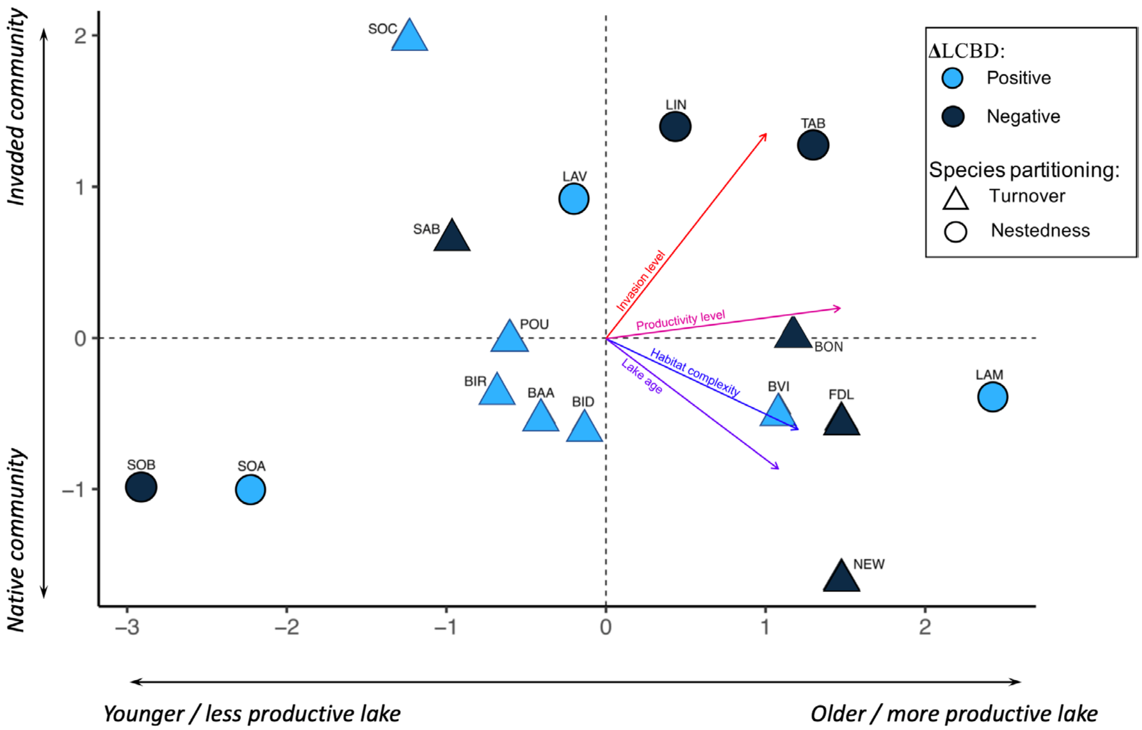

FIGURE 3 | Principal component analysis (PCA) based on lake environmental characteristics (invasion level, productivity level, habitat complexity, and lake age; variables contributing the most to both axes are displayed in red). The first axis (49.4% of the total variance explained) was mainly associated with the primary productivity and lake age, while the second axis (22.8% of the total variance explained) was mainly associated with the dominance of non-native species in fish communities. Lakes are displayed in blue when their ΔLCBD is positive and in black when it is negative. Lakes mainly influenced by changes in species nestedness are displayed with dots, whereas lakes mainly influenced by changes in species turnover are displayed with triangles.

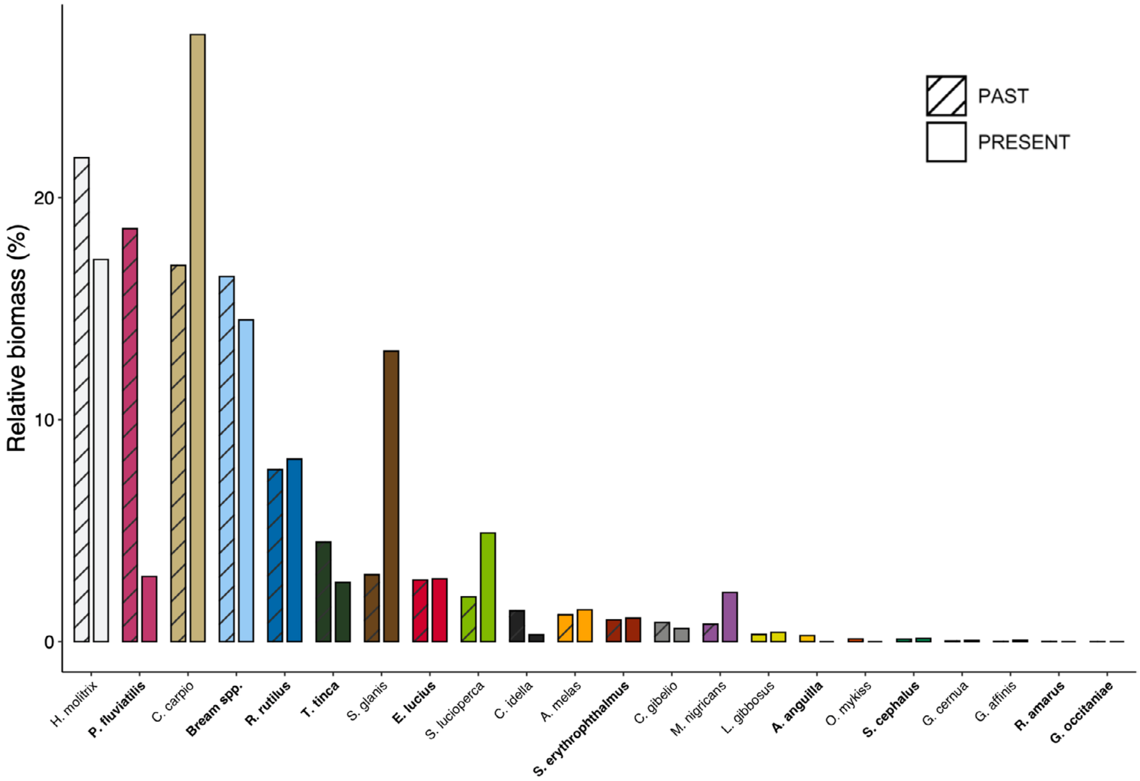

FIGURE 4 | Relative biomass (%) of each fish species pooled across all lakes within the study area. The relative biomass during the past period is displayed with striped bars; the relative biomass during the present period is displayed with empty bars. Native species names are displayed in bold.

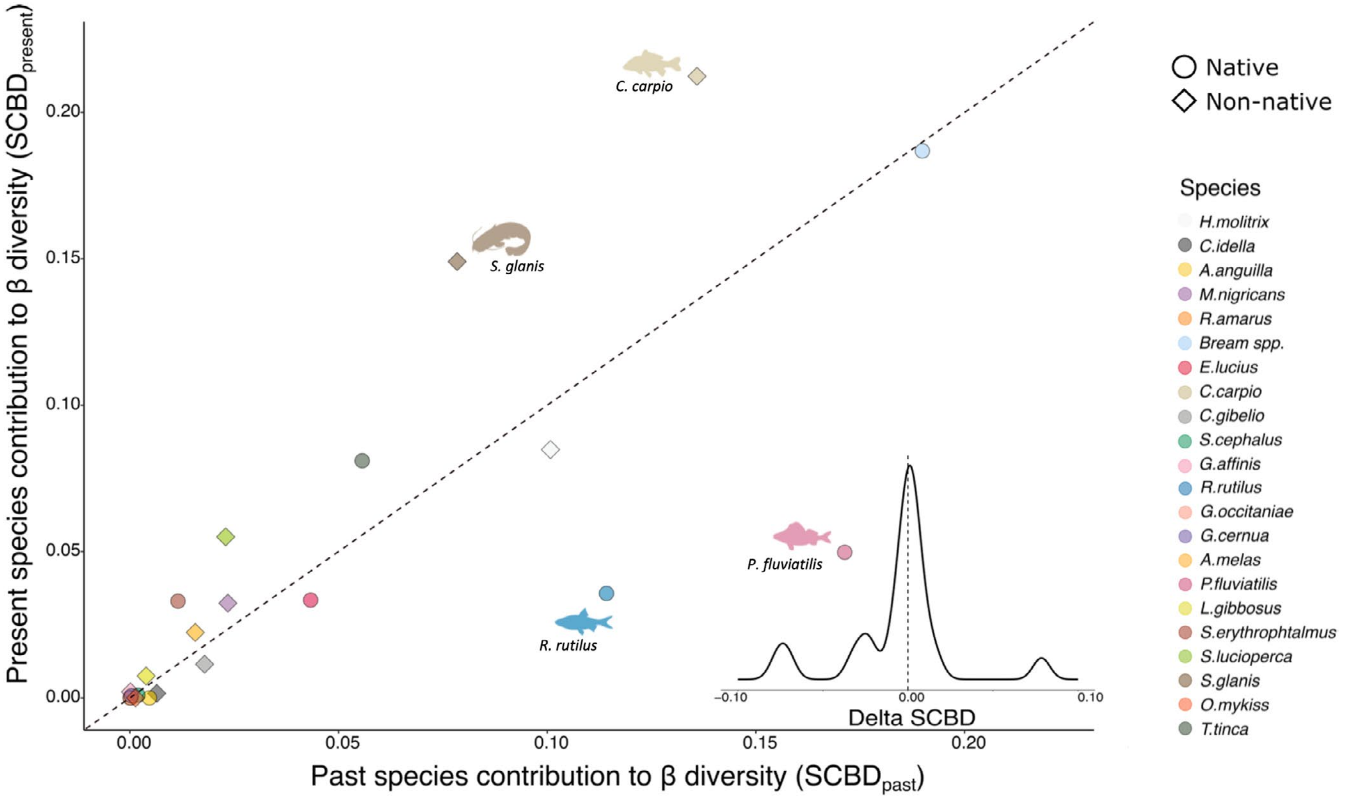

FIGURE 5 | Relationship between present species contribution to beta-diversity ($SCBD_{present}$) and past species contribution to beta-diversity ($SCBD_{past}$) for 22 fish species sampled in gravel pit lakes. The black dotted line indicates an absence of variation in SCBD between past and present. The shape of the points represents the invasive status of the species, with native species displayed with dots and non-native species with diamonds. The accompanying histogram displays the difference between $SCBD_{present}$ and $SCBD_{past}$ (ΔSCBD).

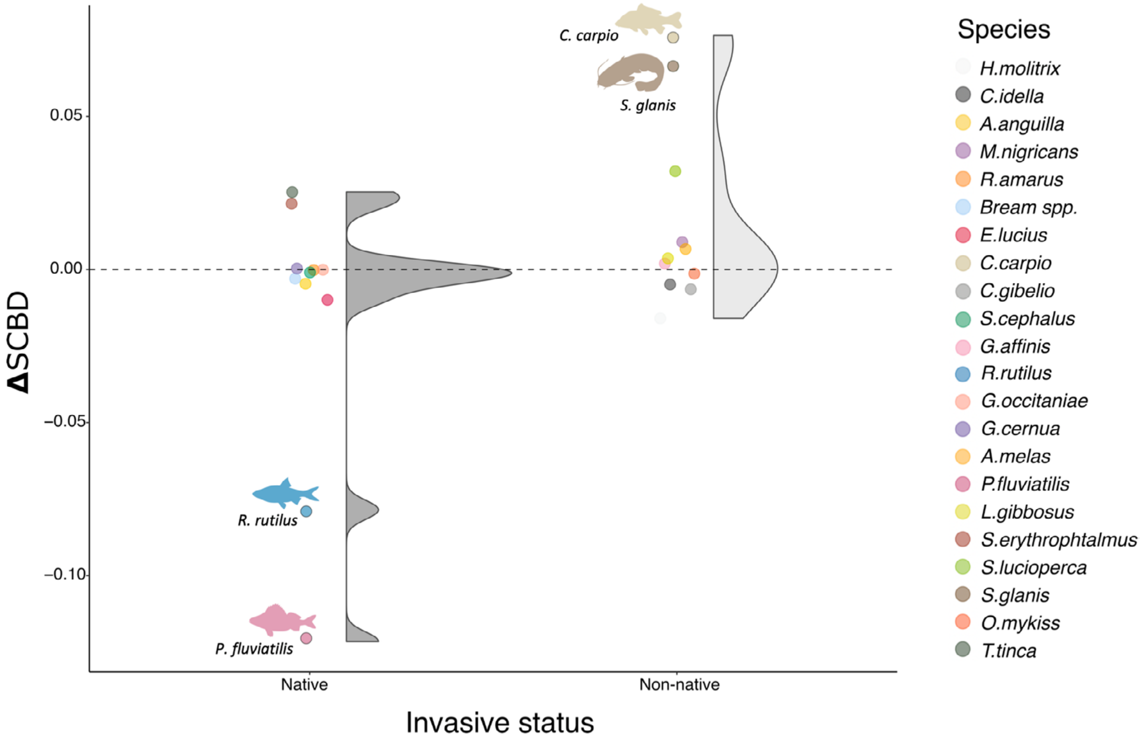

FIGURE 6 | Comparison of ΔSCBD according to the invasive status of fish species. Native species are displayed in dark grey and non-native species in light grey.

including fish communities in European shallow lakes (Menezes et al. 2023). In our study system, mature lakes are also characterised by a shift from heterotrophic to autotrophic-based metabolism, associated with high turbidity and hypoxia/anoxia (Colas et al. 2021; Paerl et al. 2001; Havens 2008). Such abiotic conditions likely foster community convergence among mature lakes by favouring species tolerant to eutrophic environments (Ludsin et al. 2001; Chalar et al. 2013). In line with this, several non-native species such as Wels catfish, largemouth bass and common carp increased in biomass over the study period. These species exhibit traits associated with eutrophication tolerance, including environmental flexibility and opportunistic feeding strategies (e.g., Cucherousset et al. 2007; Mutethya and Yongo 2021). In contrast, native species such as the European perch, which rely on visual predation and are less tolerant to such conditions (e.g., Sandström and Karås 2002), experienced drastic declines over the same period. Finally, changes in species nestedness were less pronounced in immature lakes than in mature ones. Younger systems, often dominated by pioneer species (e.g., perch, Northern pike *Esox lucius*, roach; Garcia et al. 2023), showed limited evidence of additional colonisation. This pattern contrasts with expectations based on early successional dynamics or post-disturbance recovery (Ruuhijärvi et al. 2010), and suggests a balance between changes in species relative abundance and occasional gains or losses, as also observed in newly created lakes (Degani et al. 1998).

We found a weak negative association between non-native dominance and changes in lake contributions to beta-diversity (ΔLCBD), suggesting that invasive species may contribute, albeit modestly, to biotic homogenisation. This limited effect likely reflects a combination of homogenisation and heterogenisation processes, which vary depending on lake-specific conditions and the identity of non-native species (Olden and Poff 2003; Menezes et al. 2023). Still, the observed trend is consistent with previous findings showing that non-native fish increase faunal similarity across freshwater systems, especially when species are repeatedly translocated across nearby ecosystems (Toussaint et al. 2018), such as through fish stocking in Spanish rivers (Clavero and García-Berthou 2006). Our results also revealed that heavily invaded lakes exhibited higher species nestedness than turnover. These two patterns may share common biotic mechanisms, including increased resistance to further colonisation due to the dominance of established invaders (Yurkonis and Meiners 2004; Erős et al. 2020), and local extinctions of native species via competitive exclusion or predation (Li et al. 2022). A classic illustration of such extinction-driven homogenisation comes from New Zealand, where brown trout (*Salmo trutta*) have caused the decline of endemic galaxiid fishes (McIntosh et al. 2010).

Unlike most studies, non-native species in our system did not show a reduced contribution to beta-diversity (i.e., became more common/ordinary species) than native species (Rogosch and Olden 2019; Baidya and Bagchi 2022). Indeed, stronger changes in species contributions to beta-diversity were expected among non-native species, given their potential to impact native communities through predation or competitive exclusion (Busst and Britton 2017; Mofu et al. 2019), their faster demographic dynamics (e.g., higher growth rate and reproduction) and their higher propensity for invading other lakes (Su et al. 2023). However, the majority of species, whether native or non-native, experienced minimal changes in their contribution over time.

The Wels catfish and the common carp, two non-native species, increased in relative biomass in the study area while contributing more strongly to beta-diversity. High species contribution to beta-diversity is generally seen as a positive indicator, suggesting high diversity and variability within the studied communities (Legendre and De Cáceres 2013). However, here, these two species are non-native and are known for their negative ecological impacts, including predation and habitat modification (e.g., Badiou et al. 2011; Vejřík et al. 2017). Given that both species are large-bodied fish with continuous growth (Keith et al. 2020; Bergström et al. 2022), their increasing uniqueness may reflect changes in population structure, such as increased average body size over time; a pattern observed in other taxa (e.g., large-bodied ants; Baidya and Bagchi 2022). In contrast, the European perch, a native pioneer species in the study area (Zhao et al. 2016; Garcia et al. 2023), exhibited a declining contribution to beta-diversity and increasing homogenisation of its biomass across lakes over the 10-year period, resulting in similar small populations distributed throughout the study area. Such a gradual decline of pioneer species is well-documented in plant ecological succession, where pioneer species are progressively replaced as environmental conditions shift (Losapio et al. 2021). In particular, the arrival of piscivorous species, including Northern pike, largemouth bass and pikeperch, likely contributed to this decline through predation or competitive exclusion (Degani et al. 1998). This shift from percids-dominated communities to other communities, such as cyprinid-dominated ones, has already been observed in lake fish communities (Olin et al. 2002).

In conclusion, this study highlights spatio-temporal variation in beta-diversity across a network of artificial gravel pit lakes. Changes in lake contribution to beta-diversity were closely linked to ecosystem maturity, with immature lakes (i.e., younger and less productive lakes) exhibiting greater community turnover and compositional uniqueness over time. With time, these lakes appear to shift toward more mature ecosystems (i.e., older and more productive lakes), characterised by increased eutrophication and a greater dominance of non-native species tolerant to degraded water conditions. Our results emphasise that beta-diversity, while essential for understanding ecological dynamics, must be interpreted in the context of species' ecological roles and importance. Given the strong association between taxonomical and functional contribution to beta-diversity (Mouton et al. 2020; García-Navas et al. 2022), shifts in species composition are likely to influence ecosystem stability; especially through changes in the trophic structure of fish communities, as functional diversity influences feeding-related traits in fish.

Author Contributions

F.G., J.C., and J.D.O: conceptualization; F.G. and J.C.: developing methods; F.G., J.C., and J.D.O: conducting the research; F.G. and J.D.O.: data analysis; F.G., J.C., and J.D.O.: data interpretation; F.G.: preparation of figures and tables; F.G., J.C., and J.D.O.: writing; All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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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 from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** eff70024-sup-0001-AppendixS1.pdf.