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Fish Beta Diversity Patterns across Environmental Gradients in 63 European Shallow Lakes: Effects of Turbidity, Nutrient Enrichment, and Exotic Species

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Abstract: The beta diversity among lakes is affected by natural environmental sorting, dispersal constraints, and anthropogenic disturbances. We hypothesized that fish beta diversity would increase towards lower latitudes and be higher in less disturbed lakes at within-region scale, but environmental disturbances could affect these patterns due to community homogenization or heterogenization (e.g., gain of exotic species) among lakes. We used generalized dissimilarity modeling to assess the relative importance of geographic distance, climate, and environmental heterogeneity on fish beta diversity across Denmark, Belgium/The Netherlands, and Spain. We also tested whether differences in beta diversity changed between lake types (e.g., clear vs. turbid lakes and lakes with vs. without exotics fish) within-region and across latitude. Beta diversity increased from Denmark to Spain and geographic distance and climate variability were the main drivers of community change across latitude, but the rate of change varied between lake types. At the within-region scale, factors such as turbidity, lake size, and presence of exotics had varying impacts on beta diversity (i.e., increasing, decreasing, or no effect) across the three regions. Our findings suggest that understanding the effects of environmental disturbances on beta diversity requires consideration of both biogeographic and local factors.

Keywords: environmental heterogeneity; turbidity; homogenization; heterogenization; environmental gradients; lake connectivity; exotic fish

1. Introduction

Latitudinal diversity gradients are some of the most noticeable biogeographic patterns on Earth [1], but how and why these patterns exist are still debated [2–5]. It is recognized that species diversity generally peaks at lower latitudes and declines towards the poles. This pattern is confirmed for both aquatic and terrestrial organisms [2], for both present and extinct taxa [6,7], for ectotherms and endotherms, and for taxa differing in trophic level, mode of dispersal, and body size [3,5]. However, anthropogenic processes such as habitat destruction and introduction of exotic species may affect these patterns [8,9].

As for alpha and gamma diversity, beta diversity has been predicted to decrease with increasing latitude, and extensive efforts have been made to gain insight into the factors driving these patterns [10–13]. Beta diversity can provide insights into the processes organizing ecological communities along environmental and spatial gradients, since it captures shifts in species composition at both local and regional scales [12]. Furthermore, the understanding of patterns of beta diversity and the underlying drivers is a central issue in ecology, not least given its importance for the conservation of biodiversity and ecosystem management [14–17].

Variation in community structure along latitudinal gradients has been explained by variation in species' range size [18] and dispersal ability [19], ecological drift, speciation, and environmental filtering (i.e., species sorting or selection) [10,20]. For both rivers and lakes, it has been shown that spatial patterns in fish communities in Europe are determined by environmental filtering and by dispersal constraints (e.g., vagility) related to historical processes such as isolation by mountain ranges, connectivity among river systems, and glacial history [21–23]. Previous changes in climate in the Quaternary period played a major role in shaping the present-day global patterns of spatial turnover and nestedness in the fish beta diversity [13]. However, information of how anthropogenically driven forces (i.e., habitat destruction, eutrophication, loss of lake connectivity, and introduction of exotic species) affect spatial patterns of fish beta diversity in lakes along latitudinal gradients remains scarce.

At local scales, environmental filters such as eutrophication, turbidity, lake morphometry and connectivity, and species introductions may drive compositional and diversity patterns in fish communities [9,24–29]. Eutrophication, in interaction with climatic warming, is a conspicuous driver of change in freshwater fish community structure, due to quantitative and qualitative changes in food availability, changed predation pressure by piscivores, and excessive algal growth and consequent habitat deterioration [30–32]. Aquatic plants exert multiple effects on lake ecosystem structure and functioning by affecting water's physical (e.g., turbidity) and chemical properties and, mediated by these changes in water quality, alter fish communities [33]. Aquatic plants can affect the interaction among fish species by offering physical refuges [34] and providing spawning habitats and shelter against predation for juvenile fish [35], and submerged plants also affect fish species turnover by creating heterogeneous habitats and producing multiple environmental gradients [33,36]. Moreover, high abundance of submerged macrophytes is generally associated with high water transparency [37] and high biodiversity in temperate shallow lakes [36], whereas the reversed pattern is observed in eutrophic lakes [38,39]. The environmental heterogeneity associated with lake morphometry (e.g., lake surface area and depth) may also influence fish assemblage structure and species diversity patterns, since deeper and larger lakes generally hold more available niches, while small sized lakes are more susceptible to stochastic fish kills [40]. Moreover, presence of exotic fish species may decrease fish alpha and beta diversity, create biotic homogenization of fish communities, and reduce ecosystem multifunctionality [41,42]. However, the introduction of exotic species can also increase alpha and beta diversity, and the impact of exotic species will depend on local abiotic conditions, dispersal constraints, history, and connectivity among habitats [8].

In this paper, we analyzed the variation in fish community among lakes in Western Europe along a latitudinal gradient from Scandinavia to the Mediterranean. We used data from 63 shallow lakes sampled according to a standardized protocol in three regions, a

northern region (Denmark), a mid-latitude region (The Netherlands and Belgium), and a southern region (southern Spain) following a common sampling protocol. We tested the hypothesis that fish beta diversity increases towards lower latitudes, but that this biogeographic pattern becomes less pronounced with increasing environmental disturbance (i.e., increasing turbidity, nutrient enrichment, and presence of exotic species). In less disturbed shallow lakes, a strong turnover (i.e., species replacement) is expected across the latitudinal gradient due to better overall ecosystem integrity and preservation of the environment. However, large-scale human chronic disturbances, such as increasing water turbidity, eutrophication, and introduction of exotic species, have the potential to affect this pattern by either increasing or decreasing species turnover across latitudes, driven by loss of shared species or gain of exotic species among lakes. In addition, we investigate whether environmental disturbances lead to a reduction in beta diversity (homogenization of communities) within regions (i.e., Denmark, Belgium/The Netherlands and southern Spain), regardless of their geographic location.

2. Materials and Methods

2.1. Study Sites, Environmental Variables, and Fish Sampling

We used data from 63 small-sized shallow lakes with a mean depth <3 m and a maximum depth of 5 m sampled in 2000 and 2001 following a standardized protocol. The lakes were located in three European regions at different latitudes: Denmark (Lat: 56.2° N, Long: 9.5° E; n = 29 lakes), Belgium/The Netherlands (Lat: 50.5° N, Long: 4.4° E/Lat: 52.1° N, Long: 5.2° E; n = 26 lakes), and southern Spain (Lat: 40.4° N, Long: 3.7° W; n = 8 lakes). The Spanish lakes were all situated in the southern part of the country, mainly in Andalusia (Figure 1), and the number of Spanish lakes included was lower than for the other regions as many of the lakes comprised by the original program were fishless or not sampled for fish. The physical, chemical, and biological variables used for this paper were extracted from an existing database generated within the framework of the EU project BIOMAN [36,43]. A description of the methods of sampling and analyses of these lake variables can be found in Declerck et al. [36]. The climate variables used were averages for 1970–2000 and were obtained from WorldClim [44] (Table S1). The climate in the three different regions differed, with annual mean temperature ranging from 7.8 °C in Denmark over 10.3 °C in Belgium/The Netherlands to 15.2 °C in southern Spain, and total annual precipitation ranged from 780 mm in Belgium/The Netherlands to 503 mm in southern Spain, with Denmark in between (702 mm) [44].

Monofilament nylon gillnets were used to capture fish in both the littoral and pelagic zones of the lakes. Each net was 1.5 m deep and 42 m long and consisted of 14 units of 3 m length with different mesh sizes (6.25, 8, 16.5, 75, 38, 25, 12.5, 33, 50, 22, 43, 30, 60, 10 mm) placed in random order. In each zone of the lake, littoral sinking nets were set parallel to the shore, approximately 5 m outside the reed belt or at 1–1.5 m depth, whereas pelagic sinking nets were set parallel to the shore in the middle of the lakes. The nets were set late in the afternoon and retrieved the following morning. The total number of nets used per lake varied according to lake size. For instance, in lakes with an area smaller than 2 ha, two nets were used, whereas in lakes with an area larger than 100 ha, maximum eight nets were used.

The sampling was conducted when the fish were most evenly distributed in the lakes and when young-of-the-year fish were large enough to be caught in the gill nets, i.e., between 15 August and 15 September in Denmark, between 15 August and 1 October in Belgium/The Netherlands, and between 1 July and 1 September in Spain. Catch per unit effort (CPUE, catch per net per night) of fish was calculated as the total number of individuals per net. As the number of species and their fish CPUE did not differ between pelagic and littoral regions, we merged the data from the two regions into a single species matrix.

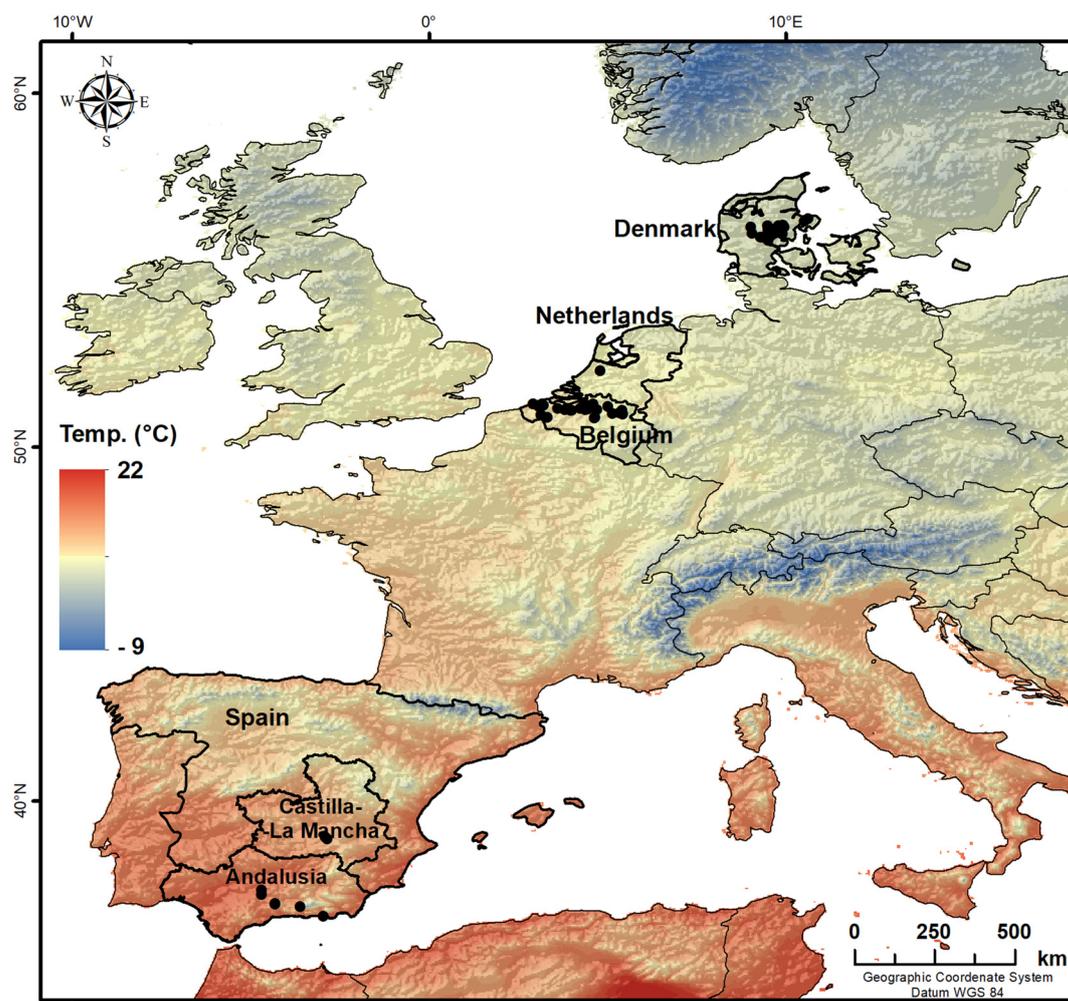


Figure 1. The study included 63 comparable shallow lakes: 29 Denmark, 26 Belgium/The Netherlands, and 8 in Spain (SP). The Spanish lakes were all situated in the southern part of the country (Andalusia and south of Castilla–La Mancha). The temperatures are annual means for 1970–2000 and were obtained from WorldClim [44].

2.2. Categorization of Lakes

The lakes were not selected randomly but along mutually independent gradients of three potentially important key variables (the ‘gradient variables’): turbidity, total phosphorus (TP), and lake surface area. We sought to create independent gradients for these variables to reduce effects of co-linearity in our analyses [36] (for more details about the gradients, see Tables S2 and S3). Firstly, to know whether the environmental gradient variables differed among regions, we used a Kruskal–Wallis test (Figure S1). A Dunn’s test of multiple comparisons using ranking sums was also used to compare the medians between regions of each environmental gradient variable [45]. We used the Benjamini–Hochberg adjustment [46] to control the false discovery rate and adjust the p -values for multiple comparisons. We used the `dunn.test` R package to perform the Kruskal–Wallis and Dunn’s tests [47]. Finally, to test if the environmental gradients were independent from each other, a Pearson correlation test was performed between gradient variables in each of the three geographic regions (Table S2).

Only meso- to eutrophic lakes were sampled (Tables S2 and S3). For this paper, the lakes were distributed over five factorial categories: water turbidity (> or <20% of the lake surface area covered by macrophytes—proxy for clear and turbid lakes, respectively), total phosphorus (<100 $\mu\text{g P l}^{-1}$ and $\geq 100 \mu\text{g P l}^{-1}$), lake surface area (<5 ha and ≥ 5 ha), lake connectivity (connected and isolated) (see Declerck et al. [36]), and presence and absence of

exotic fish species (+/− exotics) (Tables S4 and S5). We carried out our analysis contrasting lakes with and without exotic fish using both the complete dataset (including exotic fish) and with a dataset without exotic fish to assess whether the pattern is due to the inclusion of exotic fish themselves. In our study, exotic refers to fish species that are not native to Europe or not native to the focal regions of the study (Spain, Belgium/The Netherlands, and Denmark).

2.3. Measures of Beta Diversity

Total beta diversity was estimated as the average compositional dissimilarity (multivariate dispersion; [17]) within each region to the centroid formed by all lakes in that region (DK = Denmark, BNL = Belgium and The Netherlands, SP = Spain). The multivariate dispersion was computed using three different dissimilarity matrices: Bray–Curtis (β_{bray}), Sørensen ($\beta_{\text{sør}}$), and Simpson (β_{sim}). The Bray–Curtis coefficient was calculated from $\log(x + 1)$ transformed data on fish CPUE based on numbers to emphasize abundant species (dominant). The Sørensen coefficient was used for the presence-absence data to give equal weight to rare and abundant species, whereas the Simpson coefficient was used as a measure of the turnover (the replacement component of beta diversity— β_{sim}) within and among regions [48]. Turnover (β_{sim}) here means the change in species composition (i.e., species replacement) along the pre-defined gradients selected in our study.

2.4. Measures of Environmental Heterogeneity

The environmental heterogeneity components (EH_{lim} , EH_{phy} , EH_{res} , and EH_{clim}) were computed as Euclidean dissimilarity matrices by applying the method proposed by Anderson et al. [49] and were calculated from standardized environmental data from 39 limnological, biological, and climatic variables. We used five subsets of environmental heterogeneity (EH) components to explore the multifaceted nature of our datasets (Table S1). The first subset included geographic distance among all lakes (GD). The second component of heterogeneity (EH_{lim}) was based on water quality characteristics (water temperature, conductivity, pH, Secchi, total suspended matter, inorganic fraction of suspended matter, total nitrogen, total phosphorus, silicate, and orthophosphate). The third component of heterogeneity (EH_{phy}) included lake physical variables (lake surface area and mean depth). The fourth component of environmental heterogeneity (EH_{res}) was based on lake biological resources (chlorophyll a, the biomasses of cyanobacteria, cryptophytes, chlorococcales, and phytoplankton (<20 μm , 20–40 μm , and >40 μm), total phytoplankton, mixotrophic species, rotifers, cladocerans, cyclopoids, calanoids, oligotrichs, grazable and total ciliates, densities of bacterial and heterotrophic nanoflagellates, % coverage of submerged, floating, and emergent macrophytes, and % infestation of submerged macrophytes (PVI)). The fifth component of heterogeneity (EH_{clim}) included climatic variables (annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality).

2.5. Statistical Analysis

2.5.1. Categorization of Data

We used both categorical and continuous statistical approaches to test our hypotheses. First, we assessed the influence of five dichotomous categorical environmental variables on total fish beta diversity (β_{bray} and $\beta_{\text{sør}}$) and species turnover (β_{sim}) in order to separate their effects from the latitudinal gradient effect. Secondly, we tested whether the within-region variability in fish community structure differed between environmental factors (i.e., clear vs. turbid lakes, high vs. low TP, small vs. large lakes, connected vs. isolated lakes, presence vs. absence of exotic fish). Finally, we decomposed continuous environmental variables into four components of environmental heterogeneity (EH_{lim} = limnological, EH_{phy} = physical, EH_{res} = biological resources, and EH_{clim} = climate) and a component of geographical distance (GD) to assess whether the contribution of environmental heterogeneity to explaining variations in total fish beta diversity and species turnover would change across latitude between each of the five factorial environmental categories.

2.5.2. W*d-Test and Multivariate Dispersion

To assess the effects environmental factors (i.e., water turbidity, total phosphorus, lake area, lake connectivity, and lakes with and without exotic fish) on total fish beta diversity and turnover, we used both the W*d-test and the permutation test for homogeneity of multivariate dispersion (PERMDISP). To attribute lake group differences to location (location of the sample groups) and/or dispersion (spread of the sample groups), we combined W*d-test and PERMDISP analyses. Significant differences in beta diversity between groups of environmental factors (e.g., DK clear × DK turbid lakes) can be either caused by different mean values of the groups (location) or by different within-group variation in communities (dispersion) [50]. To disentangle this in our data, we used a W*d-test (a robust distance test-based on Welch's multivariate analysis of variance) to test for differences in fish community composition between the location of the sample groups [51]. The W*d-test has proven to be sensitive for unbalanced designs and when only the differences between location of sample groups are important [51], such as in our study. The W*d-test was performed with 9999 permutations to compare the differences in total beta diversity (β_{bray} and β_{sor}) and turnover (β_{sim}) between each group of dichotomous environmental variables (i.e., turbid vs. clear, high vs. low nutrient, large vs. small, connected vs. isolated and lakes with vs. without exotic fish) within each region of our study and between the geographic regions (i.e., DK = Denmark, BNL = Belgium/The Netherlands, SP = Spain). The W*d-test was performed using an R language implementation of the method available in Hamidi et al. [51]. Pairwise comparisons using the function `Tw2.posthoc.tests` available in Hamidi et al. [51] were performed to compare the total mean beta diversity and turnover values among all the groups for each dichotomous environmental variable.

We ran a permutation test for homogeneity of multivariate dispersion (PERMDISP) between all dichotomous environmental variables (aforementioned) within each region (DK, BNL, SP) to assess the effect of dispersion on fish beta diversity components (β_{bray} , β_{sor} and β_{sim}). To test if the spread of the sample groups (dispersions) between environmental factors within region differed (e.g., DK clear × DK turbid lakes), the distances of group members to the group centroid were subject to ANOVA analysis [49,52]. Higher dispersions among lakes and their group centroids denote that fish communities are more heterogeneous while lower dispersions denote that communities are more homogeneous. A Principal Coordinate Analyses (PCoA) was used to examine both the effects of location (tested with W*d-test) and dispersion (tested with PERMDISP in combination with ANOVA) on variation of fish community structure. The PERMDISP, ANOVA, and PCoA were undertaken using the R-package `vegan` [53]. For the total phosphorus factor (high vs. low nutrient), only Danish and Belgian/Dutch regions were applied in the W*d-test, PERMDISP and ANOVA analyses, as only few of the lakes in Spain had high total phosphorus concentration.

2.5.3. Generalized Dissimilarity Modelling (GDM)

To identify the relative importance of the geographic distance (i.e., GD) and environmental heterogeneity components (EH_{lim} , EH_{phy} , EH_{res} , and EH_{clim}) in driving changes in total fish beta diversity (β_{bray} and β_{sor}) and turnover (β_{sim}) across latitudes, we applied generalized dissimilarity modeling (GDM), a nonlinear statistical approach, using the R-package `gdm` [54]. Studies often assume that species replacement rate is constant along spatial and environmental gradients and generally use linear statistical approaches (e.g., linear regressions, redundancy analysis, partial redundancy analyses). However, linear statistical approaches cannot accommodate curvilinear relationships between biological and environmental variables, which prevent more realist interpretations of the data [55]. The response matrix in the main GDM was composed of all indices of fish beta diversity (β_{bray} , β_{sor} and β_{sim}), whereas the predictors were (1) dissimilarity in environmental variables (EH_{lim} , EH_{phy} , EH_{res} , and EH_{clim}) and (2) geographic distances between sites (pairwise distances). To assess the magnitude of changes in fish beta diversity and species turnover and the relative importance of each component of heterogeneity in explaining

these changes, we used the default basis function of three I-splines per predictor. We summed the coefficients of the I-splines corresponding to the maximum height obtained by the curve. The maximum height of each spline indicates the magnitude of total biological change along that gradient and thus the relative importance of that predictor's contribution to the biological turnover, while keeping all other environmental heterogeneity components constant (i.e., partial ecological distance) [54,56]. We tested the significance of environmental heterogeneity components by performing Monte Carlo analyses with 100 permutations and retained only significant variables in the results [54,56].

Graphics used to interpret GDM, W*d-test, ANOVA, and PERMDISP results were made with the R-package ggplot2 [57]. All analyses were performed in the software R version 4.2.2 [58].

3. Results

3.1. Environmental Gradients

The lake selection protocol adopted in our study avoided biases between geographic regions regarding the environmental gradients chosen, as indicated by the Kruskal–Wallis and Dunn's test analyses (Figure S1; Table S3). However, median values for total phosphorus were lower in southern Spain than in Belgium/The Netherlands and Denmark (Figure S1; Table S3), while the differences were not significant between Denmark and Belgium/The Netherlands (Figure S1). This pattern is explained by the absence of data for high-nutrient Spanish lakes that were rare in the area. The degree to which lakes were covered by submerged water plants was highly comparable between regions, and lake-size median and range had the same magnitude (Table S3).

The correlation analyses showed that the environmental gradients variables (i.e., submerged macrophyte coverage, total phosphorus, and lake size) were independent from each other, irrespective of the region selected (Tables S2 and S3).

3.2. Fish Communities

A total of 31 fish species were captured in the 63 lakes, and of these, 11 were non-native. Among the exotic species, two species have been introduced to a given region from elsewhere Europe (*Leucaspis delineatus* in Belgium/The Netherlands and *Scardinius* sp. in Spain), two are from both Central Europe and Asia (*Sander lucioperca* and *Carassius gibelio*), three from Asia (*Cyprinus carpio*, *Pseudorasbora parva*, and *Carassius auratus*), and four from North America (*Ameiurus nebulosus*, *Umbra pygmaea*, *Lepomis gibbosus*, and *Micropterus salmoides*) (Table S6). The frequency distribution graphs revealed that the composition of the most common species did not change between Danish and Belgium/Dutch lakes (i.e., many species are shared between Denmark and Belgium/The Netherlands), while there was a low overlap in species distribution between Spain and the other two regions (i.e., few species shared) (Figure 2).

In the Danish lakes, thirteen fish species were caught, of which only one was exotic (*S. lucioperca*). Three fish species only occurred in the Danish lakes (*Alburnus alburnus*, *Coregonus lavaretus* and *Osmerus eperlanus*). The average number of species caught per lake was 4.8 ± 1.8 and those most frequently caught were *Rutilus rutilus* and *Perca fluviatilis*, occurring in approximately 90% of the Danish lakes (Figure 2).

In the Belgian/Dutch lakes, a total of twenty species were caught, of which eight were exotics (*A. nebulosus*, *C. gibelio*, *C. carpio*, *U. pygmaea*, *L. gibbosus*, *L. delineatus*, *P. parva*, and *S. lucioperca*). Eight species were exclusive for Belgian/Dutch lakes (*A. nebulosus*, *Blicca bjoerkna*, *C. gibelio*, *U. pygmaea*, *L. delineatus*, *Leuciscus idus*, *P. parva*, and *Rhodeus sericeus amarus*) and five of these were exotics. The average number of species caught per lake was 5.7 ± 2.2 and the species most frequently captured were *R. rutilus*, *P. fluviatilis*, and *Scardinius erythrophthalmus*, which were found in approximately 70% of the Belgian/Dutch lakes (Figure 2).

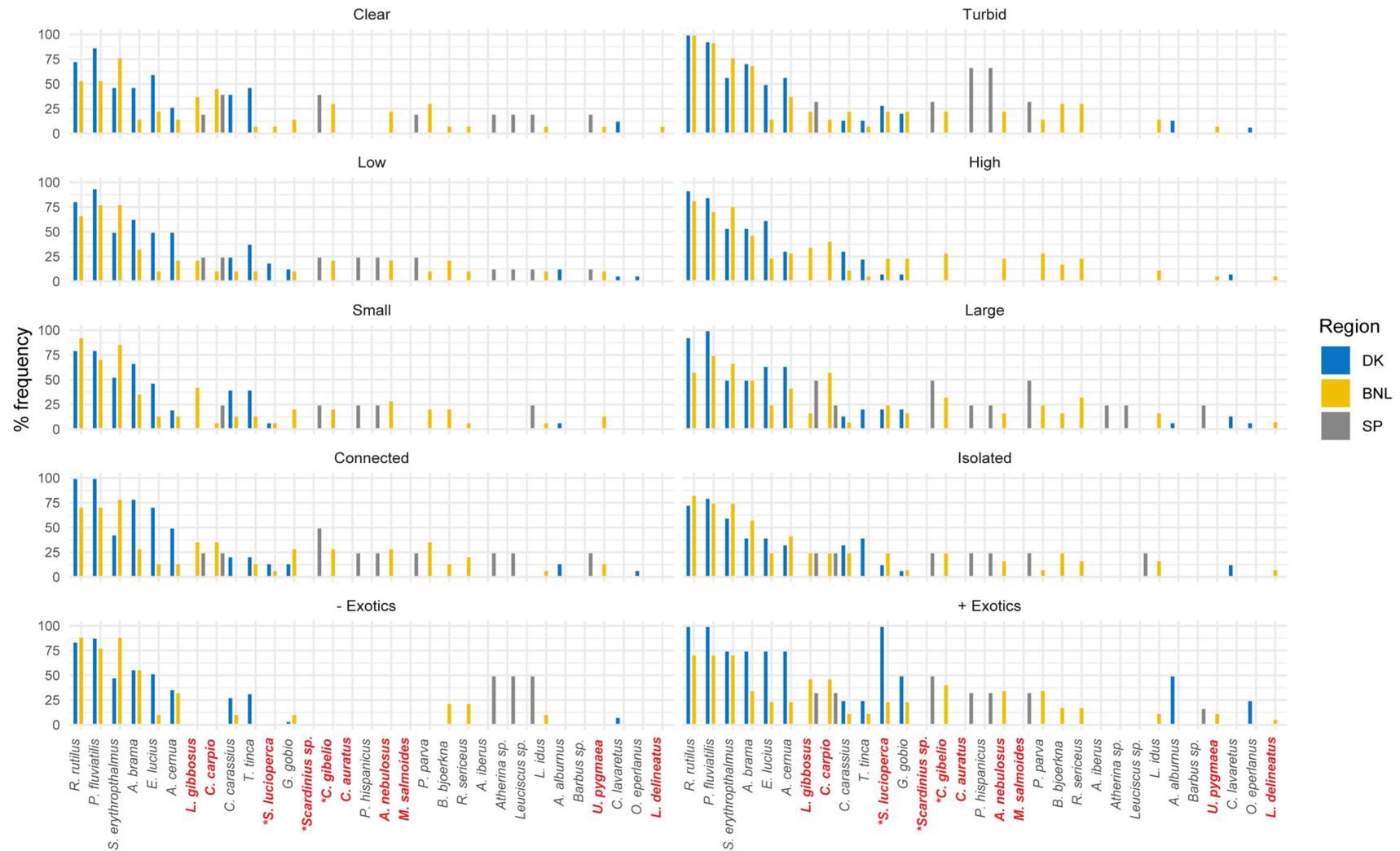


Figure 2. Relative frequency (%) of lakes occupied by each of the 31 fish species found in the 63 lakes sampled along a latitudinal gradient from northern Europe to southern Spain (DK = Denmark, BNL = Belgium, and The Netherlands, SP = Spain). Species names in bold red denote exotic species, and asterisks indicate species native in Europe but not in the region where it was captured (see Table S3 for more details).

In Spain, ten fish species were found in the eight lakes sampled, of which half were exotics (*C. carpio*, *M. salmoides*, *C. auratus*, and *Scardinius* sp.). The average number of species caught per lake was 1.8 ± 1.3 , the most frequent being *Scardinius* sp., *Micropterus salmoides*, *C. carpio*, and *Phoxinellus hispanicus* (Figure 2; Table S6). Among the ten species, four are considered small-range endemics (*Barbus* sp., *P. hispanicus*, *Atherina* sp., and *Aphanius ibericus*), with known distributions not exceeding 10,000 km² [59], and 80% of the species captured were exclusive for Spanish lakes in this study (*Barbus* sp., *Micropterus salmoides*, *Phoxinellus hispanicus*, *Leuciscus* sp., *Atherina* sp., *Aphanius ibericus*, *Carrasius auratus*, and *Scardinius* sp.), and of these, three were exotics (Figure 2; Table S6).

3.3. Location Effects on Beta Diversity Components

The results of the W^*d -test showed that total beta diversity (β_{bray} and β_{sor}) and the turnover component of beta diversity (β_{sim}) decreased from southern Spain towards Denmark in all the selected environmental gradients, with all beta diversity components generally lower in turbid than in clear lakes (Figure 3A–O; Figure S2). Increasing turbidity decreased beta diversity and turnover in Denmark, whereas in Belgium/The Netherlands and Spain, the beta diversity components were generally not affected by turbidity, except for β_{sor} in the Belgian/Dutch lakes (Figure 3A–C). Total phosphorus, in contrast, did not affect β_{bray} , β_{sor} , and β_{sim} (Figure 3D–F, J–L). In Belgium/The Netherlands, β_{bray} , β_{sor} , and β_{sim} were lower in small lakes, whereas an opposite pattern was observed for Denmark, and no difference was observed for Spain (Figure 3G–I). Lake connectivity decreased β_{sor} in Danish lakes, whereas no effect was observed in Belgium/The Netherlands and Spain. In Denmark, the presence of exotic fish decreased total beta diversity when abundant species were considered (β_{bray}), whereas no effect was observed for Spanish and Belgian/Dutch lakes (Figure 3M–O). However, in Belgian/Dutch lakes with exotic fish, total beta diversity and turnover (β_{bray} , β_{sor} and β_{sim}) were higher when exotic species were not omitted from the data, whereas an opposite pattern was observed for Danish lakes (except for β_{sim}) (Figure S3).

3.4. Dispersion Effects on Fish Beta Diversity Components

The PERMDISP in combination with ANOVA showed that the fish communities were more homogeneous (less dispersed) in turbid than in clear lakes in Denmark (only for β_{bray}) and Belgium/The Netherlands (β_{bray} and β_{sor}), while in Spain no difference was observed (Figure 4A–C; Table S7). Fish community variability (i.e., spread of the sample groups) was similar between lakes with low and high total phosphorus levels in Denmark and Belgium/The Netherlands (Figure 4D–F; Table S7). In Denmark, the fish communities were more homogeneous (β_{bray} and β_{sim}) in large than in small lakes, whereas in Belgium/The Netherlands, a reverse pattern was found but only when abundant species were considered (β_{bray}) (Figure 4G–I). No effect of lake size was observed for the Spanish lakes (Figure 4C, H, M). In Denmark, the fish communities were more homogeneous (β_{bray} , β_{sor} and β_{sim}) in connected than isolated lakes (Figure 4J–L), whereas no effect was observed for Belgian/Dutch and Spanish lakes. Fish community heterogenization (i.e., high spread of the sample groups) appeared for β_{sor} and β_{sim} in lakes with exotic fish species in Belgium/The Netherlands (β_{sor}) and Spain (β_{sim}), whereas no effects were detected in Denmark (Figure 4M–O; Table S7). However, when exotic species were not omitted from the data, fish community heterogenization was observed for all beta diversity components (β_{bray} , β_{sor} and β_{sim}) in the Belgian/Dutch lakes with exotic fish species (Figure S4). In Denmark, in contrast, when abundant species were taken into account, fish community homogenization (i.e., low spread of β_{bray} values to the centroid) was observed in lakes with exotic species, whereas no effect was observed in Spain (Figure S4).

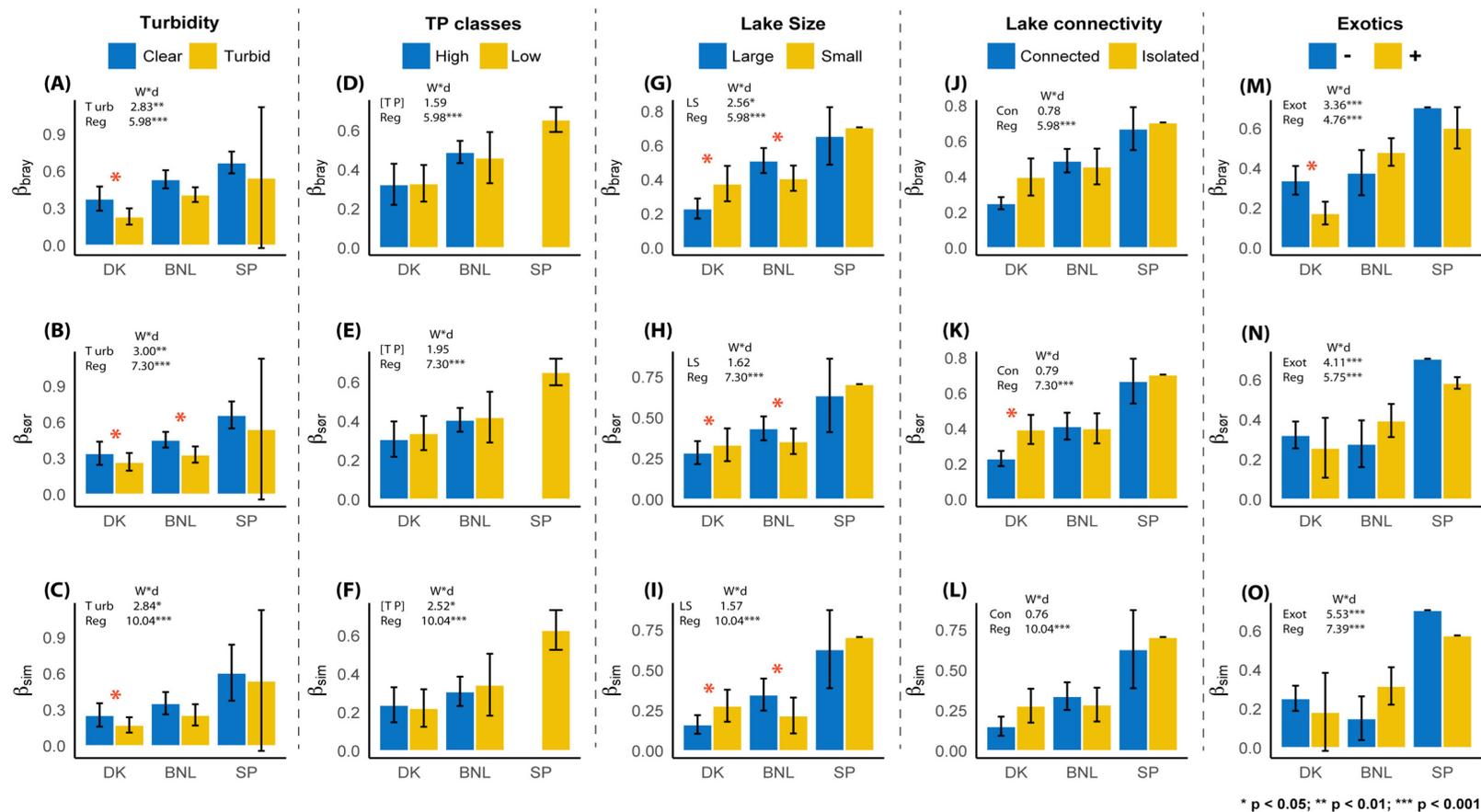


Figure 3. Results of W^*d -test to elucidate the effect of region (Reg), turbidity (clear vs. turbid), total phosphorus (high vs. low), lake size (small vs. large), lake connectivity (connected vs. isolated), and presence of exotic fish species (+ vs. – exotics) on fish beta diversity (β_{bray} and β_{sor}) and turnover (β_{sim}). A pairwise comparison among all the groups for each dichotomous environmental variable was also performed. Average distances to centroids were used to estimate fish β -diversity along a latitudinal gradient from northern Europe to southern Spain (DK = Denmark, BNL = Belgium and The Netherlands, SP = Spain). Total beta diversity (β_{bray} and β_{sor}) and turnover (β_{sim}) were calculated for clear and turbid (> or <20% of the lake surface area covered by macrophytes) (A–C), low and high nutrient-enriched (> or <100 $\mu\text{g l}^{-1}$ TP) (D–F), large and small lakes (lake surface > or <5 ha) (G–I), for connected and isolated lakes (J–L), and for lakes with presence (+) and absence (–) of exotic fish species (M–O). The error bars denote the confidence intervals and the red asterisks above the bars show that beta diversity (β_{bray} , β_{sor} , and β_{sim}) is different between the dichotomous environmental variables within the corresponding group region.

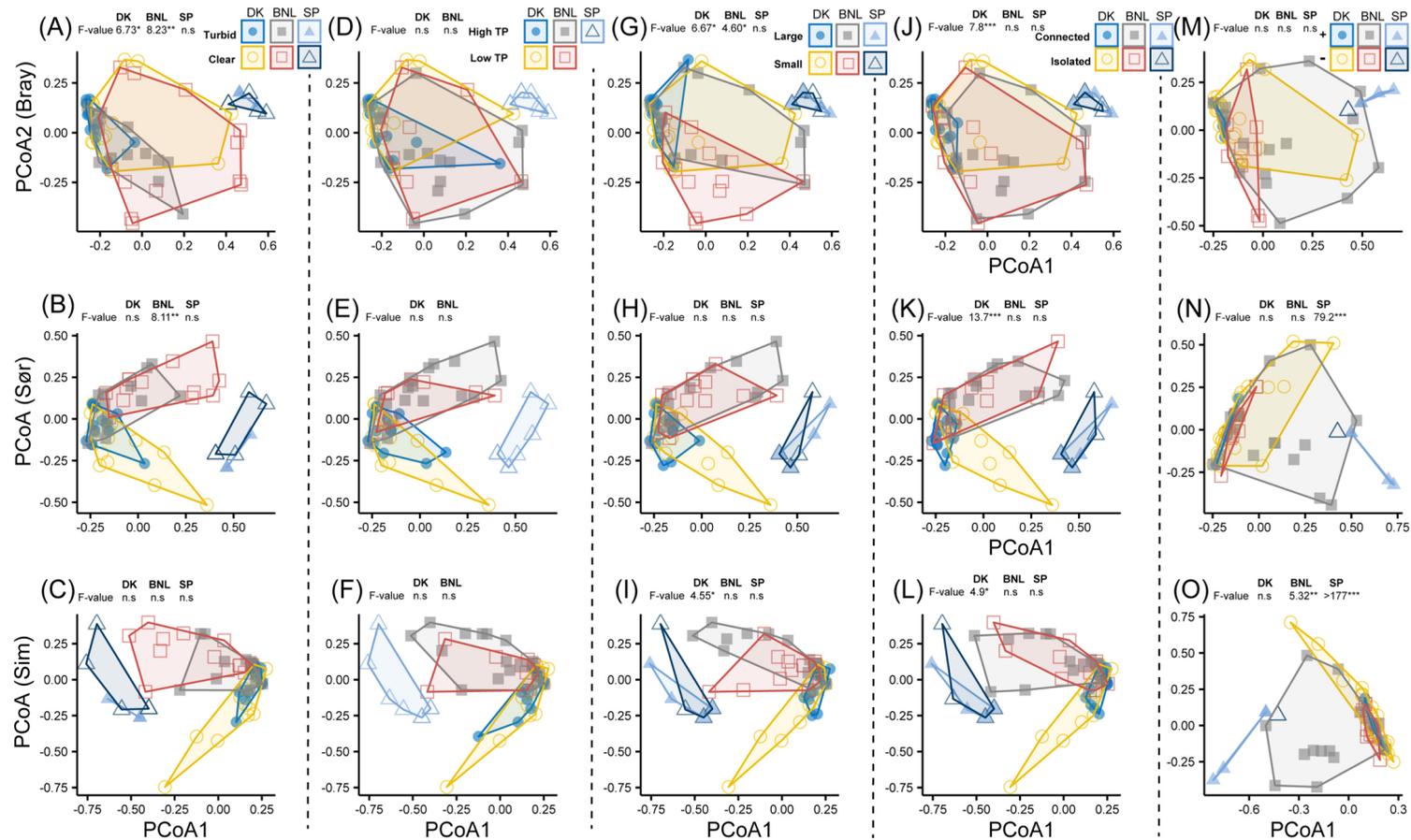


Figure 4. Results of principal coordinate and PERMDISP analyses assessing the effects of turbidity, total phosphorus, lake size, lake connectivity, and presence of exotic fish on group dispersion (spread of groups) within each region (DK = Denmark, BNL = Belgium and The Netherlands, SP = Spain). To test if the dispersions between groups within region differed (e.g., DK clear x DK turbid lakes), the distances of group members to the group centroid were subject to ANOVA analysis. The multivariate dispersions were computed using Bray–Curtis, Sørensen, and Simpson dissimilarity indices for clear and turbid (> or <20% of the lake surface area covered by macrophytes) (A–C), low and high nutrient-enriched (> or <100 $\mu\text{g l}^{-1}$ TP) (D–F), large and small lakes (lake surface > or <5 ha) (G–I), for connected and isolated lakes (J–L), and for lakes with (+) and without (−) exotic fish species (M–O). The asterisks in the F-values refer to the permutation test significance level (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s. = non-significant).

3.5. Contribution of Environmental Heterogeneity Components to Beta Diversity

The generalized dissimilarity models (GDMs) showed that across latitude, geographic distance (GD) and climate (EH_{clim}) gradients were the most important drivers of change in fish beta diversity components (β_{bray} , β_{sor} , and β_{sim}) (Table 1). The relative importance of GD and EH_{clim} in explaining variation in fish beta diversity was higher for the turbid than for the clear lakes. In lakes with low total phosphorus concentrations, GD and EH_{clim} were the most important variables contributing to changes in total fish beta diversity (β_{bray} and β_{sor}) and turnover (β_{sim}), but for lakes with high total phosphorus concentrations none of the environmental gradients affected the beta diversity components (between Denmark and Belgium/The Netherlands). For large and small lakes, connected and isolated lakes, and lakes with presence and absence of exotics fish, GD and EH_{clim} were the most important components explaining the variation in fish communities. However, the relative importance of climate for the changes in beta diversity (β_{bray} and β_{sor}) and species turnover (β_{sim}) was higher for small lakes, connected lakes and lakes without exotic fish species, whereas the relative importance of geographic distance in explaining β_{bray} and β_{sor} and β_{sim} was higher for large lakes, isolated lakes, and lakes with exotic fish species (Table 1; Figures 5 and 6). When exotic fish were omitted from the data analyses, the relative importance of climate became more important than geographic distance in lakes with exotics fish (Table 1).

Table 1. Relative importance of predictor variables (GD = geographic distance, EH_{lim} = limnological variables, EH_{phy} = physical variables, EH_{res} = resource variables, EH_{clim} = climatic variables) for fish beta diversity (β_{bray} and β_{sor}) and fish species turnover (β_{sim}) along a latitudinal gradient from northern Europe to southern Spain by summing the coefficients of the I-splines from the generalized dissimilarity models (GDMs). The analyses were performed per level of each gradient variable across the entire geographic range. Significant predictors are shown in bold. Insignificant predictors are indicated by dashes. Italicized coefficients indicate marginally significant ($0.051 < p < 0.08$) results of Monte Carlo analyses with 100 permutations. GDM analyses were also performed after removing (AR) exotics fish from the species matrix.

β -Diversity Components	GD	EH _{lim}	EH _{phy}	EH _{res}	EH _{clim}
β_{bray}					
Turbid	13.11	-	-	0.94	16.13
Clear	2.47	-	-	<i>1.06</i>	3.38
High TP	-	-	-	-	-
Low TP	6.78	3.32	-	-	5.93
Large lakes	6.91	-	-	<i>0.64</i>	5.32
Small lakes	9.13	-	-	-	20.74
Connected lakes	0.46	-	-	-	7.08
Isolated lakes	5.43	-	-	-	-
+Exotics	4.06	-	-	0.89	-
-Exotics	0.86	-	-	-	4.94
+Exotics (AR)	1.09	-	-	-	3.07
β_{sor}					
Turbid	9.00	-	-	-	6.25
Clear	2.70	-	-	-	2.64
High TP	-	-	-	-	-
Low TP	6.71	2.12	-	-	4.81
Large lakes	8.17	-	-	0.83	-
Small lakes	1.46	-	2.75	-	8.44
Connected lakes	2.88	-	-	-	4.53
Isolated lakes	5.03	-	-	-	3.04
+Exotics	2.86	-	-	0.43	2.41
-Exotics	1.33	-	-	-	-
+Exotics (AR)	1.45	-	-	0.49	2.24

Table 1. Cont.

β -Diversity Components	GD	EH_{lim}	EH_{phy}	EH_{res}	EH_{clim}
β_{sim}					
Turbid	7.23	-	-	0.31	6.82
Clear	2.80	-	-	-	1.84
High TP	-	-	-	-	-
Low TP	5.89	2.24	-	-	4.41
Large lakes	8.05	-	-	-	2.58
Small lakes	0.86	-	-	-	5.98
Connected lakes	3.08	-	-	-	4.34
Isolated lakes	4.27	-	-	-	-
+Exotics	2.29	-	-	0.36	1.37
-Exotics	0.73	-	-	-	3.25
+Exotics (AR)	1.23	-	-	-	1.79

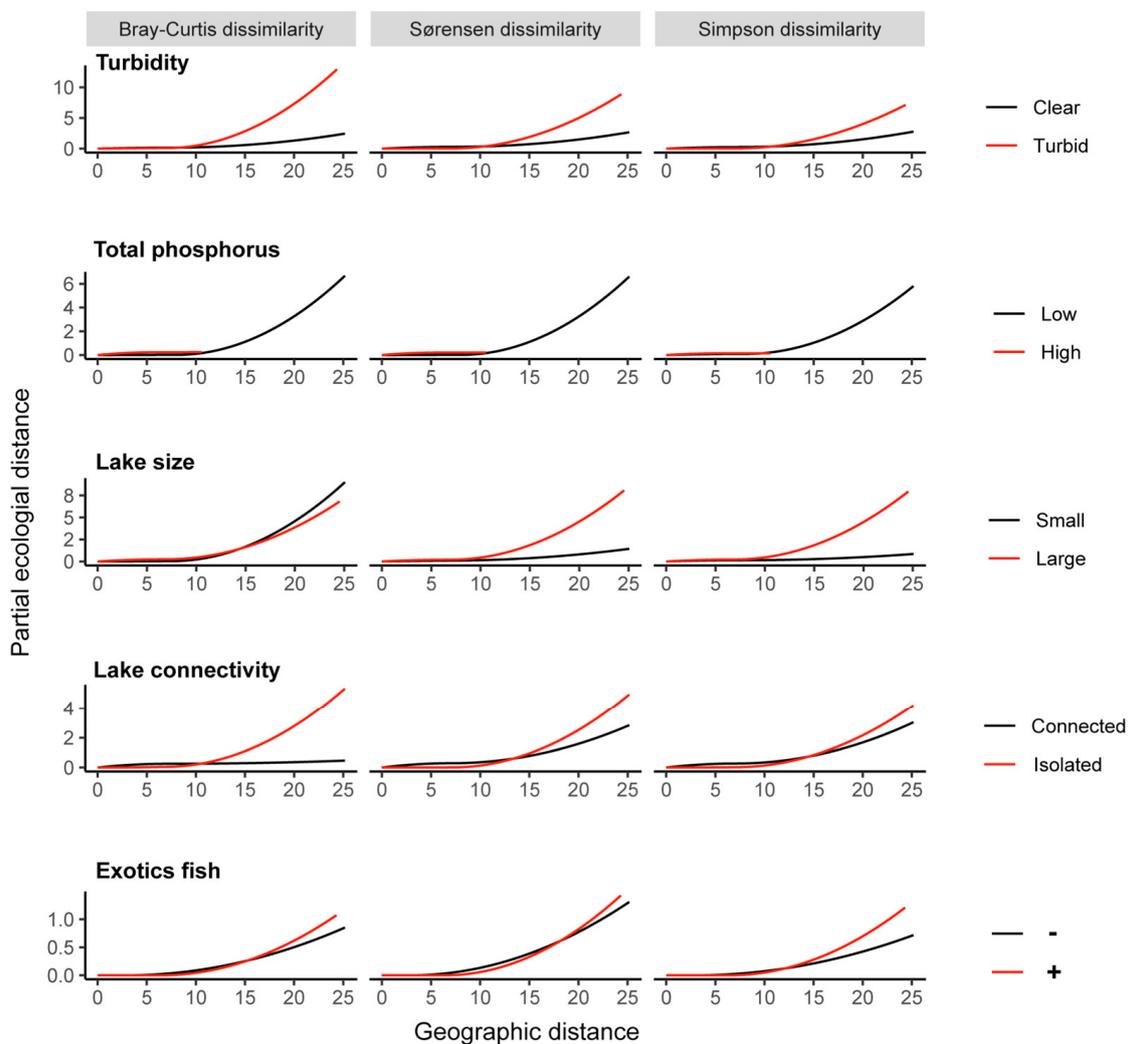


Figure 5. Generalized dissimilarity model-fitted I-splines (partial regression fits) relating geographic distance to fish beta diversity (Bray–Curtis and Sørensen) and fish species turnover (Simpson) along a latitudinal gradient from northern Europe to southern Spain. Each generalized dissimilarity model was performed for clear and turbid lakes (> or <20% of the lake surface area covered by macrophytes—proxy for clear and turbid lakes, respectively), for low and high nutrient-enriched lakes (> or <100 $\mu\text{g l}^{-1}$ TP), for small and large lakes (lake surface > or <5 ha), for connected and isolated lakes, and for lakes with (+) and without (–) exotic fish. For units of geographic distance, see Table S1.

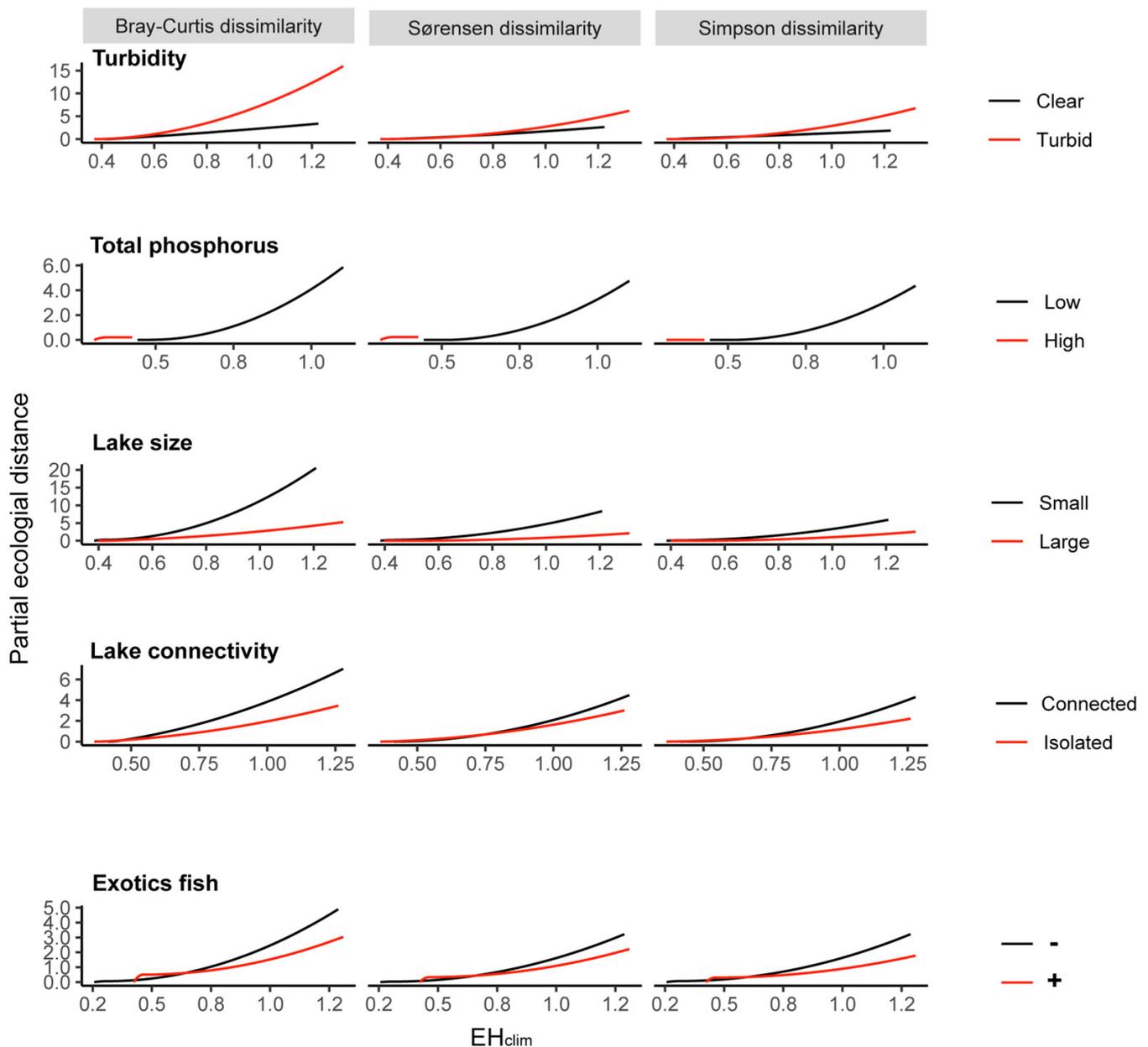


Figure 6. Generalized dissimilarity model-fitted I-splines (partial regression fits) relating environmental heterogeneity variables (EH_{clim}) to fish beta diversity (Bray–Curtis and Sørensen) and fish species turnover (Simpson) along a latitudinal gradient from northern Europe to southern Spain. Each generalized dissimilarity model was run for clear and turbid lakes (> or <20% of the lake surface area covered by macrophytes—proxy for clear and turbid lakes, respectively), for low and high nutrient-enriched lakes (> or <100 $\mu\text{g l}^{-1}$ TP), for small and large lakes (lake surface > or <5 ha), for connected and isolated lakes and for lakes with (+) and without (−) exotic fish. For units of EH_{clim} , see Table S1.

4. Discussion

Our results showed that fish beta diversity (β_{bray} , β_{sor} , and β_{sim}) increased from Denmark towards southern Spain and the geographic distance and climate variability (EH_{clim}) were the main drivers of change on fish community structure across latitude (Figure S2; Figure 3A–O; Figures 4 and 5). Contrary to our expectations, the rate of change in fish communities with geographic distance (across latitude) was higher in lakes with high turbidity, isolated, and with presence of exotics than their opposing dichotomous environ-

mental factors (Table 1; Figures 5 and 6). At within-region scale, turbidity homogenized fish communities in Danish (β_{bray}) and Belgian/Dutch lakes (β_{bray} and $\beta_{\text{sør}}$) (Figure 3A–C), whereas nutrient enrichment had no effect on fish communities within any of the regions of our study (Figure 3D–F). The increase in lake size drove homogenization of Danish fish communities (β_{bray} and β_{sim}) and the heterogenization of Dutch/Belgian fish communities (β_{bray}) (Figure 3G–I). Lake connectivity, on the other hand, homogenized only Danish fish communities (β_{bray} , $\beta_{\text{sør}}$ and β_{sim}) (Figures 3 and 4J–L). The presence of exotic fish heterogenized fish communities in Spain and in Belgium/The Netherlands (β_{sim}), whereas it caused no effect on Danish lakes. However, when exotic fish were included in the analyses, no effect was detected in Spain, while it homogenized Danish (β_{bray}) and heterogenized Belgian/Dutch fish communities (β_{bray} , $\beta_{\text{sør}}$, and β_{sim}) (Figure 3M–O; Figure S4).

The increase in fish beta diversity with decreasing latitude agrees with the beta diversity patterns reported for terrestrial, freshwater, and marine ecosystems [10,12,18,19,60]. In Europe, northern glaciated history and southern regions' isolation and/or role as a major glacial refugium (unglaciated, with dampened climatic oscillations), favoring the origination and survival of locally endemic species in the south generally explain the high dissimilarity between northern and southern European fish faunas [61–63]. In our study, however, the decreasing fish beta diversity towards higher latitudes is mostly explained by the differences observed between local and regional fish diversities within regions. For instance, in Spanish lakes, the mean local richness reported was 2.1 ± 1.4 and the regional diversity was 10, whereas in Danish lakes, the mean local richness was 4.3 ± 1.8 and regional diversity was 13 (Table S6). Furthermore, 80% of the species captured in the Spanish lakes were exclusive for the region; of these, 40% are considered small-range endemics, but the presence of some exotic fish species only in Spain also contributed importantly to the differences observed in total fish beta diversity (β_{bray} and $\beta_{\text{sør}}$) and species turnover (β_{sim}) across latitude (Figure 2; Table S3). The low local (alpha) diversity in Andalusia and south Castilla-La Mancha may be explained by the high lake-drying frequency due to alternating cycles of dry and humid conditions and prolonged droughts [64,65], leading to increased habitat heterogeneity and dispersal limitation among lakes as in other dryland systems [66]. Drought also alters availability, quality, and connectivity of lake habitats affecting the strength of species interactions, which increase beta diversity and species turnover among geographic regions in freshwater ecosystems [67,68].

Environmental heterogeneity is regarded as one of the governing factors affecting communities' structure in multiple ecosystems [69–77]. Studies have shown that decreased habitat heterogeneity, due to either natural or anthropogenic environmental disturbance, can significantly reduce beta diversity in terrestrial, marine, and freshwater ecosystems [8,71,75,78]. Further, environmental heterogeneity can also increase beta diversity, as different habitats within lakes and among regions may support different species with different adaptations over time [79]. Our results showed that environmental heterogeneity metrics associated with lake abiotic conditions within the regions (EH_{lim} , EH_{phy} and EH_{res}) had either low or no influences on changes in total beta diversity (β_{bray} and $\beta_{\text{sør}}$) and species turnover (β_{sim}) irrespective of environmental factors considered (i.e., low/high turbidity, low/high total phosphorus, small/large lake size, connected/isolated lakes, and with/without exotic fish species). However, the relative importance of geographic distance (GD) and climate heterogeneity (EH_{clim}) in explaining changes in β_{bray} , $\beta_{\text{sør}}$, and β_{sim} increased across latitude. These results reinforce that biological differences among localities are rather driven by distance and climatic variability than within-region lake abiotic variability [21,23,80]. Moreover, our study also concurs with Brucet et al. [23], who found that anthropogenic pressures had little or no effect on fish diversity across a latitudinal gradient in Europe, whereas temperature differences (related to lake gradients and morphometry) contributed importantly.

In shallow lakes, a water turbidity increase is generally associated with phytoplankton blooms and loss of macrophyte coverage [38,39], which reduces habitat heterogeneity and accordingly increases the among-lake environmental and fish assemblage similar-

ity [81]. Our results concur with this pattern and revealed that within regions, turbidity homogenized fish communities among lakes in Denmark and Belgium/The Netherlands (Figure 4A–C), highlighting the potential importance of macrophyte coverage in adding habitat heterogeneity to shallow lakes ecosystems. However, no effect of turbidity was detected in Spanish fish communities, which can be explained by the low variability in the percentage of submerged macrophytes coverage among the lakes in Andalusia and south of Castilla-La Mancha region (Figure S1; Table S3), increasing fish community similarity between lakes with low and high turbidity. Area is also an important factor determining environmental heterogeneity in ecosystems [40,82], leading to higher beta diversity in larger lakes as seen for the fish communities in the lakes from Belgium/The Netherlands (Figure 3G–I; Figure 4G–I). However, the opposite pattern was found for the Danish lakes. We can speculate that this is due to more frequent and longer duration of ice-cover in shallow Danish lakes, resulting in more erratic under-ice fish kill. No effect of lake size was detected in Spanish fish communities, likely reflecting the other strong constraints on the fish community mentioned above.

Eutrophication is one of the main causes of biotic homogenization and environmental disruption in multiple ecosystems [81,83–87]. Our results, however, showed that total phosphorus (proxy for productivity increase) had no influence on total fish beta diversity and species turnover within the regions (Figure 3F–H; Figure 4F–H), which may reflect the unbalanced representation of lakes in the defined environmental categories of our study as we in the lake sampling design strived to isolate the effect of water plants and nutrient that is usually inversely correlated in nature, but high-nutrient lakes with water plants and low-nutrient lakes without water plants were difficult to find (for details see Declerck et al. [36]).

Loss of habitat connectivity poses a serious threat to the maintenance of biodiversity and functioning of terrestrial and freshwater ecosystems [88,89]. Lake connectivity favors species dispersion and colonization among lakes, which may increase communities' similarity over space and time, whereas an opposite pattern is expected among isolated lakes [22,90]. Our results concur with this as we found that the relative importance of geographic distance to explain changes in fish communities was higher in isolated than in connected lakes across the latitudinal gradient (Table 1), though it is not clear why a reversed pattern occurred with climate variability (EHclim). However, at within-region scale, this pattern was observed only for fish communities in Danish lakes (i.e., homogenization of fish communities in connected lakes) (Figure 3; Figure 4J–L). In Spain, the limited connectivity between lakes (i.e., connectivity often occurred only between two lakes) may have reduced the dis-similarity between groups of connected and isolated lakes, whereas the lack of effect of lake connectivity in Belgium/The Netherlands is not clear. The presence of any physical or chemical barriers (e.g., atrazine) among connected lakes could prevent the exchange of fish populations of other species and limit the effect of connectivity on community similarity/dissimilarity [91]. Furthermore, the presence of competing or predatory species (i.e., exotics or endemic predators) in connected lakes may prevent fish from colonizing, which reduces the effect of connectivity on fish community similarity [92].

The introduction of exotic species poses a serious threat to the biodiversity of Earth's ecosystems [93–95], and many studies have already reported species loss and biotic homogenization of communities due to fish species' introductions in lake ecosystems [96–101]. However, studies have also shown an increase in taxonomic diversity or absence of threats to species richness and beta diversity after species introductions [8,101]. Thus, changes in beta diversity can be driven either by additive or subtractive processes [8]. In some lakes, beta diversity may increase when dominant species become extinct or when new species arrive (including via human introductions) without attaining dominance, while beta diversity may decrease when rare species are lost or when formerly rare species become dominant [8]. Our results showed that the presence of exotics in the data analyses increased fish assemblage dissimilarity in the Belgian/Dutch (community heterogenization) both by the presence of exotic fish species and native species permanence (Figure 2; Figure S4A–C).

In Denmark, however, when the only exotic species (*S. lucioperca*) was excluded from the data analyses, the patterns did not change between lakes with and without exotic fish, whereas in Spain, the exclusion of the exotics caused homogenization of the communities (Figure S4). In Belgium/The Netherlands and Denmark, when the exotic fish were removed from the data analyses, the communities became similar between lakes with and without exotic fish (except for β_{bray} in DK), whereas the reverse pattern was observed for Spanish lakes (Figure S4). However, the patterns of homogenization and heterogenization in lakes with exotic fish may have been affected by the snapshot sampling procedure (i.e., a single sampling event) and the limited amount of available data, particularly in the case of Spanish lakes where some lakes were dry during the sampling period. For instance, Moi et al. [102] have shown in long-term studies of hyperdiverse tropical ecosystems that non-native fish can drive homogenization of native species over time at local scale, reducing ecosystem multifunctionality. Long-term studies assessing the impacts of exotic fish species on native species may, therefore, be more elucidative to understand the impacts of non-native species on fish communities and ecosystem functioning [102].

5. Conclusions

Using independent gradients to assess changes in fish communities in European shallow lakes at within-region scale and across a latitudinal range, we have shown that fish beta diversity and species turnover increased from Denmark to southern Spain. The changes in beta diversity components (β_{bray} , β_{sor} and β_{sim}) were greatest in turbid lakes and were principally related to geographic distance and climatic differences across regions. Within regions, increasing turbidity drove the homogenization of the fish communities, and the presence of exotic fish species appeared to be the driver of fish assemblage heterogenization in Belgian/Dutch and Spanish lakes; in Danish lakes, however, an opposite pattern occurred, though it must be emphasized that only one exotic species was detected in the Danish lakes studied. Our findings suggest that across a latitudinal gradient, turbidity, nutrient enrichment, lake size, lake connectivity, and presence of exotic fish did not substantially affect the biogeographic patterns in small-sized European shallow lakes but can increase the rate of changes in fish communities across latitude. However, at within-region scale, these factors may cause either homogenization or heterogenization of fish communities depending on latitude and perhaps the number of exotic species present. Our results reinforce that across latitudes, biogeographic gradients are mostly driven by spatial and climatic variables, whereas at local scale, environmental conditions may disassemble fish communities. Therefore, large-scale human impacts such as those resulting from introduction of exotic species and turbidity may have a considerable influence on the mechanisms of assembly processes in fish communities at local and regional scales across environmental gradients in small-sized European shallow lakes.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w15101831/s1>, Figure S1: Kruskal–Wallis tests comparing the means among regions for submerged macrophyte coverage (SUBMCOV %), lakes size (AREA), and total phosphorus (TP); Figure S2: Results of W*d-test to assess the effect of geographical region (DK = Denmark, BNL = Belgium and The Netherlands, SP = Spain) on fish beta diversity (β_{bray} and β_{sor}) and turnover (β_{sim}); Figure S3: Results of W*d-test to elucidate the effect of presence of exotic (Exot) fish species (+ vs. – exotics) and region (Reg) on fish beta diversity (β_{bray} and β_{sor}) and turnover (β_{sim}). Figure S4: Results of principal coordinate (PCoA) and PERMDISP analyses assessing the effects of presence of exotic fish on group dispersion (variances) within each region (DK = Denmark, BNL = Belgium and The Netherlands, SP = Spain); Table S1: Environmental variables and environmental heterogeneity components (EH) used as predictors in the general dissimilarity models (GDMs). The climate variables used for EH_{clim} were averages for the years 1970–2000 and were obtained from *WorldClim* (Fick and Hijmans, 2017); Table S2: Product–moment correlation coefficients[®] and associated *p* values between gradient variables in each of the three regions; Table S3: Summary statistics of gradient variables for each of the studied geographic regions. For the analyses, we used data from 63 shallow lakes sampled from northern Europe to southern

Spain (Denmark = 29; Belgium/The Netherlands = 26; Spain = 8); Table S4: Number of lakes in the five dichotomous categories of environmental effects: water turbidity (clear or turbid), total phosphorus (low and high), lake surface area (small and large), connectivity (connected and isolated), and lakes with (+) and without (-) exotic fish species; Table S5: Lakes names, lake codes, lake regions, coordinates (decimals) and categories of environmental effects: water turbidity (clear or turbid), total phosphorus (low and high), lake surface area (small and large), connectivity (connected and isolated), and lakes with and without exotic fish species; Table S6: Fish occurrence in the different regions and number of lakes in which species appear in the Danish (DK), Belgian/Dutch (BNL), and Spanish lakes (SP). Exotic species refers to non-native fish species either within the study's region (SP, BNL, and DK) or Europe; Table S7: Permutation test for homogeneity of multivariate dispersions (PERMDISP) and W*d analyses assessing the effects of turbidity, total phosphorus, lake size, lake connectivity, and presence of exotic fish on group dispersion and on group location between environmental categories within each region (DK = Denmark, BNL = Belgium and The Netherlands, SP = Spain). References [103–108] are cited in Supplementary Materials.

Author Contributions: All authors (R.F.M., J.-C.S., H.F., L.D.M., T.L.L., M.S., J.M.C.-P. and E.J.) contributed to the study conception, sampling design, and/or analyses. L.D.M., T.L.L., M.S., J.M.C.-P. and E.J. conducted the fieldwork. R.F.M. and E.J. wrote the first draft of the manuscript and all authors contributed to the subsequent versions of the draft. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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