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Model-based decomposition of environmental, spatial and species-interaction effects on the community structure of common fish species in 772 European lakes

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Abstract

Aim: We tested whether there is a strong effect of species interactions on assembly of local lake fish communities, in addition to environmental filters and dispersal.

Location: Seven hundred and seventy-two European lakes and reservoirs.

Time period: 1993–2012.

Major taxa studied: Nineteen species of freshwater fishes.

Methods: We applied a latent variable approach using Bayesian Markov chain Monte Carlo algorithms (R package "BORAL"). We compared the contributions of six environmental predictors and the spatial organization of 772 European lakes in 209 river basins on the presence/absence of the 19 most frequent fish species and on the biomass and mean mass of the six dominant species. We inspected the residual correlation matrix for positive and negative correlations between species.

Results: Environmental (50%) and spatial (10%) predictors contributed to the presence/absence assembly of lake fish communities, whereas lake size and productivity contributed strongly to the biomass and mean mass structures. We found highly significant negative correlations between predator and prey fish species pairs in the presence/absence, biomass and mean mass datasets. There were more significantly positive than negative correlations between species pairs in all three datasets. In addition, unmeasured abiotic predictors might explain some of the correlations between species.

Main conclusions: Strong effects of species interactions on assembly of lake fish communities are very likely. We admit that our approach is of a correlational nature and does not generate mechanistic evidence that interactions strongly shape fish community structures; however, the results fit with present knowledge about the interactions between the most frequent fish species in European lakes and they support the assumption that, in particular, the mean masses of fish species in lakes are modified by species interactions.

KEYWORDS

community assembly, dispersal, environmental filters, latent variables, model-based analysis, predator–prey interactions

1 | INTRODUCTION

Macroecology traditionally considers species distributions at large spatial scales to be primarily driven by abiotic environmental conditions. In contrast, community ecology considers the interactions between species as paramount to understand the composition of local communities. Several approaches have been suggested to link macroecology and community ecology (Soberón, 2007; Staniczenko et al., 2017; Vellend, 2010). By adopting the terminology from evolutionary biology, a conceptual synthesis of community ecology suggested that patterns in the diversity and composition of species are influenced by four major processes: selection, drift, speciation and dispersal (Vellend, 2010). Selection represents deterministic differences in fitness among species, drift represents stochastic changes in species abundance, speciation creates new species, and dispersal is the movement of organisms across space. The effects of speciation and drift on local communities can be inferred only from following community composition over time, whereas information on the effects of selection and dispersal can be obtained from comparisons of community composition across large spatial and environmental gradients (e.g., Boulangeat et al., 2012; Cazelles et al., 2016; Lansac-Tôha et al., 2021). The metacommunity model of dispersal assumes a network of small local communities linked by dispersal among them (Holyoak et al., 2005). Selection processes encompass fundamental niche (mainly abiotic) filters that determine whether a species can colonize and persist in a given habitat, whereas the realized niche filters are imposed by competitive, mutualistic and agonistic (predator–prey or pathogen–host) interactions (Weiher et al., 2011). Accordingly, the assembly processes of abiotic filtering and dispersal, as considered by macroecology, are linked with the species interactions at local scales dominantly considered in community ecology.

Freshwater lakes are good model systems for exploring the relative effects of dispersal, abiotic conditions and species interactions on community assembly, because lakes can be considered as relatively discrete ecosystems within the terrestrial landscape, potentially with a hydraulic connection to other similar ecosystems (Heino et al., 2021; Jackson et al., 2001; Tonn et al., 1990). The metacommunity structure of several organism groups in freshwater lakes has been demonstrated empirically (Beisner et al., 2006; De Bie et al., 2012; Heino et al., 2015; Lansac-Tôha et al., 2021), with differences in the dispersal intensities of organisms determining the spatial extent at which environmental, spatial and hydrological processes structure aquatic communities. For example, in Brazilian floodplain lakes, environmental factors interact with hydrological period to structure communities of micro- and macro-organisms at the smallest (within floodplain) spatial scales, whereas species distributions are not dispersal limited. Between floodplains, the relative importance of environmental factors increases, whereas spatial factors become most important at the subcontinental scale, especially for poor dispersers (Lansac-Tôha et al., 2021). Other studies on freshwater invertebrates across large spatial scales suggest that, in addition to spatial factors, climatic gradients (e.g., temperature, precipitation) and ecosystem size are dominant predictors of species richness, community composition and average organismal size in lakes (Hayden et al., 2019; Meerhoff et al., 2012). Studies on processes of community assembly for fishes in freshwater lakes likewise identified dominant roles of abiotic filtering at large spatial scales (Brucet et al., 2013; Emmrich et al., 2014; Jeppesen et al., 2020).

Fish population densities and population size structure are modified primarily by productivity of the ecosystems (Arranz et al., 2016; Brucet et al., 2013), and dispersal limitation of small fish species can affect local fish species occurrences (Mehner et al., 2014; Olden et al., 2001). Strong effects of species interactions on community composition have been documented predominantly by following local communities over time; for example, in response to predator-induced trophic cascades (Carpenter & Kitchell, 1993; Meijer et al., 1994). In contrast, when comparing lake fish communities across larger spatial scales, evidence for strong effects of negative interactions between fish species on community composition was usually poor (Chu et al., 2016; Mehner et al., 2016), whereas positive covariation of occurrences and population densities for functionally similar or phylogenetically related species was common (MacDougall et al., 2018; Mason et al., 2008; Mehner et al., 2016).

These somewhat contradictory results on the importance of species interactions for assembly processes of fish communities in lakes might reflect two major intrinsic difficulties. First, interaction strength is often context dependent (MacDougall et al., 2018); hence, a strong effect of species interactions for community assembly can be identified only if abiotic filters are evaluated simultaneously. For example, temperature determines whether brown trout (*Salmo trutta*) and pike (*Esox lucius*) coexist in lakes, with co-occurrence found only in large and colder lakes (Hein et al., 2014; McLoone et al., 2018). Second, the complex interplay between interaction effects, environmental filtering and dispersal limitation generates a statistical challenge (Warton et al., 2015). The relative contribution from each process to community assembly cannot be disentangled by the usually applied distance-based ordinations (Legendre & Gauthier, 2014) or diversity measures (Magurran, 2004). For example, it can be difficult to discriminate between the effects of agonistic interactions and niche differences when two species rarely co-occur together in a set of lakes. In turn, co-occurrences of species can be driven either by facilitation between species or by similar abiotic niches.

Recent statistical developments, such as the hierarchical modelling of species communities (HMSC), facilitate the formulation of data-driven hypotheses with respect to community assembly processes (Ovaskainen et al., 2017). For example, by applying a latent variable approach, the models can isolate dispersal (spatial) and abiotic effects on fish community composition, ultimately leaving a residual correlation matrix that might reflect species interaction effects (Warton et al., 2015). Despite their conceptual advantages, it is still debatable whether the HMSC approach and the application of latent variables can identify the fundamental mechanisms behind species co-occurrences across communities, based on correlational evidence (Blanchet et al., 2020; Münkemüller et al., 2020). Recommendations to improve the reliability and validity of results obtained by the HMSC approach encompass the extension of datasets from pure presence/absence (p/a) of species to abundance or biomass contributions within a community, proper formulation of hypotheses and testable predictions, the application of the framework to a sufficiently large dataset and the report of uncertainty in the results (Blanchet et al., 2020; Hoegh & Roberts, 2020; Münkemüller et al., 2020).

Here, we used such a hierarchical model-based approach with latent variables to quantify the contributions from environmental, spatial and species-interaction effects to the composition of 772 European lake fish communities. We tested datasets on p/a, biomass and mean mass of the dominant fish species in the lakes. The dimension of the dataset was large enough to ensure that the 19 most frequent species (see Table 1) occurred in a sufficiently high number of lakes ($n \geq 30$). Abiotic predictors covered climatic conditions (temperature, precipitation and elevation), lake size (depth and area) and lake productivity (using total phosphorus concentration as a surrogate). Therefore, the major environmental filters for large-scale (continental) and local presence, biomass and size of fish species were included. Spatial effects to infer potential contributions from dispersal were modelled by assuming a higher similarity of fish community composition in lakes belonging to the same river basin. We hypothesized that all three community assembly processes (abiotic filtering, species interactions and dispersal) would be important to

TABLE 1 Overview of the 19 most frequent fish species in 772 European lakes, with Pearson correlation coefficients between empirically estimated and model-predicted presence/absence (p/a), biomass or mean mass for 19 (p/a) or six (biomass, mean mass) fish species

Common name	Scientific name	p/a	Biomass	Mean mass
Bream	*Abramis brama*	0.773	0.594	0.615
Bleak	*Alburnus alburnus*	0.837	–	–
White bream	*Blicca bjoerkna*	0.792	–	–
Crucian carp	*Carassius carassius*	0.293	–	–
Stone loach	*Cobitis taenia*	0.629	–	–
Vendace	*Coregonus albula*	0.689	–	–
Whitefish	*Coregonus* sp.	0.543	–	–
Pike	*Esox lucius*	0.462	0.342	0.844
Gudgeon	*Gobio gobio*	0.451	–	–
Ruffe	*Gymnocephalus cernuus*	0.670	0.505	0.522
Bluegill	*Lepomis gibbosus*	0.891	–	–
Sunbleak	*Leucaspius delineatus*	0.457	–	–
Burbot	*Lota lota*	0.993	–	–
Smelt	*Osmerus eperlanus*	0.701	–	–
Perch	*Perca fluviatilis*	0.833	0.851	0.979
Roach	*Rutilus rutilus*	0.661	0.538	0.858
Pikeperch	*Sander lucioperca*	0.991	–	–
Rudd	*Scardinius erythrophthalmus*	0.999	0.707	0.759
Tench	*Tinca tinca*	0.631	–	–
	Mean	0.700	0.590	0.763

Note: The models included three latent variables, six abiotic predictors and random row effects to account for spatial effects. All correlations, $p < .0001$.

model the fish datasets, but their relative contributions would be scale dependent. We predicted that environmental filtering from climatic effects and dispersal limitation would contribute strongly to the large-scale p/a structure, whereas lake size and productivity would have a stronger effect on the local biomass and mean masses of fishes. In turn, we predicted that the residual variance potentially reflecting species interaction effects would contribute strongly to predicting local fish biomass and mean masses but might be a weaker predictor for the continental p/a structure of the most frequent fish species. According to earlier studies, we expected the strongest negative interactions for predator–prey pairs, but likewise we expected to find numerous positive correlations between species with strong phylogenetic relationships in the residual correlation matrices.

2 | METHODS

We used the dataset of fish communities in 1,943 European lakes and reservoirs accumulated from standardized fishing by multi-mesh gillnets for the purpose of the European Water Framework Directive (Brucet et al., 2013; Mehner et al., 2017). Details of background, methods and basic fish community structure have been summarized previously (Brucet et al., 2013; Mehner et al., 2017). These lakes were sampled between 1993 and 2012. In short, fishing effort (number of nets per lake) was standardized according to lake area and depth, and fishing was performed using 30-m-long and 1.5-m-high benthic multi-mesh gillnets with 12 mesh sizes in a geometric row between 5.5 and 55 mm (CEN, 2015). These nets were placed at the lake bottom. In lakes deeper than 6 m maximum depth, additional pelagic gillnets were used, which were 1.5, 3 or 6 m high and had the same mesh sizes as the benthic ones (the 3 and 6 m nets lacked the 5.5 mm mesh section). The catch data were converted into a p/a matrix per species and lake. Furthermore, the species-specific catch per lake was expressed as the number or weight of fish per unit effort (NPUE or WPUE) in either benthic or pelagic areas, standardized per net and fishing night (number or biomass of fish caught per standard net and night). The difference in height of pelagic nets was considered by assuming that 3-m-high pelagic nets were equivalent to two standard benthic nets, and 6-m-high pelagic nets equivalent to four benthic standard nets. We calculated the arithmetic average NPUE and WPUE from benthic and pelagic fish catches per species. In that way, benthic and pelagic fish catches were weighted equally, hence avoiding the commonly criticized underestimation of pelagic fishes in deep lakes relative to benthic catches caused by the application of fewer pelagic nets than benthic nets per lake (Alexander et al., 2015). Finally, we divided WPUE by NPUE per species to obtain the arithmetic mean mass (in grams) of each species per lake. Subsequently, we refer to these datasets as biomass and mean mass datasets.

Environmental predictors included per lake were elevation (in metres above sea level), maximum annual air temperature (in degrees Celsius), precipitation (in millimetres per year), lake area (in square kilometres), lake maximum depth (in metres) and total phosphorus concentration (TP; in milligrams per cubic metre), as obtained from at least four samples across the seasons per year (Supporting Information Table S1). The lake descriptors were taken from national databases. We also tested whether shoreline length (in kilometres; available for 293 lakes) would be a useful additional predictor. However, in contrast to $\log_{10}$ air temperature, $\log_{10}$ lake area and $\log_{10}$ lake depth, the square root of shoreline length was not significantly related to fish species richness in the lakes (Pearson's $r = -.034$); hence, it was not considered.

The maximum air temperature and precipitation were calculated from the Climatic Research Unit (CRU) model (New et al., 2002), as based on temperature records for the years before 2008, thus matching the period when the lakes were sampled. This specific model can obtain a spatial resolution of 10′ latitude and (or) longitude and takes into account elevational differences between stations (New et al., 2002). The complete set of six environmental predictors was available for only a subset ($n = 1{,}109$) of the original $n = 1{,}943$ lakes. The dataset contained only lakes with pH > 6, to exclude the potential effect of anthropogenically induced acidification and subsequent mitigation measures on fish assemblages.

Spatial effects on fish community composition were considered by recording the river basins to which the lakes belong (for details, see subsection on model construction). These data were obtained from Catchment Characterization and Modelling (CCM) data v.2.1 provided by the EU Joint Research Centre (JRC; http://ccm.jrc.ec.europa.eu/php/index.php?action=view&id=23). The CCM2 database covers the entire European continent, including the Atlantic islands, Iceland and Turkey.

For the p/a dataset, we used all fish species that were present in ≥ 30 lakes ($n = 19$ species; Table 1; Supporting Information Table S2) and excluded lakes with only one or two species present. The limitation of the species included prevents an excessive number of zeroes in the dataset and avoids spurious correlations between species pairs occurring only rarely. Furthermore, the standardized sampling by gillnets is less reliable with respect to the occurrence of rare fish species in lakes (Diekmann et al., 2005; Olin et al., 2009; Šmejkal et al., 2015). Among the 19 species included, 18 fish species are native in the regions covered, whereas bluegill (*Lepomis gibbosus*) is the most frequent invasive species in the lakes in Europe (Trochine et al., 2018). For some of the species (e.g., genera *Esox* and *Scardinius*), populations south of the Alps can be considered a separate species (Bianco, 2014). However, the number of lakes from this geographical area in the total dataset was low (Figure 1), and there is no evidence that the ecological traits differ between the putatively different species of the genera between areas north and south of the Alps. Information on the six environmental predictors and spatial information were available for a total of $n = 772$ lakes, covering large longitudinal and latitudinal gradients in Europe (Figure 1). The final set included 43 reservoirs (5.5%) from European areas with a low density of natural lakes. Earlier studies have demonstrated that the lists of species dwelling in natural lakes and in reservoirs are almost identical (Irz et al., 2006) and that the fish community composition in reservoirs shares many predictors with those for lake fish

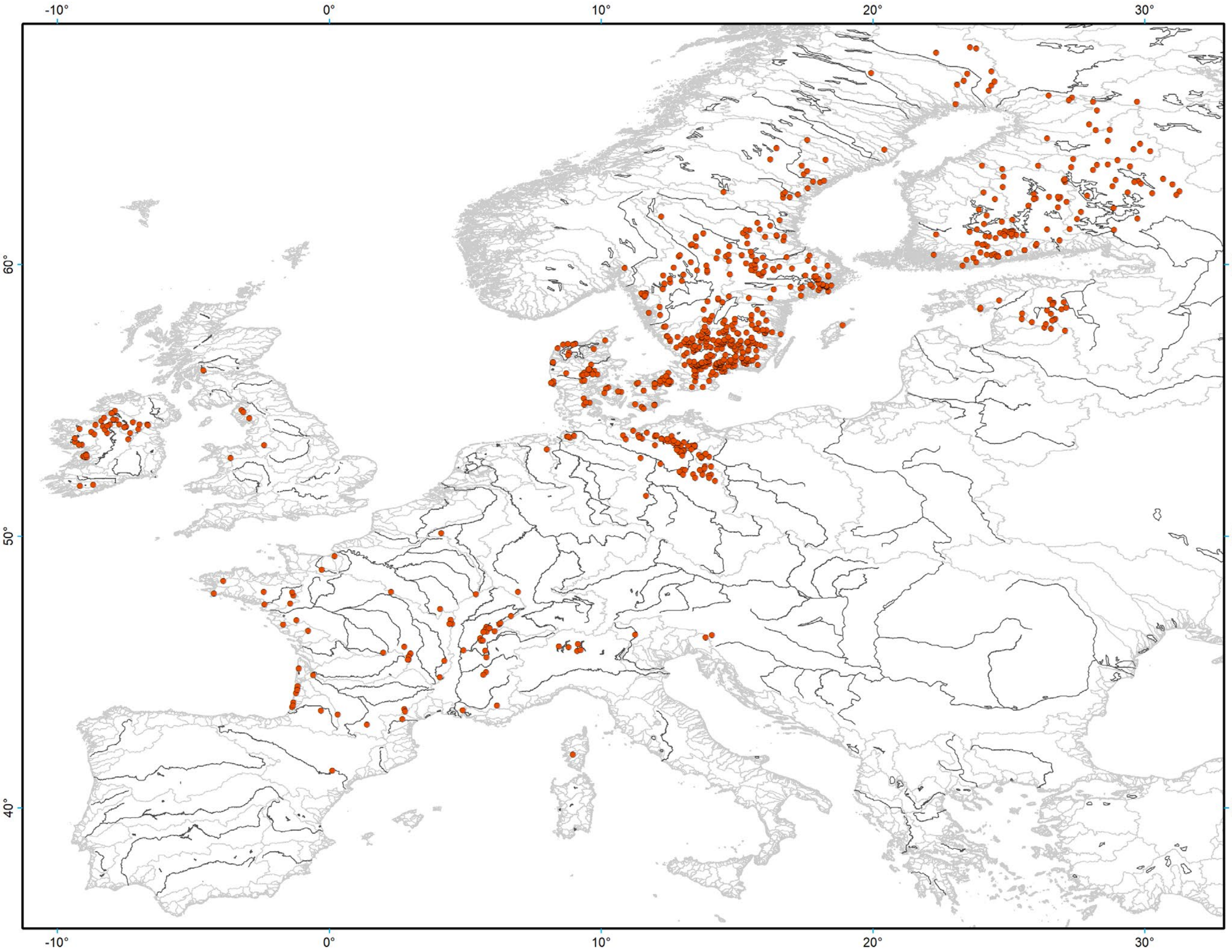

FIGURE 1 Overview of geographical locations of 772 sampled European lakes (red dots), with Catchment Characterization and Modelling (CCM2) river basins (light grey) and main rivers (black lines). Note the numerous small river basins along the shorelines, which often contain only one of the sampled lakes

communities (Irz et al., 2004). We used the identification number of the main river basins (seaoutlet) (WSO_ID in CCM2) and allocated these 772 lakes into 209 river basins (Figure 1). Most of the river basins included only one lake ($n = 119$). We found only 35 river basins with five or more lakes, with the River Elbe basin including the highest number of lakes ($n = 47$). The available data do not allow discrimination between landlocked (seapage) and drainage lakes (Heino et al., 2021; Tonn & Magnuson, 1982); therefore, we cannot infer whether the lakes within a river basin have a genuine hydraulic connection.

For the biomass and mean mass datasets, we focused on the dominant six fish species (perch, *Perca fluviatilis*; pike, *Esox lucius*; ruffe, *Gymnocephalus cernuus*; roach, *Rutilus rutilus*; bream, *Abramis brama*; and rudd, *Scardinius erythrophthalmus*) that were present in ≥ 322 (*c*. 40%) of these 772 lakes (Supporting Information Table S3). We applied a relatively high presence threshold here to reduce the number of zeroes and facilitate proper model construction for the biomass and mean mass datasets. Excessive numbers of zeroes are particularly problematic and might distort the distributions of the continuous response variables biomass and mean mass; hence, we reduced the number of species in favour of obtaining robust model results. Accordingly, the 772 lakes included are identical for all three datasets. However, we ignored rare species not passing the overall presence thresholds in some of the lakes; hence, potential interactions between dominant and rare species in these lakes are not explored. We analysed absolute values of fish biomasses and mean masses such that the raw data to calculate interaction strengths were not influenced by the exclusion of rare species.

2.1 | Model construction

We applied the HMSC approach with latent variables by running Bayesian models for analysing multivariate data as based on Markov chain Monte Carlo (MCMC) methods by the "BORAL" (Bayesian ordination and regression models for analysing multivariate data in ecology) package v.1.9 (Hui, 2016, 2020) under R v.3.6.2 (R Development Core Team, 2019). For each of the p/a, biomass and mean mass datasets, we compared purely latent models (including three latent variables without covariates) with correlated models (including environmental descriptors and three latent variables) and with spatially explicit correlated models (including three latent variables, environmental covariates and random row effects to account for spatial covariation). Purely latent models represent model-based unconstrained ordinations. With explanatory (environmental and spatial) variables, 'BORAL' fits correlated column generalized linear models (GLMs) with latent variables to account for any residual correlation between the species. Therefore, the latent variables can be interpreted as a way of accounting for any residual covariation not explained by the covariates. Our previous work on abiotic predictors indicated that (log)linear relationships describe the effects on fish communities well (Mehner et al., 2005, 2007, 2016); hence we did not include unimodal (quadratic) terms. Environmental predictors were centred and standardized. To account for the effects of dispersal, we assumed that lake fish communities within the same river basin were more similar than fish communities in lakes from different river basins, reflecting stronger dispersal within than among river basins. This spatial correlation within river basins was accomplished by adding random row effects per river basin to the model, drawn from a normal distribution with mean zero and unknown variance, analogous to a random intercept in mixed models. Dispersal among the 209 river basins was assumed to be completely random. We ran the MCMC models via JAGS (Just Another Gibbs Sampler) according to the default settings in "BORAL" (burn-in 10,000 iterations, total number of iterations including burn-in = 40,000, thinning rate = 30, very weakly informative normally distributed priors with mean zero and variance 10). Given that only one MCMC chain is run by "BORAL" (see Hui, 2020), we calculated Geweke diagnostics to check whether the MCMC chain had converged successfully. This diagnostics is a list containing *Z*-scores for all parameters in the model. If the *Z*-score exceeds *c*. 1.96, then the *p*-value of the test statistic is < .05, indicating that the MCMC chain did not converge for this particular parameter. *p*-values of multiple *Z*-tests were adjusted by the Holm method. To evaluate the fit of the final models, we calculated Pearson correlations between the observed presence, biomass or mean mass per species and the fitted values per species from the correlated response models including spatial information. For the fit, we used the posterior medians of the parameters. Note that the fitted responses for the p/a dataset form a continuous, not a dichotomous (0/1), variable.

We applied binomial distributions with probit link to the p/a datasets, and Tweedie distributions with log link for the biomass and mean mass datasets. Tweedie distributions are a special case of exponential dispersion models, often used as distributions for GLMs. The binomial and Tweedie distributions were selected according to the best visual fit of the residuals of the final "BORAL" models in comparison to other distributions. Biomass and mean mass data were Box–Cox-chord transformed (Legendre & Borcard, 2018) before running the "BORAL" models, to reduce skewness of the datasets with many zeroes (logarithmic transformation) and to obtain a double-zero asymmetrical matrix (chord transformation). The optimum logarithmic transformation exponent was 0.5 (equivalent to square-root transformation) for both the biomass and mean mass datasets.

To compare the contribution of environmental, spatial and residual (species-interaction) effects, we calculated the predicted variance averaged across the 19 (p/a) or six (biomass, mean mass) species for the environmental, spatial (row effects) and residual contributions to the final model by the cal.varpart function of the "BORAL" package (Ovaskainen et al., 2017). An alternative procedure is to estimate the reduction of trace of the residual covariance matrix induced by the latent variables between a purely latent model, a correlated model with only environmental covariates and a final correlated model including spatial (row) effects and environmental covariates (Hui, 2016). The trace of the final correlated model including environmental and spatial effects relative to the purely latent model is equivalent to the relative residual contribution (BoralModel$trace in the "BORAL" package). The reduction in trace qualitatively supported the contributions of environmental, spatial and residual variation as obtained from the predicted variance for the biomass and mean mass datasets but failed to mimic these results for the p/a dataset. The trace for the purely latent model of the p/a dataset was lower than the trace for any correlated model in several runs, such that the relative reduction in trace between the models could not be calculated properly. However, the trace calculations differed depending on the starting conditions (seed number), whereas the relative contributions from the assembly processes as calculated from the predicted variance per species were repeatable and independent of the starting conditions.

3 | RESULTS

The relative contributions of environmental, spatial and residual variance differed between the datasets. For p/a data, the sum of environmental (50%) and spatial (10%) effects was greater than the residual variance (40%), based on the amount of predicted variance averaged for the 19 species (Figure 2). Spatial effects were particularly pronounced (> 20% explained) for the p/a patterns of *Carassius carassius*, *Gobio gobio*, *Tinca tinca* and *Esox lucius*. In contrast, spatial patterns of lakes had almost no effect (< 1% explained) on p/a of *Sander lucioperca*, *Lota lota* and *Scardinius erythrophthalmus*. Significant spatial effects (posterior credibility intervals not including zero) were found for 12 of the 209 CCM2 river basins (Supporting Information Figure S1). Strong effects of dispersal and higher similarity of lake community compositions within river basins were found for the basins of the rivers Elbe, Oder, Rhine, Loire, Rhone, Neva and Kokemänjoki (plus three river basins without names in CCM2; WSO_IDs: 92, 236 and 831,220), whereas for the River Shannon (plus one river basin without a name in CCM2; WSO_ID: 84,023) the similarity of species composition within the river basin was significantly lower than expected by chance (negative posterior credibility interval).

Geweke diagnostics confirmed that the MCMC model including environmental and spatial predictors successfully converged

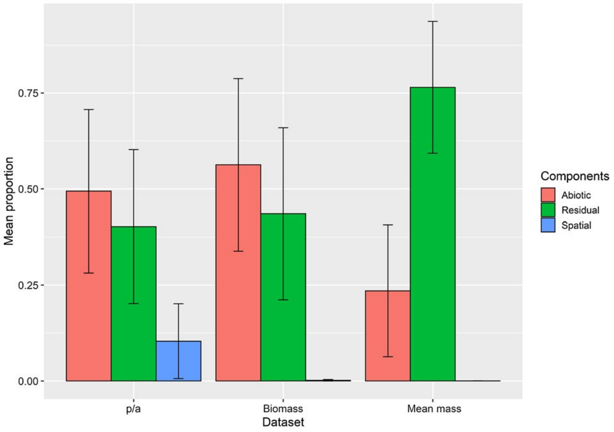

FIGURE 2 Relative contributions (mean ± *SD*) of environmental (abiotic), spatial (random row effects) and residual effects to the correlated response models for presence/absence (p/a), biomass and mean mass datasets of fishes in 772 European lakes. The contributions are averaged across 19 (p/a) or six (biomass, mean mass) fish species

(Holm-adjusted *p*-values of *Z*-scores for 209 row coefficients, 19 latent variable coefficients and six abiotic coefficients per species, all $p > .05$). Pearson correlations indicated a reasonably good fit between empirical and fitted presences and absences of the 19 species in the 772 lakes (mean Pearson's $r = 0.70$; Table 1), but the fit differed between species in the range from $r = 0.29$ (*Carrassius carassius*) to $r = 0.99$ (*Scardinius erythrophthalmus*) (Table 1).

In contrast to the p/a dataset, contributions from spatial effects were minor (<< 1%) in the biomass and mean mass datasets. The proportion of environmental contributions exceeded the contribution from residual variance to total variance for the biomass dataset (abiotic 56%, residual 44%), whereas the reverse pattern was found for the mean mass dataset (abiotic 25%, residual 75%; Figure 2). The reduction of trace between latent and correlated models confirmed the low contribution of spatial dependence on biomass and mean mass datasets and the dominance of residual variance for the mean mass dataset. Geweke diagnostics confirmed that the MCMC models including environmental and spatial predictors successfully converged for both biomass and mean mass datasets (Holm-adjusted *p*-values of *Z*-scores for 209 row coefficients, six latent variable coefficients and six abiotic coefficients per species, all $p > .05$). Pearson correlations indicated a reasonably good fit between empirical and fitted biomass (mean $r = 0.59$, range 0.34–0.85; Table 1) and mean mass (mean $r = 0.76$, range 0.52–0.98; Table 1) of the six species.

Dominant environmental predictors of the p/a dataset were variables related to meteorology (maximum temperature, significant for 14 of 19 species; precipitation 12 of 19), whereas elevation, lake area and depth and total phosphorus concentration were significant covariates for the occurrence of a lower number of species (Supporting Information Figure S2). Precipitation, maximum temperature, maximum depth and total phosphorus concentration were significant covariates for four of the six species in the biomass dataset (Supporting Information Figure S3). For the mean mass dataset, temperature, maximum depth and total phosphorus were significant covariates for three of the six species (Supporting Information Figure S4).

The matrices of residual correlations of the final models were composed of a mixture of positive and negative signs (Figures 3 and 4; Supporting Information Tables S4–S6). In the p/a dataset, there were 88 of 171 possible bivariate correlations significant at $p < .05$ (51.5%; Figure 3; Supporting Information Table S6). We found 25 species pairs with negative interactions. Among those, 14 were characterized by predator–prey pairs including the predators *Esox lucius*, *Perca fluviatilis*, *Sander lucioperca* and *Lota lota*. There were 11 negative correlations including Coregonidae (*Coregonus* sp., *Coregonus albula*) and Cyprinidae (*Carassius carassius*), which cannot be attributed to predation because these species are not piscivorous (Figure 3). There were 63 significant positive residual correlations. Among those, 18 were composed of species pairs from the family Cyprinidae (*Rutilus*, *Abramis*, *Blicca*, *Gobio* and *Alburnus*; Figure 3). Further positive correlations were frequently found for species pairs including *Sander lucioperca*, *Lota lota*, *Osmerus eperlanus* and *Gymnocephalus cernuus* (Figure 3).

In the biomass dataset with six species, only four of 15 possible species correlations were significant. Negative correlations were found between biomasses of *Perca fluviatilis* and three of the five other species (Figure 4a; Supporting Information Table S4). The negative correlations between *Perca fluviatilis* and *Rutilus rutilus* or *Abramis brama* were strong (coefficients *c.* −0.9; Supporting Information Table S4). In the mean mass dataset with 11 of 15 significant correlations, the mean mass of *Esox lucius* was correlated negatively with the mean mass of all the other five species (Figure 4b; Supporting Information Table S5). However, there were also six significant positive mean mass correlations including Cyprinidae (*Abramis brama* and *Rutilus rutilus*) and Percidae (*Gymnocephalus cernuus* and *Perca fluviatilis*).

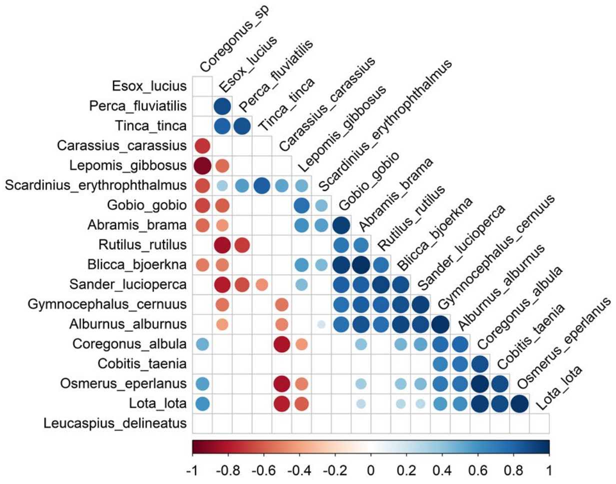

FIGURE 3 Plot of residual correlations between presence/absence of 19 fish species in 772 European lakes. Positive correlations are shown in blue, negative correlations in red. Only significant ($p < .05$) correlations are shown; the colour intensity and circle size reflect the strength of correlations. Species are displayed along the angular order of their eigenvectors

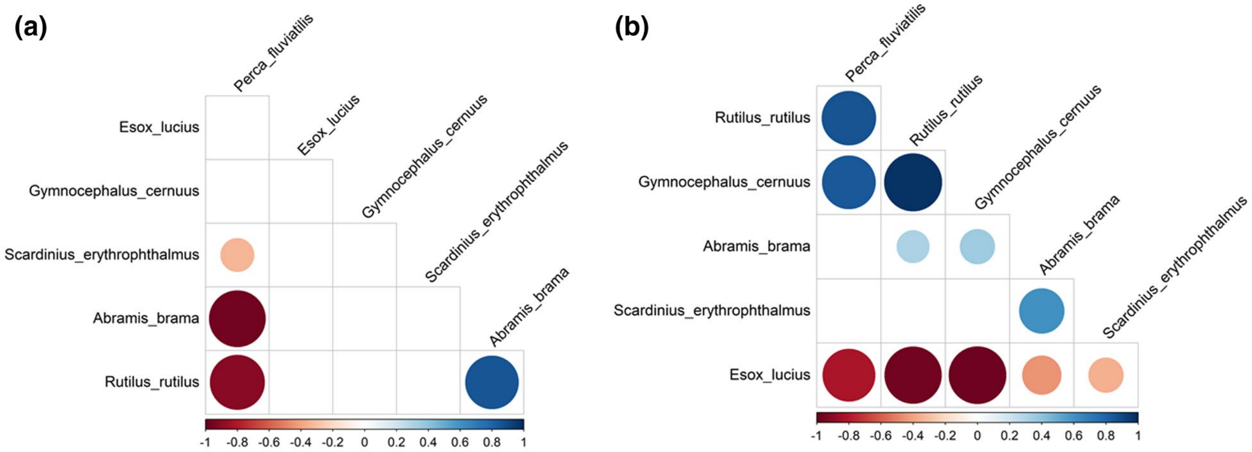

FIGURE 4 Plot of residual correlations between (a) biomass or (b) mean mass of six fish species in 772 European lakes. Positive correlations are shown in blue, negative correlations in red. Only significant ($p < .05$) correlations are shown; the colour intensity and circle size reflect the strength of correlations. Species are displayed along the angular order of their eigenvectors

4 | DISCUSSION

Our study reveals that positive and negative interactions between species are likely to be contributing substantially to the structuring of fish communities in European lakes. Despite including six key abiotic predictors for fish community composition in lakes and by accounting for spatial connectivity between lakes, addressing the effect of dispersal within river basins, there were several strong positive and negative correlations between species in the residual correlation matrices of the p/a, biomass and mean mass datasets. In the latent-variable models applied, the residual variance reflected that the species interaction effects were potentially highest for the mean mass of the six dominant fish species and lowest for the p/a of the most frequent 19 species. In contrast, environmental filtering and spatial effects reflecting dispersal between lakes within river basins were prominent contributors to the p/a structure of the lake fish species, suggesting that these processes dominate the community assembly at the continental scale. We are aware of substantial uncertainty in the estimates of contributions from the community assembly processes, and we are cautious with quantitative comparisons because the datasets contained different numbers of species. Furthermore, we do not claim that the residual correlations found by our models are equivalent to mechanistic evidence for interactions between species, which can be achieved only through replicated experiments at the community level. However, the model results correspond to our hypotheses and predictions on the dominant processes of community assembly, as based on previous empirical work on environmental filters, dispersal and species interactions of fishes in European freshwater lakes. Therefore, we conclude that species interactions are an important process in the community assembly of European lake fish communities.

Negative correlations in the residual matrix involved several predator–prey pairs, for all three datasets tested. The piscivorous species perch and pike occurred in 99% and 78% of the lakes, respectively. Perch are known for strong piscivory when they are larger than 15–20 cm (Horppila et al., 2000; Persson & Greenberg, 1990), and negative interactions including predation and interspecific competition between perch and the prey species roach and ruffe have been described from extensive experimental work and fish community surveys (Bergman & Greenberg, 1994; Persson et al., 1991; Persson & Greenberg, 1990). Likewise, the pike is a strong piscivore, with negative effects on presence, biomass or size of their prey species found in several previous studies (Bellard et al., 2019; Englund et al., 2009; McLoone et al., 2019; Persson et al., 1996). Particularly, in isolated lakes, negative co-occurrence between predators and prey has been observed and interpreted as the result of prey extinction in the presence of predators (Englund et al., 2009). Pike influenced the abundance and size distributions of crucian carp (*Carassius carassius*) and tench (*Tinca tinca*) (Brönmark et al., 1995), and introduction of perch or pike into small lakes induced rapid extinction of sticklebacks (*Gasterosteus* and *Pungitius*) (Englund et al., 2009) or brown trout (*Salmo trutta*) (McLoone et al., 2018). The third major piscivorous fish species in the dataset was the pikeperch, which was present in only 27% of the lakes. Strong effects of pikeperch on other fish species are also well described (Keskinen & Marjomäki, 2004; Kokkonen et al., 2019; Kopp et al., 2009). It is interesting to note that the dominant negative correlations of pikeperch in the p/a dataset were found with pike and perch, suggesting that intraguild predation and competition between the piscivores might contribute to structuring the local presence or absence of these three piscivorous species (Kokkonen et al., 2019; Schulze et al., 2006). The local presence of both pike and pikeperch might also be affected by intentional stocking for fisheries purposes (e.g., Henriksson et al., 2016); hence, the p/a correlations between these two predatory species might in part reflect anthropogenic effects not covered by direct species interactions.

Interspecific competition might partly explain negative correlations in the residual matrix of the p/a dataset between species not forming predator–prey pairs. For example, whitefish (*Coregonus* sp.) were correlated negatively with the presence of several cyprinid species, and crucian carp were correlated negatively with the presence of several other fish species. However, it is the fundamental limitation of the model-based approaches that positive and negative correlations in the residual correlation matrix are not equivalent to mechanistic inference of interaction effects. Although negative effects of predators on prey are a plausible outcome supported by numerous empirical studies, the extinction of competitively inferior fish species from communities by a superior competitor has rarely been documented. If interspecific competition is much stronger than intraspecific competition (Chesson, 2000), the resulting local competitive exclusion of a species would not leave a direct trace in the p/a dataset, because the communities were not followed over time. However, for the dominant fish species in European lakes, intraspecific competition and negative density-dependent growth rates are characteristic (Arranz et al., 2016), suggesting that competitive exclusion is relatively unlikely. Negative correlations between non-predatory species in our analyses might also reflect opposing responses of species to environmental variables not considered in our study. Examples of unmeasured abiotic filters include different expression of heterogeneity within ecosystems; for example, varying vertical temperature or oxygen gradients in deep lakes or varying macrophyte coverage of the littoral zones, which are known to affect the occurrence of certain species or could explain the absence of other species (Diekmann et al., 2005; Lewin et al., 2014; Mehner et al., 2005). Therefore, a finer spatial resolution of within-lake gradients might generate additional insight into factors determining species co-occurrence. Such high-resolution data were not available for the lakes included in our study. Furthermore, pH and alkalinity, a gradient of water colour or turbidity induced, for example, by dissolved organic carbon (Mooij et al., 2005; Tammi et al., 2003), and even differing anthropogenic impacts on the lakes might cause similarities and dissimilarities in species occurrences, reflected by significant correlations between species in the residual correlation matrices. For example, different responses to water colour by perch and roach (van Dorst et al., 2020) might contribute to observed residual negative correlations in the abundance and mean mass datasets.

A similar caveat applies to the numerous positive correlations between fish species in the p/a, biomass and mean mass datasets. These correlations suggest that some fish species regularly co-occur together, and often their biomasses and mean masses vary in a similar manner across the lakes, beyond the co-occurrences and correlations induced by abiotic filtering and dispersal. As mentioned already, unmeasured environmental gradients might cause these patterns. Furthermore, positive correlations in the biomass and mean mass datasets might be caused by covariation in reproduction and recruitment, as induced by similar weather conditions in larger groups of lakes in the years before sampling (Bunnell et al., 2017; Chevalier et al., 2014). However, we also have to admit that there is not much known about positive species interactions, such as mutualism and facilitation, in freshwaters (Silknetter et al., 2020). This is a fundamentally understudied topic (Collins et al., 2017; Eklöv & VanKooten, 2001). Positive interactions dominated in the processes structuring fish communities of 721 Ontario lakes, and local richness appeared to beget richness in lakes rather than to restrict it (MacDougall et al., 2018). A dominance of positive correlations was also obvious for the piscivorous pikeperch in the p/a dataset of our study, supporting the results from the Ontario lakes (MacDougall et al., 2018) that the occurrence of predators might profit from an increase in prey numbers. Additionally, it has been suggested that positive interspecific interactions between species might emerge from the shared use of social information in juvenile fish communities (Haak et al., 2020). In our dataset, positive correlations were often found between species of the same family (Cyprinidae), which is the most species-rich fish family in European lakes (Kottelat & Freyhof, 2007). We cannot exclude the possibility that there is a phylogenetic effect on co-occurrences, because related species often share traits, such as with respect to feeding and life history; hence, they are often adapted to the same environmental conditions. However, co-occurrences attributable to the effects of dominant environmental covariates were accounted for by the hierarchical approach applied here and might, therefore, not fully explain the positive correlations between species. Accordingly, covariates not included in the model construction (see above) might additionally have facilitated co-occurrences of phylogenetically related species.

The model results suggest that we included important environmental filters for fish species occurrences, biomass and mean mass. We found a dominant effect of temperature, precipitation and elevation on the large-scale occurrence of fish species, whereas ecosystem size, expressed as lake area or depth, and productivity were strong predictors of species biomasses and average mean masses. These environmental filters have been identified in previous studies on lake fish communities in Europe, North America and China (Brucet et al., 2013; Griffiths et al., 2014; Guo et al., 2019; MacDougall et al., 2018; Trochine et al., 2018). Temperature again emerged as the main driver of continental-scale differences in fish species occurrences, with lakes at higher latitudes and elevation harbouring primarily fish species of the cold- and coolwater thermal guilds (genera *Coregonus*, *Lota* and *Osmerus*), whereas the warmwater thermal guild encompasses mainly the species of the family Cyprinidae (Brucet et al., 2013; Emmrich et al., 2014). Another important abiotic predictor, lake depth, is coupled to the temperature regime of lakes via the annual stratification patterns in temperate regions and the respective availability of habitats with different temperatures (cool hypolimnion versus warm epilimnion) (Hayden et al., 2014; Mehner et al., 2005). Strong effects of temperature on the direction and strength of interactions between fish species have been detected in a study on Ontario lakes (MacDougall et al., 2018), supporting the context dependence of interactions. Temperature was also a major determinant of average fish sizes, both in the analysis presented here and in an earlier comparison of fish size spectra in European lakes (Emmrich et al., 2014). In contrast, ecosystem productivity, expressed as total phosphorus concentration, was least important for affecting the p/a structure of lake fish communities, but was important for the biomass and size structure of some of the dominant species (Argillier et al., 2013; Garcia et al., 2006). It is interesting to note that temperature and productivity seem to interact in determining the mean mass of some of the species. In contrast to the temperature–size rule, the average size of two cyprinids (bream, *Abramis brama*, and rudd, *Scardinius erythrophthalmus*) was higher in warmer lakes. This is certainly attributable to the higher productivity of the warmer (and often shallow) lakes, suggesting that the higher maintenance costs at higher temperatures affect the growth rates negatively only in conditions of resource limitation and strong intra- and interspecific competition (Bourai et al., 2020; Fugère et al., 2018). In contrast, the size of the predator species pike declined with higher temperatures, suggesting that pike cannot cover the higher energetic costs induced by increasing temperatures by higher prey uptake rates; for example, if some of their prey species, such as bream and rudd, escape into a size refuge by higher growth rates (Mehner et al., 2016).

There was some evidence that spatial effects contributed to the p/a structure of the lake fish communities, confirming earlier studies (Beisner et al., 2006; McLoone et al., 2018; Mehner et al., 2014). Lakes located in the same river basin had a higher likelihood of sharing species than lakes situated in different river basins. Similar meteorological conditions within river basins were covered by including the environmental filters; hence, they were certainly not the reason for species co-occurrences within river basins. We conclude that species distribution was facilitated by dispersal between lakes within these river basins. The contribution of spatial effects within river basins to the overall model variance was *c*. 10% for the p/a dataset, whereas no spatial effects were found on the biomass and mean mass of the six dominant fish species. This is a plausible result, because dispersal is not expected to affect population dynamics and growth rates of fish directly. However, we acknowledge that the dataset was not ideal to identify strong effects of dispersal on local fish community composition. Only 35 of 209 river basins contained more than four lakes. Among those, a significant contribution of spatial effects was found for 12 river basins, suggesting that dispersal primarily within larger and lake-rich river basins contributed to the similarity of lake fish communities. This result confirms similar studies showing that dispersal within river basins homogenizes the species composition at fine spatial scales (Beisner et al., 2006; De Bie et al., 2012; Lansac-Tôha et al., 2021). In contrast, > 80% of all river basins listed in the CCM2 database contained fewer than five lakes, and 57% ($n = 119$) of the river basins had only one lake for which we obtained the fish community data. It is, therefore, not entirely surprising that the power to detect significant dispersal effects was limited.

We applied random row effects to model stronger dispersal within than between river basins. By taking this approach, we did not test whether dispersal limitation between river basins contributed significantly to dissimilarity of fish communities at larger spatial scales. At the moment, the "BORAL" package does not allow the combination of random row effects for modelling within-basin dispersal and a distance matrix for modelling between-basin dispersal simultaneously. In addition, according to our database we could not discriminate between landlocked and drainage lakes, for which the effect of dispersal should differ fundamentally (Heino et al., 2021; Olden et al., 2001; Tonn & Magnuson, 1982). The best solution to evaluate the scale dependence of dispersal between lakes is the calculation of hydraulic distances via connecting waterways that would facilitate a quantitative comparison of within-basin and between-basin dispersal effects (Beisner et al., 2006; Mehner et al., 2014; Olden et al., 2001). This connectivity matrix could ideally be combined with flow directions of connecting rivers or streams (Olden et al., 2001) and records on in-stream barriers that fishes cannot pass (Belletti et al., 2020). Such a dataset is currently not available for the 772 lakes included in the present study, because there is an enormous complexity of spatial and geographical information needed to quantify the connectivity for even two lakes (cf. Olden et al., 2001). However, we would like to emphasize that a geographical map of hydraulic connectivity of European rivers and lakes would facilitate a much deeper analysis of the scale-dependent effects of dispersal on the community structure of dispersers with relatively large body size that are bound to water for migration, such as fishes (Heino et al., 2021; Lansac-Tôha et al., 2021).

We intended to expand our previous analyses on the effect of abiotic filtering on lake fish communities (Argillier et al., 2013; Brucet et al., 2013; Emmrich et al., 2014) to an exploration of the potential effects of species interactions on community assembly. The results of our new analyses suggest that species interactions might have strong effects, although positive interactions seem to be quantitatively even more important than the agonistic ones, which dominate the discussion in community ecology. From our perspective, this is a major step forwards in understanding the mechanisms of community assembly for lake fish communities. We are aware of several recent critical considerations about inferring processes from co-occurrence data (Blanchet et al., 2020; Münkemüller et al., 2020). However, we knew the main interactions between the species a priori and did not infer them from the data. We applied the approach to a dataset that is bigger than most of the datasets on which hierarchical models have been tested so far, and we covered large environmental gradients while including lakes from larger parts of Europe. Furthermore, we understand limitations of our approach; for example, that indirect interactions or interactions with a third species might mask the effect of direct interactions between two species (Eklöv & VanKooten, 2001; Schulze et al., 2006). This is particularly likely for the biomass and mean mass datasets, which isolated the six dominant fish species and ignored rare species co-occurring with the common ones. It was decided intentionally to ignore rare species to avoid biases in model construction attributable to excessive numbers of zeroes. However, the approach as demonstrated here elucidates that there are strong hints for a significant effect of species interactions on the assembly of lake fish communities. The comparison of p/a, biomass and mean mass datasets did not produce erratic patterns, but confirmed information that we have assembled from several earlier studies comparing lake fish communities across large spatial scales (Brucet et al., 2013; Griffiths et al., 2014; Guo et al., 2019; MacDougall et al., 2018). We agree that mechanistic experiments at ecosystem scales would be the preferred option to support the correlative evidence accumulated here. However, we are not aware of any approach that has addressed community assembly experimentally for organisms with high longevity and relatively large size at natural spatial scales, such as fishes in lakes.

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DATA AVAILABILITY STATEMENT

Data availability and access have been published (Mehner et al., 2017).

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REFERENCES

Alexander, T. J., Vonlanthen, P., Periat, G., Degiorgi, F., Raymond, J. C., & Seehausen, O. (2015). Evaluating gillnetting protocols to characterize lacustrine fish communities. *Fisheries Research*, *161*, 320–329. https://doi.org/10.1016/j.fishres.2014.08.009

Argillier, C., Causse, S., Gevrey, M., Pedron, S., De Bortoli, J., Brucet, S., Emmrich, M., Jeppesen, E., Lauridsen, T., Mehner, T., Olin, M., Rask, M., Volta, P., Winfield, I. J., Kelly, F., Krause, T., Palm, A., & Holmgren, K. (2013). Development of a fish-based index to assess the eutrophication status of European lakes. *Hydrobiologia*, *704*, 193–211. https://doi.org/10.1007/s10750-012-1282-y

Arranz, I., Mehner, T., Benejam, L., Argillier, C., Holmgren, K., Jeppesen, E., Lauridsen, T. L., Volta, P., Winfield, I. J., & Brucet, S. (2016). Density-dependent effects as key drivers of intraspecific size structure of six abundant fish species in lakes across Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 519–534. https://doi.org/10.1139/cjfas-2014-0508

Beisner, B. E., Peres, P. R., Lindström, E. S., Barnett, A., & Longhi, M. L. (2006). The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology*, *87*, 2985–2991.

Bellard, C., Englund, G., & Hugueny, B. (2019). Biotic and abiotic drivers of species loss rate in isolated lakes. *Journal of Animal Ecology*, *88*, 881–891. https://doi.org/10.1111/1365-2656.12980

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., … Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*(7838), 436–441. https://doi.org/10.1038/s41586-020-3005-2

Bergman, E., & Greenberg, L. A. (1994). Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. *Ecology*, *75*, 1233–1245. https://doi.org/10.2307/1937449

Bianco, P. G. (2014). An update on the status of native and exotic freshwater fishes of Italy. *Journal of Applied Ichthyology*, *30*, 62–77. https://doi.org/10.1111/jai.12291

Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, *23*, 1050–1063. https://doi.org/10.1111/ele.13525

Boulangeat, I., Gravel, D., & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, *15*, 584–593. https://doi.org/10.1111/j.1461-0248.2012.01772.x

Bourai, L., Logez, M., Laplace-Treyture, C., & Argillier, C. (2020). How do eutrophication and temperature interact to shape the community structures of phytoplankton and fish in lakes? *Water*, *12*, 779.

Brönmark, C., Paszkowski, C. A., Tonn, W. M., & Hargeby, A. (1995). Predation as a determinant of size structure in populations of crucian carp (*Carassius carassius*) and tench (*Tinca tinca*). *Ecology of Freshwater Fish*, *4*, 85–92.

Brucet, S., Pedron, S., Mehner, T., Lauridsen, T. L., Argillier, C., Winfield, I. J., Volta, P., Emmrich, M., Hesthagen, T., Holmgren, K., Benejam, L., Kelly, F., Krause, T., Palm, A., Rask, M., & Jeppesen, E. (2013). Fish diversity in European lakes: Geographical factors dominate over anthropogenic pressures. *Freshwater Biology*, *58*, 1779–1793. https://doi.org/10.1111/fwb.12167

Bunnell, D. B., Hook, T. O., Troy, C. D., Liu, W. T., Madenjian, C. P., & Adams, J. V. (2017). Testing for synchrony in recruitment among four Lake Michigan fish species. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 306–315. https://doi.org/10.1139/cjfas-2015-0534

Carpenter, S. R., & Kitchell, J. F. (1993). *The trophic cascade in lakes*. Cambridge University Press.

Cazelles, K., Mouquet, N., Mouillot, D., & Gravel, D. (2016). On the integration of biotic interaction and environmental constraints at the biogeographical scale. *Ecography*, *39*, 921–931. https://doi.org/10.1111/ecog.01714

CEN (2015). *Water quality—sampling of fish with multi-mesh gillnets*. European Committee for Standardization.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Chevalier, M., Laffaille, P., & Grenouillet, G. (2014). Spatial synchrony in stream fish populations: Influence of species traits. *Ecography*, *37*, 960–968. https://doi.org/10.1111/ecog.00662

Chu, C., Lester, N. P., Giacomini, H. C., Shuter, B. J., & Jackson, D. A. (2016). Catch-per-unit-effort and size spectra of lake fish assemblages reflect underlying patterns in ecological conditions and anthropogenic activities across regional and local scales. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 535–546. https://doi.org/10.1139/cjfas-2015-0150

Collins, S. F., Nelson, K. A., DeBoom, C. S., & Wahl, D. H. (2017). The facilitation of the native bluegill sunfish by the invasive bighead carp. *Freshwater Biology*, *62*, 1645–1654. https://doi.org/10.1111/fwb.12976

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., & Declerck, S. A. J. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*, *15*, 740–747. https://doi.org/10.1111/j.1461-0248.2012.01794.x

Diekmann, M., Brämick, U., Lemcke, R., & Mehner, T. (2005). Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities. *Journal of Applied Ecology*, *42*, 901–909. https://doi.org/10.1111/j.1365-2664.2005.01068.x

Eklöv, P., & VanKooten, T. (2001). Facilitation among piscivorous predators: Effects of prey habitat use. *Ecology*, *82*, 2486–2494.

Emmrich, M., Pedron, S., Brucet, S., Winfield, I. J., Jeppesen, E., Volta, P., Argillier, C., Lauridsen, T. L., Holmgren, K., Hesthagen, T., & Mehner, T. (2014). Geographical patterns in the body-size structure of European lake fish assemblages along abiotic and biotic gradients. *Journal of Biogeography*, *41*, 2221–2233. https://doi.org/10.1111/jbi.12366

Englund, G., Johansson, F., Olofsson, P., Salonsaari, J., & Ohman, J. (2009). Predation leads to assembly rules in fragmented fish communities. *Ecology Letters*, *12*, 663–671. https://doi.org/10.1111/j.1461-0248.2009.01322.x

Fugère, V., Mehner, T., & Chapman, L. J. (2018). Impacts of deforestation-induced warming on the metabolism, growth and trophic interactions of an afrotropical stream fish. *Functional Ecology*, *32*, 1343–1357. https://doi.org/10.1111/1365-2435.13065

Garcia, X. F., Diekmann, M., Brämick, U., Lemcke, R., & Mehner, T. (2006). Correlations between type-indicator fish species and lake productivity in German lowland lakes. *Journal of Fish Biology*, *68*, 1144–1157. https://doi.org/10.1111/j.0022-1112.2006.01009.x

Griffiths, D., McGonigle, C., & Quinn, R. (2014). Climate and species richness patterns of freshwater fish in North America and Europe. *Journal of Biogeography*, *41*, 452–463. https://doi.org/10.1111/jbi.12216

Guo, C. B., Chen, Y. S., Gozlan, R. E., Li, Z. J., Mehner, T., Lek, S., & Paukert, C. P. (2019). Biogeographic freshwater fish pattern legacy revealed despite rapid socio-economic changes in China. *Fish and Fisheries*, *20*, 857–869. https://doi.org/10.1111/faf.12380

Haak, C. R., Hui, F. K. C., Cowles, G. W., & Danylchuk, A. J. (2020). Positive interspecific associations consistent with social information use shape juvenile fish assemblages. *Ecology*, *101*, e02920. https://doi.org/10.1002/ecy.2920

Hayden, B., Harrod, C., & Kahilainen, K. K. (2014). Lake morphometry and resource polymorphism determine niche segregation between cool- and cold-water-adapted fish. *Ecology*, *95*, 538–552. https://doi.org/10.1890/13-0264.1

Hayden, B., Harrod, C., Thomas, S. M., Eloranta, A. P., Myllykangas, J. P., Siwertsson, A., Præbel, K., Knudsen, R., Amundsen, P. A., & Kahilainen, K. K. (2019). From clear lakes to murky waters – tracing the functional response of high-latitude lake communities to concurrent 'greening' and 'browning'. *Ecology Letters*, *22*, 807–816. https://doi.org/10.1111/ele.13238

Hein, C. L., Öhlund, G., & Englund, G. (2014). Fish introductions reveal the temperature dependence of species interactions. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132641.

Heino, J., Alahuhta, J., Bini, L. M., Cai, Y. J., Heiskanen, A.-S., Hellsten, S., Kortelainen, P., Kotamaki, N., Tolonen, K. T., Vihervaara, P., Vilmi, A., & Angeler, D. G. (2021). Lakes in the era of global change: Moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. *Biological Reviews*, *96*, 89–106. https://doi.org/10.1111/brv.12647

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology*, *60*, 845–869. https://doi.org/10.1111/fwb.12533

Henriksson, A., Yu, J., Wardle, D. A., Trygg, J., & Englund, G. (2016). Weighted species richness outperforms species richness as predictor of biotic resistance. *Ecology*, *97*, 262–271. https://doi.org/10.1890/15-0463.1

Hoegh, A., & Roberts, D. W. (2020). Evaluating and presenting uncertainty in model-based unconstrained ordination. *Ecology and Evolution*, *10*, 59–69. https://doi.org/10.1002/ece3.5752

Holyoak, M., Leibold, M. A., & Holt, R. D. (2005). *Metacommunities: Spatial dynamics and ecological communities*. University of Chicago Press.

Horppila, J., Ruuhijärvi, J., Rask, M., Karppinen, C., Nyberg, K., & Olin, M. (2000). Seasonal changes in the diets and relative abundances of perch and roach in the littoral and pelagic zones of a large lake. *Journal of Fish Biology*, *56*, 51–72. https://doi.org/10.1111/j.1095-8649.2000.tb02086.x

Hui, F. K. C. (2016). BORAL – Bayesian ordination and regression analysis of multivariate abundance data in R. *Methods in Ecology and Evolution*, *7*, 744–750.

Hui, F. K. C. (2020). *boral: Bayesian Ordination and Regression AnaLysis*. https://cran.r-project.org/web/packages/boral/index.html

Irz, P., Argillier, C., & Oberdorff, T. (2004). Native and introduced fish species richness in French lakes: Local and regional influences. *Global Ecology and Biogeography*, *13*, 335–344. https://doi.org/10.1111/j.1466-822X.2004.00109.x

Irz, P., Odion, M., Argillier, C., & Pont, D. (2006). Comparison between the fish communities of lakes, reservoirs and rivers: Can natural systems help define the ecological potential of reservoirs? *Aquatic Sciences*, *68*, 109–116.

Jackson, D. A., Peres-Neto, P., & Olden, J. D. (2001). What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 157–170.

Jeppesen, E., Canfield, D. E., Bachmann, R. W., Søndergaard, M., Havens, K. E., Johansson, L. S., Lauridsen, T. L., Tserenpil, S., Rutter, R. P., Warren, G., Ji, G., & Hoyer, M. V. (2020). Toward predicting climate change effects on lakes: A comparison of 1656 shallow lakes from Florida and Denmark reveals substantial differences in nutrient dynamics, metabolism, trophic structure, and top-down control. *Inland Waters*, *10*, 197–211. https://doi.org/10.1080/20442041.2020.1711681

Keskinen, T., & Marjomäki, T. J. (2004). Diet and prey size spectrum of pikeperch in lakes in central Finland. *Journal of Fish Biology*, *65*, 1147–1153. https://doi.org/10.1111/j.0022-1112.2004.00500.x

Kokkonen, E., Heikinheimo, O., Pekcan-Hekim, Z., & Vainikka, A. (2019). Effects of water temperature and pikeperch (*Sander lucioperca*) abundance on the stock–recruitment relationship of Eurasian perch (*Perca fluviatilis*) in the northern Baltic Sea. *Hydrobiologia*, *841*, 79–94. https://doi.org/10.1007/s10750-019-04008-z

Kopp, D., Cucherousset, J., Syväranta, J., Martino, A., Céréghino, R., & Santoul, F. (2009). Trophic ecology of the pikeperch (*Sander lucioperca*) in its introduced areas: A stable isotope approach in southwestern France. *Comptes Rendus Biologies*, *332*, 741–746. https://doi.org/10.1016/j.crvi.2009.04.001

Kottelat, M., & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Cornot and Berlin: Kottelat and Freyhof.

Lansac-Tôha, F. M., Bini, L. M., Heino, J., Meira, B. R., Segovia, B. T., Pavanelli, C. S., Bonecker, C. C., Deus, C. P., Benedito, E., Alves, G. M., Manetta, G. I., Dias, J. D., Vieira, L. C. G., Rodrigues, L. C., Carmo Roberto, M., Brugler, M. R., Lemke, M. J., Tessler, M., DeSalle, R., … Velho, L. F. M. (2021). Scale-dependent patterns of metacommunity structuring in aquatic organisms across floodplain systems. *Journal of Biogeography*, *48*, 872–885. https://doi.org/10.1111/jbi.14044

Legendre, P., & Borcard, D. (2018). Box–Cox-chord transformations for community composition data prior to beta diversity analysis. *Ecography*, *41*, 1820–1824. https://doi.org/10.1111/ecog.03498

Legendre, P., & Gauthier, O. (2014). Statistical methods for temporal and space–time analysis of community composition data. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132728.

Lewin, W. C., Mehner, T., Ritterbusch, D., & Brämick, U. (2014). The influence of anthropogenic shoreline changes on the littoral abundance of fish species in German lowland lakes varying in depth as determined by boosted regression trees. *Hydrobiologia*, *724*, 293–306. https://doi.org/10.1007/s10750-013-1746-8

MacDougall, A. S., Harvey, E., McCune, J. L., Nilsson, K. A., Bennett, J., Firn, J., Bartley, T., Grace, J. B., Kelly, J., Tunney, T. D., McMeans, B., Matsuzaki, S.-I. S., Kadoya, T., Esch, E., Cazelles, K., Lester, N., & McCann, K. S. (2018). Context-dependent interactions and the regulation of species richness in freshwater fish. *Nature Communications*, *9*, article number: 973.

Magurran, A. E. (2004). *Measuring biological diversity*. Blackwell.

Mason, N. W. H., Lanoiselee, C., Mouillot, D., Wilson, J. B., & Argillier, C. (2008). Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *Journal of Animal Ecology*, *77*, 661–669. https://doi.org/10.1111/j.1365-2656.2008.01379.x

McLoone, P., Shephard, S., Delanty, K., Rocks, K., Feeney, R., & Kelly, F. (2018). Coexistence of pike *Esox lucius* and brown trout *Salmo trutta* in Irish lakes. *Journal of Fish Biology*, *93*, 1005–1011.

McLoone, P., Shephard, S., O'Reilly, S., & Kelly, F. (2019). Shifts in diet of an apex predator following the colonisation of an invasive fish. *Hydrobiologia*, *837*, 205–218. https://doi.org/10.1007/s10750-019-03972-w

Meerhoff, M., Teixeira-de Mello, F., Kruk, C., Alonso, C., Gonzalez-Bergonzoni, I., Pacheco, J. P., Lacerot, G., Arim, M., Beklioglu, M., Brucet, S., Goyenola, G., Iglesias, C., Mazzeo, N., Kosten, S., & Jeppesen, E. (2012). Environmental warming in shallow lakes: A review of potential changes in community structure as evidenced from space-for-time substitution approaches. In: U. Jacob & G. Woodward (Eds.). *Advances in ecological research, Vol 46: Global change in multispecies systems* (pp. 259–349), Part 1. Elsevier. https://doi.org/10.1016/B978-0-12-396992-7.00004-6

Mehner, T., Brucet, S., Argillier, C., Beklioglu, M., Ferreira, T., Hesthagen, T., Holmgren, K., Jeppesen, E., Kelly, F., Krause, T., Rask, M., Volta, P., Winfield, I. J., & Podgornik, S. (2017). Metadata of European lake fishes dataset. *Freshwater Metadata Journal*, *23*, 1–8. https://doi.org/10.15504/fmj.2017.23

Mehner, T., Diekmann, M., Brämick, U., & Lemcke, R. (2005). Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human use intensity. *Freshwater Biology*, *50*, 70–85. https://doi.org/10.1111/j.1365-2427.2004.01294.x

Mehner, T., Emmrich, M., & Hartwig, S. (2014). Spatial predictors of fish species composition in European lowland lakes. *Ecography*, *37*, 73–79. https://doi.org/10.1111/j.1600-0587.2013.00432.x

Mehner, T., Holmgren, K., Lauridsen, T. L., Jeppesen, E., & Diekmann, M. (2007). Lake depth and geographical position modify lake fish assemblages of the European "Central Plains" ecoregion. *Freshwater Biology*, *52*, 2285–2297. https://doi.org/10.1111/j.1365-2427.2007.01836.x

Mehner, T., Keeling, C., Emmrich, M., Holmgren, K., Argillier, C., Volta, P., Winfield, I. J., & Brucet, S. (2016). Effects of fish predation on density and size spectra of prey fish communities in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 506–518. https://doi.org/10.1139/cjfas-2015-0034

Meijer, M. L., Jeppesen, E., VanDonk, E., Moss, B., Scheffer, M., Lammens, E., VanNes, E., VanBerkum, J. A., de Jong, G. J., Faafeng, B. A., & Jensen, J. P. (1994). Long-term response of fish-stock reduction in small shallow lakes: Interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia*, *275* , 457–466.

Mooij, W. M., Hülsmann, S., Domis, L. N. D., Nolet, B. A., Bodelier, P. L. E., Boers, P. C. M., Pires, L. M. D., Gons, H. J., Ibelings, B. W., Noordhuis, R., Portielje, R., Wolfstein, K., & Lammens, E. H. R. R. (2005). The impact of climate change on lakes in the Netherlands: A review. *Aquatic Ecology*, *39*, 381–400. https://doi.org/10.1007/s10452-005-9008-0

Münkemüller, T., Gallien, L., Pollock, L. J., Barros, C., Carboni, M., Chalmandrier, L., Mazel, F., Mokany, K., Roquet, C., Smycka, J., Talluto, M. V., & Thuiller, W. (2020). Dos and don'ts when inferring assembly rules from diversity patterns. *Global Ecology and Biogeography*, *29*, 1212–1229. https://doi.org/10.1111/geb.13098

New, M., Lister, D., Hulme, M., & Makin, I. (2002). A high-resolution data set of surface climate over global land areas. *Climate Research*, *21*, 1–25. https://doi.org/10.3354/cr021001

Olden, J. D., Jackson, D. A., & Peres-Neto, P. R. (2001). Spatial isolation and fish communities in drainage lakes. *Oecologia*, *127*, 572–585. https://doi.org/10.1007/s004420000620

Olin, M., Malinen, I., & Ruuhijärvi, J. (2009). Gillnet catch in estimating the density and structure of fish community—Comparison of gillnet and trawl samples in a eutrophic lake. *Fisheries Research*, *96*, 88–94. https://doi.org/10.1016/j.fishres.2008.09.007

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*, 561–576. https://doi.org/10.1111/ele.12757

Persson, L., Andersson, J., Wahlström, E., & Eklöv, P. (1996). Size-specific interactions in lake systems: Predator gape limitation and prey growth rate and mortality. *Ecology*, *77*, 900–911. https://doi.org/10.2307/2265510

Persson, L., Diehl, S., Johansson, L., Andersson, G., & Hamrin, S. F. (1991). Shifts in fish communities along the productivity gradient of temperate lakes—patterns and the importance of size-structured interactions. *Journal of Fish Biology*, *38*, 281–293. https://doi.org/10.1111/j.1095-8649.1991.tb03114.x

Persson, L., & Greenberg, L. A. (1990). Juvenile competitive bottlenecks: The perch (*Perca fluviatilis*)–roach (*Rutilus rutilus*) interaction. *Ecology*, *71*, 44–56. https://doi.org/10.2307/1940246

R Development Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Schulze, T., Baade, U., Dörner, H., Eckmann, R., Haertel-Borer, S. S., Hölker, F., & Mehner, T. (2006). Response of the residential piscivorous fish community to introduction of a new predator type in a mesotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 2202–2212. https://doi.org/10.1139/f06-099

Silknetter, S., Creed, R. P., Brown, B. L., Frimpong, E. A., Skelton, J., & Peoples, B. K. (2020). Positive biotic interactions in freshwaters: A review and research directive. *Freshwater Biology*, *65*, 811–832. https://doi.org/10.1111/fwb.13476

Šmejkal, M., Ricard, D., Prchalová, M., Říha, M., Muška, M., Blabolil, P., Čech, M., Vašek, M., Jůza, T., Herreras, A. M., Encina, L., Peterka, J., & Kubečka, J. (2015). Biomass and abundance biases in European standard gillnet sampling. *PLoS One*, *10*, e0122437.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, *10*, 1115–1123. https://doi.org/10.1111/j.1461-0248.2007.01107.x

Staniczenko, P. P. A., Sivasubramaniam, P., Suttle, K. B., & Pearson, R. G. (2017). Linking macroecology and community ecology: Refining predictions of species distributions using biotic interaction networks. *Ecology Letters*, *20*, 693–707. https://doi.org/10.1111/ele.12770

Tammi, J., Appelberg, M., Beier, U., Hesthagen, T., Lappalainen, A., & Rask, M. (2003). Fish status survey of Nordic lakes: Effects of acidification, eutrophication and stocking activity on present fish species composition. *AMBIO: A Journal of the Human Environment*, *32*, 98–105. https://doi.org/10.1579/0044-7447-32.2.98

Tonn, W. M., & Magnuson, J. J. (1982). Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology*, *63*, 1149–1166. https://doi.org/10.2307/1937251

Tonn, W. M., Magnuson, J. J., Rask, M., & Toivonen, J. (1990). Intercontinental comparison of small lake fish assemblages: The balance between local and regional processes. *The American Naturalist*, *136*, 345–375. https://doi.org/10.1086/285102

Trochine, C., Brucet, S., Argillier, C., Arranz, I., Beklioglu, M., Benejam, L., Ferreira, T., Hesthagen, T., Holmgren, K., Jeppesen, E., Kelly, F., Krause, T., Rask, M., Volta, P., Winfield, I. J., & Mehner, T. (2018). Non-native fish occurrence and biomass in 1943 Western Palearctic lakes and reservoirs and their abiotic and biotic correlates. *Ecosystems*, *21*, 395–409. https://doi.org/10.1007/s10021-017-0156-6

van Dorst, R. M., Gårdmark, A., Svanbäck, R., & Huss, M. (2020). Does browning-induced light limitation reduce fish body growth through shifts in prey composition or reduced foraging rates? *Freshwater Biology*, *65*, 947–959. https://doi.org/10.1111/fwb.13481

Vellend, M. (2010). Conceptual synthesis in community ecology. *Quarterly Review of Biology*, *85*, 183–206. https://doi.org/10.1086/652373

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology and Evolution*, *30*, 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2403–2413. https://doi.org/10.1098/rstb.2011.0056

BIOSKETCH

The author group has collaborated on analysing the structure and function of lake fish communities for many years. Their collaborative work has mainly focused on taxonomic, functional and size diversity of fishes and the continental-scale abiotic gradients that shape species occurrence and community composition in European lakes. The authors share expertise in lake food webs, trophic interactions, lake fish ecology, bioindication and fisheries management. They have contributed to establishment of the standardized sampling protocol and assessment of the ecological status of lake fish communities in the context of the European Water Framework Directive.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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