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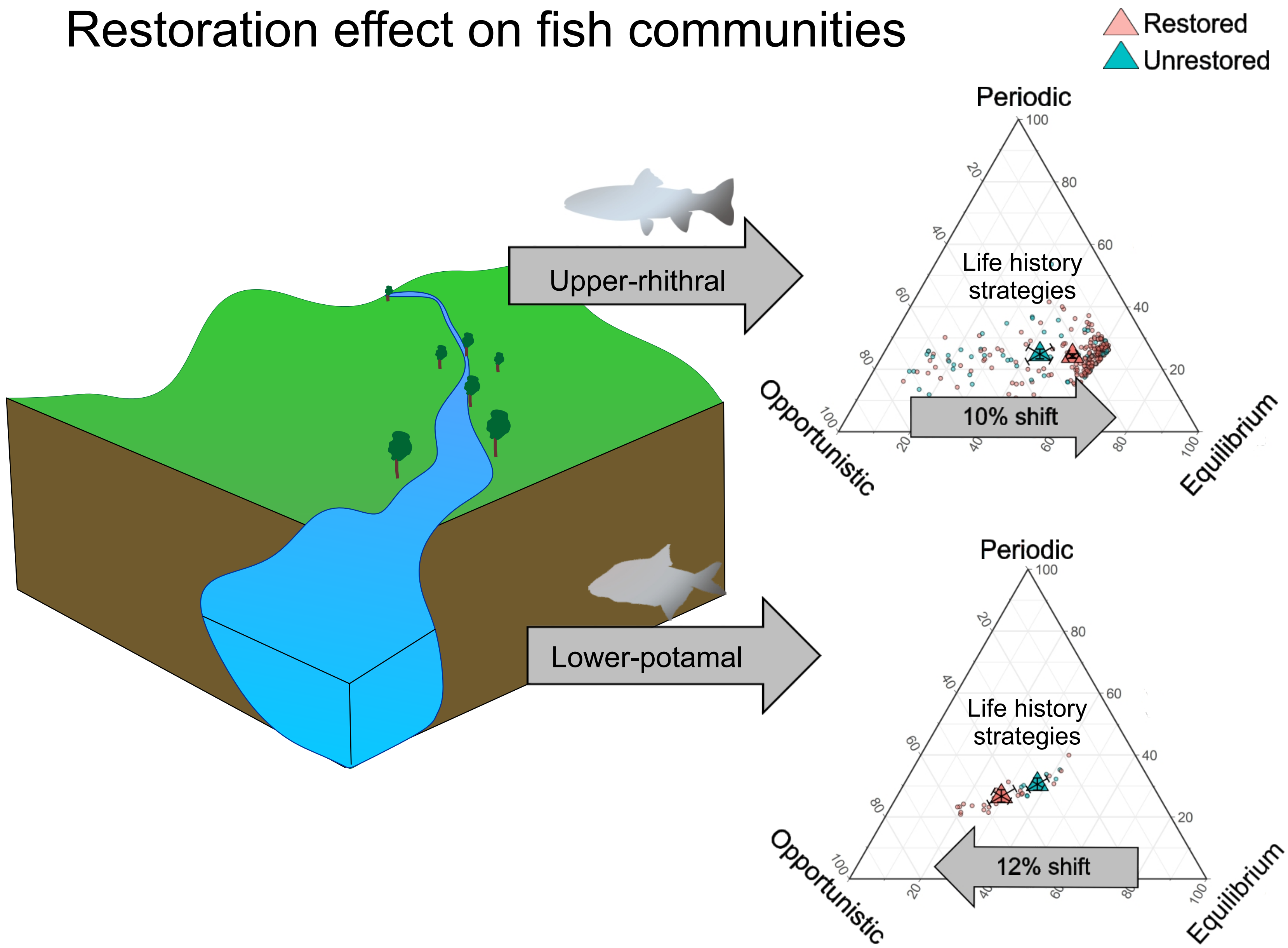
*Graphical Abstract



***Highlights (for review : 3 to 5 bullet points (maximum 85 characters including spaces per bullet point)**

- River restoration affects life-history trait composition of fish communities
- Restoration changes the ratio of opportunistic-periodic-equilibrium strategists
- Restoration outcome varies along the river continuum and successional stages
- Restored reaches show more similar trait composition then unrestored reaches
- A trait approach could be used to compare restorations across biogeographic areas

Effect of river restoration on life-history strategies in fish communities

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Abstract

Assessments of river restoration outcomes are mostly based on taxonomic identities of species, which may not be optimal because a direct relationship to river functions remains obscure and results are hardly comparable across biogeographic borders. The use of ecological species trait information instead of taxonomic units may help to overcome these challenges.

Abundance data for fish communities were gathered from 134 river restoration projects conducted in Switzerland, Germany and Finland, monitored for up to 15 years. These data were related to a dataset of 22 categories of ecological traits describing fish life-history strategies to assess the outcome of the restoration projects.

Restoration increased trait functional diversity and evenness in projects that were situated in the potamal zone of rivers. Restoration effect increased with the length of the restored river reaches. In areas with low levels of anthropogenic land use, the peak of the restoration effect was reached already within one to five years after the restoration and effect receded thereafter, while communities responded later in areas with higher levels of anthropogenic land use.

In the lower potamal zone, a shift towards opportunistic life-history strategists was observed. In the upper rhithral zone, in contrast, species with an opportunistic life-history strategy increased only in the first five years of restoration, followed by a shift towards equilibrium strategists at restorations older than 5 years. This pattern was more pronounced in rivers with higher level of anthropogenic land use and longer restored river reaches. Restoration reduced the variability in community trait composition between river reaches suggesting that community trait composition within these zones converges when rivers are restored.

This study showed how ecological traits are suitable to analyse restoration outcomes and how such an approach can be used for the evaluation and comparison of environmental management actions across geographical regions.

Keywords: functional traits, functional diversity, fish life strategies, functional composition, life-history traits, restoration success

1. Introduction

In recent decades, a great deal of energy has gone into counteracting the degradation of rivers through river restoration measures (e.g. Thomas et al., 2015). River restorations commonly aim at re-establishing natural reference conditions in terms of habitat structure. According to the habitat template theory (Southwood, 1988), this approach is commonly expected to increase habitat functioning, diversity and dynamics of stream assemblages (Palmer et al., 1997, Palmer et al., 2010). Challenges for assessment of restoration outcome are multiple, often leaving the question open, if restoration efforts indeed lead to desired results.

Position within the river continuum, catchment size or discharge regime are among the environmental variables that are discussed to influence restoration outcomes (Stoll et al., 2016). Moreover, the effect of restoration can be enhanced when the restoration is conducted in highly anthropogenic conditions compared to areas characterised by lower anthropogenic land use pressures (Lorenz and Feld, 2013; Feld et al., 2016). Restoration effects may be reduced in fragmented rivers, affecting the dispersal capacity of the surrounding species pool (Stoll et al., 2014, Kominoski et al., 2018). It is also well known that restoration outcomes can vary over time, as succession processes affect the abiotic characteristic of restored river reaches as well as the communities that establish (Stoll et al., 2014; Pilotto et al., 2018; Thomas et al., 2015). In fish communities, Höckendorff et al. (2017) showed how post-restoration successional processes lasted approximately five to eight years before reaching a level of relative ecological stability.

River restoration effectiveness is commonly assessed in terms of changes in biodiversity, as species and communities integrate anthropogenic stressors in space and time and therefore perform well as bio-indicators of the ecological status of an ecosystem (Haase et al., 2016). Many successful regional bioindication tools, many of them using fish communities, have been developed based on a taxonomic reference system, calculating deviations from a set of species defining natural reference conditions (e.g. the German fish assessment "fiBs" (Diekmann et al., 2005b), or the Index of Biotic Integrity (IBI) developed for fish communities in the USA (Karr, 1981)). A disadvantage of this common approach is that the results of these assessments are limited to comparisons only within more or less homogeneous biogeographic areas (Menezes, 2010). Each of these schemes is built based on regional species lists, focuses on common regional ecological constraints and is tied up to regional legislative regulations. This leaves a gap in the capacity to evaluate environmental management actions, such as river restorations, at the trans-national and trans-continental scale.

By shifting focus from species identity towards ecological traits of a community, comparison between highly diverse and biogeographically distinct river reaches can be made. Ecological traits are universal and largely independent of species taxonomic identities and biogeographic borders. Many studies showed that functional diversity, rather than species diversity, enhances ecosystem functions (Petchey and Gaston, 2002, Cadotte et al., 2011), and thus, ultimately, ecosystem services. Trait changes may capture important shifts in ecological functioning not reflected directly in the taxonomic assemblage (Ernst, 2006). Therefore, ecological traits are better suited to assessing the ecological functioning of a river, and hence, ecological restoration targets (Loreau et al., 2001; Mouillot et al., 2006; Thomas et al., 2015). Functional roles of ecological traits could be used as a baseline for the comparison of restoration outcomes. However, to date restoration assessment based on community trait composition is still the exception, rather than the rule (but see van Kleef et al., 2006; Höckendorff et al., 2017; Lima et al., 2018).

Stream assemblages are constrained by hydromorphological, geological and physicochemical characteristics of river ecosystems, which function as environmental filters (Poff et al., 1997; Lamouroux et al., 2002; Statzner and Bêche, 2010). The natural flow-regime paradigm postulates that adaptations of riverine assemblages are dictated by patterns of variation in river flows and habitat hydromorphology (Poff et al., 1997). These adaptations include for example ecological traits that enable riverine fish to avoid being flushed away by water peak discharge in mountain reaches or that allow survival or fast recolonization after oxygen depletion in lowland reaches (see Lytle and Poff, 2004). In fish, Winemiller and Rose (1992) differentiated three life-history strategies, each of which reflect demographical adaptations (i.e. juvenile survival, fecundity, reproduction) to a range of environmental and ecological conditions. Opportunistic strategist fishes are small-bodied, with relatively short life spans, early maturation and more than one spawning event per year characterised by low fecundity; they usually adapt to unstable and disturbed habitat conditions. Periodic strategists are large-bodied fishes with longer life spans compared to the opportunistic strategists, late female maturity, high fecundity per spawning event, and low juvenile survivorship as they do not provide parental cares; they inhabit periodically suitable habitats. Equilibrium strategists are usually associated with stable habitats and they show low fecundity per spawning event and high juvenile survivorship providing parental care and producing large eggs (Winemiller, 1989; 1992; Winemiller and Rose, 1992; Olden and Kennard, 2010). In river restorations, functional diversity of a river is maximized through the re-establishment of river functions that are considered natural in that reach and the creation of new river functions (e.g. water retention capacity). In this sense, restoration actions change the habitat structure (i.e. water flow patterns, bed structures and course) of the river favouring fish life strategies that possess functional traits which are better adapted to the new habitat conditions (Tullos et al., 2009).

The main objective of this study was to investigate the potential of implementing ecological traits to assess river restoration outcomes. We used trait data generated for 57 fish species collected over 134 restoration riverine projects conducted in Switzerland, Germany and Finland. As a first step, we analysed changes in functional diversity and evenness patterns due to restorations. Secondly, we assessed how restoration affects the proportion of the opportunistic-periodic-equilibrium strategists by changing the relative proportion (i.e. composition) of the life-history traits associated to each fish strategy. For both diversity and compositional analyses, we assessed how restoration effects relate to key environmental variables, anthropogenic land use and typology of restoration actions. All analyses were conducted along the longitudinal river gradient including the upper- and lower-rhithral zones (trout and grayling zones) and upper- and lower-potamal zones (barbel and bream zones) (Huet, 1949; Illies and Botosaneanu, 1963).

2. Methods

2.1 Data set

For this analysis, we searched for quantitative fish data from river restoration projects that were designed to serve the entire fish community, not just individual species. Per restoration project, at least two datasets (restored and unrestored control) were required. Based on a call for data in the personal networks of the authors, we received the data from three different European countries (Switzerland, Germany, and Finland).

The dataset includes a total of 134 restorations projects performed in 77 rivers. The projects were undertaken between the years 1989 and 2013. Data were collected in a time frame spanning from 15 years before to 15 years after the restoration. The monitoring schemes varied among the 134 projects including a temporal before (i.e. unrestored)–after (i.e. restored) approach (78 projects) or a spatial impact (i.e. restored)–control (i.e. unrestored) approach (55 projects). In 1 project both approaches were used (full BACI design). Sites were distributed over a latitudinal gradient from Northern to Central Europe (from 67° 37' N to 45° 53' N), and an altitudinal gradient from lowland slow-flowing rivers to mountainous streams in the pre-alpine regions (see Table S3). The dataset included at the same time lower-order river reaches with average stream widths <3 m up to larger rivers with average river width > 60m (see Table S3).

Fish data were collected using electro-fishing. Fish data from Switzerland were provided by the cantonal administrations (environmental, fisheries, and hydro-engineering departments) upon email request, and some additional data sets were extracted from scientific works, such as diploma theses and reports. Fish data collection for Switzerland and Germany is fully described in Thomas et al. (2015). Fish communities in Germany were sampled based on a standardised protocol compliant with the European Water Framework Directive (Diekmann et al., 2005a) (see methodological details in Stoll et al., 2013). Finnish fish data were gathered from Finnish Fish Sampling Data Register, Natural Resources Institute Finland and regional ELY centres, or compiled from reports (North Karelia TE Office 2001; Vihtonen, 2009). In all the Finnish restoration projects, fish sampling was conducted according to the Finnish electrofishing standard (Vehanen et al., 2013).

2.2 Life-history strategies

The composition of fish traits, informative for the opportunistic-periodic-equilibrium trichotomy of life-history strategies, was defined using 22 categories of seven biological trait classes (Table 1) (see also Olden and Kennard, 2010 for similar approach). Fish trait information was obtained at the species level from the database freshwaterecology.info (Grenouillet and Schmidt-Kloiber, 2006; Schmidt-Kloiber A. and Hering D., 2015). Gaps were filled using the available data from literature (Kottelat and Freyhof, 2007) as well as electronic datasets (Pont et al., 2006; 2007) and expert judgment of the authors. Each category was associated uniquely or as a combination of opportunistic, periodic and equilibrium life strategies (Winemiller, 1989; 1992; Winemiller and Rose, 1992; Olden and Kennard, 2010) (see Table 1).

2.3 Calculations of trait abundance and functional diversity metrics

Relative fish abundance in each site was standardised as catch per unit of effort (CPUE) per 200 m of river transect. This was done in order to have comparable fish relative abundances among the different projects. Our trait database was used to calculate a relative trait representation within each site based on CPUE of each fish species and whether or not a fish species had a certain trait (0/1).

Fish CPUE and the trait information matrices were then used to calculate Rao's quadratic entropy (RaoQ) and Functional dispersion (FDis) as functional diversity indices, using the FD package (Laliberté and Legendre, 2010) for R (R Core Team, 2015). RaoQ measures the distribution and the abundance of traits in the trait space combining both functional richness and divergence (Botta-Dukát, 2005; Peru and Dolédec, 2010). FDis measures the dispersion of species in trait space weighted by their relative abundance (Laliberté and Legendre, 2010). Both indexes are useful explaining the relationships between biotic communities and environmental constraints (Ding et al., 2017). Species Evenness Index (Eve) (Heip, 1974) was used as measurement of how uniformly are abundances of trait categories distributed in the trait space.

2.4 Surveyed environmental variables

As the restoration effect might vary due to local environmental variability and to the uniqueness of the different restoration projects, additionally to environmental variables measured during the sampling event (e.g. altitude, length of the restored river stretch, total sampled area), we calculated other variables that potentially can influence the restoration outcome. As the ecological effect of the restoration can vary over time (Höckendorff et al., 2017), the number of years since the restoration was realised, was included as an explanatory variable. Based on the work of Höckendorff et al. (2017) and Palmer et al (2010), years since the restoration were pooled in 3 main categories to assess the effect of restoration from 1 to 5 years, from 6 to 10 years and from 10 to 15 years. Among all the projects, 20 different types of restoration actions were identified. In order to achieve statistical replication, they were categorized into three main groups: actions that aimed to restore riparian section of the river (riparian actions); actions that aimed to restore the entire river course including the river bed (river bed actions); actions that aimed to improve longitudinal connectivity (connectivity actions) (see table S1) (see Simaika et al., 2015 for a detailed methodological description).

Different level of anthropogenic land use pressures of the surrounding areas can influence restoration outcome (Lorenz and Feld., 2013). To measure the extent of anthropogenic landscape modification around each sampled location, land-use data from a 10 km long and 200 m wide upstream buffer was computed (see Lorenz and Feld, 2013 for similar approach). Percent land use was derived at each site for each category of level 3 of Corine Land Cover 2006 (Büttner and Kosztra, 2007) and present in the buffer using a GIS system (ArcView GIS, ver. 3.3, Esri, 2011). In order to synthesise land-use with measure of anthropogenic pressure, the different categories of land use were combined into an Anthropogenic Index (AI) (Larsen et al., 2010; Manfrin et al., 2013; 2016), which was calculated as:

$$AI = \sum k_i p_i$$

where k_i is the specific coefficient for each land-use category (1= no anthropogenic pressure; 2= low anthropogenic pressure; 3= medium anthropogenic pressure; 4= high anthropic pressure) and p_i is the relative frequency of each category inside the buffer. The k values attributed to the land use categories are shown in Table S2. The AI ranged between 1 (minimum anthropogenic pressure) and 4 (maximum anthropogenic pressure). The AI was calculated with 10,000 x 200 m buffer distance to reflect both local riparian features and larger scale patterns acting at catchment level (see Lorenz and Feld, 2013). To differentiate river types in which restoration effects may differ, we used the following environmental variables, extracted from GIS: area (km^2) of the catchment size upstream the restored site, the total length (m) of the restored site and the altitude (m a.s.l.) at which the restoration was conducted.

2.5 Data analysis – Diversity metrics

The main effect of restoration on fish trait indices RaoQ, Fdis and Eve was analysed with linear mixed-effect (LME) models using the lme4 package (Bates et al., 2007) for R. Whether or not a site was restored, river zone, and their interaction were used as fix factors in the model. River zonation was derived from the biocoenotic region concept (Illies and Botosaneanu, 1963; see further details in Table S3). To account for repeated sampling within each project and variability among rivers and locations we used a random factor where “project” was nested in “river” which was nested in “country”. In case of significant “restoration” - “river zone” interaction, a post-hoc test was performed to examine the effects of restoration within each river zone using a LME model with the same random structure of the initial model. When necessary, weights were applied to account for heterogeneity of the variance and temporal autocorrelation was corrected for (Zuur et al., 2009b). To determine the optimal autocorrelation structure (ARMA), residuals in each model were tested using an iterative process which included an Akaike Information Criterion assessment (Zuur et al., 2009d).

Environmental variables underlying the main effect of restoration on the diversity metrics, were only analysed for the given river zone in which significant differences were found between restored and unrestored conditions. In this analysis, difference in RaoQ, Fdis and Eve were assessed as deltas (restored – unrestored value) between the two reaches restored and unrestored during the same time (Control-Impact approach), the same reach before (unrestored) and after (restored) the restoration, and between the reach before the restoration (unrestored) to which we compared reaches monitored after the restoration multiple times (Before-After approach). An LME model was used with fix factors “years since restoration” as well as “AI”, “catchment size”, “altitude”, “length of the restored reach” and their interaction with “years since restoration”. Number of restoration actions which fall into the categories “river bed actions”, “riparian actions” for each restoration project and presence or absence of “connectivity actions” were also included as fixed factors in the analysis. Fix factors were checked for multicollinearity with variance inflation factor (VIF) and Pearson correlation analyses using the mctest (Imdadullah et al., 2016) and ppcor (Kim, 2015) packages for R. The random structure, similarly to the main effect model (see above), considered projects nested in rivers nested in countries. When necessary, independent size-related variables were log-transformed to meet variance heterogeneity assumptions (Zuur et al., 2009a). Model interactions and single fix factors were backward-selected using likelihood ratio tests against reduced models (without the interaction or the fixed factor) (Zuur et al., 2009c). The variance explained by each model was calculated as marginal (R^2m) and conditional (R^2c) (Nakagawa and Schielzeth, 2013) using the MuMln package (Barton, 2016) for R. The distribution of residuals was assessed using qq-plots (Wilk and Gnanadesikan, 1968). To control for inflated false discovery rates, we used Benjamini-Hochberg corrected α-values (Waite and Campbell, 2006).

2.6 Data analysis – Trait composition

Differences in trait composition were computed as Bray-Curtis dissimilarities (Beals, 1984) on the relative abundances in trait categories in order to increase the influence of rare species (Legendre and Gallagher, 2001). NMDS was used on the trait data to visualise differences in trait composition between restored and unrestored reaches among river zones. A two-way Permutational Multivariate Analysis of Variance (perMANOVA) was performed to test for compositional dissimilarity among "restoration" and "river zones" including their interaction. Where a significant restoration- river zone interaction was detected, a one-way perMANOVA was performed within each river zone as a post-hoc comparison with the unique fix factor "restoration". For each perMANOVA, 9999 Permutations were constrained within rivers nested in countries to account for data dependency.

Similarity percentage (SIMPER) analysis (Clarke, 1993) was used to identify a ranked list of trait categories that cumulatively contributed more than 70% to significant (after one-way perMANOVA) differences between restored and unrestored site. To assess shifts in life-history strategies between restored and unrestored river reaches, we first computed a percentage of trait representation in each site for the three fish life strategies (opportunist, periodic, equilibrium). This was done by assigning a life strategy to each trait and calculating the weighted average representation of that trait in the site, weighted by CPUE. Results were visualized in a simplex/ternary plot and shifts along each of the axes was tested separately using a Fischer's exact test from the perm package (Fay and Shaw, 2010) for R.

Environmental variables underlying for the main effect of restoration on the trait composition, were only analysed when significant differences were found in post-hoc analysis for the given zone. Similarly to the analysis of the environmental variables performed on the diversity metrics with LME, also for the analysis of the composition, delta CPUE was calculated in each restored-unrestored paired condition (see above) for each trait category. The resultant matrix of compositional deltas was analysed using partial redundancy analysis (pRDA) using 9999 permutations and Euclidean distance (Oksanen et al., 2013). After VIF diagnostic for multicollinearity, environmental constrains included in the RDA were “AI”, “catchment size”, “altitude”, “length of the restored site” and their interaction with “years since restoration”. Number of “riparian actions”, “river bed actions” and presence or absence of “connectivity actions” were also included. To account for the effect of country and rivers, these factors were partialled out from the pRDA. Permutational (999 permutations) iterative test (anova) was used to assess the marginal effect of each variable.

Analysis of β-diversity was also assessed as multivariate homogeneity of groups dispersions (variance) between restored and unrestored reaches and among river zones (interaction “restoration” x “river zone”). The measure of multivariate homogeneity was calculated as the average distance of group reaches to the group centroid in multivariate space. A permutational test of the model residuals (permutes betadisper) was used to test if the dispersions (variances) of one or more groups were different and to perform pairwise comparisons between restored and unrestored condition among zones. We performed all compositional analyses using the vegan package (Oksanen et al., 2013) for R.

3. Results

3.1 Diversity metrics

Trait functional diversity measures varied between river zones (RAoQ: X^2=13.85, p=0.003; FDis: X^2=13.96, p=0.003), but generally increased due to restoration (RAoQ: X^2=3.74, p=0.053; FDis: X^2=4.22, p=0.039). However, the restoration effect on functional diversity varied between river zones (interaction "restoration" x "river zone"; RaoQ: X^2=9.44, p=0.024; FDis: X^2=11.53, p=0.009) (see complete LME results in Table S4). An interactive effect of restoration and river zone was also found for changes in trait evenness (X^2=10.34, p=0.016). Analysis of individual river zones revealed that restoration affected trait diversity similarly in lower-rhithral and upper- and lower-potamal zone, although the increase in trait diversity from unrestored to restored conditions was only significant in the upper-potamal zone (RaoQ: X^2=12.28, p<0.001; Fdis: X^2=15.01, p<0.001; Eve: X^2=15.01, p=0.023; Fig. 2). In the upper-rhithral zone, in contrast, restorations tended to decrease functional diversity and trait evenness.

Changes in functional diversity metrics and evenness between unrestored and restored conditions in the upper-potamal zone were influenced by the combination of anthropogenic pressures (AI) and restoration age (interaction "AI" x "years since restoration") (dRaoQ: X^2=7.22, p=0.027; dFDis: X^2=7.55, p=0.023) (Table S5). In the first 5 years, functional diversity increased in the restored compared to unrestored conditions independently from the AI (see Fig. S1). In older restorations, greater increases in trait diversity were observed in areas with larger AI, while trait diversity receded in areas of lower AI (see Fig. S1). A second interactive effect on functional diversity and evenness in the upper-potamal zone was found between altitude and years from restoration (dRaoQ: X^2=7.23, p=0.027; dFDis: X^2=6.54, p=0.038; dEve: X^2=7.64, p=0.022) (Fig. S2, Table S5). In the first 5 years, changes in trait functional diversity and evenness were more pronounced in rivers at low altitudes; at greater restoration ages, restoration effects were more pronounced in rivers at higher altitudes (see Fig. S2). Furthermore, greater changes in functional diversity and evenness in the upper-potamal zone were observed at longer restored site (dRaoQ: X^2=6.03, p=0.014; dFDis: X^2=5.87, p=0.015; dEve: X^2=7.35, p=0.007) (See Fig. S3) and in presence of restoration actions which were aimed to increase river connectivity (dRaoQ: X^2=15.07, p<0.001; dFDis: X^2=13.39 p<0.001; dEve: X^2=9.73, p=0.002) (See Fig. S4).

3.2 Trait Composition

Fish community trait composition varied between restored and unrestored conditions and among river zones (“restoration” x “river zone”, $F_{3, 612}$=4.05, p=0.002). Composition between restored and unrestored reaches differed in the upper-rhithral zone ($F_{1, 276}$=13.54, p=0.022) and in the lower-potamal zone ($F_{1, 28}$=5.21, p=0.044) (Fig. 3). Trait categories associated with equilibrium life-history strategy increased by 10 % in the restored conditions in upper-rhithral zones (Table 2, Figure 4a, Fischer’s exact test p < 0.001). Traits associated to opportunistic strategists decreased by 9 % in restored reaches (Table 2, Figure 4a, Fischer’s exact test p = 0.001). In contrast, in the lower-potamal zone trait categories associated with an opportunistic strategy increased by 12% after restoration (Table 2, Figure 4b, Fischer’s exact test p = 0.014), while trait categories related to equilibrium strategists decreased by 8 % (Table 2, Figure 4b, Fischer’s exact test p = 0.012).

Communities at restored reaches were more similar to each other than communities observed at unrestored reaches (“restoration” x “fish zones”; $F_{7,}$

$_{612}$=14.47, p=0.001). Restored reaches in the upper-rhithral (permutest: $p<0.001$), lower-rhithral (permutest: p=0.048) and in the upper-potamal zone (permutest: p=0.035) had lower value of β-diversity (lower variance) compared to the unrestored reaches (see Fig. 5).

Analysis of the environmental variables showed that in the upper-rhithral zone the effect of the restoration on the trait categories (delta values) varied between years from the restoration and level of anthropogenic pressure (“years since restoration” X “AI”: $F_{2,155}$ =3.62, p=0.009), years since restoration and length of the restored site (“years since restoration” X “length restored site”: $F_{2,155}$ =6.62, p=0.001) and among the number of restorations actions that focus on river bed structure ($F_{1,155}$ =22.04, p=0.001) and the riparian sector ($F_{1,155}$ =4.62, p=0.001) (Fig. 6a). Especially reaches with longer restored stretch and higher level of anthropogenic pressure showed shifts in trait composition towards an opportunistic strategy (fish species with more than 1 generation per year (st2), short life span (sl1) and with early female sexual maturation (ma1); Fig. 6a). In older restorations (6 to 10 years since restoration), species with equilibrium and periodic life-history strategies became more prevalent (fish species with late sexual maturity (ma4), large egg size (ed3), parental care (nnh) and large bodies (bl3) (Fig. 6a). Especially restorations that focused on riparian habitats led to trait shifts towards an equilibrium and periodic life-history strategy (Fig. 6a).

In the lower-potamal zone the effect of the restoration on community trait composition was mainly affected by the presence of a restoration action which aim to increase river connectivity ($F_{1,13}$ =8.37, p=0.007), but no clear relationship to life-history strategy could be observed, as the effect of measures on connectivity is associated with the first RDA axis, while the separation of traits belonging to different life-history strategies is along the second RDA axis (Fig. 6b).

4. Discussion

In this study, we showed that ecological traits can be used to compare restoration outcomes across different river types and across large geographical areas. Restoration actions have been shown to be able to influence ecosystem functions of rivers through changing trait composition in macroinvertebrates (Frainer 2018). Here, we showed that, also in fish, changes in trait composition can aid in our understanding of the secondary succession processes that take place in restored river reaches. We showed how the location of the restoration on the rhithral-potamal river continuum, as well as the level of anthropogenic pressures and the length of the restored river stretch affected the speed of trait turnover in fish communities. Using a functional approach with ecological traits, we were able to assess restoration projects across multiple countries, overcoming taxonomical difference due to geographical constrains on the local species pool (Olden and Kennard, 2010).

Restoration of hydromorphology is one of the key strategies employed in river restoration, though short term monitoring schemes have yielded varying and sometimes limited results (e.g. England 2018). We presented evidence that hydromorphological restoration can increase functional diversity and change the proportion of opportunistic-periodic-equilibrium strategists in riverine fish communities using long-term monitoring data. In particular, this was the case in the upper-potamal zone of rivers. Increases in functional diversity are widely believed to increase the resilience of an ecosystem (Dukes, 2001; Bellwood et al., 2004). Higher functional diversity is a sign of the success of restoration in stimulating self-organising of rivers and thereby creating diverse habitats with structural characteristics favourable to a wide range of fish species. This is supported by the changes away from equilibrium species and towards more opportunistic species in the lower potamal zone. Higher river-floodplain connectivity with more pronounced temporal dynamics, opens up temporary niches for opportunistic species to flourish in temporary ponds and pools, and rearrangement of substratum in unchained rivers leads to a continuous rejuvenation and provision of habitats in early succession stages. Restorations also converged communities closer to the expected reference conditions of their respective surroundings. Hence, river reaches that were already close to this potential target, which is typically the case in areas of low AI, showed a relatively smaller and more immediate restoration effect. River reaches that were further away from natural reference conditions, which typically occurs in areas with higher AI, showed greater effects, and effects took longer time to materialize. A range of studies has already pointed out the role of the status of the surrounding species pool for the colonization process at restored river reaches (Stoll et al., 2013; Sundermann et al., 2011).

4.1 Dispersion of community trait composition

Restorations reduced the trait variability (as β-diversity) across restoration projects. In this study, this was particularly true in the upper-rhithral zone for which restoration projects analysed were biogeographically distant to each other including rivers from Switzerland, Germany and Finland. Different types of degradation can lead to different functional trait compositions between communities. The greater similarity in trait composition at restored reaches, even in this set of restoration projects from geographically distant locations, underpins that natural conditions for each river zone are well defined and communities reflect these more homogenous conditions among restored reaches. If proven universal, these river zone-specific trait compositions of natural habitat conditions could serve as a robust and universal target for restoration managers that allows for comparisons across biogeographic borders.

4.2 Restoration along the river continuum

Our results suggest that the effects of restoration depend on the position of a restoration project along the river continuum. For the upper rhithral river reaches we find different response patterns for trait diversity, life-history strategies and succession dynamics compared to lower river reaches. Upper rhithral river reaches are naturally more uniform with less room for a great variety of traits. Anthropogenic influences are known to hamper restoration of fish communities (Zajicek 2019). By anthropogenic changes such as impoundment, extra (un-natural) habitat diversity is created, allowing for a wider range of traits to persist in the system. Through restoration, opportunistic traits are reduced, leading to a shift towards the more natural and less functionally diverse rhithral-zone communities. This suggests that restoring a river natural state is not necessarily associated with richer or more functionally diverse assemblages, especially in the upper rhithral zone. Degradation in the upper rhithral zone is often associated with a deterioration of the sediment quality, especially colmatation of the sediment interstitial (Scheuer et al., 2009). An accessible and oxygenated interstitial zone however is crucial especially for low fecundity equilibrium strategists in this river zone such as brown trout and bullhead.

Beside its role as the reproduction habitat, the interstitial zone is also a crucial refuge for fish species during high discharge events. In degraded reaches flushing of fish is more likely, which favours short lived, fast reproducing opportunists which can recolonize flushed-out reaches more quickly.

4.3 Time since restoration, land use and environmental characteristics affect restoration outcomes

The succession dynamics of the changes in trait composition of fish communities elicited by the restorations varied as an effect of anthropogenic pressures in the adjacent catchment area and altitudinal position of the restoration project. In areas with greater levels of anthropogenic pressure, the effect of the restoration on fish community functional aspects emerged later, but reached higher effect sizes. In contrast to analyses focusing on taxonomical species (Palmer et al 2010), we showed that, also in intensely used areas, improvements are possible by restoration actions if enough recovery time is allowed. However, these improvements may have started from a very low pre-restoration status. Here we observed a clear succession of functional patterns where in the short term opportunistic species benefited, while on the longer term equilibrium and periodic species became more prevalent. Communities in rivers exposed to lower levels of anthropogenic pressures, and thereby probably already closer to natural conditions even in the degraded state, experienced an initial increase of functional diversity. Opportunistic species are efficient in building up sizeable populations quickly (Thomas et al., 2015), especially in the situation of a temporal loss of more competitive, longer-lived equilibrium strategist species due to the disturbance associated with execution of the restoration

(Tullos et al., 2009). Later, these communities experienced a gradual return to values similar to the unrestored reaches. Within the altitudinal span from 25 m to 347 m a.s.l. in the upper potamal zone, reaches which are located at higher altitudes seem slower to return to natural functional assemblages after the restoration event than upper potamal reaches at lower altitudes.

Altitude is often correlated with slope, and thereby current velocity (Schulze, 2005). Both the natural sequence of riffles and pools as well as anthropogenic barriers to manage the flow in such river reaches contribute to a reduction longitudinal connectivity, impede free longitudinal dispersion (Aarts and Nienhuis, 2003). In these conditions, colonization events may be more stochastic and conducted mainly by nearby individuals (Stoll et al., 2014), thus take longer time showing delayed effects of the restoration.

4.4 Conclusions

This study demonstrates the usefulness of species traits in understanding general processes that take place in communities after restorations are carried out. Restoration effects at the level of community composition with regard to ecological traits and life-history strategies followed the same patterns across a large geographic area, spanning from boreal Northern Finland to the German lower mountain areas and lowlands and to the Swiss Alps. We therefore believe that the use of ecological traits, more than taxonomic information, would allow us to compare restoration results across biogeographic regions. A better comparability of results is crucial to learn from each other about experiences with different restoration approaches to reach specific targets. This synthesis of practitioner knowledge on restoration options is highly pertinent (Palmer et al., 2005; Bernhardt and Palmer, 2007). The use of ecological trait information instead of species identities also matches well with the common ultimate aim of river restoration to enhance the natural integrity and functionality of rivers. Ecological species traits are more directly coupled to ecological functioning than species identities, and thus trait-based approaches allow a more direct interpretation of restoration results. In this pilot study we focused our analysis exclusively on trait categories which are associated to the opportunistic-periodic-equilibrium life strategies, however other traits categories (e.g. feeding behaviour) are available and can be implemented to further analyse the outcome of the river restoration.

This study also reconfirmed that succession processes at restored reaches are non-linear and depend on the environmental context of where a restoration takes place. Such general ecological patterns are difficult to perceive based on highly inter-annually variable taxonomic data, but easier to spot using functionally aggregated data based on ecological traits. Too early evaluation of restoration outcomes can furthermore be misguiding, as restoration effects on communities may vary (and even may be opposite) in early and late succession stages. To further test the functional patterns observed along the river continuum in this study, trans-continental comparisons of restoration outcomes based on ecological trait information should be conducted. If successful, this could help to define overarching robust references for restoration managers. If proven to be universal, references based on community trait composition may be developed to evaluate the naturalness of species communities. Independent of taxonomic units, such an approach can be used for the evaluation and comparison of environmental management actions, e.g. restoration projects, across biogeographic regions.

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Table 1 – Life-history traits used in the study as informative of the opportunistic-periodic-equilibrium trichotomy fish life-history strategies: opportunistic (O), periodic (P), equilibrium (E), following Winemiller and Rose (1992) concept. For trait categories which were not falling specifically in one of the three life-strategies, multiple strategies were indicated as potentially suitable.

Trait Class	Trait Category	Code	Life-history strategy
maximum life span (years)	<8	ls1	O
	8-15	ls2	P/O/E
	>15	ls3	P/E
maximum body length (cm)	<20	bl1	O
	20-39	bl2	E
	>39	bl3	P
female maturity (years)	<2	ma1	O
	2-3	ma2	E
	3-4	ma3	E
	4-5	ma4	E
	>5	ma5	P
spawning time	1 per year	st1	P/E
	> 1 per year	st2	O
fecundity (no. oocytes)	< 55,000	fe1	O/E
	55,000 - 60,000	fe2	P/O/E
	> 60,000	fe3	P
egg diameter (mm)	< 1.3	ed1	P/O
	1.3 - 2	ed2	P/O/E
	> 2	ed3	E
parental care	no parental care	nop	P/O
	protection with nest or hiding eggs	pnh	E
	no protection with nest or hiding eggs	nnh	E

Table 2 –Traits that contributed to the dissimilarity in community composition (SIMPER analysis) for restored and unrestored river reaches. Only river zones in which trait composition was significantly different (perMANOVA $p < 0.05$) between the restored and unrestored reaches are shown. For each category, contribution (with standard deviation) and relative cumulative contribution (up to 70%) to the group dissimilarity are shown as well as the average relative frequency (avg %) for the restored and unrestored conditions. Life-history strategies (O=opportunistic; P=periodic; E=equilibrium) for each trait category are included.

River zone	Trait class	Trait category	Contrib(%)	sd	Cumul Contrib(%)	Avg % (Rest)	Avg % (Unrest)	Life-history strategy
Upper-rhithral	parental care	no protection with nest or hiding eggs	0.032	0.024	0.074	0.095	0.066	E
	egg diameter	>2 mm	0.032	0.026	0.147	0.110	0.075	E
	body length	>39 cm	0.030	0.022	0.218	0.093	0.070	P
	parental care	no parental care	0.029	0.024	0.287	0.030	0.061	O
	female maturity	4-5 years	0.030	0.022	0.355	0.090	0.076	E
	life span	8-15 years	0.028	0.020	0.419	0.091	0.074	P/O/E
	body length	<20 cm	0.028	0.021	0.483	0.042	0.061	O
	fecundity	<55,000 oocytes	0.024	0.021	0.540	0.114	0.096	O/E
	life span	<8 years	0.024	0.020	0.596	0.039	0.050	O
	egg diameter	<1. 3 mm	0.022	0.022	0.647	0.018	0.041	P/O
	fecundity	55,000 - 60,000 oocytes	0.020	0.020	0.694	0.020	0.037	P/O/E
Lower-potamal	female maturity	4-5 years	0.026	0.014	0.086	0.040	0.083	E
	body length	20-39 cm	0.026	0.015	0.171	0.041	0.085	E
	life span	>15 years	0.025	0.014	0.253	0.049	0.089	P/E
	body length	<20 cm	0.024	0.014	0.333	0.092	0.054	O
	fecundity	55,000 - 60,000 oocytes	0.022	0.015	0.407	0.075	0.099	P/O/E
	fecundity	<55,000 oocytes	0.019	0.012	0.469	0.050	0.015	O/E
	life span	<8 years	0.018	0.013	0.530	0.053	0.025	O
	female maturity	<2 years	0.018	0.012	0.588	0.047	0.018	O
	spawning time	1 per year	0.015	0.011	0.639	0.083	0.099	P/E
	spawning time	>1 per year	0.015	0.011	0.690	0.060	0.043	O
	egg diameter	<1. 3 mm	0.015	0.010	0.739	0.079	0.083	P/O

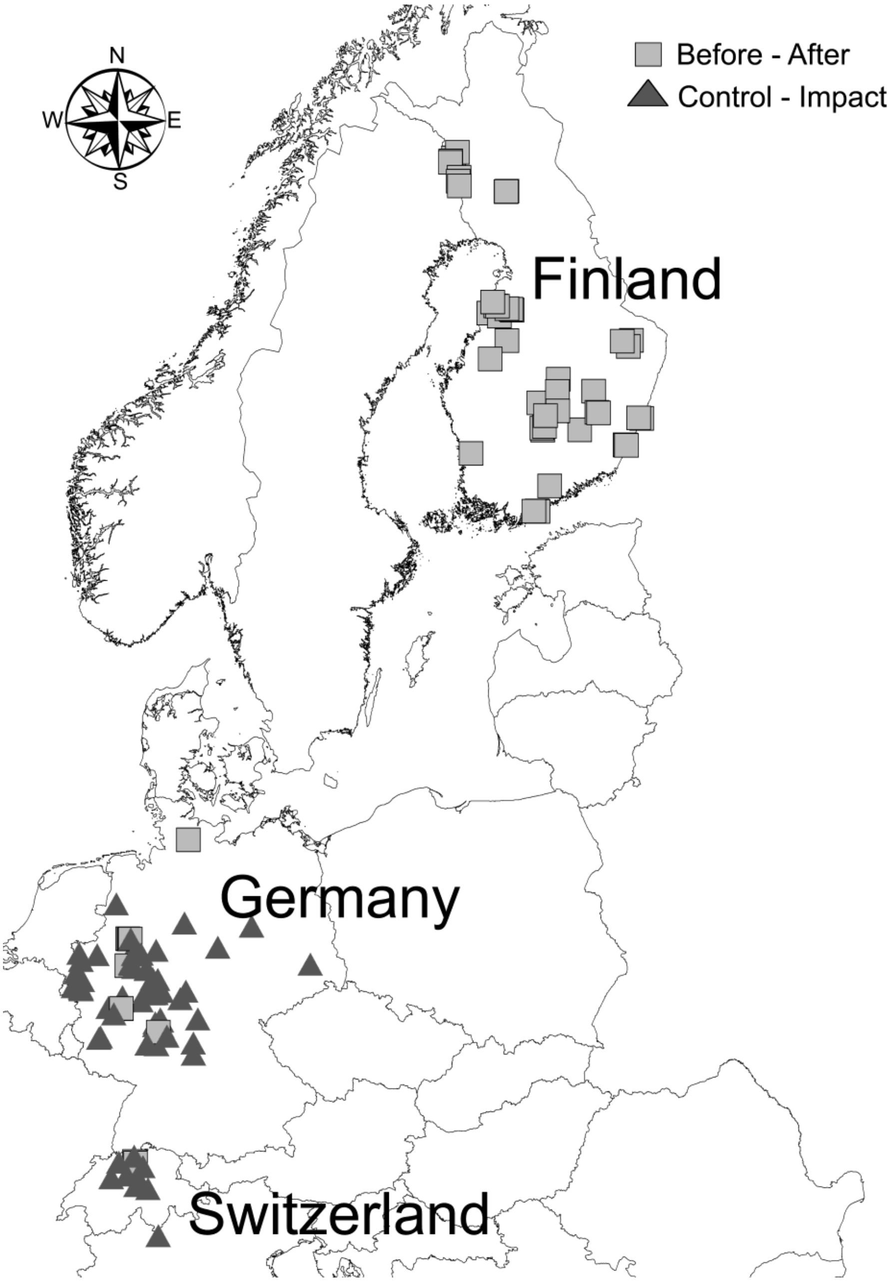

Fig. 1 – Study projects included in the study. The figure shows projects in which the same river reach was assessed before and after the restoration (BA) (squares), and projects assessed with a control – impact approach (CI) (triangles) in which an unrestored reach was compared to a restored one.

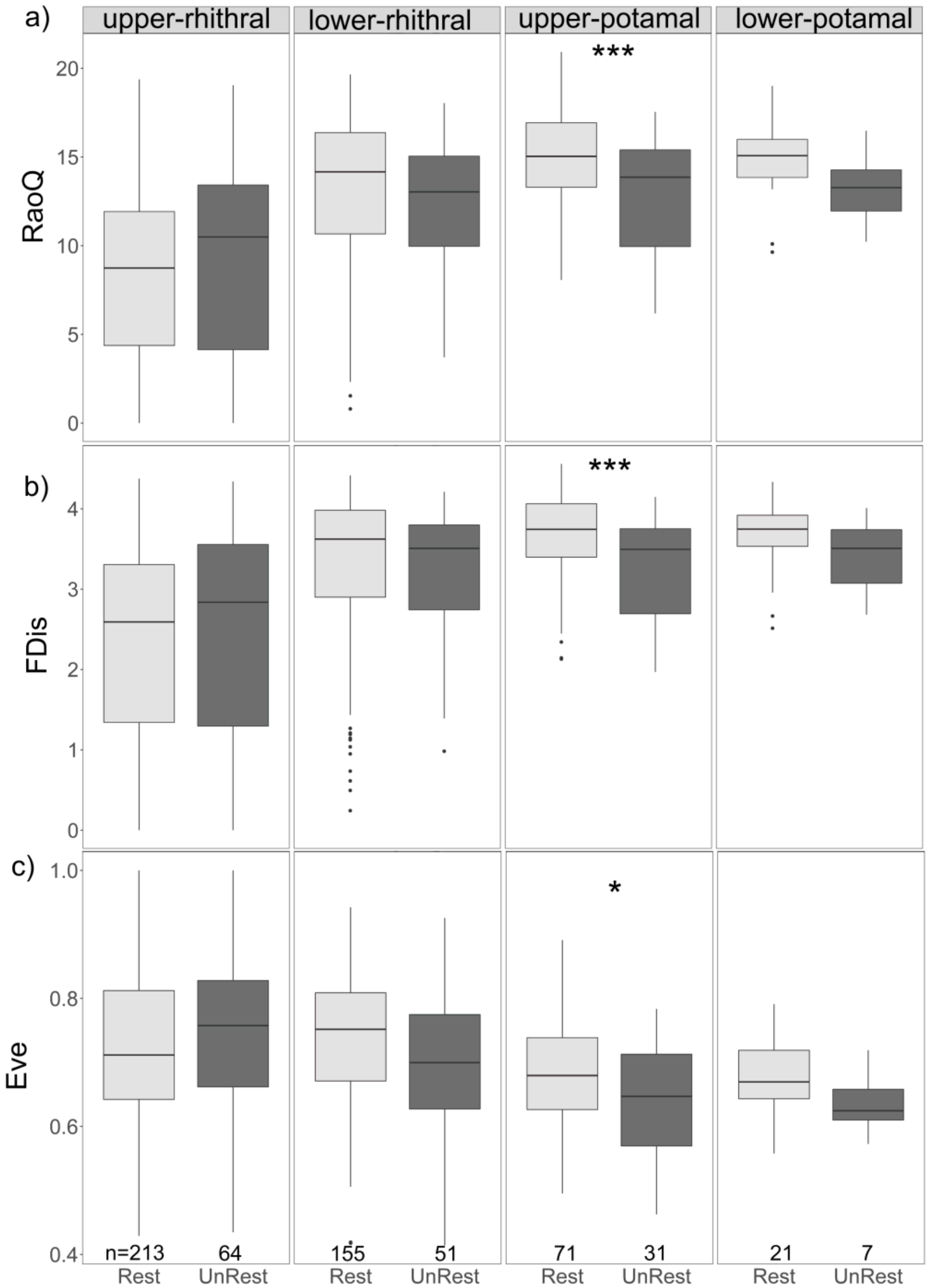

Fig. 2 – Boxplots showing Rao's quadratic entropy (RaoQ) and Functional dispersion (FDis) as functional diversity metrics together with species evenness Eve (c) in restored and unrestored conditions in the four longitudinal river zones (number of river reaches analysed are shown). Significant (LME) effect of restoration is indicated in the upper-potamal zone. (* = p<0.05; *** = p<0.001).

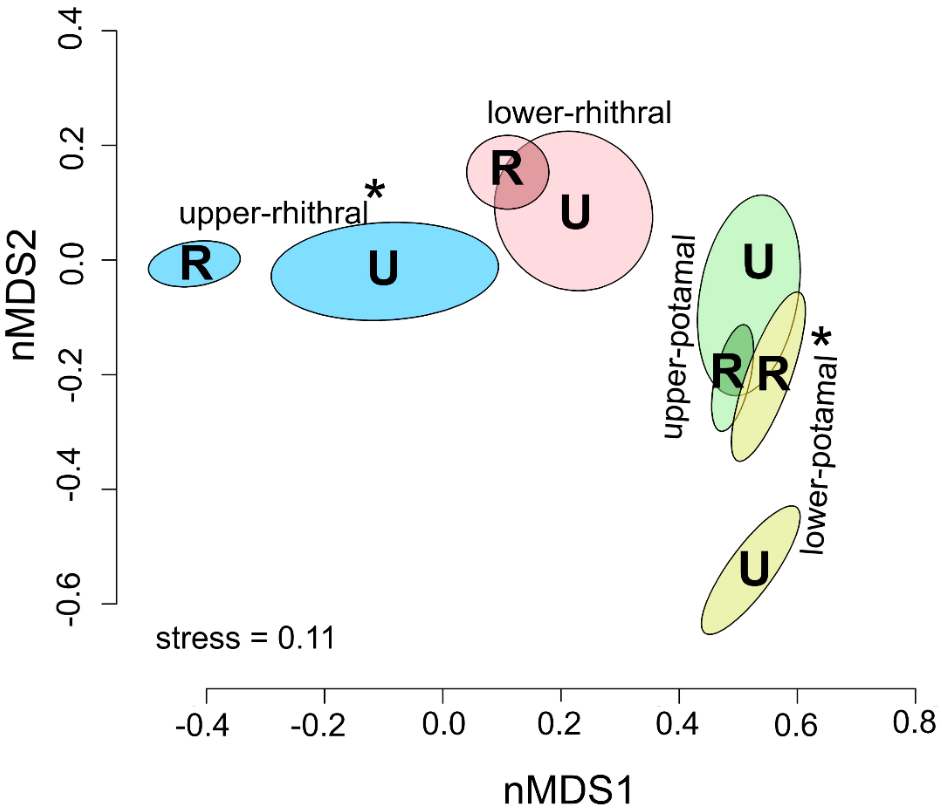

Fig. 3 – Trait composition of restored (R) and unrestored (U) conditions among longitudinal river zones is illustrated using a non-parametric Multidimensional Scaling plot (nMDS). Ellipses represent 95 % confidence intervals. Significant (perMANOVA) effect of restoration is indicated in the upper-rhithral and lower-potamal zone. (* = p<0.05).

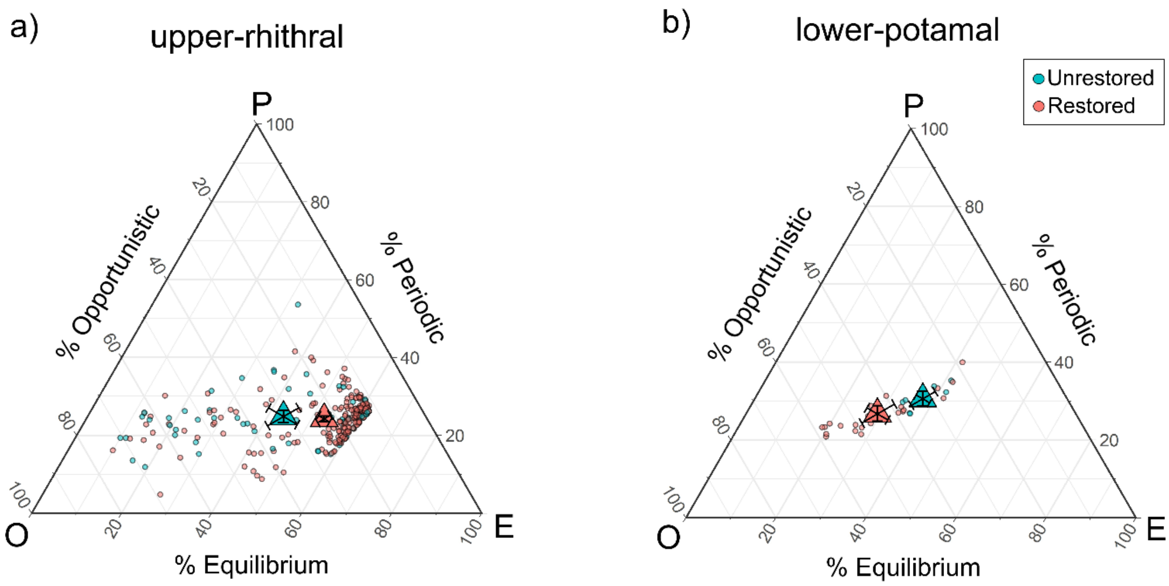

Fig. 4 – Ternary plot showing the relative proportion of opportunistic, periodic and equilibrium strategists for restored (pink dots) and unrestored (blue dots) river reaches for the upper-rhithral (a) and lower-potamal (b) zones in which significant variation in trait composition (1-way perMANOVA) was found. Coloured triangles and error bars represent centroid means and 95% confidence limits for restored (pink) and unrestored (blue) reaches. Trait proportions were calculated using only those trait categories that significantly contributed to the observed dissimilarity between unrestored and restored sites (SIMPER analysis).

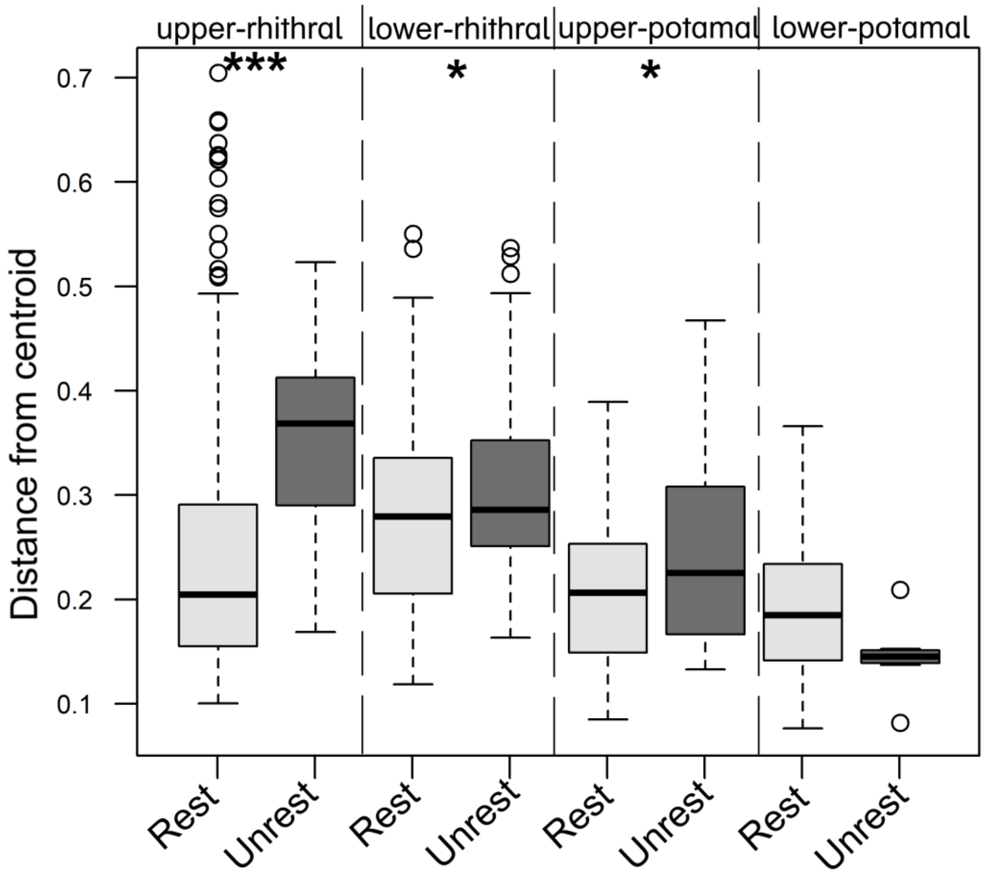

Fig. 5 – Distance from centroid in nMDS (as measure of β-diversity) on community trait composition in restored and unrestored conditions in the four longitudinal river zones (cf. Fig. 3). Significant restoration effects are indicated (*** = $p<0.001$; * = $p<0.05$). Box plots depict the 25, 50 and 75 percentiles, and whiskers the highest and lowest values excluding outliers.

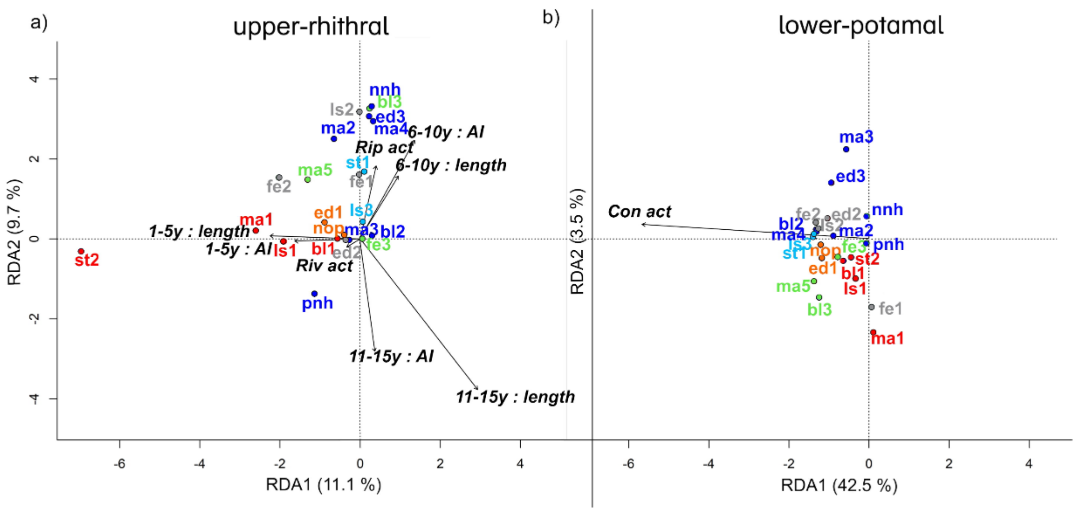

Fig. 6 – RDA plot depicting the relation between trait categories (as delta CPUE, calculated in each restored-unrestored paired condition) and environmental variables for the upper-rhithral (panel a) and lower-potamal (panel b) zones. The first two components of the RDA (with proportion explained in brackets) are included in each plot. Arrows represent significant environmental variables (anova: $p<0.05$): years since restoration (1-5y; 6-10y; 11-15y), number of actions that aimed to restore riparian section of the river (Rip act in the plot); actions that aimed to restore river bed structures (Riv act); actions that aimed to improve longitudinal connectivity (Con act). Interactive effects are shown for years since restoration with anthropic index (AI) and length of the restored river reach (length). Trait categories are color-coded according to the association with opportunistic (red), periodic (green) and equilibrium (blue) fish life strategies, or to a combination of them (orange = opportunistic/periodic; light blue = equilibrium/periodic; gray = opportunistic/equilibrium/periodic). See Table 1 for the trait category codes and relative opportunistic-periodic-equilibrium association.

Supplementary Material

Table S1 – Restoration actions were grouped in riparian, river bed and connectivity categories.

Categories	Restoration actions
Connectivity	Elimination of artificial barriers
	Mouth rehabilitation
	Transformation piping
Riparian	Creating shade shore edge strips
	Creation of gravel bars
	Creation of still water zones (pounds, lakes, backwaters)
	Elimination of embankments
	Introduction of deadwood
	Networking and floodplain reconnection
	Widening
River bed	Artificial bedload entry
	Creation of riffles and pools
	Deflectors flow diverter
	Diversify the river flow current
	Elimination of artificial structures
	Raising of the river bed
	Re-braiding of the water course
	Recreation river channel
	Re-meandering

Table S2 – Corine Land-use categories (code and description) (level 3) included in the 10 km length upstream buffer. A coefficient (k) was attributed to each of the categories based on the level of anthropogenic pressure in each category (1= no pressure; 2= low pressure; 3= medium pressure; 4= high pressure). The sum of each proportional area of each category multiplied by the correspondent coefficient k gives the anthropogenic index (AI) used for the analysis.

Code	Category description	k value
FTYP313	Mixed forest	1
FTYP324	Transitional woodland-shrub	1
FTYP512	Water bodies	1
FTYP311	Broad-leaved forest	1
FTYP321	Natural Grassland	1
FTYP322	Moors and heatland	1
FTYP332	Bare rocks	1
FTYP333	Sparsely vegetated areas	1
FTYP511	Water courses	1
FTYP412	Peat bogs	1
FTYP523	Sea and Ocean	1
FTYP411	Inland marshes	1
FTYP421	Salt marshes	1
FTYP312	Coniferous forest	2
FTYP243	Land principally occupied by agriculture, and natural vegetation	2
FTYP141	Green urban areas	2
FTYP211	Non-irrigated arable land	3
FTYP242	Complex cultivation patterns	3
FTYP231	Pastures	3
FTYP221	Vineyards	3
FTYP222	Fruit trees and berry plantations	3
FTYP142	Sport and leisure facilities	3
FTYP112	Discontinuous urban fabric	4
FTYP121	Industrial or commercial units	4
FTYP111	Continuous urban fabric	4
FTYP124	Airports	4
FTYP122	Road and rail networks and associated land	4
FTYP131	Mineral extraction sites	4
FTYP123	Port Areas	4
FTYP132	Dump sites	4

Table S3 –Number of projects as well as average width, catchment size and altitude are shown for each country according with the longitudinal river gradient used to classify the zones in the study. The longitudinal gradient was broken down according to the river biocoenotic region (Illies and Botosaneanu, 1963) and fish zonation (Huet, 1949) concepts using differentiation into rhithral (upper- and lower-) and potamal (upper- and lower-) zones. In Europe, potamal river reaches only occur in Central to Southern Europe, while in Northern Europe the potamal zone rarely occurs or is limited to the lowermost river section.

Longitudinal zonation	Country	N° of Projects	avg. width (m)	avg. catch size (Km^2)	avg. altitude (m a.s.l.)	Biocoenotic regions	Fish zones
Upper rhithral	CH	15	4.21	48.55	448.67	Epi- and Meta-rhithral	Trout
	DE	19	4.25	77.93	155.96		
	FIN	24	7.07	1029.58	103.65		
	avg.	58	6.15	718.80	158.30		
Lower rhithral	DE	22	11.59	372.60	156.17	Hypo-rhithral	Grayling
	FIN	26	35.24	4665.33	69.40		
	avg.	48	29.33	3592.15	91.09		
Upper potamal	DE	20	25.88	1651.25	77.44	Epi-potamal	Barbel
Lower potamal	DE	9	62.65	3041.00	68.35	Meta-potamal	Bream

Table S4 – Statistic summary for LME model of the main effect of the restoration among longitudinal river zones for the functional diversity metrics (RaoQ, FDis) and species evenness (Eve). In the table are included only the factors selected after model backward, for which p value was <0.06. Marginal (R^2m) and conditional (R^2c) variance of the model are indicated, as well as likelihood ratio statistic (X^2), degree of freedom (df) and significance (p).

Metric	Selected factors	R^2m; R^2c	X^2	df	p
RaoQ	Restoration*Zonation	0.10; 0.45	9.44	479	0.024
	Zonation		13.85	479	0.003
	Restoration		3.74	479	0.053
Fdis	Restoration*Zonation	0.09; 0.42	11.53	479	0.009
	Zonation		13.96	479	0.003
	Restoration		4.22	479	0.039
Eve	Restoration*Zonation	0.01; 0.28	10.34	479	0.016

Table S5 – Statistic summary for LME model of the restoration drivers for the upper-potamal river zone for the delta (restored-unrestored) functional diversity metrics (dRaoQ, dFDis) and delta species evenness (dEve). In the table are included only the factors selected after model backward, for which p value was <0.05. Marginal (R^2m) and conditional (R^2c) variance of the model are indicated, as well as likelihood ratio statistic (X^2), degree of freedom (df) and significance (p).

Metric	R^2m; R^2c	Selected factors	X^2	df	p
dRaoQ	0.55; 0.59	Age:log(AI)	7.22	44	0.027
		Age:log(Altitude)	7.23	44	0.027
		log (Length rest)	6.03	8	0.014
		Connectivity actions	15.07	44	<0.001
dFDis	0.58; 0.62	Age:log(AI)	7.55	44	0.023
		Age:log(Altitude)	6.54	44	0.038
		log (Length rest)	5.87	8	0.015
		Connectivity actions	13.39	44	<0.001
dEve	0.50; 0.76	Age:log(Altitude)	7.64	44	0.022
		log (Length rest)	7.35	8	0.007
		Connectivity actions	9.73	44	0.002

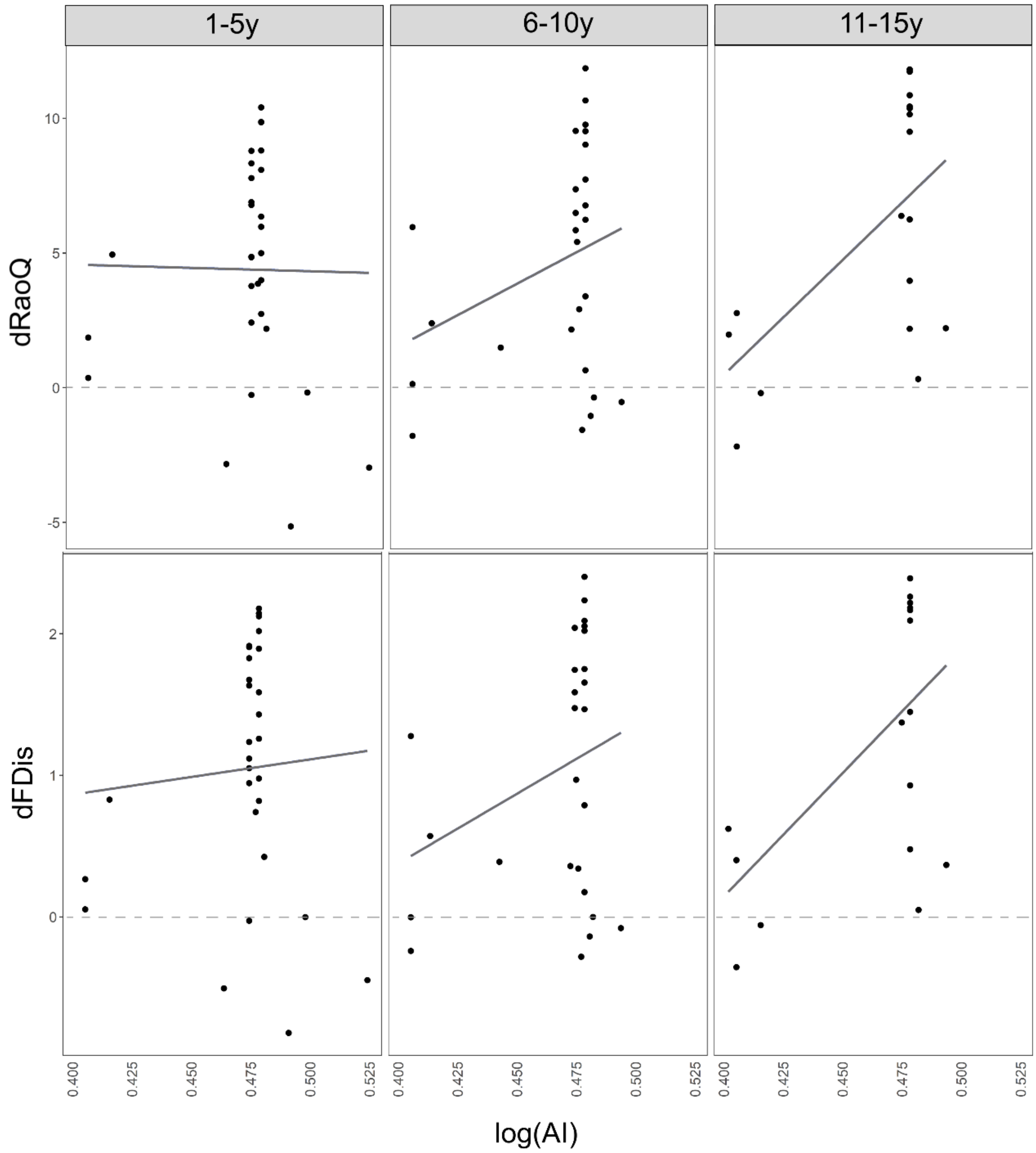

Fig. S1 – Linear relation between delta (restored-unrestored) values of RaoQ and FDis and log transformed Anthropic Index (AI) over the three age categories (1-5 years; 6-10 years; 11-15 years) in the upper-potamal river zone.

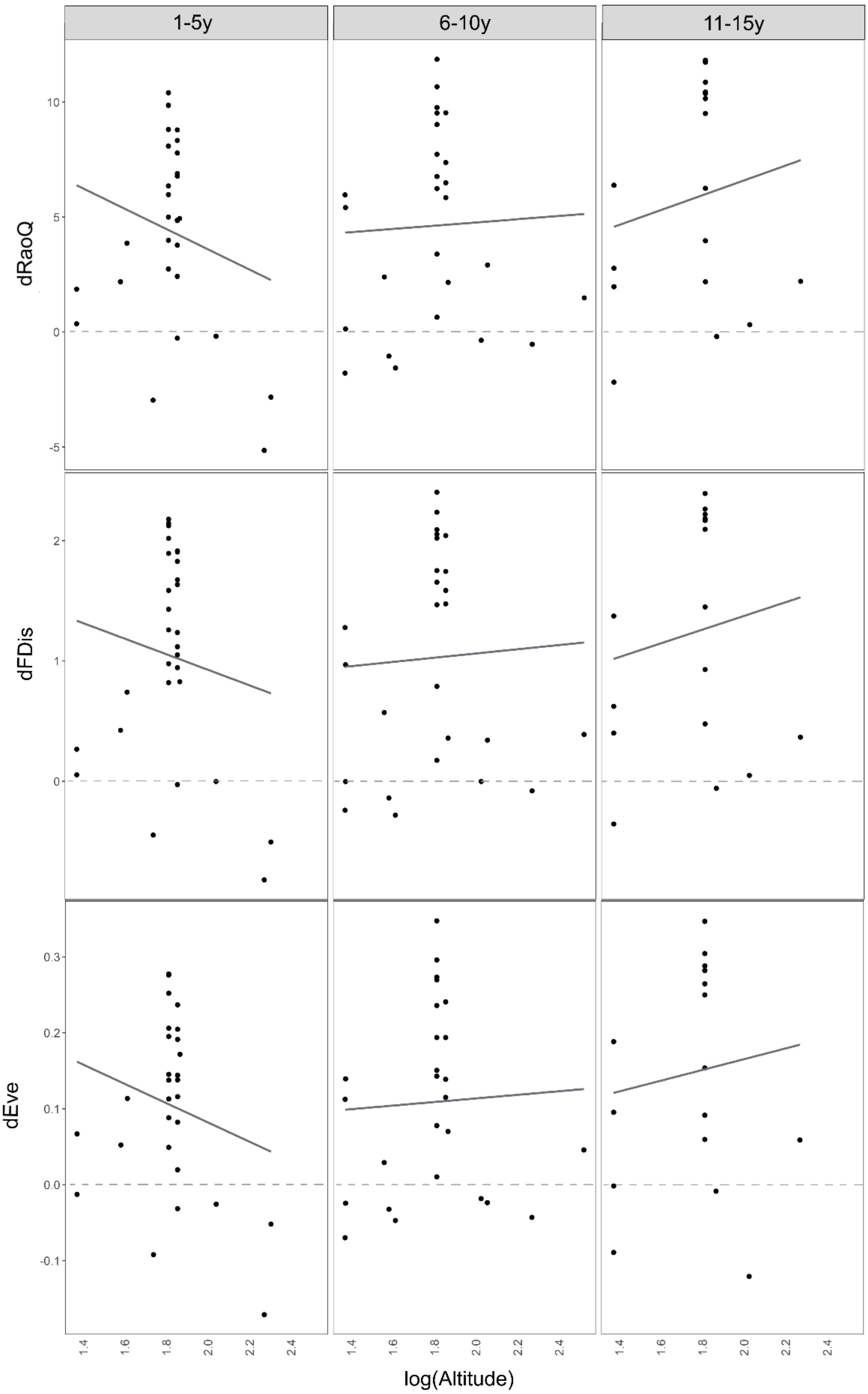

Fig. S2 – Linear relation between delta (restored-unrestored) values of RaoQ, FDis and Eve and log transformed altitude (m) (LAI) over the three age categories (1-5 years; 6-10 years; 11-15 years) in the upper-potamal river zone.

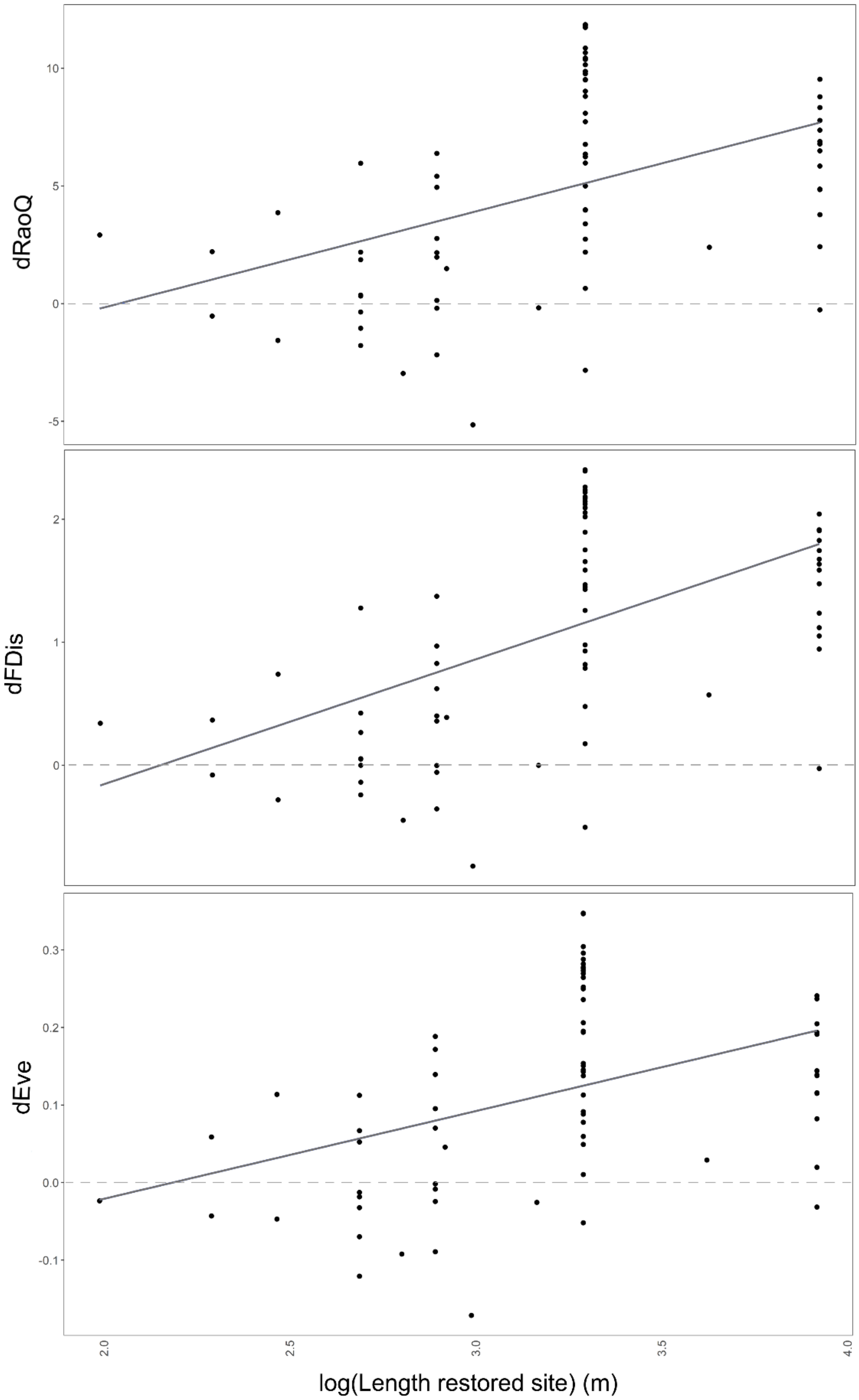

Fig. S3 – Linear relation between delta (restored-unrestored) values of RaoQ, FDis and Eve and log transformed length of the restored river reach (m) in the upper-potamal river zone.

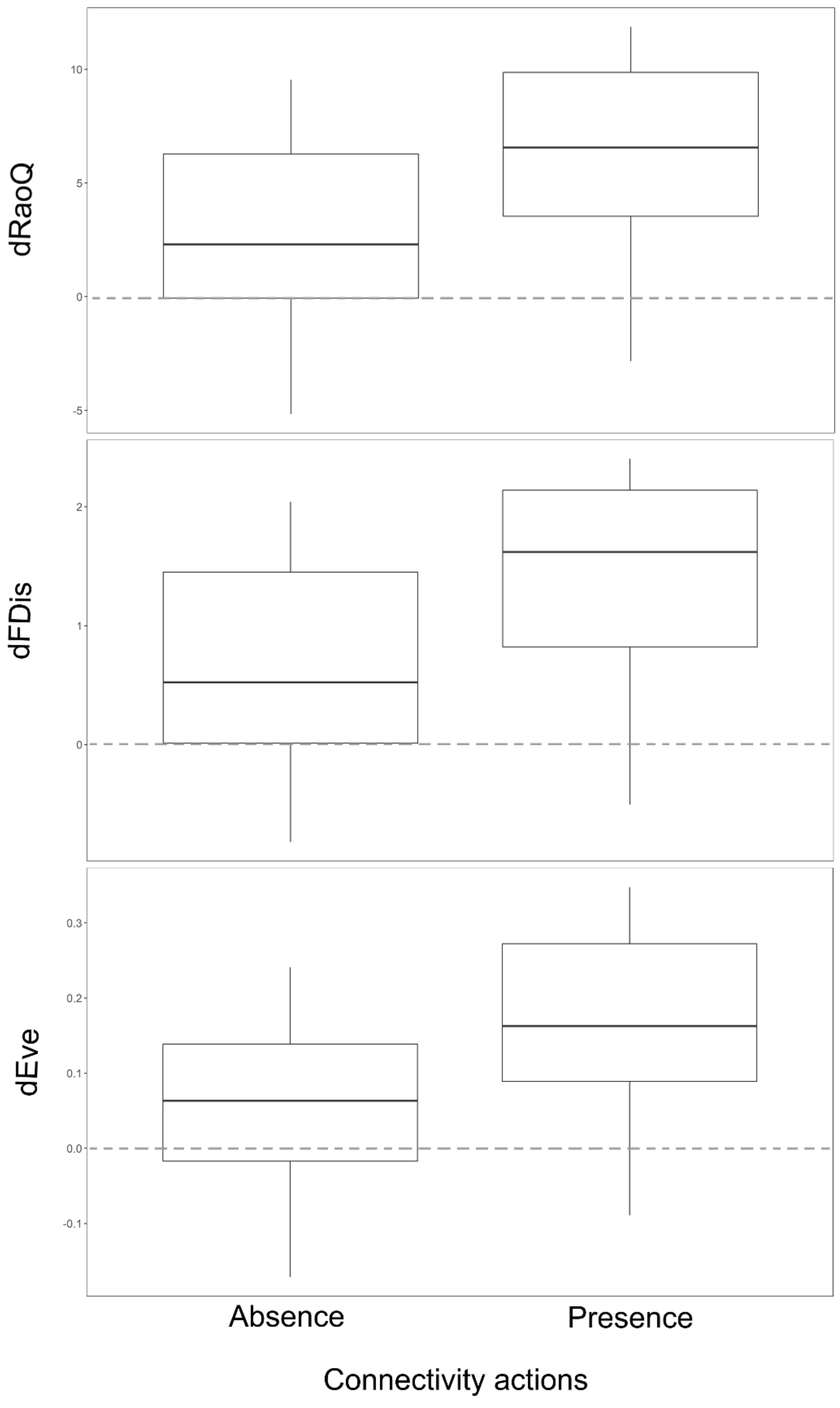

Fig. S4 – Comparison of delta (restored-unrestored) values of RaoQ, FDis and Eve and absence or presence of restoration actions that aimed to increase longitudinal connectivity in the upper-potamal river zone. Box plots depict the 25, 50 and 75 percentiles and whiskers the highest and lowest values excluding outliers.

Table 1

Table 1 - Life-history traits used in the study as informative of the opportunistic-periodic-equilibrium trichotomy fish life-history strategies: Opportunistic (O), Periodic (P), Equilibrium (E) following Winemiller and Rose (1992) concept. For trait categories which were not falling specifically in one of the three life-strategies, multiple strategies were indicated as potentially suitable.

Trait Class	Trait Category	Code	Life-history strategy
maximum life span (years)	<8	ls1	O
	8-15	ls2	P/O/E
	>15	ls3	P/E
maximum body length (cm)	<20	bl1	O
	20-39	bl2	E
	>39	bl3	P
female maturity (years)	<2	ma1	O
	2-3	ma2	E
	3-4	ma3	E
	4-5	ma4	E
	>5	ma5	P
spawning time	1 per year	st1	P/E
	> 1 per year	st2	O
fecundity (no. oocytes)	< 55,000	fe1	O/E
	55,000 - 60,000	fe2	P/O/E
	> 60,000	fe3	P
egg diameter (mm)	< 1.3	ed1	P/O
	1.3 - 2	ed2	P/O/E
	> 2	ed3	E
parental care	no parental care	nop	P/O
	protection with nest or hiding eggs	pnh	E
	no protection with nest or hiding eggs	nnh	E

Table 2
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Table 2 –Traits that contributed to the dissimilarity in community composition (SIMPER analysis) for restored and unrestored river reaches. Only river zones in which trait composition was significantly different (perMANOVA p < 0.05) between the restored and unrestored reaches are shown. For each category, contribution (with standard deviation) and relative cumulative contribution (up to 70%) to the group dissimilarity are shown as well as the average relative frequency (avg %) for the restored and unrestored conditions. Life-history strategies (E=equilibrium; P=periodic; O=opportunistic) for each trait category are included.

River zone	Trait class	Trait category	Contrib(%)	sd	Cumul Contrib(%)	Avg % (Rest)	Avg % (Unrest)	Life-history strategy
Upper-rhithral	parental care	no protection with nest or hiding eggs	0.032	0.024	0.074	0.095	0.066	E
	egg diameter	>2 mm	0.032	0.026	0.147	0.110	0.075	E
	body length	>39 cm	0.030	0.022	0.218	0.093	0.070	P
	parental care	no parental care	0.029	0.024	0.287	0.030	0.061	O
	female maturity	4-5 years	0.030	0.022	0.355	0.090	0.076	E
	life span	8-15 years	0.028	0.020	0.419	0.091	0.074	P/O/E
	body length	<20 cm	0.028	0.021	0.483	0.042	0.061	O
	fecundity	<55,000 oocytes	0.024	0.021	0.540	0.114	0.096	O/E
	life span	<8 years	0.024	0.020	0.596	0.039	0.050	O
	egg diameter	<1. 3 mm	0.022	0.022	0.647	0.018	0.041	P/O
	fecundity	55,000 - 60,000 oocytes	0.020	0.020	0.694	0.020	0.037	P/O/E
Lower-potamal	female maturity	4-5 years	0.026	0.014	0.086	0.040	0.083	E
	body length	20-39 cm	0.026	0.015	0.171	0.041	0.085	E
	life span	>15 years	0.025	0.014	0.253	0.049	0.089	P/E
	body length	<20 cm	0.024	0.014	0.333	0.092	0.054	O
	fecundity	55,000 - 60,000 oocytes	0.022	0.015	0.407	0.075	0.099	P/O/E
	fecundity	<55,000 oocytes	0.019	0.012	0.469	0.050	0.015	O/E
	life span	<8 years	0.018	0.013	0.530	0.053	0.025	O
	female maturity	<2 years	0.018	0.012	0.588	0.047	0.018	O
	spawning time	1 per year	0.015	0.011	0.639	0.083	0.099	P/E
	spawning time	>1 per year	0.015	0.011	0.690	0.060	0.043	O
	egg diameter	<1. 3 mm	0.015	0.010	0.739	0.079	0.083	P/O

Figure 1
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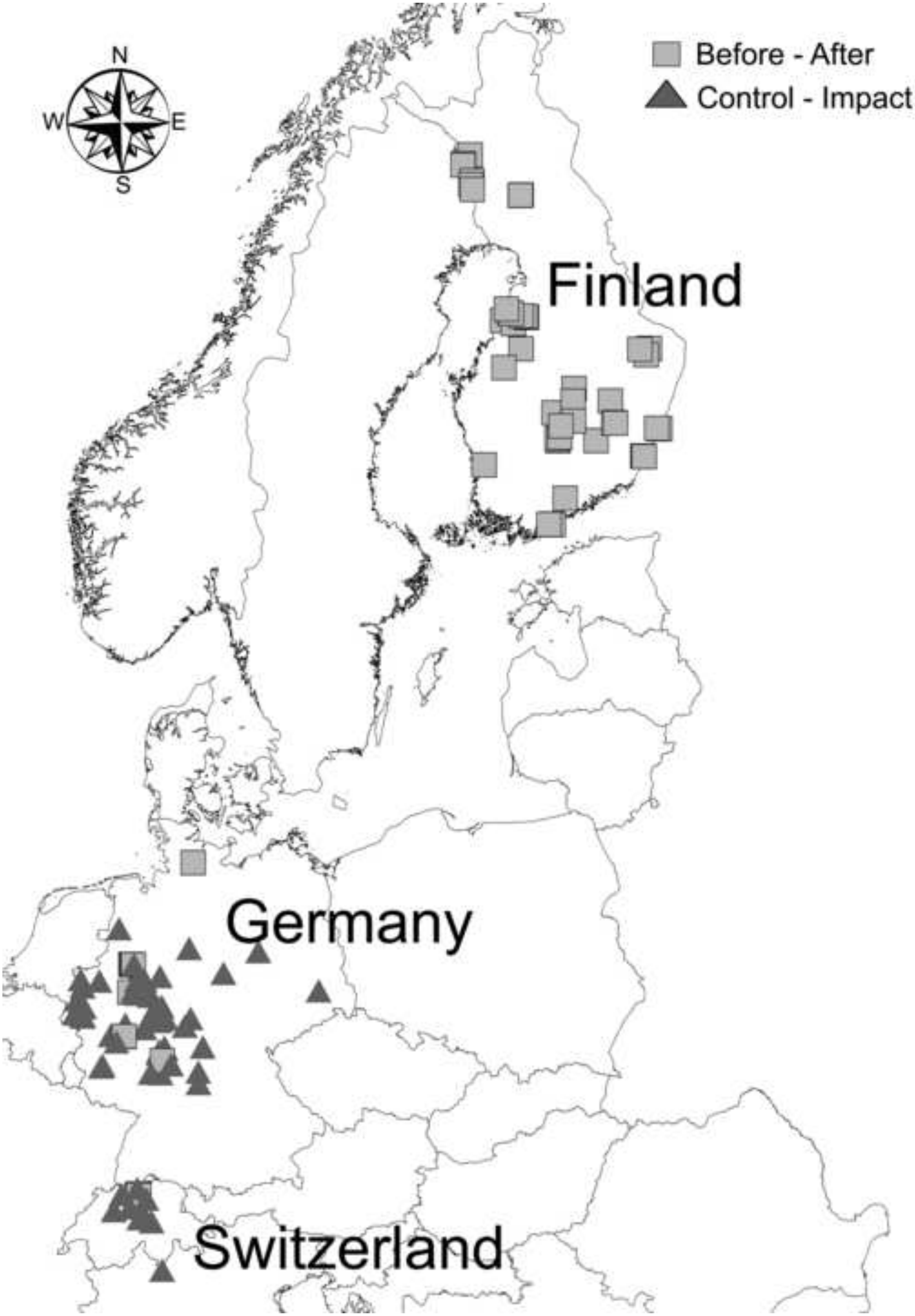

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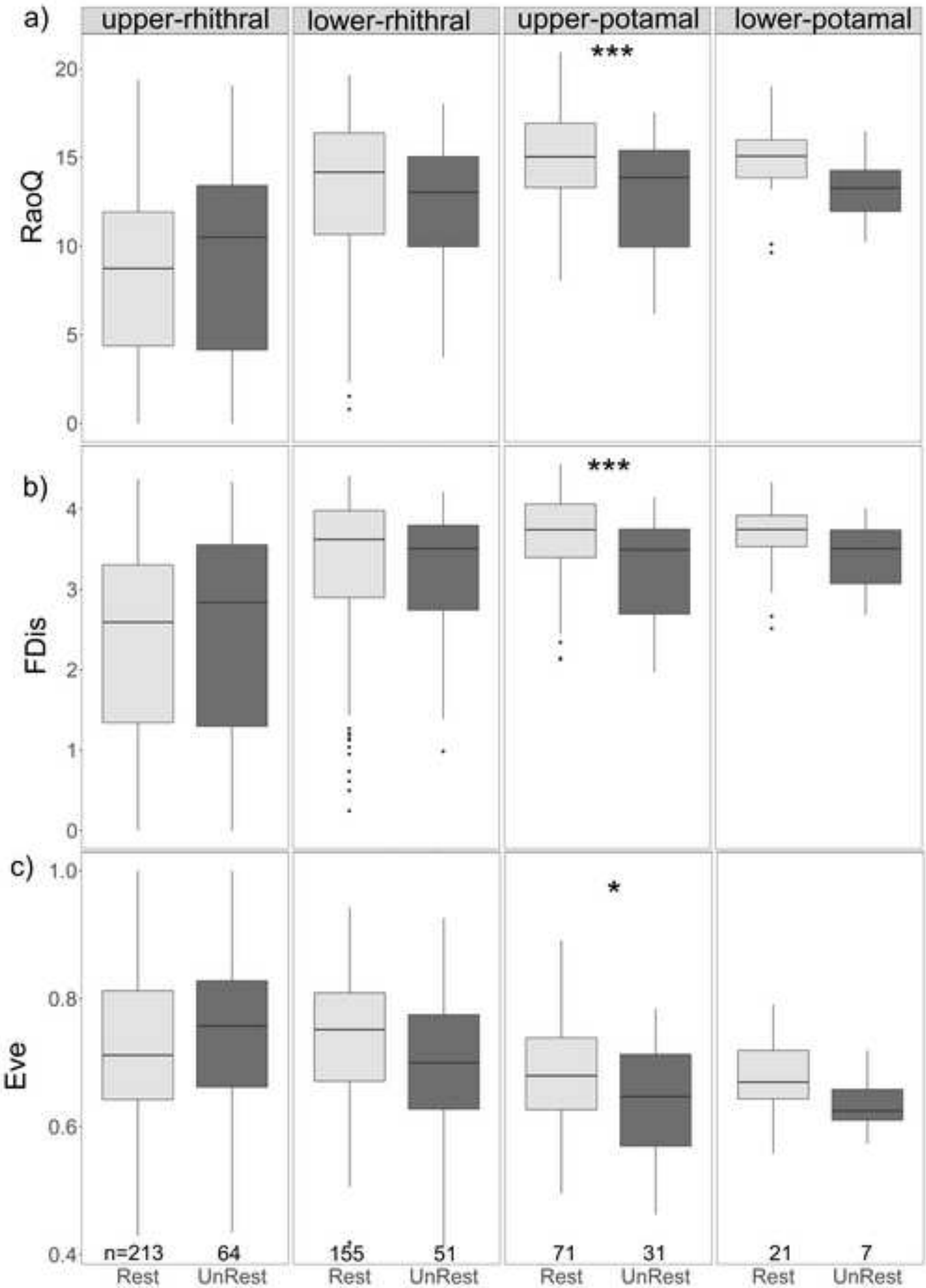

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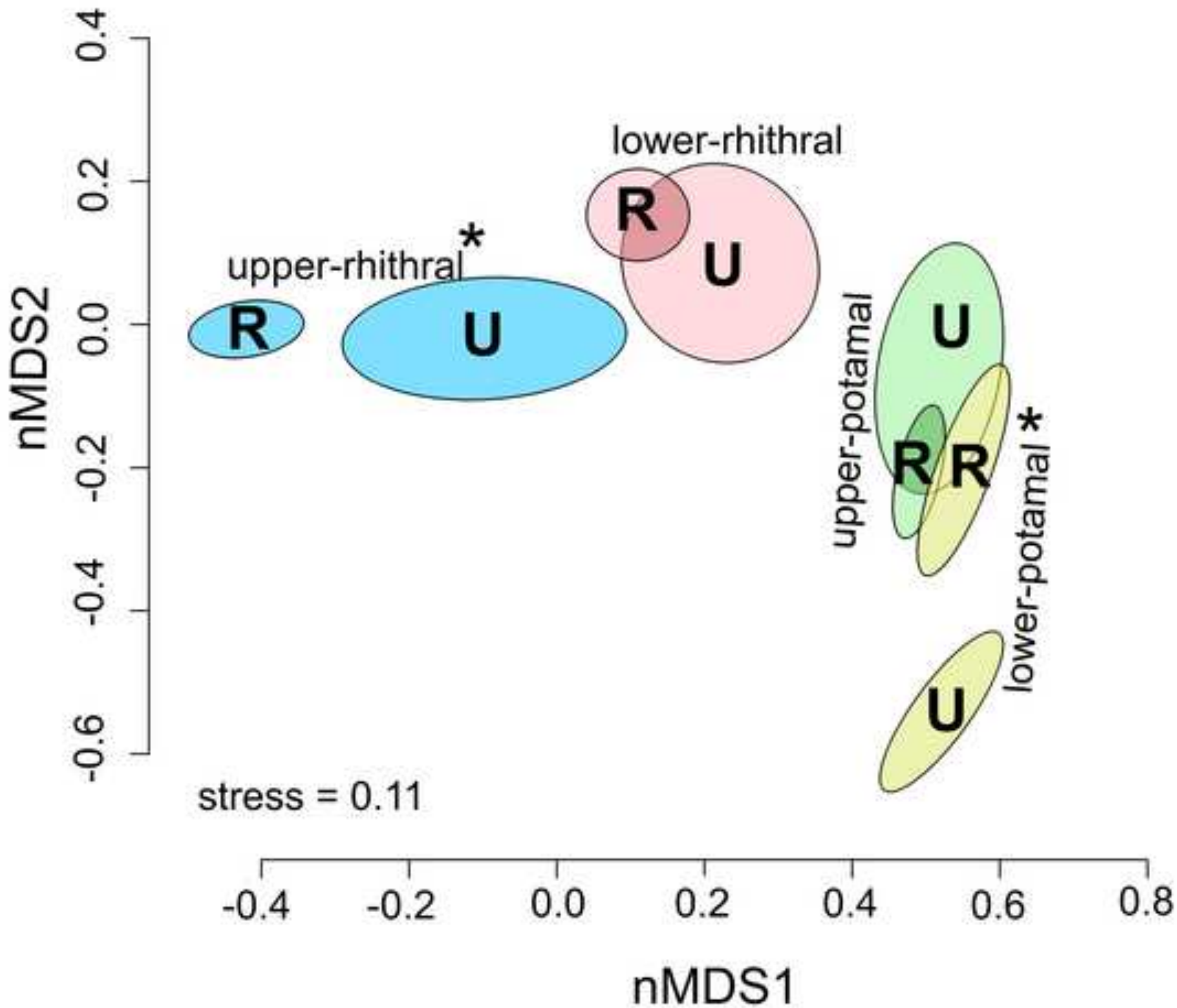

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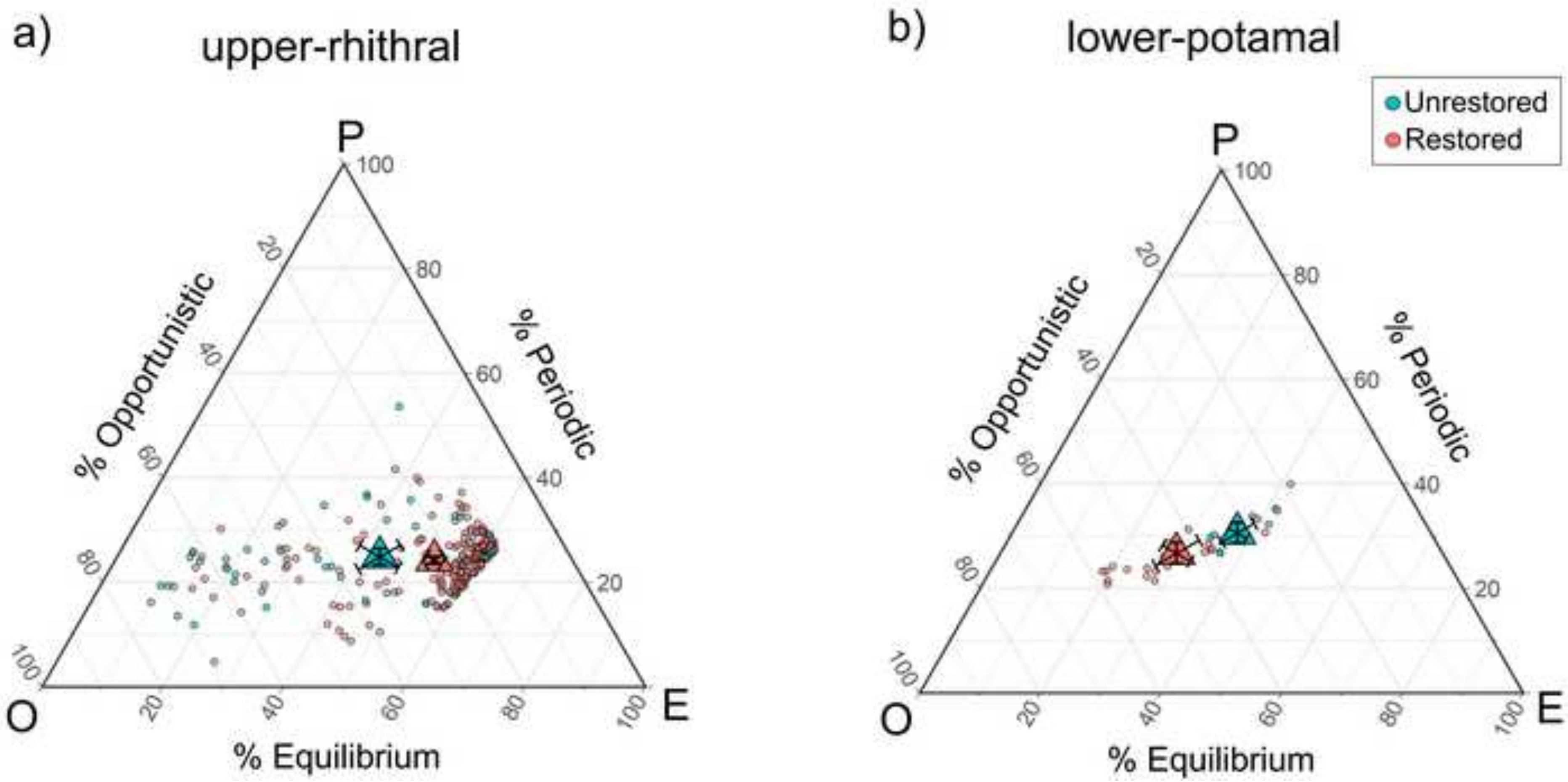

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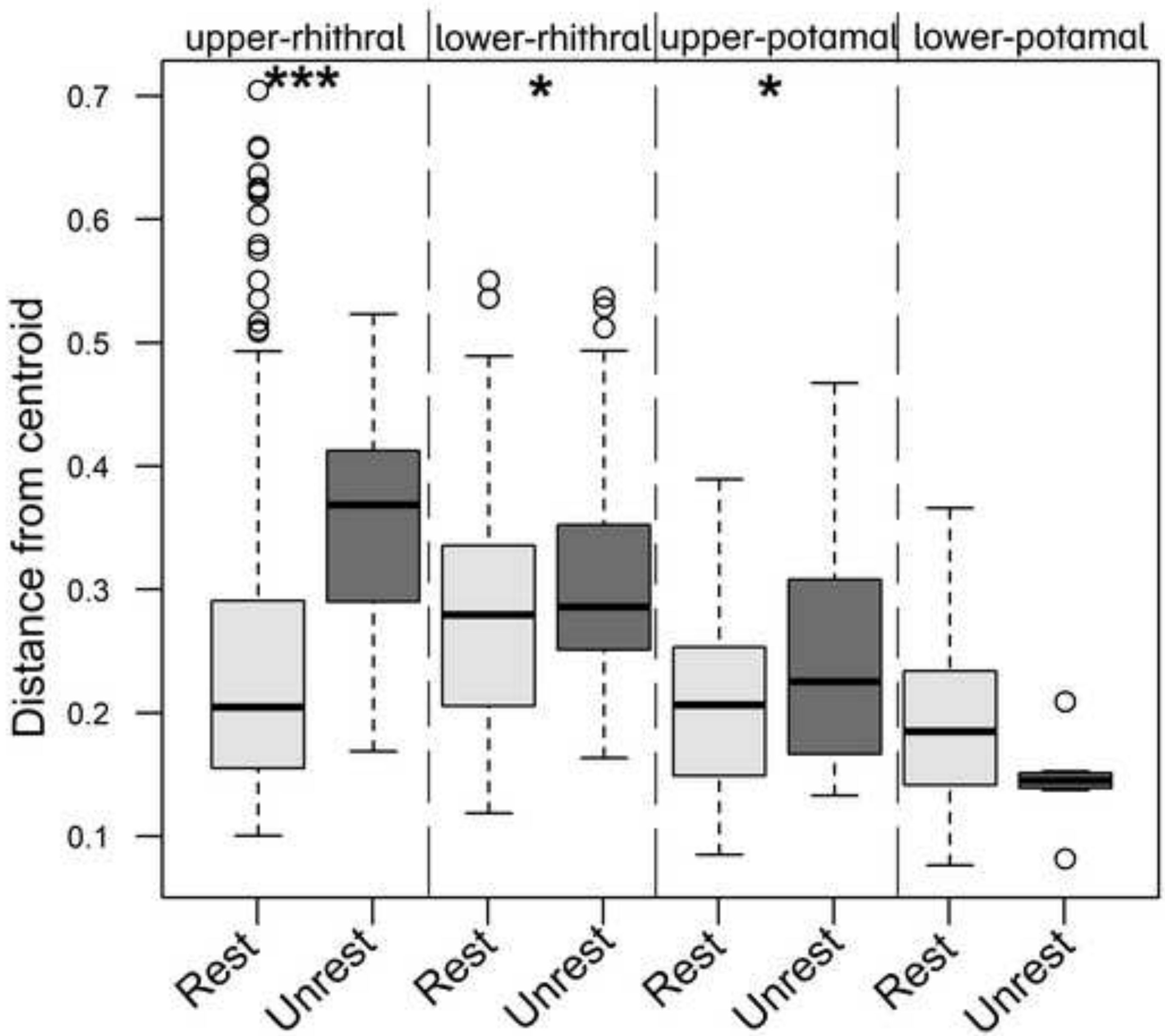

Figure 6

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