

Does functional redundancy of communities provide insurance against human disturbances? An analysis using regional-scale stream invertebrate data

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Abstract Human-induced reductions in species richness might alter the quality of ecosystem services when the remaining species are not able to substitute the functions provided by extirpated species. We examined how human disturbances (nutrient enrichment, land use intensification, instream habitat degradation and the presence of alien species) influence the species richness of stream invertebrates. Stream invertebrates (425 native species) were collected by kick and sweep sampling technique at 274 stream sites covering the entire area of Hungary. We measured the species richness, functional richness (i.e. number of unique functional roles provided by community members) and functional redundancy (i.e. the functional insurance of the community) using information on the feeding habits of each species. To remove the effect of natural variability, we tested the effect of stressors on the residuals of models relating species richness, functional richness and functional

redundancy with natural environmental gradients. Our results showed that species richness was negatively influenced by instream habitat degradation and nutrient enrichment. Independent of the way of quantifying functional richness and functional redundancy, we found that functional richness is more sensitive to human impact than functional redundancy of stream invertebrates. The finding that a reduction of species richness is associated with a loss of unique functional roles (functional richness) is important for conservation issues, because the number of unique functional roles is usually regarded as driver of ecosystem functioning.

Keywords Aquatic invertebrates · Functional richness · Functional redundancy · Human impact · Natural environmental gradient · Rivers

Introduction

The potential consequences of biodiversity loss for ecosystem functioning and services are receiving increased attention (Reiss et al., 2009; Woodward, 2009; Karlson et al., 2010; Mayfield et al., 2010). Empirical evidence indicates that species richness of communities influences ecosystem services (Diaz et al., 2006; Cardinale, 2011). More detailed analyses suggest that not necessarily species richness per se, but rather functional diversity of the community affects ecosystem services (Petchey, 2003; Yachi & Loreau,

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2007; Thibault et al., 2010). Considering species from a functional perspective, some species may perfectly replace the functional role of others (called functional redundancy; Loreau, 2004), whereas others differ in functional attributes (Petchey, 2003). Thus, human-induced reductions in species richness might alter the quality of ecosystem services depending on whether or not the remaining species can substitute the lost functional roles (Petchey & Gaston, 2002, 2006; Petchey et al., 2007).

Small-scale experimental studies suggest that the functional diversity of a community can enhance ecosystem functioning of stream invertebrates (Jonsson & Malmqvist, 2000, 2003; Cardinale et al., 2002) and perturbations reduce ecosystem functions through the elimination of species (Jonsson et al., 2002; McKie et al., 2009). On the other hand, functional redundancy (sometimes called ‘insurance’) provides resilience against loss of functions (Naeem, 1998). It follows that changes in species richness, functional diversity and functional redundancy provide a meaningful surrogate for the performance of ecosystems services in regional studies, a scale at which no experiments can be performed. A recent meta-analysis shows that both functional diversity and redundancy are affected by human disturbances and these relationships might vary considerable (Laliberte et al., 2010).

Freshwater ecosystems are among the most endangered ecosystems in the world (Dudgeon et al., 2006). Local-scale studies show that species richness of stream-dwelling native invertebrates is strongly influenced by water pollution (Dahl et al., 2004; Yule et al., 2010), instream habitat degradation (Dunbar et al., 2010; Palmer et al., 2010), land use in the watershed (Lake et al., 2010; Miserendino & Masi, 2010) and alien species (Nalepa et al., 2009; Wirth et al., 2010). However, several studies report difficulties in detecting the impact of human disturbances on the diversity of aquatic invertebrates (Heino et al., 2007; Heino, 2011). A possible explanation might be that natural environmental gradients mask the effect of perturbation (Heino et al., 2007). For example, species richness responds to stream size (Céréghino et al., 2003; Heino et al., 2005, 2008), watershed area (Voelz & McArthur, 2000; Vinson & Hawkins, 2003) or altitude (Vinson & Hawkins, 2003; Jacobsen, 2003, 2008). An additional complication is that the relationship between the species richness of aquatic invertebrates and any environmental gradient is not necessarily

linear (Clarke et al., 2008; Heino et al., 2008). Consequently, the existence of environmental gradients in large-scale community surveys provides a methodological challenge in quantifying the effects of human impact on native invertebrate richness.

In this article, we compared the effect of human disturbance on species richness, functional richness (regarded as a primary component of functional diversity, see Mason et al., 2005) and functional redundancy of aquatic invertebrates in a large-scale community survey. First, we quantified the species richness, functional richness and functional redundancy. Second, we eliminated the impact of natural environmental gradients (stream width, watershed area and altitude) from species richness, functional richness and functional redundancy to test the response of the residuals to four important forms of human disturbance: (1) degree of nutrient enrichment, (2) degree of land use intensification, (3) occurrence of instream habitat degradation and (4) presence of alien species. Our study examines human-induced reductions in species richness and their influence on the number of functional roles (measured by functional richness) and thus on the insurance of the community against disturbance (measured by functional redundancy). Based on the assumptions of the insurance hypothesis (Naeem, 1998), we hypothesise that species removal from a community due to human disturbances influences functional redundancy only. As an alternative hypothesis, we predict that species loss due to human disturbance decreases also the functional richness of stream communities.

Materials and methods

Study sites and environmental data

The “Ecological Survey of Surface Waters” programme (ECOSURV), established in Hungary in 2004 for the purpose of the Water Framework Directive, aimed to provide a large-scale, comprehensive data set for assessing the ecological status of surface waters based on biological (algae, macrophytes, aquatic invertebrates and fish), hydromorphological- and physico-chemical quality elements (<http://www.eu-wfd.info/ecosurv>, Ministry of Environment and Water, 2005a).

The assessment of habitat and water quality at the sampling sites followed the protocol of the AQEM project (Hering et al., 2003, 2004). Current velocity and stream width were measured in the field, the degree of instream habitat degradation was estimated at each sampling site and data on altitude, type of land use and size of watershed area were extracted from topological or land use maps. Physico-chemical parameters including water temperature and pH were measured using calibrated equipments. Water samples were taken and transported to the laboratory for quantitative analysis (e.g. total phosphorus) following standard methods. A detailed description of all variables can be found in van Dam et al. (2007) and the Ministry of Environment and Water (2005a).

Three natural environmental gradients were included as variables in the analyses, namely stream width, watershed size and altitude. Each of these variables has a strong but sometimes nonlinear influence on the species richness and diversity of aquatic invertebrates (Heino et al., 2003, 2007, 2008; Jacobsen, 2008). In our data set, the correlation among the three environmental variables was relatively weak (Pearson's product-moment correlation $r < 0.54$). Therefore, we considered all variables in the analyses.

The influence of four important types of human disturbances on stream ecosystems was examined: nutrient enrichment (expressed by the total amount of phosphorus in the water), land use intensification (total area of arable fields, vineyards and settlements, in % of watershed area), instream habitat degradation (i.e. presence of riverbed fixation in the channel or fixation of one or both banks) and the presence of alien species. Riverbed fixation was recorded as present or absent in the ECOSURV field survey (<http://www.eu-wfd.info/ecosurv>, Ministry of Environment and Water, 2005a). We therefore used it as a dummy variable. A high proportion of sites (61.3%) did not contain any alien species. The large number of zeros caused anomalies in handling the number of alien species as a continuous variable. Therefore, we also considered alien species as a dummy variable (present or absent). A low Pearson correlation value ($r = 0.33$), small η^2 values ($< 2.5\%$, for method see Boyero & Bailey, 2001) and a non-significant Chi-squared test showed that the examined stressors were not highly related.

Invertebrate data

Aquatic invertebrates were collected following the protocol developed in the AQEM project (Hering et al., 2003, 2004; Ministry of Environment and Water, 2005a). In short, kick and sweep sampling technique was applied at the majority of running water sites between 16 March, 2005 and 25 June, 2005 using a hand net (opening: 250 mm \times 250 mm, mesh size 0.95 mm; Kiss et al., 2006). Similar sampling methodology is generally used elsewhere for collecting stream macroinvertebrates (Carter & Resh, 2001). Morin et al. (2004) found in a comparative study that 1-mm mesh size is adequate to describe invertebrate communities. In contrast to the AQEM project (Hering et al., 2003, 2004), however, the number of replicate samples was reduced from 20 to 10, and the sampled material was sorted in the field and not in the laboratory (Kiss et al., 2006). Aquatic invertebrates were collected with a handheld net at those sites where the habitat structure did not allow the use of the kick and sweep technique (e.g. in dense aquatic vegetation). Individuals from ten taxonomic groups (Gastropoda, Bivalvia, Hirudinea, Crustacea, Ephemeroptera, Odonata, Plecoptera, Heteroptera, Coleoptera and Trichoptera) were identified to the possible lowest taxonomic level by specialists (Kiss et al., 2006). In the analyses, we used only taxa identified to the species level. Taxonomical nomenclature followed the Fauna Europae Web Service (2004).

Functional richness and redundancy

In this study, we used only presence/absence data to avoid errors as a result of abundance differences caused by different sampling methods (Elliott & Drake, 1981; Blocksom & Flotemersch, 2005; Cao et al., 2005). Furthermore, we considered only natural running water sites (i.e. human-made canals were disregarded). Records with missing data were omitted. A total of 274 sites with presence-absence data of 425 species were considered in the analyses. Species were classified as native (409 species) or non-native (alien: 16 species) based on DAISIE (2008) and grey literature. The latter was necessary because some species are alien in Western Europe, but not in Hungary.

As response variables we considered native species richness (hereafter species richness), functional richness of native species (hereafter functional richness) and functional redundancy of native species (hereafter functional redundancy). Data on species richness were obtained from the ECOSURV project. Functional richness and redundancy were calculated for each site in the following way: Each species was characterised by the affinity values of the 10 feeding habits described by Moog (1995): shredding, grazing, active filter-feeding, passive filter-feeding, detritus feeding, leaf boring, being xylophagous, a predator, a parasite or having another feeding habit. For example, *Halesus digitatus* (Shrank, 1781), a caddisfly species, might be characterised by 70% shredding, 10% grazing and 20% predatory feeding (Moog, 1995). The use of different feeding habits is expressed by affinity values varying between 0 (no affinity) and 10 (exclusive affinity) in such a way that the sum of affinity values for each species equals 10. Consequently, the affinity values of *H. digitatus* are 7, 1, 0, 0, 0, 0, 0, 2, 0 and 0, following the order of the ten feeding habits listed above. This data type is termed fuzzy coding (Chevenet et al., 1994) and frequently used in aquatic ecology (Usseglio-Polatera et al., 2000; Statzner et al., 2007). Species with identical functional roles (characterised by identical affinity values at each of the 10 feeding habits) are considered as functionally redundant and belong to the same functional unit (see Schmera et al., 2009a, b). In contrast, species differing in at least one of the affinity values of a feeding habit are considered as functionally different species. Here we define functional richness as the number of functional roles (or units) and functional redundancy as native species richness minus native functional richness. Note that the term functional role is equivalent to unique trait combination in Erős et al. (2009) and to functional species in Ricotta (2005). We used only the traits of feeding habits, because this is the trait group which can be the most directly linked to the functional role of stream invertebrates (Cummins & Klug, 1979). We should note, however, that other researchers might use additional traits in quantifying functional or rather trait-based diversity (Bonada et al., 2006; Beche & Statzner, 2009).

In a second series of analyses, we transformed the affinity values of feeding habits into a binary scale (presence/absence). This transformation compensated for some of the anomalies surrounding the

arrangements of affinity values (Moog, 1995). To make a clear separation of functional richness and functional redundancy based on quantitative and binary affinity values, we indexed the corresponding terms by a subscript q (quantitative) or b (binary). Consequently, functional richness _{q} means functional richness based on quantitative affinity values, whereas functional richness _{b} relates to functional richness based on binary affinity values.

Statistical analysis

To improve the normality of the data, environmental variables (stream width expressed in m, the size of the watershed in km², and altitude in m a.s.l.) were log-transformed and total phosphorus content (mg/l) was double square-root transformed. Pearson correlation was used to express associations between response variables. We also tested a saturating relationship between species richness and functional redundancy ($y = a + b \cdot \ln(x)$, see Beche & Statzner, 2009) and compared the fit of the model using Akaike's information criterion (AIC).

We used generalized additive models (GAM, Wood, 2006) to examine how stream width, watershed size and altitude influence species richness, functional richness and functional redundancy. This method needs smoothing curves to model the relationship between the explanatory and response variables (Zuur et al., 2007). We started with the full main-effect model (including the main effect of each explanatory variable in the model) and the minimal adequate model (the simplified model, see Crawley, 2007) was selected based on AIC. As minimal adequate models resulted in more than one explanatory variables (see “Results” section), we could only present in the figures the “additional effect” of a given explanatory variable relative to the other explanatory variables present in the minimal adequate model. This “additional effect” is quantified statistically as the “deviation from the average”.

We applied linear models (LMs, Venables & Ripley, 2002) to examine how human impacts influence the residuals of GAMs, where residuals are interpreted as the observed minus fitted values. In these models, instream habitat degradation and alien species were regarded as categorical predictors (present or absent), whereas nutrient enrichment and land use intensification were considered as continuous

predictors. Similar to the GAMs, we started with the full main-effect model and the minimal adequate model was identified based on AIC. All statistical analyses were performed in the R environment (R Development Core Team, 2009), with *mgcv* package (Wood, 2004, 2006).

Results

Correlation between response variables

We found positive correlations between species richness and functional richness_q (Pearson $r = 0.78$, $n = 274$, $P < 0.001$, Fig. 1), between species richness and functional redundancy_q ($r = 0.96$, $n = 274$, $P < 0.001$) and between functional richness_q and functional redundancy_q ($r = 0.58$, $n = 274$, $P < 0.001$). The saturating relationship between species richness and functional richness_q showed a better fit than the linear relationship (1265.90 vs. 1211.03 AIC values). Analyses based on binary affinity values showed positive correlations between species richness and functional richness_b (Pearson $r = 0.81$, $n = 274$, $P < 0.001$), between species richness and functional redundancy_b ($r = 0.98$, $n = 274$, $P < 0.001$) and between functional richness_b and functional redundancy_b.

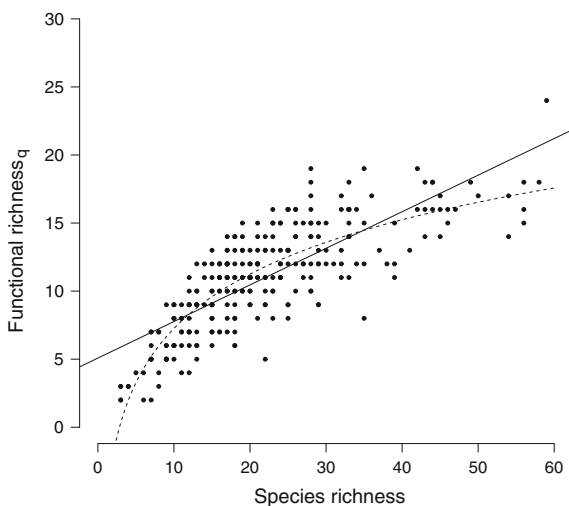


Fig. 1 The relationship between species richness and functional richness of stream invertebrates based on quantitative affinity values (functional richness_q) in Hungary. The solid line shows the linear model, whereas the dotted line indicates the saturating relationship. Each point represents one stream site

($r = 0.69$, $n = 274$, $P < 0.001$). The saturating relationship between species richness and functional richness_b showed again a better fit than the linear relationship (1084.95 vs. 1046.84 AIC values).

Species richness

The minimal adequate GAM showed that both stream width (GAM edf = 4.109, Ref.df = 5.195, $F = 5.828$, $P < 0.001$) and altitude (GAM edf = 2.828, Ref.df = 3.552, $F = 2.891$, $P = 0.027$) significantly influenced species richness of invertebrates, but not the size of the watershed (GAM edf = 3.596, Ref.df = 4.546, $F = 1.236$, $P = 0.294$):

$$\begin{aligned} \text{Species richness} = & s(\text{stream width}) \\ & + s(\text{size of the watershed}) \\ & + s(\text{altitude}), \end{aligned} \quad (\text{model 1})$$

where s denotes a smoothing function. Significant factors are typed in bold. Species richness first increased with increasing stream width but decreased in wider streams, resulting in a bell-shaped curve (Fig. 2a). In contrast, species richness gradually decreased with increasing altitude of the stream site (Fig. 2b). The minimal adequate LM revealed significant effects of nutrient enrichment and instream habitat degradation on the residuals of model 1 (Table 1).

Functional richness

The size of the watershed significantly influenced functional richness_q of stream invertebrates (GAM edf = 4.212, Ref.df = 5.245, $F = 2.366$, $P = 0.037$), whereas the effects of stream width and altitude were not significant (GAM edf = 2.081, Ref.df = 2.645, $F = 1.849$, $P = 0.146$ and GAM edf = 2.783, Ref.df = 3.500, $F = 1.845$, $P = 0.129$, respectively):

$$\begin{aligned} \text{F.richness}_q = & s(\text{stream width}) \\ & + s(\text{size of the watershed}) \\ & + s(\text{altitude}) \end{aligned} \quad (\text{model 2})$$

The relationship between watershed area and functional richness_q indicated that functional richness was more or less constant up to a watershed area of 100,000 km² (100 on the x-axis in Fig. 3) and then decreased. The minimal adequate LM showed that

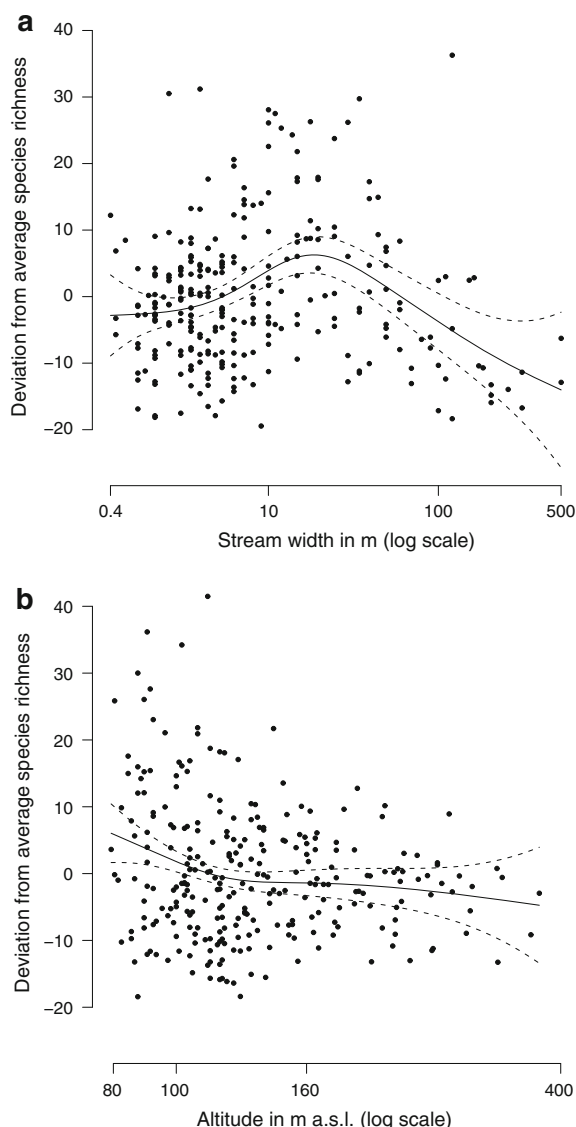


Fig. 2 Effect of stream width (**a**) and altitude (**b**) on the deviation from average species richness of aquatic invertebrates in Hungarian streams. *Solid line* shows the fitted GAM model, whereas the *dashed lines* show the 95% confidence intervals of the fitted values. Each *point* represents one stream site

both nutrient enrichment and instream habitat degradation negatively influenced the residuals of model 2 (Table 1).

Analyses based on binary affinity values revealed similar results. The size of the watershed significantly influenced functional richness_b of stream invertebrates (GAM edf = 4.316, Ref.df = 5.366, $F = 3.266$, $P = 0.005$), whereas the effects of stream width and

altitude were not significant (GAM edf = 2.122, Ref.df = 2.700, $F = 1.848$, $P = 0.145$, and GAM edf = 1.000, Ref.df = 1.000, $F = 0.054$, $P = 0.817$, respectively):

$$\begin{aligned} F. \text{richness}_b = & s(\text{stream width}) \\ & + s(\text{size of the watershed}) \\ & + s(\text{altitude}) \end{aligned} \quad (\text{model 3})$$

The relationship between functional richness_b and watershed area (not shown) was similar to that found for functional richness_q and watershed area. The minimal adequate model showed that both nutrient enrichment and instream habitat degradation negatively influenced the residuals of model 3 (Table 1).

Functional redundancy

The minimal adequate GAM revealed that stream width (GAM edf = 4.662, Ref.df = 4.735, $F = 11.361$, $P < 0.001$) and altitude (GAM edf = 2.452, Ref.df = 3.089, $F = 9.296$, $P < 0.001$) influenced the functional redundancy_q of stream invertebrates:

$$\begin{aligned} \text{Functional redundancy}_q = & s(\text{stream width}) \\ & + s(\text{altitude}) \end{aligned} \quad (\text{model 4})$$

Functional redundancy_q first increased and then decreased with increasing river width (Fig. 4a), but also decreased with increasing altitude (Fig. 4b). The minimal adequate model showed that instream habitat degradation influenced negatively the residuals of model 4 (Table 1). The size of the watershed was removed from the model.

Analyses based on binary affinity values revealed again similar results. The minimal adequate GAM indicated that stream width (GAM edf = 4.552, Ref.df = 4.609, $F = 10.610$, $P < 0.001$) and altitude (GAM edf = 2.869, Ref.df = 3.600, $F = 5.001$, $P = 0.001$) influenced the functional redundancy_b of stream invertebrates:

$$\begin{aligned} \text{Functional redundancy}_b = & s(\text{stream width}) \\ & + s(\text{altitude}) \end{aligned} \quad (\text{model 5})$$

The response of functional redundancy_b to stream width and altitude (not shown) was similar to that of the response of functional redundancy_q. The minimal

Table 1 Summary of minimal adequate linear models examining the effect of human impacts on the residuals of species richness, functional richness and functional redundancy from minimal adequate GAMs

Response variable: residuals of	Predictor	Effect size	SE	<i>t</i> value	<i>P</i>
Species richness (model 1)	(Intercept)	6.392	2.459	2.601	0.009
	Land use intensification	3.747	2.455	1.526	0.128
	Nutrient enrichment	−10.863	3.361	−3.232	0.001
	Instream habitat degradation	−2.973	1.418	−2.097	0.036
Functional richness _q (model 2)	(Intercept)	3.630	0.882	4.115	<0.001
	Nutrient enrichment	−4.739	1.171	−4.046	<0.001
	Instream habitat degradation	−1.198	0.521	−2.500	0.022
Functional richness _b (model 3)	(Intercept)	2.710	0.682	3.975	<0.001
	Nutrient enrichment	−3.508	0.905	−3.878	<0.001
	Instream habitat degradation	−0.986	0.403	−2.447	0.015
Functional redundancy _q (model 4)	(Intercept)	−1.291	1.171	−1.103	0.171
	Land use intensification	3.419	1.919	1.782	0.076
	Instream habitat degradation	−2.371	1.162	−2.040	0.042
Functional redundancy _b (model 5)	(Intercept)	3.636	1.956	1.859	0.064
	Land use intensification	3.039	1.954	1.555	0.121
	Nutrient enrichment	−6.824	2.676	−2.661	0.011
	Instream habitat degradation	−1.794	1.129	−1.589	0.113

Significant effects are highlighted in bold

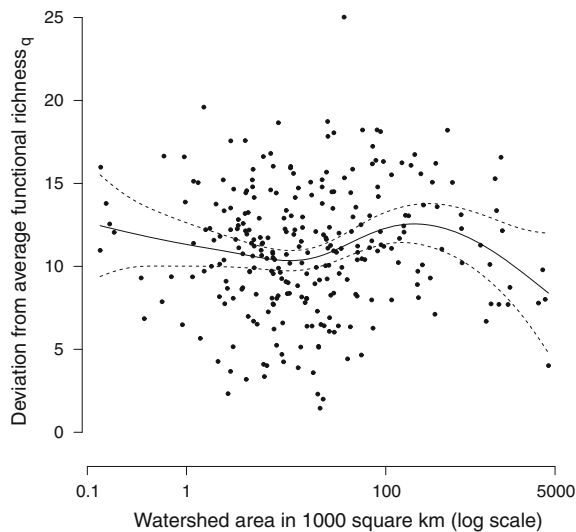


Fig. 3 Effect of watershed area on the functional richness of aquatic invertebrates based on quantitative affinity values (functional richness_q) in Hungarian streams. The *solid line* shows the fitted GAM model, whereas the *dashed lines* show the 95% confidence intervals of the fitted values. Each *point* represents one stream site

adequate model showed that nutrient enrichment influenced negatively the residuals of model 5 (Table 1).

Discussion

Our results show that human disturbances might negatively influence either both functional richness and functional redundancy, or only the functional richness components of species richness. This indicates that species removal from a community as a result of human disturbances does not necessarily influence exclusively functional redundancy. Consequently, our null hypothesis, stating that functional redundancy can protect communities against the loss of functions, should be rejected. Our results are in agreement with the findings of a recent meta-analysis performed on studies in terrestrial ecosystems: both functional diversity and redundancy are impacted by human disturbances and these relationships might vary considerably (Laliberte et al., 2010).

The positive correlations between response variables suggest that specious invertebrate communities have both higher functional richness and functional redundancy than communities with fewer species. The finding that species richness and functional richness is positively correlated is in agreement with another study examining richness gradients of stream invertebrates across the USA (Beche & Statzner, 2009).

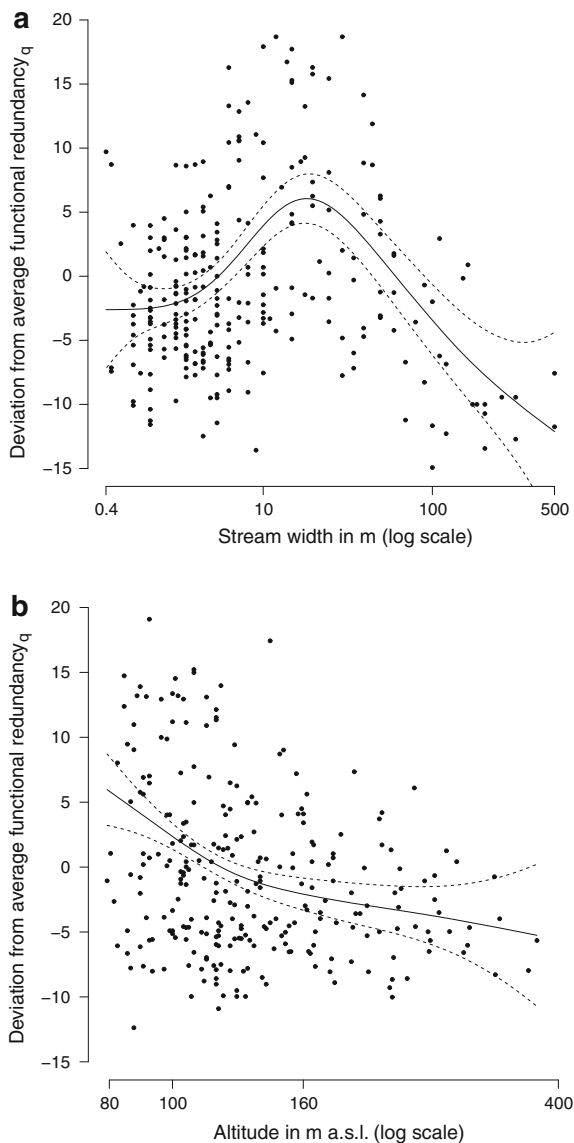


Fig. 4 Effect of stream width (a) and altitude (b) on the deviation from the average functional redundancy of aquatic invertebrates based on quantitative affinity values (functional redundancy_q) in Hungarian streams. Solid line shows the fitted GAM model, whereas the dashed lines show the 95% confidence intervals of the fitted values. Each point represents one stream site

Similar to that study, we found a saturation of functional richness at high species richness level (Fig. 1). The positive correlation between species richness and functional redundancy suggests the existence of functional redundancy in stream communities, regardless of the number of species. Finally, a

positive correlation between functional richness and functional redundancy suggests that functional richness and redundancy are not antagonistically related, as it would be assumed on the basis of additive partitioning. It follows that species richness of stream macroinvertebrate communities should not be regarded as a constant parameter that is divided into different proportions of functional richness and functional redundancy, rather than a parameter that varies considerably among localities.

We found, in agreement with previous studies, that species richness of stream invertebrates shows a hump-shaped response in relation to increasing stream width (Heino et al., 2005) and a tendency to decrease with increasing altitude (Vinson & Hawkins, 2003; Jacobsen, 2003, 2008). Furthermore, our results showed probably for the first time nonlinear relationships between functional richness and watershed area (Fig. 2), and between functional redundancy and stream width and altitude (Fig. 3).

Previous studies examining regional data sets did not find any significant impact of human disturbance and explained their results by masking effects of natural environmental gradients (Heino et al., 2007). We found that nutrient enrichment and instream habitat degradation significantly reduced species richness of stream invertebrates in Hungary provided that the effects of natural environmental variables were accounted for (Table 1; Fig. 5). However, land use intensification and the presence of alien species did not influence species richness of stream invertebrates (Table 1; Fig. 5). A possible explanation might be that these types of human disturbances do not exist along the entire range of an environmental gradient and, consequently, their overall effect might be limited. Another explanation is that presence/absence of human disturbance does not necessarily capture the real relationship between the variables studied. A recent study showed, for instance, that the number of alien invertebrate species is significantly higher in lowland than in highland streams in Hungary (Schmera & Baur, 2011). Thus, the overall effect of alien species on native species richness might not reach a statistical significant level when the whole region is considered.

Partitioning of species richness using quantitative affinity values revealed that nutrient enrichment influenced functional richness_q, but not functional redundancy_q (Table 1). This indicates that nutrient

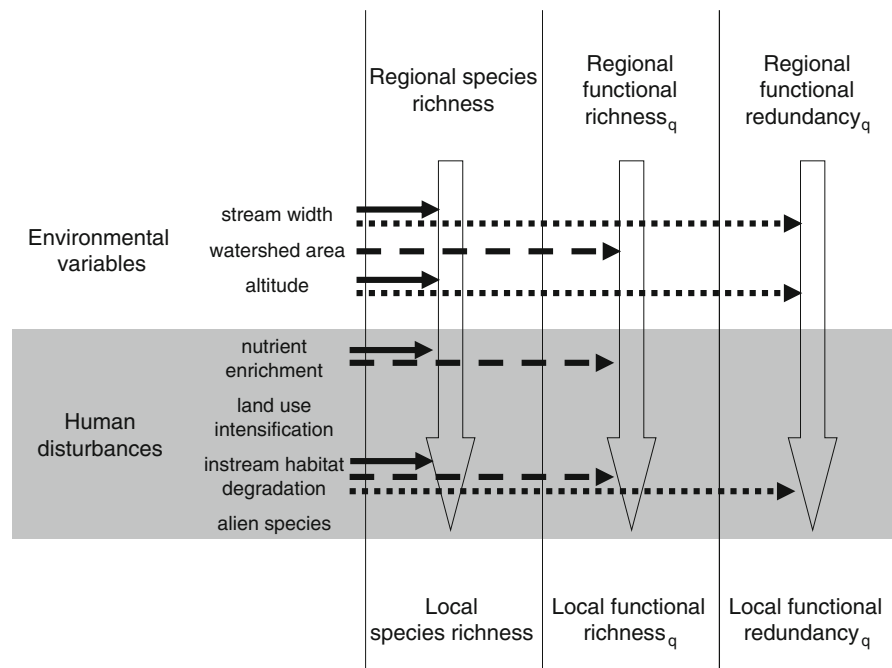
enrichment might eliminate certain species in such a way that the remaining species in the community are less complementary regarding their functional roles. This suggests that species removal from a community owing to nutrient enrichment is not random (see scenarios in Mayfield et al., 2010), and has a stronger impact on the functional richness_q than on the functional redundancy_q of the community. A possible consequence of this phenomenon is the functional homogenisation (Olden et al., 2004). However, in-stream habitat degradation had a negative effect on both functional richness_q and functional redundancy_q (Table 1; Fig. 5). Independent of the quantification of functional richness and functional redundancy, our findings suggest that some human stressors reduce species richness through its functional richness, whereas others through its functional richness and redundancy_q components (Fig. 5). Strong similarities between the results of the analyses based on quantitative and binary affinity values suggest that the observed patterns are robust. As recent meta-analyses show that the effect of human disturbance on species richness varies considerably, further studies are needed to elucidate the association between stressors and response variables, and to demonstrate the underlying mechanisms. It seems that functional redundancy, the ‘functional insurance’ of a community,

does not protect stream invertebrate communities against the types of human disturbances examined here, because—as a response to the reduction in species richness—not only functional redundancy decreased but also functional richness. This finding contrasts the insurance hypothesis proposing that biodiversity provides a buffer against the loss of functions when some species disappear (Loreau et al., 2001).

The parallel decrease in species richness and functional redundancy shown in our study indicates that functional redundancy has some role in protecting communities in Central Europe. This contrasts freshwater communities in Northern Europe, which are represented by a few confamiliar or congenetic species (Heino, 2005) and show a limited functional redundancy (Erős et al., 2009). These results suggest that stream invertebrate communities in Northern Europe might be more exposed to the loss of unique functional roles than communities in Central Europe. Obviously, further inter-regional studies are needed to test this hypothesis.

Streams are highly endangered ecosystems with dramatically decreasing biodiversity (Dudgeon et al., 2006). Our results revealed that human disturbance reduces the species richness of invertebrates in streams with environmental gradients. We found that

Fig. 5 Schematic representation of the impact of environmental variables and human disturbances on species richness, functional richness and functional redundancy of aquatic invertebrates based on quantitative traits (functional richness_q and functional redundancy_q, respectively) in Hungarian streams. For clarity, *arrows with solid line* represent the impact of environmental variables and human disturbances on species richness, whereas *arrows with dashed lines* represent the impact on functional richness_q and *arrows with dotted line* the impact on functional redundancy_q



the reduction of species richness is accompanied by low functional richness of the community. The finding that a reduction of species richness is associated with a loss of unique functional roles (functional richness) is important for conservation issues, because the number of unique functional roles is usually regarded as a driver of ecosystem functioning (Petchey, 2003).

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