Factors shaping species richness and biodiversity of riverine macroinvertebrate assemblages at the local and regional scale

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Keywords: Abiotic variables, Aquatic insects, Damming, Landscape fragmentation, (Non-)saturation, Nutrients.

Abstract: The biodiversity and species richness of benthic macroinvertebrate assemblages are under the strong pressure of environmental variables compounded with geographical and historical processes. Numerous studies that have investigated biodiversity and assemblage stability have shown the importance of choosing proper methodologies and paradigms. Consequently, the use of diversity measures and the partitioning of biodiversity at different spatial and temporal scales are of particular significance. Within habitats, only those species whose preferences remain within a tolerable range of the variability of abiotic factors are able to survive. The structure of biocoenosis at the local scale is determined mainly by current velocity/discharge, granulometry of the inorganic bottom substrate, quantity and quality of particulate organic matter, as well as water quality variables. Dispersion plays a key role in shaping regional diversity gradients, which supports the permanent inflow of individuals and their exchange between riverine basins. However, dispersion is also one of the basic aspects of the saturation/non-saturation of local communities with species from the regional species pool; a respective concept tries to determine how, why and to what degree local species richness is dependent on regional species richness.

Nomenclature: Fauna Europaea (2017).

Abbreviations: ENV – Environmental Variables; EPT – Ephemeroptera Trichoptera Plecoptera; LSR – Local Species Richness; OLS – Ordinary Least Squares; POM – Particulate Organic Matter; RSR – Regional Species Richness.

Introduction

Benthic macroinvertebrates play a key role in the circulation of organic matter and the flow of energy in running waters thanks to their feeding preferences, life histories and being prey for consumers at higher trophic levels (Cummins et al. 1983). Meanwhile a sufficiently high level of macroinvertebrate biodiversity is essential to maintain homeostasis in lotic ecosystems (Graça et al. 2004, Duan et al. 2008, 2009). One cause of increasing interest in aquatic macroinvertebrate diversity in recent years has been the intensification of human pressure on the natural environment, which usually results in a decrease in biodiversity (Burgmer et al. 2007, Smith et al. 2009, Rezende et al. 2014, Sokol et al. 2014, Fig. 1). However, reduced biodiversity may also be related to abiotic variables that regulate the abundance and structure of macroinvertebrate assemblages in aquatic ecosystems. The values of these variables can fluctuate considerably in time and space, simply as a result of natural ecological processes (Vannote et al. 1980, Graça et al. 2004, Elliott and Quintino 2007, Clarke et al. 2010, Szczerkowska-Majchrzak and Grzybkowska 2015), but some of them may also influence the environment directionally.

Many different measures are used to assess biodiversity (including macroinvertebrate diversity), the most popular being species richness and the Shannon and Simpson indices,

but the partitioning of biodiversity at different spatial scales (i.e., α for local, β for between-habitat, and γ for regional biodiversity: Whittaker 1972, Loreau 2000, Whittaker et al. 2001, Głowacki 2009, 2013) may also be essential. Using the above mentioned measures, hydrobiologists have determined that changes in the structure of macroinvertebrate communities along the course of a river can be connected to biogeographical, temporal and even historical factors operating at various scales (Vannote et al. 1980, Mykra et al. 2007). The measures are used to assess various concepts of species relations, which are mainly dichotomies such as: saturation versus non-saturation, interaction versus non-interaction, emigration versus immigration, local scale versus regional scale, and others.

Nowadays, the assessment of which variables (i.e., spatial environmental and/or temporal environmental) dominate in the structuring of diversity gradients in zoobenthos is also a widely investigated aspect (Heino et al. 2003, Mykra et al. 2007, Heino 2013, Rezende et al. 2014; Fig. 2). Many long-term field or experimental investigations conducted worldwide indicate that riverine macroinvertebrate diversity in particular habitats depends mainly on local abiotic variables, especially inorganic bottom substrate as well as quantity and quality of particulate organic matter – the main food resource for macroinvertebrates. In contrast, the most often distinguished variables that act as main determinants of the struc-
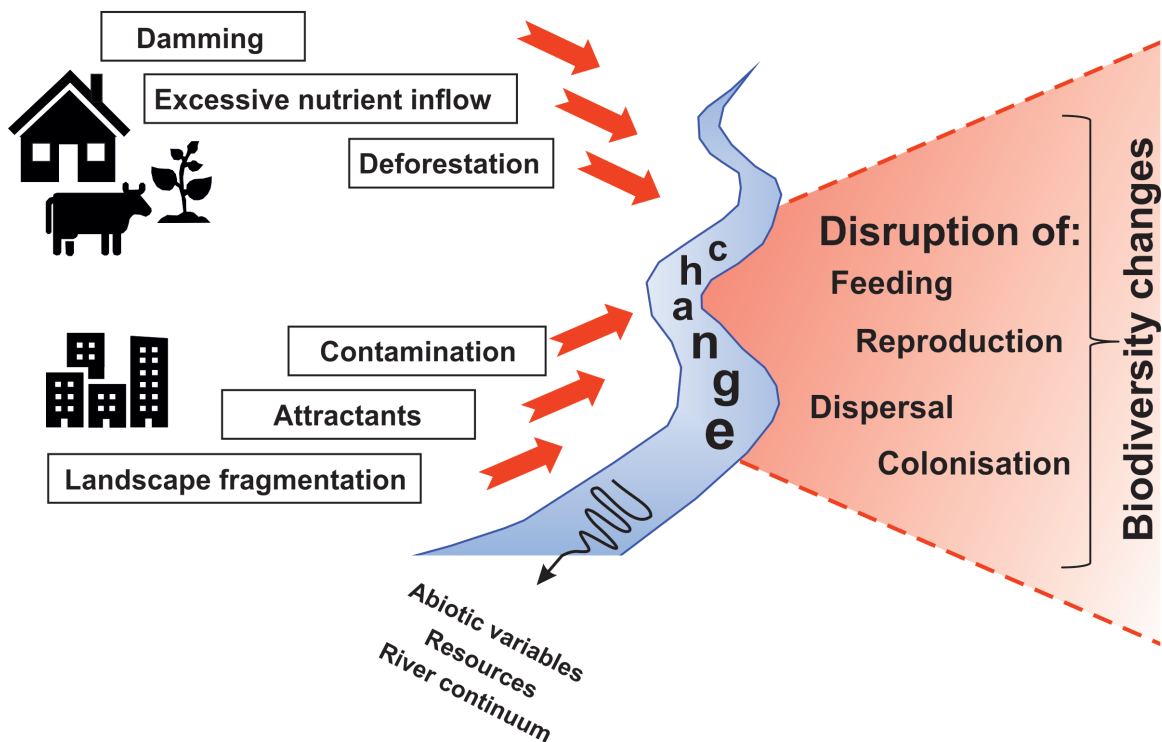
Figure 1. Different types of human impact on the natural environment.

ture of macroinvertebrate communities at the macro scale are discharge or current velocity (Minshall and Robinson 1998, Graça et al. 2004, Costa and Melo 2008, Fig. 2). Influence of environmental factors on freshwater macroinvertebrate diversity is very well investigated in Europe and North America and presented in seminal complex reviews (Malmqvist 2002, Clarke et al. 2008). The assessment of the influence of such factors from the rest of the world is still underdescribed, as was indicated by Schmera et al. (2017).

This review focuses on the impact of selected factors on riverine macroinvertebrate species richness and diversity at different spatial and temporal scales. The term 'species richness' refers here to the number of species, while 'species diversity' is expressed in diversity indices, which take into consideration both the number of species and their relative proportions. The review is based on the literature published mainly in the recent 20 years to show different and new approaches to the investigating of the relationship between environmental variables or human impact and macroinvertebrate diversity in different parts of the world. A link between well-documented knowledge from Europe and North America, and results of investigations from Asia, South America and Africa, is presented, which is a quite novel approach. The review focuses on: (i) indicating the most often described aquatic macroinvertebrate diversity factors, (ii) defining the scale of their influence (local/regional), (iii) presenting some examples of responses of macroinvertebrate communities to these factors in terms of diversity.

Results

Main factors determining macroinvertebrate diversity at the local scale or in a particular habitat

Inorganic bottom substrate. In general, it has been found that the most conductive substrate fraction for the development of zoobenthos is one consisting of gravel and pebbles, which have a positive influence on the appearance of peryphiton (a food resource for many groups of macroinvertebrates) and act as support shelters (i.e., refuges for small forms and stages of aquatic insects: Grzybkowska and Witczak 1990). This coarse fraction is usually more stable than fine sediments and can more effectively protect organisms from adverse changes in abiotic variables, such as increase in current speed inducing flow from the bottom surface and consequent drifting. This is why diversity of macroinvertebrates is often highest in habitats with substrates consisting of coarse sediments (Rezende et al. 2014).

There is no doubt that the least favourable bottom substrate for the development of macroinvertebrates is fine alluvial sand. Many recent studies (e.g., Szczerkowska-Majchrzak et al. 2010, Leitner et al. 2015, Elbrecht et al. 2016) have considered mass deposition of fine sediment as a threat for the diversity of macroinvertebrate assemblages. Among the many studied variables, a particle size < 2000 µm showed significant and negative correlations with the number of species (Wolmarans et al. 2017). However, it sometimes happens that this fraction is successfully colonised by very small forms of zoobenthos. For example, whilst the coarser
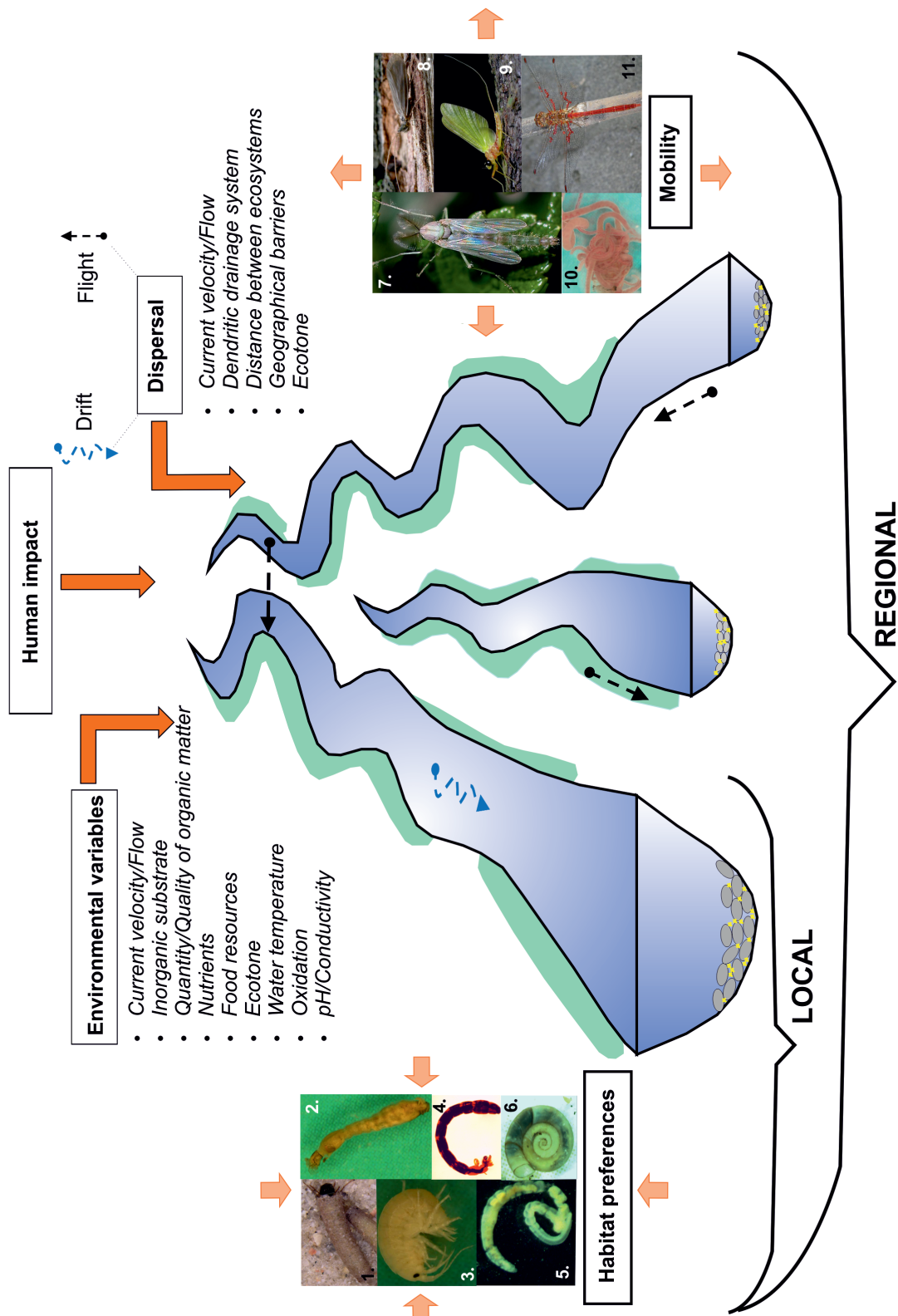
Figure 2. Potential factors determining biodiversity in the environment at various spatial scales (photo credits: 1, 9: K. Majecka; 2, 4, 6: R. Sąsiadek; 3, 5: E. Szczerkowska-Majchrzak; 7–8, 11: R. Jaskuła; 10.: M. Grabowski).

fractions of bottom sediments were preferred by about 40 taxa, good indicators for akal and psammal sediments included only two Chironomidae taxa (Leitner et al. 2015).

In fact, individual species preferences as an effect of morphological and physiological adaptations have a decisive influence on the possibility of maintaining in a given inorganic substrate of particular groups of hydrobionts. But those specific demands that can cause the high density of some organisms on some kinds of bottom can affect their dominance in biocoenoses, and not necessarily diversity (Duan et al. 2009).

Not only grain size can affect macroinvertebrate diversity, but also the structure of riverine bottom. In this respect, macroinvertebrate diversity positively correlated with both interstitial dimensions and substrate porosity, pointing to the important role of streambed heterogeneity as the preferred habitat for a larger number of macroinvertebrate species (Duan et al. 2008).

Organic matter. POM sedimenting on the bottom represents the basic food resource for many taxa and can therefore play a key role in shaping the abundance and diversity gradients of macroinvertebrate assemblages (Graça et al. 2004). Often, an increase in POM biomass can involve a corresponding increase in benthic species richness. In this respect, the number of invertebrate taxa has been found to be positively correlated with the amount of detritus available in particular habitats, hence confirming the above trend (Graça et al. 2004, Costa and Melo 2008).

The results of experiments conducted in last decades of the 20th century are also worth mentioning. Their aim was to overcome labour-intensive and time-consuming research methods for the estimation of zoobenthos abundance, and this was achieved through the use of artificial substrates. For example, Williams (1980) used baskets filled with inorganic substrate (of diverse grain diameter) and POM. This acted as an artificial substrate to obtain representative samples of zoobenthos. After a certain time, a higher biomass and abundance of invertebrates was observed in baskets with higher amounts of organic matter, independently of the heterogeneity of the inorganic bottom substrate.

Autochthonous POM, which mainly comes from decomposition of organic debris within a stream, also plays a key role in shaping species richness and diversity of invertebrates beside allochthonous organic matter, and especially its coarse fraction. Autochthonous POM increases the pool of food resources for shredders and indirectly exerts an influence on the abundance of food (i.e., fine fraction) for other aquatic organisms. Allochthonous coarse POM consists mainly of leaves and branches, which flow seasonally into the river from the ecotone area and gather in shallow, riparian zones or in places where natural flow barriers are located. As a result, a negative correlation between species richness and depth is often noted (e.g., Graça et al. 2004).

Temperature changes. Water temperature is regarded as an essential environmental variable determining the structure of benthic fauna assemblages. Global warming can have a negative impact on the species diversity of many taxa including gastropods, mayflies, beetles, caddisflies and dipterans, even though future likely scenarios are quite hard to predict (Burgmer et al. 2007). Global warming effects, but also other factors related to an increase in the water temperature of lotic ecosystems, can be lessened by canopy cover. This occurs in rivers flowing through dense forests adjoined by abundant vegetation of the ecotone zone. Moreover, canopy cover is profitable also in many other ways, as it stabilises banks, regulates nutrient content, and supports a rich habitat for many taxa (Price et al. 2003).

In the Eriora River in Nigeria, at two study sites with dense riparian vegetation (canopy cover of 70%) located in the nearest area to the source, the highest values in the diversity indices and species richness of benthic fauna were recorded (Arimoro et al. 2012). Also, in the same study, a decrease in canopy cover to 60% caused a considerable decrease in the diversity of macroinvertebrates as compared with that observed at the 70% canopy sites. Similar results were collected in the Pandeiros River (southeastern Brazil), where the lowest species richness and invertebrate diversity occurred at the study sites in which the river flows through deforested areas (Rezende et al. 2014).

Chemical variables of riverine waters. Changes in the chemical composition of riverine waters may be induced by deforestation within the river catchment as well as by other human activities. The consequences of changes in environmental variables, such as dissolved oxygen, pH, conductivity, concentration of nitrates and phosphates for the structure of benthic macroinvertebrate communities have been described (Azrina et al. 2006, Flores and Zafaralla 2012). An investigation conducted on the Mananga River (Philippines), showing that in the upper course, which was subject to weaker human pressure, species richness and diversity of benthic fauna were higher in comparison to sections located far away from the source and characterised by high anthropogenic stress (Flores and Zafaralla 2012). Along the Mananga River, at the study sites located in its lower course, human pressure mainly caused deterioration of water quality, and in particular: an increase in water temperature, in total suspended solids and biological oxygen demand, and a decrease in dissolved oxygen (Flores and Zafaralla 2012).

Differentiation in benthic structure following water quality changes caused by human pressure was also observed in the Langat River in Malaysia (Azrina et al. 2006). In the natural stream sections, 54 taxa of benthic fauna and higher values of diversity indices were recorded compared with sites modified by human activity, where only four taxa occurred. In the natural assemblages, mayflies and chironomids dominated, although caddisflies, stoneflies, dragonflies, beetles as well as other dipterans and gastropods were also present. Conversely, in the modified biocoenoses the dominant organisms were Oligochaeta and Hirudinea. Similar investigations have also been conducted in Poland, where in sections of water courses modified by human pressure Oligochaeta and Chironomidae were mainly noted (Głowacki et al. 2011, Grzybkowska and Głowacki 2011).

Influence of current velocity and flow regime at different spatial scales

Current velocity affects the inorganic structure of the bottom, the transport of organic particles, and the mobility of drifting organisms, and thereby determines species richness and biodiversity of macroinvertebrates at the habitat level (Matthaei et al. 1997). In general, the diverse structure of a biocoenosis and a greater number of macroinvertebrate species are most often connected with high values of current velocity (Grzybkowska and Witczak 1990, Fenoglio et al. 2004, Szczerkowska-Majchrzak and Grzybkowska 2015). In a study conducted in the Marico River in Africa (Wolmarans et al. 2017), the highest taxon richness was observed in habitats characterised by riffles. Only one exception to this trend was noted, namely the lowest macroinvertebrate biodiversity recorded at a site under strong pressure from dam activity, which resulted in irregular releases of water.

A similar influence of current velocity on European macroinvertebrate diversity was confirmed by a mesocosm experiment (Elbrecht et al. 2016), which showed that although reduced current speed did not result in changes in total taxon richness, it still decreased the number of the most sensitive organisms within EPT macroinvertebrates. Also, in the Tibetan-Plateau River, the number of species, diversity and share of EPT in the macroinvertebrate community was found to decrease downstream with decreasing current speed and conductivity (Jiang et al. 2013).

Yet, between particular taxa that are commonly known to be rheophilic (cf. EPT group), distinct preferences for current velocity at the local scale may be observed. These comprise changes in abundance and diversity with increased or decreased current speed. For example, from a comparison of two herbivorous insect larvae, namely the caddisfly *Agapetus boulderensis* and the stonefly *Epeorus* sp. (Plecoptera), it follows that the former favoured lower values of current speed (< 30 cm s^{-1}) whereas the latter preferred fast currents (60–80 cm s^{-1}) (Wellnitz et al. 2001). This correlation between taxa and different values of current velocity was tentatively explained in terms of different taxon mobility. Similarly, in a study on flow velocity tolerance of Limnephilidae (Trichoptera) larvae in a lowland stream, certain species were found to be characterised by different preferences for current speed (de Brouwer et al. 2017). However, for all the above studies values of current velocities of 0.6 m s^{-1}, which are often reached during peak discharges in lowland streams, are critical to maintain suitable habitat for caddisfly species because of their inability to return to the stream bottom as a result of drift.

A decrease in the share of EPT in macroinvertebrate assemblages coupled with an increase in the number of species and abundance of other taxa that are more tolerant to current velocity changes have been recorded (Elbrecht et al. 2016, Jiang et al. 2013). The taxa involved were mostly Chironomidae and Oligochaeta, which are known to be resistant to environmental changes. However, individual species' preferences for current velocity are also found within the Chironomidae family. In this respect, few species of non-biting midges can be indicators of different values of current velocity, with *Polypedilum scalaenum* preferring low current velocities and *Conchapelopia pallidula*, *Orthocladius rubicundus* and *Eukiefferiella hospital* being related to moderate ones (Chaib et al. 2013).

Not only current velocity may be essential for macroinvertebrate communities but also flow regime, which nowadays is often disrupted by different human activities. Stream channelisation, which is strictly connected to increase in the speed of runoff and loss of natural riparian zones, is regarded as the most dangerous of human impacts (Verdonschot et al. 2015). Thus, water abstraction results in an overall decrease in the amount of water supplied to rivers in dry summer periods, and this can cause low flows and streambed drying in rivers worldwide, especially in view of global warming. Based on a field experiment in which the flow regime of the river was modified from perennial into intermittent with the creation of three new habitats, namely a stagnant reach, pool and dry streambed it was determined that in the first habitat the richness and abundance of macroinvertebrates experienced a temporal drop (Verdonschot et al. 2015). In the pool, richness decreased but densities increased markedly, whereas in the dry streambed, both richness and invertebrate densities decreased, and only three taxa that were able to survive the entire experimental period in all environments, *Pisidium* sp., *Sialis* sp. and Ceratopogonidae, were distinguished. Although most taxa ($n = 31$) survived in both the control and the stagnant reaches, they were lost from the bottom of the pools or the dry streambed; these included all Ephemeroptera and Plecoptera, and most Trichoptera, as well as many Diptera and Hydracarina. It was also observed that 18 taxa that were not observed in the control samples appeared in the experimental reaches. The majority of these newcomers were not abundant, with the exclusion of mass colonization of pools by *Culex pipiens*, *C. torrentium* and *Chironomus* sp.

The potential link between macroinvertebrate diversity and hydrological regime instability was confirmed also for quite specific perennial streams in rivers of the Middle East (Oman) and Africa. High water and air temperatures and specific flow regimes caused two main taxa that are tolerant to abiotic variables changes, namely Chironomidae and Pulmonata, to survive (Boulaaba et al. 2014). Moreover, the influence of flow regime on macroinvertebrate communities is not only related to the extent of dry periods but also to episodes of heavy rainfalls, which cause local floods. Besides, a negative relationship has been found between EPT abundance and amount of heavy rainfall, suggesting lower EPT abundance during periods of heavy rains and higher densities in dry seasons (Boulaaba et al. 2014).

Saturation versus non-saturation (species pool analysis, local and regional species richness)

This important concept attempts to assess the meaning of regional factors (mainly species pools) and processes for species diversity at the local scale (i.e., its saturation with species), the diversity being understood as species richness. Such assessment is of great value in streams, because they are

among the most threatened ecosystems on Earth (Vinson and Hawkins 1998). Initially, saturation or non-saturation was believed to depend mostly on the interaction or non-interaction of species within local communities, which was tested by regressing local species richness (LSR) on regional species richness (RSR). This paradigm was formulated in the 1970s and 1980s (Cornell and Lawton 1992, Srivastava 1999), and appeared as a variant of species diversity analysis (Ricklefs 1987), which was mostly species pool analysis, although the term was coined later. According to it, one extreme of the LSR-RSR relationship is a completely unsaturated case, expressed by a linear, sloppy (and thus significant) regression line, and the other a completely saturated case, expressed by a horizontal line of no dependence. Real local communities are expressed by a curvilinear relation, located between the two above extremes, higher degree of saturation being dependent on higher degree of species interaction within the community.

Although a saturated (i.e., interaction-related) LSR community might be connected to numerous models of niche heterogeneity (classical niche, resource ratio, temporal niche) or spatio-temporal heterogeneity (lottery, random walk, aggregation, disturbance, specialist predator) (Cornell and Lawton 1992) no model was considered usual, indispensable or critical. Gradually, the LSR-RSR assessed saturation/non-saturation concept became more and more deeply related to several other general concepts, such as competitive exclusion, immigration rate versus emigration rate, historical/evolutionary versus ecological time scales, scale-dependence of both local and regional sampling areas, (lack of) speciation, disturbance versus stability, impact of environmental factors, and others. Dozens of studies exploring these concepts to higher or lower extent in the case of numerous species groups appeared in the last decade of the 20th century.

Yet, problems soon began to pile up as regards both the technical and conceptual issues of the LSR-RSR paradigm. Srivastava (1999) discovered that half of 30 such studies were pseudoreplicated, and thus provide unreliable conclusions, which may additionally be biased in frequently unpredictable way by differences in sample size and sampled area, both regional and local. Hillebrand (2005), using theoretical modelling, discovered that lack of relation or curvilinear patterns of the RSR-LRS relationship are unlikely under all but extreme conditions, hence he claimed the regression method was biased. Finally, He et al. (2005), using the island biogeographic model, mathematically formalized the LRS-RSR regression concept, incorporating probability of immigration and emigration (but also the impact of scale), and concluded that the full spectrum of linear and curvilinear relationships may be generated without invoking species interactions at all, the former relationship appearing when colonization rates are higher than extinction ones, while the latter when extinction rates are higher than colonization ones. He et al. (2005) also discovered that changing the sampling scale can make local-regional relationship appear either saturated or unsaturated. It became then obvious that the LSR-RSR concept had to be used with caution, although it cannot be discarded because most accumulated knowledge related to species richness analysis would have to be discarded as well.

In view of the difficulties, and taking them all into account, but also not to break connection with the earlier developments within the LSR-RSR paradigm, Grönroos and Heino (2012) applied a most interesting approach, at least as regards aquatic macroinvertebrates. Sampling 10 sites 50 m^2 in area in each of 10 streams differing in environmental conditions over the distance of up to 2 km from their outlets in Finland, they obtained 167 macroinvertebrate species and divided them into functional guilds. They also employed variance partitioning for a comparison of the impact of over a dozen environmental factors (ENV) with the LSR-RSR approach. Besides, they carried out all analyses for observed (and log-transformed) and for Chao-estimated (as the upper bound) species richness in both the LSR and RSR cases. The results were surprising: although the LSR-RSR relationship was linear in most cases, indicating overall regional species pool effect on LSR, variance partitioning suggested a relatively larger role of local ENV, and several environmental factors turned out significant predictors of LSR.

Although the relative importance of RSR for the guild of predators was much higher than RSR for any of the other guilds (filterers, gatherers, scrapers, and shredders), yet the importance of RSR for LSR never reached that of ENV. In the case of Chao-estimated species richness, less variation was explained than in the case of sampled species richness, but Chao richness estimation depends on rare species. As rare and common species may respond contrastingly to local and regional processes, thus suggesting unnatural results, Chao-estimated richness was further ignored. The study confirmed the hypotheses of strong regional species pool (using LSR-RSR approach) and of strong environmental impact on pooled macroinvertebrates (using variation partitioning), but did not the hypothesis of more curvilinear LSR-RSR relationships within guilds (except gatherers), and of weaker impact of RSR on given guilds, except predators. The last finding may be explained by a lower population density of predators, which increases extinction rates, as a result of which predators must rely to a greater extent on dispersal than other species.

Results that are mostly similar were obtained by Marchant et al. (2006) in Australia. However, their study differed from that of Grönroos and Heino (2012) in several respects. It was concerned with large spatial scales of 25 river basins extending over several hundred thousand square kilometers, relied mostly on the LSR-RSR approach, although considered also several environmental factors, and analysed taxonomic instead of functional macroinvertebrate categories. Besides, the number of taxa recorded was several times higher, bank and channel sites were considered separately, and there were several samples per site, whose number, however, was skillfully standardized and averaged. Despite the great difference in scale, Marchant et al. (2006) found that for all macroinvertebrates and for each of their taxonomic groups the LSR-RSR relationship was linear, as was mostly the case in Grönroos and Heino (2012). However, only conductivity was an environmental factor that was significant, and only for EPT and Coleoptera. When all taxonomic groups were considered, only longitude was related to bank data, and none to channel

data. Marchant et al. (2006) also carried out an analysis of the causes of positive rather than zero intercept of the LSR-RSR plots (earlier mentioned by Srivastava 1999), yet the problem turned out too complex for clear generalisations, and thus further research is this respect seems necessary. Grönroos and Heino (2012) and Marchant et al. (2006) seem to confirm the predictions of Hillebrand (2005) that curvilinear LSR-RSR relationships are exceptional, but this is a shortcoming of the approach, and not necessarily indication of lack of saturation in LSR.

Future development in the saturation/non-saturation concept may be related to two shortcomings of the LRS-RSR paradigm never mentioned by any scientist. One is the underestimation of the slope in the LSR-RSR relationship due to the fact that both variables are random, i.e., not controlled by the researcher (Legendre and Legendre 2012, Sokal and Rohlf 2012). Ordinary least squares method (OLS, model I regression), which has only been used so far in this paradigm, always underestimates the slope, although the scale of the underestimation may vary from slight to considerable. Methods of model II regression should be used instead. Unfortunately, at the present state of knowledge there is no model II regression method that may also be used in the case of curvilinear relations, hence new methodological developments are necessary to use model II regression instead of OLS in such cases.

The other shortcoming is parallel to the development in nestedness, a paradigm conceptually similar to the saturation/non-saturation one, although never before discussed in the same context, most probably due to applying a quite different methodology. The nestedness paradigm also relied solely on species richness, in the belief that there was an affinity between a species' frequency of occurrence and its abundance (Atmar and Patterson 1993), as a result of which abundances of species little mattered. Yet, recent developments proved that nestedness indicated by presence-absence (i.e., species richness) data is very rarely confirmed when quantitative data (abundance, for example) are used instead in the same ecosystems (Staniczenko et al. 2013), hence a reevaluation of the whole nestedness concept is necessary. It seems that a similar reevaluation of the saturation/non-saturation might be carried out using quantitative data as well. The reason why this has not been done till now is probably much greater complexity of the quantitative approach, and much more complex methodology that will be necessary.

Connection between dispersal and biodiversity (regional scale)

Environmental factors affecting local assemblages of benthic macroinvertebrates determine the possibility for a species with a particular tolerance range to thrive in a given habitat. For the presence of zoobenthos at the regional scale (γ diversity), mobility has a strong influence, allowing to overcome distance and find suitable habitat (Jocque et al. 2007, Costa and Melo 2008, Fig. 2).

Among the factors that can reduce species richness and macroinvertebrate diversity within different catchments are

distance between ecosystems (Costa and Melo 2008), geographical barriers disrupting the continuum of migration corridors (both natural such as mountain ranges and anthropogenic such as reservoirs: Monaghan et al. 2005), type of catchment land use (Sponseller et al. 2001, Smith et al. 2009, Rezende et al. 2014), and geographical location of the river (Costa and Melo 2008), meaning that a water course can be subject to specific climatic conditions (Graça et al. 2004, Burgmer et al. 2007). Overcoming these spatial barriers occurs mainly through dispersal, and permanent migrations between populations allow the free movement of alleles, increasing genetic diversity hence competition for the development of new adaptations (Bilton et al. 2001). Thanks to dipersal, organisms can colonise new habitats, escape from unfavourable abiotic conditions, and enrich neighbouring populations with the addition of new individuals (Smith et al. 2009). Notably, all of these factors play an important role for the structuring of biocenoses (Costa and Melo 2008).

It is sometimes claimed that adults of aquatic insects (females) fly upstream (colonization cycle, Müller 1973) to compensate for the loss of individuals caused by downstream drift (Macneale et al. 2005). Yet, aquatic macroinvertebrates differ in their ability for disperal (mobility), and this concerns both water stages and terrestrial, flying forms. In the case of water stages, dispersal is an effect of downstream transport within the water column and involves:

- Egg masses: some species in the centre of the egg masses have a gas bubble, which helps them flow with the river course for several hundred metres or even more (Williams 1982);
- Youngest larval stage (larvulae): these are predestined by their morphological and physiological features to float in water thanks to a great amount of body fat and the ability to feed on transported POM (Kalugina 1959);
- Individuals with developed legs (mayflies, caddisflies, stoneflies): these not only very easily and actively start to drift, but also manage to stay in suitable habitat patches (i.e., microhabitats).

Other macroinvertebrates also very often enter the drift actively or passively to escape from abiotic disturbances or to avoid predators and interference competition. Why organisms enter the drift and its meaning for riverine ecosystem functioning has been widely discussed since the 1970s (Elliott 1967, Waters 1972, Grzybkowska 2000).

The terrestrial stages of aquatic insects also have a great influence on the dispersal of species. Heino (2013) divided invertebrates according to their ability for active movement into four groups:

- Weak passive dispersers with aquatic adults: Oligochaeta, Hirudinea, Gastropoda, Bivalvia, Aranea and Crustacea;
- Weak aerial dispersers with terrestrial adults: small dipterans (Ceratopogonidae) and Chironomidae;
- Intermediate aerial dispersers with terrestrial adults: Ephemeroptera, Plecoptera, Megaloptera, Trichoptera and other Diptera (Tabanidae, Tipuloidea, Empididae);

- Strong aerial dispersers with terrestrial adults: Odonata, Heteroptera (Corixidae), Coleoptera (Dytiscidae).

In an investigation of the Oulankajoki River, the dispersal of taxa with limited possibility to move (cf. weak passive dispersers) was found to be strongly controlled by spatial factors (Heino 2013). Representatives of this group of invertebrates are not able to move independently to distant lotic ecosystems. This makes their mobility reduced to drifting with current speed within the original ecosystem, so that their occurrence in other rivers is only possible in the presence of connectivity between streams, which is favored by the dendritic network of river systems (Clarke et al. 2010).

In the case of the other groups, the distance between ecosystems ceases to represent a barrier to dispersal once the flying adult stage of the life cycle is reached. The fact that intermediate aerial dispersers are under stronger pressure of environmental variables than weak dispersers is also notable, and can be responsible for transportation over very long distances, as is the case of very light dipterans, such as Ceratopogonidae and Chironomidae. Finally, the dispersal of the most active taxa (e.g., dragonflies as well as some bugs and beetles), is controlled mainly by environmental factors, which make them able to overcome quite long distances above land and selectively choose habitats (Heino 2013).

Although particular taxa are characterised by diverse potential for dispersal, many studies have shown that the adult stages of riverine invertebrates prefer transport in the nearest area of the riverbed, as confirmed by a rapid decrease in the number of individuals together with a drift-away from the riparian zone (Sode and Wiberg-Larsen 1993, Petersen et al. 1999, Briers et al. 2002). Some cases are known when imagines choose a pathway above land to get to a stream that is located far away from the river of origin. This is a strategy that is beneficial from an energetical point of view given the loss of energy involved during flight along a stream to the nearest connection with neighbouring inlets. This type of flight above land has been observed in e.g., the dragonfly *Calopteryx splendens* (Chaput-Bardy et al. 2008) and the stonefly *Leuctra ferruginea* (Macneale et al. 2005).

Changes of land use, especially urbanisation, are becoming a serious impediment for the dispersal of invertebrates, which leads to modification of abiotic variables within the catchment (e.g., direction and strength of wind, intensity of solar radiation or temperature, and humidity gradients). This variability of environmental factors induces organisms to start migrations, and all fluctuations caused by human activity disrupt this process. Moreover, many taxa exhibit preferences to move within forested areas or corridors consisting of riparian vegetation. In this respect, deforestation can lead to loss of migration pathways and consequent reduction of dispersal, resulting in decrease of species diversity in particular river basins (Sponseller et al. 2001, Smith et al. 2009, Rezende et al. 2014). Destruction of the riparian zone, including forest in nearby areas, forces invertebrates to migrate above deforested land, and this results in increased energetic costs, but also possibility of desiccation and exposure to predator pressure (Smith et al. 2009). Moreover, these moving insects may be-

come vulnerable to other dangers, such as road infrastructure, including asphalt, vehicle lights and traffic lampposts, which can function as beacons (Smith et al. 2009).

Besides dispersal, climatic conditions exert an influence on the diversity and species richness of a biocoenosis at the regional scale, and are indirectly responsible for changes in the environmental variables of particular basins. Accordingly, species richness and diversity of benthic fauna were found to be higher in rivers located in northern and central Portugal in comparison to southern streams, and this was explained by a differentiation in riverine abiotic paramaters from other climate zones (Graça et al. 2004). On the contrary, in southern regions, precipitation is usually less heavy but becomes unpredictable. In summer, rivers often dry out resulting in the creation of small ponds, where decaying organic matter and high temperature generate microhabitats suitable for the development of microorganisms, whose physiological requirements contribute to the exhaustion of oxygen resources. The extreme environmental conditions of southern rivers in Portugal were found to allow the survival of only those species that are very resistant to oxygen deficits.

References

Arimoro, F.O., G.E. Obi-Iyeke and P.J.O. Obukeni. 2012. Spatiotemporal variation of macroinvertebrates in relations to canopy cover and other environmental factors in Eriora River, Niger Delta, Nigeria. *Environ. Monit. Assess.* 184:6449–6461.

Atmar, W. and B.D. Patterson. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382.

Azrina, M.K., C.K. Yap, A.R. Ismail and S.G. Tan. 2006. Anthropogenic impacts on the distribution and biodiversity of benthic macroinvertebrates and water quality of the Langat River, Peninsular Malaysia. *Ecotoxicol. Environ. Safety* 64:337–347.

Bilton, D.T., J.R. Freeland and B. Okamura. 2001. Dispersal in freshwater invertebrates. *Annu. Rev. Ecol. Syst.* 32:159–181.

Boulaaba, S., S. Zrelli, M. Boumaiza and B. Rossaro. 2014. Relationships between physical and chemical factors and aquatic macroinvertebrates in perennial streams in the arid northern mountain basin El Batinah, Oman. *J. Entomol. Acarol. Res.* 46:50–58.

Briers, R.A., H.M. Cariss and J.H.R. Gee. 2002. Dispersal of adult stoneflies (Plecoptera) from upland streams draining catchments with contrasting land-use. *Arch. Hydrobiol.* 155:627–644.

Burgmer, T., H. Hillebrand and M. Pfenninger. 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. *Oecologia* 151:93-103.

Chaib, N., Z. Bouhala, L. Fouzari, L. Marziali, B. Samraoui and B. Rossaro. 2013. Environmental factors affecting the distribu-

tion of Chironomid larvae of the Seybouse wadi, North-Eastern Algeria. *J. Limnol.* 72:203–214.

Chaput-Bardy, A., D. Lemaire, D. Picard and J. Secondi. 2008. Instream and overland dispersal across a river network influences gene flow in a freshwater insect, *Calopteryx splendens*. *Mol. Ecol.* 17:3496–3505.

Clarke, A., R. Mac Nally, N.R. Bond and P.S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biol.* 53:1707–1721.

Clarke, A., R. Mac Nally, N.R. Bond and P.S. Lake. 2010. Conserving macroinvertebrate diversity in headwater streams: the importance of knowing the relative contributions of α and β diversity. *Divers. Distrib.* 16:725–736.

Cornell, H.V. and J.H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.* 61:1–12.

Costa, S.S., A.S. Melo. 2008. Beta diversity in stream macroinvertebrate assemblages: among-site and among-microhabitat components. *Hydrobiologia* 598:131–138.

Cummins, K.W., J.R. Sedell, F.J. Swanson, G.W. Minshall, S.G. Fisher, C.E. Cushing, R.C. Petersen and R.L. Vannote. 1983. Organic matter budgets for stream ecosystems: problems in their evaluation. In: J.R. Barnes and G.W. Minshall (eds.), *Stream Ecology. Application and Testing of General Ecological Theory.* Plenum Press, New York, pp. 299–353.

de Brouwer, J.H.F., A.A. Besse-Lototskaja, C.J.F. ter Braak, M.H.S. Kraak and P.F.M. Verdonschot. 2017. Flow velocity tolerance of lowland stream caddisfly larvae (Trichoptera). *Aquat. Sci.* 79:419–425.

Duan, X., Z. Wang and S. Tian. 2008. Effect of streambed substrate on macroinvertebrate biodiversity. *Front. Environ. Sci. Engin. China* 2:122–128.

Duan, X., Z. Wang, M. Xu and K. Zhang. 2009. Effect of streambed sediment on benthic ecology. *Int. J. Sediment Res*. 24:325–338.

Elbrecht, V., A.J. Beermann, G. Goessler, J. Neumann, R. Tollrian, R. Wagner, A. Wlecklik, J.J. Piggott, C.D. Matthaei and F. Leese. 2016. Multiple-stressor effects on stream invertebrates: a mesocosm experiment manipulating nutrients, fine sediment and flow velocity. *Freshwater Biol.* 61:362–375.

Elliott, J.M. 1967. Invertebrate drift in a Dartmoor stream. *Arch. Hydrobiol.* 63:202–237.

Elliott, M. and V. Quintino. 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Mar. Pollut. Bull.* 54:640–645.

Fauna Europaea. 2017. Fauna Europaea version 0.6. Web service available online at: http://www.fauna-eu.org. Last accessed: May 2017.

Fenoglio, S., T. Bo and M. Cucco. 2004. Small-scale macroinvertebrate distribution in a riffle of a neotropical rainforest stream (Río Bartola, Nicaragua). *Caribbean J. Sci.* 40:253–257.

Flores, M.J.L. and M.T. Zafaralla. 2012. Macroinvertebrate composition, diversity and richness in relation to the water quality status of Mananga River, Cebu, Philippines. *Philipp. Sci. Lett.* 5:103–113.

Głowacki, Ł. 2009. Co to jest prawdziwa różnorodność oraz partycjonowanie bioróżnorodności? (What is "true diversity" and diversity partitioning?). *Kosmos* 58:97–111 (in Polish with English summary).

Głowacki, Ł. 2013. Biomonitoring a prawdziwa różnorodność rzędu pierwszego. (Biomonitoring and the true diversity of order one). *Rocz. Nauk. PZW* 26:5–19 (in Polish with English summary).

Głowacki, Ł., M. Grzybkowska, M. Dukowska and T. Penczak. 2011. Effects of damming a large lowland river on chironomids and fish assessed with the (multiplicative partitioning of) true/Hill biodiversity measure. *River Res. Applic.* 27:612–629.

Graça, M.A.S., P. Pinto, R. Cortes, N. Coimbra, S. Oliveira, M. Morais, M.J. Carvalho and J. Malo. 2004. Factors affecting macroinvertebrate richness and diversity in Portuguese streams: a two-scale analysis. *Internat. Rev. Hydrobiol.* 2:151–164.

Grönroos, M. and J. Heino. 2012. Species richness at the guild level: effects of species pool and local environmental conditions on stream macroinvertebrate communities. *J. Anim. Ecol.* 81:679–691.

Grzybkowska, M. 2000. Dryf(t) nie tylko genetyczny i kontynentalny. (Drift: not only genetic and continental). *Kosmos* 49:113–122 (in Polish with English summary).

Grzybkowska, M. and J. Witczak. 1990. Distribution and production of Chironomidae (Diptera) in the lower course of the Grabia River (Central Poland). *Freshwater Biol.* 24:519–531.

Grzybkowska, M. and Ł. Głowacki. 2011. Chironomidae (Diptera) diversity in lowland rivers of various orders and of different levels of human impact in central Poland. In: X. Wang and W. Liu (eds.), *Contemporary Chironomid Studies. Proceedings of the 17th International Symposium on Chironomidae.* Nankai University Press, Nankai, pp. 282–295.

He, F., K.J. Gaston, E.F. Connor and D.E. Srivastava. 2005. The local-regional relationship: immigration, extinction and scale. *Ecology* 86:360–365.

Heino, J. 2013. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? *Oecologia* 171:971–980.

Heino, J., T. Muotka and R. Paavola. 2003. Determinants of macroinvertebrate diversity in headwater streams: regional and local influences. *J. Anim. Ecol*. 72:425–434.

Hillebrand, H. 2005. Regressions of local on regional diversity do not reflect the importance of local interactions or saturation of local diversity. *Oikos* 110:195–198.

Jiang, X., Z. Xie and Y. Chen. 2013. Longitudinal patterns of macroinvertebrate communities in relation to environmental factors in a Tibetan-Plateau River system. *Quatern. Int.* 304:107–114.

Jocque, M., B.J. Riddoch and L. Brendonck. 2007. Successional phases and species replacements in freshwater rock pools: towards biological definition of ephemeral systems. *Freshwater Biol.* 52:1734–1744.

Kalugina, N.S. 1959. O nekotorych vozrastnych izmenenjiach v stroenii i biologii licinok chironomid (Diptera, Chironomidae). *Trudy Vsesojuz. Gidrobiol. Obsc.* 9:85–107.

Legendre, P. and L. Legendre. 2012. *Numerical Ecology.* 3rd ed. Elsevier, Amsterdam.

Leitner, P., C. Hauer, T. Ofenböck, F. Pletterbauer, A. Schmidt-Kloiber and W. Graf. 2015. Fine sediment deposition affects biodiversity and density of benthic macroinverebrates: a case study in the freshwater pearl mussel river Waldaist (Upper Austria). *Limnologica* 50:54–57.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. *Ecol. Lett.* 3:73–76.

Macneale, K.H., B.L. Peckarsky and G.E. Likens. 2005. Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. *Freshwater Biol.* 50:1117–1130.

Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biol.* 47:679–694.

Marchant, A.R., A.D. Ryan and B.L. Metzeling. 2006. Regional and local species diversity patterns for lotic invertebrates across mul-

tiple drainage basins in Victoria. *Mar. Freshwater Res.* 57:675–684.

Matthaei, C.D., D. Werthmuller and A. Frutiger. 1997. Invertebrate recovery from a bed-moving spate: the role of drift versus movements inside or over the substratum. *Arch. Hydrobiol.* 140:221–235.

Minshall, G.W. and C.T. Robinson. 1998. Macroinvertebrate community structure in relation to measures of lotic habitat heterogeneity. *Arch. Hydrobiol.* 141:129–151.

Monaghan, M.T., C.T. Robinson, P. Spaak and J.V. Ward. 2005. Macroinvertebrate diversity in fragmented Alpine streams: implications for freshwater conservation. *Aquat. Sci.* 67:454–464.

Müller, K. 1973. Life cycles of stream insects. *Aquilo. Ser. Zool.* 14:105–112.

Mykra, H., J. Heino and T. Muotka. 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Glob. Ecol. Biogeogr.* 16:149–159.

Petersen, I., J.H. Winterbottom, S. Orton, N. Friberg, A.G. Hildrew, D.C. Spiers and W.S.C. Gurney. 1999. Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, UK. *Freshwater Biol.* 42:401–416.

Price, K., A. Suski, J. McGarvie, B. Beasley and J.S. Richardson. 2003. Communities of aquatic insects of old-growth and clearcut coastal headwater streams of varying flow persistence. *Can. J. For. Res.* 33:1416–1432.

Rezende, R.S., A.M. Santos, C. Henke-Oliveira and J.F. Gonçalves Jr. 2014. Effects of spatial and environmental factors on benthic a macroinvertebrate community. *Zoologia* 31:426–434.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167–171.

Schmera, D., J. Heino, J. Podani, T. Erös and S. Dolédec. 2017. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. *Hydrobiologia* 787:27–44.

Smith, R.F., L.C. Alexander and W.O. Lamp. 2009. Dispersal of terrestrial stages of stream insects in urban watersheds: a synthesis of current knowledge. *J-NABS* 28:1022–1037.

Sode, A. and P. Wiberg-Larsen. 1993. Dispersal of adult Trichoptera at a Danish forest brook. *Freshwater Biol.* 30:439–446.

Sokal, R.R. and F.J. Rohlf. 2012. *Biometry: The Principles and Practice of Statistics in Biological Research, 4th ed*. W. H. Freeman and Co., New York.

Sokol, E.R., B.L. Brown, C.C. Carey, B.M. Tornwall, C.M. Swan and J.E. Barrett. 2014. Linking management to biodiversity in built ponds using metacommunity simulations. *Ecol. Model.* 296:36–45.

Sponseller, R.A., E.F. Benfield and H.M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biol.* 46:1409–1424.

Srivastava, D.S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *J. Anim. Ecol.* 68:1–16.

Staniczenko, P.P.A., J.C. Kopp and S. Allesina. 2013. The ghost of nestedness in ecological networks. *Nature Commun.* 4:1391.

Szczerkowska-Majchrzak, E. and M. Grzybkowska. 2015. Effects of hydrological disturbance of different magnitude on riverine habitats and benthic invertebrates. *Pol. J. Ecol.* 63:135–141.

Szczerkowska-Majchrzak, E., M. Grzybkowska and M. Dukowska. 2010. Effect of flow fluctuations on patch dynamics and chironomid distribution in a medium-sized lowland river. *J. Freshwater Ecol.* 25:437–448.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedel and C.E. Cushing. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37:130–137.

Verdonschot, R.C.M., A.M. van Oosten-Siedlecka, C.J.F. ter Braak and P.F.M. Verdonschot. 2015. Macroinvertebrate survival during cessation of flow and streambed drying in a lowland stream. *Freshwater Biol.* 60:282–296.

Vinson, M.R. and C.P. Hawkins. 1998. Biodiversity of stream insects: Variation at local, basin, and regional scales. *Annu. Rev. Entomol.* 43:271–293.

Waters, T.F. 1972. The drift of stream insects. *Ann. Rev. Ent.* 17:253–272.

Wellnitz, T.A., N. LeRoy Poff, G. Cosyleón and B. Steury. 2001. Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. *Landscape Ecol.* 16:111–120.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21:213–251.

Whittaker, R.H., K.J. Willis and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.* 28:453–470.

Williams, D.D. 1980. Temporal patterns in recolonization of stream benthos. *Arch. Hydrobiol.* 90:56–74.

Williams, C.J. 1982. The drift of some chironomid egg masses (Diptera: Chironomidae). *Freshwater Biol.* 12:573–578.

Wolmarans, C.T., M. Kemp, K.N. de Kock and V. Wepener. 2017. The possible association between selected sediment characteristics and the occurrence of benthic macroinvertebrates in a minimally affected River in South Africa. *Chem. Ecol.* 33:18–33.