

# Impact of genomic diversity in river ecosystems

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**We propose that genomic diversity in aquatic macrophytes of rivers, driven by the underlying genomic processes of interspecific hybridization and polyploidy (whole-genome duplication), play a significant role in ecosystem functioning. These genomic processes generate individuals which might differ in their demands for nitrogen (N) and phosphorus (P). This is significant because (i) N and/or P are frequently limiting nutrients in freshwater ecosystems, and (ii) nucleic acids are demanding in N and P. We suggest that N and P availability will provide a selection pressure for genetic variants in macrophytes which will, in turn, influence the nutritional quality of plant biomass, and hence their consumption by herbivores and detritivores as well as the energy flux of their biomass through the food web.**

## Freshwater macrophyte ecology and genomic diversity

The ecological significance of freshwater plants (macrophytes) in lakes and ponds is well known, where they contribute to producing a complex 3D habitat, as well as driving key nutrient cycles and acting as keystone species maintaining a clear water state (e.g., [1–3]). Far less is known about the role of macrophytes in rivers and streams, particularly in terms of how they influence the higher levels of biological organization (communities, food webs, ecosystems), and most studies of primary producers in rivers and streams only focus on the trophic roles of algae or terrestrial plant detritus at the base of the food web (e.g., reviewed in [4,5]) and on the role of macrophytes in fluvial dynamics and the physical habitat [6,7]. As with terrestrial plants, submerged or emergent macrophytes have long been assumed to enter the food web primarily as detritus after autumn die-back, rather than playing a major role as a living resource for consumers.

More recently, however, it has become clear that macrophytes are also important in river ecosystems (i) by provid-

ing energy from their living and dead tissues, and (ii) by playing a crucial role in the major nutrient cycles. Support for the first case includes isotope data which suggest a tight coupling between river macrophytes and key macroinvertebrates [8,9]. There is also direct evidence that river macrophytes are eaten by macroinvertebrates [10] and water birds [11,12]. Indeed, in some angiosperms that can be either aquatic or terrestrial it was shown that leaf loss through grazing was higher in the river populations when measured by leaf area and the same as terrestrial populations when measured by mass per unit area [13]. The second case is supported by strong empirical evidence showing how river macrophytes not only assimilate nutrients in their own tissues [6], but can also trap organic sediment [14] and facilitate the mineralization of organic carbon (C) and nitrogen (N) [15–17]. River macrophytes also provide conduits for the efflux of methane and other greenhouse gases from sediments [18].

Despite the growing appreciation of the ecological role of macrophytes in river ecosystems, we argue that the significance of their biodiversity is still underestimated. The use of macrophyte bioindicators of river ecosystem status have led to a focus on river biodiversity in terms of species richness and/or species assemblages, in conjunction with river characteristics [19]. However, some have doubted the efficacy of such approaches [20], and we suggest this may be because they miss a more fundamental aspect of biodiversity at the genomic level, a deficiency which restricts our understanding of the influence of higher plants on fluvial ecology.

## Glossary

**Allochthonous:** imported from outside the system; in other words, *ex situ* in origin.

**Autochthonous:** generated from within the system; in other words, *in situ* in origin.

**Dysploidy:** variation in chromosome numbers arising through chromosome fusion, fission, and rearrangement events, as well chromosome number losses and gains.

**Food web:** a schematic depicting the feeding connections between organisms, usually species, in an ecological community.

**Genome size:** the total amount of DNA in an unreplicated gametic nucleus.

**Interspecific hybridization:** hybridization between two or more species. Backcrossing of hybrids to parents can lead to introgression of DNA from one species to another.

**Polyploidy:** whole-genome multiplication leading to  $\geq 3$  multiples of the chromosome number found in an unreplicated gametic nucleus.

**Reticulate evolution:** the pattern of evolution arising from interspecific hybridization, which is often associated with polyploidy.

**RNA pool:** the total RNA content of a cell, the transcriptome.

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There are many evolutionary processes that influence genetic diversity – for example, genetic drift (e.g., especially associated with founder events and small populations) and selection (e.g., against herbivory) – over different geographic and temporal scales (e.g., post-glacial expansions). Here we focus on three processes which substantially influence genomic diversity in terms of genome size (see [Glossary](#)) and RNA usage. These processes are: polyploidy, interspecific hybridization, and dysploidy, which can generate substantial intra- and interspecific variation upon which selection can act over both time and space. Indeed, they are major driving forces in angiosperm evolution [21–23] and are particularly prevalent in aquatic plants [24]. Genome size varies because polyploids and dysploids have multiples (or part multiples) of the diploid DNA content, and the RNA content of cells can also be highly variable [25], especially in the context of hybrids and polyploids [26].

In this opinion article we propose that variation in the DNA and RNA content of river plants generated by these genomic processes, coupled with selection driven by the availability of the nutrients N and P, will significantly influence the nutrient stoichiometry of macrophytes and hence their nutritional quality, dead or alive, in the food web. Furthermore, we propose that this resulting genomic variation is likely to influence the consumption of macrophytes by herbivores and detritivores, and hence the flux of their biomass through the food web (summarized in [Figure 1](#)). Essentially, by ignoring such molecular aspects of plant diversity we could be missing a key link between ‘true’ biodiversity and ecosystem processes in rivers and streams.

#### **Nucleic acids are major sinks for N and P in the cell**

Genomic variation in plants is important because: (i) both N and P are frequently limiting nutrients in freshwater ecosystems [27], and (ii) nucleic acids (DNA and RNA) are demanding in both N and P (i.e., by mass, they are approximately 39% N and nearly 9% P assuming a 1:1 ratio for purines and pyridines [25]). Indeed, nucleic acids contain more P than any other major biomolecule [25]. For example, in aquatic invertebrates, up to 80% of organic P is tied up in nucleic acids [28] whereas, in plants, nucleic acids account for up to 40% of the total cell P content in some species [29,30]. Consequently, we propose that the availability of N and P provides a selection pressure that influences RNA use and genome size in macrophytes.

Although it is often stated that RNA forms the largest component of the nucleic acid fraction in the cell [31], the cellular content of P and N made up by the RNA component of nucleic acids, including ribosomal RNA, is extremely variable, can be regulated, and depends on (i) tissue, (ii) metabolic activity of the cell, (iii) species, and (iv) the growth conditions in which the species is found [26,28,32,33]. For DNA, we are unaware of data for angiosperms reporting the proportion of cellular P invested, but it is likely that DNA comprises at least 5–10% of cellular P, as in haploid and diploid algae respectively [33]. Similarly, we are unaware of the proportion of cellular N invested in DNA in angiosperms; nevertheless, this too must be significant, not least because of the high levels of N in their nitrogenous bases and in the

histones that package DNA (histones account for ~10% of all cellular proteins in mouse fibroblasts [34]). Certainly, it is unknown how N and P investment in DNA and RNA scales across the 2 400-fold range of genome sizes encountered in angiosperms [35].

Given the variation in both RNA and DNA content of cells, it is not unsurprising that RNA:DNA ratios have also been reported to vary from <1 to >10, although they are often around 2–3 except when growth is slow, when the ratio is likely to be <1 [28,31].

Genome size also correlates with other cellular properties which will impact on N and P demands of the cell. For example, there is a significant positive correlation between nucleus size and cell size in angiosperms [36]. Thus, as genome size increases, the cellular demand for other N and P-containing molecules (e.g., phospholipid membranes) will also increase [25,33] (although how cell size scales with cell number in tissues in angiosperms is unknown).

Evidence that there is indeed selection at the genome-size level under limiting N and P comes from several studies. Certainly, in suspended algae in freshwaters and oceans, diploids are favored when nutrients are abundant, and haploids favored under nutrient limitation [33]. Although we are unaware of comparable data in freshwater macrophytes, in a long-term (60 year) grassland nutrient-enrichment field experiment, there is evidence for selection of plants with lower mean genome sizes on plots receiving least P [37]. There is also evidence that plants have responded to N-limitation through selection for nucleotides and amino acids which require less N, a feature that is lost in crop plants where that selection pressure has been reduced by fertilizers [38]. There may also be a response to limiting N and P – mediated by selection for individuals with lower amounts of DNA – via its elimination (i.e., genome downsizing [39]) in polyploid genomes. Indeed, DNA elimination following polyploidy is likely to be one of the main reasons why genome sizes in angiosperms are heavily skewed towards small genomes, despite the prevalence of recurrent polyploidy in many lineages [40–42].

#### **Polyploids, hybrids, and aquatic macrophytes**

If selection is indeed acting in macrophytes at the genome-size level under limiting nutrient conditions, then it is important to consider the major processes that generate such variation. Reticulate evolution, polyploidy, and dysploidy are certainly significant processes in relation to aquatic macrophyte biology [24]. Much has been written about the ecological and evolutionary advantages associated with polyploidy, including the fixing of heterozygosity and hybrid vigor over the short term [43], and the generation of multiple gene copies from which new functions can evolve (neofunctionalization [44]) in the longer term. Furthermore, when polyploidy is coupled with interspecific hybridization (i.e., allopolyploidy), novel characters not found in either parent can evolve through the ‘mix-and-match’ of biochemical pathways (i.e., transgressive characters [45]). In addition, from its onset, interspecific hybridization and polyploidy can generate enormous genetic variation upon which selection can act. Indeed, such advantages have been proposed to explain the high

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