River Conservation
Challenges and Opportunities

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Chapter 7 Offprint

So What? Implications of Loss of Biodiversity for Ecosystem Functioning

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Chapter 7

So What? Implications of Loss of Biodiversity for Ecosystem Functioning

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A loss of biodiversity is expected to affect ecosystem properties. In most river ecosystems, the relationship between biodiversity and ecosystem functioning relies on a cascade of effects among species identity, sequence of species loss and environmental context. The resulting ecological complexity calls for applying the cautionary principle in conservation and restoration planning.

7.1. What is the problem – or why should we measure the effects of biodiversity loss on ecosystem functioning?

We live in an extraordinary rich and diverse planet, with global estimations of biodiversity ranging from 5 to 100 millions of species, from which only about 1.9 millions of species are known. However, many human activities are leading to a global biodiversity loss at a rate that is higher than what should be naturally expected. This global trend is especially worrying in freshwater ecosystems (Figure 7.1).

For instance, the Living Planet Index (LPI) has been tracking population trends of over 2,500 vertebrate species since 1970 in order to calculate a yearly average rate of changes for those populations. LPI reflects somewhat the health of

Figure 7.1: *A typical Mediterranean river. Mediterranean climate regions all over the world host high number of terrestrial and aquatic species and are considered biodiversity hotspots. Nevertheless, many Mediterranean rivers are currently threatened by rising water consumption, and face bleak prospects as a consequence of ongoing climate change*

planet ecosystems (terrestrial, freshwater, marine). Examining LPI trends shows that the abundance of more than 300 freshwater vertebrate species declined by ~55% from 1970 to 2000, while those of terrestrial and marine systems declined by ~32%. As a result, the scientific and public awareness of the ecological consequences of such a dramatic species extinction has much increased in the last two decades, as well as the budget allocated to conserve and restore biodiversity. For example, during the period 1988 and 2008 the World Bank invested more than US$6 billions to support biodiversity conservation programs. Such programs were not only meant to preserve our natural heritage but also aimed at studying the ecosystem consequences of such biodiversity loss.

The biodiversity of our every day environment results from various ecological processes. First of all, any region cannot accommodate all the potential species on the earth. For example, the platypus is only found in Australia, the hippopotamus lives only in Africa. In European waters, *Echinogammarus berilloni* (Catta 1878), an amphipod (Figure 7.2), is native of the Iberian Peninsula, but the creation of canals connecting waterways has made the species spread and establish in several French rivers beyond its native distribution (see chapter 8 for detailed mechanisms of invasion).

This means that biodiversity differs from one region to another and what we observe today is the result of 3.5 billions years of evolution and various colonisation and settlement processes. Similarly, a locality, for example a stream reach in a particular region cannot accommodate all the potential species of the re-

Figure 7.2:
A male of Echinogammarus berilloni, *an endemic crustacean amphipod of the Iberian Peninsula that lives and feeds on leaf litter of streams*

gion and only those able to pass through environmental filters that characterize the locality will be found (Figure 7.3).

In other terms, a species must possess traits (Box 7.1) that allow it to cope with several environmental constraints operating at a regional scale (essentially climate, relief, geology) and at a local scale (current velocity, temperature and so on). Dispersal ability is a further trait of the species that enables it to colonize a given locality (Figure 7.3).

Finally, in a given site, the individuals of a species have to locally find an array of biotic and abiotic conditions that allow them to survive and reproduce. However, because the resources available in the locality are not infinite, species have to share them with others, which inevitably induce competition among them. As a result, the limited number of potential habitats will ultimately limit the number of species in the site (Figure 7.3). The amount of resources in a given site thus determines the level of biodiversity. Once species are settled, by growing and reproducing they contribute to the functioning of the ecosystem.

Ecosystem functioning refers to a complex group of several functions that sustain the ecosystems. These functions include biomass production, decom-

Box 7.1

Trait, disturbance and habitat templet

Species trait

Any morphological, physiological or behavioural characteristic that characterise the life history of a species, such as body mass, the number of offspring produced each year, the type of respiration, or the type of food ingested. Every environmental change that affects the growth, survival or fecundity of individuals, or their behaviour, will affect the population size through changing birth and mortality rates. Such modification will in turn, affect the arrangement of the community, and ultimately ecosystem functioning.

Species trait state

A particular value or modality taken by a trait, which may vary along environmental conditions and temporally (e.g. small and large are trait states of body mass).

Functional trait

Characteristics of an organism that determine its effects on a given function (e.g. shredders contribute to leaf-litter decomposition).

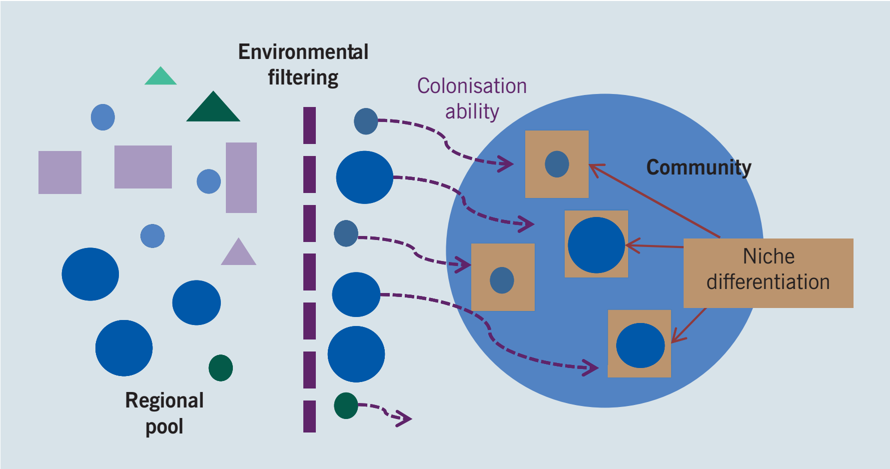
Disturbance

Unexpected event that impacts the community at a local scale and over a short time. Disturbances are defined by their intensity (including magnitude and duration), predictability and frequency. For example, floods are natural disturbances that may change stream morphology and reshape gravel bars.

Habitat templet theory

A theory assuming that habitat provides a spatio-temporal framework on which evolution forges characteristic life histories. The habitat framework adapted for rivers is built along two axes (Townsend & Hildrew 1994). The X-axis represents temporal variability (the intensity of disturbance), the Y-axis spatial heterogeneity. In streams, heterogeneity may mean refuge for organisms and a higher disturbance will have less impact in a mosaic of habitats than if the habitat is homogeneous. To survive in these habitats, species have to possess specific biological characteristics. For example, if a species inhabits a frequently disturbed habitat, then the species can either resist if it has clinging facilities or escape and return easily once the disturbance ceases. In frequently disturbed habitats, species will have short life duration and produce many offspring to ensure survival in a constrained environment. In contrast, when the intensity of disturbance is smaller, a higher diversity of species including those resistant and non-resistant and those resilient and non-resilient may occur in the community.

position of organic matter, or nutrient uptake (see Box 7.2). Many researchers have suggested that ecosystem functioning depends on biodiversity, which could be framed under the biodiversity-ecosystem functioning hypothesis (hereafter called B-EF). This has emerged as a central ecological question by the turning of the century (Loreau et al. 2001). It basically assumes that biodiversity affects ecosystem properties and, therefore, the benefits we obtain from them (ecosys-

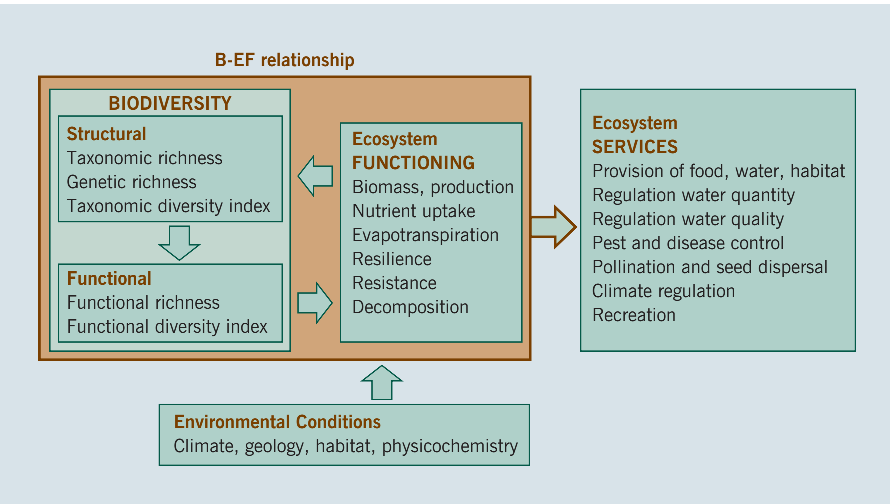


Source: Redrawn from Boulangeat (2012).

Figure 7.3: *Environmental filtering or how individuals of given species can be found in a given stream reach. The regional pool comprises all species that exist in a region. From this pool, some species are filtered out by environmental characteristics (for instance, habitat features), which are unsuitable for them to survive. The species that can survive in the conditions of this reach must also have colonisation ability to reach the locality, either actively (flying, swimming) or passively (water or wind transportation). From the species that reached the locality, only those with ecological niches different enough will be able to coexist, the rest will be eliminated by competition. Environmental filtering and niche differentiation are essential processes for explaining local biodiversity*

tem services) (Figure 7.4). Species in a community perform many ecosystem properties, such as biomass production and mineralization of the organic matter. Therefore, understanding the B-EF relationship may greatly help in understanding the consequences of the current decline in biodiversity in ecosystems.

But, how general is the B-EF hypothesis? The B-EF hypothesis is considered a “long-standing paradigm in ecology” (Caliman et al. 2010) supported by much



Source: Redrawn from Díaz et al. (2006).

Figure 7.4: *Relationship between biodiversity, ecosystem function and ecosystem services (see Box 7.2) and how environmental conditions can modify these patterns*

Box 7.2

Biodiversity, function, functioning and services

Biodiversity

Biological diversity refers to the extent of genetic, taxonomic and ecological diversity over given spatial and temporal scales. Biodiversity includes structural and functional aspects. It can be measured using variables such as richness or diversity indices but species composition may be even more informative about how species are arranged in the assemblage (their relative abundance). **Structural diversity** refers to taxonomic units (species) whereas **functional diversity** refers to the role of these units in the ecosystem (such as feeding strategies or body size).

Function

Ecosystem functions stand for ecosystem processes. They result from the interactions among biotic and abiotic elements of the ecosystem. The term is generally employed to refer to both ecosystem properties and services. Ecosystem properties include stock of energy and materials (for example biomass), fluxes of energy or material processing, (for example productivity, decomposition) (Lecerf & Richardson 2010)

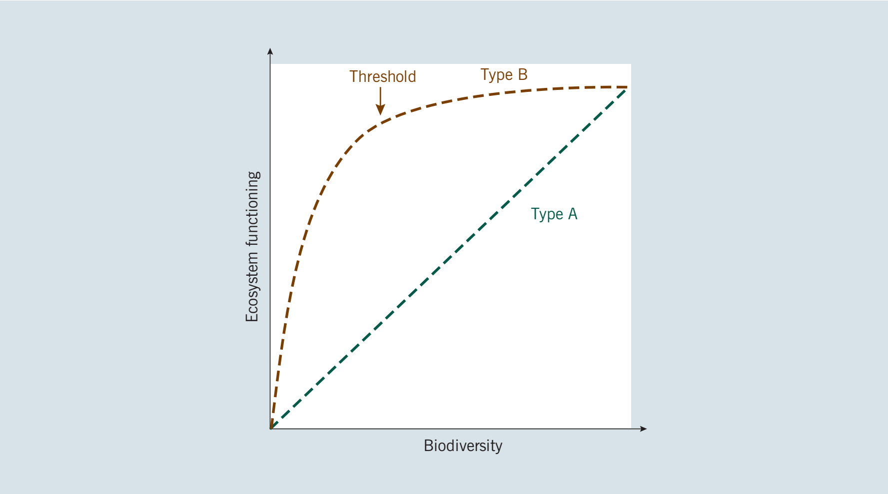
Functioning

Functioning refers to the joint effects of all functions (processes) that sustain an ecosystem. Thus, it considers the combination of biomass, production, decomposition, and nutrient uptake, among other ecosystem characteristics.

Services

Humans can benefit from the different functions that ecosystems provide. These benefits are known as **ecosystem services** and include characteristics grouped as provisioning, regulating, supporting and cultural services.

evidence, which suggests that biodiversity can positively enhance ecosystem functioning. In a literature survey, carried out with 100 studies dealing with the B-EF hypothesis, Srivastava and Vellend (2005) found that a B-EF relationship was significantly positive in 71% of the studies for at least one ecosystem function. Thus, in these cases, species-rich communities will have more efficient ecosystem functioning than species-poor communities. However, very often this relationship is only linear up to a certain point, and adding more species has no effect on the ecosystem functioning. In this case, we consider that the new added species are functionally redundant to the already existing ones. Thus, two general types of B-EF responses can be expected in ecological systems: a linear response where each species is functionally singular and contribute steadily to the ecosystem functioning (type A, Figure 7.5) and a non-linear response where ecosystem function is effectively maximized by a relatively low proportion of the total diversity (type B, Figure 7.5). In that case, few abundant species most implied in the ecosystem function live together with rare species



Source: Redrawn from Schwarz et al. (2000).

Figure 7.5:
Hypothetical relationships between biodiversity and ecosystem functioning. Type A (green) assumes a gradual decrease of ecosystem functioning with successive biodiversity loss events. Type B (brown) supposes functional redundancy (see Box 7.3) since ecosystem functioning is not immediately impacted by biodiversity loss events. The threshold on type B curve indicates the biodiversity limit below which additional species loss will involve a significant reduction of ecosystem functioning

that have a more minor contribution to ecosystem functioning. Now, when one species disappears, its function can be compensated by the increased abundance of another already existing species. As a result, ecosystem functioning does not immediately decline with biodiversity loss. Many ecological situations probably lay in-between these two extremes. Nevertheless, of the 100 studies mentioned above, only 39% showed a linear relationship (type A, Figure 7.5) whereas 61% showed a non-linear one (type B, Figure 7.5) (Srivastava and Vellend 2005).

Clearly, the two types of responses have different implications in terms of conservation. In type A, at each species loss event, ecosystem functioning decreases in a steadily way. In type B, several species may be functionally redundant (see Box 7.3) and species loss does not change ecosystem functioning beyond a certain value of biodiversity (threshold in Figure 7.5), below which further species loss events may greatly impact ecosystem functioning. Therefore, in the latter case, many species could be lost before detecting any changes in the system because many species are functionally redundant. In addition, the value of biodiversity, or that of particular species, would be very low up to a certain point above which conservation measures would not be justified, if only ecosystem services are considered. However, we have to bear in mind that the presence of a certain type of B-EF relationship depends on the type of ecosystem under study, the type and number of ecosystem functions measured, the range of biodiversity under focus, the type of biodiversity measure used, and the species identities (Ghilarov 2000; Srivastava and Vellend 2005).

Box 7.3

Functional redundancy: A reality or a myth?

Inherent to communities, functional redundancy implies that different species perform the same role in ecosystems, so that changes in species diversity should not affect ecosystem functioning. It is thus assumed that biodiversity is more sensitive to disturbance than ecosystem functioning.

The reality. Considering a single or few ecosystem functions as surrogates of functioning, species having similar functional roles can be considered redundant. For example, when looking at the processing of the matter and energy in a system, all primary producers contribute to the same function (irrespective of their relative contribution). Therefore, studies focused on a single or few functions are more susceptible to find species redundancy (Rosenfeld 2002).

The myth. In a broad sense, all functional roles that a species can perform could be seen as its functional niche. The different traits (see Box 7.1) of a species might respond to different ecosystem functions. For example, feeding traits are related to the processing of the matter and energy in a system whereas body form can be related to resistance. Therefore, local biodiversity can be only explained because species have few overlaps of their functional niche and contribute all together to the overall ecosystem functioning. Simply speaking, if "ecosystem functioning" means all compounds that plants and animals in a community have in their bodies or release in the environment, then any redundancy is impossible (Ghilarov 2000).

The reality or the myth of functional redundancy is related to how ecosystem functioning is defined, either as a single function (the reality, since current studies hardly look at more than two functions, like for example litter decomposition and algal growth in streams) or the multiple functions of an ecosystem (the myth because nobody is currently able to measure all the functions of an ecosystem).

Another important issue in considering the effects of biodiversity loss on ecosystem functioning is that species loss is never random. Some species are more prone to extinction than others for a specific pressure. For example, for regions where climate change will result in longer drought periods, those species not adapted to survive droughts will experience a higher extinction risk. Overall, type B response (shown in Figure 7.5) will occur if those species that are more susceptible to be lost contribute less to the ecosystem functioning. As a result, in addition to accounting for biodiversity, the assessment of the B-EF relationship requires addressing the functional characteristics of species (their functional role, see Box 7.2) as well as their biological traits (see Box 7.1) in relation to their extinction risk and the ecosystem function under focus. Therefore, it is difficult to forecast the impacts of environmental changes on ecosystem functioning. Moreover, it might be risky to consider a single or a few ecological functions as surrogates of global ecological functioning, as the different species may be important for different ecosystem functions.

Nature conservation is usually carried out at a regional scale, and thus humans have established protection areas over hundreds of square kilometres in natural parks. However, studies looking at the B-EF relationship have been assessed at a local scale (in a prairie, in a stream reach, or in a laboratory experiment), which cannot be directly translated to regional scales.

At the local scale, ecosystem functioning can be enhanced with the presence of one or more species because species may have a complementary action, which enhances ecosystem functioning. This action, which is called complementarity of resource use, occurs when part of the local habitat is occupied, namely there remains empty space for other species. In other terms, under the level of total biodiversity that a given site can support (shown by the vertical bar on Figure 7.6), ecosystem functioning is improved by the complementarity among species and increases with biodiversity. Above this level of "optimal" local biodiversity (vertical line), species that are added from other regional localities involve a more severe local competition. Such competition yields a global reduction of their performance and ultimately involves a local decrease of ecosystem functioning (beyond the vertical bar in Figure 7.6). In contrast, at the regional scale, species complement one another from the diverse localities of the region. As a result, additional species involve a steady increase of the regional functioning (Figure 7.6).

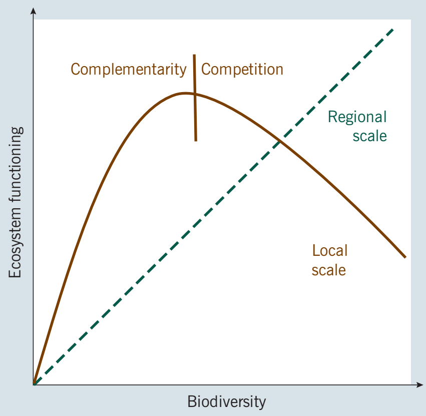


Figure 7.6: *B-EF relationships at the local and regional spatial scales. Local scale patterns cannot be directly transferred to regional scale because B-EF relationship may differ at both scales. According to these relationships, local species extinction may lead to a local improvement on ecosystem functioning up to a certain threshold (vertical line) whereas regional species extinction is immediately detrimental to ecosystem functioning*

Source: Redrawn from Bond and Chase (2002).

7.2. What do we know from stream ecology?

7.2.1. The specificity of fluvial habitats

When walking up a stream, we can easily catch a fundamental property of running waters, i.e. movement. As a fundamental part of the water cycle, the surplus precipitations that fall upon the continent (runoff) flow into the ocean allowing a permanent water turnover on Earth. When further scrutinizing the streambed at low water level, we find an amazing mosaic of different habitats (like sand, boulders, twigs, fallen leaves, algae) (Figure 7.7). The amount and the seasonality of flow induces a diversity of flow forces on the streambed, which in turn, affects the type and size of substrata (sand, cobbles, boulders) and the distribution of resources (twigs, fallen leaves, algae, and others).

In addition, stream flow implies that nutrients, dead organic matter (Figure 7.8), sediment and propagules are transferred from up to downstream as well as to the side arms in the floodplain, which makes streams and rivers open flowing systems in comparison to lakes or reservoirs. In the upper course of rivers, a large amount of the energy supply comes from the processing of dead organic matter, which originates from outside the stream channel. Part of this dead matter is processed locally by various species and another part is carried away downstream by flow. In contrast, lower courses are less affected by riparian shading and depend more on in-channel primary productivity and the organic matter coming from upstream involving different species to occur. In addition, flow and other environmental characteristics select species according to their

Figure 7.7: *Rivers flowing gently and showing the mosaic of habitats on the bottom substrate*

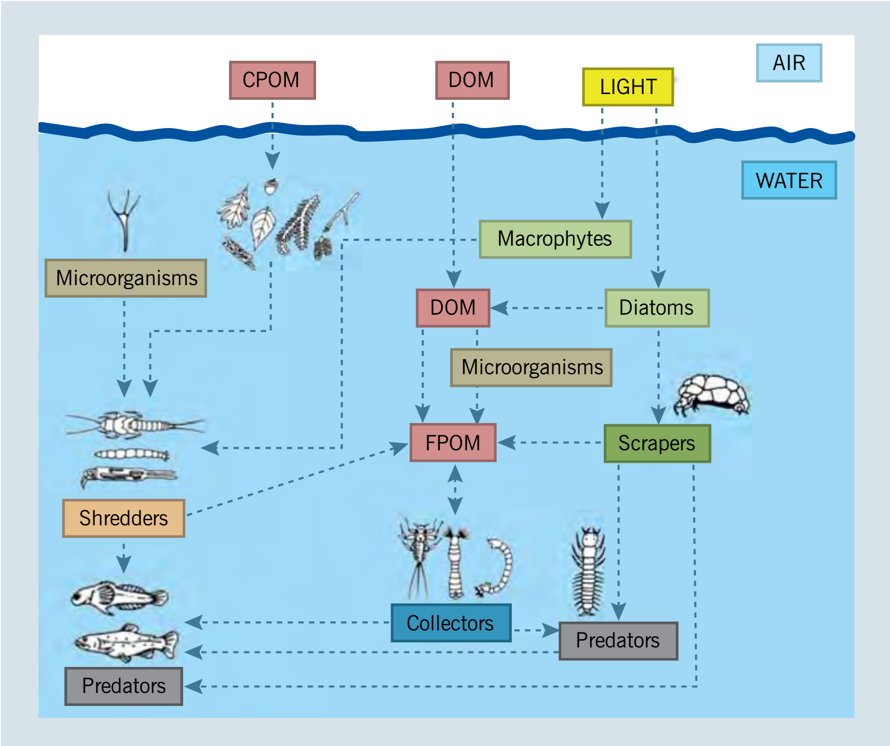
Figure 7.8:
A leaf pack in a French temperate river. Rivers transport leaves until they deposit and are processed by the stream biota (especially fungi and invertebrates). Leaf litter decomposition is one of the most studied river ecosystem functions

traits (see Box 7.1). Thus, flow is in rivers the most important driving force that affects its biodiversity and functioning.

7.2.2. Functional guilds and functional redundancy

Functional groups or guilds are groups of organisms that are believed to play the same role in ecosystems. For example, stream invertebrates can be divided, among others, into predators or shredders (animals eating large portions of dead organic matter). Cummins (1973) proposed to establish feeding guilds, known as functional feeding groups (FFG), mainly based on the mechanisms of feeding used by stream invertebrates and secondarily on the main type of food source (Figure 7.9). He, thus, implicitly recognized that knowledge on the functional role of species in streams should improve our understanding of the aquatic ecosystem functioning. Cummins (1973) especially noted that a majority of stream invertebrate consumers exhibited overlaps in their diets (i.e. they showed some functional redundancy see Box 7.3). For example, a detritivore may eat dead leaves but may also absorb small crustaceans or small insect larvae in some period. Similarly, an herbivore that usually grazes algae can potentially get dead organic matter in its food as well. In fact, stream insects cannot con-

Figure 7.9: *The various functional feeding groups (FFG) that interact to process the matter and energy in streams and rivers. As indicated in this diagram, any FFG covers various life forms. All these life forms depend on each other and on energy inputs (CPOM stands for Coarse Particulate Organic Matter, FPOM for Fine Particulate Organic Matter, DOM for Dissolved Organic Matter)*



Source: Redrawn from Cummins (1973).

trol the food they receive, and thus, must be rather polyphagous and somehow opportunistic to get their food. This contrasts a lot with so many terrestrial insects, which are restricted to eating a single or a few plant species, as is the case of many caterpillars, for example. Moreover, diets may vary according to larval stages. For example, young *Hydropsyche* larvae (see Figure 7.12) mainly feed on algae and dead organic matter whereas older larvae may still feed on algae and also on other small invertebrates.

However, organisms within a given trophic guild are not necessarily redundant, as they may differ in their ecological requirements. For example, manipulative experiments with eight species of burrowing filter-feeding bivalves (freshwater mussels) showed that in summer one mussel species *(Actinonaias ligamentina)* reached greater biomass and had a higher excretion rate than other mussel species. In these conditions *A. ligamentina* benefitted benthic algae, which took advantage of the nitrogen excreted by the mussel (Figure 7.9). These differences between mussel species disappeared in periods of lower temperatures (Vaughn et al. 2007).

One species within a given FFG may thus not totally replace another species of the same FFG and the real degree of redundancy among species is far from being known. For example, it has been shown experimentally that three stonefly species belonging to the same FFG, such as shredders for example, had a different impact on leaf mass loss (namely, leaf litter decomposition; Figure 7.10). In this case, the same number of individuals was introduced in microcosms with each species alone, and grouped by two or three species together. In species alone situations, *Taeniopteryx nebulosa* had the highest impact on leaf litter decomposition, followed by *Nemoura avicularis*, and *Protonemura meyeri* (Figure 7.10 *left*). By contrast, decomposition increased with the number of species involved (Figure 7.10 *right*). Since the same number of individuals was used, these experiments suggest facilitation among species for processing leaf litter. As a result, at least experimentally, within-guild leaf litter decomposition rates can be significantly affected by the number of species belonging to the same FFG (Jonsson and Malmqvist 2000).

7.2.3. Context-dependency of the relationships between biodiversity and ecosystem functioning

The relationship between biodiversity and ecosystem functioning can be context dependent, as it may vary across the space. In other terms, some areas of the distribution range of a given species can be more suitable than others for its survival, growth and reproduction, and thus, its ecological effects there can be

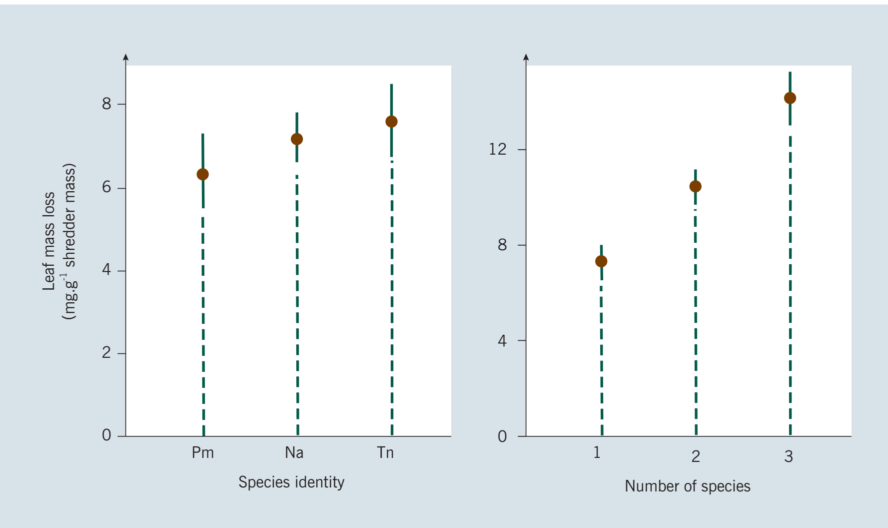


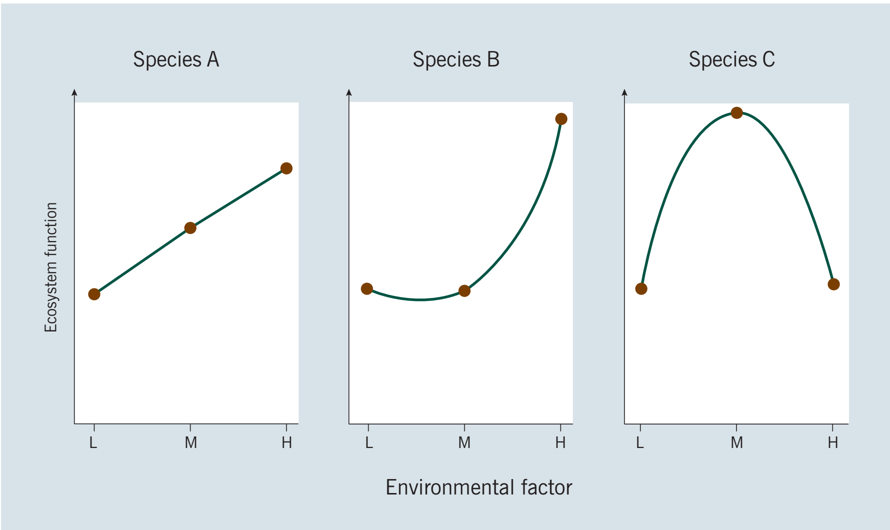
Figure 7.10: *Variation in leaf mass loss (mean ±1 SE) due to the identity of stonefly species feeding on dead organic matter* (left), *and with different species numbers* (right). *On the left, four individuals of each species alone were placed in microcosms, and decomposition increased from* Protonemura meyeri *(Pm) to* Nemoura avicularis *(Na) and* Taeniopteryx nebulosa *(Tn). On the right, grouping species together (by 2 or 3) increased the decomposition efficiency in comparison to species alone*

Source: Redrawn from Jonsson and Malmqvist (2000).

more important. For example, it has been shown experimentally that the effect of grazing insects on algal biomass changes with local current velocity (Figure 7.9). *Glossosoma verdona* (caddisfly) and *Baetis bicaudatus* (mayfly) ate less algae at slow and medium currents in comparison to fast current. In contrast, *Drunella grandis* (mayfly) had a strong effect on algal growth irrespective of current velocity. At fast current the three species had an equivalent impact on algae whereas at slow current, *D. grandis* had significantly greater impact than *B. bicaudatus*, and this one greater than *G. verdona* (Poff et al. 2003). Therefore, in some environmental conditions (in this case, low current velocity), different species may have a similar effect on ecosystem function (in this case, consumption of algae), and thus, appear as redundant, whereas the same species may differ in their effects when environmental conditions change (Figure 7.11). In other words, species with a strong effect on ecosystem processes in certain environmental conditions can become weak contributors under other environmental conditions, and this property may apply at different spatial and temporal scales.

Context dependency also relates to the degree and type of disturbances (Box 7.1). Biotic and abiotic disturbances (like grazing, predation, floods) causing mortality to organisms are key ecological factors that moderate the relationships between biodiversity and ecosystem functioning. As an example, net-spinning caddisfly larvae of the family Hydropsychidae are common in streams and feed on the dead particulate organic matter (POM) and small living organisms that drift in the water column with current. To catch their

Figure 7.11: *Hypothetical example showing how the performance of species belonging to the same guild and thus having a similar effect on an ecosystem function, may change with increasing value of a given environmental factor (L = Low, M = Medium, H = High)*



Source: Redrawn from Wellnitz and Poff (2001).

food they build nets on the bottom substrate, which enables them to capture the particles that drift in the current (Figure 7.12). In case of high densities of a more competitive hydropsychid, the nets of larvae can create flow shading and modify the hydrodynamic conditions in the immediate surroundings, which may prevent other filter-feeding species getting POM. It has been shown in manipulative experiments that disturbance could moderate such effect. The experiments consisted of creating disturbance artificially by randomly removing larvae of three species and their nets (thus imitating flood effects). By reducing the flow shading effect of the competitively superior hydropsychid, such artificial removal allowed a higher taxonomic evenness. In other terms, the other species could settle more easily. The resulting more diverse assemblage of filter feeders captured a greater fraction of POM. In contrast, in the absence of such artificial disturbance, increasing species richness led to dominance of the com-

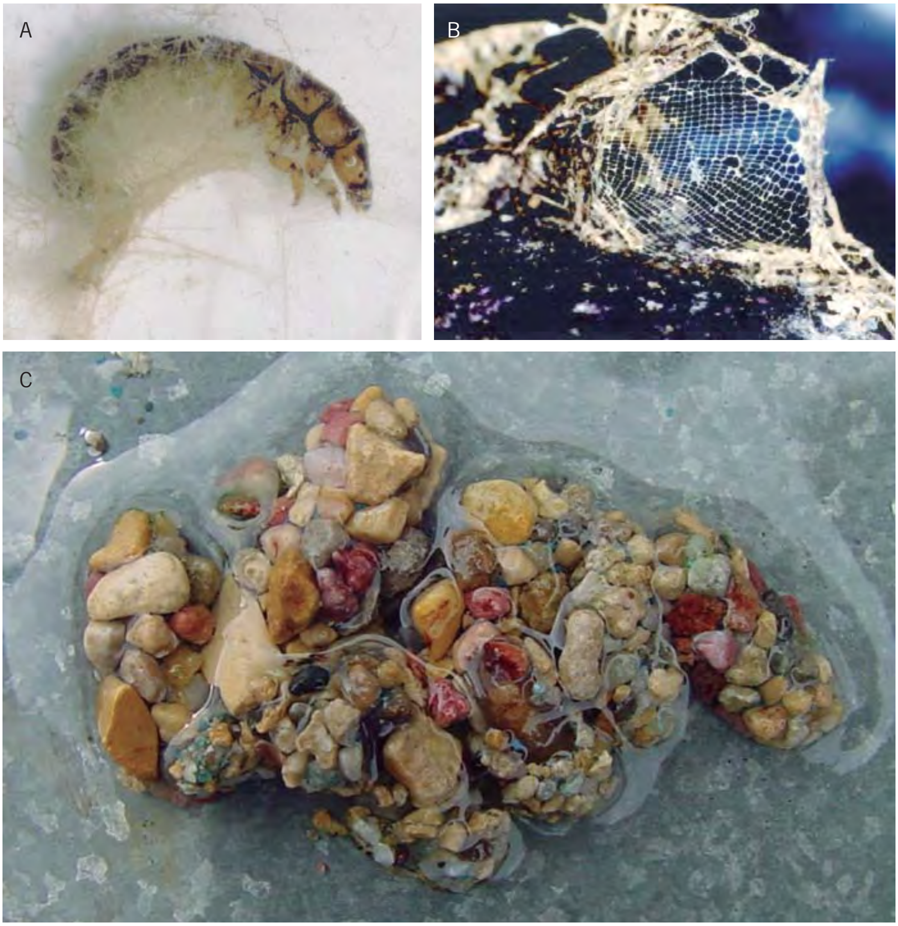


Figure 7.12:
A) A net-spinning caddisfly larvae (Hydropsyche exocellata) *surrounded by its net. B) The net itself constructed to capture particles drifting in the water column. C) A group of nymph cases with painted grain*

petitively superior hydropsychid and the amount of POM captured in water did not change when adding species.

Disturbance can also alter the indirect effect of net-spinning caddisfly larvae on other ecological processes such as algal productivity. For example, stream algal productivity partly relies on the amount of nutrients excreted by stream organisms since they use these nutrients as fertilizers. In the above manipulative experiments, it has been shown that in the absence of disturbance, namely when the competitively superior hydropsychid dominates the assemblage, the algal productivity declines. This apparently occurs because the prominent hydropsychid has particularly low rates of nutrient excretion.

Biotic and abiotic disturbance (Box 7.1) may influence ecosystem functioning in combination. For example, in the South Fork of Eel River (California) both floods and stocked fish can affect the abundance of insect larvae, and indirectly ecosystem functioning measured as algal productivity. In rainy years, floods slough insect larvae, and fish reduce the remaining insects, thus promoting algal growth. In contrast, during dry years, the insects are dominated by large armoured caddisfly grazers less vulnerable to fish predation, and algal biomass remains low (Power et al. 2008).

Disturbance can thus moderate the B-EF relationships by two mechanisms. One mechanism consists of a reduction of the effect of species with a disproportionate effect on ecological processes, like keystone species, ecosystem engineers, or species with biologically unique traits. The other mechanism relies on that preventing species dominance may result in increasing spatial heterogeneity, species richness and the rate of a given ecological process. In that case, to co-exist, species of the same guild have to differ by some amount in their biological traits so that they can feed in a complementary way on resources.

7.2.4. The importance of species dominance and identity

Most experimental studies addressing the B-EF relationship focus on species richness without considering the relative abundance of species within assemblages (evenness). In other terms, controlled experiments generally ignore that real local communities are usually dominated by few abundant species, which drive ecosystem processes and which coexist with many more rare species. However, besides species richness decline, human disturbances may produce changes in the relative abundance of species, which can greatly affect ecosystem functioning without noticeable change in species richness. For example, nutrient enrichment increases the abundance of a few species, which results in an increase of the ecosystem production. In contrast, siltation in streams fills in the interstices of the bottom substrata, which produces a decrease in the abundance of primary producers and therefore a decline of ecosystem production. In these two cases, measuring ecosystem functioning only through species richness would be misleading.

Biodiversity loss may affect ecosystem functioning. However, this effect depends on the degree and type of disturbances, the presence of dominant species and the order in which species are lost

A common emblematic example of species controlling stream ecosystem functioning concerns salmon. A run of 20 million fish getting to spawning areas can move over 50,000 t of biomass into freshwater and adjacent terrestrial ecosystems. Salmon carcasses provide nutrients, which positively impact young salmon as well as a range of vertebrates and invertebrates that consume salmon resulting in high biodiversity. Overharvesting these migratory fish, thus, greatly disturbs the transport of materials over long distance and the chain bringing marine-derived nutrients to freshwater and terrestrial environments.

Similarly, the relative abundance of shredders (as defined in Fig. 9) in assemblages may strongly influence the B-EF relationship in low-order streams where accumulation of leaf litter can be very important. It has been shown that for a given species richness, leaf litter decomposition was greater in communities with higher species dominance than in those with more even distribution of species. For instance, the crustacean *Gammarus fossarum* dominated the shredder community in a given stream throughout the year, and had a major impact on leaf litter decomposition even at low shredder diversity. In contrast, in other streams, breakdown rates peaked seasonally when two Trichopteran species dominated the community *(Sericostoma personatum* or *Chaetopteryx villosa*; Dangles and Malmqvist 2004). This example shows that species identity is a fundamental component of biodiversity with varying impact on ecosystem functioning. Hence, the biological traits of individual species strongly influence their abundance in communities and subsequently their roles in ecosystem functioning. For example, species such as *G. fossarum* showing strong specific interactions, high densities, present all year round in the stream and with a high mobility, namely able to drift and migrate upstream extensively can be expected to have strong effects on communities and ecosystem functioning. In contrast, the two above Trichopteran species demonstrate pronounced seasonal patterns in their biomass and resulting effect on decomposition, which shows in that case that the diversity effect on ecosystem functioning does not remain constant over time. As a result, deep knowledge of species identity and life cycles is mandatory for assessing further B-EF relationships and taking appropriate management measures.

7.2.5. The existence of positive interactions among species

As seen above, according to the competitive exclusion principle, two species relying on the same resources cannot coexist in a stable environment (see Figure 7.3). If one of the species has a slight advantage over the other then it will dominate, leading to either the extinction of the competitors or an evolutionary shift of their functional niche (niche differentiation). Such evolutionary shift may involve species feeding in a complementary way.

Besides the biodiversity and ecosystem functioning effects associated with such trophic niche differentiation and complementary use of resources, we should not forget positive interactions among species, which frequently occur in streams. Such positive interactions include aquatic fungi that condition leaf litter thus enhancing the palatability of leaves for shredders and initiating the detrital food chain. In addition, organism activities (e.g. for searching food, spawning, case building) contribute to sand and gravel transport or aggregation, thus, modifying both solid transport and biogeochemical processes on the streambed (two major stream functions), and the potential settlement of other species in the assemblage.

For example, net-spinning caddisfly larvae build their nymph case to metamorphose into adults (Figure 7.12). The grains that constitute the case are cemented together with silk similar to that used by spiders, and the case itself cemented onto the bottom substrate. At high densities, several cases can join together (Figure 7.12), and the ensemble can cause changes in the near-bottom flow forces. These caddisfly larvae can increase 9-fold the force necessary to mobilize gravel, thus stabilising the substrate and favouring the establishment of a diverse aquatic fauna and flora. However, here again appears complexity, since the locomotion activities of other species may be antagonistic. For example, gudgeon *(Gobio gobio)* and barbel *(Barbus barbus),* two species with different habitat preferences (near-bank gravel beds for gudgeon and coarse bed below riffles for barbel, a habitat similar to that of *Hydropsyche),* can reduce the flow forces necessary to mobilize gravels in different areas of a stream reach. We are yet far from a complete knowledge of the effect of species removal in such a complex context (Statzner et al. 2003).

The presence of a species may not only change the habitat for other species but may also affect the resource due to varying feeding efficiency. For example, it has been shown experimentally that the action of two detritivores on leaf decomposition could complement each other only if they were introduced in a well-defined sequence (Figure 7.13). The order in which the species colonize a given habitat is thus of critical importance for the functioning of the ecosystem.

7.2.6. The order in which species are lost do matter

While the sequence of colonisation of a stream reach by species affects ecosystem functioning, the sequential loss of taxonomically distinct invertebrate species

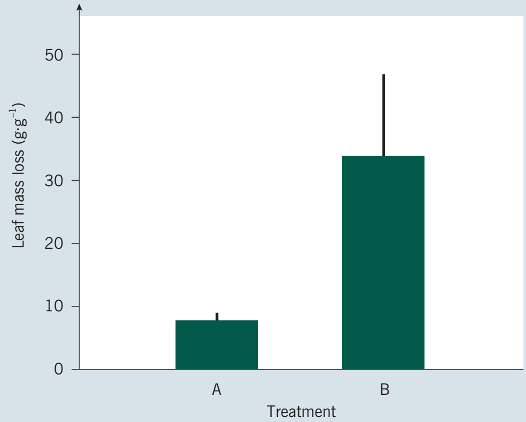


Figure 7.13: *Detritivore activity (leaf mass loss) of two shredding stoneflies introduced in sequence with (A)* Protonemura meyeri *following* Taeniopteryx nebulosa *and (B) the reverse option*

Source: Redrawn from Jonsson and Malmqvist (2003).

may also greatly affect ecosystem processes. Among the traits of species that do matter to changes in ecosystem functioning, body size has strong implications for organism metabolism. Small-sized organisms tend to have higher metabolic rates per mass unit than large-sized organisms. This can be measured by the *production-to-biomass ratio* (P/B), which represents the proportion of biomass produced by the individual of a species per time unit. Annual P/B ratio is higher for small-sized than for large-size organisms. In a modelling experiment that simulated species removal, it has been shown that the disappearance of all species of a given size class in sequences from large to small body sizes during repeated extinction events involved an increase of annual P/B (toward a value 5 times that of the initial entire assemblage; Figure 7.14). In contrast, if at each extinction event, the species are lost at random regardless of their body size, annual P/B remains relatively stable (Figure 7.14).

This simple example illustrates the outstanding importance of size in any consideration of species loss and function. Patterns similar to those simulated may occur when a stream receives pollution. In this case, diverse assemblages that include large invertebrates yielding high biomass and low production are replaced by species-poor assemblages dominated by small tolerant species with a low biomass and a high production. The order of extinction can easily be assessed for various types of anthropogenic disturbance. For instance, acidification affects mainly organisms sensitive to lack of calcium (crustaceans and molluscs), whereas organic pollution affects those sensitive to oxygen depletion. Therefore, species traits do matter for assessing the decline in ecosystem functioning.

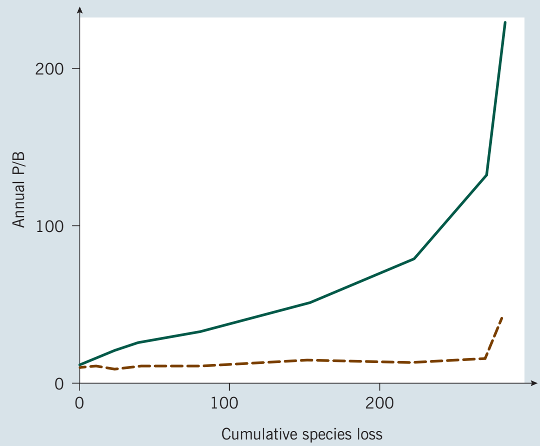


Figure 7.14: *Simulation of the effect of random species extinction independent of body size (dashed line) and of removing species sequentially from large to small body sizes (plain line) on annual production-to-biomass ratio (P/B) in hypothetical stream invertebrate assemblages. If large and intermediate size classes disappear, the annual P/B of the assemblage rapidly increases (plain line). If species go extinct at random, the annual P/B remains relatively stable with increasing species extinction, and increases only when a single species remains*

Source: Redrawn from Statzner and Moss (2004).

A further complication to bear in mind is that large animals, those likely to go extinct first, may belong to different trophic levels, such as detritivores and predators. The manipulation of large predatory invertebrates in experimental stream channel shows that their absence can promote grazers and reduce biomass of benthic algae, and even reduce sediment accumulation. The experimental exclusion of large detritivores in the same experimental channel affected both the magnitude and the rate of litter decomposition. Small-size detritivores are unable to compensate the lack of large detritivores, thus leading to a decline in leaf decomposition rate (Lecerf and Richardson 2011). As a result, large stream invertebrates may affect multiple ecosystem properties. As they will generally disappear first, their loss will critically affect ecosystem structure and functioning.

The consequences of species extinctions on ecosystem functioning thus depend on the species and its interaction with others in the food web. They may induce an increase of some species when their competitors and/or predators decline. The effects of biodiversity on ecosystem functioning may also depend on whether biodiversity loss occurs at a single trophic level, or at multiple trophic levels. From several studies covering various types of stream ecosystems, it has been shown that species richness had a weaker effect on ecosystem functions than assemblage composition of overall species, which indicates again the importance of species identity, species traits and functional diversity in comparison to taxonomic diversity. In addition, this meta-analysis showed that the species composition effect was found to be more pronounced on ecosystem function at lower trophic levels in comparison to species richness, whereas both the richness and composition of predators affected ecosystem functions equally (Lecerf and Richardson 2010). All these elements acting at different biological scales show how difficult it may be to accurately predict the effect of biodiversity loss on ecosystem functioning.

7.2.7. What about species gain?

Many human pressures involve species loss but also species gain, which derives from the establishment of non-indigenous species (deliberate or accidental introduction of organisms to an ecosystem; see chapter 8). Such biotic exchanges appear as one of the five most important determinants of changes in overall biodiversity together with changes in land use, atmospheric CO_2 concentration, nitrogen deposition and acid rain, and climate. In general, invasive species have traits (temperature tolerance, body size) that favour their establishment and population growth and may lead to the replacement of native by invasive species. However, the functional consequences of invasive species remain to be documented. For example, freshwater gammarids that are commonly considered as shredders (see above) and suggested to have a strong impact on leaf litter decomposition may exploit a wide food range. Now, the originally Ponto-Caspian gammarid *Dikerogammarus villosus* has invaded many European freshwaters where it is progressively eliminating native gammarids from European freshwaters through predation. In experimental flumes, *D. villosus* was able to withstand stronger currents than the native *Gammarus pulex*. Under high velocities, *G. pulex* tended to concentrate in flow refuges, thus being easy prey for *D. villosus* and resulting in increased mortality of *G. pulex*. However, leaf litter decomposition only moderately decreased in the presence of *D. villosus* (Felten et al. 2008) showing that the invasive species had a moderate effect on the ecosystem function. In contrast, due to their high densities, the signal crayfish *(Pacifastacus leniusclus)* has been shown to dramatically alter sediment transport thus deeply impacting ecosystem functioning (Harvey et al. 2011).

7.3. Take-home message

High species richness in streams results from an array of processes including the ability of species to cope with environmental conditions, their dispersal ability, and subtle interactions that allow them to coexist locally by partitioning the resources. Changes in species richness affect ecosystem functioning, but the species identity may matter much more than species richness per se. Looking at species richness alone may be thus misleading for addressing the effect of biodiversity loss on ecosystem functioning since changes in the abundance of some species might impact ecosystem function even in the absence of local extinctions. As an additional complexity, few scientific studies have clearly shown how the functional performance of species varies in different environmental conditions.

Rivers hold a huge biodiversity despite covering a little percentage of the Earth area. Conservation strategies should be prioritized in habitats having key species for ecosystem functioning

The role of non-trophic interactions among stream species also appears insufficiently appreciated. For instance, ecosystem engineers include beavers that build dams across rivers, thus strongly affecting their functioning. In fact, most stream species either consolidate or disturb the bed sediment, which has consequences not only on the bottom substrate mosaic, but also on resource fluxes and the establishment of other stream organisms. However, we lack evidence about the ecological consequences of removing engineer species, especially because some of them may involve bioturbation whereas in the same area other may consolidate stream. We currently do not know how the resulting antagonistic effect of both types of engineers may affect an ecosystem function such as bed sediment transport. To investigate the impact of human disturbances on ecosystem functioning, we need to establish scenarios of extinctions that are characteristic for a given type of disturbance and to consider the non-random sequential loss of species, which depends on the traits of species, among which body size is determinant.

Taking into account that predicting changes of ecological functioning from changes of biodiversity remains a complex task at regional scale (the scale at which environmental policies operate) and since most of the B-EF responses were assessed from local scale experiments, we should keep the B-EF hypothesis as a working hypothesis. B-EF tests suggest measuring biodiversity by taking into account the identity of species (their traits, their life cycles) rather than species richness alone. Once a few of such species have been recognized as keys for some ecosystem functioning in a given ecosystem then conservation measures should concentrate on preserving their environment. Preserving the environment of a key species means preserving the biotic and abiotic filters, which induce the preservation of other species and having an appropriate ecosystem functioning.

Currently, a straight match between biodiversity and ecosystem functioning in streams is thus far from obvious and urges B-EF scientists to develop new research combining field studies and laboratory experiments at different scales. It should also impulse managers to implement present scientific knowledge in conservation, management and restoration. A key implication of the B-EF hypothesis is, however, that the final target relies on receiving a service from ecosystems. Therefore, the B-EF hypothesis assumes that biodiversity should be preserved because it ensures a service rather than for its own intrinsic value. We should not forget that every form of life is unique, deserving attention regardless of the ecosystem service it provides to human society. Biodiversity is above all part of our natural and cultural heritage.

7.4. References

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