Chapter 21
Plant Litter Decomposition as a Tool for Stream Ecosystem Assessment

André Frainer, Andreas Bruder, Fanny Colas, Verónica Ferreira, and Brendan G. McKie

Abstract The decomposition of plant litter in freshwaters is an integrative process involving multiple organism groups and connecting terrestrial and freshwater ecosystems. The quantification of leaf litter decomposition has been advocated as an effective indicator of ecosystem functional integrity in the bioassessment of freshwaters. Indeed, variation in litter decomposition rates has been used to detect the impacts of a wide range of anthropogenic disturbances on the functioning of detritus-based food webs in freshwater ecosystems, particularly in streams. However, these assessments have almost exclusively been undertaken as part of research projects, and the application of litter decomposition as a tool in routine biomonitoring remains limited. We evaluate the potential for litter decomposition as a tool for ecosystem assessment by environmental agencies and managers, drawing on insights and experiences from three lines of evidence: (i) a broad selection of published research projects, (ii) an

A. Frainer (✉)
Norwegian Institute for Nature Research (NINA), Tromsø, Norway
e-mail: andre.frainer@nina.no

Faculty of Biosciences, Fisheries and Economy, UiT The Arctic
University of Norway, Tromsø, Norway

A. Bruder
Laboratory of Applied Microbiology, University of Applied Sciences and Arts of Southern
Switzerland, Mendrisio, Switzerland
e-mail: andreas.bruder@supsi.ch

F. Colas
CNRS, ENTPE, UMR 5023 LEHNA, Univ Lyon, Université Claude Bernard Lyon 1, 69622
Villeurbanne, France
e-mail: fanny.colas@univ-lyon1.fr

V. Ferreira
Marine and Environmental Sciences Centre (MARE),
Department of Life Sciences, University of Coimbra, Coimbra, Portugal
e-mail: veronica@ci.uc.pt

B. G. McKie
Department of Aquatic Sciences and Assessment, Swedish
University of Agricultural Sciences (SLU), Uppsala, Sweden
e-mail: brendan.mckie@slu.se

existing national-scale monitoring program and (iii) a meta-analysis comparing litter decomposition rates between nutrient-enriched and reference sites. We use this as a basis for discussing *inter alia* common substrates used in decomposition assays, alternatives for field protocols and sampling designs, and the use of different indices and reference conditions when arriving at an assessment of functional status.

21.1   Background

21.1.1   *The Promise of Litter Decomposition: Ecosystem Process Rates as a Tool for Stream Bioassessment and Management*

Almost two decades ago, Gessner and Chauvet (2002) advanced the suggestion to use leaf litter decomposition to complement structural indicators for stream bioassessment, to address the lack of practical, cost-effective approaches available to management authorities for quantifying the functional aspects of ecosystems (see Sect. 21.1.2). Since then, numerous studies have tested the use of litter decomposition as a measure of freshwater functional integrity. Despite intense research, major challenges remain in the implementation of litter decomposition in bioassessment as a complementary tool to established structural measures of ecosystem integrity. We revisit the methods, experiences, and developments concerning the use of litter decomposition as a tool in stream bioassessment and discuss: when is litter decomposition most suitable for use in bioassessment and what are the remaining roadblocks and knowledge gaps precluding the widespread use of litter decomposition as a tool for management?

21.1.2   *From Analyses of Structure to Functional Metrics*

Ecologists and practitioners interested in assessing freshwater ecological condition mostly rely on structural measures of biological integrity. In benthic habitats of lotic and lentic systems, such measurements include counts of invertebrate species or families, the relative abundances of some key benthic invertebrate orders, e.g., Ephemeroptera (mayfly), Plecoptera (stonefly), and Trichoptera (caddisfly) (EPT index), or country/region specific indices that weight the relative abundance of sensitive versus tolerant taxa, including the British Biological Monitoring Working Party index (Armitage et al., 1983), the New Zealand Macroinvertebrate Community Index (Collier et al., 2014) and multimetric indices (Mondy et al., 2012). These structural measures capture variation in the composition and distribution of benthic invertebrate communities, and sometimes include information about their functional traits, and thus are widely used to assess the current ecological status of habitats and to

track changes in status as management measures are applied (Burdon et al., 2020; Dahl & Johnson, 2004). Inferences of ecosystem level impacts (e.g., on ecosystem processes regulating fluxes of nutrients and energy) from these structural measurements are possible—for example a decline in abundance or diversity of invertebrates consuming algal biofilms might indicate a reduction in the importance of algae as an energy source in that system (McKie & Cranston, 2001). However, such inferences should always be heavily qualified because underlying assumptions simplify the ecological complexity of the system studied. For instance, tolerant species might adapt their functional role in a disturbed environment and partly compensate for the loss of more specialised and sensitive species, so that ecosystem process rates are maintained even as biodiversity declines (Ledger & Hildrew, 2005). Alternatively, a disturbance might have sublethal effects on the activities of functionally important species, so that functioning is affected without a marked loss of biodiversity (McKie & Malmqvist, 2009). Furthermore, structural measurements may be of little use in regions with naturally low abundance of certain groups or incomplete taxonomic information on some species. In all these cases, direct measures of ecological processes, which quantify fluxes in ecosystem functioning and are influenced by interactions of species with their environment (including resources), may serve as a complementary or even the primary approach for assessing ecosystem integrity.

Leaf litter decomposition is a pivotal ecological process, particularly in headwater streams and rivers, and also in ponds and littoral areas of lakes, and has been repeatedly proposed as an efficient bioassessment tool (Gessner & Chauvet, 2002; von Schiller et al., 2017; Young et al., 2008). Chauvet et al. (2016) provided an extended review and discussion of the use of litter decomposition for detecting impacts of different types of disturbances on ecosystem functioning. Nonetheless, leaf litter decomposition is not a one-size-fits-all tool. Boulton (1999) discussed the lack of a 'holy grail' tool for the assessment of ecosystem health (see Karr, 1999), and suggested that a combination of abiotic, structural, and functional measurements, including litter decomposition, should be used depending on the problem being addressed. Elosegi et al. (2017) further argued that ecologists should learn from millennia of development in medicine and use a combination of tools, including litter decomposition when suitable, to assess ecosystem health.

The importance of taking a multi-faceted approach to environmental assessment is explicitly recognized in the European Water Framework Directive (WFD), for example, which describes ecological status as "an expression of the quality of the structure and functioning of aquatic ecosystems associated with surface waters" (The European Parliament, 2015—Directive 2008/94/EC, pp. 423–426, Article 2, paragraph 21). Nevertheless, the biological elements mentioned in the WFD for the assessment of water quality are exclusively structural, i.e. composition and abundance of key organism groups. Environmental agencies continue to base ecological assessments on structural measurements alone (but see our Box 21.1 for an example of national-scale use of litter decomposition for bioassessment), although the desirability of developing appropriate functional metrics, including litter decomposition, as assessment tools is often acknowledged (e.g., USEPA, 2016).

The quantification of litter decomposition is fairly simple and practical, thus making it an efficient tool for assessments of ecosystem functional integrity. Furthermore, litter decomposition has already been tested across spatial (Chauvet et al., 2016; Tonin et al., 2017; Woodward et al., 2012) and temporal (Frainer & McKie, 2015; Frainer et al., 2014; Yeung et al., 2018) scales, and used to evaluate the effects of single and multiple stressors (Bruder et al., 2016; Castela et al., 2008; Colas et al., 2013; Pascoal et al., 2003), mostly in streams and rivers, but increasingly also in ponds and lakes (Quintão et al., 2013; Raposeiro et al., 2016; van Dokkum et al., 2002). Anthropogenic impacts studied include those associated primarily with changes in the abiotic environment, such as hydromorphological changes (Mendoza-Lera et al., 2012; Mollá et al., 2017; Sabater et al., 2018), nutrient loading (Ferreira et al., 2015; Woodward et al., 2012), acidification (Ferreira & Guérold, 2017), mining (Ferreira, Koricheva, Duarte et al., 2016), urbanization (Imberger et al., 2010), and pesticides (Rasmussen et al., 2012). Other studies have focused on effects of biotic changes on organic matter decomposition, such as the use of genetically modified crops (Rosi-Marshall et al., 2007), changes in forest composition driven by forest management (Ferreira, Koricheva, Pozo et al., 2016; Ferreira et al., 2019), species invasions (Alp et al., 2016; Hladyz et al., 2011), and changes in trophic interactions (Jabiol, McKie et al., 2013), including predation (Majdi et al., 2014) and parasitism (Hernández & Sukhdeo, 2008). Litter decomposition has also been used to assess the effectiveness of different types of ecological restoration and environmental mitigation measures (Entrekin et al., 2008; Flores et al., 2011; Frainer et al., 2018; Lepori et al., 2005). Below, we discuss the most prevalent methodological considerations when using litter decomposition as a bioassessment tool, including the use of different mesh sizes, litter types, temporal scales, habitats, and choice of reference conditions. We then revisit some proposed metrics for summarizing useful information from litter decomposition and suggest ways forward by addressing some of the main advantages and caveats of using litter decomposition as a tool for ecosystem assessment. We focus on the use of naturally abscised, dried leaf litter as the substrate in a litter decomposition assay because of its widespread use and the extended knowledge on this process gained over the past decades. However, we also address alternatives to the use of leaf litter to measure decomposition rates (Box 21.2).

Box 21.1: French case study

The National Office for Water and Aquatic Environments (Onema) is a French public institution created to support the implementation of public water policy in France as required by the European Water Framework Directive (WFD). Although the WFD defines the ecological status of surface water based on both *structure* and *functioning* of aquatic ecosystems, indicators developed under the WFD consider only ecosystem structure. In addition, WFD indicators have been mainly developed to focus on impacts of catchment landuse and chemical stressors. Addressing these shortcomings, Onema initiated and funded a research project (IDFun project, CNRS-Onema, 2012–2016) to develop an

indicator reflecting responses of ecosystem functioning to hydromorphological changes of streams. Leaf decomposition was selected for this purpose because of its central role in river ecosystem functioning, the considerable scientific background on both the abiotic and biotic mechanisms involved and on the effects of various physical and chemical stressors, and the relative ease and low cost of the method.

A working group composed of scientists and agents from two Onema regional services was created to propose and test a protocol that fulfils the methodological requirements (i.e., being as standardized as possible, easy to use, efficient in time and costs). Alder (*Alnus glutinosa*) litter was used due to its ubiquity along French rivers and its fast decomposition rates, thus reducing the risks associated with extended field incubation time. Coarse-and fine-mesh litter bags were used to estimate total and microbial-mediated decomposition rates, respectively. Litter bags were placed in four areas near the stream bank in each site. These locations were selected because they are natural areas of detritus accumulation. Litter bags were retrieved after 7 and 21 days, and after 21 and 42 days for coarse- and fine-mesh bags, respectively, resulting in at least 50% of mass loss on the final sampling date. Leaves were then rinsed, dried, weighed, ashed, and reweighed to estimate ash-free dry mass (AFDM). Water temperature was recorded every 30 min during the incubation using data loggers and chemical and hydromorphological parameters were assessed using national standards. Software was developed to automatically estimate decomposition rates based on an exponential model fitting AFDM data to degree-days. The project team trained all regional services in the use of the protocol. Onema agents deployed the assay on 85 streams distributed all over France over three years.

The project provided a large database for scientists to propose thresholds on 'good ecosystem functioning' and to model relationships between hydromorphology and leaf decomposition (Colas et al., 2017). The protocol was well received by stakeholders overall, although there was a frequently expressed preference for a more easily standardised substrate than leaf litter, to reduce time for the collection of leaves. Twelve working-days are needed to apply the protocol, which is comparable in terms of efforts to other WFD protocols. Nonetheless, while the protocol is used for assessing restoration projects and by stakeholders who are less constrained by regulatory requirements and frameworks of national biomonitoring networks (e.g., water agency, natural parks, and water basins managers across the country), its implementation as routine bioassessment assay in the national WFD biomonitoring scheme is not planned yet. The main reasons are the need for further standardization of the protocol, the already high cost of the national biomonitoring scheme, therefore reducing possibilities for including new indicators, and the absence of leaf litter as a parameter to be assessed in the WFD. Thus, considering the high costs of biomonitoring, the French government is reluctant to integrate new

indicators for ecosystem functioning into the national biomonitoring scheme if not specifically requested by the WFD.

21.2 Choosing the Appropriate Method

21.2.1 Litterbag: A Toolkit in Different Mesh Sizes

Different mesh sizes have been used to compare the contribution of differently sized organism groups to litter decomposition (Fig. 21.1). Large mesh sizes (often ranging between 5 and 10 mm mesh size) allow access to the litter by larger organisms (especially invertebrates that directly feed on the litter and/or litter associated biofilms). Here, the trade-off is often between a mesh size that allows enough invertebrate colonization, while retaining the leaf litter and most fragments. In some systems, larger crabs or crayfish might be important detritivores (Alp et al., 2016; Rincón & Covich, 2014), and thus larger mesh sizes (or even alternative approaches such as tying bundles of litter without enclosure in a mesh bag; Connolly & Pearson, 2013) might be needed. Small mesh sizes, often below 0.5 mm, block access by most detritivores, and thus focus on microbial contribution to decomposition, often resulting in slower decomposition rates than in large mesh. Mesh material varies. Often material such as garden trellis is used for coarse-mesh bags, whereas material with well-controlled mesh sizes (e.g., industrial filtration fabric) is used for fine-mesh bags. The role of mesh size in quantifying litter decomposition is crucial, as specific processes and organism groups contributing to litter decomposition can be studied individually (e.g., microbial processing; Bruder et al., 2014).

The effect of mesh size on decomposition rates can be illustrated by the cross-biome study conducted by Handa et al. (2014). They used three different mesh sizes, 0.25 mm, 1 mm, and 5 mm, in replicate field experiments in streams ranging from the subarctic to the tropics. The different mesh sizes allowed either (i) microorganisms alone, (ii) meiofauna (described as mesofauna by Handa et al., 2014) and microorganisms, or (iii) macrofauna, meiofauna, and microorganisms to access the enclosed leaf litter. They found that meiofauna contributed to 8.7% and macrofauna to 50.1% to carbon loss (a surrogate for leaf mass loss) in a temperate stream (Handa et al., 2014). The contribution of these size-groups to litter decomposition was substantially smaller in a subarctic stream, with 4.0% and 5.2% for the meiofauna and macrofauna, respectively. The differences in macrofauna-mediated decomposition rates between these two streams were interpreted as the consequence of differences in shredder densities in local communities. The temperate stream had a high density of *Gammarus pulex* (on average 273 individuals per m^2; Handa et al., 2014), a very efficient shredder that often reaches high densities in temperate streams (Woodward et al., 2012). In contrast, the subarctic stream supported lower densities of
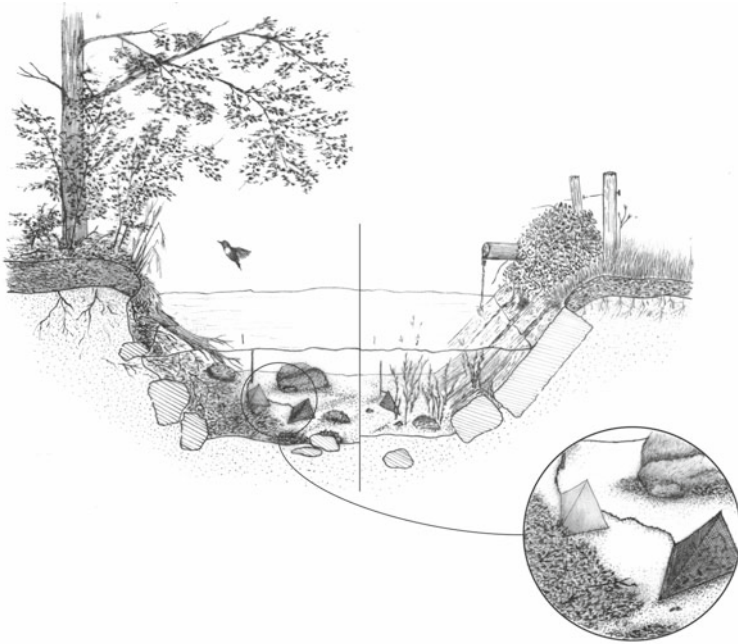
Fig. 21.1 Illustration of litter-bags of two different mesh sizes, coarse and fine, placed on the bottom of a stream. Litter bags are often attached to a rope or chain that keeps them close to the substrate, where benthic invertebrates can colonize the leaf litter inside the coarse-mesh bags. The use of litter bags as a tool in bioassessment has shown promise to detect effects of anthropogenic stressors (right side of the illustration) relative to reference conditions (left side of the illustration)

stonefly shredders (on average 44 individuals per m^2), which predominately feed by scraping biofilms growing on litter surfaces, and hence are associated with lower leaf processing rates than taxa such as *G. pulex* and many Trichoptera that chew on the litter directly (McKie et al., 2008).

21.2.2   *Leaf Litter Quality: From Recalcitrant to Labile and Nutrient Rich Leaves*

The choice of the litter material has a decisive influence on decomposition rates, and thus potentially on the capacity of a decomposition assay to detect human impacts. This choice is thus an important methodological consideration, especially when comparing decomposition rates over substantial geographic or environmental gradients along which the dominant riparian vegetation and other environmental parameters (e.g., thermal regimes) may change. Litter quality, defined by the combination of physical and chemical characteristics, affects the colonization rates, biomass, and

activity of microbial and invertebrate decomposers (Baldy et al., 1995; Ferreira et al., 2012; Frainer et al., 2015; Handa et al., 2014). Under similar environmental conditions, litter decomposition is faster for high-quality litter (i.e. high concentrations of nutrients, low concentrations of structural and secondary compounds) than for more recalcitrant litter. The most commonly considered parameters describing litter resource quality include %N, %Lignin, C:N, lignin:N, tannins, and litter toughness (Frainer et al., 2015; Lecerf & Chauvet, 2008; Ostrofsky, 1997; Schindler & Gessner, 2009). Other litter characteristics may be relevant for non-trophic effects on litter decomposition, and include those defining habitat structure in litter packs (Sanpera-Calbet et al., 2009) or the use for case-building by some groups of caddisflies (Moretti et al., 2009; Rincón & Martínez, 2006). Litter quality varies not only among litter species (Enriquez et al., 1993; Frainer et al., 2015; Ostrofsky, 1997), but also among litter from conspecific trees growing in different conditions (Graça & Poquet, 2014; Lecerf & Chauvet, 2008; Leroy et al., 2007).

For studies that aim at assessing the consequences of environmental conditions on decomposition rates, the heterogeneity in the litter material used should be minimized by standardizing the litter material across all sites sampled (Ferreira et al., 2019). Some extreme standardization procedures based on semi-natural substrates have also been applied (Box 21.2), which has the benefit of largely eliminating variability in decomposition rates due to uncontrolled (background) variation in litter quality, but at the cost of realism. Most commonly, researchers have used litter material from plant species that are present in the study area, but not necessarily collected locally, even when working across broad geographic scales (Handa et al., 2014; Irons et al., 1994; Woodward et al., 2012). This approach is justified by the very weak evidence for the so-called "home-field advantage" hypothesis, which postulates that local decomposer communities more effectively decompose litter from local species and sources, due to evolutionary adaptation. Empirical evidence for this effect is rare and might be limited to microbial adaptation to very recalcitrant litter (Yeung et al., 2019). Overall, litter quality seems to control the activity of decomposers more than litter source (Bruder et al., 2014; but see Kennedy & El-Sabaawi, 2017), although litter from contaminated sites should be avoided unless subject to specific research questions.

Differences in decomposition rates between litter species of contrasting quality has the additional advantage of yielding more information on the sensitivity of processes contributing to decomposition. For instance, high concentrations of tannins in leaf litter (e.g., in oak compared to alder leaves, Gessner & Chauvet, 1994) may reduce fungal activity due to complexation and inactivation of fungal exoenzymes (Gessner & Chauvet, 1994; McArthur et al., 1994) without affecting invertebrates directly. Differences in nutrient concentrations and specific nutrient ratios among litter species, as described by the ecological stoichiometry theory, may also be relevant for bioassessment, if, e.g., they favour or hinder feeding and growth of particular detritivore species (Abelho & Canhoto, 2020; Frainer et al., 2016; Halvorson et al., 2018).

21.2.3   Timing: Season and Duration

Litter decomposition rates may depend strongly on timing and duration of exposure. Broadly, the first days of litter decomposition in freshwaters are dominated by chemical leaching, followed by colonization by microbes. Microorganisms, fungi in particular, then initiate biological litter decomposition, thereby also increasing litter palatability for invertebrates. Although litter decomposition is often reported as a rate (thus standardized for time), the duration of exposure is relevant for the types of inferences that can be drawn. Decomposition of different litter constituents is not constant over the duration of the process, reflecting effects of litter quality (Grossman et al., 2020). Labile litter fractions (e.g., hemicellulose) are preferentially utilized before refractory fractions (e.g., lignin). The decomposer community also follows a successional pattern, with invertebrates often only gaining importance after microbial conditioning (Bruder et al., 2014; Jabiol, McKie et al., 2013). Decomposition rates differ substantially between these phases due to differences in lability of the resources but also biomass and activity of the decomposer groups. Studies have often accounted for leaching losses and calculated decomposition rates based on a measurement roughly half-way through the process (Handa et al., 2014) or based on several measurements at different stages (Bruder et al., 2014) to preclude unrepresentative estimates based on measurements during initial or terminal stages.

Seasonality and phenology are also important. Frainer et al. (2014) compared birch and alder litter decomposition rates between autumn and spring in streams of northern Sweden. They found that birch decomposed faster than alder in autumn, but in spring the difference depended on habitat characteristics, with birch decomposing faster in riffles, but alder decomposing faster in pools. These differences in decomposition rates were most likely due to differences in invertebrate community phenology, as detritivore composition differed between the two habitats. Other manifestations of phenology on litter decomposition rates may also ensue, e.g., between wet and dry seasons (Schlief & Mutz, 2011). Interannual differences in decomposition rates within the same litter species have also been reported, for instance due to differences in water current across years (Yeung et al., 2018). Overall, using litter material that is not synchronized in terms of quality and/or conditioning with background litter and decomposer community dynamics at the study site might yield unrealistic decomposition rates, e.g., due to preferential feeding of invertebrate decomposers on high-quality litter, or due to island effects, when a reduced amount of litter in the target habitat causes a disproportionately high concentration of invertebrates in the litter bags (Gjerløv & Richardson, 2004).

21.2.4   Habitat: From Lotic to Lentic Systems

Freshwaters cover a broad range of habitat types that are often characterized based on their water flow. Still water (*lentic)* habitats range from small water pools to

larger ponds, lakes, and reservoirs, but also include still-water habitats found in caves and bromeliad tanks, for example, and in so-called "pool habitats" in streams and rivers, i.e. areas of deep, very slow flowing water typical of slow meanders and other "protected" channel sections. Running water (*lotic*) habitats range from small springs to the largest rivers, and include inlets and outlets of lakes and reservoirs. Litter input is particularly important in systems where autochthonous production is low, thus litter decomposition may be a useful measure of bioassessment in several of those freshwater habitats. To date, most work on litter decomposition has been done in streams, but water tanks in bromeliads (Benavides-Gordillo et al., 2019; Migliorini et al., 2018), caves (Galas et al., 1996; Silva et al., 2013), marshes (Flury & Gessner, 2011), small reservoirs (Colas et al., 2016), and shallow lakes (Alp et al., 2016; Carvalho et al., 2015; Pope et al., 1999) have also been tested for the effects of distinct biotic and abiotic stressors on litter decomposition. For example, Frainer et al. (2014) compared decomposition rates between pools and riffles within streams, and found large differences in decomposition rates between the two habitats, which were explained by differences in the benthic invertebrate community composition and phenology (see Sect. 21.2.3).

21.2.5 *Selecting the Appropriate Reference Conditions*

A great challenge in the application of bioassessment indicators lies in the evaluation of observed differences between impacted and non-impacted ecosystems (Elias et al., 2016; Feio et al., 2014). This challenge is equally relevant for litter decomposition assays. In many studies, impacts on litter decomposition and ecosystem functional integrity in general are inferred if a difference in decomposition rates is detected between impacted and reference sites (e.g., McKie & Malmqvist, 2009). Reference sites are chosen as genuinely pristine sites if available, or else as sites representing regionally "least disturbed" conditions, or as sites on a disturbance gradient, where the least disturbed sites are used as reference (Woodward et al., 2012). The effectiveness of this approach is seen in numerous publications detecting altered decomposition rates associated with increased nutrient levels, invasive species, mining pollution, hydro-morphological alterations, and pesticides, among others (see references in Sect. 21.1.2). The approach has also been used to assess the extent to which ecological mitigation and restoration have altered ecosystem functioning (see references in Sect. 21.1.2).

Within this framework, both faster and slower decomposition rates relative to a reference condition are considered as undesirable, and may indicate impaired functional integrity. However, in some cases, the lack of difference in decomposition rates between reference and impacted sites is also informative. A healthy microbial community should be able to respond to increased nutrients by increasing activity and biomass and in turn decomposition rates. Failure to do so might indicate an impairment of the microbial community due to some additional stressors (e.g., pesticides, Gardeström et al., 2016) or other limiting factors (Bruder et al., 2016).

Finally, different stressors may cancel each other, as when nutrient enrichment leads to oxygen depletion that negatively impacts detritivores and counteracts bottom-up stimulation of microbial activity. Such hidden stressor effects and stressor interactions need to be accounted for by measurement of additional biotic and abiotic parameters (Bruder et al., 2019).

Pitfalls are potentially associated with the definition of reference conditions. The reference condition is assumed to be representative of the natural condition of ecosystems in the absence of anthropogenic disturbances. The ecological status of an ecosystem is then defined according to the discrepancy between measurements in the impacted and reference situation. The choice of reference sites thus strongly affects interpretations of decomposition rates in bioassessment (Chauvet et al., 2016; Feio et al., 2010). Defining reference conditions can be challenging if streams and rivers that have similar characteristics but are free of any disturbance do not exist anymore (e.g., Feld et al., 2011). To address this issue, the concept of 'analytical reference condition' was developed (Downs et al., 2011) involving modelling the non-disturbed state of the ecosystem (i.e. 'hindcasting modelling') (Kilgour & Stanfield, 2006; Launois et al., 2011). The analytical reference condition is obtained by lowering the value of the human disturbance variables included in predictive models, thus providing an estimation of the value of the response variable with no or reduced disturbance (Soranno et al., 2011). Development of models of 'analytical reference conditions' for thresholds in litter decomposition are conceivable, but require spatially extensive, highly standardized data sets, of which only a few examples currently exist (Woodward et al., 2012; Tiegs et al., 2019; and Sect. 21.3). It might also be possible to model reference conditions from meta-analyses of smaller projects, but the challenges arising from variation in e.g., differences in litter substrates, decomposition periods, and disturbance intensities are substantial (see Sect. 21.3).

21.2.6   Ratios Between Coarse- and Fine-Mesh Bags

Decomposition rates (k) are in most cases extracted from first-order exponential decay models (Olson, 1963). Several studies have used the ratio in decomposition rates between coarse and fine-mesh bags (i.e. k_c:k_f) as a metric that gauges the relative contribution of shredders and microorganisms to litter decomposition (Lecerf, 2017; Pascoal et al., 2003). Based on literature values, Gessner and Chauvet (2002) proposed categories of ratios of decomposition rates to estimate ecosystem alteration in streams (for streams with high potential shredder abundance): k_c:k_f ratios ranging between 1.2 and 1.5 indicate no clear evidence of environmental alteration, ratios below 1.2 or ranging from 1.5 to 2 indicate moderate disturbance, whereas ratios >2 indicate severe disturbances. However, very high values of pollution may affect even tolerant shredder species, which may translate to low k_c and consequently low k_c:k_f. Importantly, whereas moderate levels of nutrient pollution might enhance litter nutritional quality and facilitate a greater invertebrate contribution to decomposition

(i.e., increasing k_c relative to k_f), moderate levels of other disturbances, such as with hydromorphological degradation, riparian disturbances, and insecticides, may decrease invertebrate contribution to litter decomposition, thus decreasing k_c relative to k_f.

Applying Gessner and Chauvet (2002) categorization to the data from Handa et al. (2014) suggests severe alteration of the decomposition process in their temperate stream. A re-analysis of the data from Ferreira et al. (2015) suggests that a threshold ratio of 2 as an indication of severe alteration might be too low for many streams, including reference streams where shredder density and biomass may be naturally very high (see Sect. 21.3), especially when testing labile litter (Hieber & Gessner, 2002). Datasets with a broader gradient of environmental change than those used in Gessner and Chauvet (2002) suggest unimodal relationships between k_c:k_f ratio and nutrient pollution. For instance, a reanalysis of the data compiled by Ferreira et al. (2015) suggests a unimodal relationship with maximal ratios of k_c:k_f at 3.5 mg/L dissolved inorganic nitrogen (DIN) and 0.029 mg/L PO_4-P although with a high variability below the curve (see Sect. 21.3). Additionally, low k_c:k_f can also occur in stream naturally lacking efficient shredders, such as some tropical and insular streams (Bruder et al., 2014; Ferreira, Raposeiro et al., 2016).

Other approaches to the k_c:k_f ratio have been used. These include estimation of invertebrate-mediated decomposition rates ($k_{invertebrate}$) in isolation from decomposition mediated by microbes, and hence typically calculated based on the difference between percent litter mass remaining in coarse- and fine-mesh bags. A pan-European study, spanning stream sites along a very broad pollution gradient also suggests unimodal relationships of $k_{invertebrate}$ with nutrient concentrations (Woodward et al., 2012). These relationships had maximum values at approximately 3 mg/L DIN and 0.025 mg/L SRP. Unimodal relationships indicate that even tolerant shredder species become rare in highly polluted sites, e.g., due to exceedingly low levels of dissolved oxygen (Pascoal & Cássio, 2004), high concentration of ammonia (Lecerf et al., 2006), or other pollutants, resulting in low values of k_c:k_f and $k_{invertebrate}$.

21.3 Meta-Analysis Exemplifying Methodological Considerations In The Context Of Nutrient Enrichment: Reference Sites, Litter Quality and the Ratio Between Coarse and Fine-Mesh Bag Litter Decomposition Rates

21.3.1 Rationale

The effects of nutrient enrichment on litter decomposition in streams have been widely addressed, with empirical studies generally reporting a stimulation of litter decomposition with increases in dissolved nutrient concentration (Ferreira et al.,

2006; Gulis & Suberkropp, 2003; Rosemond et al., 2015). However, litter decomposition can be inhibited at high nutrient concentrations, which is generally attributed to toxicity associated with high concentrations of nitrite or ammonia, or to the concomitant change in other environmental factors (e.g., decrease in dissolved oxygen concentration or increase in fine sediment load and pesticide concentration) (Lecerf et al., 2006; Woodward et al., 2012). Even at lower to moderate nutrient concentrations, the effects of nutrient enrichment on litter decomposition have also been reported as non-significant when the stream is not nutrient limited or there are other limiting factors, such as low temperature, co-limitation by other nutrients, or low carbon quality of the litter (Baldy et al., 2007; Bruder et al., 2016; Chadwick & Huryn, 2003). Ferreira et al. (2015) summarized the effects of nutrient enrichment on litter decomposition in a meta-analysis of 99 studies that contributed 840 comparisons of litter decomposition rates in nutrient enriched and reference conditions and found an overall stimulation of litter decomposition by ~ 50% (95% CI: 41—58%). The effect was stronger when ambient nutrient concentration was lower and when the magnitude of the nutrient enrichment was higher (Ferreira et al., 2015). The magnitude of the effect also depended on litter identity (e.g., stronger stimulation of more recalcitrant oak than nitrogen-rich alder litter decomposition with nutrient enrichment), but not on climatic zone or type of decomposer community involved (microbes alone or microbes and invertebrates, assessed based on fine- or coarse-mesh bags, respectively) (Ferreira et al., 2015).

21.3.2   Methods

Here we revisit the database first analysed by Ferreira et al. (2015) to compare leaf litter decomposition rates in coarse- and fine-mesh bags and test the hypothesis that the magnitude of the effect of invertebrates on litter decomposition is (i) higher in nutrient enriched compared to reference streams as invertebrates take advantage of increased microbial biomass and activity in nutrient enriched conditions (Gulis et al., 2006), (ii) higher for more labile and nutrient-rich than for recalcitrant litter species as invertebrates play a greater role on the decomposition of the former (Hieber & Gessner, 2002), and (iii) higher for boreal than temperate regions as many shredders (e.g., from the orders Trichoptera and Plecoptera) have evolved as cold water species and microbial activity is limited at lower water temperature (Boyero, Pearson, Dudgeon et al., 2011; Irons et al., 1994; Taylor & Chauvet, 2014; Tiegs et al., 2019). The database was modified to contain only field correlative studies (not field manipulative studies) that used leaves (not woody substrates) and both coarse and fine-mesh bags (not studies that used only one mesh size, or no mesh bags). This resulted in 14 studies being retained. The matrix was then reorganized to contrast litter decomposition rates in coarse × fine-mesh bags, which resulted in 218 comparisons.

The effect of invertebrate activity on leaf litter decomposition rates (k, /d) was estimated per stream site as a response ratio (k_c:k_f; Hedges et al., 1999) and combined

using the random effects model of meta-analysis (with the restricted maximum likelihood method for estimation of between-study variance) in R (R Core Team, 2015), using the *metafor* package (Viechtbauer, 2010). The effects of invertebrate activity on the decomposition of alder (*A. glutinosa*) and oak (*Quercus robur*) litter incubated in reference and nutrient enriched streams in boreal and temperate regions were further compared by estimating effect sizes for each contrast.

21.3.3   Results and Discussion

Leaf litter decomposition was higher in coarse- than fine-mesh bags by a factor of 2.42 (95% CI: 2.12—2.66). Thirty-three k_c:kf values were detected missing to the right of the global k_c:k_f by the Duval and Tweedie's trim and fill method, which quantifies publication bias in meta-analyses (Duval & Tweedie, 2000). When these missing values are inputted into the analysis the new estimate is even higher (k_c:k_f: 2.82; 95% CI: 2.57—3.09), suggesting that the results based on the matrix are conservative. As hypothesized, the higher litter decomposition rates in coarse over fine-mesh bags was stronger for alder than for oak ($p = 0.0001$), and stronger in temperate than in boreal regions ($p < 0.001$) (Fig. 21.2).

Decomposition rates were higher in coarse- than fine-mesh bags across all sites, and this difference was observed both in nutrient enriched and reference streams ($p = 0.105$) (Fig. 21.2). This may, however, reflect our reliance on classifications of
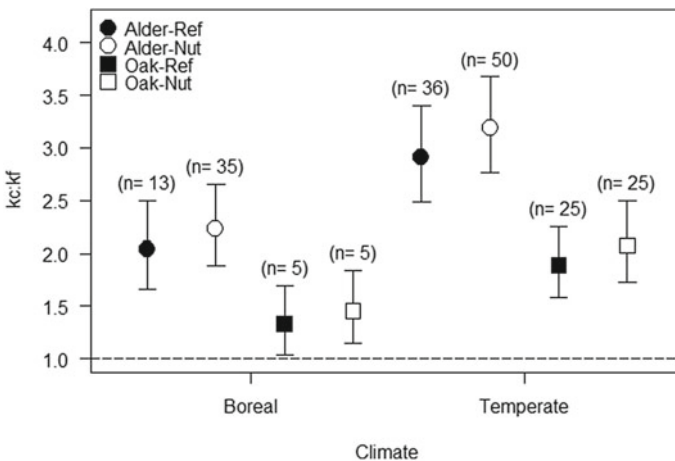

Fig. 21.2 Effects of invertebrate activity (k_c:k_f, ± 95% CI) on alder and oak leaf litter decomposition incubated in reference (Ref) and nutrient enriched (Nut) streams in boreal and temperate regions ($n = 194$). The dashed line (k_c:$k_f = 1$) indicates no significant effect of invertebrates on litter decomposition, while R > 1 indicates stimulation of litter decomposition in the presence of invertebrates. Effects of invertebrates' activities on litter decomposition are significant when the 95%CI does not include 1. Treatments significantly differ when their 95%CI do not overlap

reference and nutrient enriched streams provided by the authors of individual studies, since it is possible that reference streams in some regions have dissolved nutrient concentrations similar to those of nutrient enriched streams in other regions and vice versa (see previous section and Table S1 in Woodward et al., 2012).

To overcome this potential artifact, k_c:k_f was regressed against DIN and PO_4-P concentration (µg/L; ln-transformed) for the entire database, and separately for boreal and temperate regions using meta-regression. The ratio of litter decomposition in coarse- over fine-mesh bags increased with increasing DIN concentration, both in analyses of the entire database (slope = 0.116, $p < 0.0001$, $r^2 = 0.09$) and for boreal regions (slope = 0.131, $p = 0.005$, $r^2 = 0.07$), with a similar response also observed for temperate regions (slope = 0.09, $p = 0.058$, $r^2 = 0.02$) (Fig. 21.3). We found a clear positive relationship between k_c:k_f and PO_4-P concentration in boreal regions (slope = 0.371, $p < 0.0001$, $r^2 = 0.49$), but not in temperate regions (slope = 0.06, $p = 0.11$, $r^2 = 0.01$) or when considering the entire database (slope < 0.01, $p = 0.99$, $r^2 = 0$) (Fig. 21.3).

The hump-shaped distribution of k_c:k_f values along the nutrient gradient, particularly when values are computed for the entire dataset or only for the temperate region, is similar to that found by Woodward et al. (2012). Hence, although our meta-analysis indicates that invertebrate-mediated litter decomposition may respond positively to
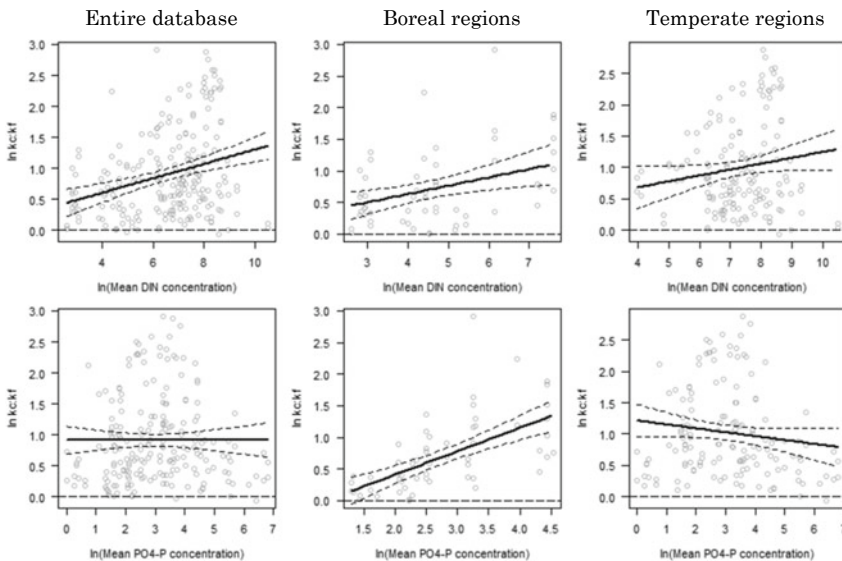

Fig. 21.3 Relationship between the effects of invertebrate activity on litter decomposition (ln k_c:k_f) and DIN and PO_4-P concentration in stream water (ln-transformed). The horizontal dashed lines (ln k_c:$k_f = 0$) indicate no significant effect of invertebrates on litter decomposition, while ln k_c:k_f > 0 indicates stimulation of litter decomposition in the presence of invertebrates. The relationships (meta-regression) are shown by the solid lines and associated 95% CI by the dashed lines

nutrient enrichment, it also shows large variability in the response of litter decomposition at medium levels of nutrient pollution. This may be due to the larger sample pool found around those medium values, which may reflect larger variability in overall background conditions, resulting in larger ecological variation as well. At the extreme levels of nutrient availability, where fewer sites are normally found, either nutrient limitation or excess nutrients seem to reduce the feeding capacity of invertebrates on leaf litter. The boreal region, which in comparison to the temperate region is often less nutrient polluted but also had fewer sites included in our analysis, did not show a hump-shaped distribution of k_c:k_f along the nutrient gradient. Instead, it had a clearer positive effect of nutrient enrichment on invertebrate-mediated decomposition rates.

Overall, the results from our meta-analysis indicate a potential positive effect of nutrient availability on litter decomposition up to a level where invertebrate-mediated decomposition starts slowing down, possibly due to deleterious effects arising from high levels of nutrient or other pollution. Our results also show a strong regional component (boreal vs temperate), with distinct responses of leaf litter and invertebrates to nutrient availability. Finally, our results illustrate the shortcomings in comparing reference *vs.* treatment streams, particularly when extrapolating the results across studies or regions that may differ in their criteria for classifying reference conditions or the availability thereof.

Box 21.2: Alternatives to the use of leaf litter

Bioassessment tools require standardization to ensure comparability of measurements among sites. Leaf litter may have shortcomings that reduce comparability of measurements, especially over larger spatio-temporal scales. These shortcomings might include low cross-scale replicability of the material being used, since even within the same litter species, spatial and interannual variability in litter C and nutrient concentration or other sources of intraspecific variation might undermine comparability of assays conducted in different years or at different locations. One approach for addressing this would be to undertake a detailed analysis of litter characteristics, to account for such variation in post-hoc analyses. Alternatively, highly standardized organic substrates have been proposed as substitutes for natural leaf litter, and include the following:

   Cotton fabrics have received most attention as alternative material to quantify organic matter decomposition and have recently been used for large-scale comparisons of decomposition rates in streams (Tiegs et al., 2019). Cotton fibres are mainly composed of cellulose, and lack significant amounts of nutrients, lignin, tannins, etc. (Colas et al., 2019), which are important litter characteristics that control decomposition rates. Moreover, the physical characteristics of cotton fibres largely preclude invertebrate feeding (van Gestel et al., 2003) and their consequences for growth of fungal decomposers are also unknown. Nonetheless, cotton fabrics have been shown sensitive to dissolved concentrations of nitrogen and phosphorus, as well as to pH and water temperature (Boulton & Quinn, 2000; Hildrew et al., 1984; Jenkins

et al., 2013) and to overall effects of agriculture and urbanization (Clapcott et al., 2012).

Wood veneers and sticks (e.g., commercially available ice cream sticks) have been used to quantify decomposition rates of plant material of low resource quality. Wood has lower nutrient but higher lignin concentration than leaves of most tree species (Arroita et al., 2012). Not surprisingly, the low resource quality is reflected in extremely low decomposition rates and low decomposer biomass compared to leaf litter (Arroita et al., 2012), and decomposition might be dominated by microbes (McTammany et al., 2008). Decomposition of wood sticks seems to respond to anthropogenic effects (Abril et al., 2015; Arroita et al., 2012; McTammany et al., 2008), and may show a hump-shaped relationship with gradients of anthropogenic impacts (Abril et al., 2015; McTammany et al., 2008), being reduced at elevated nutrients similar to leaf litter (McTammany et al., 2008). Wood veneers might provide a promising tool for studies that aim at estimating the process over longer time scales and/or in situations where physical abrasion by flow or suspended sediment is substantial.

Agar tablets, known as DECOTABs, are decomposed by microorganisms whose activity depends on the concentrations of cellulose, nutrients and minerals mixed into DECOTABs (Hunting et al., 2016; Kampfraath et al., 2012), but DECOTABs are also readily colonized and consumed by shredders and collector/gatherers (Kampfraath et al., 2012). DECOTABs can be purposely produced to reflect different organic matter resource quality (Hunting et al., 2016) and can include contaminants to the mix (Zhai et al., 2018).

Polymer sticks: decomposition in streams is governed by physical and biological processes (driven by microbial extracellular enzymes) and can be estimated by changes in the relative abundance of individual polymer ions estimated by mass spectrometry (Rivas et al., 2016).

Tea bags have been used due to the ease of implementation and high level of standardisation. Tea leaves contained within tea-bags can be considered an extreme example of leaf litter exposed in very small fine-mesh bags. Often tea bags of two contrasting types are used, and the difference in mass loss between the two may reflect differences in nutrient limitation in the system (Seelen et al., 2019). Currently, we are not aware of any data of microbial biomass and community composition measured from tea bags exposed in freshwaters. It remains to be seen if the particular litter quality often used as tea results in representative decomposition rates and decomposer activities.

21.4 Final Considerations

Litter decomposition has been tested and used as a measure of functional integrity in freshwater ecosystems for more than two decades in various ecological contexts. Most of these studies have shown negative effects of anthropogenic stressors on microbial and invertebrate-mediated decomposition rates. Nonetheless, questions regarding its suitability as a tool for stream ecosystem assessment remain. An important aspect is the lack of consensus on the consequences of altered (increased or decreased) decomposition rates for ecosystem functioning, for the integrity of local food webs, and for fluxes of energy into adjacent ecosystems.

Examples where a disturbance affects key decomposer groups and reduces decomposition rates seem straight-forward. Such cases are often interpreted as indicating impairments in ecosystem functioning, likely associated with reduced fluxes of carbon and nutrients from the litter into secondary production (Frainer et al., 2016; Halvorson et al., 2018; Kominoski et al., 2018; Rosemond et al., 2015). This can lead to accumulation of organic matter which might then either be broken down anaerobically (often associated with a greater production of CO_2 and CH_4) or else washed downstream and lost from the local food web (Lepori et al., 2005). The consequences of reduced decomposition rates on secondary production and entire food webs are still largely unknown, as compensatory mechanisms, including the use of alternative resources by consumers, could mask negative effects brought about by reduction in leaf litter availability, palatability, or nutritional quality. On the other hand, increased decomposition rates in response to stressors is not always a sign of good ecosystem integrity, and might therefore in itself be an indication of anthropogenically altered processes (McKie & Malmqvist, 2009). For example, production of fine particulate organic matter as litter fragments or of shredder fecal particles that exceeds the uptake capacity of local consumers might result in greater downstream export of carbon and nutrients, and longer, more leaky, nutrient spirals (Bundschuh & McKie, 2016).

The importance of these different scenarios depends on the goals of ecological assessment. If the goal is to assess whether ecosystem functioning has changed following a disturbance, the approach of comparing decomposition rates between impacted and reference sites, and before and after the disturbance when possible, will often be sufficient. Beyond this, development of a more specific assessment framework will require calibration of the litter decomposition assay. Such calibration requires not only accounting for how different disturbances typically affect decomposition rates (increase or decrease), but also understanding what response would be expected from a well-functioning biota compared to an impacted biota, and ultimately the consequences of changed functioning in interlinked ecosystems.

A more advanced framework for litter decomposition assays should also include guidelines on and harmonization of methodological choices, including of e.g., mesh sizes and litter species, and duration of the assay. For example, if addressing the effects of nutrient enrichment, low-nutrient litter with high quality carbon is better suited than high-nutrient litter where microbes are not nutrient limited. If physical fragmentation might be relevant at the site, the use of fine-mesh bags may

be advised; if invertebrates are an important organism group, coarse-mesh bags are required. Temporal dynamics of the decomposition process are key, since the impacts of different types of human disturbances might be best assessed at different points in the decomposition process. For example, an impact primarily on microbes might need to be assessed over a different duration than impacts on detritivores; however, this issue has not received much attention in research. Finally, regional variation is also important. Larger scale studies using litter decomposition (e.g., Boyero, Pearson, Gessner et al., 2011; Woodward et al., 2012) indicate high inter-regional variability of decomposition rates, even when identical litter material is used and hydromorphological conditions among sites are similar. This suggests that region-specific guidelines, for example for litter species or the season and length of the decomposition assay, might be required. Standardization by degree-days is one approach for increasing comparability among regions where the duration of the assay might need to vary.

The shortcomings described here are not exclusive to the use of litter decomposition as a bioassessment tool. Many countries and environmental agencies rely solely on structural measures for stream bioassessment, although they oftentimes still lack proper national or regional classification criteria for their target organisms. Also, structural measures are most commonly taken as snapshots in time, without accounting for temporal variability in community composition. These shortcomings do not prevent the use of structural measures in bioassessment and should also not prevent the use of litter decomposition assays when this measure suits the goals of bioassessment. National- or regional-level monitoring programs are likely to be the best suited for using litter decomposition in bioassessment due to the more practical evaluation and definition of reference conditions and easier standardization of the litter type (see Box 21.1). Helping to reduce costs, knowledge from these cases may even allow litter decomposition to be used as alternative to structural measures when suitable, instead of as a complementary tool.

There is increasing consensus that litter decomposition is enhanced in streams with low to moderate nutrient enrichment. Woodward et al. (2012) pointed out that this is in fact the range of nutrient enrichment levels for which structural measures (e.g., those based on EPT-taxa) may be less effective, highlighting the potential for an environmental assay based on litter decomposition to address a gap in the sensitivity of current ecological assessment approaches. At higher nutrient levels, decomposition is inhibited by toxic effects of ammonia or nitrite and other stressors, resulting in similar k_c:k_f ratios as those of reference conditions. Other stressors, e.g., habitat loss, vegetation change, hydro-morphological modifications, siltation, salinization, temperature alterations, parasites, species invasion, and other consequences of land use modification have not been assessed to the same detail as those of nutrient enrichment, but ongoing research is rapidly filling these knowledge gaps. Despite these challenges, the use of litter decomposition as a complementary tool, and in some cases, as substitute for structural measures, may provide much detail and mechanistic understanding of effects of anthropogenic stressors in freshwater ecosystems. Litter decomposition assays are fairly easy to implement and the abundant scientific literature and interest all highlight their value as an important measure of ecosystem functioning in ecosystem assessments.

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