Chapter 6
Plant Litter Decomposition in Terrestrial Ecosystems Compared to Streams

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Abstract The decomposition of dead organic matter is critical for carbon and nutrient cycles across ecosystems from the bottom of oceans to mountain tops. Despite similarities in the driving abiotic and biotic factors, and interconnected flows of organic matter between streams and their surrounding riparian zones, litter decomposition has often been studied separately in aquatic and terrestrial ecosystems, with some notable exceptions. This collaborative research across systems has identified some common patterns, which is necessary to move towards a broader litter decomposition theory and to develop a global decomposition model. Here we compare terrestrial litter decomposition with that occurring in aquatic systems, by providing an overview of the terrestrial literature and highlighting commonalities and differences with decomposition in streams. Specifically, we look at (i) the influence of climate, decomposer communities (microbes and invertebrates) and leaf litter quality (chemical and morphological), (ii) the consequences of changing diversity (in decomposer and litter communities), and (iii) the effects of global change (climate warming, nitrogen deposition and biotic invasions) on litter decomposition. Lastly, we identify recent approaches developed in terrestrial ecosystems that may help to increase our understanding of the abiotic and biotic drivers, diversity effects and global change effects on litter decomposition in aquatic ecosystems.

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6.1 Introduction

The decomposition of plant litter is one of the most important ecosystem processes in the biosphere, as it is critical for carbon and nutrient cycles across systems, including oceans, freshwater and terrestrial ecosystems. The litter produced by plants in terrestrial ecosystems may eventually reach inland surface waters such as streams and rivers, either by falling directly into the water bodies or by transport from the soil surface through runoff or wind. As a result, streams and their surrounding riparian zones are interconnected by flows of organic matter that represent a substantial contribution to the global carbon cycle (Battin et al., 2009). Common abiotic and biotic factors such as environmental conditions (climate, nutrient availability), litter quality (chemical and morphological traits) and local decomposer communities (microbes and detritivores) drive leaf litter decomposition in aquatic and terrestrial ecosystems. Consequently, current global anthropogenic changes such as biodiversity loss, warming, nitrogen enrichment and biotic invasions may impact litter decomposition in a broadly similar fashion. Unfortunately, only a handful of studies have addressed the decomposition of plant litter along the aquatic-terrestrial litter continuum. This has prevented the establishment of commonalities across ecosystems, which is important to formulate a theory on plant litter decomposition that is valid across systems.

Despite similarities in the driving abiotic and biotic factors, and interconnected flows of organic matter, litter decomposition has often been studied separately in aquatic and terrestrial ecosystems with some notable exceptions. For instance, the pioneering work of Merritt and Lawson (1992), Wagener et al. (1998), and Hutchens and Wallace (2002) encouraged communication between aquatic and terrestrial ecologists towards a more comprehensive understanding of litter decomposition. The European consortium "BioCycle", inspired by the review of Gessner et al. (2010) on diversity effects across systems, embraced this challenge and set up a collaborative research project with ecologists working in both aquatic and terrestrial ecosystems. They investigated litter decomposition in forest floors and nearby streams across five major biomes, from the tropics to the subarctic (Handa et al., 2014). Furthermore, follow-ups of this and other projects demonstrated that biotic and abiotic drivers play similar roles in aquatic and terrestrial decomposition across contrasting spatial (García-Palacios et al., 2016) and temporal (Yue et al., 2018) scales. All this and other recent research (Abelho & Descals, 2019) represent novel contributions towards the development of a global decomposition model, and although much work remains to be done, this chapter offers a first synthesis.

Here we review three major areas in litter decomposition research in terrestrial ecosystems. First, we address the main biotic and abiotic drivers of litter decomposition. Then, we assess how diversity in litter and decomposer communities affect litter decomposition rates. Finally, we review the response of litter decomposition to three global change drivers (climate warming, nitrogen enrichment and biotic invasions). Along each section, we provide insights on how previous findings in terrestrial ecosystems compare results from aquatic ecosystems. Our intention is not to review these topics in streams, which are covered in detail in other chapters of this book, nor to review terrestrial decomposition extensively, but to focus on the main commonalities and differences. We also identify recent approaches developed in terrestrial ecosystems that may help to improve our understanding of the abiotic and biotic drivers, diversity effects and global change effects on litter decomposition in aquatic ecosystems.

6.2 Main Biotic and Abiotic Drivers of Litter Decomposition in Terrestrial Ecosystems Compared to Streams

6.2.1 The Role of Litter Quality and Climatic Conditions

The triangular relationship among environmental parameters, the quality of decomposing litter, and decomposer organisms as the major control factors over decomposition is well established for terrestrial ecosystems (Berg & Laskowski, 2005; Swift et al., 1979; Fig. 6.1). It does not differ fundamentally compared to aquatic environments in general and to stream ecosystems in particular (Wagener et al., 1998). How terrestrial ecologists weighed the relative importance of these three groups of control factors, however, changed over the years and is still evolving. The classical view, that persisted over many decades, was that climatic variables control decomposition at large spatial scales among biomes and that within a specific climatic zone, litter quality was the most important driving factor (Berg et al., 1993; Meentemeyer, 1984; Fig. 6.1). This conceptual model was also referred to the Hierarchical Model of Decomposition (Lavelle et al., 1993). The spatial hierarchy of climate and litter quality control was then considered implicitly as a stratification of importance with climate being the primary control, and litter quality, the secondary control. This view was questioned in a broad synthesis of a large number of decomposition studies (Cornwell et al., 2008) showing that variability in decomposition due to differences in litter quality was at least twice as high as that observed across broad climatic gradients. In other words, the same litter type decomposing in highly contrasting climatic conditions across continental gradients may vary less in mass loss compared to contrasting litter types decomposing in the same location under identical climatic conditions. These observations required revisiting the hierarchical model of decomposition (Fig. 6.1).

The importance of litter quality effects compared to climate control also depends on how litter quality varies within and across climatic zones. Surprisingly, these differences are not that well documented presently, because studies that exhaustively report litter quality for all plant species of a given community along with their abundances, and thus their relative contribution to the overall litter pool, are rare. Community ecologists collecting good abundance data, commonly infer litter quality from live plant traits, which can at best be a proxy for the actual litter quality. Leaf

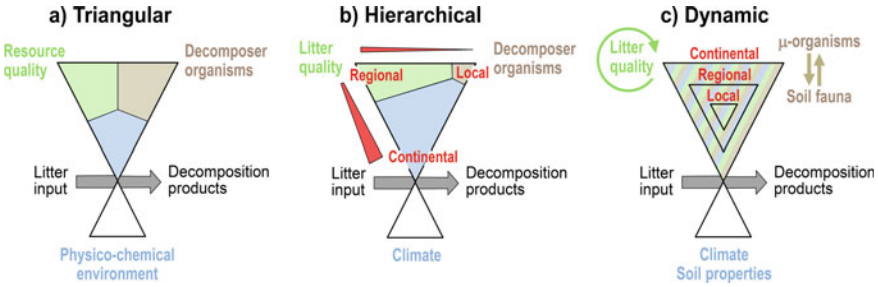

Fig. 6.1 The evolution of the conceptual model of litter decomposition over the past fifty years. The graphical representation is inspired by the original drawing by Swift et al. (1979) who used the regulation symbol (⧖) to superimpose the classical concept of the triangular control of the transformation of fresh litter input into decomposition products (**a**). The three colors referring to the three groups of factors have equal proportions because the Triangular Model did not initially propose an explicit hierarchy between the physico-chemical environment (edaphic and climatic factors), resource (litter) quality, and decomposer organisms. Over the following three decades (1980s through 2000s), studies at regional and continental scales reinforced the perception that climatic factors (essentially temperature and humidity) dominate litter quality control, and that decomposer organisms are merely reflecting climate and litter quality regulation without independent control, leading to the Hierarchical Model (**b**). The factor ranking incidentally implied a spatial stratification from local to continental scales with increasing dominance of climate control at increasing scales. The Hierarchical Model was revisited following studies that reported stronger litter quality than climate control (Cornwell et al., 2008 as a key study), which is not shown here. Instead, we propose the Dynamic Decomposition Model (**c**) emphasizing the dynamic switch among the three control factors during the decomposition process (e.g., García-Palacios et al., 2016) regardless of the spatial scale considered. In other words, all three factors can be dominant at some point during decomposition at the local as well as at the regional or continental scales. The Dynamic Model also emphasizes that litter quality changes strongly over time as do the specific traits that control decomposition. In addition, it appears inadequate to keep decomposer organisms in one single box. The distinction between at least microbial communities and soil fauna, which interact with each other, may significantly improve the understanding of decomposition and its controls

litter quality varies substantially from live foliage traits resulting from the important chemical and structural changes during leaf senescence, for example, when nutrients are resorbed (Aerts & Chapin, 2000) or when secondary metabolites undergo dynamic changes (Paaso et al., 2017). Another difficulty is that the standard set of live foliage traits commonly measured, and thus available for numerous plant species (e.g., carbon and nitrogen concentration, specific leaf area, leaf dry matter content), are not always relevant for litter decomposition. Less commonly measured litter quality traits such as condensed tannins, concentrations of Mg, Ca, Mn, or nonstructural carbohydrates often predict decomposition better, depending on the type of ecosystem and spatial scale considered (Guerrero-Ramírez et al., 2016; Hättenschwiler & Jørgensen, 2010; Makkonen et al., 2012). On the other hand, soil ecologists or biogeochemists collecting good litter quality data typically focus on a few contrasting litter types without referring to their relative abundance in the local plant community, or alternatively, on community-level litter fall without distinguishing individual species. This latter approach allows the evaluation of ecosystem-scale processes and provides a good assessment of community-level decomposition. On the contrary, it permits only a limited understanding of the driving mechanisms, especially if non-additive effects on decomposition of mixtures of litter from a range of different plant species occur, which are not predictable from community weighed-mean litter traits. We will come back to this important issue later when we discuss the role of biodiversity in litter decomposition.

Overall, litter quality control of decomposition is similar in aquatic compared to terrestrial ecosystems, especially in lower order forest streams with low autochthonous primary production and sharing the same litter inputs as neighboring terrestrial ecosystems. In one of the rare field experiments comparing terrestrial to aquatic decomposition across a broad latitudinal gradient, García-Palacios et al. (2016) identified the same set of litter traits explaining litter mass loss in forest streams and adjacent forest floors. There were some biome-specific differences, but overall, Mg and Ca concentrations were the most important litter traits associated to variation in litter decomposition across biomes in both types of ecosystems. Another, more local study in an alpine environment found that the relative role of environmental factors and litter quality were consistent in aquatic and terrestrial decomposition even at different decomposition stages (Yue et al., 2018). Collectively, these studies suggest that decomposition dynamics can be predicted from the same variables, irrespective of whether litter decomposes in a stream or on the soil surface. It is important to note, however, that these comparative studies used spatially coupled pairs of low-order streams and terrestrial sites sharing the same local environmental conditions. It is less likely that a similar coherence in the relative importance of control factors persists at larger spatial integration, with for example, varying local nitrogen deposition, heterogeneous bedrock, and thus, distinct nutrient limitation, or predominant oxygen control in higher order and more slowly-flowing streams.

Compared to biotic control factors, i.e., litter quality and decomposer organisms, environmental control during the decomposition process seems more straightforward to quantify. Technically this is certainly true, but practically, temperature, as well as humidity, which in contrast to most aquatic ecosystems (with the exception of intermittent streams) is an additional important environmental factor regulating decomposer activity in terrestrial ecosystems, may not have been characterized sufficiently well in the past. This is because microclimatic variability was mostly neglected, assuming that data from the nearest climate station can represent the climatic conditions for a particular study site reasonably well. This may not be the case as some studies suggest (Bradford et al., 2014, 2016; Joly et al., 2017). Indeed, temperature and humidity may vary strongly at very small spatial scales of only a few meters or even at the individual litterbag scale (Bradford et al., 2016), depending on microtopography, exposition, plant presence or animal activities, leading to variations that can be as large as among climate stations at regional scales (Bradford et al., 2014). The unaccounted variability in microclimate blurred the understanding of the relative importance of climate control in terrestrial decomposition and the spatial scale at which it operates. This is probably less problematic for aquatic decomposition. In these systems, water temperature and oxygen concentration, two important environmental factors controlling decomposer activity during aquatic decomposition, are standard measurements at the microsite scale because these data are not readily available from climate stations, and oxygen can vary strongly at small spatial scales. Therefore, the established relative contribution of environmental control over decomposition appears more robust in aquatic than terrestrial ecosystems.

6.2.2 The Role of Decomposer Organisms

The approaches to study temperature and litter quality control over decomposition are comparable in terrestrial and aquatic ecosystems, and share broadly the same methodological and conceptual development. However, terrestrial and stream ecologists considered the role of decomposer organisms quite differently in the past (Wagener et al., 1998). Detritivorous animals and their contribution to decomposition initially received much more attention amongst stream ecologists (Graça, 2001; Wagener et al., 1998) than amongst terrestrial ecologists, who commonly excluded detritivores by the use of litterbag mesh sizes smaller than the body sizes of most detritivores, especially soil macrofauna (e.g., earthworms, millipedes, isopods, etc.). In fact, terrestrial decomposition has been traditionally considered mostly as a microbial-driven process (Wagener et al., 1998). Microbial decomposers were seen mostly like an engine with its performance depending on available fuel (litter quality) and suitable conditions (temperature and humidity), but not on the characteristics of the ‘engine’ itself. Indeed microbial diversity and physiology was largely neglected, because the tools to measure it did not suffice, and because of the long held paradigm that the same microorganisms are everywhere. This classical view changed considerably over the last 15 years with the development of molecular tools and extensive biogeographical assessments of the occurrence and diversity of soil microbes. Recent studies showed that soil microbial communities differ substantially in time (over the course of litter decomposition; Herzog et al., 2019) and space (Baldrian, 2017). Spatial variation of a rather basic microbial parameter, such as biomass, can be an important determinant of decomposition even at regional scales alongside with climatic factors (Bradford et al., 2017), further questioning the dominant role of climate control in the classical Hierarchical Decomposition Model (Fig. 6.1). Additionally, soil fauna are increasingly considered in litter decomposition studies, showing that they are major players beyond microbial communities also in terrestrial decomposition (García-Palacios et al., 2013; Hättenschwiler & Gasser, 2005; Wall et al., 2008). Numerous studies manipulating the presence, abundance, or diversity of soil fauna (e.g., Coulis et al., 2015; Handa et al., 2014; Heemsbergen et al., 2004) clearly showed that they need to be taken into account as a control factor on their own.

Collectively, the recent findings of how microorganisms and soil fauna contribute to decomposition call for a revised role of decomposers in the control of terrestrial litter decomposition and its integration in conceptual models (Fig. 6.1). Accounting for decomposer organisms in decomposition studies is not an easy task, because of the tremendous number of different taxa, organized in highly complex food webs, which depend on plant-derived litter as the main source of energy and matter. The complexity of terrestrial decomposer communities in terms of diversity and the number of trophic and non-trophic links appears to be higher, compared to that of streams, but perhaps not of other aquatic ecosystems such as marine benthos. Because of this complexity, but also because the composition and diversity of decomposer communities can vary substantially among different plant communities, it is presently difficult to incorporate soil organisms in predictive mechanistic decomposition models.

6.2.3 Temporal Dynamics of Biotic and Abiotic Drivers of Litter Decomposition

The relative impact of environmental factors, litter quality, and decomposer communities may vary over time with proceeding decomposition. For example, García-Palacios et al. (2016) showed that control by litter microbial and nematode communities dominated during early decomposition stages, while soil moisture and legacy effects of initial litter quality increased in importance during later stages of decomposition. Such temporal shifts in control mechanisms are important to consider for a better understanding of how environmental conditions, litter quality, and decomposer communities affect decomposition interactively in a revised triangular relationship (Fig. 6.1), yet studies addressing such temporal dynamics explicitly are still rare. Changing control through time appear to be even less studied for stream ecosystems (but see Yue et al., 2018), perhaps also because litter decomposition proceeds generally quicker compared to terrestrial ecosystems. The different time scales at which freshly fallen leaf litter disappears in terrestrial and aquatic ecosystems is one of the major differences affecting the interplay of different control factors and predictive modeling of decomposition in terrestrial and aquatic systems. In certain biomes and for certain litter types it may take more than ten years in terrestrial ecosystems (Parton et al., 2007) compared to only a few weeks in stream ecosystems (Gessner et al., 2010) until the leaf litter visually disappears. These large differences actually hide the fact that smaller leaf particles resulting from detritivore activity ("fragmentation" or "comminution") are easily washed downstream with flowing water in streams, while they remain longer in place under terrestrial conditions. This means that part of the decomposition process is 'delocalized' in streams and decomposition in the strict sense of mineralization of organic matter may in the end not differ as much between terrestrial and aquatic ecosystems. This is difficult to measure correctly in either system because dissolved organic compounds and particulate organic matter move down the soil profile and down the streams.

6.3 Diversity and Litter Decomposition in Terrestrial Ecosystems Compared to Streams

6.3.1 Leaf Litter Diversity

The rapid rate of biodiversity loss worldwide has prompted research efforts in recent decades directed towards understanding if and how biodiversity influences ecosystem functioning (Eisenhauer et al., 2019; Hooper et al., 2012). Most often, diversity metrics (e.g., species richness, functional diversity) are manipulated as the independent variable, and ecosystem functions are measured to understand whether the whole is greater than the sum of its parts (net diversity effect) and if so, whether mechanisms could be identified driving such effects (Eisenhauer et al., 2019). While primary productivity is the ecosystem function having received the most attention to date and for which strong positive net diversity effects have been observed across ecosystems (Tilman et al., 2014), litter decomposition has been studied too, recognized as an ecosystem function of key importance for both terrestrial and aquatic ecosystems. Manipulative biodiversity experiments on litter decomposition have been treated in meta-analyses (Cardinale et al., 2011; Gartner & Cardon, 2004; Lecerf & Kominoski, 2010) and through large-scale collaborative experimental studies (García-Palacios et al., 2016; Handa et al., 2014). Evidence to date in terrestrial ecosystems suggests that overall net diversity effects are weak (if present at all), in comparison to plant productivity responses (Cardinale et al., 2011; Handa et al., 2014), but there is increasing evidence (Lefcheck et al., 2015; Wagg et al., 2014) suggesting that positive biodiversity effects increase when considering the ability of ecosystems to maintain multiple functions simultaneously (i.e., multifunctionality). The number of studies addressing the biodiversity-ecosystem multifunctionality relationship in streams is scarce, but novel evidence suggest an important positive linkage similar to that found in terrestrial ecosystems (López-Rojo et al., 2019).

Net diversity effects, when observed, can represent either selection or complementarity effects of species mixtures within assembled biodiversity experiments (Loreau & Hector, 2001). Selection effects are an extension of the mass ratio hypothesis (Grime, 1998), which suggests that the local dominance of a species with particular traits present within a community can be determinant to the ecosystem function under study. Complementarity effects, on the other hand, point to species differences or species interactions within a community that result in synergistic or antagonistic effects on the measured ecosystem function (Loreau & Hector, 2001). Such complementarity effects reflect niche partitioning of species favouring specialized resource use or interactions such as facilitation or inhibition that translate into diversity effects. In their collaborative study across a latitudinal gradient, Handa et al. (2014) showed that complementarity rather than selection mechanisms drove diversity effects in both terrestrial and aquatic litter mixtures. For instance, litter mixtures combining a N-rich litter and a non-recalcitrant rapidly decomposing litter led to a positive net diversity effect in this cross-system study, likely due to translocation of nitrogen through fungal hyphae from N-rich to N-poor litter thus facilitating microbial decomposition. In a recent aquatic microcosm study with a riparian forest litter mixture, López-Rojo et al. (2019) also found that complementarity effects were more prevalent in explaining observed net diversity effects, but selection effects also played a role.

Quantifying selection and complementarity effects in litter mixtures requires the measurement of litter mass loss at the species level, which is time-consuming and potentially challenging if the stage of litter decay hinders species identification. The use of community-level metrics and plant traits can partially solve this issue by establishing indirect associations with selection and complementarity effects. In this line, selection effects have been associated with the community-weighted mean of functional traits that drive the decomposition process, while complementarity effects are typically associated with the functional dissimilarity of these traits within a community (García-Palacios et al., 2017). With litter quality as one of the key drivers of decomposition, it is not surprising that idiosyncratic responses are frequently observed, leading to the conclusion 'community composition matters'. However, most litter decomposition studies addressing the role of diversity in both terrestrial and aquatic ecosystems have been performed without explicitly considering underlying mechanisms by separating individual species from litter mixtures. While these studies comparing monocultures *vs.* increasing levels of litter diversity are useful for assessing if the whole is (or is not) greater than the sum of its parts, these assessments have limited our understanding of selection and complementarity effects in both soils and streams.

6.3.2 Multi-trophic Diversity

Evidently, when considering decomposition dynamics, diversity exists not only at the level of the plant communities that provide the majority of organic matter input, but also at the level of the decomposers themselves (microbial and faunal communities). Decomposers interact in complex networks on the basis of decomposing litter substrates and connected through multiple trophic and non-trophic interactions (Wagg et al., 2019). While there is compelling evidence that multi-trophic biodiversity in general (Lefcheck et al., 2015), and soil biodiversity in particular (Wagg et al., 2014), enhances multifunctionality across ecosystems, much remains to be discovered about how varying decomposer diversity influences litter decomposition as an ecosystem function.

Contrary to the community assembly approach when studying the effect of the diversity of plants on litter decomposition, addressing the effects of varying decomposer diversity in both terrestrial and aquatic systems has, to date, more frequently relied on exclusion experiments (Handa et al., 2014). This constraint has been particularly true for manipulating microbial diversity given the many inactive or dormant microbes sampled in the environment and a high percentage of unculturable microbes (Baldrian, 2017; Jansson & Hofmockel, 2018). In a recent terrestrial grassland study, Wagg et al. (2019) sieved soils through varying mesh sizes to simplify microbial network complexity and demonstrated that reduced fungal-bacterial diversity slowed down litter decomposition. An alternate approach to simplify microbial diversity is through the dilution-to-extinction approach where, for example, Maron et al. (2018) added soil inoculum from grassland microbial communities to sterile soil in microcosms and demonstrated that decreasing diversity altered litter C cycling by favouring the decomposition of non-recalcitrant carbon over recalcitrant carbon. While the functional redundancy principle likely ensures functional stability below a particular threshold of species loss (Miki et al., 2014), a tremendous diversity of microbes contributes to litter decomposition and interact in a cross-kingdom functional succession of communities (Herzog et al., 2019).

When considering decomposer community complexity that includes meso- (up to 1-mm body size) and macrofauna (up to 5-mm body size) in addition to microbes, community exclusion litter microcosm experiments have been useful to demonstrate that increasing decomposer community complexity accelerates litter carbon and nitrogen cycling in both forests and freshwater stream ecosystems (Handa et al., 2014). However, other studies have used community assembly approaches to manipulate macrodetritivores in microcosms to assess litter decomposition. For example, in a study combining dissimilar soil detrivores such as a millipede and snail, De Oliveira et al. (2010) demonstrated both synergistic and antagonistic interactions depending on the stage of litter decomposition of Mediterranean forest litter. Other terrestrial studies have hinted at niche partitioning mechanisms reflected through functional dissimilarity (Coulis et al., 2015; Fontana et al., 2019; Heemsbergen et al., 2004) or strong litter preferences by detritivores that may account for diversity effects (Rouifed et al., 2010; Vos et al., 2011). Similarly, the literature addressing the effects of detritivores on litter decomposition in streams using exclusion procedures is also prominent (Gessner et al., 2010). More detailed analysis using community-level properties are less frequent, but Frainer et al. (2014) found that the functional diversity of detritivore communities had contrasting effects on litter decomposition in boreal streams across seasons and habitats.

In conclusion, the effects of leaf litter diversity on litter decomposition in terrestrial ecosystems and streams are reasonably well identified, but we still have a limited understanding of the biological mechanisms accounting for how plant diversity influences organic matter decomposition in both systems. With regard to the diversity of decomposer communities, emerging molecular tools and trait-based approaches are helping us move beyond exclusion experiments towards a more functional understanding of decomposer diversity in soil and stream detrital food webs.

6.4 Global Change and Litter Decomposition in Terrestrial Ecosystems Compared to Streams

The effects of global anthropogenic change on ecosystem processes has been a hot topic in the biogeochemical and ecological literature over the past 20 years, and litter decomposition is not an exception. From the multiple drivers of global change promoting planetary-scale shifts in the Earth system, here we focus on climate warming, nitrogen enrichment and biotic invasions. The effects of these three global change drivers on terrestrial litter decomposition have been synthesized in systematic reviews and quantitative meta-analyses, which are necessary to assess general patterns across different ecosystem types. Furthermore, warming, nitrogen enrichment and biotic invasions also influence the biotic and abiotic drivers of litter decomposition in streams, allowing us to look for commonalities in aquatic *vs.* terrestrial systems.

The interpretation of global change effects on terrestrial litter decomposition is not straightforward, as these effects are the result of both direct and indirect mechanisms. Specifically, climate warming and nitrogen enrichment influence litter decomposition though direct temperature effects on soil biological activity and direct nitrogen effects on soil chemistry, respectively (Wardle, 2004). However, warming, nitrogen enrichment and biotic invasions also play an indirect role mediated by shifts in plant and soil communities (Manning et al., 2006; Castro-Díez et al., 2014). Importantly, the magnitude of such indirect effects may be larger than that of direct effects mediated by changes in abiotic factors, strongly modifying the net effects of global change on litter decomposition. In short, both direct and indirect mechanisms must be considered.

6.4.1 Climate Warming

The fate of the soil carbon pool is a pressing issue under ongoing climate warming, as even subtle losses may represent a substantial contribution to the buildup of the atmospheric CO_2 pool, promoting a positive land carbon-climate feedback. Litter decomposition is a pathway of soil carbon loss to the atmosphere, and accordingly the number of studies addressing warming effects on litter decomposition increased in recent years. Different methods were used to experimentally simulate climate warming in terrestrial ecosystems, with open-top chambers, infrared lamps and soil heating cables among the most common (Fig. 6.2). Two recent global meta-analyses showed a slight positive effect of experimental warming on terrestrial litter decomposition (Lu et al., 2013; Yue et al., 2015). Across 34 different articles, Lu et al. (2013) reported a 6.8% increase, and from a slightly lower sample of 22 articles, Yue et al. (2015) reported a 4.4% increase. In streams, a recent quantitative literature review found a significant positive effect of warming on litter decomposition (Amani et al., 2019). However, as it is usually the case across different field studies,

Fig. 6.2 Different methods to experimentally simulate climate warming in terrestrial ecosystems. **a** Open-top chambers passively increasing temperature using hexagonal methacrylate sheets in Bogong High Plains, Australia (*source* https://jscamacresearch.wordpress.com/, photo credit Henrik Wahren). **b** Soil heating cables in Hubbard Brook Long-Term Ecological Research, USA (*source* https://hubbardbrook.org, photo credit: Rebecca Sanders-DeMott). **c** Infrared heaters in El Yunque National Forest, Puerto Rico (*source* https://blogs.agu.org/, photo credit: Stephanie Roe)

the overall positive warming effects on litter decomposition were strongly influenced by methodological differences among studies. For instance, the magnitude and direction of warming effects depended on the ecosystem type, study length, temperature increase, and method used to simulate elevated temperatures. When only direct effects of elevated temperatures on litter decomposition are considered, litter mass loss is typically higher in warming than in control plots, indicating higher decomposer activity under more favorable microsite conditions.

Addressing the combined direct and indirect warming effects on litter decomposition is far more complicated, and only a handful of studies have explicitly done so. For instance, Cornelissen et al. (2007) collected litter from 33 experimental warming studies in cold ecosystems and studied litter decomposition in two thermally contrasted sites in Sweden. This elegant experimental design allowed the authors to disentangle direct climate effects from indirect litter quality changes resulting from warming-induced changes in plant community composition. In fact, the site of litter incubation explained 50% of variation in litter mass loss, which was 42% higher in the warmer than colder site. Interestingly, warming promoted a shift in plant community composition from grass- and sedge-dominated communities to shrub-dominated communities. This plant community shift explained 30% of variation in litter mass loss. Increasing shrub dominance with warming resulted in an average decrease of litter mass loss of 40%. This result suggests that although climate warming seems to alleviate the temperature limitation over litter decomposition in cold ecosystems, the likely shrub expansion with warming in these high-latitude ecosystems may counteract such direct warming effects. In addition to changes in plant community composition, climate warming may also change decomposer communities, representing an additional indirect effect on litter decomposition (David & Handa, 2010). In fact, Boyero et al. (2011) found a stimulation of microbial decomposition but inhibition of detritivore-mediated decomposition with temperature in streams across a latitudinal gradient in six continents.

6.4.2 Nitrogen Enrichment

Soil nitrogen (N) enrichment through atmospheric N deposition is one of the major global change drivers affecting ecosystem functioning (Galloway et al., 2008). The effects of N enrichment are easier to simulate experimentally than those of warming, as simple inorganic N fertilization can efficiently mimic current N deposition rates. Consequently, a plethora of experimental field studies has addressed the effects of N enrichment on terrestrial litter decomposition. For instance, Knorr et al. (2005) and Zhang et al. (2018) synthesized the effects of N enrichment on litter decomposition using data from 24 and 55 articles, respectively. On average N enrichment had no significant effect on litter decomposition. Importantly, the relationship between the effect size of N enrichment and N application rate was negative, with stimulated litter decomposition at low levels of N application but suppressed litter decomposition at high levels. The same increasingly negative effects with higher N enrichment from atmospheric deposition and agricultural run-off has been demonstrated for streams with meta-analyses (Ferreira et al., 2015) and large-spatial scale observational studies (Woodward et al., 2012). High rates of N input to streams may have toxic effects for invertebrates counteracting the stimulating effect on microbial decomposition.

Nitrogen enrichment can influence litter decomposition rates via direct changes in fundamental controls of litter C mineralization and N release/immobilization patterns such as soil nutrient stoichiometry and pH, which commonly decreases with N enrichment. However, N enrichment also affects litter decomposition indirectly by altering the diversity and composition of plant and soil communities. The response of plant communities to N enrichment usually includes decreased species richness and compositional shifts towards resource acquisitive species (Isbell et al., 2013), with cascading effects on litter quality. Soil microbial communities can also mediate N enrichment effects on litter decomposition via reduced soil microbial biomass (Treseder, 2008) and oxidase enzymatic activities involved in the degradation of recalcitrant C compounds (Jian et al., 2016). Nevertheless, the relative contribution of such indirect effects on net decomposition rates vary across studies, with plant compositional shifts counteracting the direct effects of N enrichment on soil chemistry (Pichon et al., 2019) or playing a minor role compared with direct effects (Manning et al., 2006).

6.4.3 Biotic Invasions

The effects of biotic invasions on terrestrial litter decomposition rely mostly on indirect impacts via changes in the plant and soil community, as this global change driver does not commonly directly modify the environmental conditions of the invaded site. Here we focus on the indirect effects via the plant community, as studies addressing how non-native soil organisms alter litter decomposition rates are less numerous, which limits our ability to elaborate general conclusions.

Several reviews and meta-analysis have synthesized the effects of non-native plant invasions on litter decomposition, with contrasting results. The vote-counting approach of Ehrenfeld (2003) and quantitative reviews of Liao et al. (2008) and Castro-Díez et al. (2014) showed higher decomposition of non-native than native leaf litter. Specifically, Liao et al. (2008) found a 117% increase in non-native litter decomposition rates, which correlated well with the higher litter N and specific leaf area in non-native compared to native litter and green leaves. These results have contributed to the generalization that invasive plants decompose more quickly, leading to more rapid cycling of nutrients and C release in invaded ecosystems. However, neither the meta-analysis of Vilà et al. (2011) nor the multi-species study (78 deciduous forest species) of Jo et al. (2016) found significant differences in litter decomposition rates between non-native and native species. As pointed out by Zukswert and Prescott (2016), the general perception that non-native litter decomposes faster may arise from a bias in current studies focusing primarily on plant species that are known to have a major influence on ecosystem functioning, such as N fixing species like *Myrica faya* (Liao et al., 2008).

Most litter decomposition studies addressing the impacts of biotic invasions in streams have focused on exotic trees. Recently, Ferreira et al. (2016) synthesized the available literature addressing the effects of tree plantations and tree invasions in natural ecosystems. They found that litter decomposition was 26% lower in streams flowing through *Eucalyptus globulus* plantations than in streams flowing through native forests. However, the effects were not significant when non-native tree species other than *Eucalyptus globulus* were included in the comparison.

In contrast with the two previous sections on decomposition drivers and diversity effects, we are not aware of any study jointly addressing the influence of global change in terrestrial and aquatic ecosystems. However, as warming, N enrichment and biotic invasions also influence the biotic and abiotic drivers of litter decomposition in streams, we may be able to infer consistent patterns across ecosystems by comparing the results found in meta-analyses and large-spatial scale studies. Although climate warming significantly increases litter decomposition in soils and streams, warming-induced effects can change substantially after accounting for the indirect changes via the plant and decomposer communities. The effects of N enrichment on litter decomposition seem to vary as a function of the amount of N addition in both soil and stream studies. This pattern may be the result of indirect effects via changes in plant and decomposer communities, although the number of studies is still quite limited for robust conclusions. With regard to biotic invasions, the effects of exotic plants on soil and stream litter decomposition seem to be species-specific.

6.5 Suggested Approaches for Future Studies

6.5.1 Future Studies Looking at Biotic and Abiotic Drivers

It appears that the role of climate was overestimated in the past, because climatic variables were not measured at a fine enough spatial resolution, and variables related to decomposer communities were largely ignored, especially in terrestrial studies (Bradford et al., 2016). Future studies would need to measure environmental factors (climate variables, but also soil or water characteristics) at appropriate spatial and temporal scales and should include a sufficiently large array of relevant litter quality traits and a reasonably detailed characterization of decomposer communities for a better understanding of how the different factors interact in controlling decomposition.

The understanding of the fate of decomposition products is another area of research that has received insufficient attention to date. The vast majority of decomposition studies have used and still use the litterbag approach or variants of it and assess decomposition as litter mass loss from these bags. Much of this lost litter material may actually not decompose (in the sense of mineralization) during the study, but transported out of the bags in the form of particulate or dissolved organic matter. Ignoring the fate of this organic matter is likely leading to erroneous assumptions in how carbon and nutrients are cycled through the ecosystem. It will be important to address the fate of “lost litter mass” more explicitly in future studies. This may be even more critical for stream ecosystems where flowing water may transport a large amount of particulate and dissolved litter material over relatively large distances. It is methodologically challenging even with the powerful approach of using isotopically labelled litter material to follow the decomposition products, in particular in stream ecosystems where they may not easily be recovered.

We believe that from the three groups of control factors, decomposer organisms require stronger attention in future work determining how the different drivers interactively affect decomposition, in particular in terrestrial ecosystems. It is now clear that decomposers do not simply "translate" the effects of litter quality and environmental conditions, but are an important driver on their own (Bradford et al., 2017; García-Palacios et al., 2016). Interactions between microbial communities and detritivores are particularly poorly understood. The recent finding that the transformation of fresh leaf litter material into fecal pellets by an abundant millipede species can change carbon and nitrogen release during further microbial decomposition as well as the relevant traits predicting decomposition (Joly et al., 2018) suggests that such interactions can have strong impacts on decomposition. However, data are extremely limiting, especially under field conditions.

The large majority of decomposition studies focused on leaf litter, neglecting other plant tissues such as wood and roots that quantitatively contribute at least as much to the overall litter produced by plants. Root decomposition studies are strikingly few in the literature compared to leaf litter studies, although there are recent advances in terrestrial ecosystems (Guerrero-Ramírez et al., 2016; Herzog et al., 2019; Jo et al., 2016; Sun et al., 2018). There are some obvious reasons for this because roots are more difficult to access and to collect, roots from different plant species are often difficult to distinguish, and roots do not seem to readily fall into streams. A recent study following leaf litter and first-order roots (these are the few millimeter long root tips, which turnover two to three times per year) from several woody species over six years reported substantially slower decomposition of first-order roots that was controlled by completely different traits compared to leaf litter (Sun et al., 2018). Thus, at the scale of the ecosystem, we may currently understand only part of the decomposition process reasonably well, calling for more root studies in the future. Even in aquatic systems, especially in low-order stream, root decomposition may be considerable as roots from riparian vegetation can grow into the water body, but appear to have received very little attention.

6.5.2 Future Studies Looking at Diversity Effects

One major challenge to improve our understanding of how both resource and consumer diversity influences litter decomposition dynamics will be to integrate our multi-trophic understanding of food web interactions into models so as to better predict process rates across ecosystems. While some synthesis efforts have suggested that top down effects of consumer diversity are stronger than bottom up effects of resource detrital diversity (Srivastava et al., 2009), others have pointed towards strong bottom up drivers, particularly nutrient limitation and stiochiometric constraints in freshwater food webs (Frainer et al., 2016). Given the challenges of resolving food webs and the desire to develop tools that allow us to extrapolate network structure towards predicting litter decomposition, one potential approach is trait matching of consumer feeding traits to resource palatability traits (Brousseau et al., 2018). Recent work assessing trait covariation of detrivores and their resources has pointed to over one third spatial covariation of consumer and resource traits for collembolans and leaf litter (Raymond-Léonard et al., 2019), as well as for litter-dwelling detritivorous and predatory macroarthropods with their respective resources (Brousseau et al., 2019). These results suggest certain predictive bottom-up structuring forces. Linking trait-matching models that can successfully predict litter-feeding interactions (Brousseau et al., 2018) with estimates of process rates like decomposition represents a promising future research direction. Additionally, refining our understanding of microbial networks and the function of microbes will be a high priority with metagenomic tools that indicate the functional potential of communities all the way to metaphenomics, which combine this information with that of available resources (Jansson & Hofmockel, 2018). Soil viruses have been largely understudied but as demonstrated through microbial loops in aquatic systems can dramatically change ecosystem process rates (Kuzyakov & Mason-Jones, 2018). Future studies will clearly benefit from embracing all this complexity and seeking predictive tools that integrate our understanding of these multi-trophic perspectives to predict litter decomposition in the context of a changing planet.

6.5.3 Future Studies Looking at Global Change Effects

In the global change section of this chapter, we highlighted the importance of disentangling the direct effects of climate warming and nitrogen enrichment on litter decomposition from the indirect effects via changes in plant community composition. Here we propose two methods inspired in previous litter decomposition studies performed in terrestrial ecosystems, one experimental and one analytical, which may also help to tease apart these two important mechanisms in litter decomposition studies performed in streams.

The first method is a mechanistic factorial experiment that has been used to test the effects of warming (Allison et al., 2013; Cornelissen et al., 2007) and nitrogen enrichment (Manning et al., 2006; Pichon et al., 2019) on terrestrial litter decomposition (Fig. 6.3). The experimental design consists in the following factors: 'plot environment' (direct global change effect) and 'litter origin' (indirect effect via changes in plant community). First, a global change field experiment with two levels (warming or nitrogen enrichment *vs.* control) is conducted for a period long enough to allow for plant community compositional shifts (i.e., 3–5 years in grasslands). This design is replicated in a few experimental blocks. Then, naturally-senesced leaf litter is collected from the global change and control plots, and used to establish a litter reciprocal transplant. A similar approach may be followed in aquatic ecosystems, using either experimental treatments in a single stream or multiple streams along

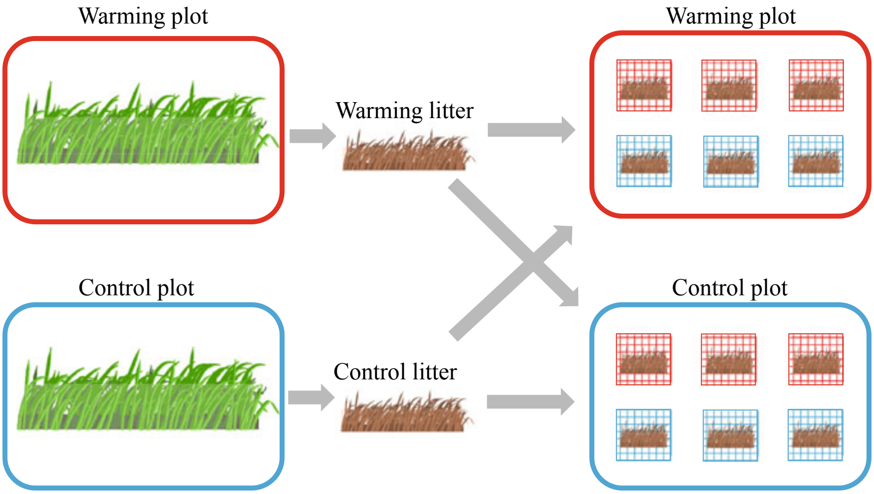

Fig. 6.3 Experimental design to disentangle the direct effects of global change (climate warming) on litter decomposition from those indirectly mediated by changes in plant community composition. First, leaf litter is harvest from warming and control plots. Then, a reciprocal transplant litterbag study is conducted to test the effects of 'plot environment' (warming *vs.* control plot) and 'litter origin' (warming *vs.* control litter). Several litterbags may be included in each block if sequential sampling is required (in this example we envisioned three harvests)

contrasting environmental conditions. Additionally, Allison et al. (2013) considered a third treatment ('microbe origin') assessing indirect effect via changes in the decomposer community. To do that, the authors gamma-sterilized all litterbags and litter material, and reinoculated them with a microbial inoculum extracted from the global change and control litter treatments. However, the validity of this approach is more uncertain due to litter microbial colonization during incubation in the field.

The second method is an analytical procedure to disentangle the direct and indirect effects of global change drivers in large-spatial scale observations. This approach assumes that the environmental gradient selected mainly encapsulates the variation in the variable of interest (i.e., temperature and nitrogen enrichment). Ideally, such environmental information should be recorded at each site in sufficient detail, knowing that environmental factors should be evaluated at an appropriate spatial resolution (Bradford et al., 2014). Then, naturally-senesced leaf litter of the dominant plant species is collected at each site, and used to fill site-specific litterbags containing litter species in the same proportions found in the native litter layer. Leaf litter traits such as nutrient concentration, morphology or stoichiometry may be used to quantify variation in plant community composition across sites. At each site, soil samples are also collected to measure physicochemical parameters as well as the abundance and diversity of microbial and animal decomposers. Finally, all the abiotic and biotic drivers of litter decomposition are linked in a conceptual path diagram similar to that shown in Fig. 6.4a. This conceptual model is then analyzed using path analyses and tested against field data. García-Palacios et al. (2017) followed a similar approach

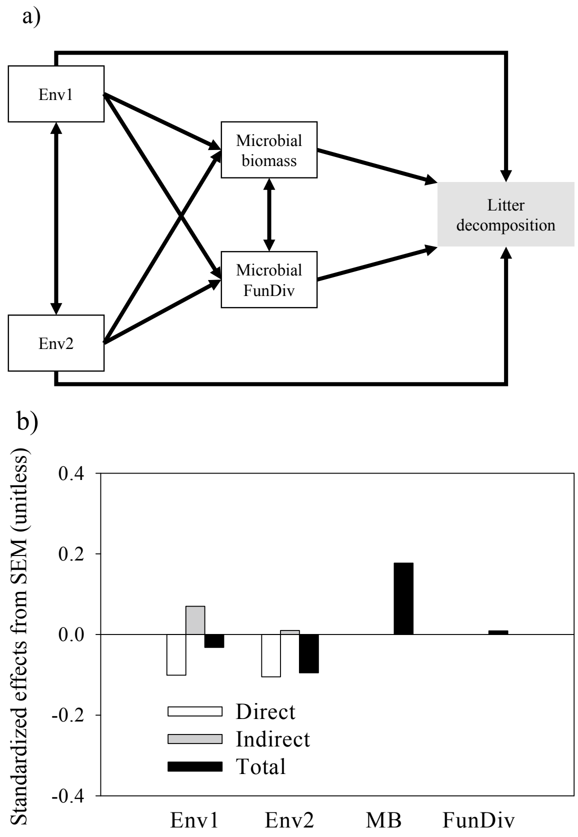

Fig. 6.4 A priori conceptual path diagram (**a**) depicting pathways by which environmental conditions (Env1 and Env2 are the two first axes of a PCA with climatic variables and soil physicochemistry), soil microbial biomass (MB) and soil microbial functional diversity (FunDiv; assessed with community-level physiological profiles) influence litter decomposition (% of litter C loss). Standardized direct, indirect and total effects (**b**) derived from the structural equation model. Redrawn from Journal of Ecology (García-Palacios et al., 2017)

when addressing the direct and indirect (mediated by the soil microbial community) effects of climate and soil parameters on litter decomposition across 10 sites located along a regional climatic gradient in southern France. Litterbags were harvested after a year of field incubation, and the total, direct and indirect effects of environment (climate and soil conditions) on litter carbon loss were calculated. The total effects of Env1 (accounting for MAP and MAT differences among sites) were small, as the indirect effects via changes in the soil microbial community partially offset the direct effects (Fig. 6.4b). This result supports the pattern found in Cornelissen et al. (2007) when assessing warming-induced effects on litter decomposition via shrub expansion in cold ecosystems. Studies at large spatial scales conducted in streams (e.g., Boyero et al., 2011) are also well-suited to perform a similar analysis.

6.6 Summary

In general, litter decomposition is faster in aquatic (stream) than in terrestrial ecosystems, as a consequence of the higher loss of water-soluble compounds due to leaching and flushing effects (Berg & McClaugherty, 2014), as well as due to abrasion by sediment transport and continuous organic matter and nutrient supplies from upstream sources (Graça et al., 2015). Despite these importance differences, it seems that the abiotic and biotic drivers, the diversity effects of plant litter and decomposer communities, and the impacts of climate warming and nitrogen enrichment on litter decomposition are surprisingly similar across terrestrial and aquatic ecosystems. However, a number of important knowledge gaps still limit the development of a cross-system decomposition model. For instance, the spatiotemporal variation at which decomposition drivers operate, the biological mechanisms behind diversity effects, and the indirect effects of climate warming and nitrogen enrichment on litter decomposition via shifts in plant and decomposer communities. Addressing these gaps in future studies that explicitly address litter decomposition across the terrestrial-aquatic continuum (e.g., in forest ecosystems) will contribute to generate a reliable predictive framework of litter decomposition at biome and global scale.

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