Biodiversity and Ecosystem Functioning: a Conceptual Model of Leaf Litter Decomposition

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1. Introduction

In this chapter we present a brief history of studies on the relationship between biodiversity and ecosystem functioning (BEF), describing the main models used to explain this relationship, as well as the biodiversity metrics most commonly used. Furthermore, we use litter decomposition as a "process model", presenting a flowchart of mechanisms that may affect the decomposition. The flowchart represents the linking between the diversity of leaves that compose the litter, which is usually called the litter mixture, to its decomposition rates. Finally, we present a simplified flowchart of the edaphic trophic web, relating it to litter decomposition, and some perspectives for future studies in this area.

2. A brief history of studies on biodiversity and ecosystem functioning — BEF

Knowledge about biodiversity has passed through various stages in recent years, resulting from an accelerated scientific production. This scientific output, in turn, is a result of concerns arising from anthropogenic disturbances, which occur on spatial scales ranging from local to global [1].

To illustrate the changes observed in the study of biodiversity, Kevin Gaston in 1996 published a book entitled "Biodiversity: a biology of numbers and difference" [2]. In the first chapter of this book, Gaston emphasizes the relative infancy of the biodiversity issue, stating that a science can be seen by passing through three stages, as it matures [3]. The first stage of biodiversity studies is called the stage "What?", in which scientists seek only to know what are the species that occur in a particular location. In the second stage, the stage called "How?", is characterized by the attempts to search for patterns of biodiversity, and the third stage (the stage "Why?"), seeks to explain the factors that lead to the patterns observed before. Also according to [1], when the book was written, biodiversity studies remained "emphatically in the second stage of development, with more discussions on the measures and standards, than with issues related to the mechanisms."

In just over a decade after the publication of Gaston, several mechanisms that determine and influence biodiversity were discussed [1], and today the statement made by the author would certainly be very wrong. Many studies have been carried out in different spatial and temporal scales [1], using several different biological systems and in different regions of the world. Much remains to be done, but it is not risky to affirm that little knowledge is still to be generated regarding the mechanisms responsible for determining biodiversity, especially with respect to the definition of biodiversity as the number of species in a given area.

Around the same time of the publication of the book by Gaston, there was a shift in the view of scientists on biodiversity: the thought that biodiversity was an expression of abiotic environmental conditions gave way to the recognition that the properties of the environment were also affected by the biota [4]. This recognition spurred the search for the elucidation of the effect of the loss of biodiversity on ecosystem functioning, generating more than 50 different hypotheses to explain how this relationship would be [5]. Ecosystem functioning can be understood as a set of biogeochemical processes and ecosystem functions [6], responsible for the flow of matter and energy, and it is directly related to the dynamics of resources and the stability of the ecosystem [7].

The hypotheses that explain the effect of biodiversity on ecosystem functioning may be classified into three major classes [8]. Within the first class fall the cases which species are assumed as redundant, and the loss of some species may be compensated by the presence of others, which perform the same function. Thus, to some extent, there would be no reduction of ecosystem functioning due to the lost of species and, on the other hand, there was no increase in the ecosystem functioning when species are added. In the second category of hypotheses are the cases when species are singular or unique, such as, for example, key species. According to this hypothesis, species lack redundancy and the loss or addition of some species would cause drastic changes to ecosystem functioning. Finally, there are hypotheses in which the ecosystem functioning effects of the loss or gain of species does not depend neither on the number nor the identity of the species present, but on the conditions under which this loss occurs, so that the effects of species on the functioning become idiosyncratic.

These model-hypotheses formed the necessary structure to the experimental tests of the relationship between biodiversity and ecosystem functioning [5]. The initial tests involved theoretical approaches, as well as the use of simplified micro and mesocosm laboratory experiments. Posterior studies incorporated actual environmental variation through observational and manipulative experiments, allowing higher applicability in public policy management and biodiversity conservation [9].

3. Biodiversity in studies of BEF

Biodiversity may be estimated through several different metrics, and the most traditional approach is to access it via taxonomic diversity [10]. Later in the studies of BEF, functional diversity started to be used as an additional metric [11, 12] and, more recently, phylogenetic diversity has been included as a proposal of metric to biodiversity [13-15].

Taxonomic diversity, in turn, may be translated by species abundance, richness and composition [16, 17] parameters that are easily accessed and that may give basic information to the generation of diversity indices (such as Simpson or Shannon). These diversity indices are useful to synthesize and compare the biodiversity in different environments or sites [18, 19]. However, the indiscriminate use of diversity indices, and as a goal in itself, rather than using them as a useful metric of diversity, prompted several authors to avoid its use in favor of species richness as a metric. Species may be identified from morphological or genetic traits and, when using taxonomic diversity as a metrics, it is assumed that the differences among species are determined by these aspects. Nevertheless, some authors suggest that taxonomic diversity may not be the most adequate metric [12] to evaluate the effect of organisms on ecosystem functioning. To better evaluate such effects, it would be necessary to use the functional diversity, even though it is expected that, with an increase in species richness, there would be an increase in functional diversity [20].

Functional diversity may be understood as the group of characteristics, of species or organisms, responsible by altering one or more aspects of ecosystem functioning [21]. Such characteristics may be related to the abilities that organisms have to engage or to alter ecosystem processes such as seed dispersal [22], pest biological control [23], pollination [24], nutrient cycling [25], decomposition [26], productivity [27, 28], amongst others. However, when inferring functional diversity from species richness, it is assumed that the relationship between species number and niche occupation is linear, which usually does not occur in nature [7].

Therefore, the use of species richness as an estimate of functional diversity has been criticized, and the estimate of functional diversity has been achieved by species classification by their trophic level, guild, as well as physiological and phenotypic characteristics. Functional diversity is usually used to estimate the biodiversity of plant communities, classifying plant species according to their physiognomy, phenology or photosynthetic pathways. Animals are frequently grouped in guilds based on their consumption, but commonly with a low level of resolution, due to the weak knowledge of their biology. Such characteristics are frequently considered to determine functional diversity because they supposedly relate to aspects of the niches occupied and, consequently, they may express the effects of the organisms in ecosystem processes [21, 29]. From the analysis of these characteristics it is possible to determine and to include species in functional groups, which assemble organisms that fulfill similar functions and, consequently, have similar effects on the ecosystem [30, 22]. This approach is the most usual when using functional diversity in BEF studies.

Functional diversity is considered an estimate that may express more powerfully the effects of biodiversity on ecosystem functioning, because it refers to those biodiversity components that directly affect in how ecosystem operates [22].

There are two questions regarding the use functional diversity as an estimate of biodiversity. The first relates to its teleological use, which involve purpose, such as some earlier discussion of the hypothesis of redundancy [31]. These discussions were full of anthropocentric analogies, describing redundant species as passengers in an automobile [32] or words in a phrase [31]. The replacement of purpose with process, as suggested by [33] and [31], "retains the intuition that if something is functional, it must do something". Therefore, to be functional, species must interact with ecological processes, a relationship that brings us to the second possible question regarding the use of functional diversity as an estimate of biodiversity: is it a tautological discussion?

Because functional diversity is an estimate derived from the relationship between species and ecological processes, it stays clear to us that an observed relationship between ecosystem functioning and functional biodiversity must be positive and highly significant. There are even suggestions that ecological processes and ecological function might be treated as synonymous [31], increasing the possibility of a positive relationship in the studies relating ecosystem functioning and functional diversity.

The above issues must be considered when using functional diversity as an estimate of biodiversity in studies relating ecosystem function and biodiversity. The definition of functional diversity is somewhat established since the proposal by [31], but this metric would only correlate two variables that are a priori related. The metric could be attractive to achieve a definition of the functional groups that are more prevalent in the effects on ecosystem processes, but the metrics alone lack an explanatory power. It is still necessary to question why biodiversity, if it estimated independently of functionality, interferes increasing or decreasing ecosystem functioning.

There has been a suggestion that animal traits that are predicted to influence ecosystem processes must be defined a priori [13]. The actual effect of each functional group on ecosystem processes is then tested and the predictions may be refined accordingly. The above authors also propose a hypothetical relationship between functional diversity and the number of taxa or groups. They suggest a loose relationship between functional diversity and species richness, and adding more families within a trophic level would add more functional trait variation than adding more species within a genus or family. Consequently, the increase in taxa variation would represent an increase of the expected functional diversity, and a priori classification of functional groups could be achieved by a metric that could capture phylogenetic diversity.

Recent studies observed the existence of a relationship between functional and phylogenetic diversities, mainly when considering functional groups as an estimate of functional diversity [16, 30, 34]. According to [30], assemblages with a higher phylogenetic diversity present higher functional diversity, possibly due to the complementarity of ecosystem functions among clades, contrasting with the expected redundancy among species that possess common ancestors.

Species functional characteristics, as well as all other traits, appear along their evolutionary history, affecting the way species distribute and relate to each other. Therefore, these traits tend to be shared among the species that have a common ancestor [30]. The latter authors propose that, since these characteristics may influence ecosystem processes, the phylogenetic history may mirror more accurately the effects of biodiversity on ecosystem functioning. This may occur because closely related species tend to occupy similar niches, and thus may play a similar role in the ecosystem processes. Consequently, communities composed by species that encompass a higher phylogenetic diversity (or more distantly related species), would also encompass a wider range of niches. These communities would be more efficient communities in maintaining ecosystem functioning (Figure. 1), due to the higher complementarity of species effect on ecosystem processes [33].

There are two main reasons to use phylogenetic diversity as a relevant biodiversity estimate in comprehension of ecosystem functioning, instead of functional groups: (1) the removal or addition of a functionally redundant species may have effects of ecosystem processes, highlighting important functional among species, non-captured by functional groupings; and (2) in the case of prediction of change in ecosystem processes like productivity, for example, functional groups may explain as much as categories of randomly chosen groups [34].

Phylogenetic diversity may be defined, in general, as the sum of phylogenetic branches that ling species [34], although several methods of estimating phylogenetic diversity may be recognized [35]. These metrics may be classified into two basic types. The type I metrics begin by calculating a distinctness score for all species of a regional phylogeny and, after this calculation, the distinctness scores of the focal subset of species are summed (or any other function to be used), to produce the phylogenetic diversity metric. Contrarily, the type II metrics use a local phylogeny, from which the distinctness scores are calculated to the focal species [35].

Important considerations regarding the choice of these estimates are presented [41], based on the available data, listing the metrics that are typically used in community ecology studies. These are: (1) Phylogenetic diversity (PD): sum of all branches lengths in the portion of a phylogenetic tree connecting the focal set of species; (2) Mean phylogenetic distance (MPD): mean phylogenetic distance between each pair of species in the focal set of species; (3) Sum of phylogenetic distances (SPD): sum of phylogenetic distances between each pair of species (MPD) multiplied by the number of species pairs; (4) Mean nearest neighbor distance (MNND): mean phylogenetic distance from each species to its closest relative in the focal species set. These metrics are primarily used on conservation biology studies that focus on species conservation, supporting conservation decisions. Nevertheless, in relation to biodiversity and ecosystem functioning studies we do not have a standard metric for usage and this lack comprises an important issue in BEF studies that uses phylogenetic diversity as biodiversity estimate. We recommend to researchers who want to use PD as biodiversity estimate, to search for a powerful background in choosing the metric. We expect that with the increase of studies using PD as metric in BEF researches will result in an improvement of using this metric.

However, even though the estimates of phylogenetic diversity may be promising in BEF studies, there are still no solid evidences about its relationship with ecosystem functioning [15], except those reported by [14]. These latter authors propose a model that partitions the effects of biodiversity into phylogenetic effects and other community properties.

There are three aspects in the studies of BEF relationship that have to be distinguished. The first aspect is the evaluation of which would be the appropriate metrics for biodiversity and for ecosystem functioning. This evaluation involves both methodological and mechanistic considerations, but certainly may affect the results of BEF relationship evaluation, for non-biological reasons. Therefore, one has to be especially careful to distinguish actual mechanistic relationships from tautological correlations, disconnected from biology itself. The second aspect of BEF studies is the evaluation of BEF relationship hypotheses, which necessarily involve regression models that must be tested against null hypothesis of no relationship, or spurious relationship due exclusively to methodological or mathematical issues.

These two first aspects of BEF studies have been often confused, and may lead to unwarranted conclusions. For example, studies on the relationship of phylogenetic diversity in relation to ecosystem functioning [12], have shown that phylogenetic diversity is more relevant to predict ecosystem functioning, at least when evaluated by primary productivity, than crude species richness or diversity. The authors argue for evolutionary reasons for this pattern, and further suggest that thus one should favor phylogenetic diversity rather than species diversity, as a metric to evaluate BEF. This should not, however, be interpreted as a test of the BEF relationship, but rather a methodological refinement, prior to an actual hypotheses testing.

The third aspect of BEF studies, which is the one that we proposed to illustrate in this chapter, regards the explanations for the actual relationship between biodiversity and ecosystem functioning. Disregarding the metrics used to depict biodiversity and the shape of the relationship between biodiversity and ecosystem function, the question why does ecosystem function vary with biodiversity remains. The mechanistic processes by which these two community parameters relate are then described below, using decomposition as the ecosystem function and the variety of species that compose the litter, the so-called litter mixture, as the biodiversity metrics.

4. The process model — Litter decomposition

Litter decomposition is a so-called support process of ecosystems, necessary to the maintenance of several ecosystem processes [36]. Due to the implications and to the importance of litter decomposition process in local scale, such as in the productivity of agricultural areas [37], and also in global scale, such as in the global carbon cycling [38], studies involving biodiversity and litter decomposition are increasingly frequent [39-43]. The central goal of these studies is to understand how the factors that drive litter decomposition interact and what are the consequences of biodiversity decrease on this process.

Litter decomposition is the process by which organic matter is progressively broken in smaller parts, since all organic molecules have been mineralized into their primary constituents: water, carbon dioxide and mineral elements [44]. Litter decomposition process is regulated by three main factors: the physico-chemical environment, the quality of the material to be decomposed and the edaphic biota [44-46].

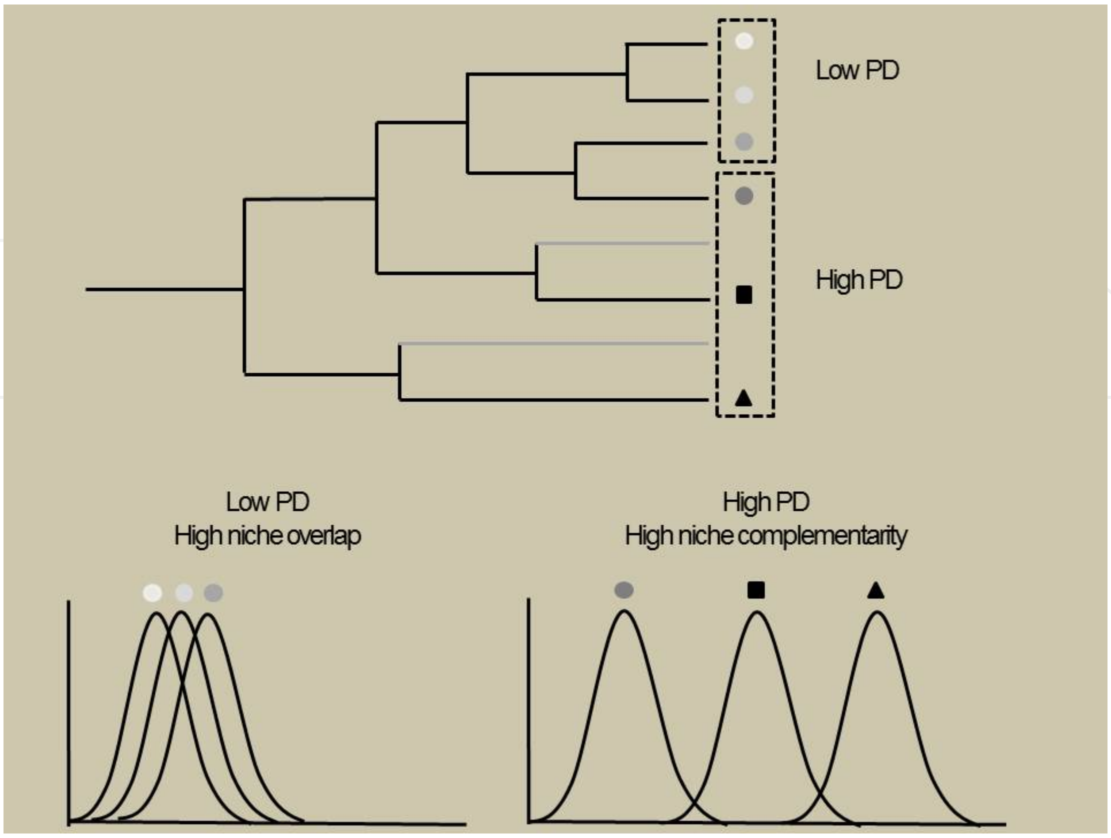

Figure 1. Relationship between functional and phylogenetic diversities in a community, considering the existence of a phylogenetic signal to the functional characteristics in question. PD: Phylogenetic diversity. Closely related species are more similar (symbols differ only in color) than distantly related species (symbols differ in shape). Adapted from [15].

The physico-chemical environment is related to climate, especially humidity and temperature [45, 47]. The climate may indirectly affect litter decomposition, changing litter characteristics, or directly, controlling the activity of decomposing organisms. Plant chemical composition may result from soil formation and from nutrient cycling, and both are regulated by the climate [47]. Therefore, nutrient mineralization may be more accelerated in hot and humid climates, resulting in higher nutrient concentration in litter, increasing its degradability and decomposition [48]. In addition, the direct effect of physico-chemical environment on decomposition occurs from favoring the activity of decomposer organisms by the higher temperature and humidity, increasing the rates of litter decomposition and nutrient release [48, 49].

The second main factor regulating litter decomposition is the quality of organic matter from litter, which is frequently associated to leaf degradability [46]. There is not a unanimity regarding a valid index of litter degradability, although certain nutrient concentrations have been usually associated to higher quality [50]. High nitrogen (N) and phosphorus (P) concentrations, as well as high proportions of easily degradable carbon compounds, such as sugars, have been associated to better litter quality [50], which translates into higher decomposition rates. Contrarily, less degradable carbon compounds (such as lignin), decrease degradability and litter quality, because these compounds require higher energy from decomposers to break the organic matter [46].

The edaphic biota is the third factor regulating decomposition and comprises a plethora of organisms, ranging from bacteria to insects. These organisms remove, mix, break and digest the organic matter, metabolizing litter constituents, mineralizing and making nutrients available to plants [51]. Even though all components of the edaphic biota may perform important roles on litter decomposition, the main decomposing agents are fungi and bacteria, being responsible by nutrient mineralization. Fungi may colonize recently fallen leaves, building up a net of hyphae that allows them the transference of carbon and nitrogen from litter to soil. Bacteria, on other hand, are the main responsible by nitrogen mineralization and availability, which make them extremely significant for the cycling of this nutrient through the soil and to the plants [52]. Several bacteria not only degrade the organic matter, but are central in nitrogen transformations, in a complex of chemical reactions of oxidation and reduction, fixing nitrogen from the air, transforming nitrites into nitrates and back to nitrites, ammonia and returning it to the air. The activity of decomposers, both fungi and bacteria, is affected by the action of detritivore arthropods, which break the litter by its ingestion and digestion, increasing the litter area available to decomposers and facilitating litter decomposition by microorganisms [53].

The diversity of plants whose leaves compose the litter, the litter mixture, may affect the decomposition process through different pathways (Figure 2). According the general findings of the relationship between biodiversity and ecosystem functioning, it is expected a positive relationship between litter mixture diversity (biodiversity) and litter decomposition (ecosystem process). Nevertheless, there are possible pathways that may conduct to the absence of such relationship (the null hypothesis), or even to a negative relationship. The importance of the flowchart depicted in Figure 2 is to generate hypotheses to explain this diversity of possible outcomes in the BEF relationship, allowing the posterior designing of experiments to test these hypotheses.

In general, the main mechanism whereby litter mixture diversity affects litter decomposition it is via resource heterogeneity [54]. In Figure 2, litter taxonomic diversity may be understood in three ways: different species richness and/or compositions, varied functional groups or phylogenetic diversity. We discussed these metrics previously in this chapter, highlighting the advantages and disadvantages of each of them, but disregarding the metrics used, we considered that an increase of each of them would result in higher litter heterogeneity.

A more diverse litter mixture would present a more varied resource supply, allowing the occurrence of a higher abundance and richness of detritivore and decomposer organisms [54]. A higher abundance and/or species richness of decomposers and detritivores would increase litter decomposition.

The heterogeneity promoted by the increase of species composing the litter mixture may occur both due to the physical and chemical plant characteristics. Leaves with certain physical characteristics, such as lower hardness and lignin content, are correlated to higher decomposition rates [55]. Chemical aspects, such as higher carbon and nitrogen concentrations, are frequently correlated to higher decomposition rates [26, 50, 55, 56], even though this pattern is not fully established [51]. According to our flowchart, there would be a positive relationship between environmental heterogeneity and the possibility of the litter mixture being explored by different decomposer species, which possess distinct nutritional needs, or different abilities to exploit resources originated from a varied plant species. The relationship between an increasing environmental heterogeneity affecting positively the species richness of the communities is a well-established pattern [57], and may be based on the amount or variety of resources that may allow the coexistence of potentially competitive species.

Theoretically, it would be possible to predict litter decomposition rates from the proportional sum of the decomposition rates observed in each plant species composing the litter mixture. However, this expected outcome does not necessarily occurs [58, 59], due to interactions between the species composing the litter mixture. When the expected prediction, decomposition rates of the litter mixture corresponds to the sum of decomposition rates of each species composing it, we say that an additive effect is occurring. However, when leaves from two or more plant species are mixed, decomposition rates of the litter mixture may not correspond to that estimated from the decomposition rates of each plant species alone, due to synergistic and antagonistic effects among species composing the litter mixture [59]. These effects may occur because nutrients may be transferred from one plant species to another one [60], altering the expected effects of diversity of litter mixture on leaf litter decomposition [26]. There are evidences that a nutrient transference from a nutrient-rich species (with a lower carbon/nitrogen ratio) to a nutrient-poor species may increase litter mixture decomposition when compared to the sum of decomposition rates of each species considered alone [56], resulting in a synergistic effect. On the other hand, the presence of some secondary plant metabolites, such as polyphenols, may decrease, revert, or even compensate synergistic mechanisms that would be occurring simultaneously. This effect would decrease the decomposition rate of litter mixture, when compared to the sum of decomposition rates observed in each of the species composing the mixture, causing the antagonistic effect [51, 59]. Thus, plant diversity that composes the litter mixture would not always have the expected positive effect on decomposition. This is so mostly because the number of species in litter [40], the environment in which the litter is decomposing [61], the origin of leaves [62], amongst other aspects, may alter the response of decomposition to plant species diversity of the litter mixture.

Moreover, the effect of litter mixture biodiversity on decomposition rates is deeply related to the edaphic biota, its activity, abundance and composition [56]. The edaphic biota may modulate the decomposition process, mainly in tropical ecosystems, where arthropods are extremely abundant and their effect on decomposition is more consistent [49, 63].

5. Effect of the edaphic biota on decomposition — Top-down/bottom-up control

The edaphic organisms organize in an intricate trophic web, and the diversity of the litter mixture would alter the interactions among these organisms and therefore the effects of this interaction on litter decomposition. The knowledge regarding trophic webs related to the decomposition process is very weak, especially in tropical biomes. This lack of knowledge is caused primarily by the weakness of taxonomic and biological knowledge [64, 65], both

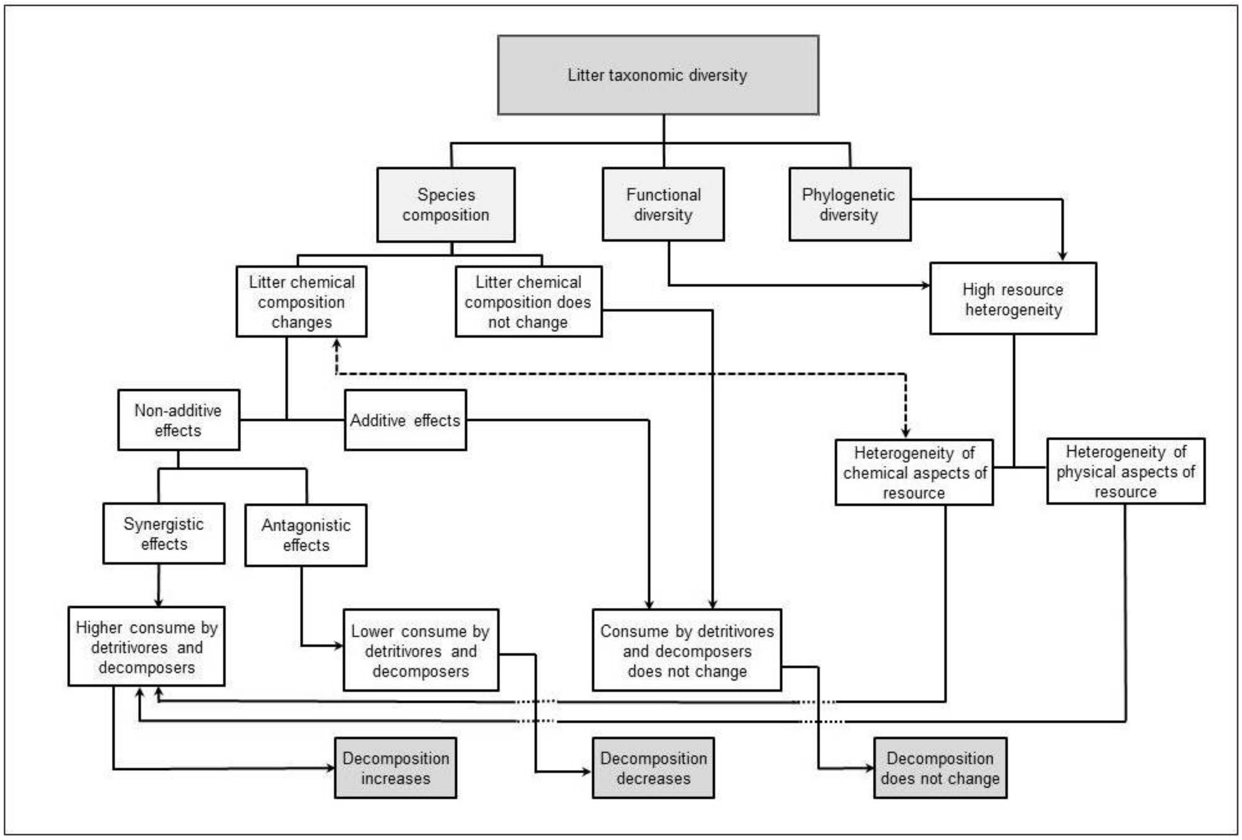

Figure 2. Factors and processes that associate plant diversity in litter mixture to litter decomposition.

regarding the decomposers themselves and their consumers, from different trophic levels, associated to the trophic web. The study of these trophic webs necessarily involves two components that may influence the litter decomposition process: (1) the diversity of litter mixture composing the litter; and (2) the diversity and the trophic links among decomposers and detritivores. Once the trophic web related to litter decomposition is, at least partially, donor-controlled – in the case, the leaf litter – it is expected these webs to be controlled predominantly by bottom-up effects, since consumers do not control resource abundance (and, in our example, nor the diversity).

In Figure 3 we represent a simplified trophic web of detritivores and decomposers, recognizing three different control pathways of the represented trophic levels. The more direct pathway, symbolized by the dotted line, represents a direct effect of the diversity of litter mixture accounting for higher resource heterogeneity to decomposers (but see Figure 2 and discussion above). This pathway may promote the increase of decomposer diversity and activity, directly augmenting the decomposition process, without the interference of organisms from other trophic levels. However, such effects would only be possible if the effects promoted by the increase of litter diversity on the edaphic biota are positive (see Figure 2 and discussion above).

The activities of the animals that inhabit litter may interfere in the above described patterns in different ways. Following the dashed line in Figure 3, the activity of litter breaking by arthropods may increase the resource availability to the decomposer community, since the passage of litter along the digestive tract of detritivores facilitates the degradation by the enzymes of decomposer organisms [66, 67]. Thus, the action of animals may increase the abundance and/or species richness of microorganisms, with a consequent increase in decomposition rates.

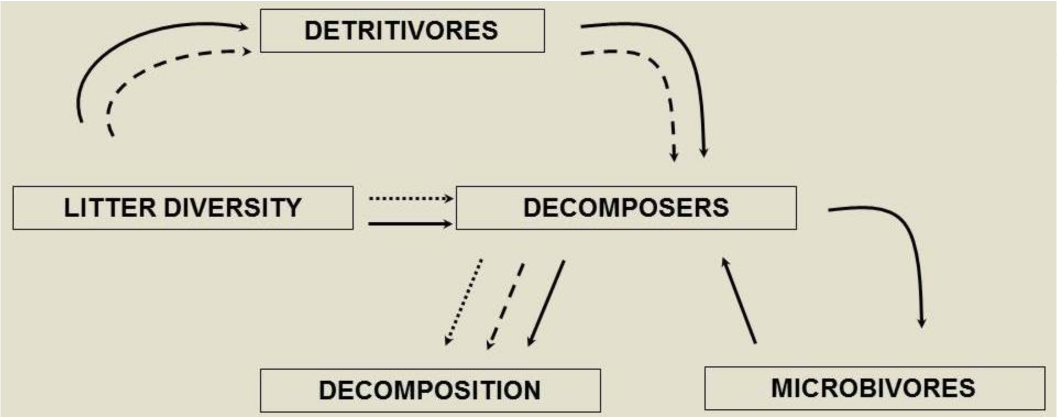

Figure 3. Simplified flowchart of the edaphic trophic web, depicting possible pathways of the effect of diversity of litter mixture on litter decomposition. See text for further information.

On the other hand, the higher abundance and/or diversity of decomposers may lead to an increase of abundance and/or species richness of fungivores and bacteriovores (called here microbivores), due to an increase of resources available to these animals. An increase of microbivores may augment a predation pressure on decomposers, decreasing their abundance and activity. As a consequence, there would be a decrease of litter decomposition (continuous line in Figure 3). This control pathway of the decomposers by the microbivores could represent a top-down control in the decomposer trophic level.

Moreover, predators, not depicted in the trophic web of Figure 3, may control top-down both detritivores and microbivores, making this trophic web more complex and difficult to interpret. The study of edaphic trophic webs, its influence on litter decomposition process and the effects of litter mixture diversity on this web must thus be studied through well designed experiments. Correlational studies may give weak evidences regarding the relative role of each group of organisms within this trophic web, since several of the involved factors in these webs tend to covariate and confound data interpretation [65]. The exclusion of some groups or trophic levels may represent, hence, an option to study these trophic webs, provided that the techniques involved in the exclusion process do not interfere in the decomposition process or in other organisms. A critique of the use of fumigation as an arthropod exclusion method is given by [65], due to the nutrient addition to litter caused by the technique.

6. Conclusions and perspectives

According to the above discussions, it is possible to notice that a single response relating the effects of litter diversity on decomposition does not exist. The interactions among the factors that determine litter decomposition is complex, and several pathways may occur. The effects of litter diversity on decomposition rates are dependent on several features, and the experimental control of these factors is absolutely necessary to clarify their relative roles and interactions.

Therefore, studies controlling, simultaneously, litter and edaphic fauna diversities, may give evidence to their joined effects on decomposition rates, allowing a better understanding of the relationship between these two factors. Furthermore, since several elements external to litter diversity (such as soil use, habitat fragmentation and others) may affect the effect of the discussed factors on litter decomposition, the incorporation of such elements would add information to the process. To do this it is necessary to design studies with manipulative control, which would render more informative studies than those that limit to compare decomposition rates in different litter mixtures.

There are some alternative for these studies, and each alternative may achieve an answer that would clarify one or more of the above discussed points. One proposal it is the use of several plant species, among which different number of species are drawn, giving an idea of the relationship between the number of species in litter mixture and decomposition. In the array of litter mixtures other parameters may also be tested, such as arthropod species richness and abundance, as well as microbial biomass and activity. This approach tends to create situations more close to the actual environments studied, since usually the plant species used are the same as those occurring in the study site. On the other hand, this approach may increase very much the variability among repetitions, creating a noise that may impair data interpretation. The alternative approach would be the use of the same plant species in all repetitions, decreasing variability among them and giving more interpretable data, although decreasing their realism towards the studied environments. These studies are particularly common in habitats involving crops, associated or not to other plants, using decomposition litterbags containing leaves of the cultivated plant, alone and together with other plant species.

In order to study the relative role of the trophic web components, manipulative studies are the most usual approach. In these studies, detritivore species are added or removed, and their effect on other species and/or on decomposition rates are observed. This approach suffers from the same problem of the manipulative studies involving litter mixtures: the distancing from biological reality. Furthermore, these studies are virtually impossible to carry out in hyper diversity habitats (as it is usual in most tropical biomes), and when the knowledge regarding taxonomic identity and/or biology of the involved species is weak. In such cases, experiments excluding litter fauna may be carried out through methods as fumigation, or by the use or other biocides, such as naphthalene. These substances, however, may cause impacts in the decomposer community, modifying decomposition process through more than one pathway of the activity of organisms, impairing once more data interpretation. Another option to exclude fauna is decomposition litterbags with different sized mesh, which may exclude selectively the fauna and modify their species composition. Nevertheless, most options to exclude fauna deal with species richness of the edaphic trophic web, and not on its species composition, weakening the interpretation of the effects of the functional and phylogenetic diversity on litter decomposition process.

Therefore, the studies involving the relationship between the plant diversity composing litter mixtures and its effects on the decomposition process, including the possible effects on the edaphic trophic webs, still need much more study and explanation. The knowledge acquisition in these subjects must necessarily be based on well-designed experiments, to elucidate the relative role of each factor and of the interactions between these factors. We hope to have contributed for future studies by the production of the flowchart of factors and processes, facilitating the isolated tests of each of the connections shown in it.

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