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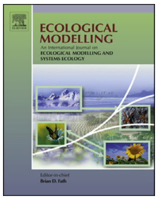

Methods for estimating the effect of litterbag mesh size on decomposition

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ABSTRACT

Litterbag is a standard apparatus used in plant litter decomposition studies. Decreasing bag mesh size hampers litter decomposition due to exclusion of large-bodied consumers and interferences with agents of litter fragmentation. The combined use of coarse and fine mesh bags in field studies is thus relevant for assessing the contribution of macrodetritivores and microbial decomposers to litter decomposition. The present paper examines methods for analyzing the effect of litterbag mesh size on decomposition. I present here a new approach derived from a mathematical analysis of the first-order decay model (i.e. the Olson's model) and use it to reanalyze a large dataset of litter decay rates in two different mesh size litterbags. The presented calculation method for the extent and rate of litter fragmentation overcomes several shortcomings of previously used indices. I also highlight potential pitfalls associated with using the Olson's model to analyze the effect of litterbag mesh size on decomposition.

1. Introduction

Plant litter decomposition has been a central focus of ecology for over a century (Berg and McClaugherty, 2008). Recent research in this field has concentrated on understanding the biotic and abiotic drivers of ecosystem functioning and biogeochemical cycles (e.g. Handa et al., 2014). There is a rich theoretical and practical framework to quantify fluxes of elements and compounds released during decomposition and to evaluate the intensity of biotic and abiotic processes accounting for these fluxes. Litter decomposition is routinely assessed in the field by the mean of litterbags which are small cages used to confined a known mass of plant litter. Litter decay rate is then estimated by fitting kinetic models to mass loss data collected on one or more occasions (Adair et al., 2010; Cornwell and Weedon, 2014). The first-order decay model elaborated by Olson (1963) has been widely applied in comparative studies. Although this model relies on over-simplistic assumptions, notably with respect to the homogeneity of the detrital pool, it does provide reasonably good fit to empirical data in many cases (Berg and McClaugherty, 2008). It is often preferred over more accurate but complex models in litterbag studies whose primary aim is to compare different conditions using small datasets. In the Olson's model, a single free parameter (k) is needed to relate detrital stock (m) to time (t) (Eq. (1)).

$$m(t) = e^{-kt} \tag{1}$$

m is actually expressed in a relative manner and thus stands for the proportion of initial detrital stock ranging from 0 to 1. k is the litter decay rate (time^{-1}) which measures the proportional change of litter mass over time.

Mesh size of litterbags influences the rate of litter mass loss primarily through interfering with physical and biological processes involved in litter fragmentation. A realistic estimate of litter decay rate is more likely to be obtained with coarse mesh bags with mesh openings large enough to ensure that the whole community of litter consumers can access the litter (e.g. Handa et al., 2014), or ultimately with unconfined litter patches (e.g. Alp et al., 2016). Finer mesh size reduces the scope of litter fragmentation through exclusion of large-bodied detritivores and the physical protection of confined litter against abrasive forces (e.g. wind, precipitations, water flow, etc.). Since litter decomposition in fine mesh bags (usually 1 mm or smaller) is mostly mediated by dissolution processes (leaching) and microbial activities, it conceivably proceeds at a slower rate than in coarse mesh bags. Thus, the combined use of coarse and fine mesh bags in field studies helps shed light on the contribution of litter fragmentation to total decomposition. This mesh size effect is often interpreted as being equivalent to invertebrate-mediated decomposition (Woodward et al., 2012; Garcia-Palacio et al., 2013; Handa et al., 2014), which

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would hold true if mesh size did not alter microbial and physical processes involved in decomposition. The latter assumption may not be strictly met since small mesh openings are likely to hinder exchanges of nutrients, water, gas, and microorganisms between the inside and outside of litterbags. This paper is not intended to discuss the strengths and weaknesses of litterbag experiments. It is concerned with methods for quantifying mesh size effect on litter decomposition. I present here a new calculation method and use it to reanalyze a large dataset of litter decay rates in coarse and fine mesh bags.

2. A review of approaches used to quantify litter fragmentation

Quantification of mesh size effect on decomposition is quite intuitive when dealing with stocks at a given instant of time. Litter mass loss owing to fragmentation (F) can be calculated as the difference in litter mass remaining between coarse (m_c) and fine (m_f) mesh bags.

$$F = m_f - m_c, F \geq 0 \tag{2}$$

Some authors have used the formula $100F/(1 - m_c)$ to estimate the percent contribution of groups of invertebrates of contrasting size classes to total decomposition (e.g. Handa et al., 2014; Alp et al., 2016). Because the effect of invertebrates changes as litter decomposition proceeds, this method is likely to give variable results depending on the decomposition stage at which litter fragmentation is assessed. The least biased estimate of F would be obtained when litter mass remaining in coarse mesh bags approaches zero.

Mesh size effect on litter decomposition has also been inferred from first-order decay constants (cf. Eq. (1)). The ratio (α) of decay rates determined empirically in coarse (k_c) and fine (k_f) mesh bags has been widely reported in the literature since the introduction of this index by Gessner and Chauvet (2002). Despite its apparent simplicity, the decay rate ratio has three interesting features:

(1) It is the only parameter needed to relate m_c and m_f:

$$m_f = m_c^{(k_f/k_c)} = m_c^{(\alpha^{-1})}, \alpha \geq 1 \tag{3}$$

(2) It is analogous to the "hazard ratio" used to compare two conditions in survival analysis (Kleinbaum and Klein, 2012). This analogy makes sense since kinetic models can be interpreted in a similar probabilistic manner as survival functions (Manzoni et al., 2009, 2012). The decay rate k can thus be defined as the probability that molecules of plant litter remaining in litterbags at time t undergo decomposition during the next instant of time.

(3) k^{-1} is equivalent to the mean residence time given by the Olson's model (Manzoni et al., 2009, 2012). Therefore, the ratio of k_c to k_f is a measure of the effect of litter fragmentation on the time that detrital molecules spent in litterbags.

Some authors have replaced m with F in the formula for calculating exponential litter decay rate based on a single sampling date (e.g. McKie et al., 2006; Woodward et al., 2012). The tweaked formula (Eq. (4)) has been thought to give the rate of invertebrate-mediated decomposition.

$$k_{invertebrate} = -\frac{\ln(F)}{t} \tag{4}$$

There are two major objections to this approach:

(1) It does not calculate a decay rate since F represents a fraction of litter that is lost rather than a fraction of litter that "survive" fragmentation.

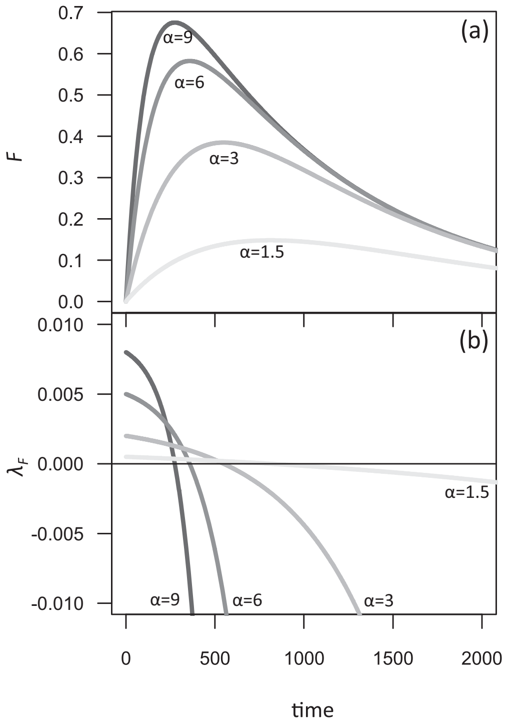

Fig. 1. Graphical representations of the functions F(t) (Eq. (5); panel a) and $\lambda_F(t)$ (Eq. (9); panel b). The curves are drawn using the parameters $k_f = 0.001$ and $\alpha = \frac{k_c}{k_f} = 1.5$, 3, 6 and 9.

(2) It pertains to the hypothesis that proportional change in litter mass owing to fragmentation is constant through time, which has not been verified.

3. Analytically derived indices

The difference in litter mass remaining between coarse and fine mesh bags (F) can be expressed as a function of time by combining Eqs. (1) and (2).

$$F(t) = e^{-k_f t} - e^{-k_c t}, k_f \leq k_c \tag{5}$$

F(t) represents the cumulative amount of litter mass lost through fragmentation processes since the origin. The graph of Eq. (5) is a hump shaped curve skewed to the right and whose intercept and upper limit are zero (Fig. 1a). The falling portion of the curve is meaningless as it suggests a net gain of litter mass. The peak value of the curve ($F_{\max}$) gives an estimate of the total mass lost through fragmentation over the full course of decomposition. $F_{\max}$ is calculated from Eq. (6) (see also Appendix A).

$$F_{max} = \frac{k_f}{k_c}^{1/(1-k_f/k_c)} \left(\left(\frac{k_f}{k_c} \right)^{-1} - 1 \right) \tag{6}$$

It is interesting to note that the ratio $k_f : k_c$ (i.e. α^{-1}) is the only parameter needed for the calculation. Multiplying F_{max} by 100 gives the percent contribution of litter fragmentation to decomposition (%F) extrapolated until complete disappearance of the litter enclosed in litterbags. This index is thus particularly useful when it is necessary to compare data collected at different stages of litter decomposition.

Some mechanistic models of litter decomposition are formulated as a sum of rates of organic matter flows transferred out of the detrital pool through different decomposition pathways (e.g. Hieber and Gessner, 2002; Alemanno et al., 2007). This approach is relevant to identify a suitable mathematical expression for the rate