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Rapid leaf litter decomposition of deciduous understory shrubs and lianas mediated by mesofauna

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Abstract Leaf litter decomposition rates (LDRs) of understory woody species vary substantially across species in temperate forest ecosystems. Using litter traits and LDR data for 78 shrub and liana species from a previous study, plus an additional litterbag experiment with varying mesh bag sizes for a subset of 17 species with rapid LDRs, we report that litter traits have nonlinear effects on LDR. In addition, we show that mesofauna, including nonnative earthworms, in general increase LDR and that the effects are greater for species of high LDR. Our results suggest that the acceleration of LDR by the co-invasion of plant species with high LDR and soil biota can promote nutrient cycling, potentially disrupting the stability of native forest ecosystems.

Keywords Litter decomposition · Litter traits · Mesofauna · Understory woody species · Temperate deciduous forest · Eastern USA

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Introduction

Litter decomposition rates (LDRs) of forest understory plants vary markedly (over 100-fold) across species (Ashton et al. 2005; Cornelissen 1996; Jo et al. 2016). For example, in a comparative litter decomposition study of 78 forest understory species, we found that some species, including nonnative invaders, had exceptionally high LDRs (litter decay rate, k [year^{-1}]-> 30), whereas others had relatively low LDRs ($k < 1$) (Jo et al. 2016). Although the variability of LDRs is often strongly correlated with litter traits (e.g., chemistry and structural properties) (Chapin III et al. 2011; Cornwell et al. 2008; Jo et al. 2016), exceptionally high LDRs for some species indicate that the soil mesofauna community may play an important role in mediating LDRs.

In addition to nonnative plants, introduced earthworms have heavily invaded forests in eastern North America, a region where native earthworms were absent before European settlement (Fridley 2008; Craven et al. 2017; Frelich et al. 2006). Indeed, in the previous decomposition study (Jo et al. 2016), we detected nonnative juvenile earthworms inside litterbags for a subgroup of nonnative invasive species with rapid LDRs. Accelerating effects on litter decomposition by the co-invasion of plant species and soil biota can change nutrient dynamics in forest ecosystems (Roth et al. 2015); however, it remains unclear the extent to which rapid LDRs are driven by the accelerated decomposition by microbes and/or selective foraging by the nonnative component of the mesofauna community.

In this study, using leaf litter traits and LDRs for 78 understory species reported by Jo et al. (2016), we explored (1) how leaf litter traits that have been found to control LDR vary according to litter decay classes (i.e., species subgroups with rapid, intermediate, and slow LDRs) and, using an additional litterbag experiment with varying mesh sizes for a subset of 17 species with rapid LDRs, we examined (2) which traits were associated with mesofauna-assisted litter decomposition.

Methods

Litter traits and decomposition rates for 78 understory species reported in Jo et al. (2016) were used to determine litter trait effects on LDRs for three classes of species exhibiting different levels of decomposition rate (rapid LDR class: $k > 75\%$ percentile of all 78 species; intermediate LDR class: 25–75% k; and slow LDR class: $k < 25\%$). In brief, litter decay rates (k) were determined based on litter mass loss in litterbags (1 mm mesh) over 18 months during in situ incubation in a forest dominated by sugar maple (*Acer saccharum*) in Pompey, New York, USA. Litter traits measured for each species included litter nitrogen (N) and carbon (C) concentrations, acid-insoluble residue concentration (AIR), water and ethanol extractive concentration (WEE), and specific leaf area (leaf area:mass ratio; SLA). Details of methods used to measure each trait can be found in Jo et al. (2016). For each class, we tested litter trait effects on LDR using a Bayesian hierarchical modeling approach which incorporated taxonomic relatedness information to account for phylogenetic autocorrelations across species in the covariates (litter traits and k) used in the models (de Villemereuil et al. 2012).

To test mesofauna effects on rapid LDR, we selected 17 species with high LDRs based on Jo et al. (2016) (Fig. 1) and measured litter mass loss after a 3-month in situ incubation for two different mesh-sized litterbags. Senesced leaves were collected immediately after abscission in autumn 2012 from 5- to 6-year-old plants established in an experimental garden in Syracuse, New York, USA and were dried at 60 °C for > 2 days. For each species, ca. 1 g of dried leaves was inserted into each of three 10 × 20 cm bags (fiberglass screening, mesh size 1 mm) and three 10 × 20 cm N-free polyester bags (mesh size 50 µm, Ankom Technology, Macedon, New York, USA). The filled bags were sealed with a heat sealer. In May 2014, samples were laid out in three adjacent 10 × 10 m blocks in a mature secondary forest in Pompey, New York, USA where *A. saccharum* was dominant with a moderate cover of some native and nonnative understory shrubs that included *Cornus racemosa*, *Ostrya virginiana*, *Prunus virginiana*, *Rhamnus cathartica*, *Rosa multiflora*, *Euonymus alatus,* and *Lonicera* spp. In each block, six leaf litterbags for each species were placed on the soil surface. Three litterbags for each species were collected after a month and the number of earthworms found on the surface of remaining litter inside each litterbag was counted. No other major mesofauna species were found inside the litterbags other than earthworms. The remaining litter mass was measured after drying at 60 °C for > 2 days to calculate earthworm density per gram of remaining litter mass. Remaining litterbags were collected after three months, dried at 60 °C for > 2 days, and weighed to determine mass loss during decomposition. Decomposition rates during a 3-month incubation for species of each mesh type were determined as the ratio log(initial litter mass [ILM]:litter mass remaining [LMR]).

Statistical analyses

We fit hierarchical Bayesian models to test the effects of traits on LDR for three subgroups of 78 species with different levels of LDR (based on 25% and 75% percentiles of ks for all species, Fig. 1) and on litter mass remaining differences after 3-month in situ incubation with differed mesh size litterbags for 17 species with rapid LDR. We accounted for phylogenetic autocorrelation across species using a phylogeny created by Jo et al. (2016), following the model of de Villemereuil et al. (2012) using JAGS in R 3.51 (Plummer 2003; R Development Core Team 2018). Decomposition rates were log-transformed to meet normality assumptions. All predictor variables were standardized by subtracting their mean and dividing by two standard deviations to enable effect size comparisons (Gelman and Hill 2006). The models allowed us to estimate posterior coefficients to determine the relative effects of parameters on dependent

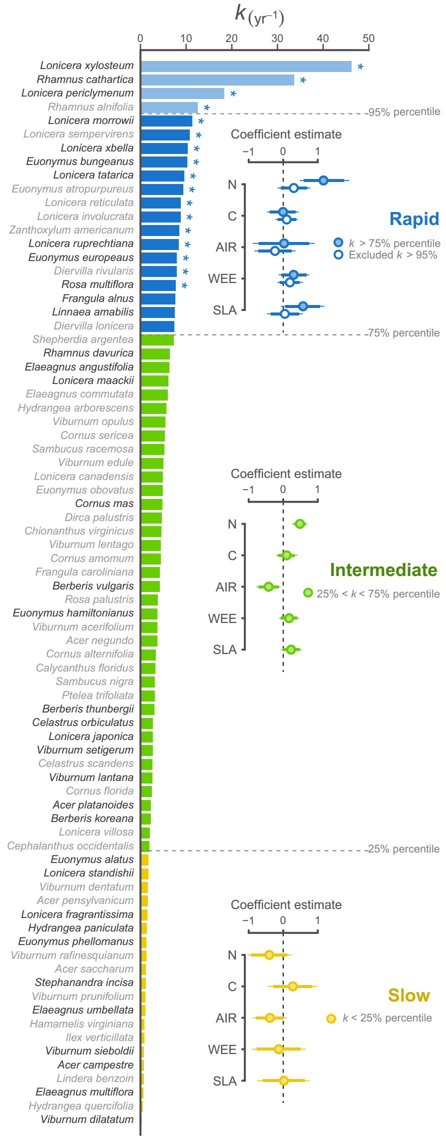

Fig. 1 Litter decomposition rates (LDRs) of 78 Eastern USA forest understory woody species from Jo et al. (2016). Species LDR classes (rapid, intermediate, and slow) are defined by 25% and 75% percentiles of litter decay rates (*k*) for all 78 species. Inset figures show the effects of litter traits on LDR in each LDR class. Dots are mean posterior coefficient estimates and thick and thin lines represent 90% and 95% credible intervals, respectively. *N* mass-based nitrogen concentration, *C* mass-based carbon concentration, *AIR* mass-based acid-insoluble residue concentration, *WEE* mass-based water and ethanol extractive concentration, *SLA* specific leaf area (leaf area:mass ratio). Species with asterisk on top of the bar (in the rapid LDR class) were used for an additional assay to test invertebrate effects on the litter decomposition using different mesh-sized litterbags (Fig. 2). Native and nonnative species names are displayed as gray and black text, respectively, based on Fridley (2008)

variables. Non-informative priors for the coefficients were sampled from a normal distribution of mean 0 and variance 100,000. To ensure convergence, we ran three parallel MCMC chains in JAGS for 20,000 iterations after a 5000-iteration burn-in.

Results and discussion

We found that litter trait control over LDR was stronger among species in the high LDR class than those in the low LDR class (Fig. 1). Consistent with previous studies (Cornwell et al. 2008; Pietsch et al. 2014; Taylor et al. 1989), LDRs in the rapid and intermediate LDR classes were strongly associated with high litter N, although the effect for species in the rapid LDR class became less significant when the exceptionally high LDR species (species with $k > 95\%$ percentile) were excluded (Fig. 1). It is noteworthy that recalcitrant compounds (AIR, acid-insoluble residue concentration), which include lignin, and specific leaf area (SLA, leaf area:mass ratio) were not significantly related to LDR values in the rapid LDR class, suggesting that LDR in the rapid LDR class may be driven by selective mesofauna feeding associated with nitrogen (N) and perhaps leaf structure (e.g., hairs) related to litter palatability, although it needs to be tested further with thorough palatability assessment. On the other hand, litter N was not a significant predictor of LDR for species in the slow LDR class. Instead, AIR had a stronger association than other litter traits (Fig. 1), suggesting that variation in LDR among species exhibiting slow decay rates may be driven by compounds that inhibit microbial decomposers (Chapin III et al. 2011). We also note that, overall, litter N was negatively associated with LDR in the slow LDR class (Fig. 1), indicating a potential effect of N-based secondary metabolites (e.g., alkaloids) which can inhibit invertebrate foraging and, in turn, result in slow LDR (Chomel et al. 2016). However, further tests are required to understand how plant-produced metabolites regulate litter palatability and LDR across species in temperate forests. This result shows that the effects of litter traits across the wide range of species LDRs typical in temperate forest ecosystems are nonlinear and suggests that soil mesofauna may contribute to the varied effects of litter traits on LDRs according to LDR classes.

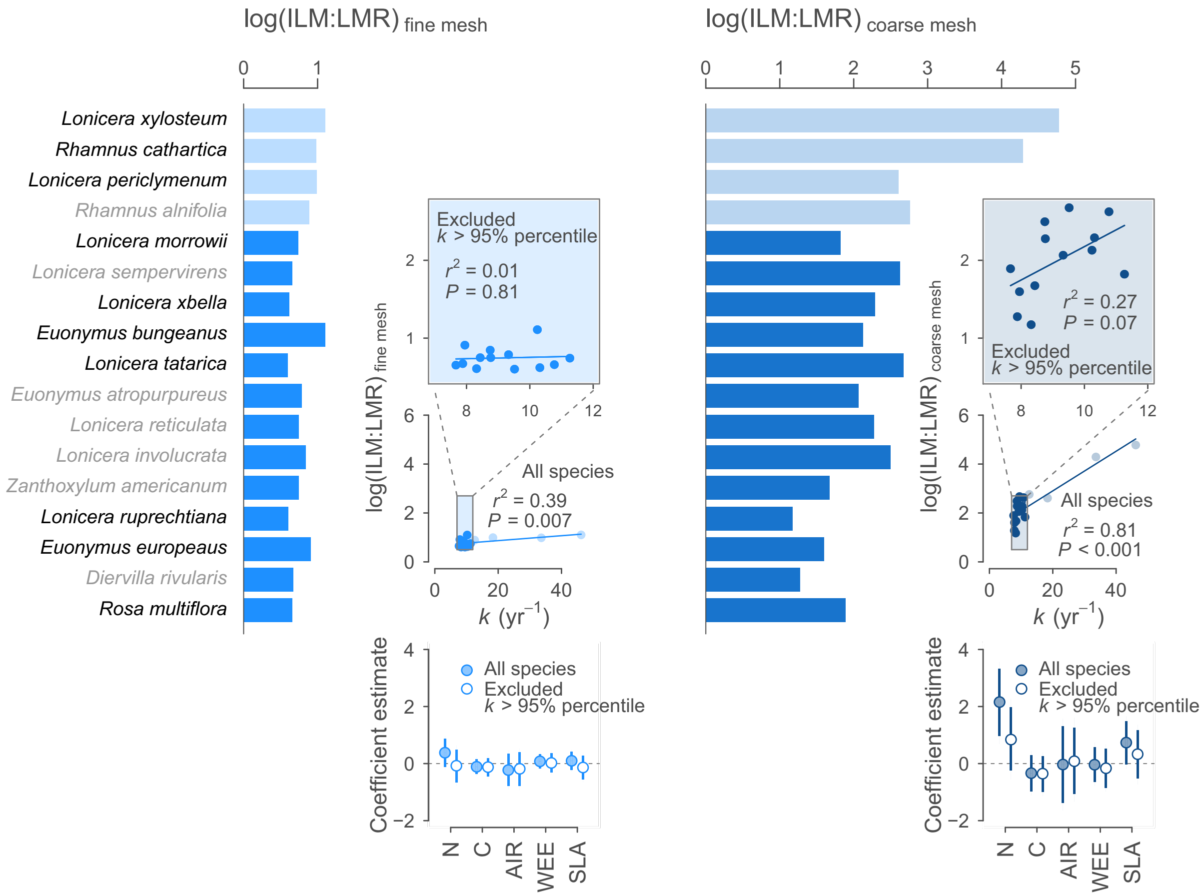

Fig. 2 Mesofauna effects on litter decomposition determined by comparing decomposition rates in litter bags with different mesh sizes (fine mesh in left panel and coarse mesh in right) for 17 species with the most rapidly decomposing litter depicted in Fig. 1. The ratio log(initial litter mass [ILM]:litter mass remaining [LMR]) during 3-month long incubation was used to assess mesofauna effects. Inset figures include bivariate relationships (linear regression) between litter decay rates (k) from Jo et al. (2016) and the ratio log(ILM:LMR) and coefficient estimates from multiple regressions for litter trait effects on the ratio log(ILM:LMR) for fine and coarse mesh litterbag incubations. Bars and dots for species with $k > 95\%$ percentile are lightly colored. *N* mass-based nitrogen concentration, *C* mass-based carbon concentration, *AIR* mass-based acid-insoluble residue concentration, *WEE* mass-based water and ethanol extractive concentration, *SLA* specific leaf area (leaf area:mass ratio). Native and nonnative species names are displayed as gray and black text, respectively, based on Fridley (2008)

In most litterbag decomposition experiments, litter decomposition patterns largely follow a single exponential decay function ($y = e^{-kt}$ where y = litter mass remaining, k = litter decay rate, and t = time). Therefore, prompt mass loss, presumably via selective feeding by soil mesofauna early during the decomposition process, will yield a high LDR. Our in situ litterbag incubation with 17 species that had high LDRs (species with asterisk on the bars in Fig. 1) included different mesh size litterbags, one with the same mesh size as Jo et al. (2016) (1 mm) and the other with a fine mesh (50 µm) which prevented invertebrates and other soil mesofauna gaining access to litter. This incubation showed significant mesofauna effects on the litter decay rate of the rapidly decomposing species group (Fig. 2). Specifically, we found a greater log ratio (ILM:LMR) for coarse mesh (mean = 2.4) than those for the fine mesh (mean = 0.8) (Fig. 2), and a positive relationship between juvenile earthworm density and litter decomposition during the first month incubation period (Fig. 3), which would be expected if the mesofauna community

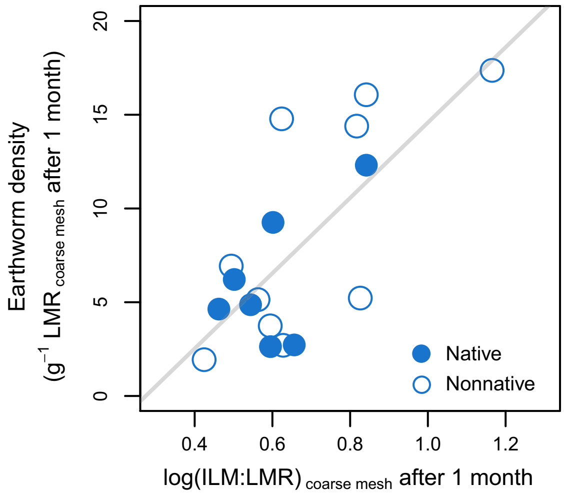

Fig. 3 Relationship between juvenile earthworm density in litter mass remaining (LMR) and the ratio log(initial litter mass [ILM]:LMR) from coarse mesh litterbags collected after 1-month incubation. Significance of the relationship was tested using linear regression ($r^2 = 0.58$, $P < 0.001$)

facilitated litter decomposition. A positive relationship of greater effect size (i.e., regression slope estimate) between decomposition rates (*k*) and log ratio (ILM:LMR) for coarse mesh than for fine mesh (Fig. 2) further suggests greater mesofauna effects on the litter decomposition of species in the rapid LDR class than those in the slow LDR class. In both fine and coarse litterbag incubations, the strong N effect on litter decomposition was retained, consistent with Jo et al. (2016). However, the effect size of litter N was greater in coarse litterbag incubations than that in fine litterbag incubations, suggesting additive effects of mesofauna on the exceptionally high LDR associated with N-rich litter.

Our analysis showed that the litter traits that influenced LDR depended on whether litter decomposed quickly or slowly. In addition, the mesofauna community was as important a control over rapid LDRs as litter traits. Although mesofauna in general increased LDR, their effects on the decomposition rate for some species, many of which were nonnative (Figs. 1, 2), were substantial. For instance, four out of five species with > 10 nonnative earthworms per unit LMR mass (g) inside the coarse mesh litterbags were nonnatives (Fig. 3). It is unclear the extent to which introduced detritivores contributed to the increased LDRs in this study. However, the presence of nonnative juvenile earthworms in the litterbags of the invasive plant species with highest LDRs suggests that the co-invasion of plant and mesofauna species may accelerate nutrient cycling and disrupt the normal soil processes of native forest ecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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