forests

MDPI

Article

Exploring Effects of Nutrient Availability, Species Composition, Stand Age, and Mesofaunal Exclusion on Leaf Litter Decomposition in Northern Hardwood Forests

Alexander R. Young [1], Brianne N. Innusa [2], Rick Biché [3] and Ruth D. Yanai [4,*]

[1] Earth Systems Research Center, Institute of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824, USA
[2] Department of Forestry and Natural Resources, College of Agriculture, Purdue University, West Lafayette, IN 47907, USA
[3] A. Crosby Kennett Middle School, Conway, NH 03818, USA
[4] Department of Sustainable Resource Management, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, USA
* Correspondence: rdyanai@syr.edu; Tel.: +1-315-345-7402

Abstract: In northern hardwood forests, litter decomposition might be affected by nutrient availability, species composition, stand age, or access by decomposers. We investigated these factors at the Bartlett Experimental Forest in New Hampshire. Leaf litter of early and late successional species was collected from four stands that had full factorial nitrogen and phosphorus additions to the soil and were deployed in bags of two mesh sizes (63 µm and 2 mm) in two young and two mature stands. Litter bags were collected three times over the next 2 years, and mass loss was described as an exponential function of time represented by a thermal sum. Litter from young stands had higher initial N and P concentrations and decomposed more quickly than litter from mature stands (p = 0.005), regardless of where it was deployed. Litter decomposed more quickly in fine mesh bags that excluded mesofauna (p < 0.001), which might be explained by the greater rigidity of the large mesh material making poor contact with the soil. Neither nutrient addition (p = 0.94 for N, p = 0.26 for P) nor the age of the stand in which bags were deployed (p = 0.36) had a detectable effect on rates of litter decomposition.

Keywords: litter bags; *Betula papyrifera*; *Prunus pensylvanica*; *Acer rubrum*; *Fagus grandifolia*; *Acer saccharum*; *Betula alleghaniensis*; nitrogen; phosphorus; MELNHE

check for updates

Citation: Young, A.R.; Innusa, B.N.; Biché, R.; Yanai, R.D. Exploring Effects of Nutrient Availability, Species Composition, Stand Age, and Mesofaunal Exclusion on Leaf Litter Decomposition in Northern Hardwood Forests. *Forests* **2024**, *15*, 1911. https://doi.org/10.3390/f15111911

Academic Editors: Robert G. Qualls, Yanlong Jia, Jūratė Aleinikovienė, Yue Pang, Zhongqi Xu, Zhidong Zhang and Li Xu

Received: 30 August 2024
Revised: 11 October 2024
Accepted: 15 October 2024
Published: 30 October 2024

1. Introduction

The decomposition of leaf litter is the main flux of nutrients from the vegetation to the soil surface [1–3]. Litter decomposition affects nutrient cycling and nutrient availability [4,5] in forest ecosystems and contributes to the creation of soil organic matter [4].

Forest succession affects rates of decomposition and nutrient turnover due to changes in species composition and forest structure [6,7]. Younger forests typically have more open canopies, allowing more sunlight and rainfall to reach the forest floor, which may increase decomposition [8,9]. Depending on the ecosystem, the opposite may occur. In Costa Rica, litter decomposition increased with stand age due to differences in soil properties, tree community composition, and fungal community structure [10]. In 27 different stands of varying age and species composition in subtropical China, the decomposition of one litter species declined with forest age, possibly because young forest stands had microclimatic conditions more favorable for litter decomposition [11]. Litter decomposition also depends on the species present, which may differ with stand age. In northern hardwood forests, the early successional species are white birch (*Betula papyrifera*), pin cherry (*Prunus pensylvanica*), and red maple (*Acer rubrum*), while mature forests are dominated by American beech (*Fagus* *grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). These species differ in foliar chemistry [12].

Experiments with different-sized litter mesh bags have become a staple for evaluating the effects of soil organisms on litter decomposition [13–15]. Microbes are defined as <100 µm in diameter, mesofauna are 0.1–2 mm in diameter, and macrofauna are greater than 2 mm [15]. Microbes include protozoa, nematodes, bacteria, and fungi [15]. Mesofauna include arthropods such as mites (*Oribatida*), springtails (*Collembola*), juvenile spiders (*Araneae*), and some insect larvae [16].

Nutrient availability might be expected to affect litter decomposition to the degree that decomposition is driven by microbial demand for nutrients [7–9,16]. The expression of enzymes involved in the degradation of lignin is reduced by N addition [17], and P addition has also been observed to limit microbial processes [18]. The decomposition of high-quality litter is commonly accelerated by N addition, while that of low-quality litter with high lignin content is inhibited [17,19]. The addition of N and P together increased decomposition more than either nutrient alone in tropical forests in southern China [20], Hawaii [21], and the Amazon [22]. There are few such reports from temperate forests, except that the decomposition of white oak litter was increased by N addition and decreased by P addition at Walker Branch, Tennessee, USA, with interactions depending on the application rates [23].

A long-term study of Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE), involving a full factorial N by P addition, was begun in 2011 in northern hardwoods in New Hampshire, USA [12,24]. Consequences of these nutrient additions to date include increased soil N and P availability [25]; increased foliar N and P [12,26,27]; increased tree diameter growth under P addition, on average [28], or N addition, in larger trees [12]; and increased root growth in response to N addition [29] or N+P addition [30]. In this study, we examined the rate of litter decomposition over a 2-year period in four stands of the MELNHE study, using two different species mixtures of litter (characteristic of young and mature stands), placed in stands of two age classes (young and mature), in bags of two mesh sizes, in plots receiving N or P addition.

2. Methods

2.1. Site Description

This study took place in the Bartlett Experimental Forest in the White Mountains of New Hampshire, USA (44° N 71° W, Figure 1). The climate is humid continental with the average July temperature being 19.8 °C and the average January temperature being 9.8 °C. The average annual precipitation is 1300 mm [31]. Soils are shallow, well-drained Spodosols formed in granitoid glacial till; soils have been described in detail based on three quantitative soil pits excavated in each stand [32,33]. Two stands, C1 and C2, are early successional, regenerated naturally after clearcutting in 1990 and 1988, respectively, whereas stands C7 and C9 are mature, having last been cut over in 1890 [28] (Table 1). Dominant tree species in the young stands were American beech (*Fagus americana* Ehrh.), white birch (*Betula papyrifera* Marsh.), pin cherry (*Prunus pensylvanica* L.), and red maple (*Acer rubrum* L.). Dominant tree species in the mature stands were American beech, sugar maple (*A. saccharum* Marsh.), and yellow birch (*B. alleghaniensis* Britt.).

Table 1. Description of the four stands at the Bartlett Experimental Forest.

Stand	Age Class	Year Last Harvested	Elevation (m)	Aspect	Slope (%)
C1	Young	1990	570	SE	5–20
C2	Young	1988	340	NE	15–30
C7	Mature	1890	440	ENE	5–10
C9	Mature	1890	440	NE	10–35

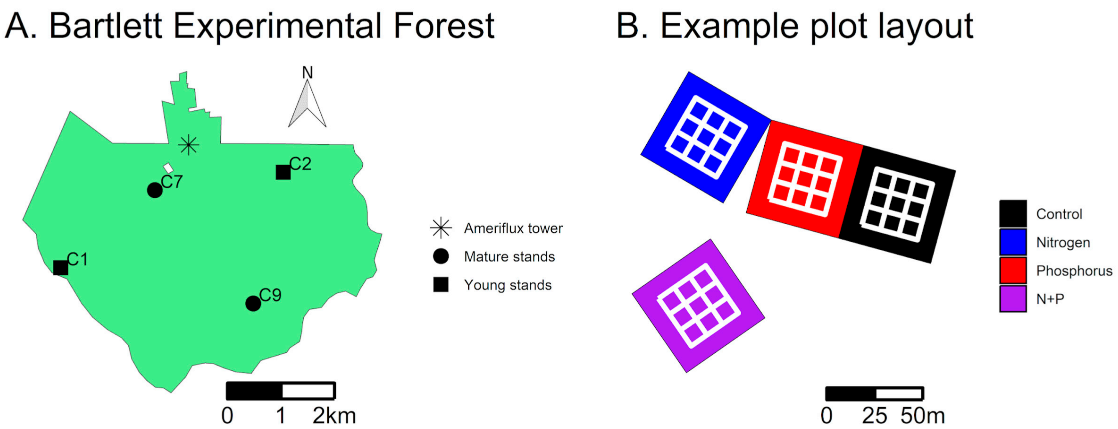

Figure 1. (**A**) Map of Bartlett Experimental Forest showing approximate locations of the two young and two mature stands used in this study. (**B**) Layout of the four experimental plots in Stand C9, each with a 50 m × 50 m treatment area and the 30 m × 30 m measurement area.

Each stand contained four treatment plots fertilized annually beginning in 2011 with either NH_4NO_3 at a rate of 30 kg N/ha/yr, NaH_2PO_4 at a rate of 10 kg P/ha/yr, or both, or neither [24]. The plots were 50 m × 50 m (0.25 ha) and included a 10 m buffer to ensure that trees, soil, and leaf litter in the inner 30 m × 30 m measurement area were fully treated (Figure 1). The measurement area was divided into nine 10 m × 10 m subplots.

2.2. Leaf Litter Collection

Fresh leaf litter from American beech, white birch, pin cherry, red maple, sugar maple, and yellow birch was collected from the four treatment plots in each of the four stands between 22 September to 25 October 2012 in deer netting suspended off the ground. Only litter that was not exposed to rainfall was used in litter bags. Litter was air-dried at room temperature and sorted by species.

2.3. Litter Bag Assembly

Litter mixes that represented young stands were created from stands C1 and C2. Litter mixes that represented mature stands were created from stands C7 and C9. The young litter mix consisted of 1.0 ± 0.02 g American beech, 0.75 ± 0.02 g white birch, 0.5 ± 0.02 g pin cherry, and 0.5 ± 0.02 g red maple. The mature stand litter mix consisted of 1.25 ± 0.02 g American beech, 1.0 ± 0.02 g sugar maple, and 0.3 ± 0.02 g yellow birch. Mixture masses were representative of dominant species found in litter traps in these stands in 2005, 2009, and 2010 [24]. Leaves collected from control, N, P, or N × P plots were deployed in the respective nutrient treatment plots.

Litter bags (10 × 10 cm) were constructed from nylon mesh and sealed with hot glue. Small mesh bags (63 µm) excluded macrofauna and mesofauna. Large mesh bags allowed detritivores (mesofauna and microfauna) and had a mesh size of 2 mm on the top portion and 63 µm on the bottom portion to minimize loss due to fragmentation. To determine the initial oven-dry weight of the samples, a subsample of bags was reserved and dried at 60 °C for 48 h and then weighed.

The large mesh material was noticeably more rigid than the fine mesh material. We assessed the force required to bend 5 bags of each type using a three-point bending test under a constant speed of 10 mm/min (Shimadzu autograph AGS-X series, Kyoto, Japan). The large mesh material averaged 3 ± 2 N/mm and the small mesh averaged 0.01 ± 0.001 N/mm.

2.4. Litter Analysis

Extra litter bags were constructed but not taken to the field. Three to four replicates of each combination of nutrient treatments (control, N, P, and N + P) and litter mix (young and old) were analyzed for tissue chemistry (31 samples). Samples were oven-dried at

60 °C and ground to pass a 40-mesh screen. For P concentration, 0.25 g of each sample was digested in 10 mL concentrated nitric acid using a MARS 6 microwave digestion system (CEM Corporation, Matthews, NC, USA), diluted to 50 mL with deionized water, and analyzed using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES, Optima 5300 DV, Perkin-Elmer, Markham, ON, Canada). For N concentration, 3.5–4.5 mg of each sample was analyzed using a CN analyzer (FlashEA 1112 analyzer, Thermo Fisher Scientific, Inc., Waltham, MA, USA).

2.5. Litter Bag Deployment

Ten sets of four litter bags were deployed in each treatment plot of stands C1, C2, C7, and C9 from 17 to 21 November 2012. One set was randomly placed in each of the nine subplots, with the 10th set in the center subplot. Each set consisted of all combinations of the two mesh sizes (large and small) filled with the two litter mixes (young and mature). Ziplock bags were used to contain the litter bags between the lab and the field to verify that material was not lost in transport. Litter bags were placed on top of the forest floor and each group of four bags was covered with 0.375 m^2 of wildlife netting held in place with landscaping staples.

2.6. Litter Bag Removal

Three replicate sets of four litterbags were collected from each of the four treatment plots in each of the four stands on three dates: 12 June 2013, 25 October 2013, and 31 October 2014. Of the 576 litter bags, only 12 were not found, and in only one case were none of the three replicates found of a treatment combination (C9 control, 27 September 2014). Collected litterbags were returned to the lab, dried at 60 °C, and weighed. Litter fragments found in the empty control bags were weighed to create a corrected initial weight. The empty large mesh bags used to control for mass gain averaged −0.04 g in July 2013, 0.10 g in October 2013, and 0.16 g in November 2014, and the small mesh bags gained 0.01 g in July 2013, 0.05 g in October 2013, and 0.05 g in November 2014.

2.7. Data Analysis

All analyses were performed with R software version 4.3 (R Core Team 2023, Vienna, Austria). We tested for differences in litter N and P concentrations prior to deployment for 31 samples using an ANOVA with species mix, N addition, P addition, and the interaction of N and P addition. The rate of decomposition was calculated by examining mass loss at 519, 2252, and 4491 cumulative growing degree days (GDD) where the soil temperature was above 4 °C [31]. The exponential decay rate constant, k (GDD^{-1}), was calculated for each plot by fitting a nonlinear model of the percentage of the initial mass remaining (A) as a function of time, using the formula $A = A_0 e^{-kt}$, where A_0 is the initial mass (100%) and t is time in GDD.

The decay constant k was the response variable in a linear mixed effect ANOVA calculated with the R package nlme [34]. The full model included N addition, P addition, the interaction of N and P addition, mesh size (small and large), species composition (litter from young and mature stands), and stand age (young and mature). The nutrient treatment plots were nested within each stand and used as random effect variables. Because few of the terms were significant with the full model, we used backward model selection. The least significant term was iteratively dropped from each model until there was no improvement in Akaike's information criterion (AIC). When the main effect of N was dropped from the model, the N × P interaction term was also dropped, because an interaction term is not meaningful without the main effects. To report the difference in decay rates predicted by the mixed effect models we used the R package emmeans [35].

The dplyr package [36] was used for data wrangling. The package ggplot2 [37] was used for data visualization, sf for spatial data wrangling [38], ggsn for scale bars [39], ggtext to display superscripts in figures [40], and patchwork for combining figures for display [41].

3. Results

Decomposition of leaf litter incubated in northern hardwood stands proceeded over time, averaging 18% mass loss over the first 7 months, corresponding to 519 growing-degree days, as this included the first winter. After 11 months, corresponding to 2252 growing degree days, the average mass loss was 34%. After 22 months, corresponding to 4491 growing degree days, the average mass loss was 49% (Figure 2).

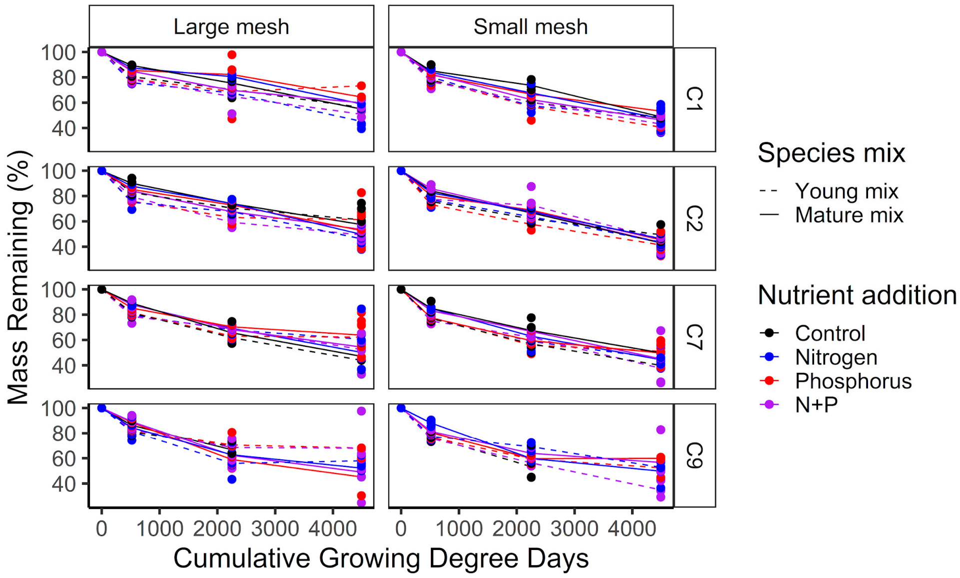

Figure 2. Mass loss of litter over time, represented by a heat sum. Litterbags were installed on 17–21 November 2012 and removed on 12 June 2013, 25 October 2013, and 27 September 2014.

Litter from P-treated plots (P and NP) had 42% higher P concentrations than litter from plots without added P (control and N plots) ($p < 0.001$ for the main effect of P in ANOVA, Figure 3). Litter from N-treated plots (N and NP) had 5% higher N concentrations than litter from plots without added P (control and P plots) but this difference was not statistically significant ($p = 0.15$). The mix of litter from young stands had 18% higher N concentration ($p < 0.001$) and 13% higher P concentration ($p = 0.06$) than litter from mature stands.

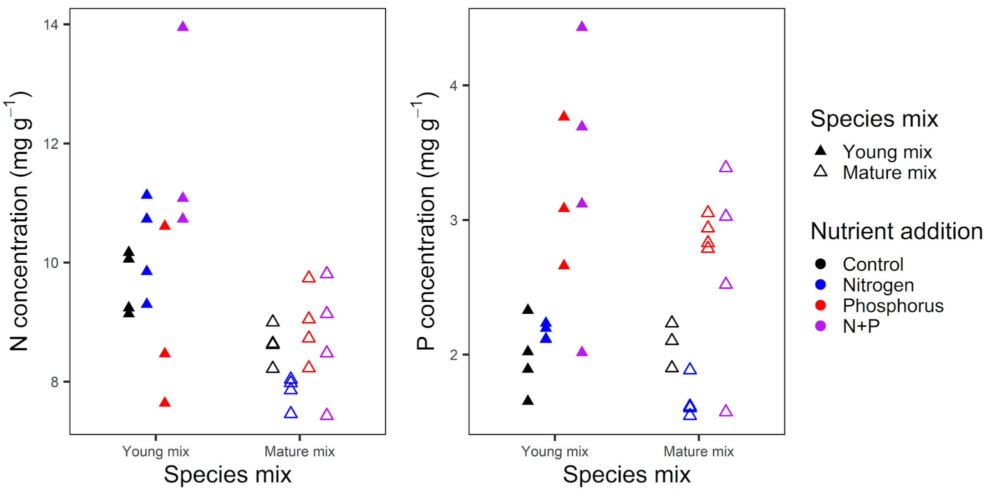

Figure 3. Foliar N and P concentrations of leaf litter from young and mature stands after 2 years of nutrient addition. These litter samples were taken from bags that were constructed but not installed.

The litter with a species composition characteristic of our young stands decomposed more quickly than the litter representing mature stands ($p = 0.01$ for species mix in the full model). The environment in which it was placed was not as important: neither the age of the stand in which it was placed (p = 0.31), N addition (p = 0.59), P addition (p = 0.41), nor the interaction of N and P addition (p = 0.13) were significant predictors of the decomposition rate, defined by fitting an exponential decay constant.

Decomposition rates were best explained by a model including only mesh type (Table 2), where bags of small mesh (63 µm) had lost 54% of their mass, whereas bags of large mesh (2 mm) had only lost 44% of their mass at the end of the experiment (Figure 2). Using the model with mesh type as the only effect, we found a 26% greater decay constant in the small mesh bags ($p < 0.001$, Figure 4).

Table 2. Five models were systematically assessed based on AIC values. The number of terms used in each model ranged from 1 to 6, with mesh representing small or large mesh type, mix representing the main effect of young or mature species litter, stand age representing 'young' and 'mature' stand ages, N and P addition representing whether that nutrient was added, and N × P representing the interaction of N and P addition. The model with all factors included was the starting point. The least significant term was dropped from each model, resulting in continuous improvement in the AIC.

Degrees of Freedom	Model Terms	AIC
6	Mesh + Mix + Stand age + N × P	−990
4	Mesh + Mix + P + Stand age	−1032
3	Mesh + Mix + P	−1054
2	Mesh + Mix	−1076
1	Mesh	−1092

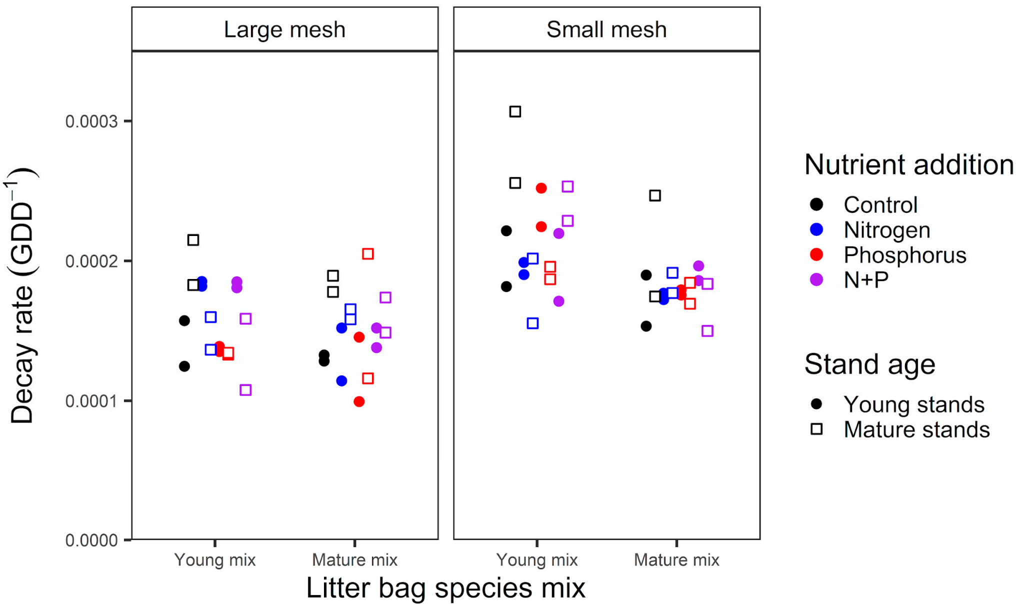

Figure 4. Rate of decay (k) in large mesh and small mesh litter bags with young or mature species mix and N or P addition incubated in two young stands (C1 and C2) and two mature stands (C7 and C9).

4. Discussion

It was surprising that decomposition proceeded more quickly in 63 µm small mesh bags than in the 2 mm large mesh bags, given the preponderance of reports of larger mesh sizes allowing faster decomposition, as seen in a meta-analysis examining 132 published litter bag studies [40]. Fine mesh bags allow entry by microfauna, such as fungi and bacteria. These organisms break down litter components such as lignin and other side products [42]. Large mesh bags allow entry by mesofauna, such as mites and springtails, in the case of our 1 mm large mesh; in other studies, even larger mesh sizes allow macrofauna, such as earthworms and small insects, to contribute to litter comminution.

Litter decomposition experiments with large mesh bags may have overestimated the effects of soil mesofauna if loss by fragmentation is mistakenly considered to have been respired [15,40,43]. In our study, fine mesh was used on the bottom of the large mesh bags to prevent the loss of litter fragments and frass.

The faster decomposition we observed in fine mesh bags could be an artifact of a difference in material stiffness. The coarse mesh plastic screen used in our study required two orders of magnitude more force to deform than the fine mesh (3 ± 2 N/mm vs. 0.01 ± 0.001 N/mm). The flexibility of the small mesh bags may have allowed them to make better contact with the soil, and thus better retain moisture. Drier conditions can result in decreased respiration [44,45], decreased soil faunal abundance [46], and lower decomposition rates [47]. A layer of large mesh included with the small mesh bags would have eliminated this unintended effect of mesh size on bag stiffness.

Decomposition proceeded more quickly for leaf litter collected in the young than mature stands, even though beech was the largest component of both mixtures (36% of the young mix and 49% of the mature mix). The other species in the young mix were early successional (white birch, pin cherry, and red maple), while those in the mature mix (sugar maple and yellow birch) were shade tolerant. These climax species would be expected to invest more in defensive compounds and have more recalcitrant litter [48–50]. It is also possible that beech foliage differs in decomposability between young and mature stands, but that question cannot be addressed in this study, where species were combined in mixtures.

Notably, decomposition rates were indistinguishable for litter placed in young and mature stands. Canopy closure occurs early in stand development in this forest type [47] and soil moisture and temperature were not consistently higher in our young than in our mature stands [51]. Thus, in the setting of our study, the differences in litter quality were more important than the differences in the environment due to stand age.

Initial differences in N concentration of litter from N-treated plots were not detectable ($p = 0.15$), and we did not find differences in the decomposition of litter due to N treatment. Initial differences in litter P were substantial (42% higher in litter from P treatment plots, $p < 0.001$), so it is perhaps surprising that we did not find differences in the decomposition of litter due to P treatment.

The young litter mix was higher in concentrations of both N (by 18%) and P (by 13%), making it a more attractive substrate to decomposers. Given the lack of effect of P concentration on decomposition rates, the difference in decomposability of litter from young and mature forests is likely attributable to their C:N ratio and not the differences in P compounds. The life history strategies of early successional tree species allow them to establish quickly, with higher quality leaf litter and more rapid nutrient cycling, while those of mature forests include greater investments in defense, more lignin, and higher C:N ratios in foliage, and lower rates of decomposition and nutrient cycling [52]. This study provides support for the importance of foliar attributes rather than the differences in the physical environment caused by forest succession.

5. Conclusions

In summary, litter from young stands had higher initial N and P concentrations and decomposed more quickly than litter from mature stands, regardless of whether it was placed in young or mature stands to decompose. Litter from trees in plots fertilized with P had higher P concentrations, but this did not detectably affect litter decomposition rates. Litter from trees in plots fertilized with N did not have as strong a signal in N concentration, and no effect of N addition was detected in mass loss rates.

Like the successional status of the stands, the addition of N or P to plots did not have a detectable effect on decomposition rates. Additional studies of decomposition in the MELNHE experiment are underway and may be more likely to detect the effects of nutrient addition; this early experiment was conducted with litter produced after only two years of fertilization.

There was a strong effect of mesh type on decomposition rates, probably due to an unintended difference in mesh stiffness: the large mesh material, intended to allow entry by mesofauna on decomposition rates, required two orders of magnitude more force to deform, and thus likely made poor contact with the soil. Care should be taken to avoid unintended artifacts of treatments; in this case, adding a large mesh layer to the small mesh bags would have equalized their stiffness.

Author Contributions: Conceptualization, R.B. and R.D.Y.; formal analysis, A.R.Y. and B.N.I.; investigation, R.B. and R.D.Y.; data curation, A.R.Y.; writing—original draft preparation, B.N.I., A.R.Y. and R.D.Y.; writing—review and editing, A.R.Y. and R.D.Y.; visualization, B.N.I. and A.R.Y.; funding acquisition, R.D.Y. and R.B. All authors have read and agreed to the published version of the manuscript.

Funding: Funding was provided by the USDA National Institute of Food and Agriculture (2019-67019-29464) and NSF Long-Term Ecological Research (DEB-1114804 and DEB-1637685).

Data Availability Statement: The original data presented in the study are openly available in Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Leaf Litter Decomposition 2012–2014 ver 1. Environmental Data Initiative at https://doi.org/10.6073/pasta/704c062966f0289818e438bee78a71fe (accessed on 10 October 2024).

Acknowledgments: A hundred 7th and 8th graders in Rick Biche's classes at Kennett Middle School, Conway, NH, sorted leaf litter by species and constructed and filled the litter bags. Kevin Richard, had the trust and vision to allow students to engage in such a project. Gracie Gilcrist and Jeff Merriam analyzed the leaf litter samples from bags that were not deployed, and Jenna Zukswert finished processing the last round of collected litterbags. Anqi Ji measured the stiffness of the mesh materials. Melany Fisk, Christy Goodale, and Geoff and Jackie Wilson provided early support and guidance. Craig See, Adam Wild, and Matt Vadeboncoeur reviewed early drafts of the manuscript. We are grateful for the cooperation and support of the U.S Forest Service Northern Research Station and the Bartlett Experimental Forest. This project is a contribution to the Hubbard Brook Ecosystem Study.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Lambers, H.; Chapin, F.S.; Pons, T.L. *Plant Physiological Ecology*, 1st ed.; Springer: New York, NY, USA, 1998; ISBN 978-1-4757-2855-2.
2. Didham, R.K. Altered Leaf-Litter Decomposition Rates in Tropical Forest Fragments. *Oecologia* **1998**, *116*, 397–406. [CrossRef] [PubMed]
3. Seastedt, T.R.; Crossley, D.A., Jr. The Influence of Arthropods on Ecosystems. *BioScience* **1984**, *34*, 157–161. [CrossRef]
4. Prescott, C.E. Do Rates of Litter Decomposition Tell Us Anything We Really Need to Know? *For. Ecol. Manag.* **2005**, *220*, 66–74. [CrossRef]
5. Cuevas, E.; Medina, E. Nutrient Dynamics within Amazonian Forests. *Oecologia* **1988**, *76*, 222–235. [CrossRef]
6. Inagaki, Y.; Miura, S.; Kohzu, A. Effects of Forest Type and Stand Age on Litterfall Quality and Soil N Dynamics in Shikoku District, Southern Japan. *For. Ecol. Manag.* **2004**, *202*, 107–117. [CrossRef]
7. Coleman, D.C.; Crossley, D.A., Jr. *Fundamentals of Soil Ecology*, 2nd ed.; Elsevier: Amsterdam, The Netherlands, 2004; ISBN 978-0-12-179726-3.
8. Chen, J.; Saunders, S.C.; Crow, T.R.; Naiman, R.J.; Brosofske, K.D.; Mroz, G.D.; Brookshire, B.L.; Franklin, J.F. Microclimate in Forest Ecosystem and Landscape Ecology: Variations in Local Climate Can Be Used to Monitor and Compare the Effects of Different Management Regimes. *BioScience* **1999**, *49*, 288–297. [CrossRef]
9. Lebrija-Trejos, E.; Pérez-García, E.A.; Meave, J.A.; Poorter, L.; Bongers, F. Environmental Changes during Secondary Succession in a Tropical Dry Forest in Mexico. *J. Trop. Ecol.* **2011**, *27*, 477–489. [CrossRef]
10. Schilling, E.M.; Waring, B.G.; Schilling, J.S.; Powers, J.S. Forest Composition Modifies Litter Dynamics and Decomposition in Regenerating Tropical Dry Forest. *Oecologia* **2016**, *182*, 287–297. [CrossRef]
11. Trogisch, S.; He, J.-S.; Hector, A.; Scherer-Lorenzen, M. Impact of Species Diversity, Stand Age and Environmental Factors on Leaf Litter Decomposition in Subtropical Forests in China. *Plant Soil* **2016**, *400*, 337–350. [CrossRef]
12. Hong, D.S.; Gonzales, K.E.; Fahey, T.J.; Yanai, R.D. Foliar Nutrient Concentrations of Six Northern Hardwood Species Responded to Nitrogen and Phosphorus Fertilization but Did Not Predict Tree Growth. *PeerJ* **2022**, *10*, e13193. [CrossRef]
13. Swift, M.J.; Heal, O.W.; Anderson, J.M. *Decomposition in Terrestrial Ecosystems*; University of California Press: Berkeley, CA, USA, 1979; ISBN 978-0-520-04001-4.
14. Bocock, K.L.; Gilbert, O.J.W. The Disappearance of Leaf Litter under Different Woodland Conditions. *Plant Soil* **1957**, *9*, 179–185. [CrossRef]

15. Kampichler, C.; Bruckner, A. The Role of Microarthropods in Terrestrial Decomposition: A Meta-Analysis of 40 Years of Litterbag Studies. *Biol. Rev.* **2009**, *84*, 375–389. [CrossRef] [PubMed]
16. Wise, D.H.; Lensing, J.R. Impacts of Rainfall Extremes Predicted by Climate-Change Models on Major Trophic Groups in the Leaf Litter Arthropod Community. *J. Anim. Ecol.* **2019**, *88*, 1486–1497. [CrossRef] [PubMed]
17. Knorr, M.; Frey, S.D.; Curtis, P.S. Nitrogen Additions and Litter Decomposition: A Meta-Analysis. *Ecology* **2005**, *86*, 3252–3257. [CrossRef]
18. Cleveland, C.; Townsend, A.; Schmidt, S. Phosphorus Limitation of Microbial Processes in Moist Tropical Forests: Evidence from Short-Term Laboratory Incubations and Field Studies. *Ecosystems* **2002**, *5*, 680–691. [CrossRef]
19. Wu, J.; Zhang, H.; Cheng, X.; Liu, G. Nitrogen Addition Stimulates Litter Decomposition Rate: From the Perspective of the Combined Effect of Soil Environment and Litter Quality. *Soil Biol. Biochem.* **2023**, *179*, 108992. [CrossRef]
20. Chen, H.; Dong, S.; Liu, L.; Ma, C.; Zhang, T.; Zhu, X.; Mo, J. Effects of Experimental Nitrogen and Phosphorus Addition on Litter Decomposition in an Old-Growth Tropical Forest. *PLoS ONE* **2013**, *8*, e84101. [CrossRef]
21. Hobbie, S.E.; Vitousek, P.M. Nutrient Limitation of Decomposition in Hawaiian Forests. *Ecology* **2000**, *81*, 1867–1877. [CrossRef]
22. Barantal, S.; Schimann, H.; Fromin, N.; Hättenschwiler, S. Nutrient and Carbon Limitation on Decomposition in an Amazonian Moist Forest. *Ecosystems* **2012**, *15*, 1039–1052. [CrossRef]
23. Kelly, J.M.; Henderson, G.S. Effects of Nitrogen and Phosphorus Additions on Deciduous Litter Decomposition. *Soil Sci. Soc. Am. J.* **1978**, *42*, 972–976. [CrossRef]
24. Yanai, R.D.; Fisk, M.C.; Vadeboncoeur, M.A.; Zukswert, J.M.; Mann, T.; Young, A.; Walsh, G.; Morley, M.; See, C.R. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Litterfall Mass 2009–2022 ver 1. Environmental Data Initiative. 2024. Available online: https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-hbr.404.1 (accessed on 11 October 2024).
25. Fisk, M.C.; Ratliff, T.J.; Goswami, S.; Yanai, R.D. Synergistic Soil Response to Nitrogen plus Phosphorus Fertilization in Hardwood Forests. *Biogeochemistry* **2014**, *118*, 195–204. [CrossRef]
26. Gonzales, K.; Yanai, R. Nitrogen–Phosphorous Interactions in Young Northern Hardwoods Indicate P Limitation: Foliar Concentrations and Resorption in a Factorial N by P Addition Experiment. *Oecologia* **2019**, *189*, 829–840. [CrossRef] [PubMed]
27. Gonzales, K.E.; Yanai, R.D.; Fahey, T.J.; Fisk, M.C. Evidence for P Limitation in Eight Northern Hardwood Stands: Foliar Concentrations and Resorption by Three Tree Species in a Factorial N by P Addition Experiment. *For. Ecol. Manag.* **2023**, *529*, 120696. [CrossRef]
28. Goswami, S.; Fisk, M.C.; Vadeboncoeur, M.A.; Garrison-Johnston, M.; Yanai, R.D.; Fahey, T.J. Phosphorus Limitation of Aboveground Production in Northern Hardwood Forests. *Ecology* **2018**, *99*, 438–449. [CrossRef] [PubMed]
29. Shan, S.; Devens, H.; Fahey, T.J.; Yanai, R.D.; Fisk, M.C. Fine Root Growth Increases in Response to Nitrogen Addition in Phosphorus-Limited Northern Hardwood Forests. *Ecosystems* **2022**, *25*, 1589–1600. [CrossRef]
30. Li, S.; Fisk, M.C.; Yanai, R.D.; Fahey, T.J. Co-Limitation of Fine Root Growth by Nitrogen and Phosphorus in Early Successional Northern Hardwood Forests. *Ecosystems* **2024**, *27*, 33–44. [CrossRef]
31. Richardson, A.; Hollinger, D. *AmeriFlux BASE US-Bar Bartlett Experimental Forest*; Ver.6-5 AmeriFlux AMP, (Dataset); Lawrence Berkeley National Laboratory (LBNL): Berkeley, CA, USA; Northern Arizona University: Flagstaff, AZ, USA, 2023. [CrossRef]
32. Vadeboncoeur, M.A.; Hamburg, S.P.; Blum, J.D.; Pennino, M.J.; Yanai, R.D.; Johnson, C.E. The quantitative soil pit method for measuring belowground carbon and nitrogen stocks. *Soil Sci. Soc. Am. J.* **2012**, *76*, 2241–2255. [CrossRef]
33. Vadeboncoeur, M.A.; Hamburg, S.P.; Yanai, R.D.; Blum, J.D. Rates of sustainable forest harvest depend on rotation length and weathering of soil minerals. *For. Ecol. Manag.* **2014**, *318*, 194–205. [CrossRef]
34. Pinheiro, J.; Bates, D.; R Core Team. Nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-166. 2023. Available online: https://CRAN.R-project.org/package=nlme (accessed on 11 October 2024).
35. Lenth, R. Emmeans: Estimated Marginal Means, Aka Least-Squares Means. R Package Version 1.10.5. 2023. Available online: https://cran.r-project.org/web/packages/emmeans/index.html (accessed on 11 October 2024).
36. Wickham, H.; François, R.; Henry, L.; Müller, K.; Vaughan, D. A Grammar of Data Manipulation. R Package Version 1.1.2. 2023. Available online: https://dplyr.tidyverse.org (accessed on 11 October 2024).
37. Wickham, H. *Ggplot2*, 2nd ed.; Use R! Springer International Publishing: Cham, Switzerland, 2016; ISBN 978-3-319-24275-0.
38. Pebesma, E.; Bivand, R. *Spatial Data Science: With Applications in R*; Chapman and Hall/CRC: Boca Raton, FL, USA, 2023.
39. Santos Baquero, O. ggsn: North Symbols and Scale Bars for Maps Created with 'ggplot2' or 'ggmap'_. R Package Version 0.5.3. Available online: https://github.com/oswaldosantos/ggsn (accessed on 25 September 2024).
40. Frouz, J.; Roubíčková, A.; Heděnec, P.; Tajovský, K. Do Soil Fauna Really Hasten Litter Decomposition? A Meta-Analysis of Enclosure Studies. *Eur. J. Soil Biol.* **2015**, *68*, 18–24. [CrossRef]
41. Pedersen, T. Patchwork: The Composer of Plots_. R Package Version 1.1.3. Available online: https://cran.r-project.org/package=patchwork (accessed on 25 September 2024).
42. Bani, A.; Pioli, S.; Ventura, M.; Panzacchi, P.; Borruso, L.; Tognetti, R.; Tonon, G.; Brusetti, L. The Role of Microbial Community in the Decomposition of Leaf Litter and Deadwood. *Appl. Soil Ecol.* **2018**, *126*, 75–84. [CrossRef]
43. David, J.F. The Role of Litter-Feeding Macroarthropods in Decomposition Processes: A Reappraisal of Common Views. *Soil Biol. Biochem.* **2014**, *76*, 109–118. [CrossRef]
44. Bradford, M.A.; Tordoff, G.M.; Eggers, T.; Jones, T.H.; Newington, J.E. Microbiota, Fauna, and Mesh Size Interactions in Litter Decomposition. *Oikos* **2002**, *99*, 317–323. [CrossRef]

45. Bunnell, F.L.; Tait, D.E.N.; Flanagan, P.W.; Van Clever, K. Microbial Respiration and Substrate Weight Loss—I: A General Model of the Influences of Abiotic Variables. *Soil Biol. Biochem.* **1977**, *9*, 33–40. [CrossRef]
46. Aupic-Samain, A.; Baldy, V.; Delcourt, N.; Krogh, P.H.; Gauquelin, T.; Fernandez, C.; Santonja, M. Water Availability Rather than Temperature Control Soil Fauna Community Structure and Prey–Predator Interactions. *Funct. Ecol.* **2021**, *35*, 1550–1559. [CrossRef]
47. Tan, B.; Yin, R.; Zhang, J.; Xu, Z.; Liu, Y.; He, S.; Zhang, L.; Li, H.; Wang, L.; Liu, S.; et al. Temperature and Moisture Modulate the Contribution of Soil Fauna to Litter Decomposition via Different Pathways. *Ecosystems* **2021**, *24*, 1142–1156. [CrossRef]
48. Côté, B.; Fyles, J.W. Leaf Litter Disappearance of Hardwood Species of Southern Québec: Interaction between Litter Quality and Stand Type. *Écoscience* **1994**, *1*, 322–328. [CrossRef]
49. MacLean, D.A.; Wein, R.W. Weight Loss and Nutrient Changes in Decomposing Litter and Forest Floor Material in New Brunswick Forest Stands. *Can. J. Bot.* **1978**, *56*, 2730–2749. [CrossRef]
50. Melillo, J.M.; Aber, J.D.; Muratore, J.F. Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics. *Ecology* **1982**, *63*, 621–626. [CrossRef]
51. Fahey, T.J.; Yanai, R.D.; Li, S.; Mann, T. Multiple Element Limitation in Northern Hardwood Experiment (MELNHE): Soil Respiration at Hubbard Brook Experimental Forest, Bartlett Experimental Forest and Jeffers Brook, Central NH USA, 2008—Present; ver 2; Environmental Data Initiative. 2021. Available online: https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-hbr.269.2 (accessed on 1 September 2024).
52. Cramer, J.; Fahey, T.; Battles, J. Patterns of Leaf Mass, Area and Nitrogen in Young Northern Hardwood Forests. *Am. Midl. Nat.* **2000**, *144*, 253–264. [CrossRef]