

Article

Meta-Analysis of Effects of Forest Litter on Seedling Establishment

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Abstract: Litter plays an important role in seedling establishment (emergence, survival, and early growth). Here, we performed a meta-analysis on 404 datasets from 33 independent studies to analyze the effects of litter cover on seedling emergence, survival, height, and biomass (root, stem, leaf, and total). Each dataset was stratified according to experimental conditions, litter type (broadleaf versus needle litter), litter amount (thickness), and seed size. The results showed that litter cover had an overall negative effect on seedling emergence and survival, a neutral effect on root, leaf, total biomass, and a positive effect on stem biomass and seedling height than the no-litter cover control. Compared to thin (<250 g m⁻²) and medium (250–500 g m⁻²) litter layers, thick litter (>500 g m⁻²) was more detrimental for seedling emergence, survival, and total biomass, which could be an adaptation mechanism to prevent the growth of young seedling among high densities of other plants (trees). Broadleaf litter cover had a stronger negative effect on seedling emergence and total biomass than needle litter. Litter cover had a stronger negative effect on emergence of small seeds than on emergence of larger seeds. Similarly, litter cover had a stronger overall negative effect on seedling emergence than on seedling survival. In field and common garden experiments, litter effects were negative for emergence and positive for total biomass. In glasshouse and germination chamber experiments, litter effects were negative for emergence, survival and total biomass. These findings would contribute to advancements in forest management, improving conservation and restoration efforts.

Keywords: plant biomass; litter thickness; litter type; seed size; seedling emergence; seedling survival



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1. Introduction

Plant litter is an important part of forest ecosystems, acting as a link between plants and soil [1,2], while influencing the natural regeneration of forests and accompanying tree growth [3–5]. However, available research on forest litter has mostly focused on litter decomposition [6–8], litterfall production, litterfall dynamics [9–11], ecological function of litter, such as how litter influences soil and water conservation [12,13], and nutrient cycling [14,15]. Litter cover is a rarely studied factor that affects the natural regeneration, although it is the first physical environment that seeds immediately encounter after they land on the ground [16–18]. This proximity means litter cover should have a major influence on seedling establishment (seedling emergence, survival, and early growth), the most sensitive stage in the plant life cycle and critical to the successful establishment of species [19–22]. The effect of litter cover on seedling emergence, survival and early growth depends on litter type, litter amount, seed size, and environmental conditions [23–30].

Meta-analyses are a useful method for examining litter effects on seedling emergence, survival and establishment in different ecosystems [31,32]. For example, the meta-analysis of Xiong and Nilsson [32] showed that litter had a greater impact on seedling emergence than on the other aspects of seedling establishment. Moreover, they found that field tests yielded stronger litter effects than greenhouse tests, and tree and forb litter influenced seedling establishment than grass litter. It has been also demonstrated that litter presence had a neutral effect on seedling emergence and survival, but a positive effect on biomass accumulation. Furthermore, litter had no effect on seedling establishment in field experiments but a positive effect on seedling emergence under common garden studies. However, in glasshouse experiments, litter effects were negative for emergence and positive for biomass accumulation. Finally, the meta-analysis indicated that litter presence had a stronger effect on large seeds than small seeds, with the former exhibiting improved emergence and survival, although biomass remained unaffected. Despite these advances, we still lack an overall understanding of how litter type, coverage thickness, and seed size differentially influence seedling emergence, survival, and growth.

Therefore, in this study, we performed a systematic meta-analysis to explore the effects of litter cover on seedling emergence, survival, and the early growth in forest ecosystems. Through our analysis of available literature, we grouped different litter attributes (litter type, litter thickness, seed size, and experimental condition) to determine their influence on seedling establishment. We specifically addressed three main questions. First, do needle and broadleaf litter covers differ in their effects on seedling emergence due to the vast differences in the physical structure between needles and broadleaf leaves? It is expected that large litter pieces may produce more physical barrier than the same mass of small litter particles, probably because small litter particles do not cover seedlings as large particles do. In addition, because litter surface area is closely related to the degree of light absorption, broadleaf litter would have greater light interception than needle litter, and yet light quantity and quality are important cues for seedling emergence. Thus, we predicated that broadleaf litter would inhibited seedling establishment more than needle litter. Second, is there a threshold for the effect of litter cover thickness on seedling establishment? We hypothesized that thick litter cover not only reduces the light quantity and then altering the light quality under the litter layer, but also can create a physical barrier that hamper seedlings to pierce through the litter from below to reach the light. We expect that a threshold of litter amount is occurred for seedlings establishment. Third, do the effects of litter cover on seedling emergence vary with seed size? Since larger seed sizes generally lead to larger seedling sizes, we expect that seedlings of large-seeded species possess a better ability to penetrate a layer of litter than small seedlings. We hypothesized that the emergence of small seeds was more inhibited than large seed under deeper litter layer. In addition, we examine the effects of experimental conditions (field, common garden, glasshouse and germination chamber experimental settings) on seedling emergence and establishment due to the fact that the experimental conditions could possibly influence the effects of litter cover.

2. Materials and Methods

The meta-analysis focused on published studies investigating forest ecosystems or forest species that explicitly manipulated litter cover and assessed the response of at least one of the following seedling attributes: emergence, survival, height, or biomass. A literature search spanning 1900–2018 (last search date: 31 December 2018) was performed in the database ISI Web of Science (keywords: “plant litter” AND “seed*” AND “forests”), yielding 2170 papers. After scanning through abstracts, methods, figures, and tables to determine relevance, all selected papers were determined using the following criteria:

1. Plant litter was manipulated in field experiments on litter cover in forest ecosystems or treatments under controlled conditions.
2. Independent experiments had both a test group and a control group, along with experimental replications.

3. At least one of the following seedling attributes was included: emergence, survival, height, biomass of seedling parts, and total biomass.
4. Sample size, mean, standard deviation, standard error of the sample, or raw data for calculating these values were included.
5. Studies using artificial litter were excluded.
6. With repeated-measures experiments, only a single measurement was included in the meta-analysis to ensure data independence.

Finally, 33 studies and 404 valid data points were retained, and the location of selected studies are shown in Figure 1. We performed a random effects meta-analysis for each of the seven datasets: emergence, survival, height, root biomass, stem biomass, leaf biomass, and total biomass. Litter type was classified as broadleaf versus needle; litter thickness as thin ($<250 \text{ g m}^{-2}$), medium ($250\text{--}500 \text{ g m}^{-2}$) and thick ($>500 \text{ g m}^{-2}$); seed size as small ($<1 \text{ mg}$) and large ($>1 \text{ mg}$); and experiment conditions as field, greenhouse, common garden, and germination chamber.

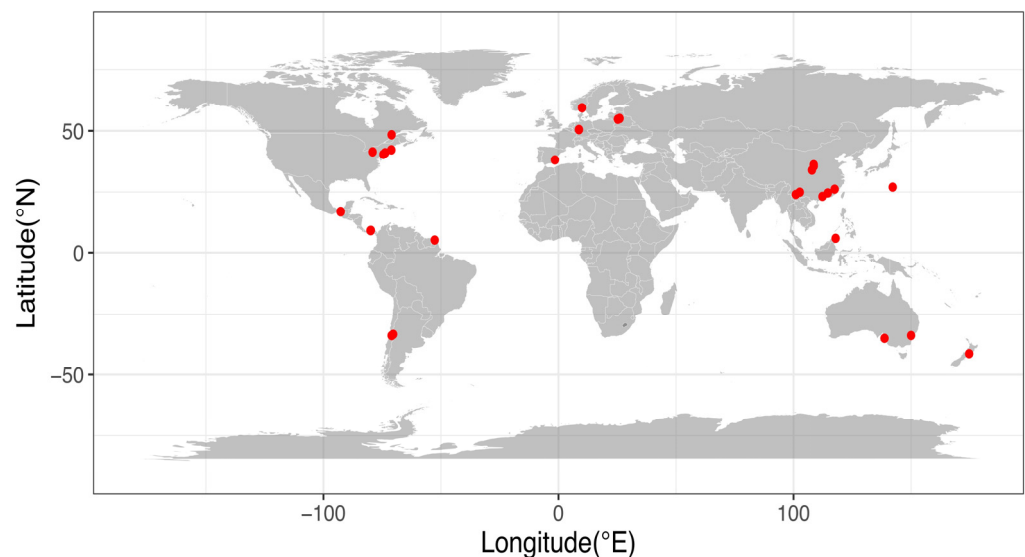


Figure 1. Locations of the collected studies.

All meta-analyses were conducted in META-WIN V.2.0 (Sinauer Associates, Sunderland, MA, USA). Random effect models were used to determine differences in mean effect sizes between groups, with confidence intervals (CI) calculated using the bootstrapping method (9999 iterations). A difference between means was significant ($p < 0.05$) if the 95% CI did not overlap with zero or the CIs of other groups. For every analysis, total heterogeneity (QT) was calculated to determine whether variance in effect size was greater than chance. QT is the weighted sum of squares, equivalent to total sum of squares in analysis of variance. The variance explained by the model (QM, equivalent to between-study variance in analysis of variance) was used to test for between-group differences.

3. Results

3.1. Overall Effect of Litter Cover on Seedling Establishment

Litter cover significantly decreased seedling emergence by 13.4% compared with no litter cover. Litter cover did not significantly affect seedling survival. In terms of biomass, litter cover did not significantly influence root, leaf, or total biomass of seedlings, although there was a positive trend for the former two traits and a negative trend for the latter. Litter cover significantly increased seedling height by 22.7% and increased stem biomass accumulation by 21.6% (Figure 2).

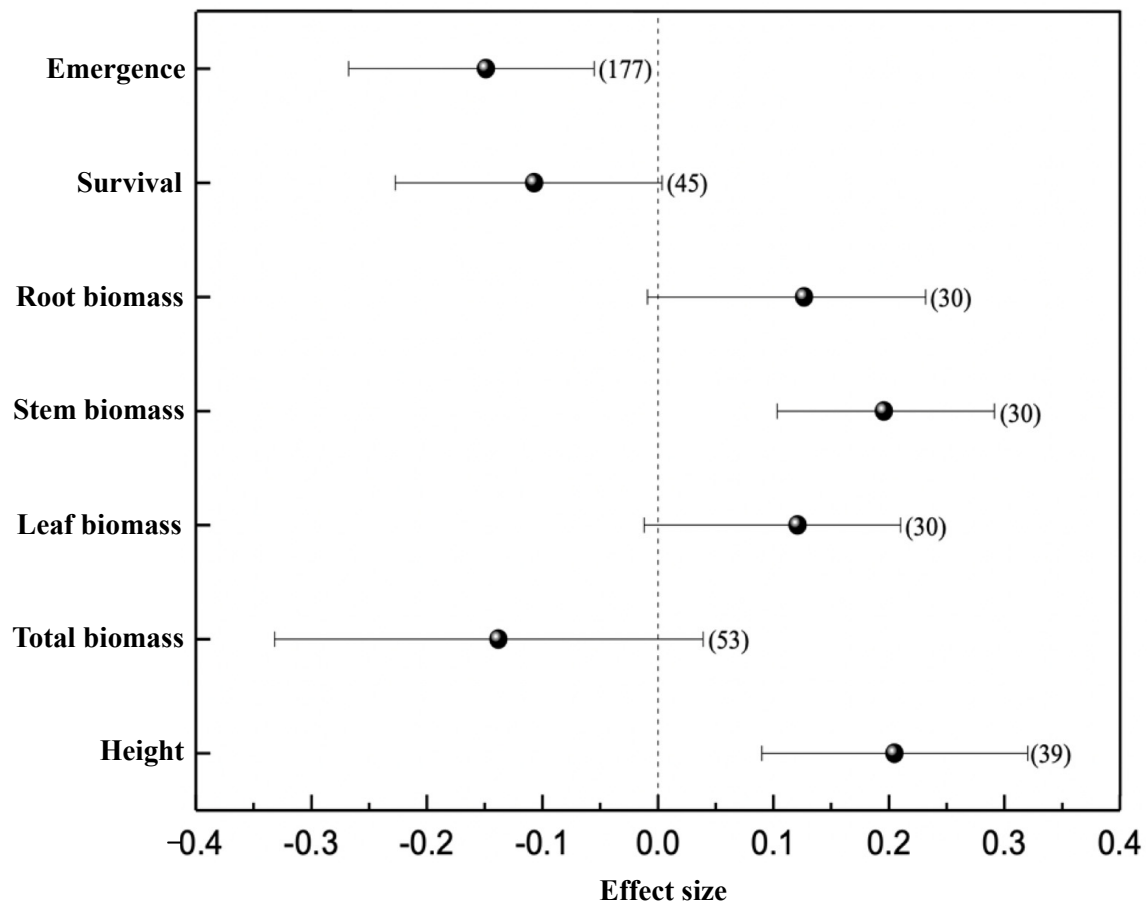


Figure 2. Mean effect size for each seedling-related trait under litter cover. The numbers in brackets represent the sample size of each indicator. An effect size > 0 indicates a positive effect of litter cover, while values < 0 indicate a negative effect. Error bars are 95% confidence intervals (CI).

3.2. Effects of Litter Types on Seedling Establishment

Broadleaf litter cover inhibited seedling emergence, leaf biomass, and total biomass accumulation, promoted seedling height and stem biomass accumulation, but did not influence seedling survival or root biomass accumulation (Figure 3). Conifer needle leaf litter cover inhibited seedling survival and total biomass accumulation, promoted stem biomass accumulation, but did not affect seedling emergence, leaf and root biomass accumulation, or seedling height (Figure 3).

3.3. Effects of Litter Thickness on Seedling Establishment

Thin litter ($< 250 \text{ g m}^{-2}$) had a negative effect on seedling survival and positive effects on stem and leaf biomass accumulations, but did not influence seedling emergence, root biomass, or total biomass (Figure 4). Medium litter ($250\text{--}500 \text{ g m}^{-2}$) negatively affected seedling survival, as well as leaf and total biomass accumulation, but had no effect on seedling emergence, seedling height, and stem and root biomass (Figure 4). Lastly, thick litter ($> 500 \text{ g m}^{-2}$) hindered seedling emergence, survival, leaf biomass, and total biomass, without influencing seedling height, stem biomass, or root biomass (Figure 4).

When we examined the effect of litter amount by litter type, we found that for broadleaf litter, a thin layer ($< 250 \text{ g m}^{-2}$) decreased seedling emergence by 4.3% compared with no litter cover, whereas medium thickness ($250\text{--}500 \text{ g m}^{-2}$) had no effect. Thick litter ($> 500 \text{ g m}^{-2}$) decreased seedling emergence by 45.1% (Figure 5a). For needle litter, both thin and medium litter layers negatively influenced seedling emergence, while a thick layer decreased emergence by 50.6% compared with no litter cover (Figure 5b).

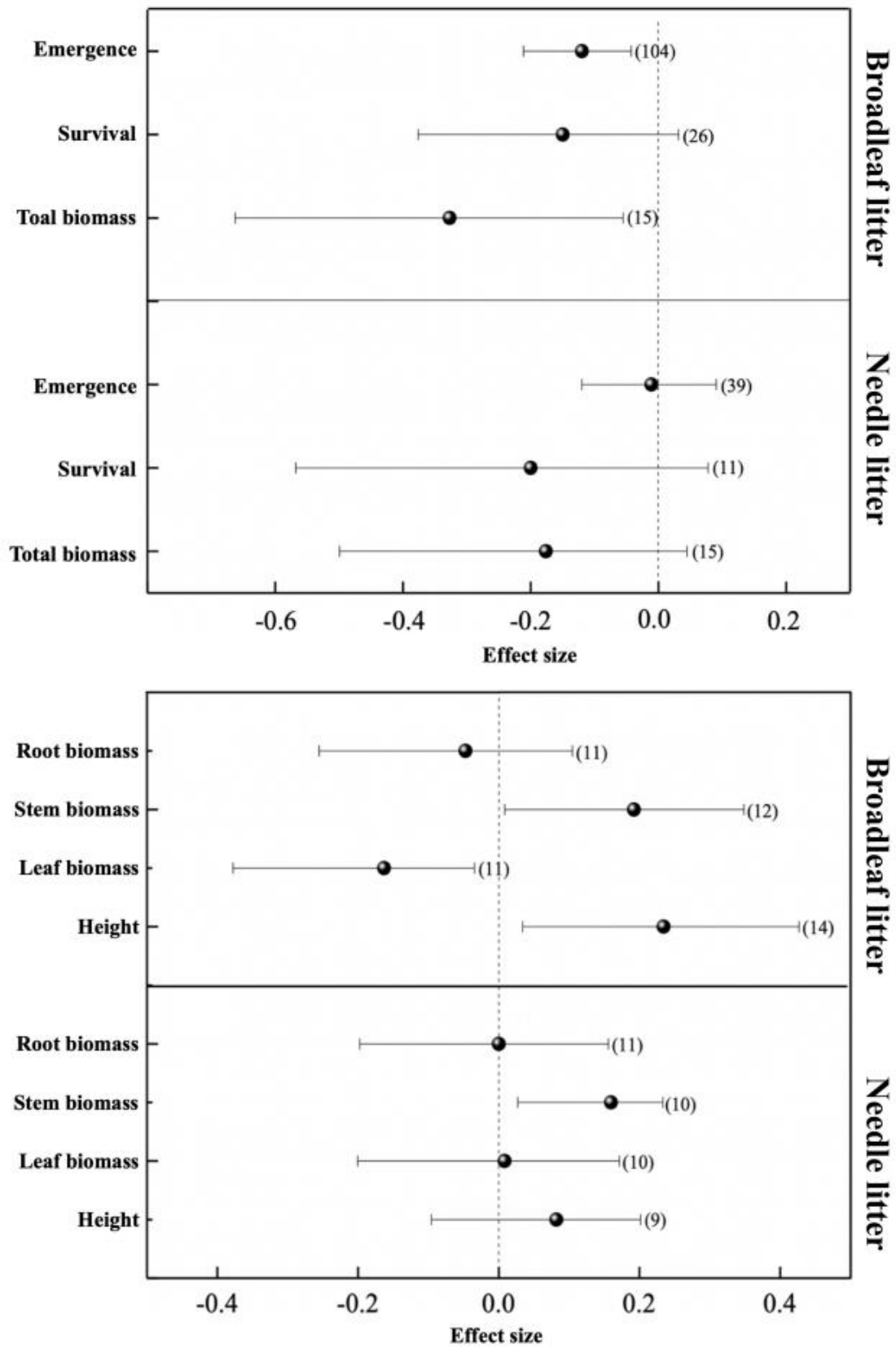


Figure 3. Mean effect size for seedling emergence, survival, total biomass, root, stem, leaf biomass, and height under broadleaf litter and conifer needle litter cover. Error bars represent 95% CIs. The numbers in brackets represent the sample size of each indicator.

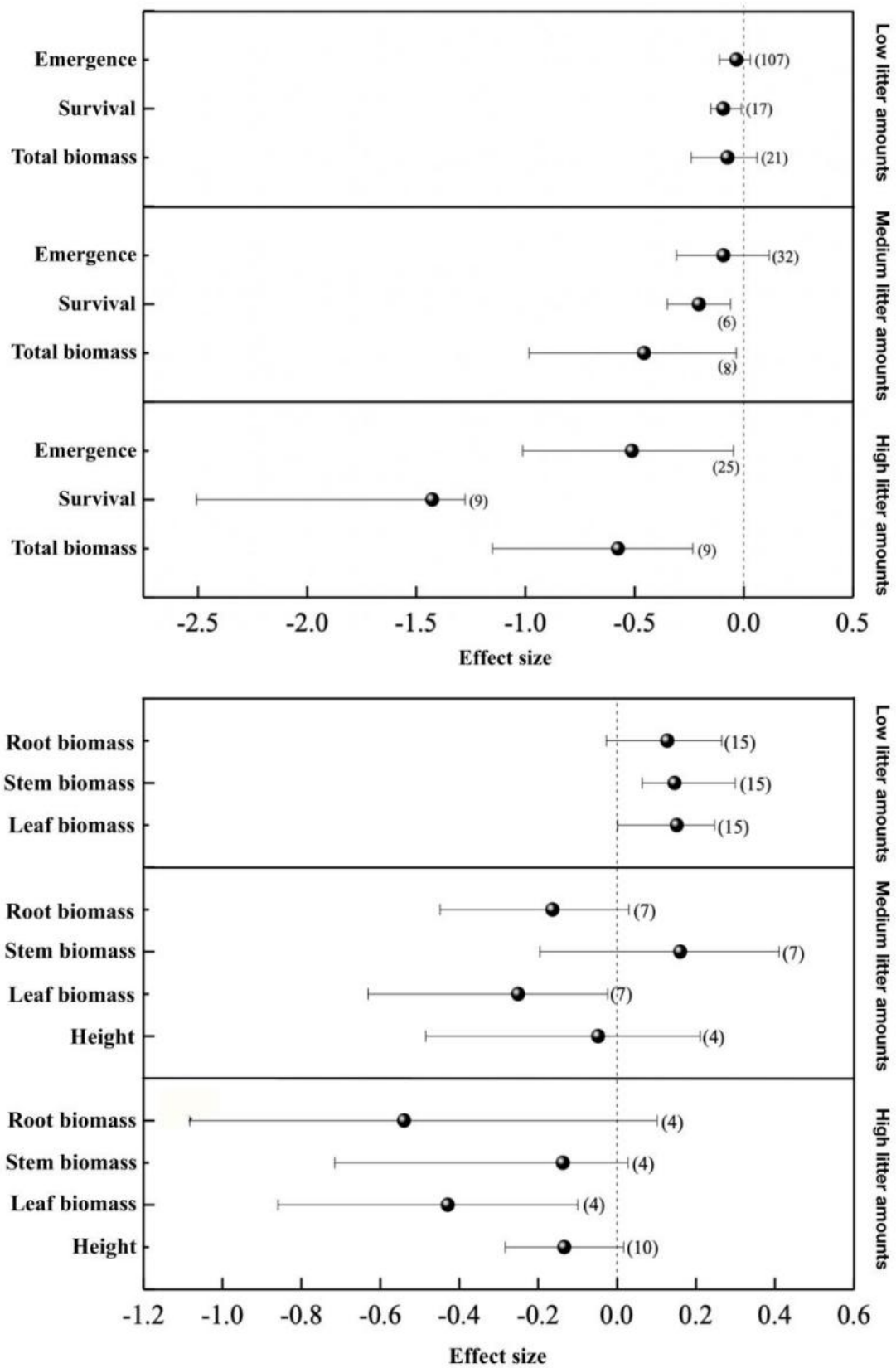


Figure 4. Mean effect size for seedling emergence, survival, total biomass, root, stem, leaf biomass, and height under low litter amounts cover (<250 g m⁻²), medium litter amounts cover (250–500 g m⁻²), and high litter amounts cover (>500 g m⁻²). Error bars represent 95% CIs.

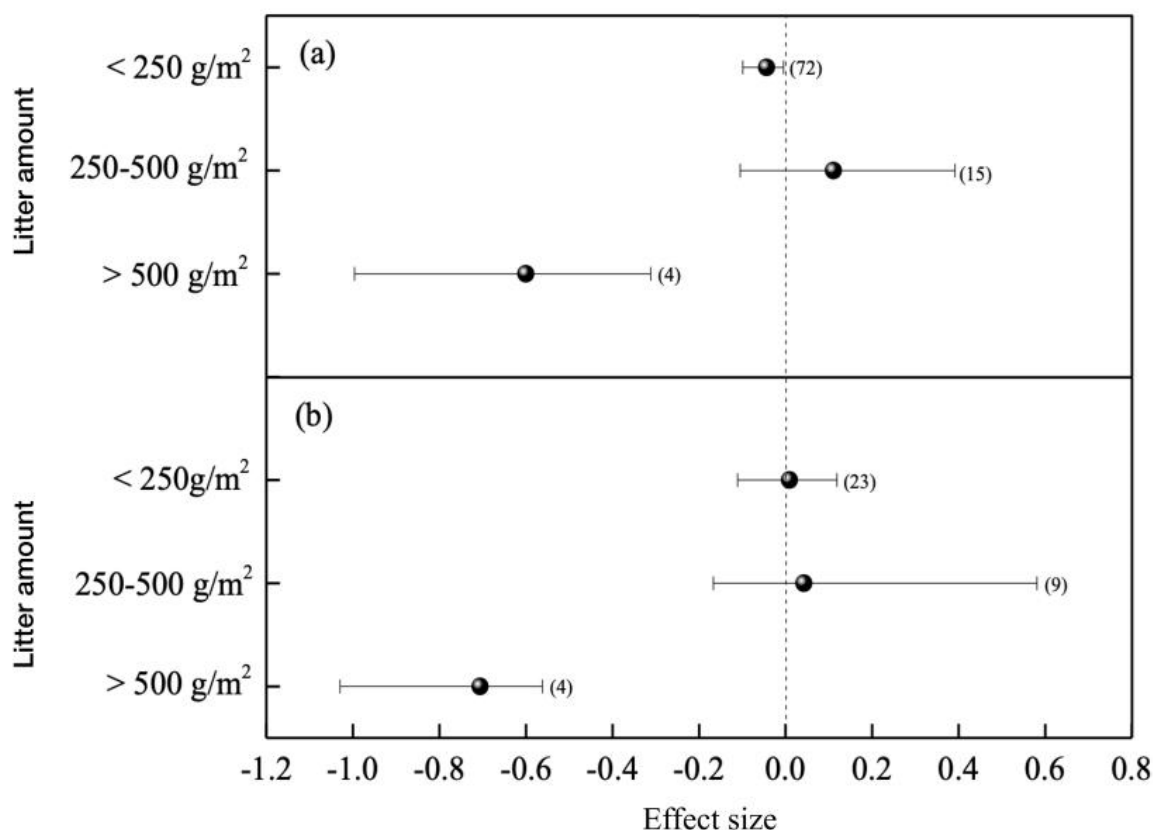


Figure 5. Mean effect size for seedling emergence under different litter amounts cover of broadleaf (a) and needle (b) litter. Error bars represent 95% CIs. The numbers in brackets represent the sample size of each indicator.

When we examined the interaction of litter amount and experiment conditions, we found that in greenhouse studies, thin and medium litter thickness had no effect on seedling emergence. However, thick litter had a negative effect (Figure 6a). In field studies, a thin litter layer did not influence seedling emergence, but a medium thickness had a beneficial effect (Figure 6b). In germination chamber studies, none of the three litter thicknesses affected seedling emergence (Figure 6c).

In terms of how seed size modulated the effect of litter amount, thin and medium thickness had negative effects on emergence of small seeds (<1 mg) (Figure 7a). For large seeds (>1 mg), thin and medium litter layers did not influence emergence, whereas thick litter had a negative effect (Figure 7b).

3.4. Effects of Litter on Seedling Establishment under Different Experimental Conditions

The effects of litter on seedling emergence, survival and growth under different experimental conditions showed differential response. In field studies, litter cover showed non-significant effect on seedling emergence and total biomass, but a negative effect on seedling survival (Figure 8a). Greenhouse studies showed a negative effect of litter cover on seedling emergence, survival, and total biomass (Figure 8b), whereas common garden studies showed no effect of litter cover on seedling emergence but had a positive effect on total biomass (Figure 8c). Finally, litter cover in germination chamber studies negatively influenced seedling emergence, survival, and total biomass (Figure 8d). Likewise, greenhouse studies showed a neutral effect of litter on leaf and root biomass, and a positive effect on stem biomass and height (Figure 9a). Litter cover in common garden studies had no effect on seedling height, but benefited root, stem, and leaf biomass growth (Figure 9b). Field studies showed a positive effect on seedling height (Figure 9c).

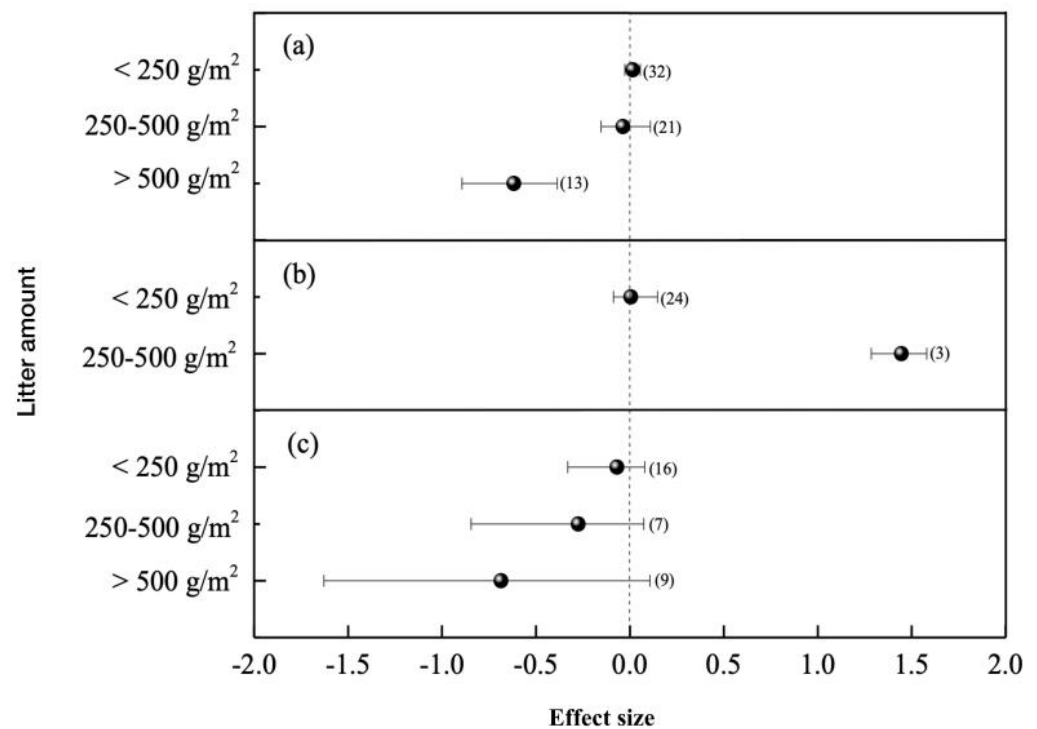


Figure 6. Mean effect size of litter amount on seedling emergence under greenhouse (a), field (b), and germination chamber (c) studies. Note that data on thin and medium thicknesses were included in field studies due to lack of studies on thick litter layer under this condition. Error bar represents 95% confidence interval.

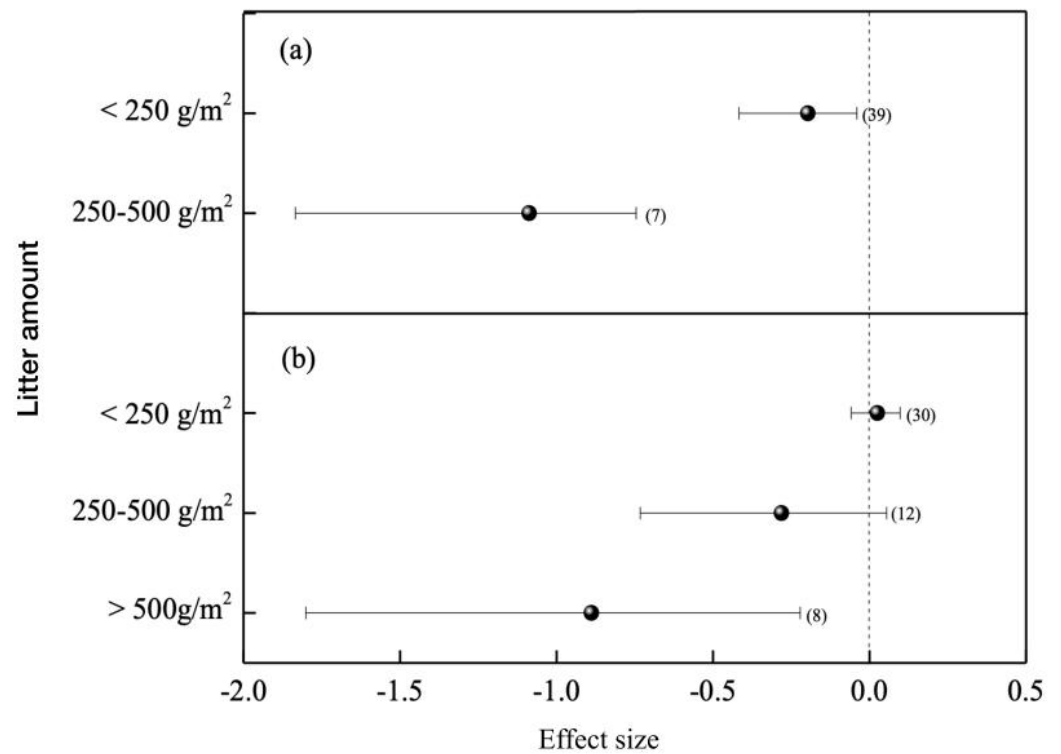


Figure 7. Mean effect size for emergence under different litter amounts of small (a) and large (b) seed sizes. Error bars represent 95% CIs.

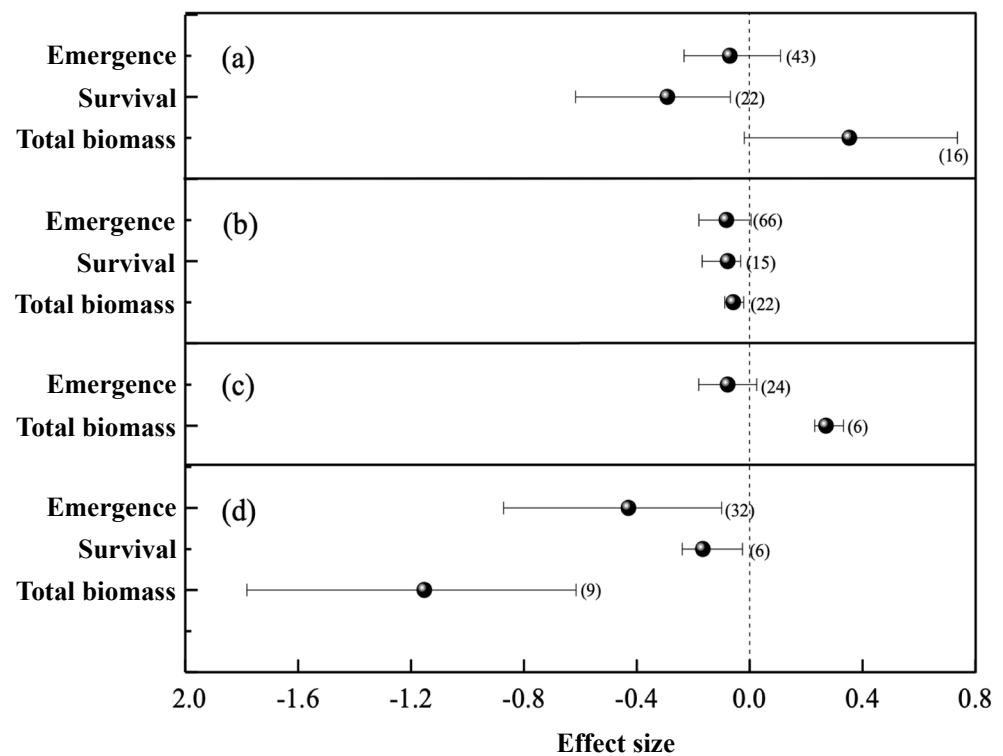


Figure 8. Mean effect size of litter cover for seedling emergence, survival, and total biomass in field (a), greenhouse (b), common garden (c), and germination chamber (d) studies. Error bars represent 95% CIs. The numbers in brackets represent the sample size of each indicator.

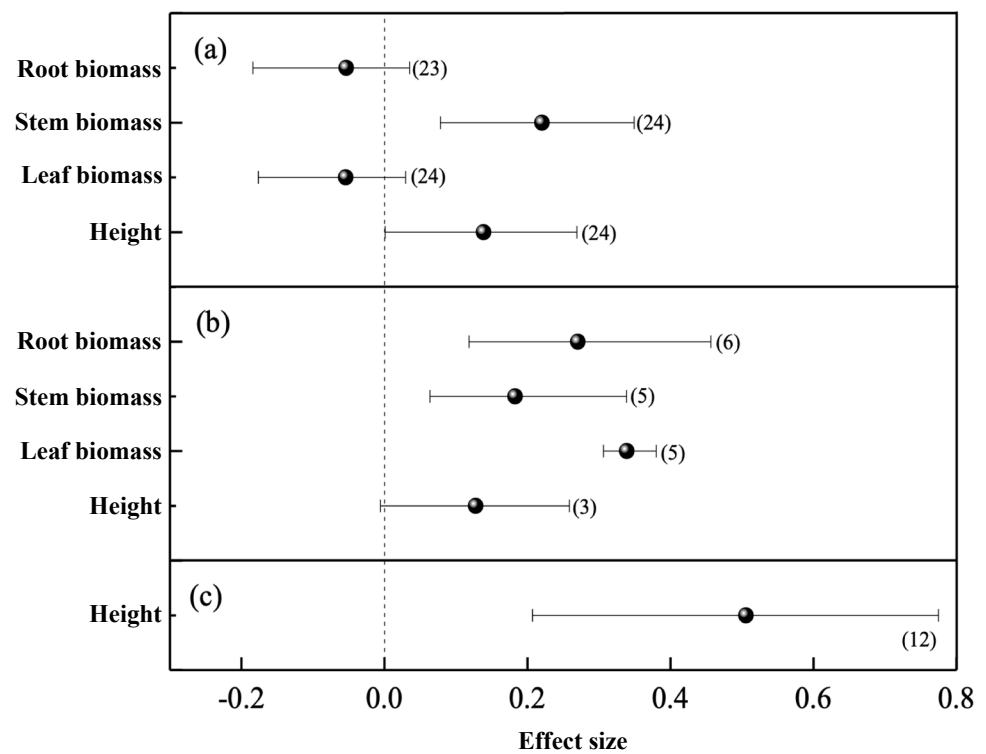


Figure 9. Mean effect size for seedling root, stem and leaf biomass, as well as height in greenhouse (a), common garden (b), and field (c) studies. Error bars represent 95% CIs.

4. Discussion

Our results showed that litter presence had a negative effect on seedling emergence in forest ecosystems, contrasting with grassland ecosystems, where litter cover has no significant effect [32]. The reason for this difference may be that forests have more litter than grasslands, and the forest canopy also lets in less light, leading to unfavorable conditions for photoblastic seedling emergence [33–35]. We also found that litter presence had a slight (not significant) inhibitory effect on seedling survival but increased seedling height. This result is consistent with previous studies demonstrating that under low-light conditions such as litter cover, seedlings promote height growth to intercept light [3,36–38]. Relatedly, litter present only promoted stem biomass accumulation and did not influence root, leaf, or total biomass. Because light intensity decreases under litter cover [5,39], seedlings must devote resources to stem growth, thus increasing height and their chances of obtaining more light energy for survival [16,40,41]. Litter cover had a significantly stronger influence on seedling emergence than on seedling survival [3].

Litter type is a key factor in determining the effects of litter on seedling establishment [24,26,42]. Deciduous, evergreen, coniferous, and broadleaf litter all differ considerably in their influence on seedling emergence, growth, and development because of variation in decomposition rates, leaf characteristics, and degradation-induced chemicals [43–52]. Our meta-analysis revealed that broadleaf litter cover significantly inhibited seedling emergence and total biomass, and had no effect on survival, whereas coniferous litter cover had a neutral effect on seedling emergence, survival and total biomass. Our results do in fact provide support for our first prediction that large litter pieces may produce more physical barrier than the same mass of small litter particles, probably because small litter particles do not cover seedlings as large particles do. These results indicate that differential effects between two litter types may in part be caused by differences in litter structure, i.e., mechanical litter effects. In support of this view, Xiong and Nelsson [32] showed that negative litter effects increased with leaf area, which could be because broadleaf with large planar structures have more smothering effect than easily displaced needle leaves. Additionally, the relative light interception was adjusted by the structure of the litter as litter surface area is closely related to the degree of light absorption [39]. Broadleaf litter has greatly reduced light quantity and quality (red/far-red ratio) than needle litter given the same litter mass. Thus, the coverage of broadleaf litter negatively effect seedling emergence than needle litter cover because light quantity and quality are important cues for photoblastic seeds germination [48–50].

Alongside litter type, litter amount is another important driver of litter effects on seedling establishment [53–58]. In grassland ecosystems, low ($\leq 250 \text{ g m}^{-2}$) and medium litter thickness ($250\text{--}500 \text{ g m}^{-2}$) benefited seedling emergence, whereas thick litter ($>500 \text{ g m}^{-2}$) had an inhibitory effect [32]. Likewise, it was found that a thin layer of litter cover ($<200 \text{ g m}^{-2}$) promoted seedling emergence [31]. In contrast to these findings, our meta-analysis showed that low ($\leq 250 \text{ g m}^{-2}$) and medium litter ($250\text{--}500 \text{ g m}^{-2}$) thickness had no effect on seedling emergence in forest ecosystems, while thick litter has a negative effect on seedling emergence. Our results suggest that the presence of a physical barrier and accompanying mechanical damage overrode positive effects from the litter providing a suitable environment for seedling growth under high litter amount cover [3,44,56]. Our results showed that seedling survival were negatively affected under all litter cover, especially under high litter amount cover. These results indicated that despite successful emergence under litter cover, the physical interception that impedes seedlings from accessing light before reserves are depleted renders seedling survival unlikely [3,39]. This phenomenon was observed in previous studies that seeds were able to germinate under thick litter cover, but failed to penetrate through the litter layer [24,56].

Seed size is a proxy for the resource available to a growing plant [59,60]. It is therefore an extremely important variable to consider when investigating seedling emergence, survival, growth, and development, as well as a forest's natural regeneration ability. Seed size is a particularly good predictor of litter effects on seedling establishment [59–61]. Our

meta-analysis showed that seedling emergence of small seeds (≤ 1 mg) was negatively affected through litter present than that of large seeds (> 1 mg), with even low and medium litter thickness inhibiting small seed emergence while having no effect on large seeds. There are several possible explanations for this phenomenon. First, small seeds usually need light for germination, and so their emergence would be particularly affected by the reduced light quantity and quality under litter cover [62,63]. Second, small seeds have fewer energy reserves that are likely to be exhausted before they can break past the physical barrier of litter [64]. Third, small-seeded species produce smaller seedlings that have more difficulty pushing through the litter layer. In contrast, large seeds can better cope with dense litter cover, being more likely to germinate and rapidly escape low-light conditions [35,64].

We found that experimental conditions differentially affected seedling establishment [65–69]. For seedling emergence, field and common garden studies showed neutral effect of litter present but showed positive effects of litter present on total biomass. Field and common garden experiments usually have variations in temperature and water stress, glasshouse and germination chamber experiments usually conducted under optimal moisture and temperature conditions. It has been thought that leaf litter may play a greater role in facilitating seedling emergence under stress condition.

5. Conclusions

Our meta-analysis synthesized research that investigated litter effects on seedling establishment in forest ecosystems, successfully identifying general patterns in how litter mediates the development of plant communities. First, we concluded that litter type influenced seedling emergence, survival, and early growth, with broadleaf litter inhibiting seedling establishment more than needle litter cover. Second, thick litter cover had a significant negative effect on seedling establishment, whereas thin and medium litter cover either did not affect or else benefited seedling survival and growth. Third, the effect of litter cover on seedling establishment is closely related to seed size. Fourth, litter cover affected seedling emergence significantly more than it affected seedling survival. Even though our meta-analysis only considers short-term effects of litter on seedling emergence, survival and early growth, the impact of litter on forest stand in the long-run is found to be complicated by many factors, and it is difficult to define common rules that apply under differing environmental conditions. Thus, it is necessary to analyze the complex interaction between litter effect and different ecological variables.

Our analysis has an important limitation, specifically the small number of independent studies for some estimators. This restricts statistical inference and power, affecting our conclusions about different covariates. To improve our understanding of the relationships between litter cover and seedling establishment, we recommend that future studies explore the influence of physical (temperature, light, and moisture) and biological (invertebrates and fungi) factors on the impact of litter. A full understanding of these relationships and processes of litter effect on seedling establishment will allow us to incorporate litter-mediated mechanisms in restoration ecology through application/maintenance of litter on degraded sites as restoration techniques.

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