Plant-plant interactions change during succession on nurse logs in a northern temperate rainforest

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March 25, 2021

Abstract

Plant-plant interactions can vary depending on the severity of the environment. Positive interactions, such as facilitation, are important in early life stages while negative interactions, such as competition, predominate in later stages. Through succession, plant-plant interactions often change from facilitative to competitive. In northern temperate rainforests, gap dynamics result in tree falls that facilitate tree regeneration (nurse logs) as well as bryophyte succession. While the importance of nurse logs for tree seedlings is known, how the interactions of bryophyte communities and tree seedlings vary through succession of the log remains unclear. We examined the relationships of tree seedlings, bryophyte community composition, bryophyte depth, and percent canopy cover in 166 plots on nurse logs and the forest floor in the Hoh rainforest in Washington, USA. Tree seedling density was highest on young logs with early-colonizing bryophyte species (e.g., Rhizomnium glabrescens), and lowest on decayed logs with Hylocomium splendens, a long-lived moss that reaches depths >20 cm. As a result, bryophyte depth increased with nurse log decay and was negatively associated with tree seedling density. Tree seedling density was 4.6x higher on nurse logs than on the forest floor, which was likely due to competitive exclusion by H. splendens. Nurse logs had 17 species of bryophytes while the forest floor had six, indicating that nurse logs contribute to maintaining bryophyte diversity. Nurse logs are essential for forest dynamics as they enable both tree seedlings and smaller bryophyte species to avoid competition with the dominant forest floor bryophyte, H. splendens. Given that H. splendens has a global distribution and is often dominant in forested systems across the northern hemisphere, it is likely a widespread driver of plant community structure. Our findings indicate that plant-plant interactions shift with succession on nurse logs from facilitative to competitive and, thus, influence forest community structure and dynamics.

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ABSTRACT

1. Plant-plant interactions can vary depending on the severity of the environment. Positive interactions, such as facilitation, are often important in early life stages of plants whereas negative interactions, such as competition, predominate in later stages of growth. Thus, through succession, plant-plant interactions often change from facilitative to competitive. In northern temperate rainforests, gap dynamics result in tree falls that facilitate tree regeneration (nurse logs) as well as bryophyte succession. While the importance of nurse logs for tree seedlings is known, how the interactions of bryophyte communities and tree seedlings vary through succession of the log remains unclear.

2. We surveyed tree seedlings, bryophyte community composition, bryophyte depth, and percent canopy cover in 166 plots on nurse logs and the forest floor in the Hoh rainforest in Washington. We examined the relationship of bryophyte community composition, bryophyte depth, percent canopy cover, and tree seedling density on nurse logs of three decay classes and the forest floor.

3. Tree seedling density was highest on young logs with early-colonizing bryophyte species, such as *Rhizomnium glabrescens* , and lowest on decayed logs with *Hylocomium splendens* a long-lived moss that can reach depths of >20 cm. As a result, bryophyte depth increased with nurse log decay stage and was negatively associated with tree seedling density. Tree seedling density was 4.6x higher on nurse logs than on the forest floor, which was likely due to competitive exclusion by *H. splendens* . Nurse logs had 17 species of bryophytes while the forest floor had only six, indicating that nurse logs contribute to maintaining bryophyte diversity.

4. Nurse logs are, therefore, essential for forest dynamics as they enable both tree seedlings and smaller bryophyte species to avoid competition with the dominant forest floor bryophyte, *H. splendens* . Given that *H. splendens* has a global distribution and is often dominant in forested systems across the northern hemisphere, it is likely a widespread driver of plant community structure.

Synthesis: Our findings indicate that plant-plant interactions shift with succession on nurse logs from facilitative to competitive and, thus, influence forest community structure and dynamics.

KEY WORDS: determinants of plant community structure; moss; nurse log; Olympic rainforest; plant-plant interactions; Stress Gradient Hypothesis; structural diversity; temperate rainforest

INTRODUCTION

Plant-plant interactions are complex and can vary from facilitative to competitive depending on the severity of the external environment (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Callaway & Walker, 1997). Most positive plant interactions have been found to occur in severe environments (e.g., arid, salt marshes, polar tundra), and happen through the amelioration of those stressful conditions (Brooker & Callaghan, 1998; Callaway et al., 2002). Facilitation, in particular, appears to be important in colonization and early community development as environments in early succession are typically severe (Callaway & Walker, 1997; Clements, 1916; Connell & Slatyer, 1977; Egler, 1954; Gómez-Aparicio, 2009). As the community develops, the amelioration of disturbance and stress by the physical presence of plants (e.g., stabilizing slopes, herbivory protection, microclimate), results in competitive interactions becoming more important over time (Brooker & Callaghan, 1998; Egler, 1954; Ricklefs, 1977; Walker & Chapin, 1987; but see Maestre, Valladares, & Reynolds, 2005). While vascular plants have largely been the focus of plant-plant interaction research, bryophytes can have facilitative or competitive interactions with vascular plants depending on multiple abiotic and biotic factors (Doxford, Ooi, & Freckleton, 2013; Gornall, Woodin, Jónsdóttir, & van der Wal, 2011; Gough, 2006; Sedia & Ehrenfeld, 2003; Soudzilovskaia et al., 2011; Staunch, Redlecki, Wooten, Sleeper, & Titus, 2012). In locations where bryophytes dominate the ground cover, such as in the arctic and boreal forest, bryophytes can structure the composition of vascular plant communities (Gavini, Suárez, Ezcurra, & Aizen, 2019; Gornall et al., 2011; Gough, 2006). However, how various stages of bryophyte succession influence vascular plants remains largely unexplored.

In old-growth forests, forest regeneration is often triggered by disturbances, such as tree falls, that create gaps into which early colonizing species proliferate (*i.e.* , small-scale gap dynamics, McCarthy, 2001; Ricklefs, 1977; Yamamoto, 2000). These gaps often result in a change in light levels that facilitate regeneration of early-colonizing shade-intolerant plants if the gaps are large, and shade-tolerant climax species if the gaps are small (< 200 m^2); colonization of small gaps by the canopy dominants can perpetuate the current canopy species composition (Denslow, Schultz, Vitousek, & Strain, 1990; McCarthy, 2001; Runkle, 1981). In Appalachian forests in Tennessee, for example, shade-intolerant trees were only able to establish in gaps created by multiple tree falls whereas small gaps were colonized by shade-tolerant trees (Barden, 1981). In contrast, in subalpine fir forests of coastal British Columbia, Pacific silver fir (*Abies amabilis*) preferentially colonized all gaps regardless of gap size (Lertzman, 1992). However, western hemlock (*Tsuga heterophylla*) was more dominant on stumps in gaps (Lertzman, 1992), suggesting that substrate changes during gap

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formation could also influence forest dynamics. In temperate coniferous forests of the Pacific Northwest, gap regeneration after tree falls can be quite slow (>25 yr, Spies, Franklin, & Klopsch, 1990), which results in large areas occupied by canopy gaps (13.1%, Spies et al., 1990). The trees that fall to create these gaps become essential sites of forest regeneration (*i.e.*nurse logs, Franklin et al., 2002) that cover more area in these forests (up to 25%) than in other forests (<4%) (Harmon et al., 1986). Similar to the subalpine fir forests of British Columbia, these nurse logs provide safe germination sites for late succession tree species', such as shade-tolerant *Tsuga heterophylla* (Christie & Armesto, 2003; Harmon & Franklin, 1989). Nurse logs are thought to facilitate seedlings through several means, such as by becoming a physical barrier between plants and terrestrial fungal pathogens, limiting competition between seedlings, herbaceous species, and bryophytes on the forest floor, and providing nutrients for potential seedling growth (Franklin, Shugart, & Harmon, 1987; Graham & Cromack Jr., 1982; Harmon, 1986; Harmon & Franklin, 1989). They may also be key to maintaining bryophyte diversity.

Nurse logs are sites for bryophyte colonization and succession. In coniferous forests in Colorado, bryophytes were found to colonize logs after lichen establishment (McCullough, 1948), and in coniferous forests of the Pacific Northwest, epiphytic plants from standing trees were replaced by bryophytes more commonly found on the forest floor (Sharpe, 1956). In the Hoh Rainforest in Washington, bryophyte cover on fallen logs reached approximately 90% in 11-19 y, and succession followed dominance by *Dicranum* spp. and *Hypnum circinale* in early succession, *Rhizomnium* spp. in mid succession, and feather mosses*Kindbergia oregano* and *Hylocomium splendens* in late succession (Harmon, 1989b). Given that late successional bryophytes are tall and dense enough to prevent tree seedling establishment (Harmon, 1986), they may also out-compete early- and mid-successional bryophyte species. Thus, nurse logs with moderate decay may be a refuge for early- and mid-successional terrestrial bryophytes that have difficulty establishing on the forest floor either due to insufficient light or competition with late successional bryophyte species. Thus, gap dynamics may also be important for the maintenance of bryophyte diversity.

These changes in bryophyte communities may have facilitative or competitive interactions with tree seedlings. In the Hoh rainforest, seedling density was highest when logs were dominated by the mid successional bryophytes *Rhizomnium* spp. and lowest when logs were dominated by late succession bryophytes (Harmon, 1989b). Harmon & Franklin (1989) argue through their controlled experiments that the interaction of mosses with seedlings changes from facilitative to competitive once the moss layer exceeds 5 cm in depth. Previous research on bryophyte-vascular plant interactions found that thicker mosses can hinder vascular plants by reducing temperatures and nutrient availability (Gornall et al., 2011; Pearce, Woodin, & Van Der Wal, 2003). However, they could also hinder vascular plant seedlings by reducing light levels if the bryophytes are thick and dense enough. In coniferous forests, removal of forest floor mosses showed positive effects on tree seedlings (Wardle, Lagerström, & Nilsson, 2008; Zackrisson, Nilsson, Dahlberg, Jäderlund, & Jaderlund, 1997). Thus, the importance of nurse logs for tree regeneration may be mitigated by bryophyte communities.

Here we build on the findings of previous studies (Harmon, 1986, 1989b; Harmon & Franklin, 1989) by diving deeper into the role of bryophyte species on tree seedling density. Over the course of three years, we conducted separate studies in northern temperate rainforests on the Olympic peninsula in Washington State (Hoh rainforest) to examine the importance of nurse logs for tree seedlings focusing on the effects of the nurse log bryophyte community, how that could change with nurse log decay class, and how it may differ from the forest floor. We tested the following predictions: 1) tree seedling density would be higher on nurse logs than on the forest floor, as shown previously (Christie & Armesto, 2003; Harmon & Franklin, 1989); 2) bryophyte community composition and the depth of bryophyte mats on nurse logs would influence tree seedling densities (Fukasawa & Ando, 2018; Harmon & Franklin, 1989); and 3) the decay class of the nurse log would influence both bryophyte communities and tree seedling densities. Because bryophytes vary in their growth patterns, we also examined if particular bryophyte species were more abundant on the forest floor or nurse logs and were associated with high and low tree seedling density as found previously (Harmon, 1989b). We focused on the dominant feather moss, *Hylocomium splendens* , given its abundance in these forests and its impact on tree seedling growth in other studies (Fukasawa & Ando, 2018; Harmon & Franklin, 1989). We tested our hypothesis that the effect of *H. splendens* on seeding growth was due to competition for light

by measuring light under and beside this moss. If bryophyte communities on nurse logs change predictably through succession and influence tree seedlings differently at different successional stages, it would further limit the degree of safe regeneration sites in these forests for trees, and highlight the essential role of nurse logs and plant-plant interactions in forest dynamics and diversity maintenance.

MATERIALS AND METHODS

Study site

Our study was conducted in the Hoh rainforest in the Olympic National Park, a World Heritage Site and Biosphere reserve in Washington State, USA (47°50'08" N, 123°58'54" W). The climate is mild and extremely wet with an average annual temperature of 10°C (range = -11°C – 36°C) and annual rainfall of 3200 mm (Harmon & Franklin, 1989). These forests are characterized by large degrees of vertical and horizontal heterogeneity formed by large and tall trees (> 80 m) that are dominated by *Picea sitchensis* and *Tsuga heterophylla* , an abundance of large nurse logs (>1 m diameter), a luxurious cover of bryophytes and herbs on the forest floor, and an abundance of epiphytic bryophytes (Franklin et al., 2002; Harmon & Franklin, 1989).

Survey methods

We conducted this study over the course of three summers (2016 – 2018). We counted *Tsuga heterophylla* and *Picea sitchensis*seedlings in 166 randomly placed 1 m x 1 m plots on the forest floor (n = 52) and 1 m x nurse log diameter on nurse logs (defined as >30 cm diameter and at least 2 m in length; nurse log diameter ranged from 30 to 104 cm; n = 114). For a subset of the nurse log plots (n = 86) and forest floor plots (n = 12), bryophyte composition was surveyed using the point-intercept method. Percent canopy cover was measured as a potential confounding factor using a densiometer placed in the center of each plot. Bryophyte depth was measured (cm) using a caliper in the center of each plot. Because Harmon & Franklin (1989) found that seedlings that receive less than 0.6% of light (< 12.5 μmol/m^2/sec) would not be able to survive, and seedling survival was reduced with high moss biomass (an indicator of moss depth), we also measured light irradiance with a photometer in 50 pairs under and beside thick bryophyte mats focusing on the predominant moss in the forest, *Hylocomium splendens* . Decay class of each nurse log for each plot was measured using the kick test, which included three levels of decay classes: 1 = bark still intact upon contact, 2 = some to various debris falls upon contact, 3 = foot completely in log, several pieces fragmented off of the log (modified from Christy & Mack, 1984; Sollins, Cline, Verhoeven, Sachs, & Spycher, 1987, and Fogel, Ogawa, and Trappe, *unpublished report*). These classes correlate with the age of the nurse log so we used them as an indicator of nurse log age (Harmon, 1989b).

Statistical analysis

To examine if tree seedling density (number of seedlings per m^2) was higher overall on nurse logs than on the forest floor, we used a Wilcoxon rank test because the data did not meet parametric model assumptions of normality and homogeneity of variance across groups. We used seedling density per area of the plot because area of the plot varied with nurse log diameter. We then examined whether substrate type including forest floor and all three decay classes of nurse logs influenced tree seedling density, bryophyte depth, percent canopy cover, percent cover of the three most abundant bryophyte species (*Rhizomnium glabrescens* , *Hylocomium splendens* ,*Antitrichia curtipendula*) using 1-way ANOVA or Kruskal-Wallis tests if parametric model assumptions couldn't be met. Bryophyte depth was missing from one plot and percent cover of *H. splendens* had to be square-root transformed to meet parametric model assumptions.

To determine the factors associated with seedling density, we used a generalized linear model (GLM) with a Poisson error distribution. Explanatory variables included substrate type (nurse log or forest floor), decay class of nurse log, bryophyte depth, % canopy cover, and bryophyte species with a total percent cover of >300 across all plots and that were found in at least 10 plots (Table S1). The bryophyte species included as predictors were: *Hylocomium splendens* , *Rhizomnium glabrescens* , *Antitrichia curtipendula* , *Rhytidiadelphus loreus* , *Sphagnum girgensohnii* , and *Kindbergia praelonga* . We used the dredge function

in the MuMIn package to determine the model with the lowest Akaike Information Criterion (AIC) value (Barton, 2009). We calculated Spearman rank correlation coefficients for all pairs of explanatory variables using the rcorr function in the Hmisc package in R (Harrell & with contributions from Charles Dupont and many others, 2020). We included forest floor as decay class 5 in our model. We also calculated variance inflation factors (vif) to test for collinearity among our predictor variables using the vif function in the car package; any vif < 5 was deemed not correlated.

To examine the influence of substrate (forest floor and nurse logs characterized by decay class) on bryophyte community composition, we conducted a non-metric multi-dimensional scaling ordination (NMDS) using the metaMDS function in the vegan package in R (Oksanen et al., 2010). We used a Bray-Curtis distance matrix on bryophyte percent cover in each plot. Only plots that had at least two bryophyte species were included (n = 98). We used ellipses to denote variances in bryophyte species composition among substrate types. We fit bryophyte depth (BD), tree seedling density (seedling), and percent canopy cover (CC) as environmental vectors to the NMDS ordination using the envfit function in the vegan package in R with 1000 permutations (Oksanen et al., 2010). To test for significant differences in species composition among substrate types, we used the adonis function in the vegan package, which is essentially a multivariate analysis of variance. We then used the pairwiseAdonis function in the vegan package to compute all pairwise comparisons among substrate types with adjusted p-values (Martinez Arbizu, 2020).

To test the light levels under and beside *Hylocomium splendens* mats, we used a paired t-test.

RESULTS

Substrate type

In a total of 166 plots, tree seedlings were found in 50% of our plots. Of those 166 plots, 52 were on the forest floor and 114 were on nurse logs; 36% of the forest floor plots had tree seedlings whereas 57% of the nurse log plots had tree seedlings. *Tsuga heterophylla* was the dominant tree species found as seedlings (87% of all seedlings found). On nurse logs, we found a total of 18 different non-vascular species. Of these 18, there were 16 mosses, one liverwort, and one lichen (Table S2). We found only six different bryophyte species on the forest floor (Table S2).

Tree seedling density was significantly influenced by substrate type, as average tree seedling density on nurse logs (20.1 ± 3.6) was 4.6x greater than on the forest floor (4.5 ± 1.8; W = 2027.5, $P< 0.001$). Substrate type significantly influenced moss depth ($F_{3,93} = 6.6$, $P < 0.001$, Fig. 1B), and the percent cover of *H. splendens* ($F_{3,94} = 17.8$, $P < 0.001$, Fig. 1E). No other factor was significantly influenced by substrate type (Fig. 1).

Decay class was significantly positively associated with moss depth and the percent cover of *Hylocomium splendens* (Table 1). Moss depth was positively correlated with the percent cover of *H. splendens* and *Rhytidiadelphus loreus* and negatively correlated with the percent cover of *Rhizomnium glabrescens* (Table 1). Percent cover of *H. splendens* was negatively correlated with the percent cover of *Kindbergia praelonga* . Finally, the percent canopy cover was positively correlated with the percent cover of *Antitrichia curtipendula* (Table 1).

The GLM model that best predicted tree seedling density included substrate type, percent canopy cover as a positive factor, and percent cover of *Hylocomium splendens* as a negative factor (Table 2). Interestingly, moss depth was a negative factor and percent cover of *Rhizomnium glabrescens* was a positive factor, so their exclusion from the model may be due to their correlative relationships with the percent cover of *H. splendens* .

Bryophyte composition varied significantly with substrate type (adonis, $F_{3,97} = 6.8$, $P = 0.001$, Fig. 3). Decay class 1 was significantly different from decay class 3 ($P = 0.006$) and the forest floor ($P = 0.006$); there were no other significant differences in bryophyte composition among substrate types ($P > 0.01$, Fig. 3). These differences were driven by bryophyte species that create thick mats (>4 cm), such as *Hylocomium splendens* (HylSpl), which were associated with the forest floor and later decay classes of nurse logs (class two and three),

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whereas bryophyte species that don't create thick mats were associated with early decay classes of nurse logs (one), such as *Rhizomnium glabrescens* (RhiGla) and *Scapania bolanderi* (ScaBol) (Fig. 3). Bryophyte depth was the only factor that had a significant correlation with bryophyte community composition ($r^2 = 0.47$, $p < 0.001$). While seedling density was higher on nurse logs that were in the early decay class, it did not significantly correlate with bryophyte composition ($r^2 = 0.02$, $p = 0.4$). Canopy cover did not significantly correlate with the NMDS ordination but showed a trend towards decay class 2 ($r^2 = 0.06$, $p = 0.06$).

Light levels were significantly lower under *Hylocomium splendens* than beside it (paired t-test, $t = -10.3$, df = 49, $P < 0.001$, Fig. S1).

DISCUSSION

Our study found that tree seedlings were largely affected by bryophyte species identity and the thickness of the bryophyte cover. We found overall that tree seedlings were much more abundant on nurse logs than on the forest floor as found previously (Christy & Mack, 1984; Harmon & Franklin, 1989). However, not all nurse logs were created equal; nurse logs at early decay classes supported many tree seedlings and small bryophyte species, such as *Rhizomnium glabrescens* and *Scapania bolanderi*, while later decay classes had few tree seedlings and bryophyte species with greater depths, such as *Hylocomium splendens*. Moreover, the percent cover of *H. splendens* was negatively associated with tree seedling density and positively associated with bryophyte depth. Our findings are in accordance with Harmon (1989) who found seedling densities highest when nurse logs were dominated by *Rhizomnium* spp. and lowest when dominated by *H. splendens*. Our findings are also supported by another study conducted in old-growth subalpine spruce forests in Japan where tree seedlings on nurse logs were found to be positively associated with a small liverwort, *Scapania bolanderi*, and negatively associated with *H. splendens* (Fukasawa & Ando, 2018). As in our study, Fukasawa & Ando (2018) also found that bryophyte community composition shifted from dominance by *S. bolanderi* to *H. splendens* as nurse logs decayed. Thus, bryophyte succession on nurse logs influenced tree seedlings differently depending on the stage of succession.

As nurse logs decayed, the relationship of bryophyte communities and tree seedlings changed from facilitation to competition. We found support for this in our study as the pattern of seedling density mirrored that of the percent cover of *Rhizomnium glabrescens* (Figure 1A and 1D) while opposite that of the percent cover of *Hylocomium splendens* (Figure 1A and 1E), and *H. splendens* came out in the model as the only negative driver of seedling density. These patterns are consistent with other studies. In subalpine forests of Japan, *Tsuga* seedling survival was restricted to nurse logs covered with small bryophyte species (Nakamura, 1992), and in the Hoh Rainforest, seedling establishment was highest on logs with thin mosses as seed retention on bare logs was low, and thick mosses excluded seedlings (Harmon & Franklin, 1989). While our study and others found correlative support of these relationships, findings from manipulative field experiments provide the strongest evidence. In old-growth forests in western Oregon, for example, seedling emergence was higher on nurse logs of decay class 3 (our class 2) when bryophytes were present than when they were removed (Christy & Mack, 1984), and in a field experiment in the Hoh Rainforest testing the influence of moss depth on seedling density, seedling density of *Tsuga* was higher in a moss mat of 3.7 cm than in 1.4 cm or 7.8 cm (Harmon & Franklin, 1989). The positive effect of bryophytes on tree seedlings could be due to protection from herbivores, increasing moisture or nutrient availability, protecting seeds from being blown off by the wind, or providing a humus substrate into which seedling roots can grow (Graham & Cromack Jr., 1982; Harmon & Franklin, 1989; Nakamura, 1992). Many studies have found competitive interactions between bryophytes and tree seedlings (Christy & Mack, 1984; Fukasawa & Ando, 2018; Harmon & Franklin, 1989; Nakamura, 1992). The negative effect of thick bryophytes on tree seedlings could be due to preventing seeds from reaching the humus or soil layer, which can inhibit germination (Iijima & Shibuya, 2010), the reduction of light levels below the threshold needed for tree seedling germination and survival as found in our study and others (Harmon, 1986; Iijima & Shibuya, 2010), or reducing nitrogen availability to vascular plants as found in the boreal forest (Gornall et al., 2011). The "window of time" for tree seedling establishment on logs of a particular stage of decomposition seems to be driven by bryophyte succession on logs (Fukasawa & Ando, 2018), and suggests that the available substrate for successful seedling regeneration is even more

limited than the area covered by nurse logs would suggest.

The benefits of nurse logs to tree seedlings could be due to a release from competition with forest floor plants. In western Oregon old-growth forests dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* , 98% of the seedlings in the plot were on nurse logs despite the fact that nurse logs only covered 6% of the plot, and *T. heterophylla* emergence was higher on mineral soil when litter, bryophytes (such as *Hylocomium splendens*) and herbaceous plants were removed than in the forest floor control where nothing was removed (Christy & Mack, 1984). In the Hoh Rainforest where our study took place, tree seedling survival was significantly higher on the forest floor when bryophytes and vascular plants were removed (Harmon & Franklin, 1989). Our findings corroborate this, as we found lower seedling densities on the forest floor where *H. splendens* was in high abundance. Our finding that *H. splendens* reduces light levels below the threshold for seedling survival (< 12.5 μmol/m^2/sec) suggests that the mechanism by which *H. splendens* out-competes tree seedlings is through light competition as suggested previously (Harmon & Franklin, 1989). Christy & Mack (1984) also suggest that nurse logs enable seedlings to avoid being covered by litter that dominates the forest floor in western Oregon forests. Interestingly, the small tree seedlings (<15 cm) that were on the forest floor in our study were on areas covered by litter where bryophytes were not abundant. The tree seedlings we did find on the forest floor or mounds of very decayed nurse logs that were covered in *H. splendens* were quite tall (>15 cm), which suggests that seedlings that establish on nurse logs prior to *H. splendens* could grow tall enough to surpass the height of the moss. This could add bryophyte cover as a contributor to the decrease in tree seedling survival after the first 1-2 years of growth (Christy & Mack, 1984; Friesner & Potzger, 1944; Haig, Davis, & Weidman, 1941). While litter may negatively impact tree seedlings, manipulative field experiments with long-term seedling survival data are further required to disentangle the relative influence of bryophytes and litter on tree seedlings both on the forest floor and on nurse logs.

On nurse logs, what drives the initial colonization and subsequent turnover in species composition is largely unknown. Rodents and slugs have been found to disperse lichen and bryophyte propagules (Asplund, Larsson, Vatne, & Gauslaa, 2010; Barbé et al., 2016; Kimmerer, 1994; Kimmerer & Young, 1995), and mammals use fallen logs as trails through the forest, so it could be a combination of differences in propagule dispersal ability, germination requirements, and biotic interactions that determine these changes. Alternatively, different decomposer fungi could influence bryophyte community structure on nurse logs as found in alpine forests in Japan (Ando, Fukasawa, & Oishi, 2017). Thus, the influence of bryophytes on tree seedlings could be mediated by other biotic interactions through a trophic cascade. Regardless, we did find that nurse logs are not only essential for forest regeneration but for the maintenance of bryophyte diversity in late stage forests. We found 17 bryophyte species on nurse logs and only six on the forest floor, and there were significant differences in species composition between our nurse log decay class 1 and the forest floor. Without gap-phase dynamics driven by large tree falls, these early nurse log bryophyte species would eventually be competitively excluded by the late stage bryophytes.

Our results support the predictions of the Stress Gradient Hypothesis that plant-plant interactions are complex and can vary from facilitative to competitive depending on the severity of the external environment (Bertness & Callaway, 1994). For tree seedlings, some level of bryophyte cover on nurse logs seems to be needed to facilitate germination and seedling establishment, while too much bryophyte cover inhibits germination and seedling survival. *Hylocomium splendens* , in particular, has been found to consistently exclude seedlings (Fukasawa & Ando, 2018; Harmon & Franklin, 1989). This is likely due to *H. splenden* 's distinctive "stairstep" architecture, which lends it unusual height for a bryophyte. The average lifespan of *Hylocomium splendens* is 8 years (Binkley & Graham, 1981), and it dominates nurse logs that are >30 years old (Harmon, 1989a). Forest floor bryophytes may have an almost unlimited life span given their continued upward growth (Fenton & Bergeron, 2006). Thus, unless there is a disturbance that disrupts the dominance by these forest floor bryophytes, the regeneration of the dominant trees will be limited to the small window of opportunity found in early successional stages of bryophytes communities on nurse logs, which is less than 30 years. Interestingly, above the alpine tree line in subarctic tundra in Sweden, spruce tree establishment was improved when planted in bryophyte mats of *Hylocomium splendens* (Lett, Nilsson, Wardle, & Dorrepaal, 2017) further supporting that species interactions fall along a spectrum depending on site conditions. Bryophytes, though

often overlooked in forested ecosystems, could be an important driver of plant community composition and dynamics.

AUTHOR CONTRIBUTIONS

ACKNOWLEDGEMENTS

DATA ACCESSIBILITY

Variables used as predictors of tree seedling density in the GLM, a list of non-vascular species found on all substrate types, and light irradiance under and beside *Hylocomium splendens* are uploaded as online supporting information. A list of tree seedling density, percent canopy cover, bryophyte depth, and the percent cover of the most abundant bryophyte species in each plot are deposited in the Dryad depository:

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Figure 1. Average ($\pm$ SE) tree seedling density of *Picea sitchensis* and *Tsuga heterophylla* (A) bryophyte depth (B), percent canopy cover (C), percent cover of *Rhizomnium glabrescens*(D), percent cover of *Hylocomium splendens* (E) and percent cover of *Antitrichia curtipendula* (F) on the forest floor (n = 12) and each decay class of nurse logs (NL 1 = nurse log decay class 1, n = 31; NL 2 = nurse log decay class 2, n = 30; NL 3 = nurse log decay class 3, n = 25) in a northern temperate rainforest, Olympic peninsula, WA. Bryophyte depth was missing from one plot. Substrate type significantly influenced bryophyte depth ($F_{3,93} = 6.6$, $P <$ 0.001). Substrate type significantly influenced percent cover of *H. splendens* ($F_{3,94} = 17.8$, $P < 0.001$).

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Figure 3. Non-metric multi-dimensional (NMS) ordination of bryophyte community composition on nurse logs (n = 98) of varying decay stages and the forest floor using a Bray-Curtis distance matrix on percent cover. Two-dimensional stress = 0.16 with 1000 permutations. The ellipses show the covariance matrix centered on the mean of each nurse log decay stage and the forest floor (solid black line). Nurse logs were classified into three decay stages (modified from Christy & Mack 1984): NL1 = bark still intact and can hold weight when

stepped on (light grey dotted line solid black line), NL2 = some to various debris falls upon contact (grey dashed dot line), NL3 = foot completely in log, several pieces fragmented off of the log (dark grey dashed line). Species codes are from Table S1. Environmental variables that significantly correlated with NMS axes are shown in black, heavy arrows and those that did not significantly correlate with axes are shown in grey. Bryophyte depth (BD) correlated significantly with the axes ($r^2 = 0.47$, $p < 0.001$) but not canopy cover (CC, $r^2 = 0.06$, $p = 0.08$) or tree seedling density (seedling, $r^2 = 0.02$, $p = 0.4$). Species codes are in red and are the first three letters of the genus and the first three letters of the species (found in Table S2).

Table 1. Spearman rank correlation coefficients between explanatory variables for the generalized linear model for seedling density.

	Decay class	Bryophyte depth	*Hylocomium*	Canopy cover	*Rhizomnium*	*Antitrichia*	*Rhytidiad*
Decay class							
Bryophyte depth	**0.41***						
Hylocomium	**0.56***	**0.58***					
Canopy cover	-0.16	-0.1	-0.02				
Rhizomnium	-0.18	**-0.25***	-0.17	-0.13			
Antitrichia	-0.13	0.05	-0.17	**0.32****	-0.19		
Rhytidiadelphus	0.05	**0.4***	0.04	-0.16	0.03	-0.1	
Sphagnum	0.12	0.19	-0.01	-0.05	-0.12	-0.12	-0.03
Kindbergia	-0.13	-0.21	**-0.24***	-0.14	0.11	-0.08	-0.11

Values in bold indicate a significant correlation between variables. ***P < 0.001; **P < 0.01; *P< 0.05

Table 2. Results of the generalized linear model (GLM) analysis showing the predictors of tree seedling density from the best model.

Factor	Estimate	SE
Canopy cover	0.019***	0.005
Hylocomium cover	-0.009***	0.001
Substrate	0.315*	0.136
AIC of the best model	4269.6	

*P < 0.05; ***P < 0.0001