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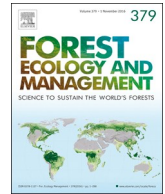
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Bryophyte abundance, composition and importance to woody plant recruitment in natural and restoration forests

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ABSTRACT

Restoration of tropical forests can lead to enhanced ecosystem services and increases in native biodiversity. Bryophytes may be an integral part of the forest restoration process and can serve a critical role in forest functioning. However, the recovery of bryophytes and their ability to facilitate woody plant establishment during restoration remains poorly studied, especially in the tropics. We investigate how bryophyte abundance and community composition, as well as woody plant seedling associations with bryophyte mats and other ground cover types change from under the canopy of intact forest to under trees in restoration corridor plantings in Hawaii. Restoration corridors consisted of corridors of koa (*Acacia koa*) trees that were planted roughly 30 years ago. Some corridors were planted around remnant ʻōhiʻa trees (*Metrosideros polymorpha*) that can be several hundred years old. We sampled under ʻōhiʻa in intact forest and both koa and ʻōhiʻa trees in restoration corridors. In restoration corridors, bryophyte abundance was low relative to intact forest and species diversity was a subset of that found in intact forest despite restoration corridors being several decades old. Seedlings strongly associated with bryophytes across all habitats suggesting that bryophytes may significantly enhance forest seedling establishment when present in restoration corridors. Other ground cover types like woody litter and nurse logs also had a positive association with forest seedlings but were rare in restoration corridors. Grass remained a dominant ground cover type in restoration corridors under koa and remnant ʻōhiʻa trees and only a single seedling was ever found growing in this grass. Enhancing bryophyte growth and recovery within restoration plantings through the reduction of grass cover could facilitate native plant establishment.

1. Introduction

Across the tropics there is strong interest in restoring native forest communities on abandoned pastures to enhance ecosystem services (Chazdon, 2014; Lamb et al., 2005). In these pastures, passive regeneration can effectively lead to forest establishment in some sites (Crouzeilles et al., 2017). Many areas, however, require human intervention due to any number of barriers to woody plant re-establishment including competition from invasive pasture grasses (Aide et al., 1995), lack of viable seed of forest species (Slocum and Horvitz, 2000), harsh microclimatic conditions (Holl, 1999), or altered soil properties (Yelenik, 2017). Even with human intervention and intensive active management, forest restoration can still be slowed because barriers may act synergistically or unidentified barriers may be hindering restoration efforts.

Often thick layers of exotic grasses dominate the ground in abandoned pastures. In order to establish and survive, seeds of woody plants may need to germinate in non-grass covered microsites. Nurse logs and other downed woody debris for example, are consistently shown to be microsites where woody seedlings recruit within abandoned pastures (Sanchez et al., 2009; Santiago, 2000). Other substrates such as bryophyte (mosses, liverworts and hornworts) mats can occur around remnant or new trees in pastures and they too may be viable substrates for woody plant establishment. To date, bryophytes have received much less attention compared with nurse logs as potential recruitment sites for native seedlings, especially in tropical settings.

Where studied, the importance of bryophytes to seedling germination has been shown to vary across habitat type, climatic conditions, and study system. Bryophytes can provide positive benefits to native plant recruitment through a variety of mechanisms including regulating moisture loss from soil, harboring beneficial mycorrhizae and providing grass-free microsites for germination (During and Van Tooren, 1990;

Staunch et al., 2012). Conversely, seeds may get caught in bryophyte mats leading to germination but soon die due to the lack of connectivity with soil substrate (Soudzilovskaia et al., 2011; Staunch et al., 2012). In temperate forests in Sweden, *Picea abies* seedling establishment was enhanced by elevated microsites of *Sphagnum* and *Pleurozium* (moss) on logs although some seedlings were overgrown by the mosses (Hörnberg et al., 1997). Greenhouse experiments conducted by Tavili et al. (2017) demonstrated that cryptogamic (moss and lichen covered) soils had angiosperm germination and establishment that averaged roughly 8 times that of non-cryptogamic soils. Such results suggest that bryophyte covered substrates could be important for restoration of forest plants but their role in woody plant establishment, particularly during restoration continues to be overlooked.

Tropical forests in Hawai'i were subject to deforestation and pasture conversion since the mid 19th century (Denslow et al., 2006; Scowcroft, 2013; Scowcroft and Jeffrey, 1999). Declining profits from ranching have caused the abandonment or sale of high elevation ranches, prompting efforts to restore forests and provide habitat for endangered species (Scowcroft and Jeffrey, 1999). To date however, passive restoration has generally been unsuccessful since most abandoned pastures are dominated by vigorous introduced perennial grasses (McDaniel et al., 2011; Yelenik, 2017). Active planting of canopy trees and understory is taking place in some areas with the hope that this will lead to a naturally functioning forest environment with continued woody plant recruitment (Pinto et al., 2015; Scowcroft and Jeffrey, 1999).

Studies done in *Metrosideros polymorpha* dominated wet forests in Hawai'i show woody seedlings are found in association with coarse woody debris, as well as areas dominated by moss (Cole and Litton, 2014; Santiago, 2000; Scowcroft and Jeffrey, 1999). In one study where all bryophytes were lumped into a single category of 'moss', moss was the only significant predictor of seedling density on decaying logs, and was found to be important for predicting sapling density (Santiago, 2000). While bryophytes show promise as facilitators of seedling regeneration in intact forest, recovery of bryophyte communities during forest restoration has been poorly documented in Hawai'i and to our knowledge, no studies have documented how bryophytes aid forest recovery in degraded sites that are being actively restored in tropical systems. If bryophytes increase the passive recruitment of native woody species, then fostering bryophyte communities may be a faster and more cost-effective way to restore degraded areas than logistically challenging and expensive large-scale outplanting.

In this study we ask two specific questions; (1) How do bryophyte abundance and community composition change from habitat types of intact forest, to remnant trees in pastures, to planted corridors of trees? and (2) Do woody seedlings associate differentially with bryophyte mats versus other ground cover types across these habitat types? Our sampling included ~30 year old trees planted in corridors throughout grassy pastures, remnant forest trees embedded within these corridors and intact forest. Our goal was to evaluate whether on-going forest restoration plots in the study area are lacking in a potentially critical component of understory substrate that is hindering recovery.

2. Methods

2.1. Study area

This study took place at Hakalau Forest National Wildlife Refuge (Fig. A1) on the eastern slope of Mauna Kea on Hawai'i island, Hawai'i USA. Native forests in the upper elevations (approximately 1600 m.a.s.l. and higher) of the refuge were cleared during the 1800s and planted with introduced pasture grasses. Active grazing ended in the 1980s and efforts have been underway to restore the grass-dominated pastures to native forest. Beginning in the late 1980s, restoration efforts consisted of planting corridors of the native tree *Acacia koa* (hereafter, koa) throughout the pasture areas in the hopes that over

time corridors would expand outward and form more contiguous native forest dominated by *Metrosideros polymorpha*, (hereafter, 'ōhi'a) and koa. However, the understory composition of these corridors continues to be dominated by invasive perennial grass species including *Cenchrus clandestinus* (kikuyu) and *Ehrharta stipoides* (meadow ricegrass) with little evidence of native plant regeneration.

We focused data collection in three habitat types around the two focal tree species. These included: (1) 'ōhi'a trees in intact forest, (2) 'ōhi'a trees in the planted koa corridors, and (3) koa trees in the koa corridors. Intact 'ōhi'a occur in undisturbed forest that has never been cleared and was fenced from ungulate grazing throughout the period of forest clearing. Intact 'ōhi'a forest typically has an understory dominated by native woody species with few, if any, non-native species present. 'Ōhi'a in koa corridors (referred to as "corridor 'ōhi'a") are remnant trees, often hundreds of years old (Hart, 2010), that were not cleared during forest conversion to pasture and have persisted within the grass matrix. Many of these remnant 'ōhi'a have since been surrounded by planted koa during forest restoration. The understory of corridor 'ōhi'a can range from all grass to a well-developed ring of native woody plants that extends from the tree trunk to the edge of the crown (Yelenik, 2017). The source of this variation in corridor 'ōhi'a understory is the subject of ongoing research (E. M. Rehm, unpublished data). Koa in koa corridors (referred to hereafter as "corridor koa") are all ~ 30 years old and have little to no native understory development because exotic grasses dominate the ground cover (Yelenik, 2017).

2.2. Tree selection for bryophyte surveys

We selected 20 trees of each of the three tree types (hereafter 'habitats') based on the following selection criteria. To avoid any possible edge effects, intact 'ōhi'a were located at least 50 m from remnant fence lines that marked the historic boundary of forest clearing. To identify corridor 'ōhi'a and koa, we walked koa corridors and selected trees based on the following criteria. For corridor 'ōhi'a, we chose trees with a minimally branching upright (i.e. not prostrate) trunk, that did not have more than 50% canopy coverage by native understory species in a 5 m radius around the base of focal tree. We avoided trees with > 50% native plants in the understory as we were interested in how bryophyte communities may affect seedling establishment, whereas trees with understory development > 50% already had high seedling and sapling cover which itself could be altering the bryophyte community and seedling establishment. For corridor koa we first selected a corridor at random and then randomly chose a tree within the corridor to sample. All trees were at least 50 m from each other and were scattered throughout the refuge to minimize spatial clustering of samples (Fig. A1). We excluded trees that were located in a gulch, on a steep slope, or other topographic anomalies as such trees occurred in unique microhabitats (e.g. higher moisture, lower light) relative to the majority of trees in intact forest and restoration corridors and thus may potentially have different bryophyte communities.

2.3. Bryophyte and seedling sampling

At each tree, we placed four, 2 m long transects starting from the base of the tree and extending outwards in the four cardinal directions. Along each transect we established five 0.25 m² (0.5 × 0.5 m) subplots centered at 1.75, 1.25, 0.75, and 0.25 m away from the base of the tree with the last subplot placed at the tree base and extending vertically along the trunk. Within each subplot we estimated percent cover of all ground cover types including bryophytes (any surface covered with bryophyte was counted as bryophyte rather than the underlying material), grass, woody litter (leaf litter or dead wood < 2 cm diameter from woody plants), fine roots (exposed roots < 0.5 cm diameter that normally formed thick mats), live tree (trunks, exposed roots larger than 0.5 cm diameter or other live structures), nurse log (dead wood > 2 cm diameter and not covered in bryophytes), lichen, and

bare soil. We also further identified and estimated coverage of each bryophyte species in each subplot where possible. We attempted to identify every bryophyte to the species level following Bartram (1933) and Staples et al. (2004) but in many cases this was not possible due to the lack of current bryophyte taxonomic guides or identification resources for the region. In these cases, we identified each morpho-species and created a reference catalog to ensure consistency in identification. We refer to bryophytes with the term 'species', but this includes those identified to species, several that could only be identified to genus and others that are identified as distinct morpho-species. We also classified bryophytes into life-form categories based on Bates (1998), as life-form categories can help explain ecological roles of bryophytes and their distributions

In each plot we counted all woody plant seedlings (< 10 cm in height from the base to apical meristem) and recorded the ground cover type in which they were rooted. We did not record larger seedlings as the ground cover under seedlings likely changes over time and therefore we could not be confident that the ground cover present during our survey was the ground cover present when larger seedlings first established. As we were interested in relationships between seedlings and specific bryophyte species, when a woody seedling was rooted in a bryophyte mat, we recorded the species of bryophyte in which it was rooted. Woody plant seedlings were identified to species when possible but ~39% of seedlings were unidentified because they were not developed past the cotyledon stage.

2.4. Statistical analysis

All analyses were completed in R 3.1.1. (R development core, 2016). We were first interested in determining if total bryophyte coverage and other ground covers changed across habitat type and therefore modeled ground coverage by habitat type with a generalized linear model (glm) with a gamma distribution and log link. As sampling area was the same for each tree (20 subplots of 0.25 m^2 for a total of 5 m^2), ground cover types were first converted to total ground cover type per tree (m^2) by summing across all 20 subplots. To conform to a gamma distribution we added a small positive value (1×10^{-6}) to zero values. A Tukey's Honestly Significant Difference (HSD) test from the multcomp package in R (Hothorn et al., 2008) was used to look for pair-wise differences ($p < 0.05$) in ground cover coverage between habitats when the main effect of habitat type was significant.

We used non-metric multidimensional scaling (NMDS) to compare bryophyte community differences among the three habitat types. NMDS is a nonparametric method that does not assume linearity between community distance measures and represents changes in beta diversity in low-dimensional space that allows easy visual interpretation. Bryophyte coverage per species was used to represent the bryophyte community instead of simple presence/absence as coverage gives information on relative abundance of each bryophyte species and thus differences among tree types. We conducted a NMDS on Bray-Curtis dissimilarity index with 1000 random starts using the metaMDS function in the vegan package (Oksanen et al., 2017). We then used permutational multivariate analysis of variance on the Bray-Curtis distance matrices using the Adonis function in vegan with 9999 permutations to check for differences in Bray-Curtis dissimilarity between habitat types.

To assess seedling associations with ground cover types, we calculated the number of seedlings per cm^2 of ground cover type for each tree. All seedlings were combined as we were unable to identify 38.9% of seedlings to species. This resulted in the number of seedlings per area for each ground cover type present at a given tree. These data contained large amounts of zeros because many trees had no seedlings for a given ground cover type. We therefore modeled seedlings per area of ground cover type using a two-step hurdle model that consisted of (1) a logistic glm to predict the probability of seedlings being present or absent and (2) a gamma glm that predicts seedling abundance for those tree and ground cover type combinations where at least one seedling was

present (Zuur and Ieno, 2016). To aid with model convergence, three ground cover types (lichen, bare soil, and grass) were excluded from this analysis due to the lack of seedlings present in these types. Lichen was often present on the trunks of live trees or downed wood but no seedlings were recorded in this cover type. Bare soil covered less than 2% of ground cover in all habitats and only two seedlings were ever found in this ground cover type. Similarly, only a single seedling was found growing in grass despite grass comprising 25 and 31% of ground cover at corridor 'ōhi'a and koa, respectively.

We predicted probability of a single seedling being present by first converting seedlings per area to a binary response (0 if no seedlings were present or 1 if seedlings were present). We then predicted this binary response in a logistic glm with fixed effects of habitat and ground cover type and their interaction. As we were interested in how seedling associations changed from intact 'ōhi'a to other habitat types and from bryophytes to other ground cover types, we used intact 'ōhi'a and bryophytes as the reference group for our two fixed effects, habitat and ground cover type respectively. We tested if the interaction of habitat and ground cover was necessary using AIC selection and the interaction term was excluded if it did not increase AIC by at least 2 units relative to the model with no interaction (Burnham and Anderson, 2002). We then used a Tukey's HSD test to look for pair-wise differences ($p < 0.05$) when the main effect of habitat type or ground cover type was significant in predicting the probability of seedling presence.

For the second step in the hurdle model, we were interested in how seedling density changed across habitat and ground cover types. Therefore, we modeled seedlings per area of ground cover type only for those trees and habitat cover type combinations that had at least one seedling present using a gamma glm with log link with fixed effects of habitat and ground cover type and their interaction. Model selection then proceeded as stated above for the first step in the hurdle model.

3. Results

3.1. Bryophyte composition and cover

Bryophyte coverage differed by habitat (Tukey HSD; $p < 0.05$ for all comparisons) with mean coverage being highest for intact 'ōhi'a (1.64 ± 0.14 SE m^2), moderate for corridor 'ōhi'a (0.28 ± 0.07 SE m^2) and lowest in corridor koa (0.04 ± 0.02 SE m^2; Fig. 1). When summed by habitat, bryophytes comprised 33% of the total area under intact 'ōhi'a, 6% for corridor 'ōhi'a and less than 2% for corridor koa. Conversely, grass cover was 25 and 31% in corridor 'ōhi'a and koa, respectively, while composing less than 2% in intact 'ōhi'a. Abundance of other ground cover types were fairly consistent across habitats with woody litter (composed largely of leaf litter) and live tree (mainly trunks) being relatively abundant while lichen, bare soil, and nurse logs were relatively rare in all habitat types.

Byrophyte composition showed a nested and varied structure across habitats largely due to species gain/loss rather than species turnover (Adonis function $p < 0.0001$; Fig. 2). Corridor 'ōhi'a contained 11 bryophyte species and corridor koa contained nine, with eight species being found in common in both of these habitats (Fig. 3). All but one species (Moss 2 morpho-species; see Table A1 for description) found in the corridor koa and 'ōhi'a habitats were also found in intact 'ōhi'a habitats. Intact 'ōhi'a bryophyte communities, in contrast, included five additional species that were not found in the other habitats. The most dominant bryophyte also varied across habitats (Fig. 3). *Bazzania* spp. and *Leucobryum* spp. were dominant at 19 of 20 trees in the intact 'ōhi'a while these two species were of minor occurrence in corridor koa and *Leucobryum* spp. was dominant at only one tree in corridor 'ōhi'a. The dominant species in corridor koa were *Sematophyllum* c.f. *hawaiiense* (8 trees), *Macromitrium microstomum* Hook. & Grev. (5 trees) and *Pyrrhobryum spiniforme* (4 trees). For corridor 'ōhi'a, *Campylopus* spp. was the most common dominant (15 trees).

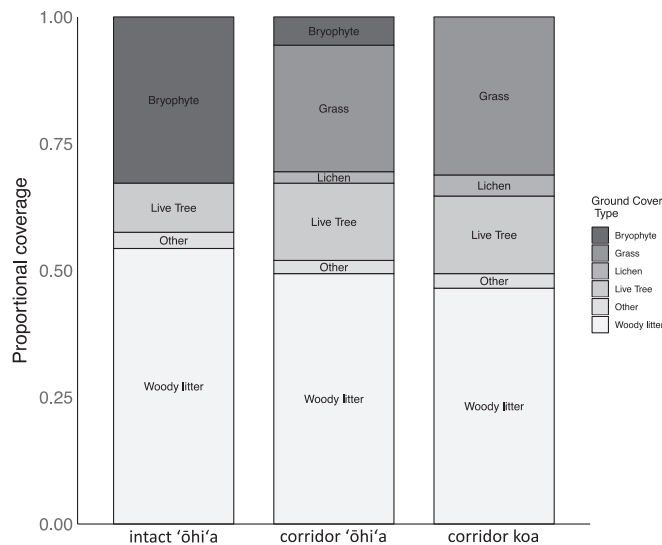Bryophyte life-form changed among habitats with the majority of

Fig. 1. Proportional coverage of ground cover types pooled across the 20 trees within each habitat type. Any ground cover type that composed < 2% of the total coverage within a habitat type was grouped into the 'other' category (e.g. bryophytes in corridor koa). Additional ground cover types of bare soil, fine roots, and nurse logs never covered more than 2% of the area and therefore are also included in the other category.
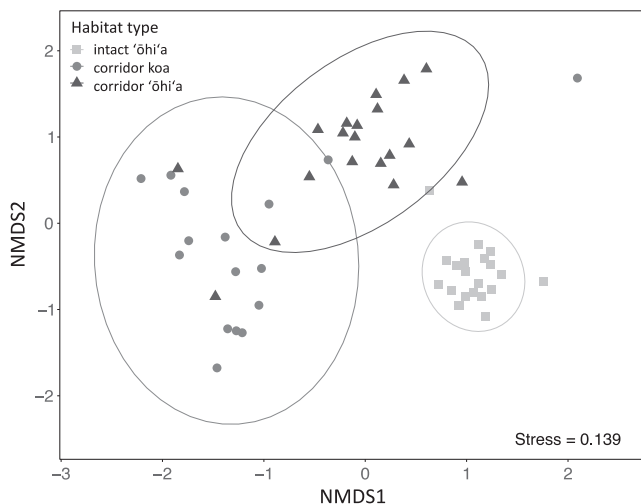

Fig. 2. Community composition of bryophytes at different habitats (n = 20 trees sampled within each habitat) using non-metric multidimensional scaling (NMDS) on Bray-Curtis dissimilarity index. All habitats have different community composition according to a permutational multivariate analysis of variance on the Bray-Curtis distance matrices (Adonis function p < 0.01).

bryophyte area in intact 'ōhi'a being largely composed of tall turf (*Bazzania* spp.) or large cushions (*Leucobryum* spp.). In corridor 'ōhi'a there was a shift towards short turf (Campylopus spp.) with some large cushion still present (*Leucobryum* spp.). In the koa corridor, short turf still dominated but with rough (*M. microstomum*) and smooth mats (*S. hawaiiense*) becoming more common.

3.2. Woody seedling preference for ground cover type

The number of seedlings encountered varied greatly across habitats. We found 2905 seedling in intact 'ōhi'a, 807 in corridor 'ōhi'a but just 34 in corridor koa. In addition, seedlings in intact 'ōhi'a were found at all 20 trees and 17 trees had seedlings in corridor 'ōhi'a. In contrast only 3 corridor koa had seedlings, with 30 of the 34 seedlings being found at a single tree.

For both steps of the hurdle model, the most parsimonious models did not include the interaction term between habitat type and ground cover type (Table 1). In the first step, the logistic glm, the presence of seedlings varied by habitat type and ground cover type (Fig. 4). Seedling presence was highest in intact 'ōhi'a, moderate in corridor 'ōhi'a and lowest in corridor koa. Seedling presence was also higher in bryophytes and woody litter than in fine roots, live tree, and nurse logs irrespective of habitat.

For combinations of habitat and ground cover type where seedlings were present, their density no longer varied with habitat type. However, seedling density did vary based on ground cover type with densities being highest for bryophytes and lowest for woody litter and live tree (Table 1, Fig. 4). Nurse logs and fine roots had seedling abundances similar to bryophytes despite having lower probability of having a seedling present. No statistical test was needed to show that lichen, bare soil, and grass ground cover were poor recruitment sites for forest seedlings because no seedlings were ever found growing on lichen, bare soil only had two seedlings present, and only a single seedling was found growing in grass despite grass covering 19% of all the plot area across all habitats and being the second most abundant ground cover type in corridor koa and 'ōhi'a.

Seedlings appeared to show associations with specific bryophyte species and life-forms. In intact and corridor 'ōhi'a a disproportionate number of seedlings were found in *Leucobryum* spp., which is a large cushion life-form (Fig. 3). In contrast, *Bazzania* spp., which is a tall turf, was relatively abundant in intact 'ōhi'a but contained a low number of seedlings (Fig. 3). In corridor 'ōhi'a seedlings occurred in about the same proportion as availability as *Campylopus* spp., a short turf. All seedlings found in bryophytes in koa corridor were found in *Campylopus* spp. but all of these seedlings (28 of the 34 seedlings found in any ground cover type in koa corridor) were encountered in a single patch of *Campylopus* spp. at a single tree so our ability to draw inferences about seedling associations with specific bryophytes in koa corridors is limited.

4. Discussion

Given the importance of bryophytes to many ecosystem processes (e.g. biogeochemical cycling, decomposition rates; Lindo and Gonzalez, 2010), bryophytes may serve a critical function in the restoration of native forest on abandoned pastures. Yet the influence of bryophytes on seed germination and seedling recruitment as well as their recovery after disturbance and restoration in most systems have largely been overlooked (Paillet et al., 2010). Our study demonstrates the potential importance of bryophytes to successful seedling recruitment and clearly shows that bryophytes are slow to colonize these restoration sites, even at remnant trees within pasture. Bryophyte abundance and species diversity was highest in intact forests and lowest in the manually planted koa restoration corridors despite these trees being 30–40 years old. Across all habitat types, seedlings were strongly associated with bryophytes suggesting that, at least in Hawai'i, bryophytes can provide important substrates for seedling establishment. Yet, bryophyte abundance is exceedingly low in restoration areas, offering one explanation as to why passive regeneration rates of native forest species in degraded habitats is also extremely low.

The very low abundance of bryophytes in both corridor 'ōhi'a and koa relative to intact 'ōhi'a suggests that bryophyte recovery during restoration is slow. Corridor 'ōhi'a presumably suffered loss of their bryophyte communities due to grazing throughout the period of live-stock presence and today have some but still limited bryophyte recovery. In Canada, bryophyte persistence and abundance are known to decrease after forest canopy reduction through partial logging because the opening of the canopy may alter moisture regimes, negatively impacting bryophyte abundance (Caners et al., 2010). The restoration corridors in our study have yet to form canopies as dense as intact forest. Therefore, these restoration corridors may mimic partially logged forests in that they negatively impact bryophytes through drier
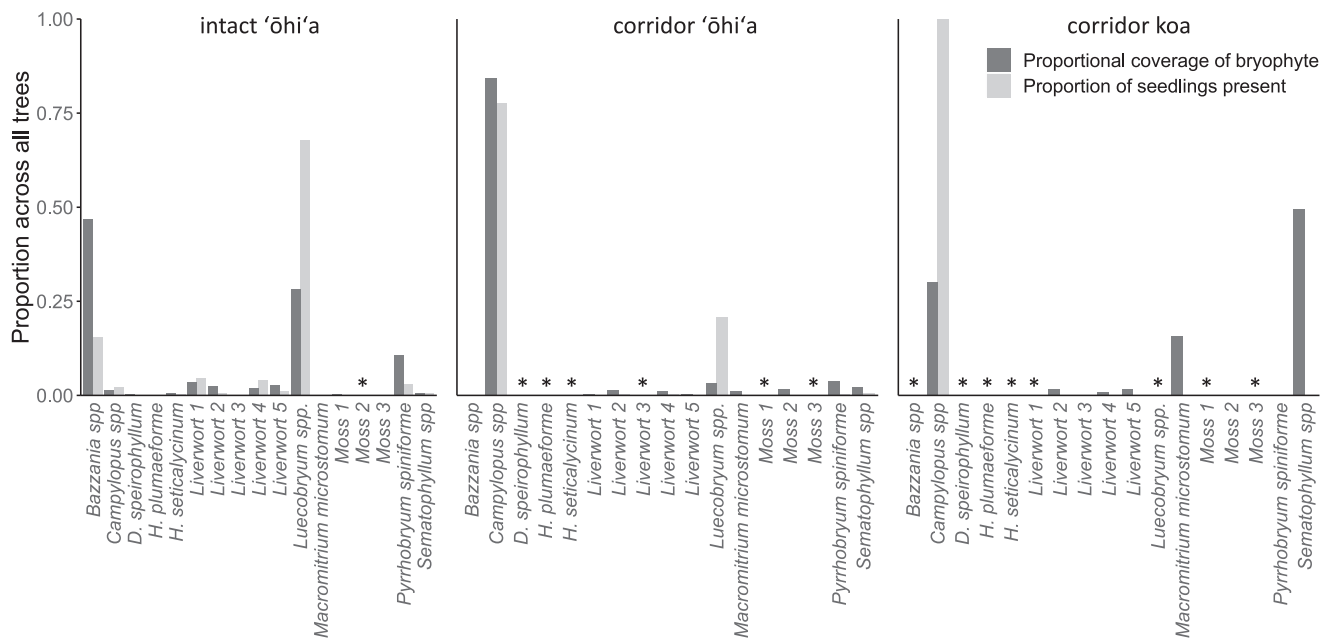
Fig. 3. Proportional composition of bryophytes within each habitat type and the proportion of seedlings found growing in each bryophyte within each habitat type. Proportions were calculated across all 20 trees within each habitat type. '*' represents a bryophyte that was never found within that habitat type and therefore could not contain seedlings. Full species description can be found in Table A1.

Table 1

Model outputs for the most parsimonious model for both stages of a two-step hurdle model used to predict seedling presence-absence and abundance in different ground cover types at different habitats. The logistic generalized linear model (glm) was used to predict seedling presence-absence in each ground cover type within each habitat. For those habitat and ground cover combinations where seedlings were present, we then used a gamma glm to predict seedling abundance per area for each habitat and ground cover type. Parameter estimates for habitat variables are relative to intact 'ōhi'a and ground cover are relative to bryophyte. In both steps, interaction terms between habitat type and ground cover type were not included in the final model based on AIC selection criteria. To help with model convergence, lichen, bare soil, and grass were excluded from the analysis due to lack of significant seedlings presence in these ground cover types, see main text for details.

Model	Parameter	Estimate	SE	Z-value	p
Logistic glm	Intercept	3.25	0.60	5.40	< 0.001
	Habitat				
	koa	−5.48	0.72	−7.62	< 0.001
	'ōhi'a in corridor	−1.49	0.41	−3.60	< 0.001
	Ground Cover				
	Fine Root	−2.95	0.67	−4.39	< 0.001
	Live Tree	−2.75	0.62	−4.41	< 0.001
	Nurse Log	−2.52	0.69	−3.65	< 0.001
	Woody Litter	0.16	0.66	0.24	0.813
Gamma glm	Intercept	−4.90	0.24	−20.03	< 0.001
	Habitat				
	koa	−0.96	0.69	−1.40	0.163
	'ōhi'a in corridor	0.35	0.26	1.38	0.17
	Ground Cover				
	Fine Root	−0.23	0.44	−0.53	0.60
	Live Tree	−2.64	0.38	−7.01	< 0.001
	Nurse Log	0.20	0.44	0.46	0.65
	Woody Litter	−2.55	0.30	−8.42	< 0.001

and brighter conditions relative to intact forest. Conversely, following slash and burn of Tasmanian forest, bryophytes recovered quickly and dominated ground cover for the next several years despite growing in a system with little to no canopy cover (Brasell and Mattay, 1984; Duncan and Dalton, 1982). This difference in bryophyte abundance recovery between Tasmanian forests and Hawai'i restoration sites could

be due to differences in the intensity and duration of the disturbance, resident bryophyte species pools available for recovery, ecosystem productivity, and rates of regrowth of other ground vegetation (i.e. grass) relative to bryophytes.

Similar to bryophyte abundance, species diversity was lower in corridor 'ōhi'a and koa trees relative to intact 'ōhi'a, with all but one bryophyte species present in corridor 'ōhi'a and koa also present in intact 'ōhi'a. Due to drastic changes in microclimatic conditions and substrate during clearing and conversion to introduced grass it is likely that the intact forest bryophyte community was completely or mostly lost in pastures even under the remnant corridor 'ōhi'a. Therefore, the species present in corridor 'ōhi'a and koa likely represent those species that have been able to colonize these restoration habitats while other bryophyte species found only in intact forest will colonize as propagules arrive and/or the habitat within restoration areas becomes suitable. In general, bryophyte species richness tends to be lower in forests that are subject to disturbance due to active management relative to undisturbed forests (Baker et al., 2016; Rudolphi and Gustafsson, 2011). Recovery of bryophyte communities following disturbances such as partial logging may take several decades as has been documented in Tasmania (Baker et al., 2016). Furthermore, 70-year-old stands that were previously clear cut had lower bryophyte species diversity than old growth forest in Fennoscandia (Rudolphi and Gustafsson, 2011) and bryophyte abundance and species composition have yet to recover to primary forest levels in 110 year old secondary forest in China (Song et al., 2011). Given this evidence from temperate sites and the long time between forest clearing and restoration initiation in our system, bryophyte communities in restoration corridors may take several more decades, or longer, to reach community composition similar to intact forest sites. Observationally, we usually found corridor bryophytes on nurse logs or the focal tree itself, away from the introduced grasses, whereas in the intact forest bryophytes were found on many surface including the soil or bare rock. Slow bryophyte recovery may be exacerbated by feedbacks between bryophytes needing shadier growing conditions, yet woody seedlings whose success would ultimately lead to those shadier conditions need bryophytes to initially recruit.

The changing pattern of life-form composition across habitat types provides additional support for the idea that bryophyte communities
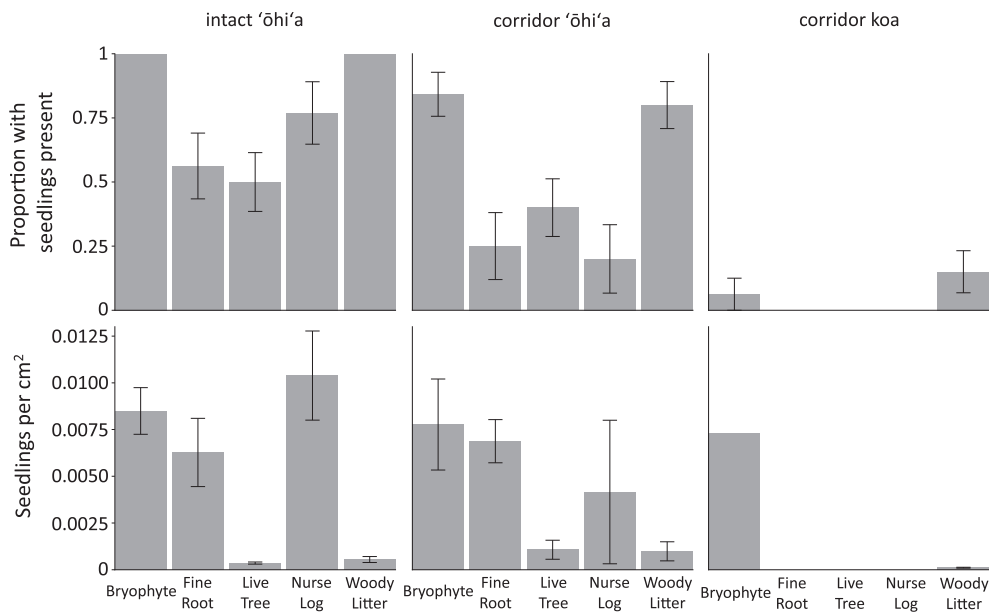
Fig. 4. Top row – Mean proportion (with SE bars) of habitat and ground cover combinations with at least one seedling present. For corridor koa, no seedlings were ever found in fine root, live tree and nurse logs. When no error bars are shown that means all locations of the given ground cover type had seedlings present. Bottom row – Mean seedling per cm² (with SE bars) of habitat and ground cover combinations when at least one seedling was present. For corridor koa, no seedlings were ever found in fine root, live tree and nurse logs. Lichen, grass and bare soil were also excluded from the analysis and figure due to low numbers of seedlings present in these ground cover types, see main text for additional details. There is no SE bar for bryophyte in corridor koa because a single tree contained all seedlings found in bryophyte and therefore there was no variation in seedling density.

are slow to recover in corridor habitats due to environmental conditions. Intact 'ōhi'a was dominated by several life-forms that occur in darker habitats such as large cushion and small mats (Bates, 1998). In addition, the tall turf life-form, which was the most abundant life-form in intact 'ōhi'a, associates with wetter sites (Bates, 1998). Conversely, bryophytes in corridor habitats were largely of short turfs and rough mats, which are thought to be more common in drier and brighter habitats (Bates, 1998). Therefore, the more open and potentially drier corridor habitats may limit bryophyte life-forms.

4.1. Seedling substrate preferences

Despite their slow colonization under corridor 'ōhi'a and koa, bryophytes were one of the most important seedling recruitment sites in both intact forest and restoration corridors. Out of all possible substrates, bryophytes and woody litter were most commonly found to have woody seedlings across all habitats and in corridor koa they were the only substrates where seedlings were found at all. Other substrates that supported seedlings in intact forest, such as fine root mats, live tree trunk, and nurse logs did not support any seedlings in corridor koa. Our findings also highlight that the second most abundant substrate in corridor koa, grass, is an extremely poor substrate for forest seedling establishment and additional efforts need to be taken to replace grass with other substrates in restoration sites.

Bryophyte mats had seedlings present considerably less often in corridor koa than in either 'ōhi'a type, which could be due to differences in the bryophyte species composition among tree types. The dominant bryophytes in corridor koa and 'ōhi'a were prostrate mosses (*S. hawaiiense* and *Campylopus* spp.; Fig. 3, Table A1) that are of the short turf life-form. These form densely packed shoots that may act to reduce evaporative losses in drier environments (Bates, 1998) but simultaneously repel falling seeds instead of retaining them. Similarly, the dominant bryophyte species in intact 'ōhi'a (*Bazzania* spp.) is classified as a tall turf that isn't as densely packed as a short turf but still likely acts to repel seeds due to the prostrate and impenetrable growth. Indeed, while we found some seedlings in *Bazzania* spp., seedlings occurred here disproportionately less often based on the availability of *Bazzania* spp. even though *Bazzania* spp. was the most dominant species in intact 'ōhi'a. Conversely, seedlings in intact and corridor 'ōhi'a strongly associated with *Luecobryum* spp. which is a large cushion, with many erect stems that accumulate organic matter over time and presumably may capture seeds as well. The presence of humus may further

be beneficial to seeds as a rooting substrate and adding to moisture stability, even during dry periods. Besides differences in architecture and moisture, it is possible that the different bryophyte communities also differed in nutrient retention, mycorrhizae associations or temperature regulation in ways that potentially led to recruitment differences.

Other factors also likely play a role in poor seedling establishment under koa. Across all ground cover types, there was an overall reduction in the proportion of locations containing seedlings from intact and corridor 'ōhi'a to corridor koa. These factors may include differing environmental conditions (e.g. light and moisture), reduced seed rain due to differing patterns of bird visitation, altered soil nutrient levels, and allelopathy under koa. For example, koa canopies tend to let in more light than 'ōhi'a canopies (McDaniel and Ostertag, 2010), which could lead to drier conditions and/or greater grass growth. Similar to constraints on bryophyte establishment, these factors could reduce seedling establishment relative to 'ōhi'a; several of these constraints are currently under study by our group.

Despite bryophyte mats and woody plant litter having a similar proportion of sites with seedlings present, mean seedling abundance per unit area of bryophytes was over ten times higher than woody litter when pooled across all habitat types. This difference in seedling abundance suggests that bryophytes may be a better substrate for forest seedlings than woody litter. Similarly, fine roots and nurse logs had a lower proportion of sites with seedlings present than bryophytes, yet when seedlings were present, seedling abundance was similar between fine roots, nurse logs and bryophytes. For nurse logs, our findings corroborate previous work showing that this substrate can be very important for seedling dynamics in Hawaiian forests (Cole and Litton, 2014; Santiago, 2000). How certain substrates like bryophytes or nurse logs promote seedling establishment remains unclear but could relate to substrate properties like the ability to capture and hold seeds, moisture regulation or simply providing a location away from the grass where almost no seedlings were found growing (Inman-Narahari et al., 2013).

5. Conclusions

Our study shows the positive influence of bryophytes on forest seedling recruitment in tropical forest restoration sites. Efforts to restore Hawaiian forests on abandoned pastures may be hindered by the slow recovery of bryophytes under planted trees. In addition, bryophyte sites under koa are less likely to have seedlings present than bryophytes

under 'ōhi'a suggesting that bryophyte species and/or environmental conditions under koa may impede seedling recruitment. Yet koa continues to be the dominant species used in restoration efforts at mid-elevations throughout the Hawaiian islands, largely because it is faster growing and easier to propagate than 'ōhi'a (Jeffrey and Horiuchi, 2003; McDaniel and Ostertag, 2010). If this trend of predominantly using koa for canopy tree restoration in Hawai'i continues, additional efforts to restore bryophyte communities within restoration sites may be needed to accelerate the establishment of additional native forest plants. While it is not yet clear how to increase bryophyte cover, some possibilities could include increasing nurse log abundance and the transplantation of bryophyte mats or spores from intact forest to re-

storation sites on nurse logs or other structures above the grass matrix.
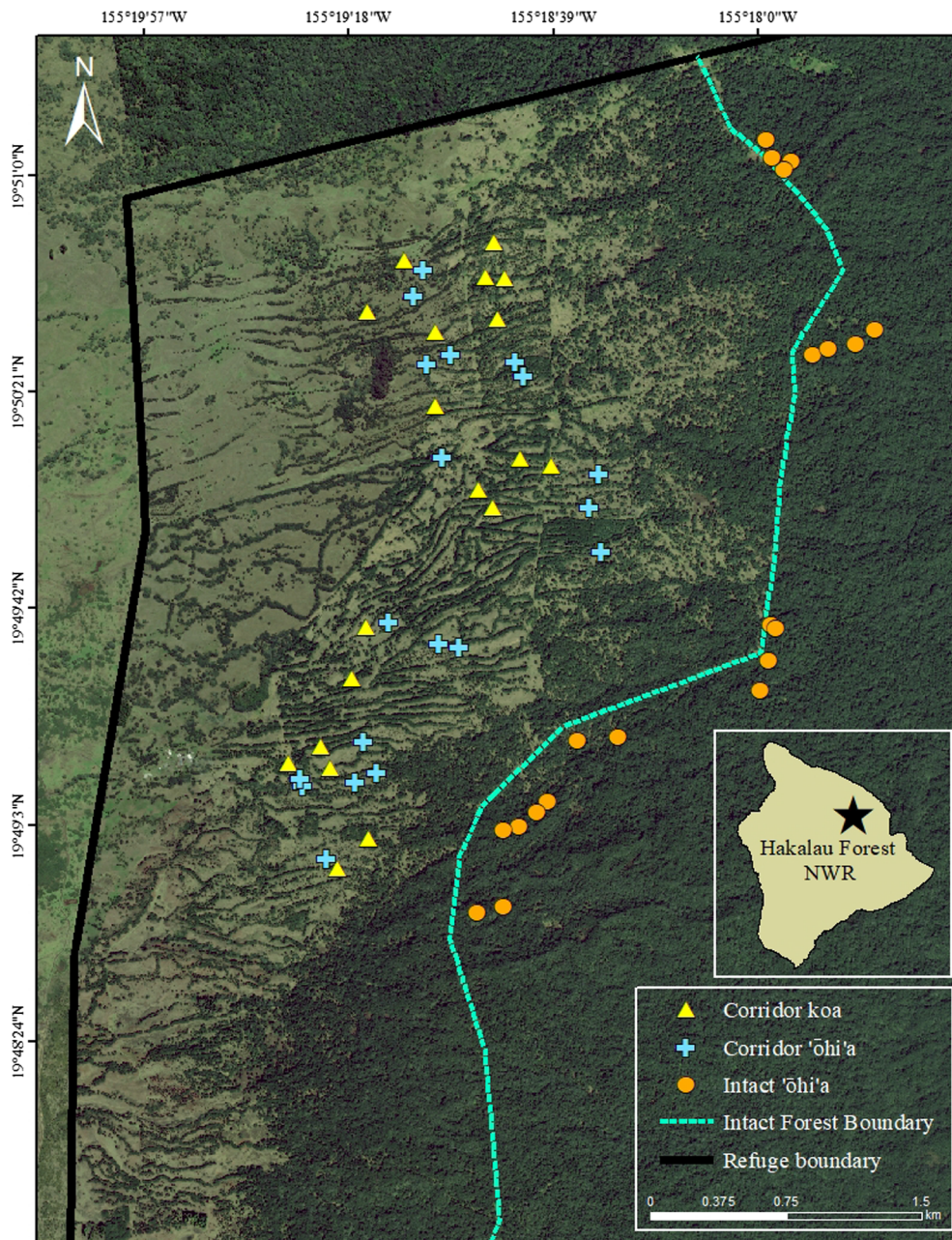
Appendix A

Fig. A1. Map of the study area and sample trees at Hakalau Forest National Wildlife Refuge on Hawai'i Island, USA.

Table A1

Name used to identify the species in the field, the type of bryophyte, a description of the species including important functional traits, bryophyte life-form and additional notes used to identify the species. When possible, bryophytes were identified to the species or genus level but if they could not be identified to this taxonomic resolution they were defined by their functional characteristics based of of morphology, habitat, and life-form.

Species or morpho-species name	Type	Functional description	Life-form*	Other notes
Bazzania spp.	Liverwort	Loosely dense tufts of dichotomously branching plants. Leaves in 2 rows, overlapping and minute	Tall turf	Growth habit is characteristic among other leafy liverworts. Rather robustly spreading plant, common as an epiphyte in wet forests. Some species occasionally creeping
Liverwort1	Liverwort	Prostrate, compound leaves, glabrous	Smooth mat	Often found in exposed areas like rocks in the sun
Liverwort 2	Liverwort	Prostrate, epiphytic and spreading	Smooth mat	Leaves close and overlapping in two rows, minute to no serrations along leaf margin to smooth. Midrib absent
Liverwort 3	Liverwort	2 + rows of leaves, stems erect and branching. Loosely clumping plants	Tall turf	Plants can be green to red and are nearly always epiphytic, but also found on nurse logs. (What appear to be) basal gemmae are tubular.
Liverwort 4	Liverwort	2 rows of alternating leaves, midrib absent. Loosely matted plants that develop into a few centimeters thick	Smooth mat	Leaves with 2–3 distinct teeth near and around the apex. Leaves minutely overlapping. Branches prostrate to ascending towards the new growth. Plants medium to dark green, older stems brown.
Liverwort 5	Liverwort	Plants forming thin mats on trees and nurse logs. Bryophyte mat ~1 cm at most	Smooth mat	
Macromitrium microstomum Hook. & Grev.	Moss	Prostrate stem with short, erect secondary branches forming small rosettes of alternating leaves. Stems tomentose.	Rough Mat	Epiphytic and epigeous, also found on rock surfaces. Sporophytes formed on lateral branches. Leaves often incurved and twisted when dry
Sematophyllum c.f. *hawaiiense*	Moss	Prostrate and creeping moss with crowded leaves, sometimes forming dense mats.	Smooth mat	Plants seen are epiphytic. Seta smooth and red below, capsule horizontal or inclined. Peristome teeth in two unequal rows with a constriction just below the rim of the capsule.
Leucobryum spp.	Moss	Dense, tuft forming moss with erect stems. Accumulates significant amounts of humus within older stems.	Large Cushion	Plants are epiphytic and epigeous. Easily recognizable by pale, glaucous color and leaves more than 1 cell layer thick. 3 species are recognized in Hawai'i, often found overlapping in habitat and differing in the length of leaves as well as growth pattern, but all form dense matts.
Campylopus spp.	Moss	Dense to loosely dense, tuft forming plants with erect stems and thin leaves. Accumulates significant amounts of humus.	Short Turf	Epiphytic, epigeous, and lithophytic. Roughly 9 species in Hawai'i, most characterized by a cygneous setae and dense colonies. Most species are distinguishable only by the cell layers and the presence of excurrent or incurrent costae.
Holomitrium seticalycinum Müll. Hal.	Moss	Small dense plants found on trees. Perichaetal leaves long, nearly same length as setae.	Small Cushion	
Pyrrhobryum spiniforme (Hedw.) Mitt.	Moss	Loosely dense tufts with lots of air spaces compared to other moss encountered.	Rough mat	Epiphytic or epigeous. Secondary branch with lanceolate, serrated leaves that turn a gold/brown when mature and remain pale/green when young or in shade.
Hypnum plumaeforme Wilson	Moss	Spreading well branched moss that makes dense mats on ground and on trees. Leaves branched with a tapering of large basal tertiary branches to smaller distal branches. Leaves acute.	Tall turf	Plants brown on older stems and gold-yellow at younger tissue. Branches gradually reducing in size in a pinnate fashion in clusters along main stem. At study site, found almost exclusively along roadsides and disturbed areas but was found at one study site away from road.
Moss1	Moss	Spreading slender plants with prostrate stems that are weakly branching. Leaves lanceolate forming loose mats along tree trunks.	Smooth mat	Plants light green to yellow-green. Leaves acute to acuminate in more than 3 rows. Sporophyte not seen.
Moss2	Moss	Plants forming dense mats with spreading primary stems and erect secondary stems. Leaves are not as crowded as much compared to taxa like *Leucobryum*. Found growing epiphytically and on nurse logs.	Short turf	Leaves 1–2 mm, ovate and loosely crowded along erect secondary stems. Plants a medium green to light green. Leaves slightly involute when dry. Stems tomentose. Sporophyte not seen.
Moss3	Moss	Plants forming mats similar to *Hypnum* though not as dense. Occurring in small patches on a small portion of our sample trees.	Smooth mat	Leaves broader and color is a darker green. *Hypnum* seems to form more dense mats while this moss was more open. The former species also possesses leaf tips that curl downward in a "hook" like fashion. This moss has leaves not so. Epiphytic. Sporophyte not seen.

* Life-form categories according to Bates, J. 1998. Is 'life-form' a useful concept in bryophyte ecology. Oikos 82:223–237.

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