RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Planting diversity and density shape native plant survival and community assembly in tropical forest restoration

Michala L. Phillips[1,2], Corie Yanger[3], Jonah Kuwahara-Hu[4], Erin Datlof[4], Stephanie Yelenik[5]

Abstract

Introduction: Forest restoration in Hawaii is underway due to past large-scale conversion of forests to pastures dominated by invasive grasses. Secondary succession is limited by grass dominance and a lack of native seed rain, making outplanting a viable restoration strategy.

Objective: We conducted a multi-year field experiment at Hakalau Forest National Wildlife Refuge to test how species richness and planting density influence outplant survival, cover, and growth.

Methods: We planted eight native species representing trees, a shrub, a fern, and a vine in combinations of two, four, and eight species at single and double planting densities. We measured survival and growth of outplants as well as percent cover of all plants in the experimental plots for 3 years.

Results: Overall survival across all species was high (76 ± 2.5%) but varied by species; shrubs and vines had the lowest survivorship, likely due to grass competition, while a four-species combination of trees and a fern had the highest survivorship. Outplant cover increased over time, with the greatest cover observed in double-density plantings of four and eight species. Invasive grass cover also increased across all treatments, with little evidence that outplantings reduced grass cover relative to controls. Relative growth rates were unaffected by species combination or density.

Conclusions: While overall cover differences were modest by the final monitoring period, planting density and species selection shaped early establishment. These results support multi-species, high-density planting as a strategy to enhance survivorship, accelerate canopy development, and support habitat creation.

Implications for Practice: High-density plantings may accelerate tree canopy development in wet forests dominated by invasive grasses, offering a pathway to reestablish forest structure in degraded pasturelands. Because shrubs and vines had higher mortality, phased restoration strategies, where canopy-forming tree species are planted first and more vulnerable understory species are introduced once canopy cover has developed, may improve establishment outcomes for those more susceptible species. Multi-species combinations pairing fast-establishing trees with fewer understory species appear to balance early survivorship with long-term structural diversity. These findings offer restoration practitioners working in similar systems additional evidence on how planting density and species sequencing shape trajectories of canopy development.

Key words: ecological restoration, exotic grass, fern, Hawaii, invasive species, shrub, species assemblages, tree, vine

Introduction

Tropical forests cover a vast area and possess substantial value for global- and local-scale ecosystem processes and services, yet they have been drastically transformed over the last 200 years due to deforestation for pasture and agriculture (Fearnside 1993; Davidson et al. 2012). This pastureland is often abandoned, leaving large swaths of unmanaged land that are converted into either grasslands or savannas (Holl et al. 2000; Perroy et al. 2016; Farrant et al. 2023). There is potential for tropical forests to regenerate; however, regeneration following land use conversion from forest to pasture is halted when little to no native seed banks remain and when invasive grasses with competitive advantage dominate (Holl 1999; Ashton et al. 2001; Guariguata & Ostertag 2001; Rehm et al. 2023). The most common intervention to support forest regeneration is large-scale tree planting, often done in a plantation style (Holl

Author contributions: MLP analyzed the data and drafted the first draft of the manuscript; SY conceived of the experiment and received funding for the project; MLP, SY, CY, JK-H performed field work for the project; ED assisted with figure generation; all authors reviewed drafts and contributed to writing.

[1]Pacific Island Ecosystems Research Center, U.S. Geological Survey, 1 Crater Rim Drive, Building 344, Hawaii National Park, HI 96718, U.S.A.
[2]Address correspondence to M. L. Phillips, email mphillips@usgs.gov
[3]Three Mountain Alliance, P.O. Box 52, Resources Management, Hawaii National Park, HI 96718, U.S.A.
[4]Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo, P.O. Box 44, Hawaii National Park 96718, HI, U.S.A.
[5]Rocky Mountain Research Station, USDA Forest Service, 920 Valley Road, Reno, NV 89512, U.S.A.

doi: 10.1111/rec.70539
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70539/suppinfo

et al. 2013). Plantation-style planting typically focuses on trees alone, excluding other plant life forms such as shrubs, ferns, and vines that characterize native forest structure. Planting one or few tree species with even spacing and in rows may lead to canopy recovery, but not necessarily recovery of diverse forest structure, composition, and ecosystem processes characteristic of native forests (Powers et al. 1997; Ostertag et al. 2008; Holl et al. 2013). Studies that incorporate multiple plant life forms in restoration plantings are therefore important for understanding how to better replicate native forest communities.

Species assemblages of plantings can affect restoration outcomes. Restoration outcomes in grass-invaded tropical pastures include successful establishment of native species, development of native canopy cover, and suppression of invasive grasses that inhibit succession. Specifically, plant communities with higher species and/or functional diversity are more likely to contain species that occupy the same niche as invasive species and thus may have greater resistance against invasion (Levine 2000; Funk et al. 2008; Ostertag et al. 2015). Including multiple plant functional types in restoration efforts also increases the likelihood that planted species will occupy different niches (Yu et al. 2020) and thus take up different resources, potentially leading to greater native productivity over time (Tilman et al. 1996; Hooper & Dukes 2010). This may lead to greater competitive exclusion of invasive species such as grasses in old pastures as compared to plantings that only use monocultures, or one functional type. However, restoration outcomes may also depend strongly on species identity if certain species or functional groups have low competitive advantage against invasive species. In such cases, including vulnerable species in diverse plantings may lead to higher mortality. While it has long been suggested that higher species and functional diversity may lead to better restoration outcomes (e.g. Funk et al. 2008), these questions are rarely tested experimentally, particularly in woody ecosystems where community-level effects may emerge over longer-time scales (Ostertag et al. 2015; Carlucci et al. 2020).

Mimicking natural processes and facilitating succession have proven to increase the success of tropical forest restoration (Lamb et al. 2005; Chazdon 2008). In many systems, plant establishment following disturbance occurs in clusters, with vegetation expanding outward over time (Yarranton & Morrison 1974; Archer et al. 1998). The density of plants in restoration outplantings may influence similar processes by altering plant–plant interactions and rates of vegetation establishment. However, higher-density planting can also intensify competition for resources and potentially lead to self-thinning of native woody species (Westoby 1984; Pyke & Archer 1991). The likelihood of such competitive thinning may depend on resource availability and environmental conditions. Even if some mortality occurs due to self-thinning, higher-density planting could increase seed inputs and suppress invasive grasses (Rehm et al. 2023). Consequently, these denser plantings might facilitate a faster increase in desired woody species than more widely spaced plantation-style planting. Beyond community-level factors such as diversity and density, individual plant characteristics at the time of outplanting may also influence establishment success. In grass-dominated systems, taller individuals may have a competitive advantage over invasive grasses, potentially leading to higher survival rates.

Designing optimal planting density and species assemblages offers promising opportunities to increase forest restoration success across tropical old pasture ecosystems. In Hawaii, abandonment of pasture and agricultural land has led to an abundance of unmanaged land (Perroy et al. 2016; Farrant et al. 2023), some of which is undergoing restoration activities that range from passive (e.g. fencing and ungulate removal) to intensive forest restoration (Yelenik et al. 2024). A lack of secondary succession to diverse forest species communities (e.g. D'Antonio et al. 2017; Yelenik 2017) led to efforts to reforest old pasture systems to achieve a variety of goals including wildlife habitat and water security. However, additional information could help inform effective reforestation strategies (Yelenik et al. 2022), and questions relating to diversity and density of restoration plantings have not been addressed.

To address this gap, we established a factorial field experiment on the Island of Hawai'i manipulating planting density and species assemblages to evaluate early restoration outcomes over 32 months. Specifically, we examined how these factors influence survival and growth of outplanted individuals, native plant cover, and grass cover. We hypothesized that: (1) higher density and more diverse species assemblages would lead to greater overall cover of outplanted species, (2) higher density and more diverse species assemblages would lead to lower grass cover, (3) growth of outplanted species would be lower and mortality greater in higher-density plantings due to competition between outplants, and (4) individuals that were taller at the time of outplanting would have higher survivorship.

Methods

Site Description

We conducted our study in Hakalau Forest National Wildlife Refuge on the Island of Hawai'i, established in 1985 to provide habitat for endangered forest species (U.S. Fish and Wildlife Service 2010). The refuge spans over 32,700 acres of montane rainforest. Elevation ranges from 610 to 1900 m asl; with 2700 mm mean annual rainfall, and a mean temperature of 12°C (Giambelluca et al. 2013). Restoration goals include reestablishing Koa (*Acacia koa*) and 'Ōhi'a (*Metrosideros polymorpha*) forest (U.S. Fish and Wildlife Service 2010). Between 1985 and 1990, over 252,000 plants, including 'Ōhi'a and Koa were planted in corridors extending into former pasturelands to support native bird habitat (Horiuchi & Jeffrey 2002; Paxton et al. 2018; Hunt et al. 2025). Despite canopy cover and bird increases the understory remains dominated by the introduced pasture grass, Kikuyu grass (*Cenchrus clandestinus*; Yelenik 2017).

We established five sites (blocks) in April 2021, each with eleven 6 m × 6 m plots beneath Koa canopy, with a 1 m buffer on all sides and spaced ≥5 m apart (Figure 1). We randomly assigned treatments to the plots in each site. Treatments consisted of different species combinations (two-, four-, or eight-species combination) and density treatments (16 or 32 plants per plot, equivalent to 10,000 or 20,000 plants per hectare), with

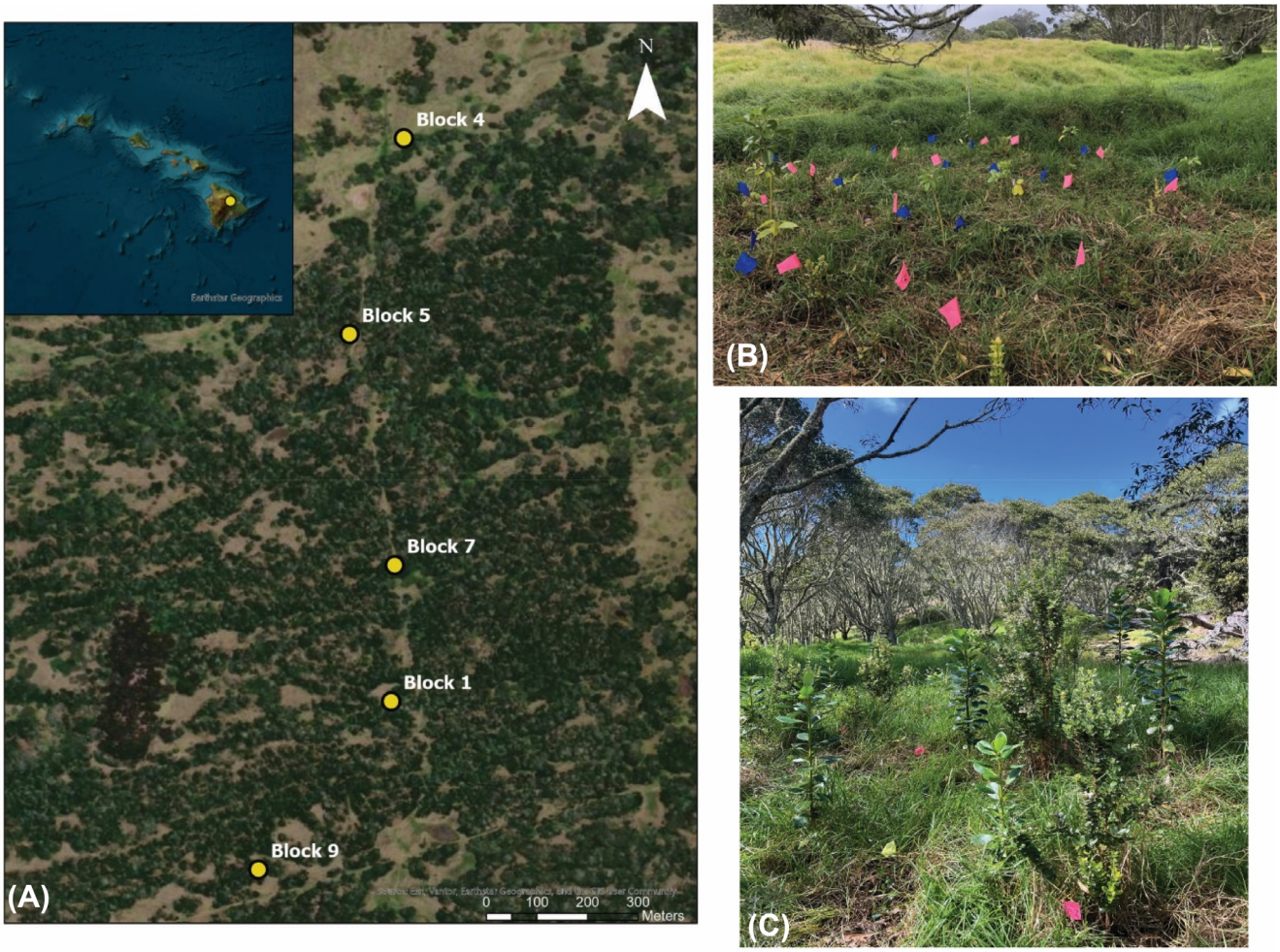

Figure 1. (A) Map of outplanting field sites at Hakalau Forest National Wildlife Refuge. (B) Photo of outplanting plot 1 year after planting. (C) Photo of outplanting plot 3.5 years after planting. Photos taken by J. Kuwahara-Hu and M. Phillips.

one unplanted control per site. The two-species combinations included varied functional groups (Figure 2). Plants were outplanted in four rows within the plots, with rows spaced 1 m apart in both treatments. Within rows, plants were spaced 1 m apart in single-density treatments and 0.5 m apart in double-density treatments. Within plots, we randomly assigned species to locations. Species combinations are illustrated in Figure 2. We considered ʻŌhiʻa (*Metrosideros polymorpha*), Kāwaʻu (*Ilex anomala*), ʻŌlapa (*Cheirodendron trigynum*), and Pilo (*Coprosma rhynchocarpa*) as trees or subtrees, ʻĀkala (*Rubus hawaiensis*), and Pūkiawe (*Leptecophylla tameiameiae*) as shrubs, Laukahi (*Dryopteris wallichiana*) as a fern, and Māʻohiʻohi (*Stenogyne calaminthoides*) as a vine. Prior to planting, we cleared Kikuyu grass using a weed trimmer and then used a mechanical auger to drill holes for plants. We outplanted a total of 1200 plants, with 240 at each site, at the end of April 2021. In June 2021, about 1 month after the initial planting, we completed our first monitoring effort and noted that some plants, particularly *M. polymorpha*, had died likely due to transplant shock or improper planting. Because our research questions centered on relationships between established plant species and not early mortality, we decided to replace plants that had died at our first monitoring time point. We therefore replaced the dead *M. polymorpha* (62 plants total) and thereafter hand weeded around all seedlings every few months for 1 year.

Monitoring

We monitored all plots a total of five times between June 2021 and January 2024, recording survival, plant height, width, and basal diameter (except for non-woody species). We measured height from the base of the plant to the tallest living part of the plant and width at the widest point of its canopy, using a measuring tape. We measured basal diameter to the closest mm with calipers at 10 cm above soil height as measured along the main stem. If we were unable to take measurements at 10 cm (e.g. due to branching), we recorded the measurement at the next whole cm available. For plants with multiple stems, we measured the main stem. If there was not a main stem, we measured the root collar and counted all stems. If the root collar was not

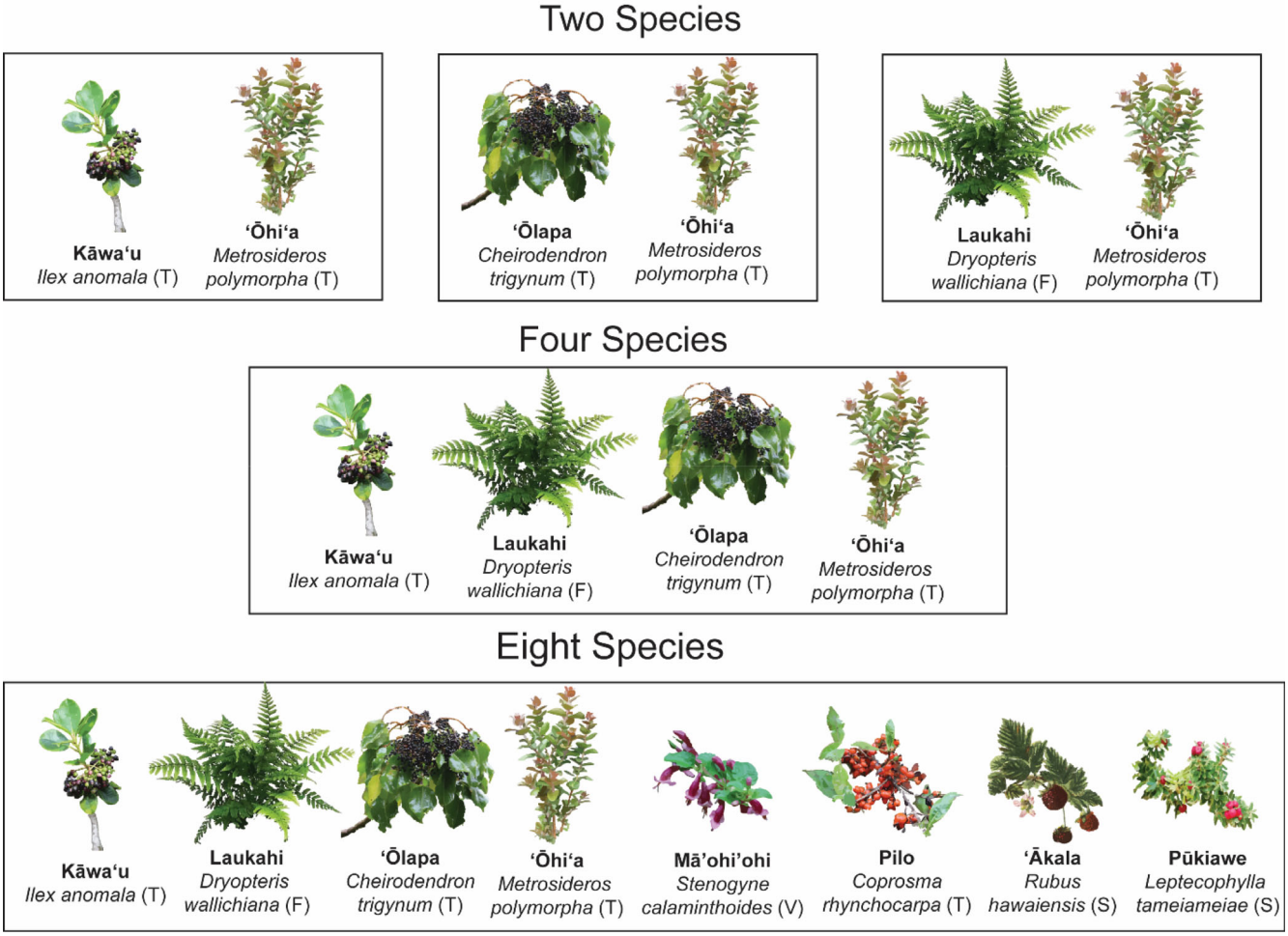

Figure 2. Species combinations used in experimental design with ‘Ōlelo Hawaii in bold, scientific names in italics, and functional group in parentheses (T = tree, S = shrub, F = fern, V = vine). Botanical families represented include Myrtaceae (*Metrosideros polymorpha*), Aquifoliaceae (*Ilex anomola*), Araliaceae (*Cheirodendron trigynum*), Rubiaceae (*Coprosma rhynchocarpa*), Rosaceae (*Rubus hawaiensis*), Ericaceae (*Leptecophylla tameiameiae*), Dryopteridaceae (*Dryopteris wallichiana*), and Lamiaceae (*Stenogyne calaminthoides*). All species combinations were planted in single and double densities. Functional group representation varies among the two-species combinations.

measurable, we measured all stems. We did not measure basal diameter for the fern (*D. wallichiana*) or shrubs (*L. tameiameiae* and *S. calaminthoides*) due to their lack of one main stem. We also measured vegetation cover using a line-point intercept approach (Herrick et al. 2005), using an 8 m transect that ran diagonally from the southeast corner to the northwest corner of the plot. We recorded the occurrence of vegetative hits along a tent pole placed on the right side of the transect line, starting at 1 m and then every 0.5 m along the transect. We recorded the substrate (litter, woody litter, soil, log, or plant base) at the bottom of the stake and then every plant species that hit the stake between the 10 cm, 50 cm, 1 m, and 2 m height intervals. This allowed us to capture the multi-level structure of the plant canopy as it formed.

Data Analysis

H1: Effects of Density and Species Diversity on Outplant Cover. All analyses outlined below were conducted in R version 4.4.1 (R Core Team 2024). Data are available in Yanger et al. (2026). To assess how treatments structured plant cover, we calculated plant and substrate cover from line-point intercept transect data as a proportion of the intercept hits per species or substrate. We pooled cover of all outplanted species in each transect to understand when outplants were large enough to have a signal in plot-level plant cover. We analyzed proportional outplant cover using a zero-inflated beta regression model implemented in the "glmmTMB" package in R (McGillycuddy et al. 2025). Because beta models require response values strictly between 0 and 1, cover values were rescaled using the transformation $(y+0.001)/1.002$, and values equal to 1 after transformation were adjusted slightly (0.999) to ensure all observations fell within the open interval (0,1). The model included density, species combination, time, and their interactions as fixed effects. A zero-inflation component with an intercept-only structure was included to account for excess zeros, and dispersion was allowed to vary across survey periods. We evaluated model diagnostics using simulated residuals generated with the "DHARMa" package (Hartig 2024). Tests

indicated no evidence of overdispersion or additional zero inflation beyond that accounted for by the model. We assessed temporal autocorrelation in the residuals using the autocorrelation function (ACF) from "stats" package, and no substantial autocorrelation was detected. We evaluated the significance of fixed effects using Type II Wald χ^2 tests. Where significant effects were detected, we conducted pairwise post hoc comparisons using the "emmeans" package (Lenth 2023), with Tukey adjustment for multiple comparisons.

H2: Effects of Density and Species Diversity on Grass Cover. We evaluated treatment effects on *C. clandestinus* cover calculated from the line-point intercept data using a generalized linear model built using the "stats" package in R. Proportional cover values were logit-transformed to account for the bounded nature of the response variable. The transformed response was modeled as a function of density, species combination, time, and their interactions. We assessed model significance using analysis of variance (ANOVA). We evaluated model assumptions evaluated using residual diagnostic plots and quantile–quantile plots, which indicated approximately normally distributed residuals and no evidence of heteroscedasticity. We evaluated temporal autocorrelation using the ACF from the "stats" package, and no substantial autocorrelation was detected. Where significant effects were detected, we conducted pairwise post hoc comparisons using the "emmeans" package (Lenth 2023), with Tukey adjustment for multiple comparisons.

H3: Effects of Density and Species Composition on Survival and Growth. To assess survivorship of outplanted species within each treatment, we generated plot-level survival curves using the non-parametric Kaplan–Meier method (Kaplan & Meier 1958). This method estimates the probability of survival over time based on the number of outplants at risk and the number of mortality events recorded at each monitoring time point. We estimated outplant survival probability for each species and treatment using the "survival" R package (Therneau & Lumley 2015). We used a log-rank test to determine if there was a difference between survival curves. Lastly, we calculated pairwise comparisons between species and treatment levels using the "survminer" R package (Kassambara et al. 2016).

Three of the four primary species we used in our experiment (used the most extensively across the treatments) were woody—*M. polymorpha*, *I. anomala*, and *C. trigynum*—and have species-specific allometric regression equations to estimate biomass from height and diameter (Aplet & Vitousek 1994). We used these equations to estimate biomass in grams at each time point. We then calculated a relative growth rate (RGR) for each individual of these three species using this equation:

$$\mathrm{RGR} = \frac{(\ln(W_2) - \ln(W_1))}{(t_2 - t_1)}$$

In this equation, W represents the biomass estimate (g) and t represents time (days). For our purposes t_1 was the outplanting date and t_2 was the last date of our monitoring period. Residuals of RGR for all three species conformed to normality and heteroscedasticity assumptions. Thus, we used an ANOVA to test for differences in RGR between treatments.

H4: Effects of Initial Plant Height on Survival. We assessed how plant height and species influenced survival using a logistic regression model in the "glmmTMB" package in R (McGillycuddy et al. 2025). We coded survival as a binary response (alive = 1, dead = 0) and included height, species, and their interaction as predictors. We evaluated model fit using simulated residuals from the "DHARMa" package (Hartig 2024), which indicated no severe violations of assumptions. We tested the significance of fixed effects with Type II Wald χ^2 tests. To examine how height affected survival for each species, we calculated species-specific slopes using "emtrends" from the "emmeans" package (Lenth 2023) and performed pairwise comparisons of these slopes with a Tukey adjustment to account for multiple testing.

Results

H1: Effects of Density and Species Diversity on Outplant Cover

Outplanted species established successfully across treatments, and their cover increased through time. Total outplant cover increased through time ($\chi^2 = 85.14$, $p < 0.001$; Table S1), reflecting gradual establishment and growth of planted individuals during the monitoring period (Figure 3A). Outplant cover was greater in double-density than single-density plantings ($\chi^2 = 35.22$, $p = 0.002$; Table S1; Figure 3B). Outplant cover increased with species richness ($\chi^2 = 13.95$, $p = 0.007$; Table S1). Pairwise comparisons among species combinations revealed that the eight-species combination had greater outplant cover than both two-species combinations (*Metrosideros polymorpha–Ilex anomala* and *M. polymorpha–Dryopteris wallichiana*; $p = 0.007$ and $p = 0.033$, respectively), while all other pairwise comparisons among species combinations were not different. Estimated mean cover ranged from 5.6% in the *M. polymorpha–I. anomala* two-species combination to 11.0% in the eight-species combination. In contrast, interactions among density, species combination, and time were not detected (all $p > 0.05$; Table S1), indicating that these effects remained relatively consistent over time. Across all planted treatments, mean total outplant cover reached 16 ± 3% (mean ± SE) by the end of the experiment. Individual species typically contributed 3–4 ± 1% cover, and overall cover increased steadily through time, although variability among plots remained high.

Differences among treatments were apparent in several survey periods. For example, during the March 2023 monitoring period the eight-species double-density treatment had higher outplant cover than both two- and four-species single-density treatments (Figure 3A). When we aggregated data across species combinations to isolate density effects, double-density planting consistently produced greater cover than control plots across multiple survey periods (Figure 3B). Differences between single- and double-density treatments were most pronounced

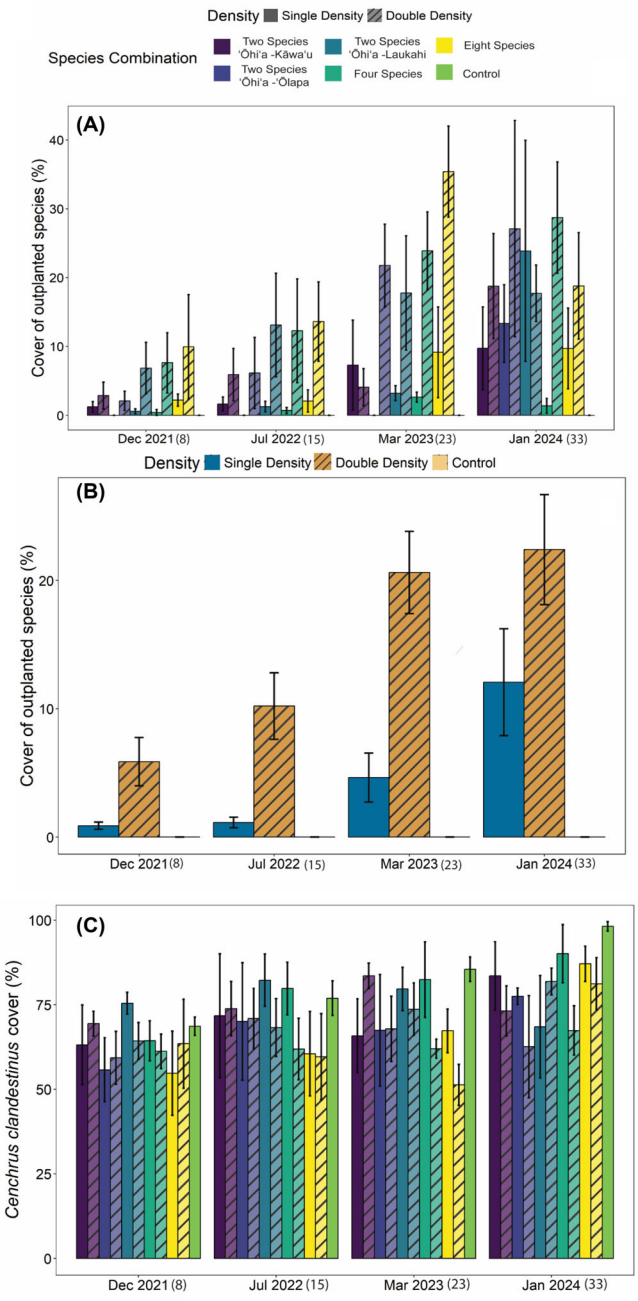

Figure 3. (A) Mean cover ± SE of all outplanted species within each of the species combinations (represented by different colors) at single and double density (represented by solid or hatched bars). The control treatment is represented by the last bar at each time point, but had no cover present. (B) Mean cover ± SE of all outplanted species aggregated across species combinations at single and double density (represented by solid or hatched bars). (C) Mean cover + SE of Kikuyu grass (*Cenchrus clandestinus*) within each of the species combinations (represented by different colors) at single and double density (represented by solid or hatched bars). *x*-axis labels in panels (A–C) show the survey date followed by time since outplanting in months in parentheses.

in July 2022 and March 2023, although these differences were smaller by the final monitoring period in January 2024. When density and species combination were considered together, double-density four-species and double-density eight-species treatments had greater cover than several single-density two-species treatments and the single-density control (all $p < 0.05$).

H2: Effects of Density and Species Diversity on Grass Cover

Cover of *Cenchrus clandestinus* varied through time but showed limited response to outplanting treatments (Figure 4). Grass cover increased through time ($F = 20.52$, $p < 0.001$). Grass cover was lower in double-density than single-density plantings ($F = 5.83$, $p = 0.017$; Figure 3C). In contrast, species combination did not influence grass cover ($F = 1.72$, $p = 0.13$).

We did not detect interactions among density, species combination, and survey period (all $p > 0.05$), indicating that treatment effects remained relatively consistent through time. Grass cover generally increased across surveys, likely reflecting regrowth following initial mechanical suppression and subsequent hand weeding. Despite this increase, grass cover in planted treatments did not consistently differ from that observed in unplanted control plots (Figure 3C).

H3: Effects of Density and Species Composition on Survival and Growth

Survival. Overall survival of outplanted individuals was high, averaging 76 ± 2.5% by the end of the experiment. Survival varied substantially among species. The highest survival occurred in *I. anomala* (92 ± 2.6%), *Rubus hawaiensis* (93 ± 7.5%), and *Coprosma rhynchocarpa* (90 ± 5.5%), followed by *D. wallichiana* (84 ± 5.1%), *Cheirodendron trigynum* (83 ± 3.5%), and *M. polymorpha* (67 ± 5.2%). The lowest survival occurred in *Leptecophylla tameiameiae* (47 ± 14.7%) and *Stenogyne calaminthoides* (23 ± 13.2%).

Kaplan–Meier survival curves differed among species and treatments (Figs. 4 & S1; log-rank $p < 0.0001$). Species combinations affected survival, with some combinations showing higher survivorship than others (Fig. S2; $p < 0.0001$). The *M. polymorpha–I. anomala* combination had higher survival than the *M. polymorpha–D. wallichiana* combination, while the four-species mixture had higher survival than the eight-species mixture. In contrast, planting density did not influence survival (Fig. S3; $p = 0.22$).

Species responses to treatments varied. *M. polymorpha* exhibited its lowest survival in the eight-species combination, regardless of planting density. In contrast, *I. anomala* and *C. trigynum* tended to have higher survival in four-species mixtures, while *D. wallichiana* showed no differences across treatments.

Relative Growth Rate. RGRs of the three woody species (*M. polymorpha*, *I. anomala*, and *C. trigynum*) did not differ among species combinations, planting densities, or their interactions. For *M. polymorpha*, RGR did not vary among species combinations ($F_{[2,21]} = 0.79$, $p = 0.47$), planting densities ($F_{[1,21]} = 0.04$, $p = 0.85$), or their interaction ($F_{[2,21]} = 0.77$, $p = 0.48$; Fig. 5A). *Ilex anomala* and *C. trigynum* showed similar patterns, with no treatment effects (Figs. 5B & 5C).

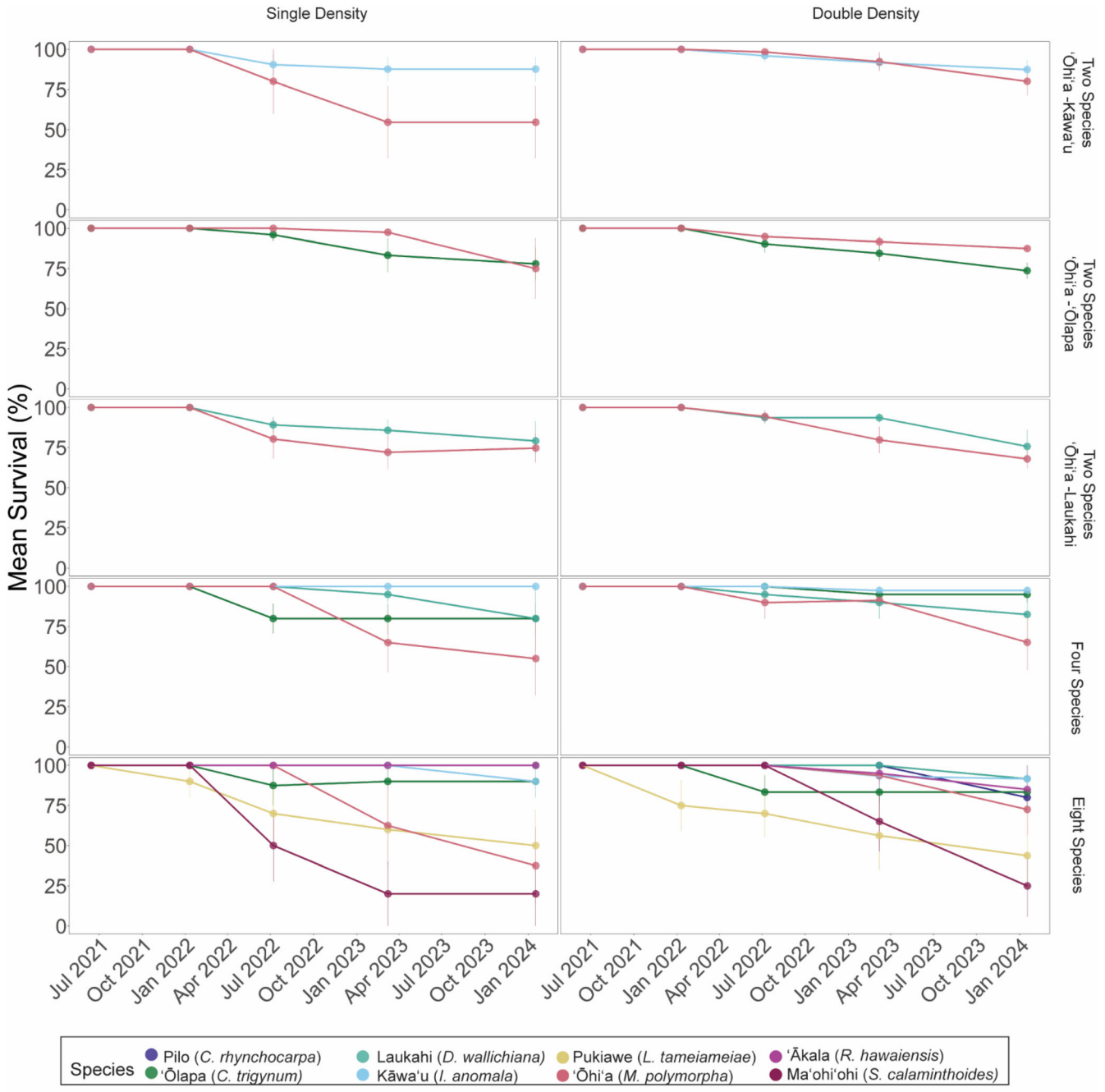

Figure 4. Mean survival ± SE of each species under single density (left panels) and double density (right panels) by species combination (rows) over the course of the experiment.

H4: Effects of Initial Plant Height on Survival

Initial plant height influenced survival probability across species ($\chi^2 = 23.23$, $p < 0.001$; Table S2; Figure 6), and survival also differed among species ($\chi^2 = 40.26$, $p < 0.001$; Table S2). However, there was no interaction between height and species ($\chi^2 = 7.94$, $p = 0.34$; Table S2), indicating that the relationship between height and survival was broadly similar among species.

Species-specific slopes showed that survival increased with initial height for *D. wallichiana*, *I. anomala*, and *M. polymorpha*, indicating that taller individuals of these species were more likely to survive. For the remaining species, the effect of height on survival was not different from zero. Pairwise comparisons among species slopes were not significant after Tukey adjustment, suggesting that the magnitude of the height effect did not differ among species.

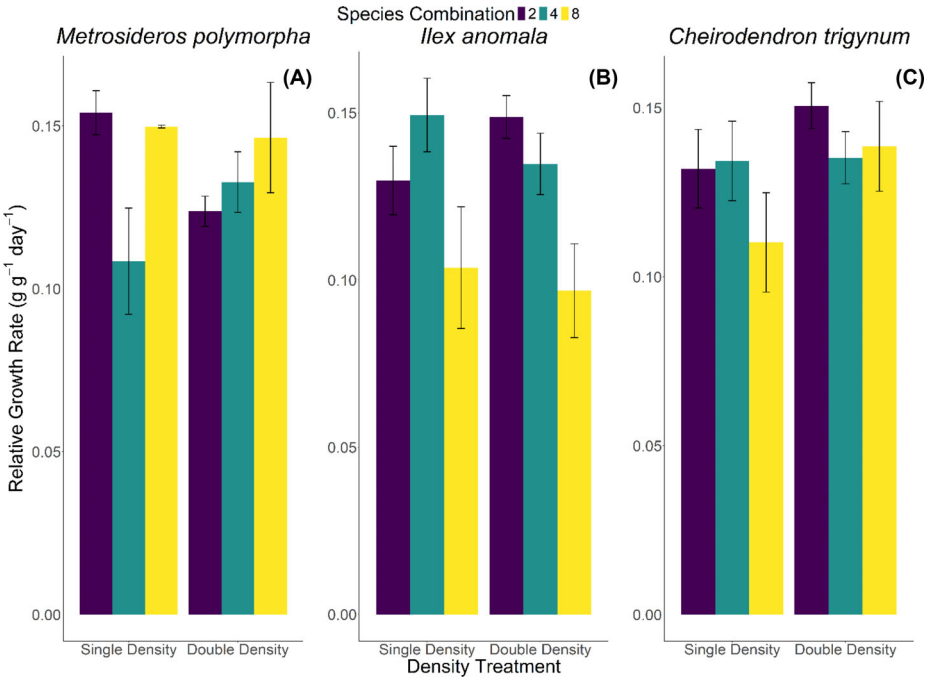

Figure 5. Mean relative growth rate ± SE by species combination (represented by color) and density treatment (*x*-axis) of (A) ʻŌhiʻa (*Metrosideros polymorpha*), (B) Kāwaʻu (*Ilex anomola*), and (C) ʻŌlapa (*Cheirodendron trigynum*).

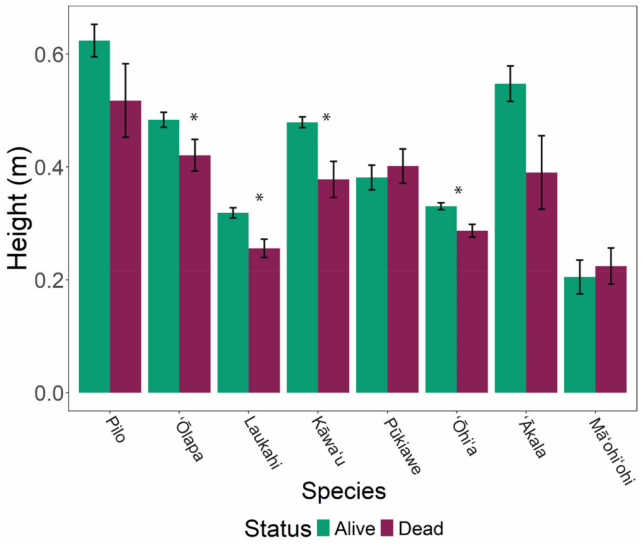

Figure 6. Mean height (m) ± SE of each species at the time of outplanting that were alive (green) or dead (brown) by end of the experiment. Bars with * between them indicate significant differences in height at *p* less than 0.05.

Discussion

Overall, we found high survivorship of multiple species in both single- and double-density plantings, with taller individuals showing higher survival for the fern and all tree species. As hypothesized, higher-density plantings produced greater outplant cover, particularly during early and mid-stage observations, although differences diminished by the final monitoring period and were not driven by mortality. Species composition also influenced cover, with the eight-species treatment showing reduced cover over time due to higher mortality of vine and shrub species. In contrast, we did not find consistent evidence that higher planting density reduced grass cover within the first 3 years. Similarly, increased density did not lead to reduced growth or survival, suggesting limited short-term competition among outplants. These patterns suggest that height and growth form may be important factors influencing establishment in this system. Together, these results suggest that restoration in tropical wet forests may benefit from carefully selected multi-species assemblages and higher planting densities.

H1: Effects of Density and Species Diversity on Outplant Cover

While we observed differences in survivorship between the species combinations, we observed minimal differences in total cover of outplants in our treatments when compared to the control due to a high degree of variability in the data. We found that the four- and eight-species combinations planted at double density had higher outplant cover than the control 2 years after outplanting. This pattern only remained for the four-species combination at nearly 3 years after outplanting, likely due to the high mortality of some species in the eight-species combination. Although evidence that outplant cover differed between treatments was limited, increases in the abundance of some outplanted species suggest early indications of shifts in planted species dominance, which is a common restoration goal (Stanturf et al. 2014). This may reflect the early stages of a sampling effect, where a subset of species begins to dominate and

influence community trajectory (Huston 1997; Huston & McBride 2002; Hooper et al. 2005). Additionally, *Metrosideros polymorpha* was included in all of the outplanting treatments, which may influence its relative contribution to observed patterns.

We found that species combination did impact survivorship, and this may be explained in part by plant type. These species combinations represented different growth forms (trees, shrub, fern, and vine). We found that the vine (*Stenogyne calaminthoides*) and a shrub (*Leptecophylla tameiameiae*) had the lowest survivorship out of all species we planted. Additionally, the fern (*Dryopteris wallichiana*) and a shrub (*Rubus hawaiensis*) had lower survivorship than some of the tree species. Three of these species (*S. calaminthoides*, *L. tameiameiae*, and *R. hawaiensis*) were only included in the eight-species combination, likely driving lower survivorship when compared to other species combinations. Yet, because species richness was confounded with species identity and growth form, caution is advised before attributing these patterns solely to diversity effects. It appeared that these species were easily covered by the invasive grass, likely decreasing their survivorship. Shorter-stature outplant species have been associated with lower survival at this site in the past (Yelenik et al. 2022).

Our results, which show that there is lower native plant cover in the eight versus four-species plots, do not align with expectations from biodiversity-ecosystem functioning theory (e.g. Tilman et al. 1996, Hooper & Dukes 2010) although interpretation is limited by the confounding described above. Our results may be due to a "negative selection effect" (Jiang et al. 2008), wherein disproportionate mortality among a few species drive the cover differences between treatments. From a management perspective, these results suggest that it may be beneficial to use a phased planting approach (Coiffait-Gombault et al. 2012; Stanturf et al. 2014) where important understory species that are likely to be easily outcompeted or smothered by grass are added in once the canopy is more established and there is evidence of grass suppression.

H2: Effects of Density and Species Diversity on Grass Cover

Some evidence supports that revegetation following invasive-plant removal can suppress the reestablishment of invasive species (Schuster et al. 2018); however, an earlier meta-analysis highlighted that few invasive-plant removal studies (30%) examined revegetation as a tool for invasive suppression (Kettenring & Adams 2011). Further investigation could help determine the effectiveness of this approach. We expected that higher-density plantings would suppress grass cover through shading, but we found limited evidence to support this within the first 3 years of planting. It remains unclear how effective revegetation is at grass suppression in woody systems as most evidence supporting this strategy comes from grasslands (Schuster et al. 2018). However, it is possible that grass suppression will occur once the plants are larger, and a closed canopy is present as suggested by McDaniel and Ostertag (2010). The limited canopy closure observed by three and a half years after planting is consistent with the slow-growth rates characteristic of Hawaiian montane forest species, particularly *M. polymorpha* (Friday & Herbert 2006). Unlike faster-growing tropical tree species, the species used in this experiment may require substantially longer time frames to achieve the canopy closure necessary to shade out invasive grasses. Past research at this site has shown that high-density plantings lead to roughly half of the grass biomass compared to plantings at half the density, although this result took 4 years to emerge (D'Antonio et al. 2024). This agrees with evidence from a review that found that revegetation experiments aimed at suppressing invasive plants that were less than 3 years had a higher rate of negative results when compared with longer-term experiments (Schuster et al. 2018), which could be investigated with further sampling of these plots over time.

The line-point intercept method captures occurrence at fixed points but does not directly quantify grass biomass or canopy density, and it is therefore possible that grass biomass declined in planted treatments even when cover as recorded by point intercepts did not change detectably. This is especially true for *Cenchrus clandestinus*, which is rhizomatous and grows in multiple overlapping layers in productive habitats such as these sites. Thus, biomass could decrease while still showing high cover. Future studies could benefit from combining cover estimates with biomass harvests (Rehm et al. 2023). Additionally, *C. clandestinus* can tolerate moderate shade (Holm et al. 1977; McDaniel & Ostertag 2010), which may partly explain the limited suppression observed even as outplant cover increased.

While our results support high-density, multi-species planting as a restoration strategy, the practical implications of doubling planting density may be a consideration. Increased density raises implementation costs, including seedling production, planting labor, and ongoing maintenance. Within the first 3 years, we did not observe a corresponding benefit of higher density in reducing invasive grass cover, and these tradeoffs will vary in importance depending on restoration budgets and objectives. The potential long-term benefits of accelerated canopy development and eventual grass suppression, as suggested by D'Antonio et al. (2024) remain plausible but have yet to be demonstrated over longer time frames in this system.

H3: Effects of Density and Species Composition on Survival and Growth

Intraspecific competition between tree species is well known to lead to self-thinning in dense stands (Westoby 1984). It is assumed that high-density restoration plantings will result in self-thinning (Osawa & Allen 1993; Jones et al. 2015) and tree density will decrease over time (Sansevero et al. 2011). We did not find evidence of self-thinning in our experiment as survival and RGR were not different between single- and double-density plantings. However, the relatively short duration of the study may have limited our ability to detect changes in tree density, and longer-term monitoring will be needed to determine whether self-thinning emerges as trees increase in size and canopy closure develops. Other studies have also found that self-thinning does not occur or occurs at low rates in restored forests, which could be due to planting slow-growth species that are

long-lived (Suganuma & Durigan 2015; de Oliveira et al. 2019). The species that we planted are relatively slow-growing, especially *M. polymorpha*, when compared to other tropical tree species (Friday & Herbert 2006). It is hard to predict how long self-thinning processes may take to start for the different species; however, some work suggests that gap turnover ranges from 80 to 136 years in tropical forests (Hartshorn 1978; Denslow 1987). Planting densely may be an effective approach, even if self-thinning eventually occurs, if the resulting canopy closure can suppress invasive grasses.

H4: Effects of Initial Plant Height on Survival

Shorter stature outplant species have been associated with lower survival at this site in the past (Yelenik et al. 2022). Our results support this conclusion, as we found higher survivorship of taller outplants for several of the species included in our study. We found the highest survivorship in our four-species combination (*Ilex anomala*, *Cheirodendron trigynum*, *M. polymorpha*, and *D. wallichiana*), canopy-forming tree species, and one fern.

Our results suggest that carefully selected multi-species, high-density plantings can be a viable strategy for restoring wet forest ecosystems in Hawaii. Specifically, we found that dense outplantings can establish successfully without early signs of self-thinning or reduced growth, suggesting that this approach may be effective when aiming to accelerate canopy development and shift community composition. Species-specific differences in survivorship highlight the importance of selecting resilient species, particularly in grass-dominated areas, and suggest that phased planting may be a more effective approach for establishing sensitive understory species. These results suggest potential management options beyond the single-species approaches historically used in this area. Establishing more diverse, functionally complementary species at the start of (or early on in) pasture reforestation efforts may contribute to improved habitat quality for native forest birds and provide broader ecosystem benefits. Long-term monitoring may reveal whether these approaches yield durable shifts in vegetation structure and function, but our findings offer a strong design approach for more effective and ecologically aligned restoration strategies across the Hawaiian archipelago.

Acknowledgments

We thank S. Bechtel, K. Fukunaga, L. R. Guieb, L. Messer, C. Smith, Warner, M. Iwamoto, and E. Bell, for help with fieldwork. Hakalau Forest National Wildlife Refuge staff provided access and S. Kendall of U.S. Fish and Wildlife Service (USFWS) helped locate specific sites and we thank B. Horiuchi for growing native plants. This research was funded by a U.S. Fish and Wildlife Service Science Support Partnership Grant and the U.S. Geological Survey, and in part, by the U.S. Department of Agriculture (USDA) Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and should not be considered to represent any official USDA determination or policy. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Data generated during this study are available in Yanger et al. (2026).

LITERATURE CITED

Aplet GH, Vitousek PM (1994) An age – altitude matrix analysis of Hawaiian rain-forest succession. Journal of Ecology137–147

Archer S, Scifres CR, Bassham CR, Maggio R (1998) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58:111–127. https://doi.org/10.2307/1942463

Ashton MS, Gunatilleke CVS, Singhakumara BMP, Gunatilleke I (2001) Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. Forest Ecology and Management 154:409–430. https://doi.org/10.1016/S0378-1127(01)00512-6

Carlucci MB, Brancalion PHS, Rodrigues RR, Loyola R, Cianciaruso MV (2020) Functional traits and ecosystem services in ecological restoration. Restoration Ecology 28:1372–1383. https://doi.org/10.1111/rec.13279

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458–1460. https://doi.org/10.1126/science.1155365

Coiffait-Gombault C, Buisson E, Dutoit T (2012) Using a two-phase sowing approach in restoration: sowing foundation species to restore, and subordinate species to evaluate restoration success. Applied Vegetation Science 15:277–289. https://doi.org/10.1111/j.1654-109X.2012.01182.x

D'Antonio CM, Rehm E, Elgersma C, Yelenik SG (2024) Influence of native woody understory on invasive grasses and soil nitrogen dynamics under plantation and remnant montane tropical trees. Ecosystems 27:797–814. https://doi.org/10.1007/s10021-024-00922-z

D'Antonio CM, Yelenik SG, Mack MC (2017) Ecosystem vs. community recovery 25 years after grass invasions and fire in a subtropical woodland. Journal of Ecology 105:1462–1474. https://doi.org/10.1111/1365-2745.12855

Davidson EA, de Araújo AC, Artaxo P, Balch JK, Brown IF, Bustamante MM, Coe MT, DeFries RS, Keller M, Longo M (2012) The Amazon basin in transition. Nature 481:321–328. https://doi.org/10.1038/nature10717

de Oliveira CDC, de Oliveira IRC, Suganuma MS, Durigan G (2019) Overstory trees in excess: a threat to restoration success in Brazilian Atlantic forest. Forest Ecology and Management 449:117453. https://doi.org/10.1016/j.foreco.2019.117453

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 1:431–451. https://doi.org/10.1146/annurev.es.18.110187.002243

Farrant DN, Roberts DA, D'Antonio CM, Larsen AE (2023) What follows fallow? Assessing revegetation patterns on abandoned sugarcane land in Hawai'i. Agriculture, Ecosystems & Environment 355:108603. https://doi.org/10.1016/j.agee.2023.108603

Fearnside PM (1993) Deforestation in Brazilian Amazonia: the effect of population and land tenure. Ambio 22:537–545. https://doi.org/10.1016/0006-3207(94)90222-4

Friday JB, Herbert DA (2006) Metrosideros polymorpha ('ōhi'a lehua). Species Profiles for Pacific Island Agroforestry 3:2

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution 23:695–703. https://doi.org/10.1016/j.tree.2008.07.013

Giambelluca TW, Chen Q, Frazier AG, Price JP, Chen YL, Chu PS, Delparte DM (2013) Online rainfall atlas of Hawai'i. Bulletin of the American Meteorological Society 94:313–316. https://doi.org/10.1175/BAMSD-11-00228.1

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management 148:185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Hartig F (2024) DHARMa: residual diagnostics for hierarchical (multi-level/-mixed) regression models. R package version 0.4.7. http://florianhartig.github.io/DHARMa/ (accessed 15 May 2025)

Hartshorn GS (1978) Tree falls and tropical forest dynamics. Pages 617–665. In: Tomlinson PB, Zimmermann MH (eds) Tropical trees as living systems. Cambridge University Press, Cambridge, United Kingdom

Herrick JE, Van Zee JW, Havstad KM, Burkett LM, Whitford WG, Bestelmeyer BT, et al. (2005) Monitoring manual for grassland, shurbland, and savanna ecosystems. USDA-ARS Jornada Experimental Range, Las Cruces, New Mexico

Holl KD (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31:229–241. https://doi.org/10.1111/j.1744-7429.1999.tb00135.x

Holl KD, Loik ME, Lin EH, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology 8:339–349. https://doi.org/10.1046/j.1526-100x.2000.80049.x

Holl KD, Stout VM, Reid JL, Zahawi RA (2013) Testing heterogeneity-diversity relationships in tropical forest restoration. Oecologia 173:569–578. https://doi.org/10.1007/s00442-013-2632-9

Holm LG, Plucknett DL, Pancho JV, Herberger JP (1977) The world's worst weeds: distribution and biology. University Press of Hawaii, Honolulu, Hawaii

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, et al. (2005) Effect of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35. https://doi.org/10.1890/04-0922

Hooper DU, Dukes JS (2010) Functional composition controls invasion success in a California serpentine grassland. Journal of Ecology 98:764–777. https://doi.org/10.1111/j.1365-2745.2010.01673.x

Horiuchi B, Jeffrey J (2002) Native plant propagation and habitat restoration at Hakalau Forest National Wildlife Refuge, Hawai'i. In: National proceedings: forest and conservation nursery associations. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah

Hunt NJ, Kendall SJ, Bak TM, Camp RJ (2025) Status and trends of forest bird populations at Hakalau Forest National Wildlife Refuge, 1987–2024. Hawai'i Cooperative Studies Unit Technical Report HCSU-117. University of Hawai'i at Hilo, Hilo, Hawai'i. http://hdl.handle.net/10790/5400 (accessed 5 Jan 2025)

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 111:449–460. https://doi.org/10.1007/s004420050180

Huston MA, McBride AC (2002) Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. Pages 47–60. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning. Oxford University Press, Oxford, United Kingdom

Jiang L, Pu Z, Nemergut DR (2008) On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. Oikos 117:488–493. https://doi.org/10.1111/j.0030-1299.2008.16401.x

Jones CS, Duncan DH, Rumpff L, Thomas FM, Morris WK, Vesk PA (2015) Empirically validating a dense woody regrowth problem and thinning solution for understory vegetation. Forest Ecology and Management 340:153–162. https://doi.org/10.1016/j.foreco.2014.12.006

Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481. https://doi.org/10.1080/01621459.1958.10501452

Kassambara A, Kosinski M, Biecek P (2016) survminer: drawing survival curves using ggplot2. R Package. https://cran.r-project.org/web/packages/survminer/index.html (accessed 15 May 2025)

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology 48:970–979. https://doi.org/10.1111/j.1365-2664.2011.01979.x

Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. Science 310:1628–1632. https://doi.org/10.1126/science.1111773

Lenth R (2023) emmeans: estimated marginal means, aka least-squares means. R package version 1.8.5. https://github.com/rvlenth/emmeans/ (accessed 15 May 2025)

Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854. https://doi.org/10.1126/science.288.5467.852

McDaniel S, Ostertag R (2010) Strategic light manipulation as a restoration strategy to reduce alien grasses and encourage native regeneration in Hawaiian mesic forests. Applied Vegetation Science 13:280–290. https://doi.org/10.1111/j.1654-109X.2009.01074.x

McGillycuddy M, Popovic G, Bolker BM, Warton DI (2025) Parsimoniously fitting large multivariate random effects in glmmTMB. Journal of Statistical Software 112:1–19. https://doi.org/10.18637/jss.v112.i01

Osawa A, Allen RB (1993) Allometric theory explains self-thinning relationships of mountain beech and red pine. Ecology 74:1020–1032. https://doi.org/10.2307/1940472

Ostertag R, Giardina CP, Cordell S (2008) Understory colonization of Eucalyptus plantations in Hawai'i in relation to light and nutrient levels. Restoration Ecology 16:475–485. https://doi.org/10.1111/j.1526-100X.2007.00321.x

Ostertag R, Warman L, Cordell S, Vitousek PM (2015) Using plant functional traits to restore Hawaiian rainforest. Journal of Applied Ecology 52:805–809. https://doi.org/10.1111/1365-2664.12413

Paxton EH, Yelenik SG, Borneman TE, Rose ET, Camp RJ, Kendall SJ (2018) Rapid colonization of a Hawaiian restoration forest by a diverse avian community. Restoration Ecology 26:165–173. https://doi.org/10.1111/rec.12540

Perroy RL, Melrose J, Cares S (2016) The evolving agricultural landscape of post-plantation Hawai'i. Applied Geography 76:154–162. https://doi.org/10.1016/j.apgeog.2016.09.018

Powers JS, Haggar JP, Fisher RF (1997) The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. Forest Ecology and Management 99:43–54. https://doi.org/10.1016/S0378-1127(97)00193-X

Pyke DA, Archer S (1991) Plant–plant interactions affecting plant establishment and persistence on revegetated rangeland. Journal of Range Management 44:550–557. https://doi.org/10.2307/4003035

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (accessed 15 May 2025)

Rehm EM, D'Antonio CM, Yelenik SG (2023) Crossing the threshold: invasive grasses inhibit forest restoration on Hawaiian Islands. Ecological Applications 33:e2841. https://doi.org/10.1002/eap.2841

Sansevero JBB, Prieto PV, de Moraes LFD, Rodrigues PJP (2011) Natural regeneration in plantations of native trees in lowland Brazilian Atlantic forest: community structure, diversity, and dispersal syndromes. Restoration Ecology 19:379–389. https://doi.org/10.1111/j.1526-100x.2009.00556.x

Schuster MJ, Wragg PD, Reich PB (2018) Using revegetation to suppress invasive plants in grasslands and forests. Journal of Applied Ecology 55:2362–2373. https://doi.org/10.1111/1365-2664.13195

Stanturf JA, Palik BJ, Dumroese RK (2014) Contemporary forest restoration: a review emphasizing function. Forest Ecology and Management 331:292–323. https://doi.org/10.1016/j.foreco.2014.07.029

Suganuma MS, Durigan G (2015) Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. Restoration Ecology 23:238–251. https://doi.org/10.1111/rec.12168

Therneau TM, Lumley T (2015) survival: R package. https://cran.r-project.org/web/packages/survival/index.html (accessed 15 May 2025)

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720. https://doi.org/10.1038/379718a0

U.S. Fish and Wildlife Service (2010) Hakalau Forest National Wildlife Refuge comprehensive conservation plan. http://www.fws.gov/refuge/Hakalau_Forest/what_we_do/planning.html (accessed 5 Jan 2025)

Westoby M (1984) The self-thinning rule. Advances in Ecological Research 14:167–225. https://doi.org/10.1016/s0065-2504(08)60171-3

Yanger C, Kuwahara-Hu J, Yelenik S, Phillips M, Datlof EM (2026) Hakalau forest national wildlife refuge testing plant diversity and density for restoration

from 2021-2024: U.S. Geological Survey data release. Pacific Island Ecosystems Research Center, Hawaii National Park, Hawaii. https://doi.org/10.5066/180810

Yarranton GA, Morrison RG (1974) Spatial dynamics of a primary succession: nucleation. Journal of Ecology 62:417. https://doi.org/10.2307/2258988

Yelenik S, Trauernicht C, McDaniel S, Wolkis D, Chambers T (2024) Increasing wildfire incidence and the need for seed in Hawai'i. Native Plants Journal 25:61–67. https://doi.org/10.3368/npj.25.2.61

Yelenik SG (2017) Linking dominant Hawaiian tree species to understory development in recovering pastures via impacts on soils and litter. Restoration Ecology 25:42–52. https://doi.org/10.1111/rec.12377

Yelenik SG, Rehm EM, D'Antonio CM (2022) Can the impact of canopy trees on soil and understory be altered using litter additions? Ecological Applications 32:e02477. https://doi.org/10.1002/eap.2477

Yu R, Huang J, Xu Y, Ding Y, Zang R (2020) Plant functional niches in forests across four climatic zones: exploring the periodic table of niches based on plant functional traits. Frontiers in Plant Science 11:841. https://doi.org/10.3389/fpls.2020.00841

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Kaplan–Meir survival curve showing cumulative survival probabilities of each species under single density (left panels) and double density (right panels) by species combination (rows) over the course of the experiment.

Figure S2. Kaplan–Meir survival curve showing cumulative survival probabilities of all plants under each species combination over time (in days).

Figure S3. Kaplan–Meir survival curve showing cumulative survival probabilities of all plants under single and double density plantings over time (in days).

Table S1. Chi-square test results from a generalized linear mixed model (GLMM) examining the effects of density, species combination, and time on proportional outplant cover. The model included all two- and three-way interactions, with a beta error distribution, a logit link, and a zero-inflation component. Dispersion was modeled as a function of time. Significant effects ($p < 0.05$) are shown in bold.

Table S2. Analysis of deviance (Type II ANOVA) results from a generalized linear model (GLM) examining the effects of density, species combination, and time on grass cover (logit-transformed grass cover). The model included all two- and three-way interactions. Significant effects ($p < 0.05$) are shown in bold.

Coordinating Editor: Csaba Tölgyesi

Received: 27 March, 2026; First decision: 5 June, 2026; Revised: 20 August, 2026; Accepted: 24 August, 2026