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Experimental translocation of a rare Hawaiian tree reveals disparity between remnant and potential habitat

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ABSTRACT

Translocation is implemented worldwide as a conservation strategy for rare and endangered plant species, yet the factors that influence long-term success remain poorly understood. Remnant wild populations are often used as indicators to model habitat preference and select translocation sites, but such populations may be refugia from past biological or anthropogenic stressors and represent sub-optimal habitat conditions for focal taxa. To test assumptions about habitat preferences of rare species, we conducted a four-year experimental translocation of the Critically Endangered Hawaiian tree, 'ohe mauka, *Polyscias bisattenuata* (Araliaceae), planting 3,700 saplings across eleven sites spanning diverse environmental conditions both within and beyond the species' extant range. We measured seventeen predictor variables at the site and individual plant level in categories of climate, surrounding vegetation, soil chemistry, and genetic provenance. We used linear mixed effects models to assess relative effects of predictors on translocated plant survival, growth, and vigor. The factors which influenced plant performance shifted across ontogeny. The height of surrounding vegetation showed an initial negative relationship with two-year survival, but later showed a positive relationship with four-year growth. Four-year growth demonstrated a strong positive relationship with site annual mean temperature. Successful translocation sites were lower in elevation and warmer in temperature than conditions represented by remnant wild populations. Results demonstrate that basing translocation sites solely on limited extant wild occurrences can lead to suboptimal restoration practices, and experimental outplanting across broad conditions may help identify rare species' contemporary habitat preferences.

1. Introduction

As the extinction rate of plant species accelerates worldwide (Bachman et al., 2024; Pimm et al., 2014), the persistence of plant diversity depends on effective conservation interventions such as ex situ collections and in situ translocation (Corlett, 2016; Heywood, 2017). While human-induced climate change and habitat degradation drive most twenty-first century species extinctions (IPCC, 2014; Pyron and Pennell, 2022), the conservation of biodiversity is now paradoxically dependent on well-informed human action (COP CBD; IPBES et al., 2019). While significant advances have been made in plant conservation, global efforts have largely fallen short of goals set by the Convention on Biological Diversity (CBD) (Heywood, 2017), and species extinction rates continue to rise (IUCN, 2023). Applied research designed to optimize plant conservation success is imperative to inform management and increase knowledge of focal species' biology.

Plant translocation is a conservation tool used to prevent the extinction of rare plant species when less intensive in situ management strategies are insufficient (Maunder, 1992; Sarrazin and Barbault, 1996). Translocation aims to promote self-sustaining populations through the deliberate movement of plants to suitable habitat (IUCN, 2013; Maschinski and Albrecht, 2017; Maunder, 1992). Propagules are

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planted to re-establish historic populations (reintroduction), enlarge current populations (augmentation), or establish new populations in novel geographic distributions (conservation introduction). Translocation is integrated into recommendations of the International Union for Conservation of Nature (IUCN), and federal agencies of countries worldwide (IUCN/SSC, 2013; Maschinski and Albrecht, 2017).

Multiple reviews of plant translocation efforts have sought to identify universal determinants of initial and long-term success on the international (Dalrymple et al., 2012; Godefroid et al., 2011; Menges, 2008) and regional scales (Bellis et al., 2023; D'Agostino et al., 2024; Liu et al., 2015; Silcock et al., 2019). While mean initial (1–4 year) survival rates are high in these reviews (52 % by Godefroid et al., 2011; 65 % by Dalrymple et al., 2012), a decreasing proportion of translocated populations achieve the life-cycle benchmarks of reproduction, dispersal, and recruitment (Bellis et al., 2023; Dalrymple et al., 2012). Additionally, there are few patterns consistently supported across existing reviews. For example, D'Agostino et al. (2024) found that intrinsic species characteristics had no relationship with translocation survival rates, in contrast to Liu et al. (2015) and Bellis et al. (2023), who identified life form as a significant factor determining outcomes. Some meta-analyses emphasize the importance herbivory reduction and competition removal (Corli et al., 2023; Godefroid et al., 2011), while others find these management techniques have lower relative importance than habitat quality (Bellis et al., 2023; D'Agostino et al., 2024). These contrasting patterns highlight the challenge in utilizing global and regional reviews to inform species-specific translocation decision-making for rare plant species.

In contrast to ecosystem restoration practices that aim to restore broad assemblages of typically common species, ideally with known reference habitat (Gann et al., 2019; Holl and Aide, 2011), rare plant translocation projects often lack information on the realized or potential niche of focal species (Maschinski et al., 2012a). While species distribution models (SDM) are typically used to identify such niches, results can be misleading due to small sample sizes, limited knowledge of historical distributions, microclimate variability, shifting suitable climates, and novel species interactions (Araujo and Townsend Peterson, 2012; Crisfield et al., 2024; Maclean and Early, 2023; Steen et al., 2017). Populations of rare plants may persist under suboptimal climatic conditions if the remnant population's location is a refugium from historic disturbances such as wildfire, herbivory, or deforestation, or if climatic conditions have changed since population establishment. For example, populations of rare herbaceous species in the Hawaiian Islands are often found on cliffs or steep slopes, which provide a refugia from herbivory by invasive goats, despite the species not being adapted to cliff habitat (Nyberg et al., 2023).

Experimental translocation therefore represents an important tool to determine the contemporary habitat preferences of rare plant species at a fine environmental resolution. Translocation has the capacity to address two questions fundamental to the conservation of rare species: *Where did populations occur in the past, and where could populations succeed in the future?* Because of limited propagule material and the high motivation for success, rare species are often augmented into remnant populations or nearby analog habitat without experimental design (Armstrong and Seddon, 2008; Dalrymple et al., 2012). For species which have experienced range contractions, using remnant populations as habitat reference can lead to the establishment of translocated populations in suboptimal climate conditions. Structured experimental approaches may experience higher initial outplant mortality in unsuitable sites, but can increase long-term success by identifying alternative distributions and best management practices under shifting climates.

Experimental translocation can also test commonly held assumptions on how to source seed for restoration efforts. Best practice translocation guidelines generally suggest sourcing seed from local geographic provenance to preserve local genotypes and microhabitat adaptations (IUCN/SSC, 2013; Krauss and Koch, 2004; Maschinski and Albrecht, 2017). There is considerable evidence that locally adapted plant genotypes provide higher fitness within corresponding habitat (Atkins and Travis, 2010; Becker et al., 2006; Leimu and Fischer, 2008). However, climate change might result in mismatches between local genotypes and suitable climatic conditions (Aitken and Whitlock, 2013). In the case of rare species with small extant populations, the negative effects of inbreeding depression might outweigh concerns of preserving local adaptations (Neale, 2012), and there are few experiments that assess the legitimacy of guidelines to exclusively source seeds for translocation from local populations.

The Hawaiian Islands are a leader in plant conservation efforts and offer insight to the global discourse on plant translocation. Translocation projects have been implemented for ~350 endemic species across the archipelago (HRPRG, 2024), including the state flower, *Hibiscus brackenridgei* (Rovzar et al., 2018) and the iconic silversword, *Argyroxiphium sandwicense* (Robichaux et al., 2017). While plant species extinctions have been historically concentrated on islands due to geographic isolation and endemism, extinction is now accelerating across continental ecosystems (Ricketts et al., 2005). Lessons from translocations in the Hawaiian Islands are globally relevant to understanding how remnant populations may or may not represent optimal habitat, how novel interactions shape fitness outcomes, and reimagining how plant populations can be translocated for future success within anthropogenically impacted landscapes.

We conducted a four-year experimental translocation study of a rare endemic Hawaiian tree species. We aimed to identify the species' contemporary habitat preferences through planting individuals across broad climatic and environmental gradients both within and beyond the species' known geographic range. To accurately identify the preferred habitat of the species within contemporary conditions at high resolution, we assessed the effect of 17 predictors in the categories of climate, surrounding vegetation composition, soil chemical characteristics, founder genetic group, and site management. These predictors have been identified in the translocation literature as variably influencing the translocation outcomes (Bellis et al., 2023; D'Agostino et al., 2024; Dalrymple et al., 2012; Liu et al., 2015; Silcock et al., 2019), and we hypothesized that translocated plant performance would vary across the broad habitat conditions represented by the selected sites. We asked two questions, 1) How does translocated plant survival, growth, and vigor vary as a function of environmental variables and genetic provenance? 2) Do the habitat conditions of successful translocation sites correspond or differ from the conditions of remnant populations? We discuss how our results can inform rare plant translocation strategies within the Hawaiian Islands and compare results to regional and global translocation reviews.

2. Methods

2.1. Study site: Rarity of the Hawaiian flora

Optimizing translocation success is particularly relevant to places experiencing precipitous declines of native plant diversity. The Hawaiian Islands are a global hotspot of plant endemism; of the state's 1367 native species, 90 % of angiosperms and 71 % of pteridophytes are endemic, with many endemic to single islands (Rønsted et al., 2022; Wagner et al., 1999). The oceanic isolation and spectacular adaptive radiations which led to this high diversity have culminated in contemporary vulnerability; ecosystem degradation is widespread due to naturalized invasives such as Polynesian rats (*Rattus exulans* Peale), black rats (*Rattus rattus* L.), feral Eurasian pigs (*Sus scrofa* L.), mosquitoes, and invasive plant species (Sax and Gaines, 2008; Ziegler, 2002). The endemic flora of Hawai'i has experienced rapid declines throughout the past century due to habitat loss and associated threats; 45 % of listed U.S. Fish and Wildlife Service (USFWS) Threatened and Endangered species are Hawaiian endemics, 260 plant species in Hawai'i have less than 50 individuals left in the wild, and approximately 10 % of the Hawaiian flora has gone extinct within the past century (PEPP, 2023; USFWS, 2021).

2.2. Study species: ‘ohe mauka, Polyscias bisattenuata (Araliaceae)

Known by its Hawaiian name ‘ohe mauka or ‘ohe‘ohe, *Polyscias bisattenuata* (Sherff) Lowry & Plunkett is a perennial tree species in the Araliaceae and is endemic to Kaua‘i, the northwestern-most island of the Hawaiian Islands (Lowry and Plunkett, 2010; Wagner et al., 1999). This tree is an extremely rare component of Kaua‘i's forest; approximately thirty mature trees remain across three wild populations (Wood, 2007). The species is characterized by sprawling trunks creating thickets on steep slopes, pinnately compound glabrous leaves with 5–7 attenuate leaflets, compound-umbellate magenta inflorescences, and ovoid purple fruit (Fig. 1a, b) (Sherff, 1952). The species is assessed as ‘Critically Endangered’ on the IUCN Red List and ‘Endangered’ by the USFWS (Tangalin, 2015; USFWS, 2020). Biological threats include habitat degradation by feral pigs, competition from invasive vegetation, and seed predation by non-native rats (Wood, 2007). The remnant populations are in decline; the demographic structure is only composed of mature individuals, and there is no in situ seedling recruitment.

2.3. Translocation methods and design

The *P. bisattenuata* translocation experiment was initiated in 2016 by the National Tropical Botanical Garden (NTBG). Seed was collected from nineteen wild founders at each of the three extant wild populations. 3742 *P. bisattenuata* saplings were cultivated under identical growing conditions in NTBG Horticulture Center nursery and prepared for translocation at eleven selected sites on windward Kaua‘i. Four sites represented augmentations where saplings were planted <1 km from extant remnant populations, while the other seven sites were conservation introductions in which saplings were planted into novel habitat. To test assumptions about *P. bisattenuata* habitat preferences, we selected introduction sites across windward Kaua‘i that ranged from approximately 500 m lower (106 m at the lowland forest of Lower Limahuli) to 500 m higher (930 m at the wet forests of Upper Limahuli) than extant populations (~550–650 m) (Table 1). This 1000 m range represented a broad climatic gradient due to the mountainous topography and orographic precipitation patterns of Kaua‘i. Mean annual temperature of introduction sites ranged from 18.5 °C to 24.6 °C, approximately 2 °C lower and 3 °C higher than mean temperature of extant populations. Annual precipitation of introduction sites ranged from 147 cm to 969 cm, approximately 200 cm less and 600 cm more than average annual rainfall at extant populations (Longman et al., 2024).

Because of the large portion of eastern Kaua‘i that is privately owned, translocation site selection and management was constrained by land ownership and access. Three selected sites occurred within NTBG preserves, three within State Forest Reserves, and five within private land (Table 1). The degree of management varied across sites, and included ungulate fenced areas, unfenced areas, no weed control, sporadic weed control, and consistent weed control. Site replicates were limited due to logistical difficulties in establishing long term agreements with landowners and transporting saplings to mountainous backcountry locations.

To control for the influence of genotypic adaptation to local microclimate, an approximately equal proportion of material from each of the 19 wild founders was planted at each translocation site. Exceptions included Makaleha, in which three founders were represented, and Lower Limahuli, in which two founders were represented. All saplings

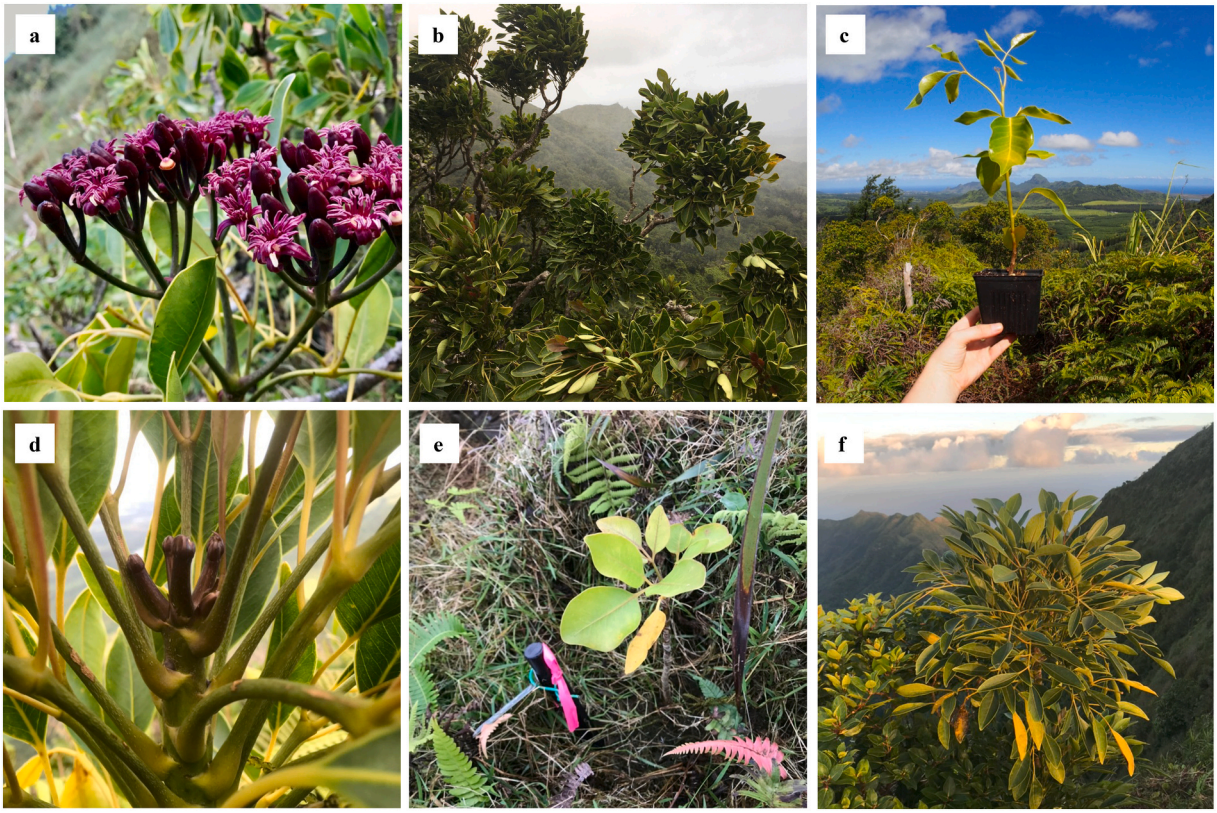

Fig. 1. Photographs of wild and translocated ‘ohe mauka, *Polyscias bisattenuata* (Araliaceae) on the island of Kaua‘i.
a) The compound-umbellate magenta inflorescence of wild mature *P. bisattenuata*; b) a wild *P. bisattenuata* individual with sprawling multi-stemmed habit in a remnant population on windward slopes of Kaua‘i; c) a year-old nursery grown sapling, ~20–40 cm tall upon outplanting, photo by N. Tangalin; d) the first observation of flower buds on translocated sapling, 4 years post-outplanting; e) a translocated *P. bisattenuata* in the ‘poor’ vigor category, ~30 cm in height; and f) a translocated *P. bisattenuata* in the ‘healthy vigor category, ~150 cm in height. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Variation in climate and management across the selected *P. bisattenuata* translocation sites on the Hawaiian island of Kauaʻi.

Site	Elevation (m)	Land Ownership [a]	Management [b]	Average annual precipitation [c] (mm)	Average annual temperature [c] (°C)	Translocation Category [d]
McBryde Garden	67	P (NTBG managed)	F, consistent weed cont.	1473	24.6°	Introduction
Lower Limahuli Preserve	106	P (NTBG managed)	NF, consistent weed cont.	3248	24.0°	Introduction
Nounou	280	S (Nounou Forest Reserve)	NF, no weed control	1885	23.3°	Introduction
Lower Hāʻupu	335	P (unmanaged)	NF, no weed control	1758	23.2°	Introduction
Puʻu Kolo (Kāhili)	542	P (unmanaged)	NF, no weed control	3121	21.3°	Augmentation
Laʻauhihaihai (Kāhili)	576	P (unmanaged)	NF, no weed control	3658	21.1°	Augmentation
Kanaele Bog	600	P (Nature Conservancy managed)	F, sporadic weed cont.	4127	20.2°	Introduction
Makaleha	619	S (Keālia Forest Reserve)	NF, no weed control	3732	20.6°	Augmentation
Blue Hole (Upper Wailua)	643	S (Līhuʻe Kōloa Forest Reserve)	F, no weed control	9689	18.9°	Introduction
Hāʻupu Summit	673	P (unmanaged)	NF, sporadic weed cont.	1793	20.8°	Augmentation
Upper Limahuli Preserve	930	P (NTBG managed)	F, consistent weed cont.	3914	18.5°	Introduction

[a] P, private landowner; S, State of Hawaiʻi owned and managed by the Department of Land and Natural Resources.
[b] F, site fenced; NF, site not fenced. Degree of weed control categorically assessed by local managers: no weed control; sporadic, <5× annually; consistent, >5× annually (refer to Appendix S1).
[c] Climate data accessed through the Hawaiʻi Climate Data Portal (Longman et al., 2024); mean annual precipitation and temperature calculated for study period November 2017 through November 2021.
[d] Introduction, site beyond geographic range of extant populations; Augmentation, saplings within geographic range of extant populations, < 1 km from a remnant extant population.

were approximately one year old, 20–40 cm in height, and of similar vigor upon planting (Fig. 1c). To minimize variation in establishment conditions, all *P. bisattenuata* saplings were planted during the 4-month wet season (October 2017–January 2018) when soil moisture levels were highest (Longman et al., 2024). Apart from the removal of non-native herbaceous species at certain sites and three sites protected by ungulate fencing (refer to Table 1), translocated *P. bisattenuata* did not receive aftercare; saplings were not irrigated, and no additional herbivory or predation protection was conducted.

2.4. Field monitoring and assembly of response variables

We monitored survivorship, growth, and vigor of the translocated populations at two- and four-years post-planting (2019 and 2021). We located each *P. bisattenuata* sapling and assessed individuals as living or dead. Two-year survival per site was quantified as the proportion of initially translocated individuals that were observed alive after two years (n2019/n2017). Four-year survival was quantified as the proportion of individuals alive after two years that were observed alive after four years (n2021/n2019). Among living plants, we measured height to the apical meristem, basal diameter at 10 cm vertical from rooting point, and assessed reproductive status. To quantify plant condition that was not captured by survival nor growth measurements, we recorded qualitative plant vigor as one of three categories: poor (no recent growth, insect damage, persistence unlikely), moderate, and healthy (observation of recent growth, no insect damage, and persistence likely).

Per individual plant, we recorded seven potential growth metrics including two- and four-year height and basal diameter, change in height and diameter between censuses, and relative growth rate between censuses. Pairwise Pearson correlation coefficients were calculated for the seven potential response variables. Height and diameter at two years were strongly correlated with height and diameter at four years ($r = 0.71$, $p < 0.001$ and $r = 0.88$, $p < 0.001$), and change in height was strongly correlated with four-year height ($r = 0.83$, $p < 0.001$). We therefore retained four-year plant height as our single metric of plant growth.

Upon completion of monitoring, we retained four response variables to assess translocation outcomes: four-year plant height (proxy for plant growth) at the individual level, four-year plant vigor at the individual level, two-year survival at the site level (0 to 2 years), and four-year survival at the site level (2 to 4 years).

2.5. Assembly of predictor variables

Through both field measurement and accessing pre-existing data, we generated twenty-five potential predictor variables of *P. bisattenuata* translocation success in the categories of site climate, surrounding vegetation composition, habitat quality, soil chemical characteristics, population genomics, and site management (Appendix S1).

We accessed climate data for the time-period of *P. bisattenuata* planting and growth (October 2016–November 2021) through the Hawaiʻi Climate Data Portal (Longman et al., 2024; Lucas et al., 2022) to generate seven site-level climate variables; elevation, mean wet season temperature (November–April), mean dry season temperature (May–October), mean wet season rainfall, mean dry season rainfall, mean annual temperature, and mean annual rainfall for each translocation site.

We conducted field measurements to assemble eleven individual-level predictors in the categories of surrounding vegetation composition and habitat quality (Appendix S1). We characterized the understory and overstory vegetation community using 1-m^2 circular plots centered around each translocated *P. bisattenuata* living after four years. We only sampled plots at living individuals because of the inaccuracy in determining the precise location of dead individuals in dense understory vegetation. We consider 'understory' as any non-woody plant rooted within the 1-m^2 plot, and 'overstory' to be the trees which fall within a 45° vertical cone above each sapling (Lemmon, 1956). Percent overstory cover was recorded within categorical bins of 10 %, and a spherical densiometer was used every five observations to calibrate estimates. Average understory height was recorded within categorical bins of 0.25 m. We measured the microtopography around each seedling, as this can affect plant success (Gill et al., 2023; Questad et al., 2014). Slope angle was estimated using 10° bins within a 10-m^2 area surrounding each sapling, and a clinometer was used every five observations to calibrate

estimates. Categorical slope aspect (cardinal and sub-cardinal) was estimated using a compass within a 10-m^2 area surrounding each sapling. Understory species composition was assessed by quantifying the percent cover of the five most abundant species. The five most abundant species consistently represented the majority of observed biomass in the 1-m^2 plots. We aggregated the understory composition data into eight vegetation predictors based on morphological descriptions in the Manual of the Flowering Plants of Hawai'i (Wagner et al., 1999) and standardized descriptions of plant growth form (Pérez-Harguindeguy et al., 2013) (Appendix S2). We incorporated the percentage of each vegetation category as individual-level predictors.

We took five surface soil samples at each translocation site to generate three site-level variables in the category of soil characteristics: mean percent organic matter (OM), mean nitrogen (N), and mean carbon (C). The soil sample locations were selected to represent the site's spatial scope and taken 50 cm from a translocated *P. bisattenuata* stem. We used a hand trowel to dig 10–15 cm into the soil and removed a soil core 5–7 cm in diameter. The samples were dried, sieved through 4.75-mm wire mesh, and analyzed by the University of Hawai'i at Hilo Analytical Laboratory (Appendix S3). We averaged the five samples to obtain site-level OM, N, and C values.

Two additional site-level variables were included in the category of land management: categorical frequency of weed control (no weed control; sporadic, <5× annually; consistent, >5× annually) and ungulate fencing (site fenced or unfenced) (Appendix S1). These categories were assessed at each site with knowledge by local managers.

We included two categorical variables as predictors to assess the effect of founder provenance on translocated *P. bisattenuata* success. First, we used the population genomic results (refer to Results 3.4) to assign translocated saplings to one of three categorical genetic clusters identified in the genetic distance PCA (Hā'upu, Kāhili, and Makaleha). Because the subset of translocated individuals included in the genomic analysis (5–10 per site) corresponded to the genetic group of their maternal founder (refer to Results 3.4), the genetic group of maternal founder was used to inform genetic group of all translocated saplings. We generated an individual-level binary variable to represent type of translocation: introduced individuals (planted >1 km from remnant population of the same genetic group), and augmented individuals (planted <1 km from remnant population of the same genetic group).

To address multicollinearity, we calculated pairwise Pearson correlation coefficients for all 25 predictor variables considered and assembled a correlation matrix using 'corrplot' (Wei and Simko, 2024). For pairs with correlation coefficient > 0.8, we retained only the most ecologically relevant predictor. Upon completion of data processing, we retained 17 predictor variables (Appendix S1).

2.6. Identifying subsets of predictors to outplanting performance

We analyzed the effect of the 17 assembled predictor variables on the four independent metrics of performance: two- and four-year survival, growth, and vigor of translocated *P. bisattenuata*. To narrow the pool of candidate predictors to minimize overfitting, we used the 'dredge' function in the 'MuMIn' package which evaluates all combinations of a saturated global model and ranks them based on AICc. (Barton, 2023). We identified a subset of the 17 predictor variables that demonstrated consistent relationships with translocated 'ohe mauka growth and vigor (individual-level response variables). The first dredge analysis was conducted on a global linear model with the natural logarithm of four-year height as the continuous response, and the 17 assembled variables as fixed effects predictors without interactions (Appendix S4a). The second dredge analysis was conducted on a global proportional odds logistic regression model odds using the 'polr' in the package 'MASS' (Ripley et al., 2024) with 4-year vigor as the ordinal response, and the 17 assembled variables as fixed effects predictors without interactions (Appendix S4d). From the growth and vigor dredge output, we retained models with ΔAICc <2 relative to the top ranked model, calculated variable importance scores as the sum of Akaike weights for all retained models in which the predictor was included, and retained variables with importance scores >0.5 for further analysis (Burnham and Anderson, 2002) (Appendix S4c, S4f).

Because two- and four-year survival had limited data points (site-level variable, $n = 11$), dredge was not an appropriate tool for reducing the pool of 17 candidate predictors. We therefore selected four variables (see Methods 2.7) to include in the survival predictor subset that represented each of the variable categories (climate, soil chemistry, surrounding vegetation, and genetic factors), and are identified in meta-analysis reviews as associated with translocation survival outcomes (Bellis et al., 2023, 2025; Dalrymple et al., 2012). Final variable selection was also informed by expert field knowledge; the included variables are frequently observed determinants of rare plant translocation outcomes in the Hawaiian Islands.

We subsequently explored the relationships of the three respective predictor subsets with survival, growth, and vigor using linear regressions (LM), linear mixed effects models (LMM), and proportional odds logistic regression (POLR), and analysis of variance (ANOVA). All analysis was conducted in R, version 4.3.1 (R Core Team, 2024).

2.7. Survival analysis

We created linear regression models to test the independent effects of predictors on site-level two- and four-year *P. bisattenuata* survival. Because survival was analyzed at the site level and sample size was extremely limited (n = 11), we used Gaussian linear regressions to explore broad associations between survival and the four predictors. We acknowledge that inference is constrained by potentially imprecise effect size estimates, and results should be interpreted as exploratory. The four predictors identified in the preceding analysis step included mean OM (%), mean annual temperature (°C), mean understory height (m), and translocation category (binary). We constructed two separate models that included two-year and four-year survival as response variables and the selected subset of predictors as fixed terms without interactions (Appendix S5a, S5b). We sequentially removed non-significant predictors and used likelihood ratio tests to confirm that predictor removal did not worsen model fit. We used the corrected Akaike Information Criterion (AICc) and adjusted R^2 to inform final model selection.

2.8. Growth analysis

We applied linear mixed-effects models to test relationships between the identified subset of predictors and individual plant growth. The subset of predictors identified in the dredge analysis included naturalized fern (%), naturalized herbaceous (%), native fern (%), native herbaceous (%), understory height (m), mean annual rainfall (mm), and mean annual temperature (°C). Using the function 'lmer' (Bates et al., 2024), we constructed a saturated model that included the natural logarithm of individual level four-year height as the growth response variable, the forementioned predictors without interaction terms, and site treated as a random effect to account for unmeasured site-level variation (Appendix S5c). We removed non-significant predictors and used likelihood ratio tests to confirm that removal did not decrease model fit. Final model selection was informed by AICc and conditional R^2 values (Appendix S5c).

Given that categorical factors may have been excluded from the dredge results due to collinearity in the large set of predictors, we used univariate analysis of variance (ANOVA) to evaluate if variation in growth differed significantly by the categorical predictors of site, degree of weed control, genetic group, and translocation category. We chose to test the independent effects of these treatments because they directly inform management decisions. We used individual-level four-year plant height as the response variable and performed a one-way ANOVA for each categorical predictor independently (Appendix S6). We conducted

a post-hoc Tukey Honestly Significant Difference (HSD) test to compare treatment means between the levels of each categorical predictor.

2.9. Vigor analysis

We applied ordinal logistic regression using the function 'polr' (Ripley et al., 2024) to test the relationships of the subset of predictors with the individual-level response variable of four-year plant vigor. Predictors identified in the dredge analysis included mean annual rainfall (mm), naturalized herbaceous (%), understory height (m), naturalized fern (%), weed control (binary), annual mean temperature (°C), and mean OM (%). We used 'polr' because it is compatible with dredge analysis, and accounts for ordered factor levels without assuming equal distance between levels. We transformed categorical vigor ('poor', 'moderate', and 'healthy') into an ordinal response variable (1,2,3). The saturated model included all seven predictor variables without interaction terms (Appendix S5d). Naturalized herbaceous and naturalized fern cover were removed from the saturated model due to convergence issues (limited replication across factor categories). We then sequentially removed non-significant predictors and used likelihood ratio tests (ANOVA) to confirm that predictor removal did not worsen model fit. Final model selection was informed by AICc and conditional R^2 values (Appendix S5d).

2.10. Population genomic analysis

We collected leaf material from 5 to 10 individuals at each of the translocation sites and included samples from the NTBG Herbarium (114 *P. bisattenuata* samples total) (Appendix S7). DNA samples were sent to Beijing Genomics Institute-Shenzhen (BGI-Shenzhen) and sequenced using the MGI-T7 sequencing platform. A GATK 4.0 Haplotype Variant Caller was used for the SNP calling (McKenna et al., 2010). The raw SNP dataset was filtered using variant quality score recalibration (VQSR) (Poplin et al., 2017). Population genetic structure and phylogenetic relationships of *P. bisattenuata* were analyzed using ADMIXTURE (v1.3.0) (Alexander et al., 2009) with 5-fold cross-validation (CV) from K = 2 to 10. A Principal Component Analysis (PCA) was conducted to visualize the relatedness and clustering of populations. The top 10 PCs of the variance-standardized relationship matrix were extracted using VCF2PCACluster (v1.40) (VCF2PCACluster, 2008) with the default parameter. To quantify the relatedness between individuals, the p_distance matrix of all samples was calculated using VCF2Dis (v1.46) (VCF2Dis, 2008). A neighbor-joining (NJ) phylogenetic tree was constructed using MEGA (v4.0) (Kumar et al., 2018) based on the distance matrix.

2.11. Post hoc species distribution model

To compare the suitable *P. bisattenuata* habitat identified through experimental translocation with the habitat identified through species distribution modeling, a post hoc SDM was constructed using wild and translocated *P. bisattenuata* occurrence data (see Appendix S8 for methods).

3. Results

Of the 3742 *P. bisattenuata* translocated across eleven sites on Kaua'i, 647 individuals were alive two years after outplanting (0–2 year survival 17.3 %), and 430 individuals were alive four years after outplanting (0–4 year survival 11.5 %). Mean height two years after outplanting was 53.51 cm (±27.15 SD), increasing to 69.03 cm (±40.63 SD) four years after outplanting (Table 2). We found significant variation in growth across translocation sites (ANOVA: $F = 26.19$, $p < 0.001$) (Fig. 2b, Appendix S6), indicating variability in habitat suitability. Of the total 430 *P. bisattenuata* saplings alive four years after translocation, four individuals had reached reproductive maturity and were observed with buds, flower, and fruit (0.9 % of the population).

3.1. Survival analysis results

Initial two-year survival of translocated *P. bisattenuata* populations varied widely across the eleven translocation sites (Table 2). Certain sites experienced high mortality (i.e., McBryde, 1.3 % survival), while others supported a survival rate of greater than 50 % (i.e., Lower Limahuli, 56.4 % survival). Across all sites, higher mortality occurred in the initial period following planting compared to the period between two to four years. When aggregating survival rates across all sites, initial 0–2 year survival was 17.3 %, while 2–4 year survival was 66.6 %. Once established, individuals had a higher probability of persistence compared to the initial two-year period following translocation.

Of the candidate models for *P. bisattenuata* initial two-year survival, the model of best fit included mean understory height as a single predictor variable (AICc = −9.72, adjusted $R^2 = 0.57$) (Table 3a, Appendix S5a). Understory height showed a significant negative relationship with initial plant survival (estimate = −0.29, $p = 0.004$). Of the 17 variables originally included in the global model, understory height of surrounding vegetation was the only variable that significantly explained variation in initial survival across sites (Fig. 3a).

Of the candidate models for *P. bisattenuata* four-year survival, the model of best fit once again included understory height as the single predictive variable (AICc = 0.31, adjusted $R^2 = -0.09$) (Appendix S5b). However, the model had poor explanatory power and the relationship

Table 2
Survival, growth, and vigor of translocated *P. bisattenuata* saplings across eleven sites.

		Survival % (n)		Four-year growth (SD)		Vigor
Translocation Site	Initial population size (n)[a]	Two-year[b]	Four-year[c]	Mean height (cm) (SD)	Mean diameter (cm) (SD)	% population 'healthy'
McBryde	856	1.3 % (11)	72.7 % (8)	130.62 (71.2)	1.53 (0.55)	75.00
Lower Limahuli	165	56.4 % (93)	65.6 % (61)	117.1 (44.7)	1.46 (0.62)	70.49
Nounou	125	4.8 % (6)	50 % (3)	132.7 (90.2)	1.33 (0.87)	66.67
Lower Hā'upu	82	41.5 % (34)	50 % (17)	59.9 (29.9)	0.87 (0.3)	41.18
Pu'u Kolo	312	7.7 % (24)	83.3 % (20)	79.1 (25.7)	1.35 (0.48)	90.00
La'auhihaihai	540	20.2 % (109)	26.6 % (29)	77.1 (23.05)	0.99 (0.24)	31.03
Makaleha	73	27.4 % (20)	19.2 % (14)	46 (22.9)	0.86 (0.31)	64.29
Kanaele Bog	200	4.8 % (5)	20 % (1)	39	0.6	–
Blue Hole	586	20.0 % (117)	71.8 % (84)	44.85 (24.5)	0.77 (0.35)	27.38
Hā'upu Summit	499	32.5 % (162)	95.1 % (154)	65.6 (2.8)	1.21 (0.61)	61.44
Upper Limahuli	304	21.7 % (66)	60.6 % (40)	44.4 (10.97)	0.75 (0.2)	22.50
Total (sites aggregated)	3742	17.3 % (647)	66.5 % (430)	69.03 (0.63)	1.09 (0.56)	51.20

[a] Variation in population sizes due to challenging backcountry topography and logistical difficulty in transporting *P. bisattenuata* saplings to translocation sites.
[b] n 2019/ n 2017.
[c] n 2021/ n 2019.

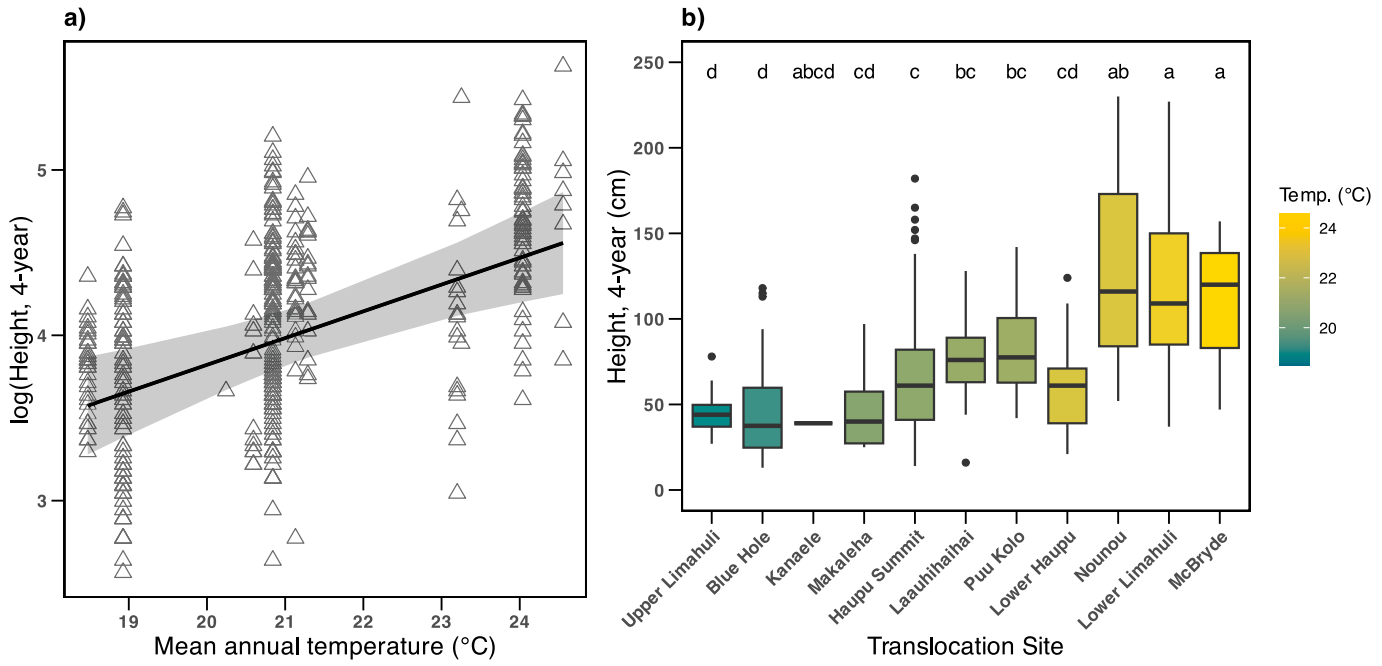

Fig. 2. Translocated *P. bisattenuata* growth varied as a function of site temperature: a) In the linear mixed-effects model of best fit, individual *P. bisattenuata* height demonstrated a significant positive relationship with site mean annual temperature (exp. estimate = 1.18, SE =0.04, $p = 0.006$, cond. $R^2 = 0.47$). Observed data points are represented by triangles, regression line represents model-predicted values ('ggeffects' package; Lüdecke, 2018), and the 95 % confidence interval in shaded grey. b) Variation observed in *P. bisattenuata* growth across sites (ANOVA, F = 26.19, $p \leq 0.001$). Lowercase letters indicate significant differences ($p < 0.05$) in comparisons among sites using Tukey HSD tests, error bars show Standard Deviation, and sites are ordered by ascending mean annual temperature which is negatively correlated with site elevation.

Table 3
Results of, a) the linear regression of best fit (AICc = −9.72, adjusted $R^2 = 0.57$), showing the relationship between understory height and initial two-year *P. bisattenuata* survival, b) the linear mixed effects regression model of best fit (AICc = 545.9, conditional $R^2 = 0.47$, marginal $R^2 = 0.3$), showing the independent effects of mean annual temperature, understory height, and surrounding cover of naturalized ferns on *P. bisattenuata* growth, and b) the ordinal logistic regression model of best fit (AICc = 708.16, residual deviance = 698.11, McFadden's pseudo $R^2 = 0.095$), showing the independent effects of mean annual rainfall, understory height, and mean annual temperature on *P. bisattenuata* observed vigor (Appendix S5).

a) Survival, 2-year, site-level ~ Under. height.

Predictor	Coefficient	Std. Error	*t* value	*p* value
Understory height (m)	−0.29	0.08	−3.79	0.004*

b) log(Height, 4-year, individual-level) ~ Under. height + Annual temp. + Nat. fern + (1 | site).

Predictor	Exponentiated coefficient	Std. Error	*t* value	*p* value
Understory height (m)	1.47	± 0.06	6.67	0.029*
Mean annual temperature (° C)	1.18	± 0.04	3.18	0.006*
Naturalized fern (% cover)	1.01	± 0.002	3.9	<0.001*

c) Vigor, 4-year, individual-level ~ Annual rainfall + Under. height + Annual temp.

Predictor	Coefficient	Odds ratio	95 % Conf. interval	*t* value	*p* value
Mean annual rainfall (m)+	−0.14	0.87	0.81–0.94	−3.4	0.001*
Understory height (m)	1.12	3.03	1.71–5.54	3.71	<0.001*
Mean annual temperature (° C)	0.34	1.4	1.23–1.64	4.51	<0.001*

* statistical significance indicated by $p < 0.05$.
\+ Scaled from millimeters to meters for model convergence.

between four-year survival and understory height was not significant (estimate = −0.01, $p = 0.733$) (Fig. 3b). This result indicates that while surrounding vegetation had a strong negative relationship with initial survival, the strength of that relationship weakened once the translocated saplings had established.

3.2. Growth analysis results

Of the candidate models for *P. bisattenuata* growth, the model of best fit included annual mean temperature, surrounding understory height, and surrounding percent cover of naturalized ferns as fixed effects, with site as a random effect (AICc = 545.9, conditional $R^2 = 0.47$, marginal $R^2 = 0.30$) (Appendix S5c). Both annual mean temperature (estimate = 1.18, $p = 0.006$) and understory height (estimate = 1.47, $p < 0.001$) showed significant positive relationships with *P. bisattenuata* growth (Table 3b, Fig. 2). Percent cover of surrounding ferns had a significant yet weak relationship with growth (estimate = 0.01, $p < 0.001$), however its inclusion increased the condition R^2 and lowered the AICc of the model and was therefore retained.

Growth of translocated *P. bisattenuata* saplings varied significantly across translocation sites (ANOVA: $F = 26.19$, $p < 0.001$) (Table 2, Fig. 2b, Appendix S6). The site with the highest growth was Nounou (mean four-year height 132.7 cm ± 90.2 SD), while the lowest growth was observed at Blue Hole (44.3 cm ± 10.82 SD). Variation in sapling heights within a site was broader for the high performing sites, indicating height means of these sites were driven by a few large individuals. Post hoc Tukey tests revealed that Lower Limahuli, McBryde, and Nounou sites had significantly higher growth than the other sites ($p < 0.001$), while Upper Limahuli, Blue Hole, and Makaleha were significantly lower ($p < 0.001$). The Kanaele site had a single surviving individual four years after translocation, resulting in no within-site variance and reduced power for post hoc comparisons involving this site. Growth of saplings also varied significantly by degree of weed control (ANOVA, $F = 18.1$, $p < 0.001$), and post hoc Tukey tests demonstrated that sites with consistent weed control had higher growth than sites with none or

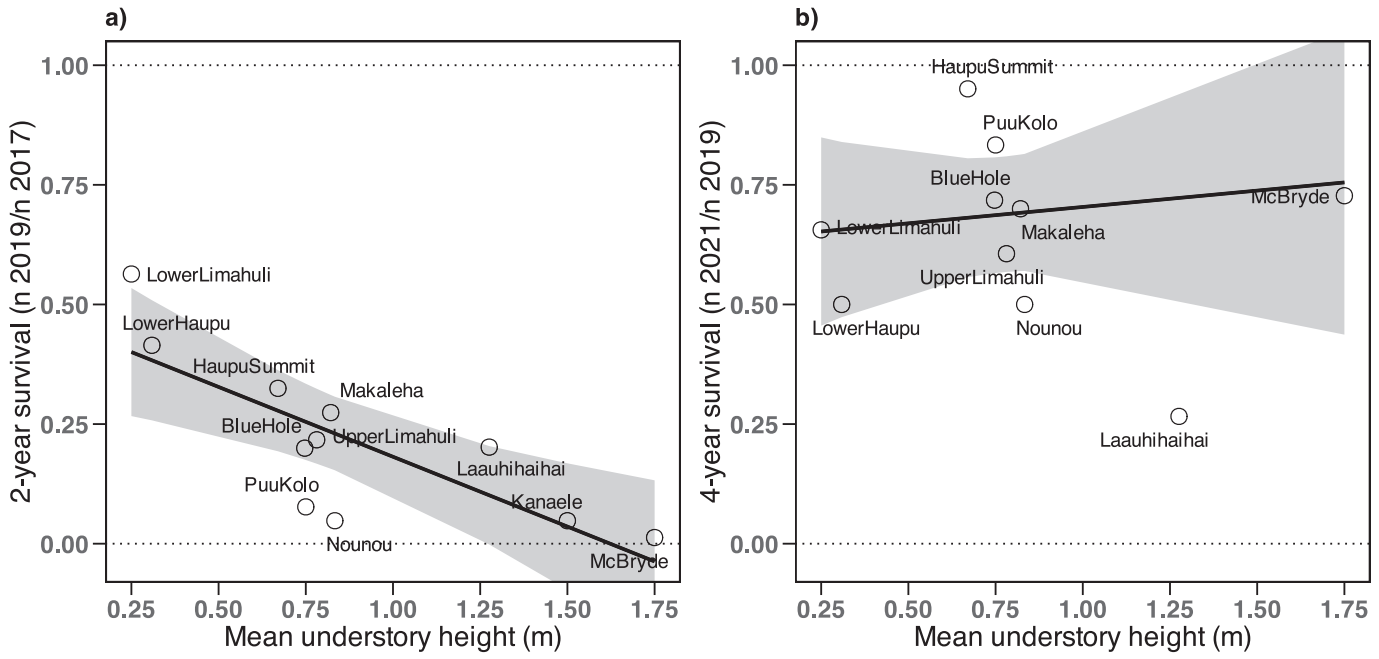

Fig. 3. The survival of *P. bisattenuata* populations demonstrated shifting relationships with understory height throughout time: a) Initial site-level survival was strongly predicted by a negative relationship with mean height of surrounding vegetation (estimate = −0.29, SE = 0.08, $p = 0.004$, adjusted $R^2 = 0.57$). b) In contrast, four-year survival showed no significant relationship with height of surrounding vegetation (estimate = 0.07, SE = 0.03, $p = 0.61$) and the linear model did not explain variation in four-year survival (adjusted $R^2 = -0.09$). Observed survival proportions are represented by circles, regression line represents model-predicted values (Lüdecke, 2018), and 95 % confidence intervals are shown in shaded grey.

sporadic weed control management (None-Consistent: $p = 0.007$) (Appendix S6c). Because the categorical predictors of site and weed control are likely linked to other continuous environmental predictors, the ANOVA results are best viewed as exploratory as they may partially reflect the effects of covarying predictors.

We found subtle yet significant variation in translocated *P. bisattenuata* sapling growth in relation to the three identified genetic groupings (ANOVA, $F = 5.39$, $p = 0.001$), suggesting that the distinct genetic groups display variable in situ growth rates (Appendix S6a, S6d). However, the mean four-year height of the three genetic groups were similar, 65 ± 35.9, 75 ± 45.7 and 42.6 ± 16.5 cm respectively, indicating that the effect of genetic grouping on growth was subtle in comparison to the strong relationship found between growth and annual mean temperature. We found no significant difference in sapling growth across translocation categories (whether the individual had been augmented or introduced) (ANOVA, $F = 0.73$, $p = 0.48$) (Appendix S6a).

3.3. Vigor analysis results

The observed vigor of translocated *P. bisattenuata* saplings varied across sites, and ranged from 90 % of the reintroduced population described as 'healthy' (Puʻu Kolo), to only 20 % of the population described as 'healthy' (Upper Limahuli) (Table 2). Of the candidate models for plant vigor, the model of best fit included mean annual rainfall, surrounding understory height, and mean annual temperature (AICc = 708.11), however the variation in vigor explained by the model was low (McFadden's $R^2 = 0.095$) (Table 3c, Appendix S5d). In the model of best fit, height of surrounding understory vegetation demonstrated a positive relationship with translocated 'ohe mauka vigor; a 1 m increase in height was associated with a 203 % increase in the odds of a sapling being observed in a higher vigor category. Mean annual temperature also had a positive relationship with likelihood of a sapling moving upward in a vigor category; for every degree °C increase in annual temperature, the odds ratio of the sapling being observed in a higher vigor category increased by 40 % (95 % CI, 23 %–66 %). By contrast, mean annual rainfall had a negative relationship with the likelihood of a sapling moving upward in a vigor category; for every 1 m increase in mean cumulative rainfall at a translocation site, the odds ratio of a sapling being observed in a higher vigor category decreased by 13 % (95 % CI, 81 %–94 %) (Table 3c).

3.4. Population genomic results

Population genomic results demonstrated three significantly distinct genetic groups with clear geographic associations among sampled *P. bisattenuata* (Fig. 4). Sampling covered the extant and translocated populations of *P. bisattenuata* across Kauaʻi and generated 4.04 Tb of data. Using the chromosome-level reference genome, we obtained 32.6 million high quality SNPs/Indels using a strict filtering standard. PCA divided the samples into three major clusters (Fig. 4A) which were geographically associated with the Hāʻupu, Kāhili, and Makaleha mountain ranges. ADMIXTURE analysis indicated that the deepest splits ($K = 3$) occurred between cluster1 (Hāʻupu), cluster2 (Kāhili), and cluster3 (Makaleha) populations. A neighbor-joining (NJ) tree further supports such a pattern (Fig. 4C). The results indicated that wild remnant populations of 'ohe mauka at Hāʻupu, Kāhili, and Makaleha mountains are genetically distinct groups. Genetic group of seed material had subtle explanatory power on variation in translocated plant growth (ANOVA, $F = 5.39$, $p = 0.001$) (Appendix S6a, S6d).

3.5. Post hoc species distribution model results

The generalized-additive SDM model of wild *P. bisattenuata* occurrences excluding the Makaleha site had the best predictive performance (see Appendix S8 for complete results). Utilizing this SDM, regions of predicted high habitat suitability were higher in elevation than both remnant wild populations and successful translocation sites.

4. Discussion

Through experimentation with translocation across broad habitat characteristics, we found that the preferred environmental conditions

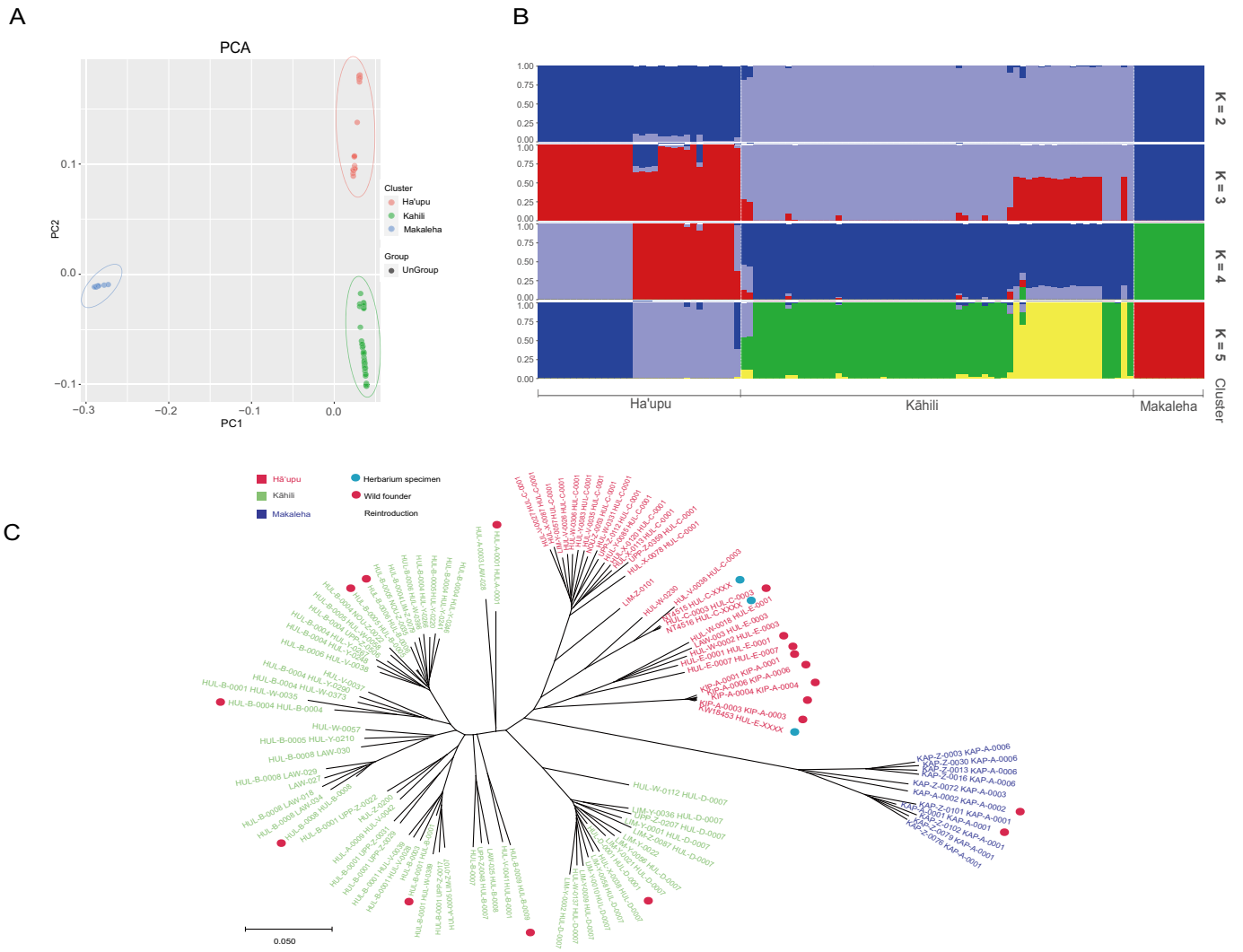

Fig. 4. Population genomic analysis of *P. bisattenuata* indicated three significantly different genetic clusters associated with Kauaʻi topographic regions of Hāʻupu, Kāhili, and Makaleha moutains: PCA analysis (A), structure analysis (B), and phylogenetic analysis (C).

for translocated ʻohe mauka growth were lower in elevation (~500 m) and warmer (~4 °C) in mean annual temperature than the habitat of remnant populations. We also found that the strength and direction of environmental and climatic predictors of translocated ʻohe mauka success shifted through time and across ontogeny. Height of surrounding vegetation showed a negative relationship with initial survival, no significant relationship with four-year survival, and surprisingly a positive relationship with four-year growth. Site annual temperature had no detectable effect on two-year nor four-year survival but emerged as the strongest single predictor of longer-term plant growth and vigor. Our results suggest that selecting translocation sites for rare plant species based exclusively on limited extant wild occurrences can potentially lead to maladaptive restoration practices. Similarly, a post hoc modeling of habitat suitability based solely on *P. bisattenuata* wild occurrences using standard SDM was misleading, and did not accurately represent the complex patterns uncovered in our analyses. Instead, these SDM results showed areas of predicted high habitat suitability higher in elevation than our successful translocation sites (Appendix S8).

4.1. ʻOhe mauka translocation survival rates in local and global contexts

ʻOhe mauka four-year survival across eleven sites was 11.5 %, with high variability in survival between translocation sites (lowest 0.9 %, highest 36.9 %). A survival rate of 11.5 % is low in comparison with global translocation reviews which find initial mean survival across taxa to range from 52 to 65 % (Dalrymple et al., 2012; Godefroid et al., 2011). However, there is bias in the literature towards projects with high survival, as translocation efforts with high mortality unfortunately often go unreported, despite providing insights on unsuitable habitat or unsuccessful strategies (Abeli and Dalrymple, 2023; Menges, 2008). Within the contexts of Hawaiʻi, initial survival rates of rare plant translocations are highly variable due to unmanaged biological threats and lack of reference habitat (Adamski et al., 2020; Kawelo et al., 2012; Robichaux et al., 2017; Rovzar et al., 2018). For example, some Hawaiian rare plant translocation projects reported >90 % initial survival, such as populations of *Argyroxiphium sandwicense* subs. *Macrocephalum* on the slopes of Haleakalā (Krushelnycky et al., 2023), while others reported <10 % survival, such as attempts with *Flueggea neowawraea*, an endangered tree from Oʻahu (Kawelo et al., 2012).

Initial survival rates are not inherently representative of multigenerational establishment (Dalrymple et al., 2012; Drayton and Primack, 2012; Maschinski and Albrecht, 2017). Accurately assessing translocation success requires monitoring the population through flowering, pollination, seed dispersal, and recruitment of subsequent generations (Albrecht et al., 2019; Bialic-Murphy et al., 2022; Menges, 2008). A translocation study of the Hawaiian shrub *Delissea waianaeensis* found that metrics of initial survival did not predict long-term population growth because of barriers to seedling regeneration (Bialic-Murphy

et al., 2022). In turn, a study of translocated *Tephrosia angustissima* in Florida found that habitat conditions which supported the highest initial survival differed from the niche which supported germination (Wendelberger and Maschinski, 2015). Other studies have also noted that the niche which supports initial translocated plant survival often differs from niches which support subsequent growth, persistence, and recruitment (Albrecht et al., 2019; Bellis et al., 2023). Our present study acknowledges that initial survival may not be an accurate metric of long-term success. Nonetheless, within four-years of translocation, a relatively narrow window into the life cycle of ʻohe mauka which is a long-lived perennial species (Wood, 2007), we identified multiple drivers to indicators of translocated plant fitness which shifted through time. After four years, <1 % of the translocated individuals were reproductive, and the suite of environmental variables determining ʻohe mauka reproduction and recruitment remain unknown. Multi-decadal monitoring of translocated populations could help assess the environmental determinants of success across multiple generations.

4.2. Historic land use contexts for ʻohe mauka rarity

The human history of Kauaʻi's lowlands provides insight to ʻohe mauka's status of extreme rarity, and the strong relationship we found between temperature and translocation growth rate. Hawaiian lowland forests are heavily impacted by anthropogenic activities (Price et al., 2012; Vorsino et al., 2014), and taxa with distributions in coastal and low elevations are at higher odds of extinction risk (Sakai et al., 2002). Plantation agriculture of the 1800s, cattle ranching, and urban development throughout the twentieth century have been concentrated in low elevations of the Hawaiian Islands (Hawaii Statewide GIS Program, 2021; Perroy et al., 2016). Fossil evidence from Māhāʻulepū limestone cave on Kauaʻi revealed that extinctions of flora occurred precipitously following European arrival, and genera currently restricted to higher elevations of the islands were once common components of historic lowland communities (Burney et al., 2001). Rare plant populations in Kauaʻi are commonly found on cliff faces, as they serve as refugia against biological threats (Nyberg et al., 2023; Wood, 2005) and are a further indication that remnant high-elevation populations of rare plants do not necessarily represent habitat optimums. We suggest that remnant ʻohe mauka populations on the steep slopes of Hāʻupu and Laʻauhihaihai represent refugia at the upper elevational limit of the species. The strong positive relationship we found between translocated ʻohe mauka growth and vigor with low elevation and high annual temperature sites supports this assessment. ʻOhe mauka may have once been common throughout 0–500 m elevation in Kauaʻi, and only currently persists in the higher altitudinal distributions as lowland habitat was altered by agriculture, development, and introduced species.

4.3. Relationship between temperature and growth suggests range expansion

Translocated ʻohe mauka growth was highest at sites where habitat conditions differed considerably from remnant wild populations. We found a strong positive relationship between mean annual site temperature and ʻohe mauka four-year growth and vigor (Fig. 2a). Each 1 °C increase in mean annual temperature was associated with a 17.6 % increase in predicted ʻohe mauka height, and increasing annual mean temperature significantly increased the likelihood of a sapling moving upward in a vigor category. The sites with highest growth rates are approximately 500 m lower in elevation and annual mean temperature is between 3 and 4 °C higher than remnant wild populations (Fig. 2b). The three remnant ʻohe mauka populations occur in mid-montane slopes 400–700 m elevation, with 20–22 °C annual mean temperature. In contrast, one of the translocation sites with overall highest survival, growth, and vigor was Lower Limahuli, a coastal valley at 120 m elevation and 24 °C annual temperature.

Our findings support that ʻohe mauka's potential range is not fully represented by remnant populations, but includes habitats at lower elevations. In the discussions on performing assisted migrations to track climate envelopes, the majority of studies, which range from Costa Rica to Hawaiʻi, focus on mobilizing species towards higher elevation (Colwell et al., 2008; Corlett and Westcott, 2013; Vitt et al., 2010). For example, Adamski et al. (2020), found survival of *Cyanea superba* increased when individuals were planted at elevations higher than historic populations in the Waiʻanae mountains of Oʻahu. While these studies illustrate a pattern in optimums shifting upward in response to warming climatic conditions, these altitudinal patterns are not ubiquitous. Our results serve as a reminder that assisting species towards suitable habitat will not be unidirectionally upwards in elevation, and optimum habitat may exist far below the current range of a species.

4.4. Shifting effects of competition throughout translocated plant ontogeny

We found the effect of surrounding vegetation on translocated plant fitness to shift throughout the timespan of our study. Understory height showed a negative relationship with initial survival, no significant relationship with four-year survival, and a positive relationship with four-year growth (Fig. 3). Although based on a limited number of site-level observations, this pattern suggests a dynamic influence of competition from surrounding vegetation as the translocated plants established within the landscape. At the Kanaele site, initial survival was 4.8 %, mean understory height was 1.5 m, and entirely composed of uluhe (*Dicranopteris linearis)*, a fast-growing stoloniferous fern which forms dense mats in Hawaiʻi. Uluhe is a competitive early successional species known to inhibit regeneration of tree species (Mueller-Dombois and Boehmer, 2013; Russell et al., 1998). Similarly, the McBryde site had an initial survival rate of 1.3 %, and a mean understory height of 1.75 m composed of invasive Guinea grass (*Megathyrsus maximus)*. Guinea grass forms monotypic stands throughout Hawaiʻi's dry ecosystems, where it outcompetes native species and leads to grass-fire cycles (Ammondt and Litton, 2012; Soti and Thomas, 2022; Trauernicht et al., 2015). The strong negative relationship between initial survival with understory height suggests a competitive effect of uluhe and Guinea grass on initial ʻohe mauka survival.

While the effects of ungulate fencing and weed control frequency on translocation outcomes were not experimentally tested in this study, these management factors likely influenced the observed variation in ʻohe mauka survival and growth. For example, the two sites that were exceptions to the strong linear relationship between understory height and survival, Puʻu Kolo and Nounou (Fig. 3), are both unprotected by ungulate fencing and high feral pig activity was observed. The negative impacts of feral pig foraging behavior on native Hawaiian forest species is well-documented (Cole and Litton, 2014; Long et al., 2017), and may explain the low initial survival rates of these two translocation sites (7.7 % and 4.8 % respectively). Similarly, an exception to the strong relationship between site mean annual temperature and plant growth was Lower Hāʻupu (mean 4-year height, 59.9 ± 29.9) which did not receive weed control; mean ʻohe mauka height at Lower Hāʻupu was significantly lower than sites of similar mean temperatures that experienced consistent weed control (McBryde and Lower Limahuli) (Fig. 3).

Low competitive capacity is speculated as a cause of plant species rarity and extinction risk (Murray et al., 2002; Walck et al., 1999). Isolated Pacific floras are often described as particularly vulnerable to biotic invasion, and competition with invasive plants is identified as a cause of species decline (Denslow, 2003; Kueffer et al., 2010; Vitousek, 1988). As such, controlling threats, including invasive plant competitors and feral ungulates, prior to rare plant reintroduction is recognized as a key determinant of survival and long-term persistence, and is a foundational component of translocation guidelines (IUCN/SSC, 2013; Maschinski and Albrecht, 2017). Our results support the notion of low ʻohe mauka competitive capacity at the establishment stage (0–2 years) but show that the influence of competitive surrounding vegetation

decreases through time. If saplings survived the initial two-year period, the competitive influence of surrounding vegetation appeared to decrease, potentially due to the saplings growing taller than the surrounding vegetation and overcoming light limitation (Yelenik et al., 2022; Young et al., 2015). Another possible explanation is facilitation, or positive plant-plant interactions between translocated saplings and surrounding species, through amelioration of abiotic stress (Brooker and Callaway, 2009; Bulleri et al., 2016). Despite initial high mortality at sites dominated by competitive invasive species, the subsequent success of ʻohe mauka saplings within novel lowland habitat indicates the potential of the species to naturalize and succeed within non-native plant communities.

Overall, our results illustrate how a high-risk and high-mortality translocation effort revealed insight into a species' habitat preference. This insight would not have been detected had saplings been planted as augmentations into remnant populations or had SDM been exclusively utilized for site selection. Despite certain sites experiencing near total mortality, the insights gained inform iterative rounds of translocation, which could ultimately achieve long-term population persistence in the contemporary landscapes of Kauaʻi. If a species is well-represented in ex situ collections, greater experimentation with habitat ranges in translocation projects across Hawaiʻi and other regions with imperiled flora may yield similar insights. Although translocation experiments are rarely implemented due to upfront costs and the risks associated with project failure, the long-term expense of translocation to suboptimal habitats likely outweighs the initial investment in experimentation. By identifying suitable habitats early on, conservation practitioners can optimize resource allocation and improve overall success of translocation efforts.

4.5. *The importance of public participation and the future of ʻohe mauka*

The long-term success of translocated plant populations requires iterative rounds of experimentation and biological threat management (Corli et al., 2023; IUCN/SSC, 2013), and the continuation of these programs is contingent on public awareness, involvement, and support (Ban et al., 2013; Bennett et al., 2017; Serota et al., 2023). Facilitating opportunities for people to participate, interact with, and experientially learn about rare species engenders community investment in translocation projects (Maschinski et al., 2012b; Nazarea, 2006). In the recovery effort of ʻohe mauka, over 200 local citizens participated in translocation planting and monitoring. In Hawaiian language and lifeways, the word *pilina* translates to connection or relationship, and can refer to the interconnection between people and *ʻāina,* the living land, which is nourished through stewardship (Kealiikanakaoleohaililani et al., 2018; Pukui and Elbert, 1986). Facilitating *pilina* by including the public in translocation efforts can restore rare species not only as biotic components of the ecosystem, but as valued elements of collective biocultural heritage. Future ʻohe mauka translocation programs could include the public through experimental planting in public and private lands throughout Kauaʻi's low elevations. Iterative rounds of experimental translocation across broad conditions combined with public participation may help to ensure that ʻohe mauka, along with rare plant species around the world, will have a place in our future.

CRediT authorship contribution statement

Julia Douglas: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Mingzhou Bai:** Visualization, Formal analysis. **Lucas Berio Fortini:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Stephanie G. Yelenik:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Nina Rønsted:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Article impact statement

Optimization of translocation practice for species' conservation requires experimental planting across broad habitat and climate conditions.

Target audience

This work may be insightful to managers and researchers who focus on the conservation and translocation of rare plant species with few remnant populations available for habitat reference.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111686.

Data availability

All data collected and references in this work is publicly available through the Forest Service Research Data Archive: https://doi.org/10.2737/RDS-2024-0063

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