

Influence of Light and Substrate Conditions on Regeneration of Native Tree Saplings in the Hawaiian Lowland Wet Forest¹

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Abstract: Understanding microsite preferences of species at the sapling stage is crucial for successful forest restoration, as efforts can be concentrated onto the most promising sites, and invaded sites can be manipulated toward more suitable conditions for target species. The Hawaiian Lowland Wet Forest is a highly endemic and endangered ecosystem that has received limited attention in terms of research on recruitment dynamics. Our study combined density records and sapling-based measurements within a forest reserve, an invaded forest, a traditional restoration project and a novel restoration project. We recorded substrate type, soil depth, surface roughness, and light availability for 382 saplings of the four native tree species *Metrosideros polymorpha*, *Myrsine lessertiana*, *Pipturus albidus*, and *Psychotria hawaiiensis*, and 146 spots where the target species were absent. The invaded forest had the lowest native sapling density, lower light availability, and lower surface roughness than the remaining management units. The novel restoration project had more moss/nurselog sites and higher light availability than the remaining management units. The traditional restoration project was mainly characterized by rocky substrate. *Metrosideros* and *Pipturus* showed significantly higher light demand than *Myrsine* and *Psychotria*. *Pipturus* was associated with rough microsites and *Metrosideros* with moss/nurselog substrates. Our findings suggest that restoration strategies considering manipulation of the canopy light environment and microsite preferences of target species can better facilitate native recruitment into heavily invaded forests.

Keywords: abiotic microsite preferences, restoration ecology, *Metrosideros polymorpha*, *Psychotria hawaiiensis*, *Pipturus albidus*, *Myrsine lessertiana*, forest restoration planning

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THE ABUNDANCE AND DIVERSITY OF SAPLINGS in a forest ecosystem provide information about future forest conditions as forest composition and dynamics are predominantly influenced by variation in the survival of saplings (Kobe et al. 1995, Kobe 1996). Recruitment is mainly limited by high mortality in the early juvenile stages (Poorter and Arets 2003), and mortality of recruits was found to decrease with increasing plant size (Clark and Clark 1992). It is therefore likely that saplings have already withstood abiotic and biotic forces including self-thinning, seasonal fluctuations and extreme climatic events during the phases of seed dispersal, germination and the seedling stage (Rother et al. 2013). Thus, the abundance of saplings can be seen as a predictor for persistence of the forest community composition.

Determining the best conditions for the establishment of a juvenile tree up to the sapling stage requires knowledge of its ecological niche, defined as the physiological ability to respond to the set of given site conditions (Hutchinson 1957, Pocheville 2015). Niche theory predicts that the location of a sapling indicates that site conditions and resources at that particular spot are sufficient for survival (Marques and Burslem 2015). Additionally, understanding the site requirements and preferences of saplings of target species can facilitate forest restoration success, which is becoming an increasingly important topic (Lamb et al. 2005, Van Andel and Aronson 2005, Rey Benayas et al. 2009) in light of global forest ecosystem decline and degradation (Lamb et al. 2005). Restoration projects are only promising if successful recruits of target tree species can secure the next generation of mature trees and viable populations in the long run.

Determining beneficial site conditions is challenging as requirements and preferences vary across species, developmental stages, and sites (Schupp and Fuentes 1995, Kobe 1999, Battaglia et al. 2000, Peña-Claros 2001, Poorter and Arets 2003, Aiba and Nakashizuka 2007, Baltzer and Thomas 2007, Marques and Burslem 2015). However, an approach to enhance understanding of context dependency of vegetation patterns by Jones

and Callaway (2007) suggests that abiotic factors have a more predictable effect on plant community composition than biotic factors. Abiotic site conditions affecting seedlings and saplings have been found to vary at small spatial scales (Carlton and Bazzaz 1998) of 1 m or less (Molofsky and Augspurger 1992, Nicotra et al. 1999, Born et al. 2015) rather than at larger spatial units (García et al. 2005).

We examined abiotic factors influencing native sapling establishment in the Hawaiian Lowland Wet Forest (HLWF), an ecosystem characterized by high endemism, but also substantial habitat loss and susceptibility to biotic invasion (Carlquist 1980, Kirch 1982, Wagner et al. 1999, Ziegler 2002). These characteristics have been suggested as definitive of global hotspots for forest restoration (Myers et al. 2000, Olson and Dinerstein 2002). Restoration of HLWF is challenging (Friday et al. 2015) as many introduced species are more abundant than native species in the HLWF (Hughes and Denslow 2005, Mascaro et al. 2008, Ostertag et al. 2008, Zimmerman et al. 2008). In contrast, natural regeneration of native species is low (Zimmerman et al. 2008, Cordell et al. 2009), contributing to radical ecosystem change. Forest conservation ecologists are thus confident that without restoration intervention, the remaining endemic Hawaiian forest ecosystems cannot be preserved (Cabin et al. 2000, Zimmerman et al. 2008, Ostertag et al. 2009). Several small-scale restoration projects have been established throughout the Hawaiian Islands. Some of these projects entail restoration costs up to tens of thousands of US Dollars per hectare as well as intensive work including manual removal of invasive plants (Friday et al. 2015). However, in comparison to continental tropical forest ecosystems, little research has been conducted on the potential of HLWF restoration (Ostertag et al. 2009, Cordell et al. 2016), especially on recruitment preferences of native tree species (Cordell et al. 2009).

The motivation of our study was to increase the understanding of recruitment ecology of native tree species and identify site characteristics under which forest restoration with native tree species is most promising. This understanding could be used to design

more targeted and effective restoration projects. An objective of our study was to gain further understanding of how variability in management strategy influences sapling establishment and thus the future regeneration outcomes of forest restoration strategies applied. Management strategy is associated with variation in abiotic characteristics, degree of invasion, maintenance frequency, project size, and duration of project. Thus, four management strategies (treatments) were compared: HLWF severely degraded by invasive species (invaded forest), two different experimental restoration projects (traditional restoration project and novel restoration project), and a managed forest reserve (reserve). The invaded forest serves as a reference site without restoration intervention. The traditional restoration project (Cordell et al. 2009, Ostertag et al. 2009) tested the strategy of assisted succession (as described in Chazdon and Guariguata 2016); all undesirable nonnatives were removed and the facilitation of native recruitment was attempted through continued maintenance (i.e., weeding). In contrast, the novel restoration project (Ostertag et al. 2015) tested a functional trait approach: after undesirable nonnatives had been removed, selected species were planted, which would provide resistance to invasion in conjunction to continued maintenance. The reserve shows less invasion yet still has the need for restoration efforts. In the reserve, invasive plants were removed and natives were planted. However, it differs from the traditional restoration and novel restoration projects in not being an experimental research project. In order to understand how variability in management strategy influences sapling establishment, we asked the following questions: (Q1) Do management units differ in microsite characteristics relevant for sapling establishment and survival? We hypothesize that the four management units, each with a different management strategy, will differ in abiotic conditions. (Q2) What is the difference in naturally established native sapling density across the four management units? We hypothesize that sapling density will be highest in the reserve due to the lower

invasion found at this site, intermediate in the two restoration projects, and least in the invaded forest. We also hypothesize that the novel restoration project will have higher native sapling density than the traditional restoration project as the functional trait-based plantings create suitable canopy cover thereby providing invasion resistance and facilitating native recruitment. We suspect that abiotic differences in light and substrate characteristics will relate to the differences in the sapling density, although with our study design we cannot determine whether the abiotic conditions differed before management or if management altered abiotic conditions.

Within the management units, we compared four native tree species: *Metrosideros polymorpha* (Myrtaceae), *Myrsine lessertiana* (Primulaceae), *Psychotria hawaiiensis* (Rubiaceae), and *Pipturus albidus* (Urticaceae), in regard to their preferences for substrate type, soil depth, surface roughness (rugosity), and light availability. At the species level, we investigated the following question: (Q3) Do these species differ in their microsite preferences? We hypothesize that *Metrosideros* and *Pipturus* as pioneer species (Drake 1998, Schulten et al. 2014) will be associated with bare rock substrate, shallow soils, greater surface roughness, and high light environments, while *Psychotria* and *Myrsine*, as functionally similar and shade tolerant species (Mascaro 2011) will be associated with moss or soil substrates, deeper soils, and lower light environments.

MATERIALS AND METHODS

Characteristics of the Hawaiian Lowland Wet Forest

Once widespread, the HLWF is a unique and rare ecosystem. It is diminishing in its extent and quality due to historical, cultural, and biological reasons (Kirch 1982, Ziegler 2002) and now is found only in remnant fragments (Price et al. 2007, Zimmerman et al. 2008). These remnant forests are characterized as “lowland” by being located at <800 m elevation (Gagné and Cuddihy 1999) and “wet”

based on >3,000 mm precipitation (Price et al. 2007, Zimmerman et al. 2008). Forest structure and functioning differ from continental tropical rain forests (Hughes and Denslow 2005). First, light availability in an intact HLWF can be five times higher than in a comparable continental forest (Pearcy 1983, McDaniel and Ostertag 2010, Schulzen et al. 2014). Second, on Hawai'i Island (Hawai'i) where the most HLWF is left, the predominant substrate in the current natural range of the HLWF is lava rock less than 1,500 years old (Moore and Trusdell 1991). Soils are predominantly porous, thin, rocky, often lack organic material and available nutrients, and have low water capacity (Kitayama et al. 1995, Soil Survey Staff 2012). In contrast, soils of continental tropical rain forests are usually millions of years old, several meters deep and heavily leached (Hallett and Caird 2017). Most plant species of the HLWF are endemic (Wagner et al. 1999), but locally the diversity of native species is low compared to continental tropical rain forests (Carlquist 1980, Inman-Narahari et al. 2013). The tree flora is

disharmonic and comparably depauperate, lacking tall climax species (Carlquist 1974, Drake and Mueller-Dombois 1993), which leads to open niches compared to continental tropical wet forests (Zimmerman et al. 2008). Most intact HLWF communities, especially on lava flows younger than 300 years, are dominated or codominated by the native tree species *Metrosideros polymorpha* (Carlquist 1980, Wagner et al. 1999, Zimmerman et al. 2008). On lava flows older than 200 years, other native tree species gradually establish beneath the *Metrosideros* canopy (Zimmerman et al. 2008). One of the main threats for the HLWF is the invasion by nonnative plant species. Invasion has been found to be less on lava flows younger than 300 years and at elevations over 350 m (Hughes and Denslow 2005, Zimmerman et al. 2008, Mascaro 2011).

Description of the Study Sites

Our study sites are situated on the windward east coast of Hawai'i, on the lower East Rift Zone of Kīlauea Volcano (Figure 1;

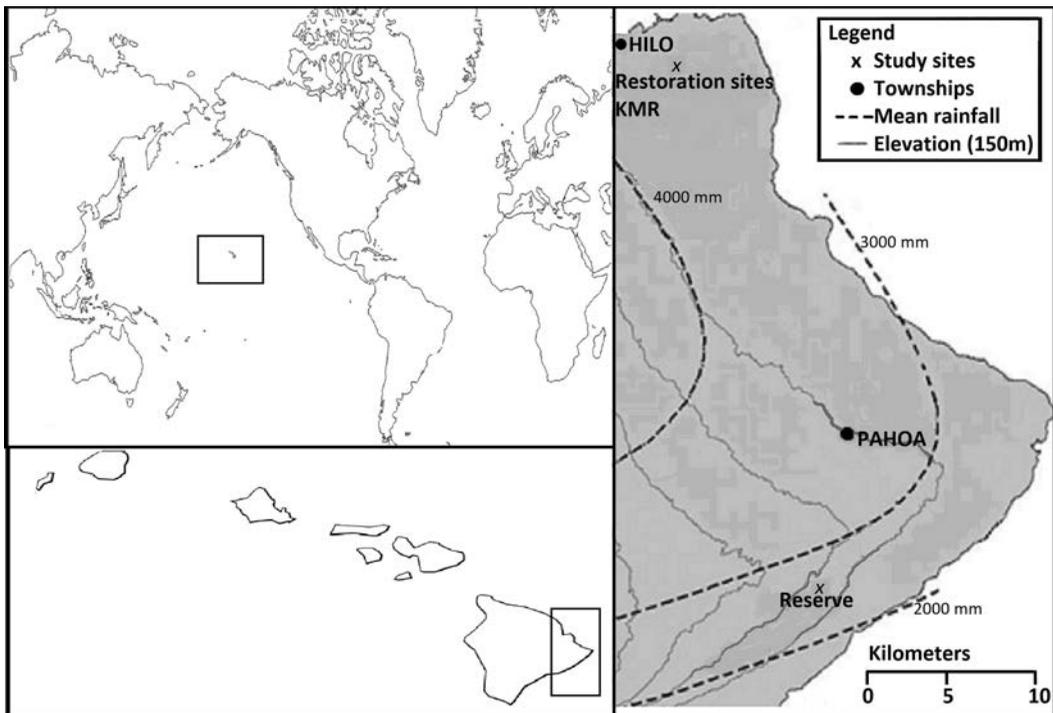


FIGURE 1. Map of the study sites in relation to regional and global geographic areas (Zimmerman et al. 2008; d-maps.com 2017; printableworldmap.net 2017; modified).

Zimmerman et al. 2008, Ostertag et al. 2009). They are classified as *Metrosideros-Diospyros* forest communities (Gagné and Cuddihy 1999, Wagner et al. 1999, Price et al. 2007). Their canopy is still dominated by the native species *Metrosideros polymorpha* and *Diospyros sandwicensis*. A variety of native species, for example, *Psychotria hawaiiensis*, *Pipturus albidus*, and *Pandanus tectorius* are common in the subcanopy layers (Cordell et al. 2009). However, the understory is increasingly colonized by invasive woody species, in particular, *Psidium cattleianum*, *Macaranga mappia*, *Melastoma septemnerium*, *Falcataria moluccana*, and *Clidemia hirta* (Zimmerman et al. 2008, Cordell et al. 2009, Dupuis 2012). These species have been found to be outcompeting native tree species, especially by dominating the seed bank and inhibiting germination of light demanding native tree species (Cordell et al. 2009).

Two experimental restoration projects (traditional restoration project and novel restoration project) are located within the Keaukaha Military Reservation (KMR; 19° 42' 14" N, 155° 02' 30" E; Zimmerman et al. 2008). KMR comprises 43.3 ha of HLWF at an elevation of 30 m (Schulzen et al. 2014). Annual rainfall averages at approximately 3,300 mm (Giambelluca et al. 2013). Parent rock is a 750–1,500-year-old 'a'ā lava flow of Kīlauea Volcano. Overlying soil is classified as isohyperthermic Typic Udifolists of the Papai Series (Ostertag et al. 2009). The soil has an available water capacity of less than 5.6 cm (Soil Survey Staff 2012). A prior census at KMR revealed that woody species density was 1,591 individuals/ha (~8% of total) for native species and 17,199 individuals/ha (~92% of total) for nonnative species (Zimmerman et al. 2008).

The traditional restoration project comprises four square plots of 100 m² each, resulting in a management unit totaling 400 m². In 2004, all nonnative tree and understory species were removed. Within the following 40 months, the site was manually weeded three times a year (Cordell et al. 2009, Ostertag et al. 2009), and annually thereafter (Ostertag, Cordell; personal communication). The traditional restoration project had been designed to test a strategy of assisted succession that relied upon natural

recruitment occurring after the removal of nonnative species; additional plantings were not incorporated in the experimental design.

The novel restoration project emerged as a follow-up experiment and comprises 16 treatment plots of 400 m² each, resulting in a total project area of 6,400 m². In 2013, all nonnative tree and understory species were removed from the treatment plots. Although the overstory at KMR is still dominated by native woody species, with a basal area of 19.8 m²/ha compared to 16.4 m²/ha for nonnative species (Zimmerman et al. 2008), seed rain is limited for *Myrsine* and *Psychotria* and only seeds of *Pipturus* have been found to persist in the seed bank. Thus, subsequently, plant communities comprising native and nonnative, noninvasive species showing specific functional traits to impede performance of invasive species were planted within the treatment plots. The functional trait-based design of this novel restoration project (Ostertag et al. 2015) includes four different treatments with different experimental assemblages of selected species. Species richness was kept constant ($n = 10$ species per treatment), with densities varying slightly (i.e., 120–130 planted individuals depending on treatment; DiManno et al. in preparation). All undesirable nonnative herb, grass, and tree species recruiting within the novel restoration project plots are removed by manual weeding twice a year.

To evaluate the regeneration success resulting from these two different restoration strategies, we compared the experimental projects with the adjacent invaded forest of KMR and Keau'ohana forest reserve (reserve). Data in the invaded forest were collected from areas that had minimal recent human disturbance and had not undergone any type of experimental manipulation or management. The reserve is situated in the Puna District approximately 40 km apart from KMR (19° 32' 11" N, 154° 57' 19" E; Zimmerman et al. 2008). Elevation ranges from 220 to 240 m (Giambelluca et al. 2013). Mean annual temperature is 23 °C and mean annual precipitation ranges from 2,500 to 3,000 mm. Geological substrate is tholeiitic basalt, resulting from a 200–400-year-old 'a'ā lava flow (Zimmerman et al. 2008). The reserve, although not fully native-dominated,

represents the largest and best preserved remaining fragment of this forest type on Hawai'i (Zimmerman et al. 2008), and thus is an important reference point. Woody species basal area was 54.3 m²/ha for native species and 0.2 m²/ha for nonnative species. Density was 2,700 individuals/ha (~89% of total) for native woody species and 340 individuals/ha (~11% of total) for nonnative woody species (Zimmerman et al. 2008). Although the reserve is less invaded than KMR (Zimmerman et al. 2008), invasive species are still a problem. Thus, since 2005, removals have been conducted in a small area of the reserve on a quarterly basis. Since 2014, management intensity has been increased with removals of understory invasive species and native trees plantings in an area encompassing 100 acres (Larish 2015, Dupuis; personal communication). In the reserve, we took measurements in an area of approximately 12 hectares within this actively restored area.

Study Species

We focused on saplings of *Metrosideros polymorpha*, *Myrsine lessertiana*, *Pipturus albidus*, and *Psychotria hawaiiensis*. All four species are endemic to the Hawaiian Islands (Wagner et al. 1999) and common components of the HLWF (Schulten et al. 2014). Sapling refers to juvenile trees of these four species between 1 m and 2.5 m in height.

Metrosideros is the dominant native species in most Hawaiian forests, reaching to up to 30 m in height in the HLWF (Little and Skolmen 1989). *Metrosideros* exhibits many pioneer characteristics (Drake 1998). It is the first species to colonize fresh lava flows (Little and Skolmen 1989) due to its ability to grow on nutrient poor rocky soils (Schulten et al. 2014). *Metrosideros* produces a multitude of minute wind-dispersed seed all year round (Drake 1992, Drake 1998), yet most are infertile (Drake 1992, Drake 1998) and do not form a seed bank (Cordell et al. 2009). Best regeneration conditions for *Metrosideros* in the HLWF are high light, dry soil, and low nutrient availability (Mascaro 2011). Prior research conducted in the traditional restoration project has found the regeneration capacity of *Metrosideros* to be nonexistent under closed canopy (Cordell et al. 2009).

Myrsine is a small to medium sized tree, up to 18 m in height and 0.3–0.6 m in diameter (Little and Skolmen 1989). It is widespread throughout all the main Hawaiian Islands (Schulten et al. 2014) occurring in lowland to montane mesic to wet forests and open lands (Wagner et al. 1999, Native Plants 2009). *Myrsine* prefers dry, well-drained cinder and organic soils (Native Plants 2009). It has been identified on opposite ends of the successional spectrum, both as a pioneer species (Drake and Mueller-Dombois 1993), and as a shade-tolerant species (Mascaro 2011). Seeds of *Myrsine* are assumed to be bird dispersed (Carlquist 1980, Foster and Robinson 2007), and only form a temporary seed bank (Drake 1998). In a greenhouse experiment, seedlings proved to have a comparably high adaptability to changing water and light environments (Schulten et al. 2014).

Pipturus is a polymorphic shrub or small tree up to 9 m in height and 0.3 m in diameter (Little and Skolmen 1989, Wagner et al. 1999). *Pipturus* is distributed in the understory of mesic to wet climax forests (Hughes and Denslow 2005), shrublands, and wet gulches at altitudes from 0 to 1,800 m throughout all the main Hawaiian Islands (Little and Skolmen 1989, Wagner et al. 1999, Native Plants 2009). It is a light demanding (Pattison et al. 1998, Wagner et al. 1999) pioneer species (Buck 1982, Schulten et al. 2014), especially following disturbances, with germination occurring quickly after canopy gaps are created (Drake 1998, Wagner et al. 1999, Hughes and Denslow 2005). It is not found in dry areas or on lava fields (Wagner et al. 1999). *Pipturus* prefers well-drained moist to wet soils and clay, cinder or organic substrate and has a broad amplitude regarding soil moisture and light requirements (Native Plants 2009). Seeds of *Pipturus* are dispersed in a large radius (Cordell et al. 2009) by birds (Carlquist 1980, Foster and Robinson 2007, Loh and Daehler 2008) and persist in the seed bank (Drake 1998, Cordell et al. 2009). A greenhouse experiment resulted in seedlings having 100% survival under high light, compared with 60% under low light and growth rates were significantly greater under the high light conditions (Schulten et al. 2014).

Psychotria grows up to 15 m in height (Native Plants 2009) and 0.3 m in diameter

(Little and Skolmen 1989). It is a scattered subcanopy tree species (Little and Skolmen 1989) of climax forests (Hughes and Denslow 2005). *Psychotria* is distributed throughout Hawai'i, Moloka'i and Maui up to 1,500 m (Native Plants 2009), from lowland mesic and wet forests to montane mesic forest (Wagner et al. 1999). *Psychotria* requires well-drained moist soils and partial sun (Native Plants 2009) and is tolerant to changing light conditions (Schulten et al. 2014) and shade (Mascaro 2011). Seeds of *Psychotria* are assumed to be bird dispersed (Carlquist 1980, Foster and Robinson 2007). Seed rain is limited and seeds do not persist in the seed bank. *Psychotria* is able to regenerate underneath nonmanaged, nonnative species domi-

nated forests (Cordell et al. 2009, Mascaro 2011). In a greenhouse experiment, seedlings proved to have a comparably high adaptability to changing water environments (Schulten et al. 2014).

Field Design

Field work was conducted between February and April 2017. We used an individual-based experimental design to analyze the abiotic microsite conditions where native saplings are established (sensu Baraloto and Goldberg 2004, Otto et al. 2010; Figure 2A). We measured only saplings that were not tagged as planted individuals and thus were naturally recruited. We focused on the four parameters:

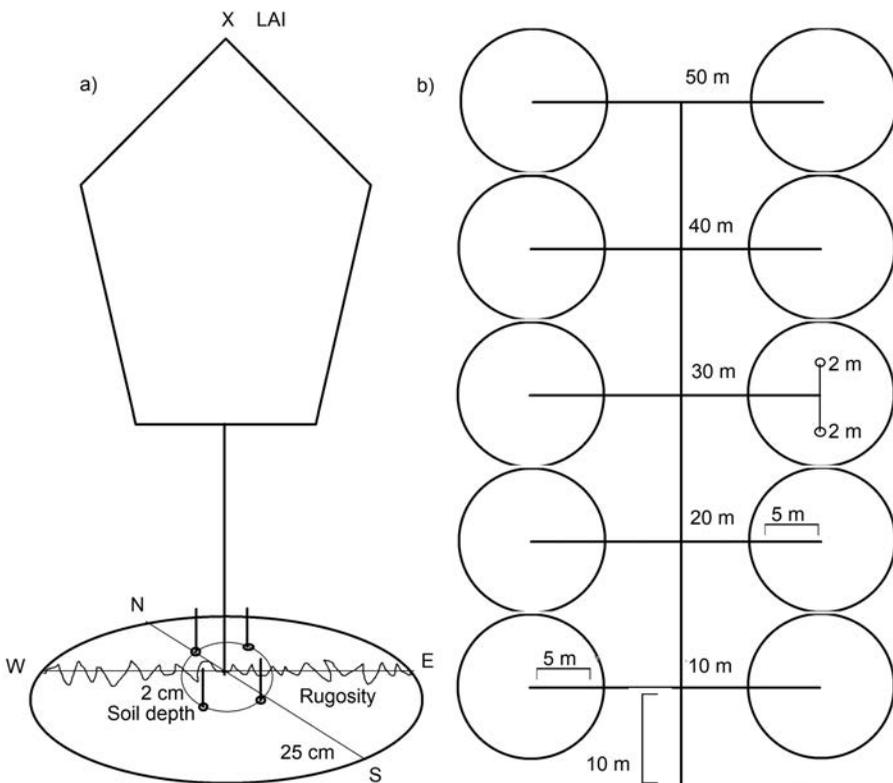


FIGURE 2. (A) Field design around each sapling: soil depth was measured on four spots in all cardinal directions 2 cm off the rooting point. Rugosity was measured with a string in horizontal distance of 25 cm north and south of the rooting point. Leaf area index (LAI) was measured right above the sapling. (B) The point-center quadrat method applied in the invaded forest and in the reserve. Eight such transects were conducted in each of these two management units orthogonally off the road, respectively the footpath. Transects were 50 m long and had 10 circular plots of 5 m radius each running 10 m off the transect all 10 m in an angle of 90°. All saplings within these plots were counted and the sapling of each species closest to the central point was recorded following the procedure of (A). If no saplings were found in the 5-m circular plot, two absence spots per 5-m circular plot, each 2 m off the central point, parallel to the transect were measured analogously to (A) in order to be able to characterize the micro-sites in the case of sapling absence

substrate type, soil depth, surface roughness (rugosity), and light availability, because these were comparably easy to record and proved to be important for recruitment in former studies. Of these four parameters, light is considered the most limiting factor for tree growth in the understory of tropical rainforests globally (Whitmore 1996, Grubb 1998, Ledo et al. 2015). Substrate type and soil depth affect tree recruitment by provisioning of nutrients and water (Clark et al. 1999). Seedling survival has been associated with increased surface roughness in the HLWF (Palupe, unpublished data) as well as in a Malaysian dipterocarp forest (Born et al. 2015).

We defined microsite as a circle of 25 cm radius around the sapling for substrate conditions and directly above the sapling for light availability. We measured soil depth at four points, each 2 cm off the saplings rooting point (Figure 2A), with a sturdy wire. Measurements were taken from 1 to ≥ 30 cm and rounded to the closest cm. Data analyses were conducted with the mean of the four measurements. Surface roughness was measured with the surrogate $\text{rugosity} = \text{Contoured distance} / \text{Planar distance}$ (sensu Du Preez 2015) from the rooting point of the sapling toward north and south with a string running in a 25 cm horizontal radius. The string was bent to follow all unevenness of the ground (Figure 2A). Measurements were taken from 1 to ≥ 100 cm and rounded to the closest cm. Data analyses were conducted with the mean of the two measurements.

Light availability was recorded indirectly using a leaf area index (LAI) as a proxy for canopy cover (Nicotra et al. 1999, Unger et al. 2013, LI-COR 2017). LAI is defined as half the cumulative foliage surface per unit ground surface (Watson 1947, Thimonier et al. 2010). Three LAI measurements were taken with a LI-COR LAI-2000C plant canopy analyzer (LI-COR Inc., Lincoln, NE, USA). The optical sensor of the LAI-2000C consists of a fish-eye lens and an optical system. The fish-eye lens records a hemispherical image, which the optical system projects onto the optical sensor consisting of five concentric rings. Each of the five rings records a different

portion of the sky or canopy centered on one of the five view angles (LI-COR 2020).

LAI was measured directly above each sapling with a sensor unit with uncovered lens parallel to the ground. Simultaneously, a control unit was automatically recording the open sky conditions every five seconds in a clearing less than two km away. We paired below-canopy and control measurements closest in time and calculated the mean of the three measurements per sapling using the postcorrection software FV2000 (LI-COR Inc.). Transmittance for recordings which did not deliver an LAI value (e.g., due to high canopy openness in the novel restoration project) was clipped at 0 (LI-COR, personal communication 2017). Rings 3 to 5 were excluded from analyses to minimize measurement errors due to clearing size. This setting reduces the zenith angle from 0–68° to 0–22° (Nicotra et al. 1999).

Substrate was classified into the following four categories:

- rock: mean soil depth <2.5 cm;
- soil: mean soil depth ≥ 2.5 cm;
- moss: sapling sitting on mossy surface;
- nurselog: sapling sitting on coarse woody debris.

Selection of Sampled Saplings

To compare microsite characteristics across the management units and microsite preferences of native saplings, we aimed at measuring 50 saplings per species in each management unit. Thus, we randomly designated 50 saplings per species from the recruitment database of the novel restoration project prior to field work. If the designated sapling was too tall, or had died since the most recent census, the closest sapling was measured instead. In the traditional restoration project, we subdivided each 100 m² plot into 25 four m² large subquadrats and measured the sapling of each species closest to the north-eastern corner. In contrast to the two restoration sites with clearly determined surface areas, the reserve and the invaded forest have much larger expansions. Thus, in the reserve and the invaded forest, saplings were located by the point-center-quadrat-

method (Figure 2B). To compare sapling density across management units, we counted all saplings within the traditional restoration and novel restoration project plots and the 5-m circular transect plots of the reserve and the invaded forest.

Data Analysis

To identify microsite differences across the four management units (Q1), we conducted Pearson's chi-squared-tests (X^2 -tests) and the corresponding Bonferroni corrected chi-squared-post-hoc-tests (X^2 -post-hoc-tests) for the categorical value substrate type. We combined the two substrate categories moss and nurselog into moss/nurselog as these showed a low sample size and the X^2 -test requires all expected values to be >5 . To compare continuous data (soil depth, rugosity and LAI) we used Kruskal–Wallis rank sum tests (KW-tests) and subsequent pair-wise Bonferroni-corrected Wilcoxon tests (Wilcoxon tests) as well as Bonferroni-corrected Kolmogorov–Smirnov-tests (KS-tests). To answer Q2, we compared density of all saplings and each species across management units using the KW-test as well as Wilcoxon tests. To identify microsites preferences across species (Q3), we applied the testing analogous as for Q1 for all management units combined along with each management unit separately. All statistical analyses were conducted using R software (R Development Core Team 2017). Specifically, we used the R-packages *fifer* (Fife 2017) *ggbiplot* (Vu 2011) and *lattice* (Sarkar 2017). P -values ≤ 0.05 were considered as significant.

RESULTS

Microsite Differences Across Management Units (Q1)

We measured 160 saplings in the novel restoration plots, 104 saplings in the reserve plots, 105 saplings in the traditional restoration plots, and 14 saplings in the invaded forest. Furthermore, we measured 146 absence spots in the invaded forest. Although the sampling design in the reserve and the

invaded forest was identical, no absence spots in the reserve were recorded because each 5-m circular plot contained at least one native sapling. Only the novel restoration project had saplings of all species. Of all measured spots, 40 showed the combined substrate type moss/nurselog, 299 rock, and 190 soil. Figure 3 shows the distribution of substrate type across management units. The novel restoration project showed more microsites of the type moss/nurselog than expected. The invaded forest and the reserve showed more microsites of the type soil than expected. The traditional restoration project showed more microsites of the type rock than expected. Differences between observed versus expected values were significant across all management units (X^2 -test; $X^2 = 35.7$; $p < 0.001$) except for the invaded forest and the reserve (X^2 -post-hoc-test; Supplemental online material: Appendix S1).

Management units varied significantly in median soil depth, median rugosity and median LAI (KW-test; $p < 0.001$). The invaded forest had significantly higher median LAI values and significantly lower median rugosity values than the other management units. The novel restoration project had significantly lower median LAI values than the other management units. The traditional restoration project had significantly deeper median soil depth values than the invaded forest and the novel restoration project (Wilcoxon tests; Supplemental online material: Appendix S1). These variations were also reflected in the KS-tests (Supplemental online material: Appendix S1) and in the Kernel density plots (Figure 4A–C).

Sapling Density as Proxy for Habitat Suitability Across Management Units (Q2)

We counted 190 saplings in the novel restoration project, 199 saplings in the traditional restoration project, 14 saplings in the invaded forest and 1,195 saplings in the reserve (Table 1). Sapling density varied significantly between the four management units across all species (KW-test, $X^2 = 16.291$; $p < 0.001$) and was highest in the traditional

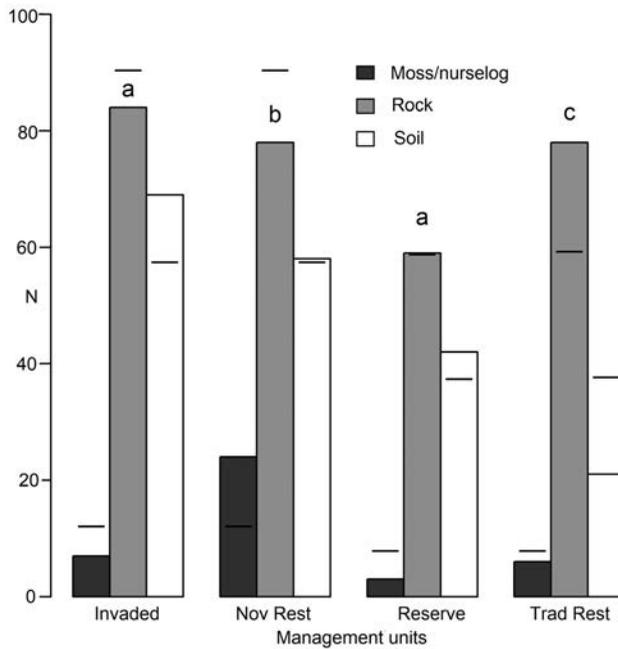


FIGURE 3. Distribution of expected vs. observed values of sapling substrate types per management unit. Above each bar, letters a–c differ where the X^2 -test showed a significant p -value. Lines within and above bars indicate expected values; Invaded = invaded forest; Nov Rest = novel restoration project; Trad Rest = traditional restoration project.

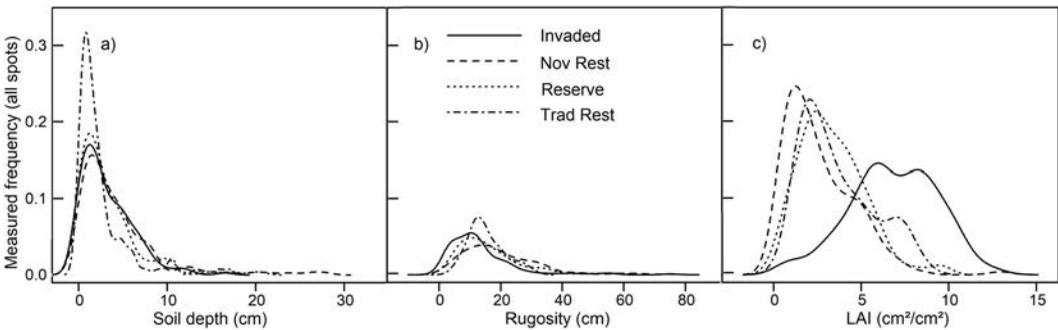


FIGURE 4. Kernel density plots comparing distribution of continuous variables across the four management units. The curves for the invaded forest contain presence and absence spots; Invaded = invaded forest; Nov Rest = novel restoration project; Trad Rest = traditional restoration project; LAI = leaf area index.

restoration project ($0.49/m^2$), followed by the reserve ($0.187/m^2$) and the novel restoration project ($0.029/m^2$) and lowest in the invaded forest ($0.002/m^2$). The high sapling density in the reserve was mainly influenced by the high density of *Pipturus* ($0.174/m^2$).

Differences in Microsite Preference Across Species (Q3)

We found 103 *Metrosideros*, 25 *Myrsine*, 95 *Pipturus*, and 159 *Psychotria* saplings across all management units. *Metrosideros* was found neither in the invaded forest nor in the

TABLE 1

Total Numbers (*N*) and Density per m² of Native Saplings per Species Across the Different Management Units

	METPOL		MYRLES		PIPALB		PSYHAW		Total/Presence
	<i>N</i>	density/m ²	<i>N</i>						
Invaded	0	0.000	2	0.0003	0	0.000	12	0.002	14
Nov Rest	53	0.008	16	0.002	44	0.007	77	0.012	190
Reserve	0	0.000	4	0.001	1,114	0.174	77	0.012	1,195
Trad Rest	74	0.185	3	0.0075	0	0.000	122	0.305	199

Invaded = invaded forest; Nov Rest = novel restoration project; Trad Rest = traditional restoration project; METPOL = *Metrosideros polymorpha*; MYRLES = *Myrsine lessertiana*; PIPALB = *Pipturus albidus*; PSYHAW = *Psychotria hawaiiensis*.

reserve. *Pipturus* was not found in the traditional restoration project. *Myrsine* and *Psychotria* were found across all management units.

The distribution of substrate types for species was specific to each management unit

(Figure 5A). Substrate-type distribution differed significantly across all species (X^2 -test; $X^2 = 64.1$; $p < 0.001$) except for *Pipturus*—*Psychotria*. Figure 5B–E shows the distribution of substrate types for sapling presence (and absence spots in the case of the invaded forest)

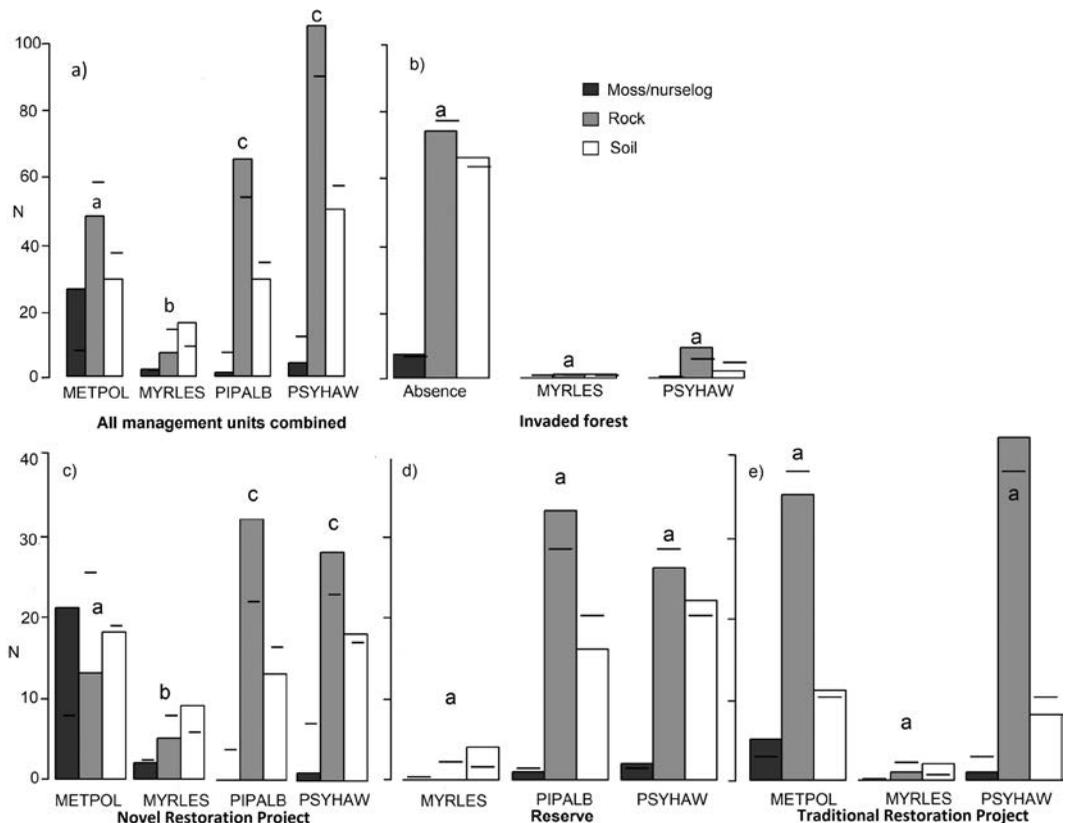


FIGURE 5. (A) Distribution of substrate types per species across all management units. (B–E) Distribution of substrate types per species within each management unit – and absence spots within the invaded forest. Within each plot, letters *a–c* differ where X^2 -test showed a significant *p*-value. Lines within and above bars indicate the expected values; METPOL = *Metrosideros polymorpha*; MYRLES = *Myrsine lessertiana*; PIPALB = *Pipturus albidus*; PSYHAW = *Psychotria hawaiiensis*.

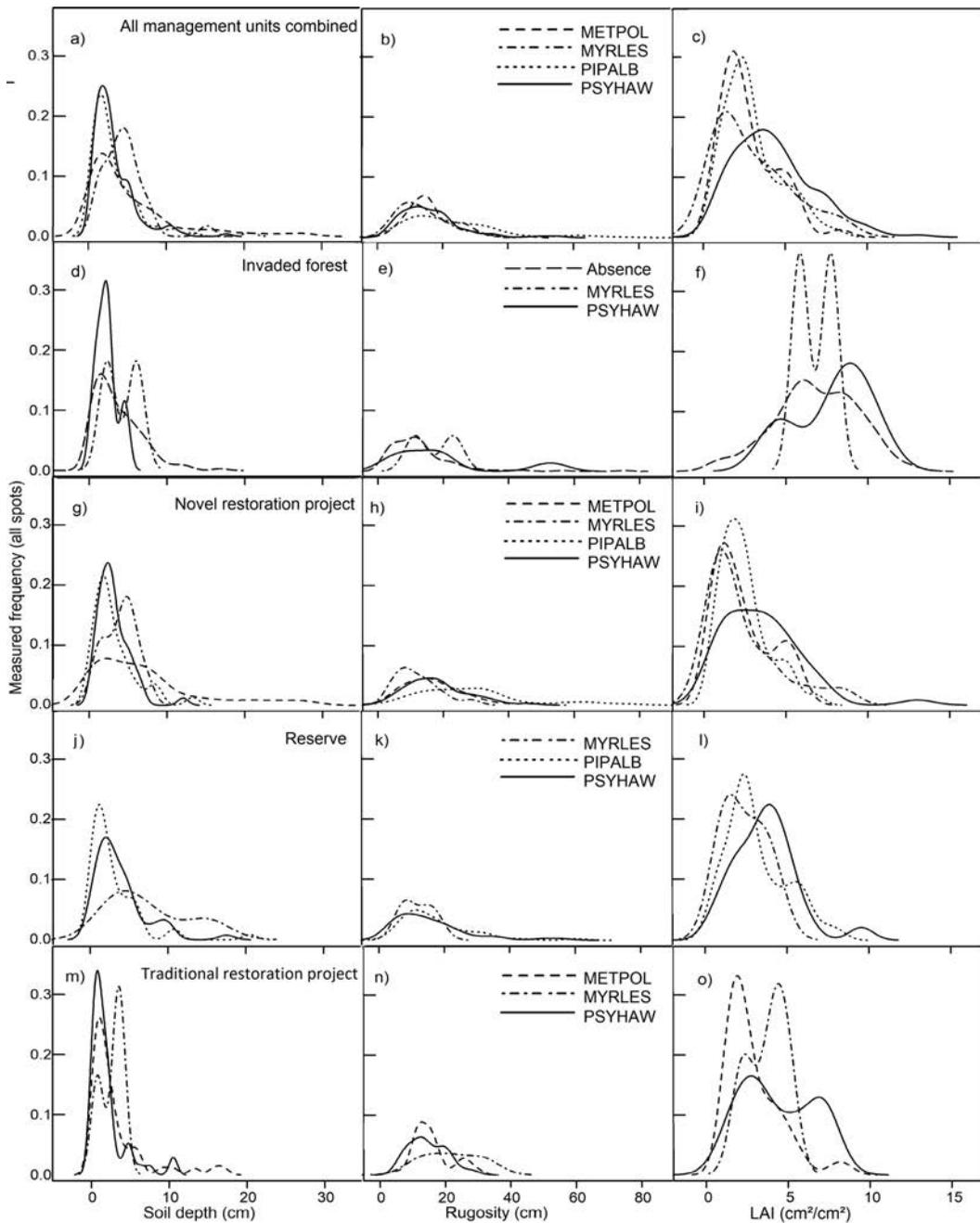


FIGURE 6. (A–C) Kernel density plots for the three continuous variables comparing distribution between each species across all management units. (D–O) Kernel density plots for the three continuous variables comparing distribution between each species within each management unit and absence spots within the invaded forest; Nov Rest = novel restoration project; Trad Rest = traditional restoration project; METPOL = *Metrosideros polymorpha*; MYRLES = *Myrsine lessertiana*; PIPALB = *Pipturus albidus*; PSYHAW = *Psychotria hawaiiensis*; LAI = leaf area index.

within each management unit separately. Substrate-type distribution only differed significantly within the novel restoration project (X^2 -test; $X^2 = 49.65$; $p < 0.001$) with differences in expected versus observed values being significant for all species except for *Pipturus*—*Psychotria* (X^2 -post hoc test; Supplemental online material: Appendix S2). *Metrosideros* occurred more often on moss/nurselog and less often on rock than expected. *Pipturus* and *Psychotria* showed rock as the prevailing substrate type, with occurrences greater than expected. *Myrsine* was the only species found on soil substrate more often than expected.

Across all management units, species varied significantly in median soil depth, median rugosity, and median LAI (Figure 6A–C; KW-tests). *Myrsine* was found at spots with significantly deeper median soil depth than *Pipturus* and *Psychotria*. *Pipturus* was found at spots with significantly higher median rugosity than all other species. *Psychotria* was found at spots with significantly higher median LAI values than *Metrosideros* and *Pipturus* (Wilcoxon tests; Supplemental online material: Appendix S2). Distribution of soil depth values differed significantly across all species except for *Pipturus*—*Psychotria*. Distribution of rugosity values differed significantly across all species except for *Metrosideros*—*Psychotria* and *Myrsine*—*Psychotria*. Distribution of LAI values differed significantly across all species (KS-test; Supplemental online material: Appendix S2).

The distribution of continuous variables for species was specific to each management unit (Figure 6D–O). Median values for species within management units varied in the novel restoration project for all three variables (KW-tests; soil depth: $p < 0.05$, rugosity: $p < 0.001$; LAI: $p < 0.05$), in the reserve for median soil depth ($p < 0.05$) and in the traditional restoration project for median LAI ($p < 0.01$). Within the invaded forest, none of the species differed in any of the variables, nor did the sapling-presence spots differ from the absence spots in any of the variables (KW-test). Differences in microsite distribution were significant across the following management units and species; in the novel restoration project: *Metrosideros* was

found on significantly deeper soil spots than *Psychotria*; *Pipturus* was found on spots with significantly higher rugosity than all remaining species. In the traditional restoration project *Metrosideros* was found on spots with significantly higher median LAI than *Psychotria* (Wilcoxon tests; Supplemental online material: Appendix S2). Significant differences in the distribution of variables were found in the novel restoration project for soil depth across all species except for *Pipturus*—*Psychotria*; for rugosity across all species except for *Metrosideros*—*Psychotria*; for LAI across all species except for *Metrosideros*—*Myrsine*. In the reserve soil depth differed significantly between *Pipturus*—*Psychotria* and *Pipturus*—*Myrsine*. In the traditional restoration project differences across species were neither significant for soil depth nor rugosity, but all three species differed significantly from each other in LAI distribution (KS-test; for p -values see supplemental online material: Appendix S2).

DISCUSSION

Management units differed in sapling microsite characteristics (Q1) and in density of native saplings (Q2). This finding indicates that manipulation of environmental conditions could enhance native regeneration, provided that there is sufficient seed rain. The four examined tree species differed in microsite preferences (Q3). Understanding how manipulation of the abiotic environment and site management conditions affects regeneration and recruitment of key species will allow a more targeted approach toward the restoration of this disappearing and biologically important forest type.

Native Sapling Establishment Can be Increased Through Conscious Restoration Planning and Management

Our results suggest that, within the restrictions of our individual-based sampling design, abiotic conditions varied greatly across the four management units. It is well established that high light availability is crucial for native recruitment in the HLWF (Burton and

Mueller-Dombois 1984, Drake 1993, Drake and Mueller-Dombois 1993), with native species recruiting almost exclusively in artificially created light gaps (Cordell et al. 2009, Ostertag et al. 2009). Accordingly, we hardly found any native recruitment in the invaded forest. As this absence is likely due to the shaded environment that was found to inhibit native recruitment (Cordell et al. 2009), our findings support previous assertions that canopy opening facilitates recruitment of all native species.

The high native sapling density in the reserve suggests that recruitment of native tree species is facilitated by putatively intact ecological processes and a relatively high abundance of native species in all layers. This finding is supported by a study in tropical lowland forests in Taiwan (Loo et al. 2017). Intact old-growth forest remnants offer complex, diverse, and heterogeneous habitats (Holl et al. 2000, Liebsch et al. 2008, Pardini et al. 2010) that have been found to facilitate multispecies restoration projects. For example, habitat heterogeneity has proved to facilitate sapling survival in a tropical rainforest in Costa Rica (Clark et al. 1999). However, younger HLWF sites are less prone to plant invasions (Zimmerman et al. 2008). Thus, microsite conditions as well as high native sapling density in the reserve are likely to be positively influenced by the fact that the reserve lies on a lava flow that is at least 350 years younger than that of the three other management units.

Contrary our hypothesis, we found native sapling density to be 2.5 times higher in the traditional restoration project than in the reserve. This finding suggests that the approach of assisted succession applied in the traditional restoration site facilitated the local establishment of native saplings (Cordell et al. 2016). In light of low native seedling abundances in the traditional restoration project four years after the project installation (Cordell et al. 2009), and the current biannual weeding interval, this finding is remarkable as it suggests that consideration of microsite preferences in a restoration project can improve native recruitment in the long run even in a formerly heavily invaded forest. In

contrast, in an independent project in a different area of the invaded HLWF of KMR, attempts to restore the forest community by native plantings alone, without management of invasive pressure, have not proven successful: in that project, planting native seedlings beneath the invaded canopy, has yielded less than 10% seedling survival six years after planting (Blaisdell; unpublished data). Comparing this low survival rate of previous restoration attempts with the findings of the traditional restoration project suggests that the reintroduction of native species into strongly degraded and invaded forest sites is possible through active management, and should include considerations of microsite preferences. Also, the high abundance of native saplings and seedlings (Kandert; personal observation) in both examined restoration projects emphasizes the benefit of conscious restoration planning and implementation. The novel restoration project offered the broadest range of microsites and was the only management unit where saplings of all four species were present. This finding indicates that site-adapted restoration planning and implementation have the potential to increase microsite diversity, which in turn has a positive influence on the recruitment of multiple native species.

Microsite variations of the two experimental restoration projects may have existed before management interventions, but it is likely that the removal of invasive species altered not only light-related but also substrate-related microsite conditions. Comparing the present differences in substrate composition between the two experimental restoration projects and the adjacent invaded forest suggests that removal of invasive species may have: (i) shifted substrate from soil to rock in the traditional restoration project, (ii) created more microsites of the type moss/nurselog in the novel restoration project, and (iii) increased rugosity in both restoration projects. These putative changes could be tested in the future by taking microsite measurements before and after clearing. We believe that the biomass produced from litterfall and woody debris of invasive species fills out crevices and thus levels out the ground

surface. Therefore, removal of invasive species may decrease litter biomass, which in turn increases rugosity and rocky substrate. Comparing substrate conditions in the invaded forest and the remaining management units suggests that a rocky substrate and a minimal soil layer are suitable conditions for most saplings. In addition, we found that microsites in the invaded forest tended to be about 1.5 times lower in rugosity. An explanation for the preference of native saplings for spots with comparably high rugosity could be that surface roughness could offer shelter from extreme moisture conditions (Born et al. 2015). In invaded sites, in addition to manipulating light environments, restoration practitioners can assist sapling establishment through careful removals that focus on promoting higher rugosity, while retaining pockets of deeper soil, and some areas of bare lava to facilitate recruitment of target species. However, extrapolating conclusions regarding variation in environmental variables does warrant some caution because as already stated, absence spots were only recorded in the invaded forest but not in the remaining management units. We decided to include the data derived from the absence spots into our analysis as these do not differ from the 14 presence spots of the invaded forest and characterize the microsites of the invaded forest. Excluding the absence spots from our analysis would have prevented answering Q1 asking for differences in microsite characteristics across all four management units. The fact that our experimental design resulted in no absence spots in the reserve stresses the high native sapling density in the reserve.

Most likely, the full range of environmental conditions and sapling microsite preferences of each of the four surveyed management units are not reflected thoroughly due to our individual-based sampling design and the fact that we did not record absence spots in each management unit.

Different Species Have Different Microsite Preferences

We found that the four examined native tree species of the HLWF differed in soil, substrate, and light microsite preferences (Table 2), with most results supporting our hypotheses. We found recruitment of *Metrosideros* to be clearly associated with high light conditions. This finding is in accordance with numerous studies across various light and nutrient conditions and different degrees of invasion arguing that *Metrosideros* requires large light gaps for regeneration (Drake 1998, Hughes and Denslow 2005, Funk and Vitousek 2007, Mascaro et al. 2008, Zimmerman et al. 2008, Cordell et al. 2009, Ostertag et al. 2009, Mascaro 2011). Our substrate-related findings are also in accordance with former studies in Hawaiian wet forests that found *Metrosideros* to be positively associated with tree fern substrate (Inman-Narahari et al. 2013) and moss (Mueller-Dombois 1987). Recruitment of *Pipturus* was positively associated with high light conditions and high rugosity, much more so than other species. This finding suggests that there is a great potential for restoration with *Pipturus* in sites with rough substrate, especially when canopy manipulations are part of the restoration

TABLE 2
Summary of Microsite Preferences Across the Four Examined Species

	Soil Depth	Rugosity	Light	Preferred Substrate
METPOL	- to ++	0	++	Moss, nurselog
MYRLES	+	0	0	Soil
PIPALB	-	++	++	Rock
PSYHAW	-	0	-	Rock

METPOL = *Metrosideros polymorpha*; MYRLES = *Myrsine lessertiana*; PIPALB = *Pipturus albidus*; PSYHAW = *Psychotria hawaiiensis*; +/0/- indicate the influence each variable has on sapling development across species: ++ strong positive influence; + positive influence; 0 neutral; - negative influence; - strong negative influence. These effects cannot be interpreted quantitatively.

strategy. Indeed, broadcasting seeds of *Pipturus* has resulted in successful recruitment of this species in the reserve (Cindy Dupuis, personal communication). Absence of *Pipturus* in the invaded forest strongly suggests that canopy opening is needed to encourage this pioneer species. *Psychotria* proved to be the most shade tolerant among the sampled species. Accordingly, other studies throughout the range of *Psychotria* found it recruiting well in nonnative dominated forests (Mascaro et al. 2008, Mascaro 2011). *Psychotria*'s ability to coinhabit nonnative-dominated forests can be attributed to similar survival, growth rates (Schulten et al. 2014), and light compensation/saturation points when compared to some invasive species (Wong 2007) and a highly plastic reaction to canopy openings (Ostertag et al. 2009). One finding that contradicted our hypothesis was that *Psychotria* was associated with shallow soil and rocky substrate. However, our original hypothesis was based on an assumption of forest succession that a closed canopy produces more litter which levels out the ground surface and covers the bare rock with soil. As a subcanopy species of later successional forest communities, we expected *Psychotria* to be associated with deeper soils, but we also found it to germinate one year after canopy opening in the 11 of the 16 plots of the novel restoration project (DiManno; personal observation). *Myrsine* proved to be shade tolerant as well and was the only species to be clearly associated with soil substrates. However, statements regarding *Myrsine* have to be interpreted cautiously due to the low sample size. Other studies in several forest sites found *Myrsine* to be recruiting in very low abundance (Mascaro et al. 2008, Zimmerman et al. 2008, Mascaro 2011, Inman-Narahari et al. 2013). As *Myrsine* is functionally similar to *Psychotria* (Mascaro 2011), low abundance could be explained by seed limitation (Inman-Narahari et al. 2013, Schulten et al. 2014).

We are aware that our findings regarding species microsite preferences for each sampled variable are limited to the management units we surveyed and the abiotic variables measured. Potentially, the species have broader niches than the results of this study suggest. To gain deeper understanding

of this unique and endangered ecosystem, further research on the recruitment ecology and microsite preferences or requirements of additional native species needs to be conducted. Future studies could focus on the connection between canopy opening and substrate related microsite conditions. Studies should include other influences on recruitment, such as water regime, nutrients, or properties of the organic layer; these variables are known to have an influence on recruitment of several species (e.g., Everham et al. 1996, Battaglia et al. 2000, Schupp et al. 2002, Marod et al. 2004, Jurinitz et al. 2013, Sterck et al. 2014, Rother et al. 2015).

CONCLUSION

The combination of individual sapling-based measurements and density estimates among management unit allows understanding of how management techniques influence abundance and distribution of native saplings. Our results strongly suggest that consciously planned and implemented restoration strategies that respect microsite preferences of target species have the potential to bring back native recruitment into heavily degraded and invaded forest sites. Given that the association between light, rugosity, and soil depth determine the establishment and survival of native saplings, restoration sites should at least be evaluated for these variables before outplanting. Our study reveals light and substrate related microsite preferences of four endemic tree species of the HLWF and contributes to a better understanding of their recruitment ecology. This understanding allows better planning and implementing of forest restoration projects in accordance with the microsite preferences of the target species and natural ecosystem dynamics and thus has the potential to increase restoration success and can help to conserve the unique forest ecosystem of the Hawaiian Lowland Wet Forest.

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Literature Cited

- Aiba, M., and T. Nakashizuka. 2007. Variation in juvenile survival and related physiological traits among dipterocarp species co-existing in a Bornean forest. *J. Veg. Sci.* 18:379–388.
- Baltzer, J. L., and S. C. Thomas. 2007. Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *J. Ecol.* 95:1208–1221.
- Baraloto, C., and E. D. Goldberg. 2004. Microhabitat associations and seedling bank dynamics in a neotropical forest. *Oecologia* 141:701–712.
- Battaglia, L., S. Fore, and R. Sharitz. 2000. Seedling emergence, survival and size in relation to light and water availability in two bottomland hardwood species. *J. Ecol.* 88:1041–1050.
- Born, J., R. Bagchi, D. Burslem, R. Nilus, C. Tellenbach, A. R. Pluess, and J. Ghazoul. 2015. Differential responses of dipterocarp seedlings to soil moisture and microtopography. *Biotropica* 47:49–58.
- Buck, M. G. 1982. Hawaiian treefern harvesting affects forest regeneration and plant succession. Research Note PSW-355. Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, Berkeley.
- Burton, P. J., and D. Mueller-Dombois. 1984. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. *Ecology* 65:779–791.
- Cabin, R. J., S. G. Weller, D. H. Lorence, T. W. Flynn, A. K. Sakai, D. Sandquist, and L. J. Hadway. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conserv. Biol.* 14:439–453.
- Carlquist, S. 1974. *Island biology*. Columbia University Press, New York.
- . 1980. *Hawai'i: a natural history*. Second edition. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawai'i.
- Carlton, G. C., and F. A. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* 79:1305–1319.
- Chazdon, R. L., and M. R. Guariguata. 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica* 48:716–730.
- Clark, D. A., and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol. Monogr.* 62:315–344.
- Clark, D. B., M. W. Palmer, and D. A. Clark. 1999. Edaphic factors and the landscape-scale distribution of tropical rainforest trees. *Ecology* 80:2662–2675.
- Cordell, S., R. Ostertag, B. Rowe, L. Schweinhart, L. Vasquez-Radonic, J. Michaud, T. C. Cole, and J. R. Schulten. 2009. Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. *Biol. Cons.* 142:2997–3004.
- Cordell, S., R. Ostertag, J. Michaud, and L. Warman. 2016. Quandaries of a decade-long restoration experiment trying to reduce invasive species: beat them, join them, give up, or start over? *Restor. Ecol.* 24:139–144.
- DiManno, N., R. Ostertag, L. Warman, D. Rayome, S. Cordell, A. Uowolo, W. Buckley, J. Rosam, T. Winters-Barcelona, and P. M. Vitousek. in preparation. Hybrid ecosystem restoration in Hawaiian forests: performance of novel species mixtures based on plant functional traits. *Ecol. Appl.*

- d-maps.com. 2017. World Pacific Ocean Centered. http://d-maps.com/pays.php?num_pay=275&lang=en. Accessed 28 October 2017.
- Drake, D. R. 1992. Seed dispersal of *Metrosideros polymorpha* (Myrtaceae): a pioneer tree of Hawaiian lava flows. *Am. J. Bot.* 79:1224–1228.
- . 1993. Germination requirements of *Metrosideros polymorpha*, the dominant tree of Hawaiian lava flows and rain forests. *Biotropica* 25:461–467.
- . 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *J. Veg. Sci.* 9:103–112.
- Drake, D. R., and D. Mueller-Dombois. 1993. Population development of rainforest trees on a chronosequence of Hawaiian lava flows. *Ecology* 74:1012–1019.
- Du Preez, C. 2015. A new arc-chord ratio (ACR) rugosity index for qualifying three-dimensional landscape structural complexity. *Landsc. Ecol.* 30:181–192.
- Dupuis, C. J. 2012. Vegetation patterns in lowland wet forests of Hawai‘i. Master’s thesis. University of Hawai‘i, Hilo.
- Everham, E. M., R. W. Myster, and E. Van De Genachte. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *Am. J. Bot.* 83:1063–1068.
- Fife, D. 2017. Package “fifer” – a biostatisticians toolbox for various activities, including plotting, data cleanup, and data analysis. CRAN.
- Foster, J. T., and S. K. Robinson. 2007. Introduced birds and the fate of Hawaiian rainforests. *Conserv. Biol.* 21:1248–1257.
- Friday, J. B., S. Cordell, C. P. Giardina, F. Inman-Narahari, N. Koch, J. J. Leary, C. M. Litton, and C. Trauernicht. 2015. Future directions for forest restoration in Hawai‘i. *New For.* 46:733–746.
- Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081.
- Gagné, W. C., and L. W. Cuddihy. 1999. Vegetation. Pages 45–114 in W. L. Wagner, D. R. Herbst, and S. H. Sohmer, eds. *Manual of the flowering plants of Hawai‘i*. University of Hawai‘i Press/Bishop Museum Press, Honolulu, USA.
- García, D., J. R. Obeso, and W. E. Martínez. 2005. Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? *J. Ecol.* 93:693–704.
- Giambelluca, T. W., Q. Chen, A. G. Frazier, J. P. Price, Y. L. Chen, P. S. Chu, J. K. Eischeid, and D. M. Delparte. 2013. Online rainfall atlas of Hawai‘i. *Bull. Am. Met. Soc.* 94:313–316.
- Grubb, P. J. 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspect. Plant Ecol. Evol. Syst.* 1:3–31.
- Hallett, S. H., and S. P. Caird. 2017. Soil-Net: development and impact of innovative, open, online soil science educational resources. *Soil Sci.* 182:188–201. http://www.soil.net.com/dev/page.cfm?pageid=casestudies_trf&loginas=anon_casestudies. Accessed 29 November 2017.
- Holl, K. D., M. E. Loik, E. H. Lin, and I. A. Samuels. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Rest. Ecol.* 8:339–349.
- Hughes, R. F., and J. S. Denslow. 2005. Invasion by a N₂-fixing tree alters function and structure in wet lowland forests of Hawai‘i. *Ecol. Appl.* 15:1615–1628.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harb. Sym.* 22:415–427.
- Inman-Narahari, F., R. Ostertag, S. Cordell, C. P. Giardina, K. Nelson-Kaula, and L. Sack. 2013. Seedling recruitment factors in low-diversity Hawaiian wet forest: towards global comparisons among tropical forests. *Ecosphere* 4:1–19.
- Jones, C. G., and R. M. Callaway. 2007. The third party. *J. Veg. Sci.* 18:771–776.
- Jurinitz, C. F., A. A. de Oliveira, and E. M. Bruna. 2013. Abiotic and biotic influences on early-stage survival in two shade-tolerant tree species in Brazil’s Atlantic forest. *Biotropica* 45:728–736.

- Kirch, P. V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. University of Hawai'i Press, Honolulu.
- Kitayama, K., D. Mueller-Dombois, and P. M. Vitousek. 1995. Primary succession of Hawaiian montane rain forest on a chronosequence of eight lava flows. *J. Veg. Sci.* 6:211–222.
- Kobe, R. K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecol. Monogr.* 66:181–201.
- . 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201.
- Kobe, R. K., S. W. Pacala, J. A. Silander, and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5:517–532.
- Lamb, D., P. D. Erskine, and J. A. Parotta. 2005. Restoration of degraded tropical forest landscapes. *Science* 310:1628–1632.
- Larish, M. 2015. Keau'ohana Forest Restoration. Keola Magazine, Keau, USA. <https://keolamagazibe.com/land/keauohana-forest-restoration/>. Accessed 31 January 2020.
- Ledo, A., L. Cayuela, R. Manso, and S. Condés. 2015. Recruitment patterns and potential mechanisms of community assembly in an Andean cloud forest. *J. Veg. Sci.* 26:876–888.
- LI-COR. 2017. LAI-2000C plant canopy analyser – Operating manual. Licor, Inc., Lincoln.
- . 2020. LI-2200C plant canopy analyzer. https://www.licor.com/env/products/leaf_area/LAI-2200C/science/. Accessed 24 October 2020.
- Liebsch, D., M. C. M. Marques, and R. Goldenberg. 2008. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biol. Cons.* 141:1717–1725.
- Little, E. L., and R. G. Skolmen. 1989. Common forest trees of Hawai'i. Agriculture Handbook No. 679. United States Department of Agriculture, Washington, DC.
- Loh, R. K., and C. C. Daehler. 2008. Influence of woody invader control methods and seed availability on native and invasive species establishment in a Hawaiian forest. *Biol. Invasions* 10:805–819.
- Loo, L. C., G. Z. M. Song, and K. J. Chao. 2017. Characteristics of tropical human-modified forests after 20 years of natural regeneration. *Bot. Stud.* 58:36.
- Marod, D., U. Kutintara, H. Tanaka, and T. Nakashizuka. 2004. Effects of drought and fire on seedling survival and growth under contrasting light conditions in a seasonal tropical forest. *J. Veg. Sci.* 15:691–700.
- Marques, M. C. M., and D. F. R. P. Burslem. 2015. Multiple stage recruitment limitation and density dependence effects in two tropical forests. *Plant Ecol.* 216:1243–1255.
- Mascaro, J. 2011. Eighty years of succession in a noncommercial plantation on Hawai'i Island: are native species returning? *Pac. Sci.* 65:1–15.
- Mascaro, J., K. K. Becklund, R. F. Hughes, and S. A. Schnitzer. 2008. Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i. *For. Ecol. Manag.* 256:593–606.
- McDaniel, S., and R. Ostertag. 2010. Strategic light manipulation as a restoration strategy to reduce alien grasses and encourage native regeneration in Hawaiian mesic forests. *Appl. Veg. Sci.* 13:280–290.
- Molofsky, J., and C. K. Augspurger. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73:68–77.
- Moore, R. B., and E. A. Trusdell. 1991. Geologic map of the lower east rift zone of Kilauea Volcano, Hawai'i. Miscellaneous Investigations Series; Map 1–2225. United States Geological Survey, Washington, DC.
- Mueller-Dombois, D. 1987. Forest dynamics in Hawai'i. *Trends Ecol. Evol.* 2:216–220.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000.

- Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Native Plants Hawai'i. 2009. <http://nativeplants.hawaii.edu/plant/index>. Accessed 8 August 2017.
- Nicotra, A. B., R. L. Chazdon, and S. V. B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1–17.
- Olson, D. M., and E. Dinerstein. 2002. The global 200: priority ecoregions for global conservation. *Ann. Mo. Bot. Gard.* 89:199–224.
- Ostertag, R., C. P. Giardina, and S. Cordell. 2008. Understory colonization of eucalyptus plantations in Hawai'i in relation to light and nutrient levels. *Restor. Ecol.* 16:475–485.
- Ostertag, R., S. Cordell, J. Michaud, T. C. Cole, R. J. Schulten, K. M. Publico, and J. H. Enoka. 2009. Ecosystem and restoration consequences of invasive woody species removal in Hawaiian lowland wet forest. *Ecosystems* 12:503–515.
- Ostertag, R., L. Warman, S. Cordell, and P. M. Vitousek. 2015. Using plant functional traits to restore Hawaiian rainforest. *J. Appl. Ecol.* 52:805–809.
- Otto, R., B. O. Krüsi, J. D. Delgado, J. M. Fernández-Palacios, E. García-Del-Rey, and J. R. Arévalo. 2010. Regeneration niche of the *Canarian juniper*: the role of adults, shrubs and environmental conditions. *Ann. For. Sci.* 67:709–709.
- Pardini, R., A. de Arruda Bueno, T. A. Gardner, P. I. Prado, and J. P. Metzger. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*, 5.
- Pattison, R. R., G. Goldstein, and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117:449–459.
- Pearcy, R. W. 1983. The light environment and growth of C3 and C4 species in the understory of a Hawaiian forest. *Oecologia* 58:19–25.
- Peña-Claros, M. 2001. Secondary forest succession: processes altering the regeneration of Bolivian tree species. Promab Scientific Series. Doctoral dissertation. Utrecht University, Utrecht.
- Pocheville, A. 2015. The ecological niche: history and recent controversies. Pages 547–586 in Herams et al. eds. *Handbook of evolutionary thinking in the sciences*. Springer, Dodrecht.
- Poorter, L., and E. J. M. M. Arets. 2003. Light environment and tree strategies in a Bolivian tropical moist forest: a test of the light-partitioning hypothesis. *Plant Ecol.* 166:295–306.
- Price, J. P., J. D. Jacobi, and D. Matsuwaki. 2007. Mapping plant species ranges in the Hawaiian Islands: developing a methodology and associated GIS layers. The Nature Conservancy.
- printableworldmap.net. 2017. Hawai'i Blank Map. https://www.printableworldmap.net/preview/hi_blank_1. Accessed 28 October 2017.
- R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>.
- Rey Benayas, J. M., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325:1121–1124.
- Rother, D. C., P. Jordano, R. R. Rodrigues, and M. A. Pizo. 2013. Demographic bottlenecks in tropical plant regeneration: a comparative analysis of causal influences. *Perspect. Plant Ecol.* 15:86–96.
- Rother, D. C., M. A. Pizo, T. Siqueira, R. R. Rodrigues, and P. Jordano. 2015. Community-wide spatial and temporal discordances of seed-seedling shadows in a tropical rainforest. *PLoS One* 10:1–12.
- Sarkar, D. 2017. Package "lattice", Trellis Graphics for R. CRAN.
- Schulten, J. R., T. C. Cole, S. Cordell, K. M. Publico, R. Ostertag, J. E. Enoka, and J. D. Michaud. 2014. Persistence of native trees in an invaded Hawaiian lowland wet forest: experimental evaluation of light and water constraints. *Pac. Sci.* 68:267–285.

- Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2:267–275.
- Schupp, E. W., T. Milleron, and S. E. Russo. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pages 19–34 *in* D. Levey, W. Silva, and M. Galetti, eds. *Seed dispersal and frugivory: ecology, evolution, and conservation*. CAB International, Wallingford.
- Soil Survey Staff. 2012. Soil survey of island of area, Hawai'i. Natural Resources Conservation Service, U.S. Department of Agriculture. Accessed 17 August 2017.
- Sterck, F., L. Markesteijn, M. Toledo, F. Schieving, and L. Poorter. 2014. Sapling performance along resource gradients drives tree species distributions within and across tropical forests. *Ecology* 95:2514–2525.
- Thimonier, A., I. Sedivy, and P. Schleppi. 2010. Estimating leaf area index in different types of mature forest stands in Switzerland: a comparison of methods. *Eur. J. For. Res.* 129:543–562.
- Unger, M., J. Homeier, and C. Leuschner. 2013. Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador. *Trop. Ecol.* 54:33–45.
- Van Andel, J., and J. Aronson. 2005. *Restoration ecology: the new frontier*. Blackwell Science, Oxford.
- Vu, V. Q. 2011. Package ggbiplot – biplot for principal components using Ggplot2. GitHub.
- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. *Manual of the flowering plants of Hawai'i*. University of Hawai'i Press, Bishop Museum Press, Honolulu.
- Watson, D. J. 1947. Comparative physiological studies in the growth of field crops: I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Ann. Bot.* 11:41–76.
- Whitmore, T. C. 1996. A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. The ecology of tropical forest tree seedlings. Pages 3–39 *in* M. D. Swaine, ed. *Man and the Biosphere Series 17*. UNESCO, Paris.
- Wong, C. P. 2007. Hawaiian lowland wet forest: impacts of invasive plants on light availability. *J. Young Investig.* 16:1–5.
- Ziegler, A. C. 2002. *Hawaiian natural history, ecology and evolution*. University of Hawai'i Press, Honolulu.
- Zimmerman, N., R. F. Hughes, S. Cordell, P. Hart, H. K. Chang, D. Perez, R. K. Like, and R. Ostertag. 2008. Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai'i. *Biotropica* 40:277–284.