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RESEARCH ARTICLE

Light quality and spatial variability influences on seedling regeneration in Hawaiian lowland wet forests

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Abstract

1. Tropical forest understories tend to be light-limited. The red-to-far-red ratio (R:FR) is a useful and reliable index of light quality and its spatial variability can influence competition between native and non-native seedlings. While per cent light transmittance has been quantified in some Hawaiian lowland wet forests (HLWF), no information exists on how the spatial distribution of understorey light varies in relation to species invasion, or if patterns of seedling regeneration and light are linked.
2. We measured the R:FR of light in the understorey to assess light quality in three HLWF forest types: native-dominated, partially invaded and *Psidium cattleyanum*- (strawberry guava) dominated to quantify light quality in the understorey (0–50 cm height). We also identified relationships between light quality and native and non-native seedling presence, diversity and abundance. Together, these data can help to determine the restoration potential of HLWF.
3. Linear mixed-effect modelling showed that native-dominated forests had significantly greater R:FR than *P. cattleyanum*-dominated forests, demonstrating a transformation in the light environment with increased invasion. Heterogeneity in R:FR varied more across sites than among forest types. In both native-dominated and partially invaded forests, there were more native seedlings in the low-quality R:FR (0.0–0.40) category and fewer in the medium- (0.41–0.70), and high-quality (≥0.71) light categories than would be expected by chance, and there were no native seedlings in the *P. cattleyanum*-dominated forests.
4. Native-dominated forests had greater species richness and abundance of native seedlings than the partially invaded forests, likely due to propagule availability. However, the spatial clustering of seedlings, the mismatch of native seedlings in light environments less suitable, and a considerable proportion of open high-quality microsites, highlights that conditions are not optimal for native species in HLWF in the long term.
5. *Synthesis and applications*. The native-dominated and partially invaded forests still hold conservation value, despite variation among sites. Seedling additions could

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be targeted to different R:FR environments and at different spatial scales, but the lack of a strong relationship between R:FR and seedling number suggests that other factors besides light quality should be considered in seedling enrichment or other management activities.

KEYWORDS
Hawai'i, red-to-far-red ratio, restoration, spatial patterning of light, understorey

1 | INTRODUCTION

Closed-forest understories tend to be the most light-limited terrestrial habitat, where both the quantity and quality of light available to seedlings is influenced by canopy, sub-canopy and understorey structure. The amount of photosynthetically active radiation (PAR) that is available at the forest floor ranges from 10%–15% in boreal forests, to 1%–5% in temperate forests (Coomes & Grubb, 2000), and <2% in tropical lowland rainforests (Chazdon, 1988; Chazdon & Fetcher, 1984; Montgomery & Chazdon, 2001). The quantity of light a plant receives is a fundamental regulator of the plant energy balance, photosynthesis and other aspects of growth and development; and in dense tropical understories, these low PAR levels strongly influence the slow growth of many seedlings (Clark & Clark, 1992).

Light quality, however, can be as important as light quantity in tropical forests. As light penetrates through a forest canopy, red and blue (R) wavelengths (475 and 650 nm, respectively) are preferentially absorbed by green leaves, while green and far-red (FR) wavelengths (510 and 730 nm, respectively) are preferentially reflected (Tinoco-Ojanguren & Pearcy, 1995). Thus, understorey plants in dense tropical rainforest understories receive low-quality light that is rich in far-red wavelengths and relatively poor in red ones (Li et al., 2001; Méthy & Roy, 1993). While the ratio of red-to-far-red wavelengths (R:FR) is approximately 1.0 in unfiltered sunlight, this ratio can be reduced to an average of 0.2–0.3 (Daws et al., 2002; Lee, 1987). The R:FR is logarithmically related to leaf area index (Jordan, 1969). Thus, it can be used to estimate per cent transmittance, and can be a valuable tool for understanding the light environment in tropical understories when per cent light transmittance is low (Capers & Chazdon, 2004). R:FR is particularly useful when light levels are too low for reliable hemispherical photograph analyses (Chazdon & Field, 1987). Quantifying R:FR can provide a relative index of understorey per cent transmittance in addition to, or instead of, the use of paired quantum sensors and hemispherical techniques (Capers & Chazdon, 2004), and it can also be used as an index of light quality (Morgan & Smith, 1981; Tan et al., 2022).

Depending on forest physiognomy, tropical understorey light environments can range from uniform to highly heterogeneous (Nicotra et al., 1999). The spatial patterning of understorey light quality can play a role in the germination of seeds, as well as seedling establishment, growth and survival (Messaoud & Houle, 2006; Montgomery & Chazdon, 2002; Nicotra et al., 1999). Within forest stands, the spatial variability of light in the understorey is largely determined by canopy and sub-canopy structure characteristics (including foliage distribution, species composition and vertical and horizontal architecture), and plays a role in the distribution of understorey species (Clark & Clark, 1992). Canopy gaps have been an important focus of literature on light environment in tropical forests (e.g. Chazdon & Fetcher, 1984; Svenning, 2000); yet these gaps only represent around 25% of the area within forests (sensu Connell et al., 1997). In tropical rainforests, the understorey layer can intercept much of the remaining light, altering both the quantity of light a newly germinated plant receives and the spectral quality of this light (George & Bazzaz, 1999; Lorimer et al., 1994; Messier et al., 1989, 1998). Ultimately, the structure and distribution of vegetation in the understorey, sub-canopy and canopy may regulate microsite environments and understanding these relationships may provide useful information regarding seedling recruitment and species distributions along the forest floor.

Light environments can also be drastically reduced by invasive species, which can strongly impact native species regeneration. Vitousek et al. (1997) demonstrated that invasive species prevent the establishment of native seedlings by occupying 'safe sites' and by outcompeting native seedlings for specific limiting resources. In Hawaiian lowland wet forests (HLWF), light is the most limiting factor for photosynthetic rates and relative growth rates of both native and non-native species (Schulten et al., 2014). Native-dominated forests in Hawai'i are unique, and tend to have more open canopies relative to their tropical continental counterparts (Funk & McDaniel, 2010; McDaniel & Ostertag, 2010; Wong, 2006). Because of their openness, most native canopy species require relatively high-light conditions for both germination and survival (Burton, 1982; Drake, 1993; Drake & Mueller-Dombois, 1993). However, HLWF in Hawai'i are changing as invasive species rapidly infiltrate the understorey, displacing native species and eventually entire forest stands. These invasive species are good competitors, proving to be more efficient in light use than native species (Pattison et al., 1998). Furthermore, these invasive species are capable of germinating and growing well in low-light conditions, unlike many of Hawaii's native species (Cordell et al., 2009).

Unfortunately, the majority of remaining HLWF are highly invaded, but as a result, they present unique opportunities to understand invasion processes and to test restoration approaches. Most current restoration efforts in HLWF are focused on invaded areas which retain some degree of native canopy but have low levels of native regeneration and recruitment (e.g. see Cordell et al., 2009; Ostertag et al., 2009). In HLWF, invasive understorey plants are densely occupying microsites that would otherwise be available for native seedlings, thus are likely altering the light conditions important for native seedling regeneration (Zimmerman et al., 2008). Wong (2006) found that non-native species in a HLWF had created a dense sub-canopy (1–10 m) that limited light heterogeneity and decreased light transmittance by 51%. Because invasive species are decreasing the amount of light available to native seedlings, management practices have focused primarily on invasive species removal. But large-scale removal projects can be labour intensive for years to come; as an example, Ostertag et al. (2009) estimated it took 40 person h/m^2/year in a HLWF to maintain it as all native, after the initial removal. In addition, opening the understorey only facilitates further secondary invasive species colonizations (D'Antonio et al., 2017). Understanding how light is distributed throughout the understorey and how that is linked to seedling success may help managers use a more focused approach to selecting suitable outplanting sites at a small scale rather than undertaking large-scale removal.

Using R:FR as an index of light quality, the primary objectives of this study were as follows: (a) to quantify spatial patterns of light quality in the understorey within and between native-dominated, partially invaded and non-native-dominated HLWF, (b) to identify relationships between seedling presence and light quality and (c) to use these data to determine the restoration potential of HLWF. A better understanding of the spatial distribution of light in the understorey and how that in turn relates to seedling recruitment could be a valuable tool for land managers attempting to restore native species to native-dominated and also partially invaded HLWF.

2 | MATERIALS AND METHODS

2.1 | Study sites

According to altitude (<800 masl) and precipitation (>2500 mm annual precipitation), all sites are classified as lowland wet as defined by Gagné and Cuddihy (1999) and Price et al. (2007), and receive similar cloud frequency as estimated by Giambelluca et al. (2014). We selected nine sites on the eastern (windward) side of Hawaiʻi Island, based on the predominance of native and non-native species at each site. Access to field sites was provided via agreements with Kamehameha Schools, the Keaukaha Military Reservation, the Hawaiʻi Department of Land and Natural Resources and an anonymous land owner. Three sites each (Table 1) were designated as native-dominated (estimated at ≥80% of native species in the canopy), partially invaded or dominated (estimated at ≥80% of the canopy) by the invasive tree, *Psidium cattleyanum*, based on site observations. These categories naturally followed an earlier study by Zimmerman et al. (2008), surveying vegetation plots of woody vegetation and understorey cover in remnant HLWF in east Hawaiʻi Island. Given the scarcity of remaining HLWF patches, it is logical to determine their category; native-dominated sites were forests with expected structure and only a small presence of non-native species, partially invaded forests had only remnant native species in low abundance and *P. cattleyanum*-dominated sites were transformed into near monocultures.

2.2 | Light quality data collection and spatial patterns

At each site ($n = 9$), we established a 20 × 80 m plot with an internal grid system measuring 5 × 5 m. All plots were set up to maintain a minimum distance of 10 m from any roadway or clearing. At each intersection point ($n = 85$ per site), we took a series of 24 light quality measurements with a SKR 110 Red/Far-red sensor (SKYE Instruments, London, UK). The sensor was mounted on a levelling arm that extended 25 cm from the intersection point and R:FR readings were taken at six different heights (0, 10, 20, 30, 40 and 50 cm) in the four cardinal directions. The four directional measurements at each height were averaged to obtain one value.

TABLE 1 Site characteristics of the nine lowland wet forest sites on the east side of Hawaiʻi Island.

Forest type	Elevation (m)	Mean annual precip. (mm)[a]	Lava type	Flow age (year)	Latitude (N)	Longitude (W)	Abbreviation
Native-dominated	253	2800	ʻaʻā	200–400	19.250556	154.416944	KH_1
Native-dominated	790	5900	ʻaʻā	3000–5000	19.694444	155.518333	KI_10.5
Native-dominated	298	3000	ʻaʻā with ash	500–750	19.450278	155.518333	PK_1
Partially invaded	15	3300	ʻaʻā	750–1500	19.703889	155.041667	KMR
Partially invaded	253	2800	ʻaʻā	200–400	19.418056	154.951111	KH_2
Partially invaded	298	3000	ʻaʻā with ash	500–750	19.448889	154.926667	PK_2
P. cattleyanum-dominated	10	3000	ʻaʻā	200–400	*Contact author*		VD_1
P. cattleyanum-dominated	10	3000	ʻaʻā	200–400	*Contact author*		VD_2
P. cattleyanum-dominated	310	3000	ʻaʻā	200–400	19.394167	154.996389	BS

[a] Mean annual precipitation derived from the Online Rainfall Atlas of Hawaiʻi, Giambelluca et al. (2013).

Thus, for each sampling point, the light environment was quantified in a 50 × 50 cm area. In few cases, a fallen log or other barrier precluded sampling at a given point/height combination ($n = 20$ missing points for R:FR).

Although Capers and Chazdon (2004) have previously shown that sunny conditions increase variability in R:FR ratios, preliminary calculations in this study found no differences between sunny and overcast conditions. However, we did find increased variability between windy and non-windy conditions, so experimental measurements were restricted to non-windy days. All measurements were taken during the summer months (June–September) of 2014 and between 1000 and 1400 h in order to minimize effects of seasonal and diurnal differences in sun azimuth.

For each of the three forest types, the collected R:FR light data were assigned local coordinates (x, y, z origin for each plot arbitrarily set at 100/100/0 m) and imported into a GIS software program (ArcGIS Pro 3.2, ESRI, Redlands, CA). Empirical Bayesian Kriging, a geostatistical interpolation method (Gribov & Krivoruchko, 2020) was used to generate an interpolated three-dimensional model of R:FR values for each individual forest plot. The Empirical Bayesian Kriging method, which uses an intrinsic random function as the kriging model and subsets input data to repeatedly estimate localized semivariograms, has been successfully used to model a wide variety of three-dimensional phenomena (Kim et al., 2022; Mourad et al., 2021; Wickramathilaka et al., 2023). The Empirical Bayesian Kriging 3D tool with default settings, including the power semivariogram option, was accessed via the 'Geostatistical Wizard' within ArcGIS Pro 3.2. The resulting three-dimensional geostatistical layers for each site were then converted into netCDF format (*.nc) files for further visualization as voxel layers.

2.3 | Seedling patterns

In addition to light, all seedlings (defined as having at least two true leaves) were measured within a 50 × 50 cm quadrat in each grid cell. All woody seedlings were identified to species, and fern and grass species were grouped together as native or non-native morphospecies. The height at the top of each individual seedling was measured and grouped into five height classes corresponding to the heights at which light quality readings were taken: 1–10, 11–20, 21–30, 31–40 and 41–50 cm. These data were also imported into the GIS software.

2.4 | Statistical analyses

To determine the intensity of horizontal spatial clustering in the measured R:FR light data near the forest floor (measurements collected between 1 and 10 cm, $n = 85$ for each site), we ran the Incremental Spatial Autocorrelation geoprocessing tool within ArcGIS Pro 3.2 with a beginning distance of 5 m. This tool measures spatial autocorrelation within the input data and repeatedly generates a series of statistical measures over increasing distances to identify the particular extent that corresponds to the maximum degree of spatial clustering, typically indicated by the maximum z-score (Francis et al., 2023; Parvin et al., 2021; Wu et al., 2023).

To examine quantitative differences in R:FR values and seedling abundance among the three forest types, statistical tests were conducted in R 4.2.2 (R Core Team, 2022). Because light levels and seedlings at a given height may not be fully independent of another height, we first examined trends across heights. But, given lack of strong patterns (Table S1), we decided to average averaged R:FR values across heights for every point. To examine how R:FR varies among forest types, we used linear mixed-effect models and estimated parameters by restricted maximum likelihood using the function lmer of the lme4 1.1–35.1 package (Bates et al., 2015). The significance of forest type (native-dominated, partially invaded and *P. cattleyanum*-dominated) as a fixed-effect predictor was tested with the ANOVA command, and the nine sites were tested as a random factor using the ranova command. When R:FR was square-root transformed, the model met the normality and homogeneity of variances assumptions of the residuals. We conducted post hoc tests for multiple comparisons across forest types in the emmeans package (version 1.8.9) (Lenth, 2022). The same linear mixed-effect model analysis was carried out on the coefficient of variation (CV) of R:FR, which was log-transformed in order to meet the assumptions of normality and homogeneity of variances of the residuals in the model.

To examine differences in the distribution of native seedlings, and non-native seedlings across forest types, R:FR measurements were summarized into low (0.0–0.40), medium (0.41–0.70) and high-quality (≥0.71) categories based on histograms (see Figure S1). We chose to make R:FR a categorical variable for this analysis because there were many sample points in the forest sites that had zeroes (no seedlings). We used G tests to determine if the number of seedlings in each category fit a theoretical expectation (goodness-of-fit). In this case, the fit we were testing against was the proportion of each R:FR category found from sampling light quality in each of the three forest types. Actual seedling counts were tested against these proportions using the DescTools package.

3 | RESULTS

3.1 | Spatial patterns of light quality

Vertical and horizontal profiles of light quality across forest types display native forests with more areas with high-light quality, while *P. cattleyanum*-dominated forests tend to have homogeneously low-quality light environments (Figure 1). Although there is variation within and across sites, the vertical profile of native-dominated forests tends to have more areas of high-quality light (24.1% of the points) than the partially invaded or *P. cattleyanum*-dominated forests (5.9% and 0.98%, respectively), and for the most part, native-dominated forests have fewer low-quality microsites (Figure 1). Partially invaded forests have few high-quality microsites with R:FR values >0.71, but do have areas with very low light quality, while the

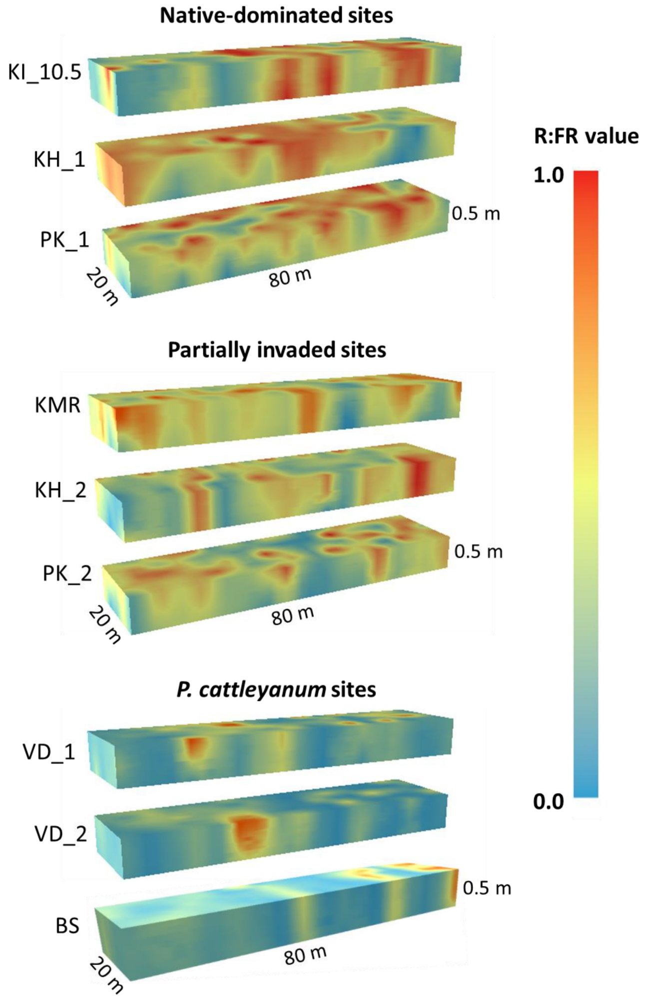

FIGURE 1 Visualizations of 3D Empirical Bayesian Kriging for R:FR measurements of all nine sites. Warmer colours indicate higher R:FR value and thus higher light quality environment. The mapped areas are based on sampling points with the 20 × 80 m sampling grid, and taken at six different heights (0, 10, 20, 30, 40 and 50 cm). Vertical exaggeration of 20 applied to height values for visualization purposes.

R:FR in *P. cattleyanum*-dominated forests were primarily low-quality microsites (84.5%; Figure 1).

All three of the native-dominated sites, two of the partially invaded sites and two of the *P. cattleyanum* sites showed spatial autocorrelation in R:FR values based on the Moran's Index (Table S2). In these seven sites, the R:FR values are more spatially clustered than would be expected by chance, that is, if underlying spatial processes were random. The peak distance for spatial autocorrelation ranged from 15 to 20 m in the native-dominated sites, 25 to 35 m in the partially invaded sites and 25 to 30 m in the *P. cattleyanum*-dominated sites (Table S2).

3.2 | Light quality across and within forest types

There was a pattern where R:FR values tended to increase with height above-ground for all three forest types (Figure 2). For a given height, a visual inspection shows that forest types did not have similar R:FR values, but the light environment at 40 cm height in partially invaded forests was similar to that of native forests at ground level (Figure 2).

When R:FR values were averaged across heights, R:FR was significantly related to the fixed effect of forest type and the random effect of study site, with the fixed effects explaining more of the variation (marginal $R^2 = 0.30$, conditional $R^2 = 0.34$; Table 2). Native-dominated forests exhibited the greatest understorey mean R:FR and *P. cattleyanum*-dominated forests had about 50% lower mean values of R:FR (Figure 3).

3.3 | Variability in light quality across and within forest types

The coefficient of variation (CV) of R:FR (log-transformed) varied across sites, but not across forest types (Table 3). Overall, the linear mixed model for CV had a much lower fit than for R:FR (marginal $R^2 = 0.0081$, conditional $R^2 = 0.08$). These results show that there was considerable variability in R:FR values among sites, regardless of the forest type, and thus, it was important to have sites as a random variable in the models.

3.4 | Light quality and seedlings

Across sites, there were 3641 seedlings present representing 40 different species or morphospecies (Table S3). The majority of seedlings in the study plots (86%) were non-native, and the most common taxa recorded included *Ardisia elliptica* (shoebutton ardisia), *Oplismenus hirtellus* (basket grass), *Miconia crenata* (formerly *Clidemia hirta* [Koster's curse]), *Psidium cattleyanum* (strawberry guava) and non-native ferns, primarily *Nephrolepis multiflora* (sword fern). We found 19 species of native seedlings, the most numerous of which were herbaceous *Peperomia* (ʻalaʻala wai nui) spp., as well as *Psychotria hawaiiensis* (kōpiko) and *Metrosideros polymorpha* (ʻōhiʻa). One listed endangered endemic species, *Cyrtandra nanawaleensis* (haʻiwale), was also present at one native-dominated site (Table S3). Native-dominated forests showed the pattern of having the most native species/morphospecies, and partially invaded forests had the most richness of non-native species/morphospecies (Table S3). Seedlings generally showed a pattern of decreasing abundance with height (Figure S2).

The distribution of native seedlings did not meet the expected distribution in the native-dominated site or in the partially invaded site. In both cases, there were more seedlings in the low-quality R:FR category and fewer in the medium and high-light categories than would be expected by chance (Table 4; Figure 4). The lack of native seedlings in the *P. cattleyanum* sites precluded the use of a statistical test. Non-native seedlings had a distribution similar to that of the native species; in the native-dominated and partially invaded sites, there were more seedlings in the low-quality microsites and fewer in the medium- and high-quality microsites than would be expected by chance (Table 4;

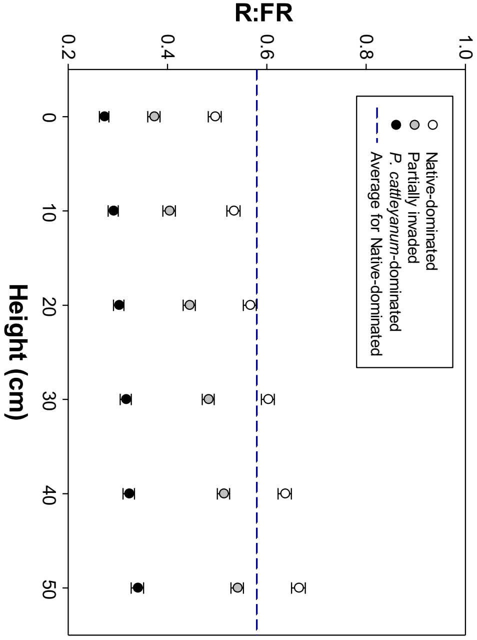

FIGURE 2 Pattern of red-to-far-red ratios (R:FR) and height above-ground (cm) in native-dominated, partially invaded and *Psidium cattleyanum*-dominated forests. Light values were averaged across the five heights per site, and then the three sites were averaged and a standard error was calculated ($n = 3$, but no statistical test was conducted). Dotted line represents the average of all R:FR points across heights in the three native-dominated forests as a baseline comparison.

Figure 4). It is important to note, that there is a large number and proportion of open microsites in these forests that could still be colonized by seedlings (Figure 5), and that most of the native seedling abundance and richness is in the native-dominated sites (Figure 6).

4 | DISCUSSION

4.1 | Relationships between light quality and seedling presence

Few studies have quantified the R:FR in tropical forests. One study by Lee (1987) conducted in two neotropical forests found low-quality R:FR microsites dominate shaded sites and high-quality R:FR microsites dominate gaps. Another study by Capers and Chazdon (2004) found R:FR in La Selva, Costa Rica to average 0.41 in the understorey. In contrast, our study examined R:FR spatially, and we found striking differences among forest types, as well as vertical partitioning of the light environment (Figure 1). Given that native canopy species prefer high-light conditions (Burton, 1982; Drake, 1993; Drake & Mueller-Dombois, 1993), and native Hawaiian rainforests contain higher light environments than their continental counterparts with up to five times greater per cent light transmittance (McDaniel & Ostertag, 2010; Pearcy, 1983), we hypothesized that the native-dominated forests would have higher quality light environments, and correspondingly would have greater amounts of seedling regeneration.

While there is a clear progressive decrease in light quality, as estimated by R:FR, between the native-dominated, partially invaded and *P. cattleyanum*-dominated forests (Figures 1 and 4), the seedling findings are more complicated and do not fully support our

TABLE 2 Results of a linear mixed effects model testing differences in R:FR (square root-transformed) among forest types, with site as a random effect.

Factor	SS	MS	NumDF	DenDF	*F* value	*p* value	AIC	LRT	df	*p* value
Forest type	0.815	0.408	2	9	23.685	<0.001				
Site							−869.23	36.444	1	<0.001
Parameter	**Coefficient**	**95% CI lower/upper limit**	***t* value**	***p* value**	**Effects**	**Group**	**SD coefficient**	**SD coeff 95% CI upper/lower limit**	**Fit**	
Intercept	0.54	[0.49, 0.58]	24.2	<0.001	Fixed		−0.7	[−0.97, −0.43]		
Forest type (native)	0.22	[0.15, 0.28]	6.89	<0.001	Fixed		1.32	[0.94, 1.69]		
Forest type (partial)	0.13	[0.07, 0.19]	4.1	<0.001	Fixed		0.78	[0.41, 1.16]		
	0.04				Random	Site				
	0.13				Random	Residual				
AIC									−867.78	
AICc									−867.7	
BIC									−844.62	
R^2 (conditional)									0.34	
R^2 (marginal)									0.28	
Sigma									0.13	

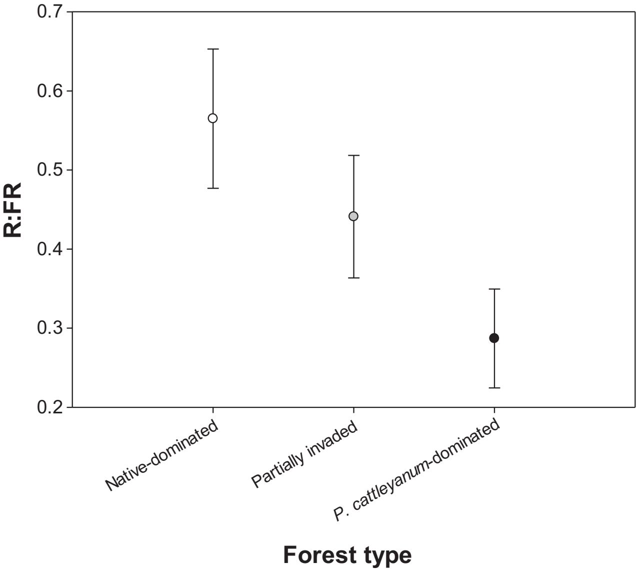

FIGURE 3 Estimated marginal means and 95% CI for a linear mixed-effect model with site as a random factor, to test differences in R:FR among forest types. Letters that are different indicate statistical significance with a post hoc test.

hypothesis. In native-dominated forest sites, there were more native and non-native seedlings in the low-quality microsites than would be expected by chance, with many high-quality microsites unoccupied (Figures 4 and 5). Similarly, there were more native seedlings than expected in the low-quality microsites in the partially invaded forests. We do not know if those low-quality sites represent a 'preference' by seedlings, because our study was a snapshot that did not follow seedling success over time. In addition, we do not know the R:FR at which a given seedling first germinated and established, and seedlings in a taller height class may provide some shade for those in shorter height classes. However, in these three forest types, the relationship between R:FR category and height class was inconsistent (Table S1). Collectively, these data suggest that light quality cannot fully explain seedling establishment, and we need to examine other factors such soil conditions, microclimate, competition and seed availability (Beckman & Rogers, 2013; Denslow et al., 2006).

In the context of maintaining native species within HLWF, several possibilities should be considered. The first is that the predominance of seedlings in the low-quality microsites could be an ecological trap (Robertson & Hutto, 2006), in which seedlings are mismatched into an environment for which they are less suited (Najberek et al., 2020). Second, the native-dominated forest had 3.5 times more native seedling individuals (Table 2) and 2.8 times more native species/morphospecies richness (Figure 6) than did the partially invaded forest. This difference in native species is due to the forest composition—partially invaded sites tend to have only support native remnant canopy trees, while the native-dominated sites support native understorey, sub-canopy and canopy species (Zimmerman et al., 2008). While there is no solid documentation for us to know when each site became infiltrated by invasive species, variation in the abundance and life forms of invasive species

TABLE 3 Results of a linear mixed effects model testing differences in coefficient in variation (CV, log-transformed) among forest types, with site as a random effect.

Factor	**SS**	**MS**	**NumDF**	**DenDF**	***F* value**	***p* value**	**AIC**	**LRT**	**df**	***p* value**
Forest type	0.132	0.066	2	9	0.502	0.621				
Site							677.07	36.298	1	<0.001
Parameter	**Coefficient**	**95% CI lower/upper limit**	***t* value**	***p* value**	**Effects**	**Group**	**SD coefficient**	**SD coeff 95% CI lower/upper limit**	**Fit**	
Intercept	1.11	[0.99, 1.23]	18.14	<0.001	Fixed		−0.05	[−0.37, 0.27]		
Forest type (native)	−0.01	[−0.18, 0.16]	−0.15	0.882	Fixed		−0.03	[−0.48, 0.42]		
Forest type (partial)	0.07	[−0.10, 0.24]	0.78	0.434	Fixed		0.18	[−0.27, 0.63]		
	0.1				Random	Site				
	0.36				Random	Residual				
AIC									654.02	
AICc									654.1	
BIC									677.2	
R^2 (conditional)									0.08	
R^2 (marginal)									0.0081	
Sigma									0.36	

TABLE 4 Observed (and expected) number of seedlings under each of the three R:FR categories representing low-, medium- and high-quality light microsites, for both native (a) and non-native (b) seedlings. Observed values are summed from the three different replicate sites within each forest type (native-dominated, partially invaded and *Psidium cattleyanum*-dominated). Results of G test of goodness-of-fit with the expected values (in parentheses) based on the proportion of microsites found in each forest type are shown.

(a) Native seedlings	R:FR category		
Forest type	≤0.40	0.41–0.70	≥0.71
Native-dominated	151 (95.4)	211 (233.3)	99 (132.3)
$G=38.837$, df $=2$, $p=3.687\times10^{-9}$			
Partially invaded	50 (33.2)	34 (47.8)	4 (7.0)
$G=13.19$, df $=2$, $p=0.001367$			
P. cattleyanum-dominated	0	0	0
No statistics needed			
(b) Non-native seedlings			
Forest type	≤0.40	0.41–0.70	≥0.71
Native-dominated	209 (183.4)	415 (448.3)	262 (254.3)
$G=6.5028$, df $=2$, $p=0.03872$			
Partially invaded	583 (618.0)	902 (887.8)	150 (129.2)
$G=6.1888$, df $=2$, $p=0.0453$			
P. cattleyanum-dominated	462 (463.2)	118 (123.0)	20 (13.8)
$G=2.6517$, df $=2$, $p=0.2656$			

is clearly seen among the sites, and site was a significant random effect in statistical models (Tables 2 and 3). Third, seedling presence itself could influence the light availability to other seedlings and this factor was not accounted for in this study. And finally, although medium- and high-quality microsites should have native seedlings present, we found that a large proportion of these sites were unoccupied (Figure 5). This absence may be explained by the lack of seed availability in some of these forests, including seed predation (Shiels & Drake, 2011). The fact that it is possible to have a fair number of native seedlings in low-quality microsites but still have open medium- and high-quality microsites (e.g. KI_10.5) or have very few native seedlings even though there is native vegetation (e.g. PK_1) is enigmatic (Figure 4). It is also noteworthy that there is considerable variation among sites, even within a forest type (e.g. PK_1 and PK_2 stand out within their forest type; Figure 4), and site was a significant random effect. These results suggest that there may be an under-developed regeneration niche in both native-dominated and partially invaded forests, and that this niche could be exploited and enhanced with careful and selective management, but that site differences are also important to consider.

Importantly, the light environments favoured by native species were also the environments favoured by non-native species. As others have noted, hot spots of native plant diversity, which are likely due to favourable abiotic conditions, may also be hot spots for invasive species (Questad et al., 2012; Stohlgren et al., 1999). Seedling presence in a given microsite may stem in part from protection from environmental conditions. High-light environments may experience stressful microclimatic conditions, which could be even more pronounced near the ground. For example, when comparing humidity between treefall gaps and the forest understorey, Schultz (1960) found that differences between 10 cm and 1.5 m above-ground were as great as those between 1.5 m and above the canopy, and found vast differences in air and soil temperature near ground level. Given that the lava-based substrates in HLWF are very porous, and droughts occur every 1.5–3 years (Michaud et al., 2015), seedlings may be congregated in areas that are less prone to soil desiccation and extreme daytime heating. In addition, Hawaiian forests are also prone to seed predation and herbivory by invasive animals such as rats and slugs (Joe & Daehler, 2008; Shiels & Drake, 2011) and soil disturbance by ungulates (Cole & Litton, 2014). Given the many factors that can influence seedling germination and establishment (e.g. soil moisture, soil nutrients, topography, competition and invasive animals), further examination of how R:FR influences seedlings directly is warranted.

This study focused on the seedling establishment stage, and there are likely differences in light requirements necessary for germination versus seedling establishment, as seen in tropical forests elsewhere. The R:FR at forest floor is a key determinant in breaking dormancy in certain seeds and provoking germination. For example, canopy gaps can alter the R:FR in such a way that the germination of pioneer species such as *Cecropia* is encouraged (Vásquez-Yanes & Orozco-Segovia, 1990). In addition, some large-seeded shade-tolerant species can often germinate successfully under low-light conditions but require a light gap to reach reproductive maturity (Amezquita, 1998). The light quality requirements for Hawaiian species are less understood. A study by Drake (1993) showed that the seeds of ʻōhiʻa (*Metrosideros polymorpha*), the dominant native tree species in HLWF, germinate more readily in red (650 nm) versus far-red (750 nm) light (i.e. they prefer high-quality light environments) and germinate poorly in the dark (low-quality light environments). Furthermore, germination was twice as rapid in intermediate temperatures (22°C) versus high (34°C). While the correlation between temperature and R:FR is not known in HLWF, future research could examine temperature effects and R:FR requirements on both germination and seedling establishment in Hawaiian lowland wet forest species.

4.2 | Using R:FR to guide restoration actions

In most studies, understorey light environments are examined by measuring light transmittance, or the fraction of photosynthetic photon flux density (PPFD) in the understorey, relative to PPFD in

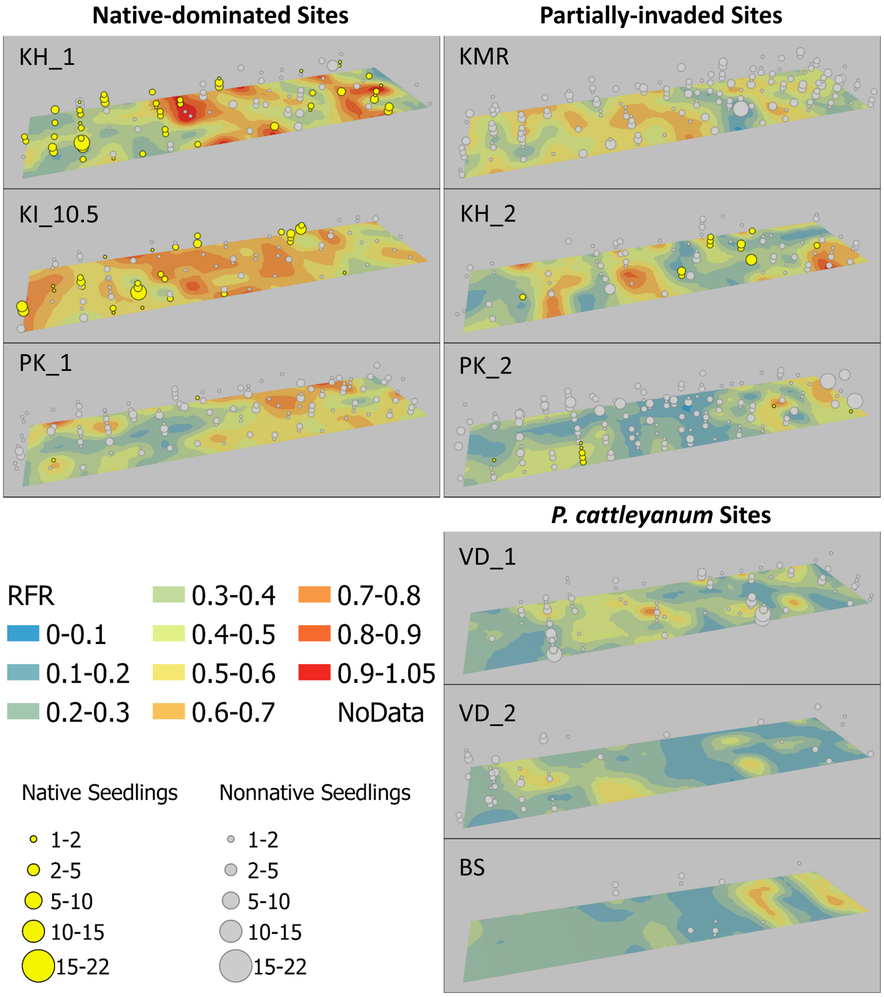

FIGURE 4 Native (yellow) and non-native (grey) seedling counts measured at five different heights for each site, plotted over a two-dimensional representation of the R:FR values estimated at the forest floor via Empirical Bayesian Kriging.

the open (Chazdon & Fetcher, 1984). While this method is useful to understand how stand composition influences understorey light, measurements taken on either clear or overcast days provide variable results (Messier & Puttonen, 1995) and require the use of paired-sensors, one which measures understorey conditions and another that measures 'open' conditions, either in a clearing or on a tower above the canopy, often difficult to obtain in the field. Other methods such as hemispherical photographs also present challenges, including requiring suitable sky and weather conditions, subjectivity in analysis and its inability to accurately depict light conditions in low light ranges (Roxburgh & Kelly, 1995). Due to the nature of conditions in HLWF, these tools for measuring per cent light transmittance are not ideal, while measuring R:FR allows for an opportunity to relate the differences in forest types to light quality. Because plants absorb most of the red wavelengths of light available to them in photosynthesis and reflect or transmit most of the far-red light, nearby plants (e.g. invasive species in high densities) reduce the amount of red light available at and just above the forest floor. Additionally, R:FR will decrease as the density of plants in the mid- and upper-canopy increases, indicating competition for light resources in these understorey and midstory niches. In this study, the vegetation influenced the light environments in the different forest types, as well as considerable variation among sites (Figure 1, Table S2). The resource heterogeneity among sites may be an important driver of diversity (Bartels & Chen, 2010; Grubb, 1977).

From an ecological standpoint, the forest types vary in their conservation value. *Psidium cattleyanum*-dominated forests ultimately lack understorey vegetation altogether and form a dense and uniform canopy (see Barbosa et al., 2016; Huenneke & Vitousek, 1990; Zimmerman et al., 2008). Only a few relict *Metrosideros polymorpha* remained in the canopy or within 1 km of the site, and there was no native seedling regeneration. These forest types also contained only 16% of all total seedlings counted, and most of these seedlings belonged to only three species other than *P. cattleyanum* (*Ardisia elliptica*, *Clusia rosea* and *Zingiber zerumbet*), all of which are considered invasive in Hawai'i. The low-quality understorey environment combined with the high fecundity, long-lived seeds, soil seed bank and clonal growth of *P. cattleyanum* (Huenneke & Vitousek, 1990; Uowolo & Denslow, 2008) is creating an uninhabitable environment for native seedlings. In addition, this species is altering more than just light quality when it is present in dense monotypic stands. For example, *P. cattleyanum* has been shown to alter the water balance (Takahashi et al., 2010) and litter nutrient cycling (Enoki & Drake, 2017) of Hawaiian forests. Given the influence of this species on ecosystem processes and the lack of native vegetation in the *P. cattleyanum*-dominated sites, a new alternative stable state (sensu

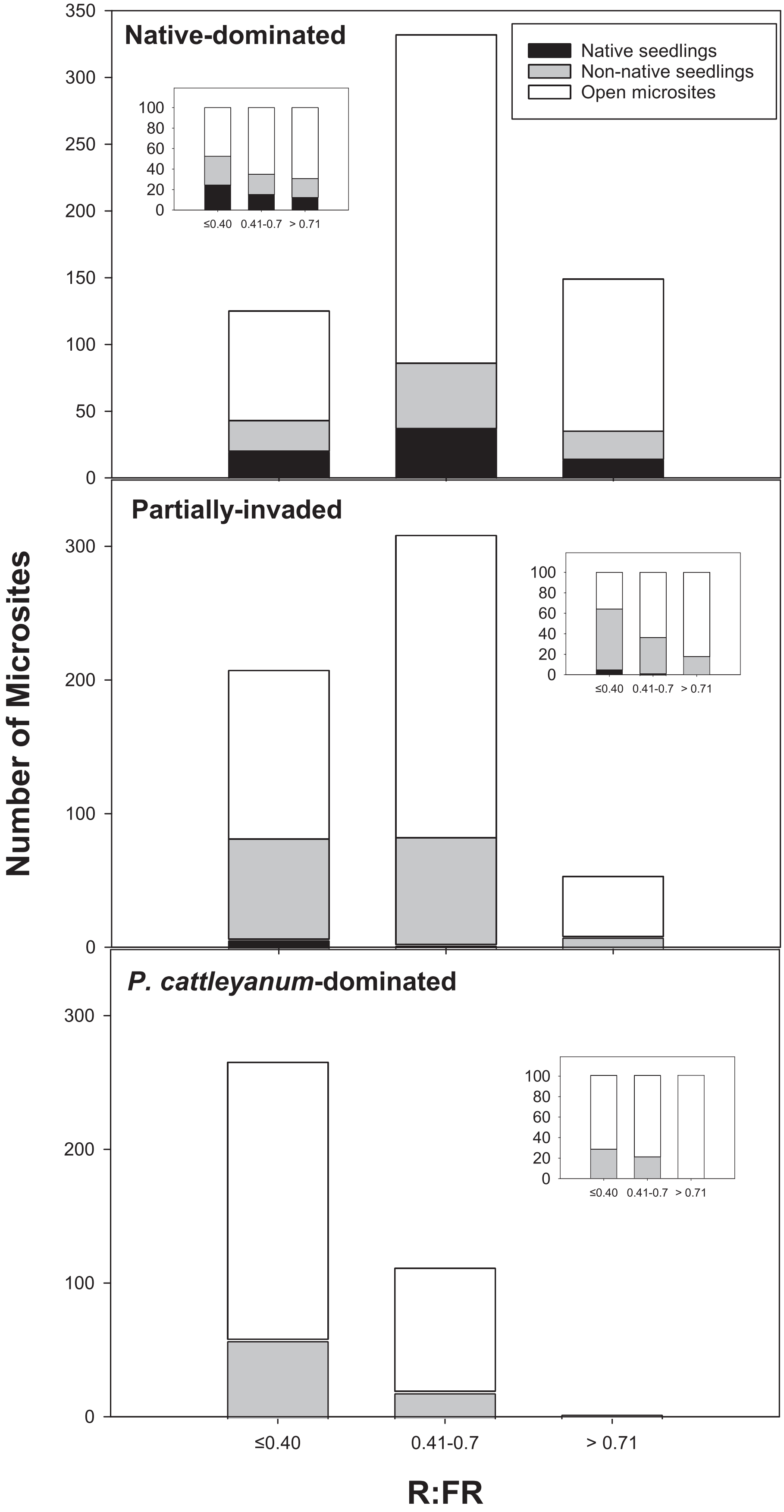

FIGURE 5 The abundance of microsites across the three R:FR levels and across forest types at ground level (0 cm height). Stacked bars show the number of native (black) and non-native (grey) seedlings, and the open areas represent microsites without seedlings. Insets show the percentages of microsites as a percentage.

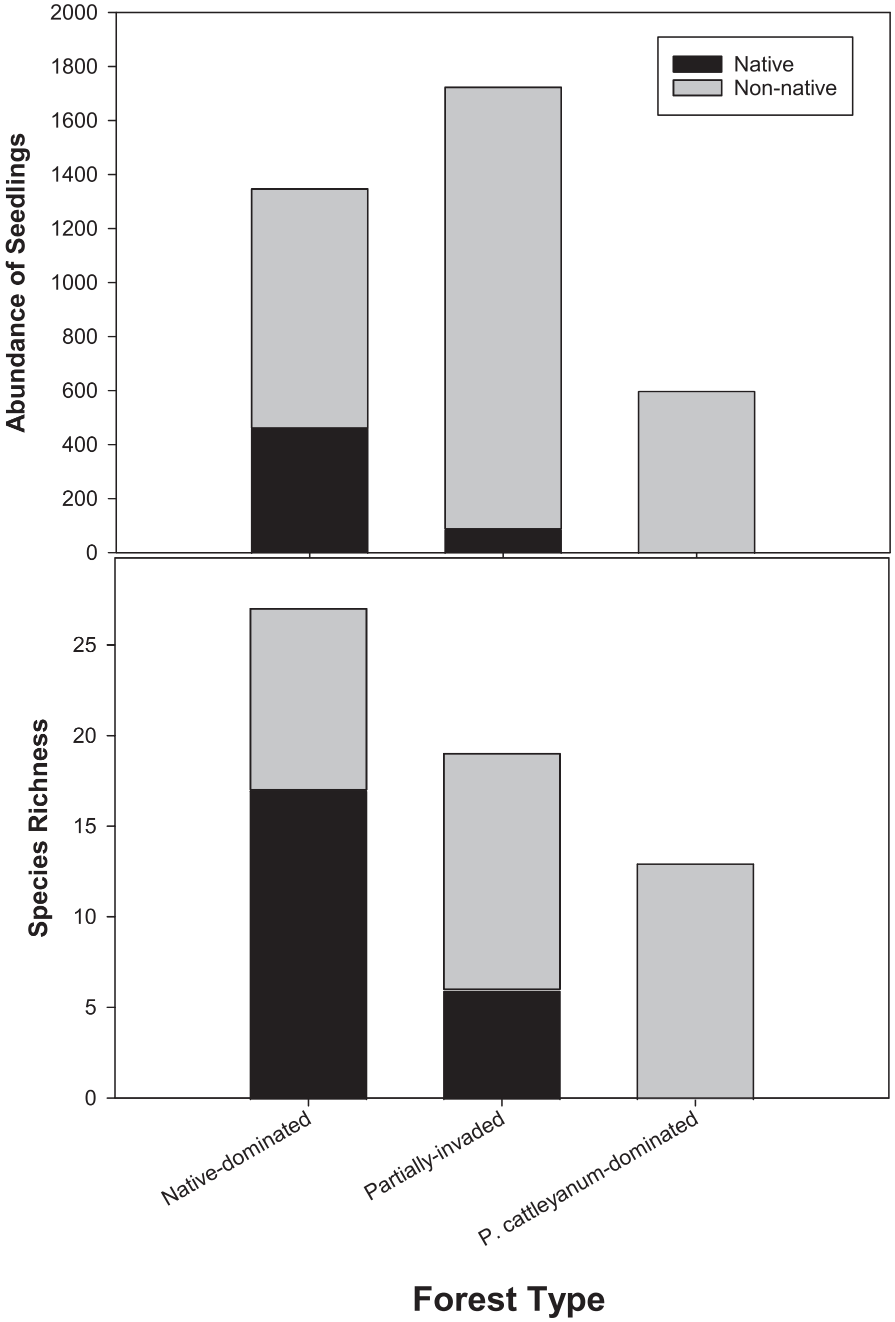

FIGURE 6 Abundance of native and non-native seedlings and the number of species/morphospecies of native and non-native seedlings across forest types. Seedling species/morphospecies described in Table S1. Refer to Table 4 to see abundance of seedlings in each light category.

Beisner et al., 2023) may have occurred that cannot be reversed without removal of this species. The restoration potential of this forest type is limited unless a major removal effort is undertaken. On the other hand, the native-dominated and the partially invaded forest types do hold conservation value. Based on our experience, neither of these forest types are likely in a stable state, but are constantly changing due to new propagule arrival and invasion. The partially invaded forests have been particularly maligned because previous research in HLWF has shown that, despite contributing to the seed rain, there are few native seedlings and saplings regenerating in them (Cordell et al., 2009; Kandert et al., 2021; Zimmerman et al., 2008). However, from a restoration standpoint, the partially invaded forests are not devoid of potential—they still serve as reservoirs of native biodiversity to some degree. Equally important to note is that the native-dominated forests can easily slip into the partially invaded category due to disturbances that open the canopy. In fact, two of the native-dominated sites have had major canopy decline since our sampling, likely due to proximity to volcanic gases from the 2018 lava flow, a fungal disease of the canopy dominant tree (Cannon et al., 2022), and ungulate damage.

Knowing the range of R:FR could allow managers to develop management actions. One possibility is that managers could pinpoint microsites suitable for seedling establishment, to conduct enrichment seeding or planting to increase native species regeneration. For example, the native-dominated sites are spatially autocorrelated in R:FR to the shortest distance, probably because the dominant native trees have a small canopy spread and higher understorey light levels in comparison to other forest types (Funk & McDaniel, 2010; McDaniel & Ostertag, 2010; Wong, 2006). Given the spatial autocorrelation in these forests, seedling additions could be targeted to different spatial scales and different R:FR environments, depending on the forest type. Planted microsites could be monitored for seedling relative growth rates, photosynthetic rates and survival, which could aid in native seedling regeneration and ultimately could be strategized to assist in native forest recovery. While this approach could possibly work, the lack of a strong relationship between R:FR and seedling number suggests that other factors besides light quality should be considered in any kind of seedling enrichment. Finally, in partially invaded forests, light quality above 40 cm was similar to that of native-dominated forests at ground level. These results could be interpreted to indicate that native seedlings are being hindered by low-lying non-native vegetation, and that if this vegetation were to be removed, it would result in a light environment conducive to successful establishment by native seedlings. Non-native vegetation could be selectively removed, allowing native seedlings to grow beyond the seedling stage and into small trees without creating too large of a gap that will hinder native seedling success, especially through competition with the seed bank (Cordell et al., 2009, 2016; Drake, 1998). R:FR could be measured before and after removal of invasive vegetation as a means to quantify the forest microsites. Managers will have to make decisions on the appropriate understorey interventions based on the health of the canopy, adapting their practices to leave the existing canopy trees, selectively remove understorey vegetation, outplanting and encourage already-present native seedlings.

This study aimed to use the patterning of light quality in the understorey of Hawaiian lowland wet forests to explain the lack of native seedling regeneration. While forests dominated by *Psidium cattleyanum* have poor light quality and native-dominated forests have high-light quality, we were unable to attribute native seedling regeneration patterns to light quality alone. Given evidence that seedling and sapling regeneration in these forests is light limited (Cordell et al., 2009; Kandert et al., 2021), light quantity could have been a useful parallel measurement. However, research should probably also be geared towards understanding other microsite conditions surrounding seedlings (local topography, substrate type, soil moisture, soil temperature and relative humidity), assessing propagule pressure and the interaction between the two components. For both invasive and native species, the interaction between seed establishment and microsite conditions plays a critical role in determining the future fate of partially-invaded forests (e.g. Colautti et al., 2006; Lockwood et al., 2005). Accurate understanding of how invasive species thrive in native environments, and the conditions necessary for native species to successfully reach reproductive maturity, is essential for the conservation of native biodiversity in Hawai'i and across tropical forest systems.

AUTHOR CONTRIBUTIONS

Jodie R. Rosam, Laura Warman and Susan Cordell conceived the ideas and designed methodology; Jodie R. Rosam collected the data; Jodie R. Rosam, Ryan Perroy and Rebecca Ostertag analysed the data; Jodie R. Rosam and Rebecca Ostertag led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interests to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.x95x69pt4 (Ostertag et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Frequency histograms of the red-to-far-red ratios (R:FR) in (a) native-dominated, (b) partially invaded and (c) *Psidium cattleyanum*-dominated forests. Light quality was categorized as low (≤0.40), medium (0.41–0.70) and high (≥0.71).

Figure S2. Number of individual seedlings found in the five height categories from the forest floor upwards in native-dominated, partially invaded and *Psidium cattleyanum*-dominated forests. Each point represents the total across three sites per forest type.

Table S1. Observed (and expected) number of seedlings under each of the three R:FR categories representing low-, medium- and high-quality light microsites, for six heights, for both native (a) and non-native (b) seedlings. Observed values are summed from the three different replicate sites within each forest type (native-dominated, partially invaded and *P. cattleyanum*-dominated). Results of *G*-tests of goodness-of-fit based on the proportion of microsites are shown.

Table S2. Results from the Incremental Spatial Autocorrelation geoprocessing tool to determine the distance corresponding to the maximum degree of spatial clustering for R:FR values measured near the forest floor. When $p \leq 0.05$ (in bold), and the Moran's Index values are positive, the R:FR values are more spatially clustered than would be expected by chance, that is, if underlying spatial processes were random. When no valid peaks were found, the Moran Index test was not significant. Site names for the native-dominated, partially invaded and *P. cattleyanum*-dominated forest types are shown in Table 1.

Table S3. Species present in seedling surveys across forest types (NAT = native-dominated, INV = partially invaded and PSI = *Psidium cattleyanum*-dominated). Origin indicates native (N), indigenous (I) or non-native (NN), status indicates Hawai'i endemic (HE) or endangered (E), and abundance is number of occurrences.

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