

**ASSESSMENT OF LIGHT QUALITY, VARIABILITY, AND SEEDLING  
PRESENCE IN HAWAIIAN LOWLAND WET FORESTS**

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## **Abstract**

Hawaiian lowland wet forest (HLWF) plant species are light-limited, yet no information exists on how the understory light varies in relation to species invasion, or if patterns of seedling regeneration and light are linked. I measured the red-to-far-red ratio (R:FR) of light to assess light quality and quantified diurnal variability in three forest types: native-dominated, partially-invaded, and fully invaded by strawberry guava (*Psidium cattleianum*). I asked: (1) how does understory light quality vary relative to invasion? (2) Are there differences in light quality moving vertically among forest types? (3) Are patterns of seedling regeneration and understory light related? Native-dominated forests had the greatest light quality (highest R:FR), and *Psidium cattleianum*-dominated forests had the lowest. While I predicted that native seedlings would prefer high-quality light sites, all seedlings preferred medium quality environments. In invaded HLWF, native seedling regeneration is hindered, and restoration efforts should focus on non-native understory removal.

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## **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 understory 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). Tropical lowland rainforest understory plants often receive less than 2% of available PAR (Chazdon & Fetcher 1984; Chazdon 1988; Montgomery & Chazdon 2001). Given these low PAR levels, seedling growth rates in dense tropical understories are slow because the quantity of light a plant receives is a fundamental regulator of the plant energy balance, photosynthesis, and other aspects of growth and development (Clark & Clark 1992).

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, understory plants in dense tropical rainforest understories receive low-quality light that is rich in far-red wavelengths and relatively poor in red ones (M  thy & Roy 1993; Li et al. 2001). While the ratio of red to far-red wavelengths (R:FR) is approximately 1.0 in unfiltered sunlight, this ratio is reduced under canopies to as low as 0.2-0.3 (Lee 1987; Daws et al. 2002). The R:FR is logarithmically related to leaf area index (Jordan 1969). Thus, it can be used to estimate percent transmittance, and can be a useful tool for measuring light quantity and quality in tropical understory environments when percent light transmittance is low (Capers & Chazdon 2004). R:FR is particularly useful when levels are too low for reliable hemispherical photograph analyses (Chazdon & Field 1987). Quantifying R:FR can provide a relative index of understory percent transmittance in addition to, or instead of, the use of paired quantum sensors and hemispherical techniques.

As well as light quantity and quality, the spatial and temporal patterning of light in dynamic tropical forest understories may provide insight into species composition and distribution. In these environments, sunflecks (i.e., brief periods of solar irradiance) contribute to the daily variation of light in the understory, as well as influence photosynthetic and growth rates of understory seedlings and saplings (Chazdon 1988 and references within). Depending on forest physiognomy, tropical understory light environments can range from quite uniform to highly

heterogeneous. This has many consequences, as the environment beneath and within low-lying vegetation is important for seedling growth and survival. Light quality in these understory environments is often low and potentially limits seedling success. Thus, the spatial and temporal patterning of understory light quality likely plays a vital role in the germination, establishment, photosynthetic rates, and growth rates of seedlings.

Within forest stands, the spatial variability of light in the understory is largely determined by canopy structure characteristics (including foliage distribution, species composition, and vertical and horizontal architecture), and plays a role in the distribution of understory species (Clark & Clark 1992). Most studies examining the variability in understory light environments have focused on the effects of canopy gaps, yet these gaps only represent around 25% of the area within forests (*sensu* Connell et al. 1997) and these studies neglect the forest structure that exists beneath the canopy. In tropical rainforests, the understory layer can intercept much of the remaining light, altering both the quantity of light a plant receives and the spectral quality this light (Messier et al. 1989; Lorimer et al. 1994; Messier et al. 1998; George & Bazzaz 1999). Thus, the structure and distribution of vegetation in the understory, sub-canopy, and canopy may regulate microsite environments and understanding these relationships may provide us with useful information regarding seedling recruitment and species distributions along the forest floor.

Light availability 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 in regard to photosynthetic rates and relative growth rates of both native and non-native species (Schulten et al. 2014). Native-dominated forests in Hawai‘i are typically more open than their tropical continental counterparts, and thus most native canopy species require relatively high light conditions for both germination and survival (Burton 1982; Drake 1993; Drake & Mueller-Dombois 1993). However, non-native species have infiltrated the understory and subcanopy in these forests. Many non-native invasive species have been found to be more efficient in light use than native species (Pattison et al. 1998), and non-native species are able to germinate and grow in low-light conditions.

The majority of remaining Hawaiian lowland wet forests are highly-invaded, and as a result, presents 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 (for example, see Cordell et al. 2009; Ostertag et al. 2009). In these forests, invasive understory and subcanopy plants are likely altering the light conditions important for native seedlings, and potentially occupying the “safe sites” that native plants would otherwise occupy. While percent light transmittance has been quantified in some examples of HLWF (Wong 2006; Funk & McDaniel 2010; McDaniel & Ostertag 2010), there is a knowledge gap regarding how the spatial and temporal distribution of light in the understory varies in relation to forest composition (native-dominated to fully invaded). It is also unknown whether patterns in seedling regeneration in HLWF are linked to spatial light patterning. The primary objectives of this study are: a) to quantify vertical patterns of light quality and diurnal patterns of light variability in the understory within and between native dominated, partially invaded, and non-native dominated HLWF, b) to compare vertical light quality differences at different heights above the forest floor, and c) to identify whether correlations exist between seedling presence and light quality.

## Materials and Methods

### STUDY SITES

I selected nine sites on the eastern (windward) side of Hawai'i Island, according to the predominance of native and non-native species at each site. Three sites each (Table 1) were designated as native-dominated, partially-invaded, or dominated by the invasive tree, *Psidium cattleianum*, based on site observations. According to altitude (<800 masl) and precipitation (>2500 mm annual precipitation), all sites are classified as lowland wet as defined by Gangé & Cuddihy (1999) and Price et al. (2007), and receive similar cloud frequency as estimated by Giambelluca et al. (2014).

### SPATIAL PATTERNS OF LIGHT QUALITY

For each of the three forest types (native-dominated, partially-invaded, and *P. cattleianum*-dominated), the collected light data (see 'data collection: light quality and quantity' for methods) was assigned local coordinates (x,y,z origin for each plot arbitrarily set at 100/100/0m). An empty 3D rectangular cuboid mesh grid covering the area of the collected data, with individual x,y,z cell dimensions (0.5 m x 0.5 m x 0.05 m) was created for each forest type. The cell values of this mesh grid were populated with interpolated light values via the "TriScatteredInterp" function (natural neighbor method) in MATLAB. For visualization purposes, 'slices' of the interpolated 3D light environment were extracted at 5 m spacing along the x-axis.

I examined semivariograms using Arc Map 10.2 to assess the degree of spatial autocorrelation at each height within each site. I used a lag distance of 5 m and an active lag of 12 m. In these analyses, the range is the distance on the x-axis at which the semivariogram curve stops increasing, and in terms of a spatial environment, this is indicative of spatial independence.

### DATA COLLECTION: LIGHT QUALITY AND QUANTITY

At each site, I established a 20 x 80 m plot with an internal grid system measuring 5 x 5 m (n=9; Figure 1). 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, 765 total), I took a series of 24 light quality measurements with a SKR 110 Red / Far-red sensor (SKYE Instruments, London, UK). The sensor mounted on a leveling 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. Thus the light environment was quantified in a 50 x 50 cm area. 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 I did find increased variability between windy and non-windy conditions, so experimental measurements were restricted to non-windy days.

An assessment of temporal variability was performed using gallium arsenide phosphide photodiodes (GaAsP, Hamamatsu Photonics K.K., Hamamatsu, Japan) individually wired to an analog relay multiplexer (Model AM416, Campbell Scientific Inc., Logan, Utah). These photodiodes were attached, in turn, to a datalogger (CR-1000, Campbell Scientific Inc., Logan, Utah) and powered by a 12 V deep cycle battery. Sensors were attached to nine metal stakes, arranged 3.5 m apart in a circular pattern, and haphazardly-placed at each site for >96 hours. Each sensor was leveled, and readings (in mV) were recorded in 30 sec intervals. During the sample period, weather conditions varied from sunny and dry to overcast and rainy, encompassing typical weather patterns in Hawai'i's lowland tropical rainforests. Because the focal unit of measurement for this study was diurnal variability rather than a quantification of total diurnal light transmittance, I did not compare in-forest readings to open-ground or above-canopy readings. Furthermore, while photosynthetic photon flux density, or PPF (units of  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), is the quanta equivalent measure of PAR (units of  $\text{W m}^{-2}$ ), their units are not directly convertible because of the difference in energy transferred by photons of different wavelengths. I attempted to correlate PPF to PAR output using linear regression, and though there was a significant relationship between the two ( $F_{1,101}=25.77$ ,  $p<0.0001$ ), the relationship was not strong ( $R\text{-sq}=20.5\%$ ). All sites were sampled between June and September, 2014, in order to minimize effects of seasonal differences in sun azimuth.

## SEEDLING PATTERNS

In addition to light, all seedlings (defined as having at least two true leaves) were measured within a 50 x 50 cm quadrat. All woody seedlings were identified to species, fern and grass species were grouped together as native or non-native, and tallied at 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.

## STATISTICAL ANALYSES

All statistical analyses were performed in R version 2.15.3. Two-way analysis of variance (ANOVA) was used to analyze mean R:FR values across forest types, heights, and the interaction of forest type and height. Tukey's post-hoc tests were used to further examine differences. Two-way ANOVA was also used to examine variability of R:FR within and across forest types and heights, using the coefficient of variation (CV) as the response rather than the raw R:FR values themselves.

I reduced the temporal data set to focus on the hours when the sun was at its highest point in the sky (from 1100-1400 hours) over three consecutive days (29,160 records per site). These values were used to examine temporal diurnal variability, and 1-way ANOVA was used to assess differences in diurnal variability across forest types (with CV as the response).

Two-way ANOVAs were also used to examine differences across the total number of seedlings, native seedlings, and non-native seedlings across forest types and within each height class. R:FR measurements were summarized into low (0.0 – 0.40), medium (0.41 – 0.70), and high quality ( $\geq 0.71$ ) categories based on histograms. I then looked for differences in seedling presence (total number of seedlings, native seedlings, and non-native seedlings) relative to R:FR category within forest type using chi-squared tests. I also attempted to identify a light quality 'threshold' at which seedlings (native, non-native, and grouped) are no longer able to survive using logistic regression, and identify the best model predicting seedling presence (including forest type, height, and R:FR) using generalized additive models (GAM; Zuur et al. 2014). In addition to total seedling presence, I identified eight primary species with the highest relative abundance across sites, linear regression was used to examine what relationships, if any, between the primary species and R:FR levels.

## Results

### SPATIAL PATTERNS OF LIGHT QUALITY

Light maps for both the vertical and horizontal profiles of light quality across forest types using interpolated values showed native forests have the most heterogeneity and more areas with high light quality. Meanwhile *P. cattleianum*-dominated forests tend to have homogeneously low quality light environments (Figure 2). More specifically, the vertical profile of native-dominated forests tends to have more areas of high quality light (24.1% of the points) than do partially-invaded or *P. cattleianum*-dominated forests (5.9% and 0.98%, respectively). For the most part, native-dominated forests also lack very low-quality sites. Partially-invaded forests have few light quality sites R:FR values greater than 0.71, but do have areas with very low light quality (0.1). R:FR in *P. cattleianum*-dominated forests were low quality for the most part (84.5%; Figure 3). Across sites, we found that the distance at which points were no longer spatially autocorrelated (range) fluctuated from 9 – 51m, with a median distance of 15m across forest types. There were no differences in range values across forest types or height above ground.

### LIGHT QUALITY ACROSS AND WITHIN FOREST TYPES AND HEIGHTS

Across forest types native-dominated forests exhibited the significantly greatest understory light quality (R:FR mean value=0.58), followed by partially-invaded forests (R:FR mean value=0.47; Table 2, Figure 4). *P. cattleianum*-dominated forests had the lowest quality of light, nearly 50% lower than native-dominated forests (R:FR mean value=0.31). While there were significant differences in R:FR across heights, there was no significant interaction between height and forest type (Table 2). The quality of light at ground level was always the poorest across forest types (R:FR mean value=0.38), and quality increased with height above ground (R:FR mean value=0.41 then 0.51 at 50 cm). In native-dominated forests, mean R:FR values from ground level to 50 cm ranged from 0.50-0.66, while partially-invaded forests ranged from 0.37-0.54. The light environment above 30cm in partially-invaded forests was similar to that of native forests at ground level and 10cm (R:FR mean value=0.49; see dotted line in Figure 4). *Psidium cattleianum*-dominated forests have homogeneously low light quality across heights (R:FR mean value at 0 cm=0.27 and at 50 cm=0.34).

## VARIABILITY IN LIGHT QUALITY ACROSS AND WITHIN FOREST TYPES

Light quality differed in its spatial variability across forest types (Table 2). Partially-invaded forests were the most variable (CV mean value=0.14); nearly twice that of *P. cattleianum*-dominated forests (CV mean value=0.08; Figure 5). There was no significant interaction between height and forest type, nor were there significant differences in the CV across heights (Table 2). It should be noted that while the *P. cattleianum*-dominated forests tended to be the least variable on average, they tended to show a different relationship between CV and height than native or partially-invaded forests. Native and partially-invaded forests showed a general trend of decreasing CV decreasing with increasing height above ground. However, in *P. cattleianum*-dominated forests, CV remained relatively constant (Figure 5).

The forest types also differed in their diurnal patterns ( $F_{2,8} = 8.8581, p \leq 0.0001$ ). Partially-invaded forests have approximately three times greater variability than either native or *P. cattleianum*-dominated forests (CV mean value=0.022 vs. 0.007 and 0.008, respectively; Figure 6). When considering all forest types and including light data for an entire day (0600-1800 hours), native-dominated forests have the greatest maximum mV values (942 mV) but the smallest range (594 mV, from 348 to 942 mV). Partially-invaded forests receive slightly lower maximums (928 mV) but display the greatest range (779 mV, from 149 to 928 mV), and *P. cattleianum*-dominated forests have the lowest maximum daily mV (840 mV) and an intermediate range (644 mV, from 197 to 840 mV; Figure 7). The opposite pattern was true in regard to CV; that is, *P. cattleianum*-dominated forests showed the most variability throughout the span of a full day (CV ranging from 0.04 to 0.71), while partially-invaded and native-dominated forests were somewhat less variable (CV ranging from 0.001 to 0.73 and 0.002 to 0.39, respectively; Figure 8).

## RELATIONSHIPS BETWEEN LIGHT QUALITY AND SEEDLING PRESENCE

Across sites, I measured 3641 seedlings from 40 different species (Table 3). Native-dominated forests had the greatest richness of native species, and partially-invaded forests had the greatest richness of non-native species (Figure 9). The majority of seedlings in the study plots (86%) were non-native, and the most common species recorded included *Ardisia elliptica* (shoebutton ardisia), *Oplismenus hirtellus* (basket grass), *Clidemia hirta* (Koster's curse), *Psidium cattleianum* (strawberry guava), and non-native ferns, namely *Nephrolepis multiflora* (sword

fern). I found 19 species of native seedlings, the most numerous of which were herbaceous *Peperomia* spp., as well as *Psychotria hawaiiensis* (kopiko) and *Metrosideros polymorpha* (‘ōhi‘a). One listed endangered endemic species, *Cyrtandra nanawalensis* (kanawao), was also present at one native site.

Overall, more native seedlings were present in native-dominated forests ( $F_{2,44}=8.9513$ ,  $p=0.0009$ ), and more non-native seedlings were in partially-invaded forests ( $F_{2,44}=8.0407$ ,  $p=0.001$ ). No native seedlings were measured in any *P. cattleianum*-dominated forests. When considering all seedlings (both native and non-native), I observed significantly fewer seedlings in forests dominated by *P. cattleianum* (618 seedlings) ( $F_{2,44} = 7.5705$ ,  $p=0.0021$ ), with no differences in the number of seedlings found in either native-dominated (1357 seedlings) and partially-invaded forests (1723 seedlings). Furthermore, across forest types, most seedlings tended to be smaller; nearly three times more seedlings were below 10 cm tall (1245 seedlings) than compared to 41-50 cm tall (408 seedlings) (Figure 10).

Most seedlings (both native and non-native) were present in medium quality microsites (1692 seedlings), followed by low quality (1471 seedlings), and the fewest in high light quality microsites (535 seedlings) ( $\chi^2=629.554$ ,  $df=4$ ,  $p<0.0001$ ; Table 4). Native seedlings also followed this trend ( $\chi^2=23.818$ ,  $df=2$ ,  $p<0.0001$ ), as did non-native seedlings (1435 versus 1254 and 1321 seedlings, respectively) ( $\chi^2=623.952$ ,  $df=4$ ,  $p<0.0001$ ). *Psidium cattleianum*-dominated forests tended to have more seedlings than expected in low quality light environments but fewer in medium and high quality light environments (based on chi-squared analyses). In native-dominated forests, I also measured fewer seedlings than expected in low quality environments and more in medium and high quality ones. Partially-invaded forests tended to have more seedlings in the medium quality microsites than expected and fewer in high and low quality (Table 4). I observed a similar pattern when following the dominant woody seedling species. The majority (45%) were found in medium quality microsites, followed by 40% in low and only 15% in high quality microsites (Figure 11). The dominant native seedling species were often found in the medium quality category rather than in low or high quality microsites (166 seedlings versus 84 and 76, respectively). This pattern was also found in non-native seedlings, although the contrasts across light quality categories were less pronounced: many seedlings were found in medium quality or low quality conditions (1058 and 983, respectively), while few (322) were found in the high quality conditions. Because the relationship between seedling presence

(regardless of species or origin) and light quality was not linear, I was unable to fit logistic regression models successfully. It should also be noted that the best fit model of seedling presence included forest type, height, and R:FR, this model had a very low  $R^2$ -value (2.2%), and the deviance explained by the model was only 1.9%.

When considering the height classes of the dominant species, nearly 60% of seedlings were 0-30 cm tall, and favored the low and medium light quality categories within the height classes. Few native seedlings (<1%) were over 30 cm tall. A similar pattern existed among the non-native seedlings, although the drop in taller seedlings was less drastic. Over 75% of the non-native seedlings reached up to 30 cm, and the other 46% were distributed equally than across the remaining height classes. I did not find any patterns between the dominant seedling species and R:FR values, as linear regression models had extremely low  $R^2$ -values, ranging from 0.15-2.6%.



## Discussion

### RELATIONSHIPS BETWEEN SEEDLING PRESENCE AND LIGHT QUALITY

Previous research in HLWF has shown that, despite contributing to the seed rain, native species do not regenerate in partially-invaded forests (Cordell et al. 2009). Given that native canopy species prefer high light conditions (Burton 1982; Drake 1993; Drake & Mueller-Dombois 1993), and native Hawaiian rainforests are much higher-light environments than their continental counterparts (with up to five times greater percent light transmittance; Pearcy 1983; McDaniel & Ostertag 2010), I hypothesized that the low light quality in the understory of partially-invaded forests may inhibit seedling regeneration, either at the germination or establishment stage. However, the data from this study suggest a different scenario. I found that a greater proportion of all seedlings (both native or non-native) were found in sites where R:FR values correspond to medium light quality levels, and few seedlings were found in high quality environments (Figure 12). While 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 dominate shaded sites, and high quality R:FR dominate gaps, and another by Capers and Chazdon (2004) found R:FR in La Selva, Costa Rica to average 0.41 in the understory. In addition, I did not find the predicted positive linear relationship between R:FR and seedling presence. Importantly, results also show that the light environments favored by native species (like those found in native-dominated and partially-invaded forests) were also the environments favored by non-native species. As others have noted, hotspots of native plant diversity, which are likely due to favorable abiotic conditions, may also be hotspots for invasive species (Stohlgren et al. 1999, Questad et al. 2012).

The preference of all seedlings for medium-quality sites may stem in part from protection from environmental conditions. Although tropical rainforests are not usually considered to be water-limited environments, they do exhibit seasonal variation in rainfall (Windsor 1990) and occasionally experience drought conditions (Walsh & Newberry 1999; Allen et al. 2010). Droughts (defined as periods during which soil moisture remains below a threshold) have been found to occur every 1.5-3 years in HLWF, (Michaud et al. *in press*), and to reoccur at 2-year intervals in rainforests in Panama (Engelbrecht et al. 2007). Understory soil desiccation during drought conditions can be detrimental to seedlings not adapted to handle low-water availability.

High-light environments may experience a different microclimate than those with medium or low light conditions, and this difference may be even more pronounced near the ground. For example, when comparing humidity between treefall gaps and the forest understory, 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 water availability varies seasonally in HLWF (Michaud et al. in press), and lava-based substrates are very porous, these findings may reflect that seedlings prefer microsites with limited sun exposure and therefore less prone to soil desiccation. While Hawaiian rainforests do not experience treefall gaps as often as do other tropical rainforests, gaps related to canopy openness or to disturbance likely create a treefall gap-like environment that seedlings must endure. Regardless, it would be worthy to examine not only the effects of gaps on the R:FR environment near the ground, but also the intensity of light received, as well as soil moisture conditions.

While resource quantity (and in this case light quality as well) is often an important driver of species composition within a forest (Davis et al. 2000), resource heterogeneity (Grubb 1977) is also thought to explain plant diversity. There is general consensus among ecologists that resource availability can influence plant establishment, but the role of spatial and temporal resource heterogeneity within a forest has received less attention. In the case of partially-invaded lowland wet forests, species that are able to withstand variability in light and soil resources are more likely to establish successfully than are species that depend on a given combination of resources (both on spatial and temporal scales). A synthesis by Bartels and Chen (2010) found that the resource heterogeneity hypothesis was more commonly associated with old growth forest stands, probably as a result of the shift from resource limitation during succession (Chen & Popakiouk 2002). In this study, partially-invaded forests were the most variable (both spatially and temporally), and forests dominated by *P. cattleianum* were the least variable. The combination of a generally open native canopy and an abundance of understory vegetation within partially-invaded forests may lead to more opportunities for sunflecks and therefore increased light heterogeneity and greater overall light variability. On the other hand, *Psidium cattleianum*-dominated forests ultimately lack understory vegetation and have a very dense and uniform canopy. While native-dominated and partially-invaded forests were species rich and contained a high relative abundance of seedlings, *P. cattleianum*-dominated forests contained

few seedlings (only 16%), and the majority of these seedlings belonged to only four species (*Ardisia elliptica*, *Clusia rosea*, *Psidium cattleianum*, and *Zingiber zerumbet*). Because the most seedlings, both native and non-native, were present in the forests with more variability, I feel as though resource heterogeneity is a predictor of species distributions in Hawaiian lowland wet forests, in addition to resource quantity and the quality of these resources.

In addition to resource distribution, Hawaiian plant seeds and seedlings are also subject to predation by invasive species. A common canopy species, *Diospyros sandwicensis*, is rarely seen regenerating in the understory, due in part to predation of the large, fleshy fruits by the invasive black rat, *Rattus rattus* (Shiels & Drake 2011). Black rats have also been documented as dispersers of invasive species such as *Clidemia hirta* (Shiels & Drake 2011), and invasive mammals are not the only animal affecting native seedling growth and survival. Invasive slugs have been shown to negatively affect the survival of endangered and threatened plant species in Hawai'i (both herbaceous and woody species) through direct consumption of plant tissue (Joe & Daehler 2008). Non-native species were found to be less vulnerable to predation by slugs. It is possible invasive slugs could have affected the seedling census in this study, and further research into the presence of slugs and their effects on native seedling regeneration should be considered.

This study focused on the seedling establishment stage, and there are likely differences in light requirements found between germination and 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, large-seeded shade-tolerant species can often germinate successfully under low-light conditions, while small seeded species require some form of a gap or sunfleck to germinate. For example, Amezcua (1998) found that after one year, seedlings of *Psychotria aubletiana* were able to grow twice as tall in light gaps and gap edge conditions than were shaded seedlings. This genus like many others in tropical rainforests is able to germinate in the understory, but requires a light gap to reach reproductive maturity. The problem Hawaiian species face is that they are typically small seeded. For example, a study by Drake (1993) showed that the small seeds of the dominant native species *Metrosideros polymorpha* germinate more readily in red versus far-red light (that is, they prefer high quality light environments) and germinate poorly in the dark. Furthermore, germination was twice as rapid in intermediate

temperatures versus extremes; microsite environments potentially correlated to those of medium quality light. The deep shade cast by non-native vegetation may be inhibiting native species such as *Psychotria hawaiiensis*, a common understory and mid-canopy species, from reaching reproductive height. Future research could examine differences in R:FR requirements between germination and seedling establishment in native Hawaiian rainforest species.

## IMPLICATIONS FOR RESTORATION

I hypothesized that native regeneration was inhibited by the effects of understory non-native vegetation on light quality. In partially-invaded forests, light quality above 30cm 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. However, the results of the seedling study do not support this hypothesis because there was no significant relationship between seedling presence and light quality. Native seedlings may be more successful in native-dominated forests due to higher native propagule abundances in native-dominated forests. This could be tested using a reciprocal transplant experiment. In this study, all three of the *P. cattleianum*-dominated sites had few relict native *Metrosideros polymorpha* in the canopy or within 1km of the site, and seeds from *M. polymorpha* were reaching these forests (J. Rosam, personal observation). I suggest that the combination of a low light quality understory environment combined with the high fecundity and rapid growth rates of *P. cattleianum* could be creating an uninhabitable environment for native seedlings. Additionally, it should be noted that this forest type lacked non-native seedlings aside from *P. cattleianum* seedlings. It is likely that this species is altering more than just light quality when it is present in dense monotypic stands. For example, *P. cattleianum* has been shown to alter the water balance of Hawaiian forests. A study by Takahashi et al. (2010) documented a native-dominated forest to have twice the canopy water storage capacity and a 27% lower annual evaporation rate than a *P. cattleianum*-dominated forest. It should also be noted that if this study included invaded forests dominated by other species than *P. cattleianum*, relationships between spatial light quality and seedling presence may be different, depending on the canopy architecture and foliage distribution (as well as density) of the dominant invasive species.

While I hypothesized that there would be a ‘light quality threshold’ below which native seedlings are not able to survive, this was not the case. Identifying this threshold would have had significant importance from a restoration standpoint as it would have indicated that manipulating the light environment in the understory (i.e., maintaining light levels above that threshold) would allow for successful regeneration of native seedlings and thus greater restoration potential for invaded HLWF. However, our results indicate it may not be that simple. In this study, native seedlings favored mid-quality light environments, but these are also the environments preferred by non-native seedlings. As Stohlgren (2003) stated: “...non-native plant control efforts will have to be targeted and even more carefully conducted in areas of high native species richness.” It would make sense that if this non-native vegetation were 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, native seedling regeneration may be successful. The work of the managers will be to adapt their strategies from a more destructive first step for restoration practices to leaving the existing canopy trees and selectively remove understory vegetation prior to outplanting, or encouraging already-present native seedling success. One must be mindful, however, that creating open sites will also favor non-native species, as the dominance of the seed bank will enable non-natives to increase in abundance following site disturbance (Drake 1998). It is probable that herbaceous ferns were once much more abundant in the understory of native HLWF than they are today, and provided shade and drought protection to native seedlings. While the native fern species are no doubt less diverse today, a successful restoration technique may choose to focus on reintroducing some of these shade-producing native fern species prior to focusing on native tree species.

This study aimed to use the patterning of light quality in the understory of Hawaiian lowland wet forests to explain the lack of native seedling regeneration. While forests dominated by *Psidium cattleianum* did have poor light quality and native-dominated forests have high light quality, I was unable to attribute light quality alone to native seedling regeneration patterns. In terms of restoration, more focus should 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 (Lockwood et al. 2005, Colautti et al. 2006). If partially-invaded forests still harbor light conditions that can support native regeneration, managers may choose to focus on removing invasive understory vegetation to remove the direct competition for resources, as well as outplanting native seedlings into mid-quality light environments and monitoring their relative growth rates, photosynthetic rates, and survival. This technique may be preferred to the previous large-scale removal techniques, in which all non-native biomass is removed at one time, creating large forest gaps and disturbance that encourages invasion. Accurate understanding of how invasive species thrive in native environments, and the conditions necessary for native species to successfully reach reproductive maturity, is essential to preserving native biodiversity in Hawai'i and across tropical forest systems.

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Table 1. Site characteristics of nine lowland wet forest sites on the east side of Hawai'i Island

Site	Forest Type	Elevation (m)	* Mean Annual Precip. (mm)	Lava type	Flow age (yr)	Latitude (N)	Longitude (E)
Keauohana Forest Reserve	native-dominated	253	2800	'a'ā	200-400	19.250556	154.416944
Kipuka 10.5	native-dominated	790	5900	'a'ā	3000-5000	19.694444	155.518333
Pu'u Kali'u	native-dominated	298	3000	'a'ā with ash	500-750	19.450278	155.518333
Keaukaha Military Reservation	partially-invaded	15	3300	'a'ā	750-1500	19.703889	155.041667
Keauohana Forest Reserve	partially-invaded	253	2800	'a'ā	200-400	19.418056	154.951111
Pu'u Kali'u	partially-invaded	298	3000	'a'ā with ash	500-750	19.448889	154.926667
Lower Puna guava site (a)	<i>P. cattleianum</i> -dominated	10	3000	'a'ā	200-400	<i>contact author</i>	
Lower Puna guava site (b)	<i>P. cattleianum</i> -dominated	10	3000	'a'ā	200-400	<i>contact author</i>	
Lower Puna guava site (c)	<i>P. cattleianum</i> -dominated	310	3000	'a'ā	200-400	19.394167	154.996389

\* Mean annual precipitation derived from the Online Rainfall Atlas of Hawai'i. Giambelluca, T.W., Q. Chen, A.G. Frazier, J.P. Price, Y.-L. Chen, P.-S. Chu, J. K. Eischeid, and D. M. Delaporte, 2013: Online Rainfall Atlas of Hawai'i. Bull. Amer. Metero. Soc. 94, 313-316, doi: 10.1175/BAMS-D-11-00228.1.

Table 2. Results from 2-way ANOVAs testing for differences in a) red/far-red ratio (R:FR) and b) coefficient of variation (CV) among forest types (native-dominated, partially-invaded, and *Psidium cattleianum*-dominated) among heights (0, 10, 20, 30, 40, and 50 cm) and interaction

a) R:FR

Source	df	Mean square	F	<i>P</i>
Forest type	2	0.34208	88.15	≤0.0001
Height	5	0.02296	5.92	0.0004
Interaction	10	0.00167	0.42	0.9261
Error	36	0.00338		
Total	53			

b) CV

Source	df	Mean square	F	<i>P</i>
Forest type	2	0.192084	17.34	≤0.0001
Height	5	0.008262	0.75	0.5945
Interaction	10	0.003431	0.31	0.9738
Error	38	0.011079		
Total	53			

Table 3. Species present in seedling surveys across forest types (NAT=native-dominated, INV=partially-invaded, and PSI=Psidium cattleianum-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

Species	Forest type	Origin	Status	Abundance
<b>INDIGENOUS</b>				
<i>Cordyline fruticosa</i>	PSI	I		3
<i>Freycinetia arborea</i>	NAT, INV	I		3
<i>Pandanus tectorius</i>	INV	I		1
<b>NATIVE</b>				
<i>Acacia koa</i>	NAT	N	HE	2
<i>Alyxia oliviformis</i>	NAT, INV	N	HE	9
<i>Broussaisia arguta</i>	NAT	N	HE	1
<i>Cheirodendron trigynum</i>	NAT	N	HE	9
<i>Cibotium glaucum</i>	NAT	N	HE	5
<i>Coprosma ochracea</i>	NAT	N	HE	2
<i>Cyrtandra nanawalensis</i>	NAT, INV	N	HE, E	2
<i>Cyrtandra platyphylla</i>	NAT	N	HE	21
<i>Diospyros sandwicensis</i>	NAT	N	HE	4
<i>Metrosideros polymorpha</i>	NAT	N	HE	110
<i>Myrsine lessertiana</i>	NAT	N	HE	1
native ferns	NAT	N	HE	10
<i>Melicope clusiifolia</i>	NAT	N	HE	9
<i>Peperomia</i> spp.	NAT, INV	N		235
<i>Pipturus albidus</i>	NAT	N	HE	7
<i>Psychotria hawaiiensis</i>	NAT, INV	N	HE	43
<i>Vaccinium calycinum</i>	NAT	N		27
<b>NON-NATIVE</b>				
<i>Ageratum conyzoides</i>	NAT, INV	NN		83
<i>Albizia falcataria</i>	INV	NN		2
<i>Ardisia elliptica</i>	PSI	NN		156
<i>Begonia hirtella</i>	INV	NN		1
<i>Cecropia obtusifolia</i>	INV	NN		1
<i>Clidemia hirta</i>	NAT, INV, PSI	NN		573
<i>Clusia rosea</i>	PSI	NN		36
<i>Dioscorea pentaphylla</i>	NAT, INV, PSI	NN		105
<i>Ficus</i> spp.	PSI	NN		1
<i>Macaranga mappa</i>	INV	NN		11
<i>Melastoma</i> spp.	NAT, INV	NN		150
<i>Microlepidia strigosa</i>	INV	NN		55
<i>Nephrolepis multiflora</i>	NAT, INV	NN		153
non-native ferns	NAT, INV, PSI	NN		405
non-native grasses	NAT	NN		47
<i>Oplismenus hirtellus</i>	NAT, INV, PSI	NN		667
<i>Paederia foetida</i>	PSI	NN		44
<i>Psidium cattleianum</i>	NAT, INV, PSI	NN		509
<i>Psidium guajava</i>	PSI	NN		2
<i>Rubus rosifolius</i>	NAT	NN		3
<i>Zingiber zerumbet</i>	PSI	NN		133

Table 4. Number of expected and observed seedlings (from chi-square analyses) of (a), native seedlings (b), and non-native seedlings (c) in each R:FR category across forest types

<b>a) All Seedlings</b>	Observed			Expected		
	R:FR Category			R:FR Category		
<u>Forest Type</u>	<u>≤0.40</u>	<u>0.41-0.70</u>	<u>≥0.71</u>	<u>≤0.40</u>	<u>0.41-0.70</u>	<u>≥0.71</u>
Native-dominated	361	635	361	540	621	196
Partially-invaded	633	936	154	685	788	249
<i>P. cattleianum</i> -dominated	477	121	20	246	283	89

<b>b) Native Seedlings</b>	R:FR Category			R:FR Category		
	<u>≤0.40</u>	<u>0.41-0.70</u>	<u>≥0.71</u>	<u>≤0.40</u>	<u>0.41-0.70</u>	<u>≥0.71</u>
Native-dominated	151	211	99	169	206	86
Partially-invaded	50	34	4	32	39	16
<i>P. cattleianum</i> -dominated	0	0	0			

<b>c) <i>P. cattleianum</i>-dominated</b>	R:FR Category			R:FR Category		
	<u>≤0.40</u>	<u>0.41-0.70</u>	<u>≥0.71</u>	<u>≤0.40</u>	<u>0.41-0.70</u>	<u>≥0.71</u>
Native-dominated	209	415	262	356	407	123
Partially-invaded	583	902	150	657	752	226
<i>P. cattleianum</i> -dominated	462	118	20	202	90	48

**Figure 1.**

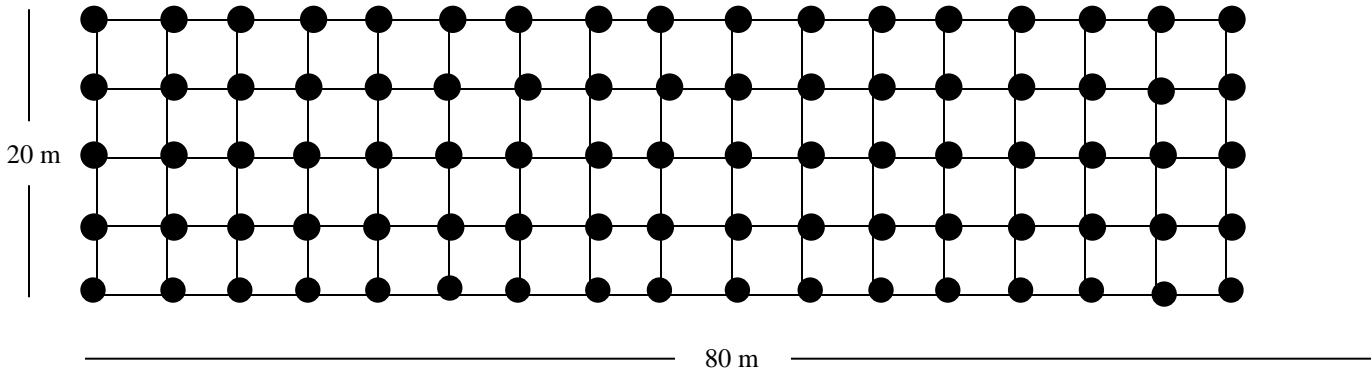


Figure 1. Layout of sampling grid at each site (circles represent sampling locations)

**Figure 2.**

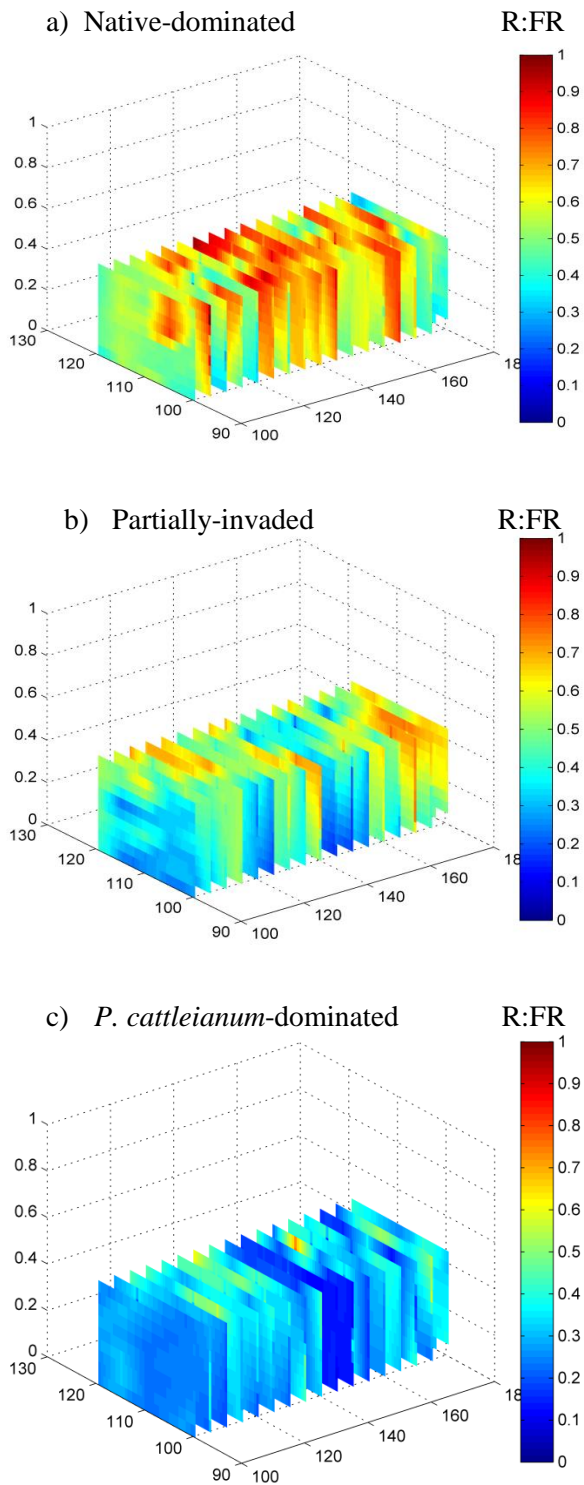


Figure 2. Interpolation of the average R:FR measurements of three sites per forest type: a) native-dominated, b) partially-invaded, and c) *P. cattleianum*-dominated. Maps were generated using kriging in MATLAB. Warmer colors indicate higher R:FR (higher light quality environment)



**Figure 3.**

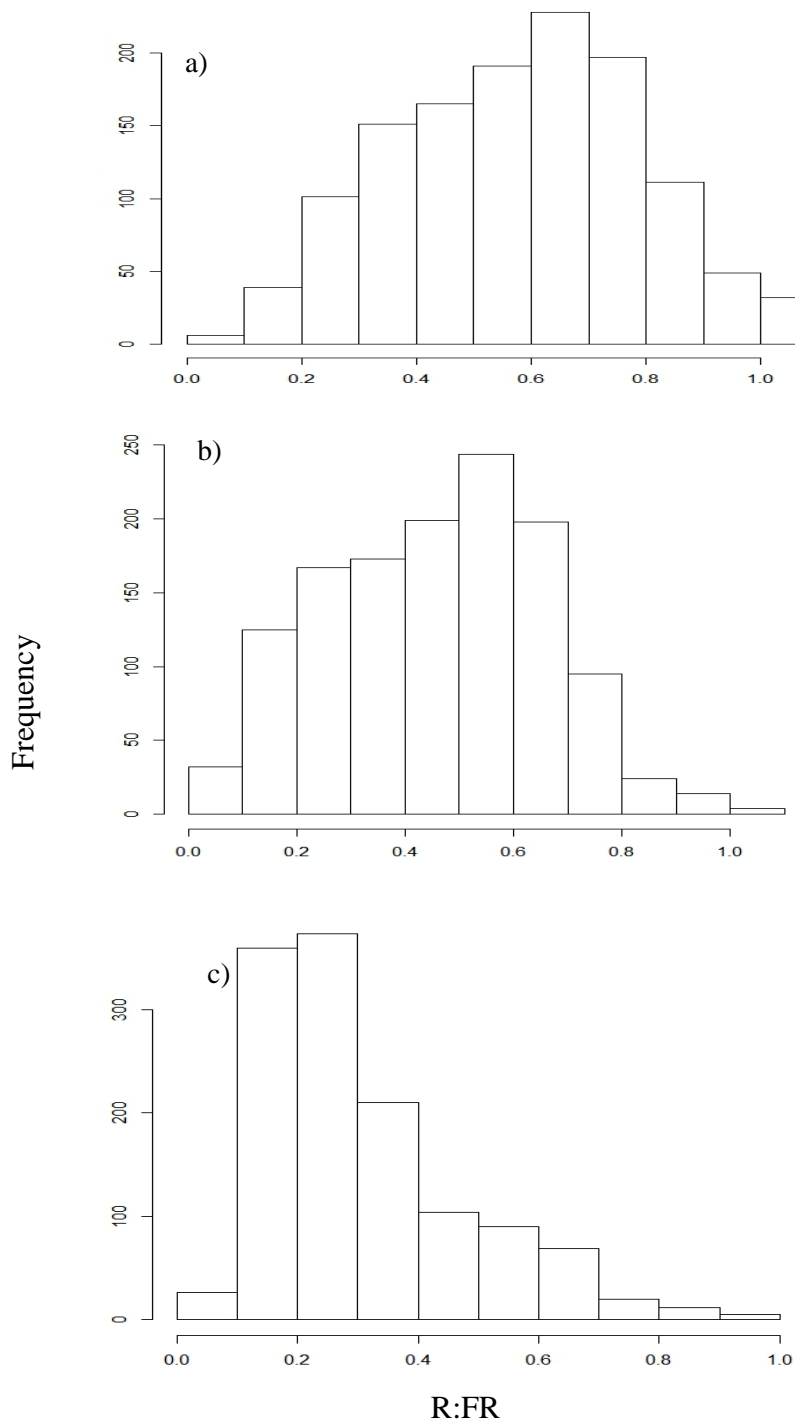


Figure 3. Frequency histograms of the red-to-far-red ratios (R:FR) in a) native-dominated, b) partially-invaded, and c) *Psidium cattleianum*-dominated forests. Light quality was categorized as low ( $\leq 0.40$ ), medium (0.41-0.70), and high ( $\geq 0.71$ )

Figure 4.

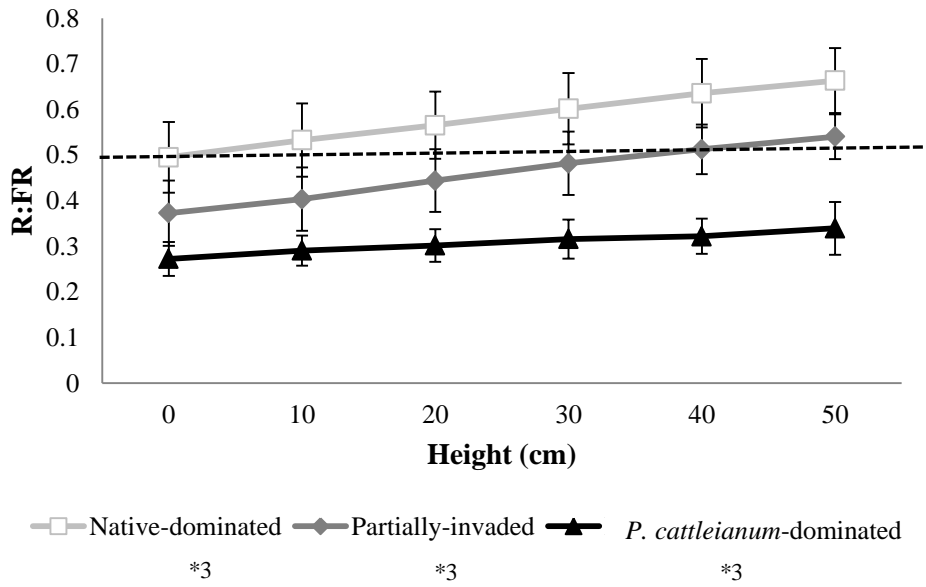


Figure 4. Interaction of red-to-far-red ratios (R:FR) and height above ground (cm) in native-dominated, partially-invaded, and *P. cattleianum*-dominated forests. Error bars represent standard deviation, asterisks (\*) represent number of replicates. Dotted line represents the baseline R:FR for native forests as a comparison

Figure 5.

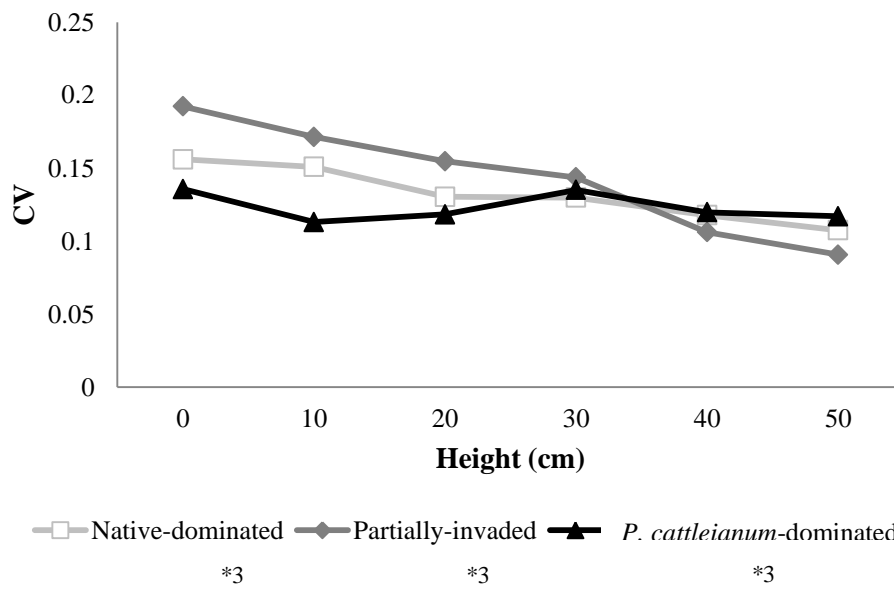


Figure 5. Interaction of the average coefficient of variation (CV) and height (cm) in native-dominated, partially-invaded, and *P. cattleianum*-dominated forests. Asterisks (\*) represent number of replicates

**Figure 6.**

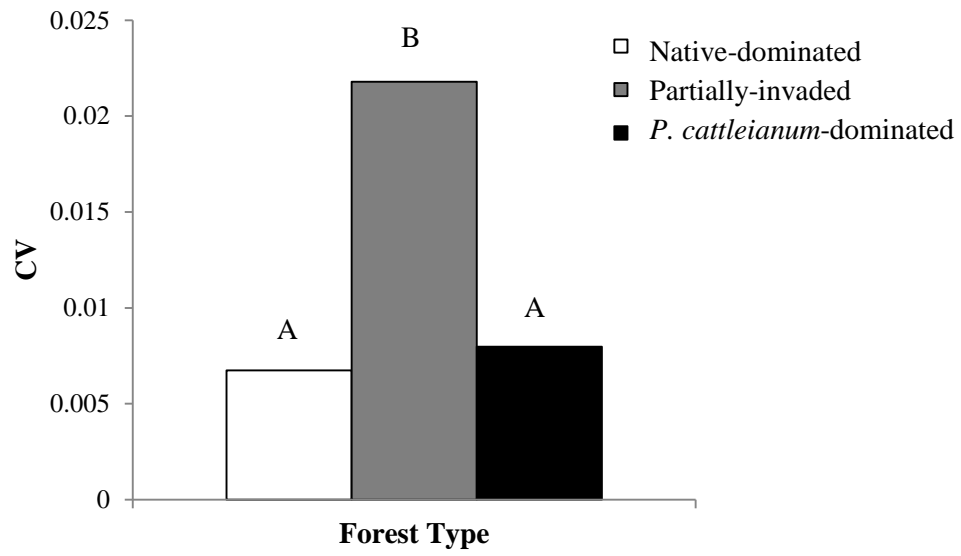


Figure 6. Diurnal variability (expressed as the coefficient of variation – CV) between 1100-1400 hours across forest types, averaged over three consecutive

Figure 7.

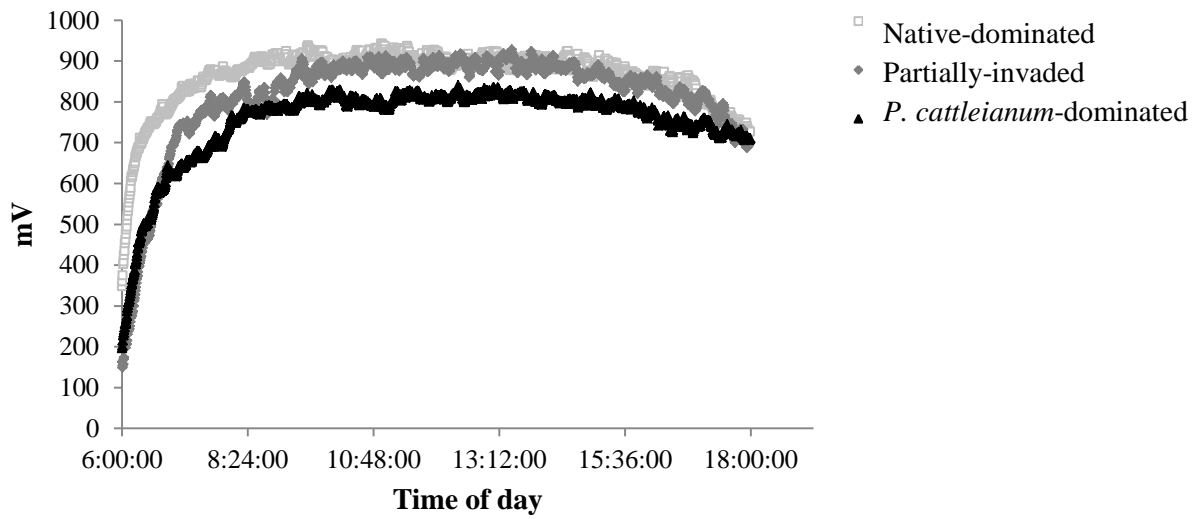


Figure 7. Average daily mV output in native-dominated, partially-invaded, and *P. cattleianum*-dominated forests

**Figure 8.**

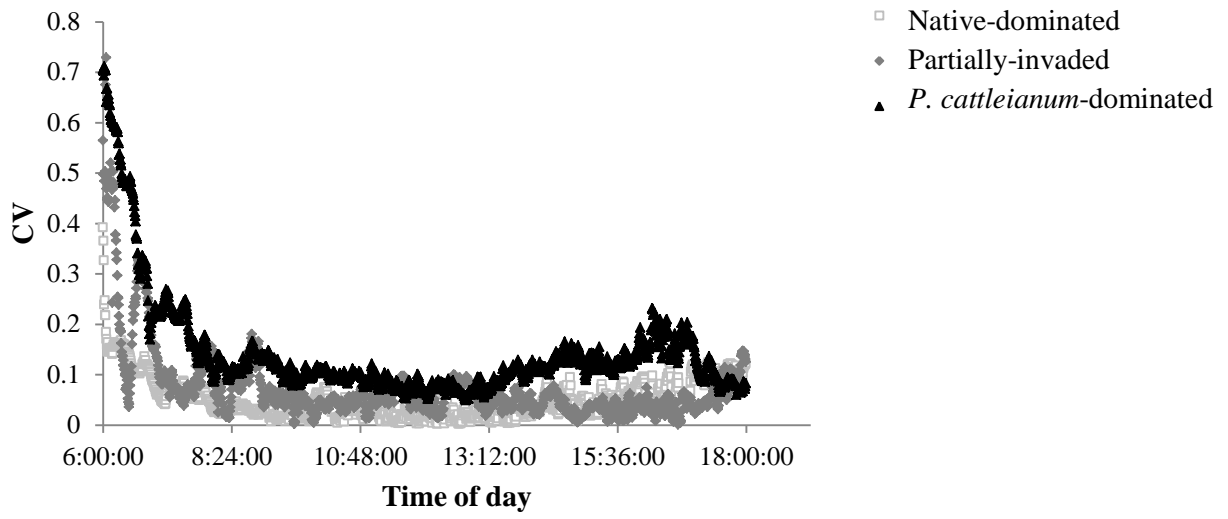


Figure 8. Average daily variation (CV) in native-dominated, partially-invaded, and *P. cattleianum*-dominated forests

**Figure 9.**

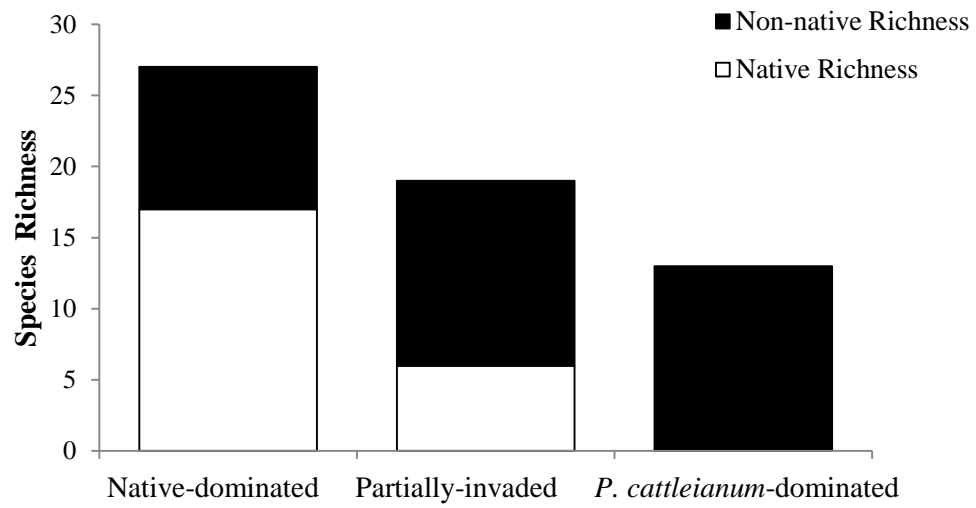


Figure 9. Species richness values native and non-native seedlings across forest types

Figure 10.

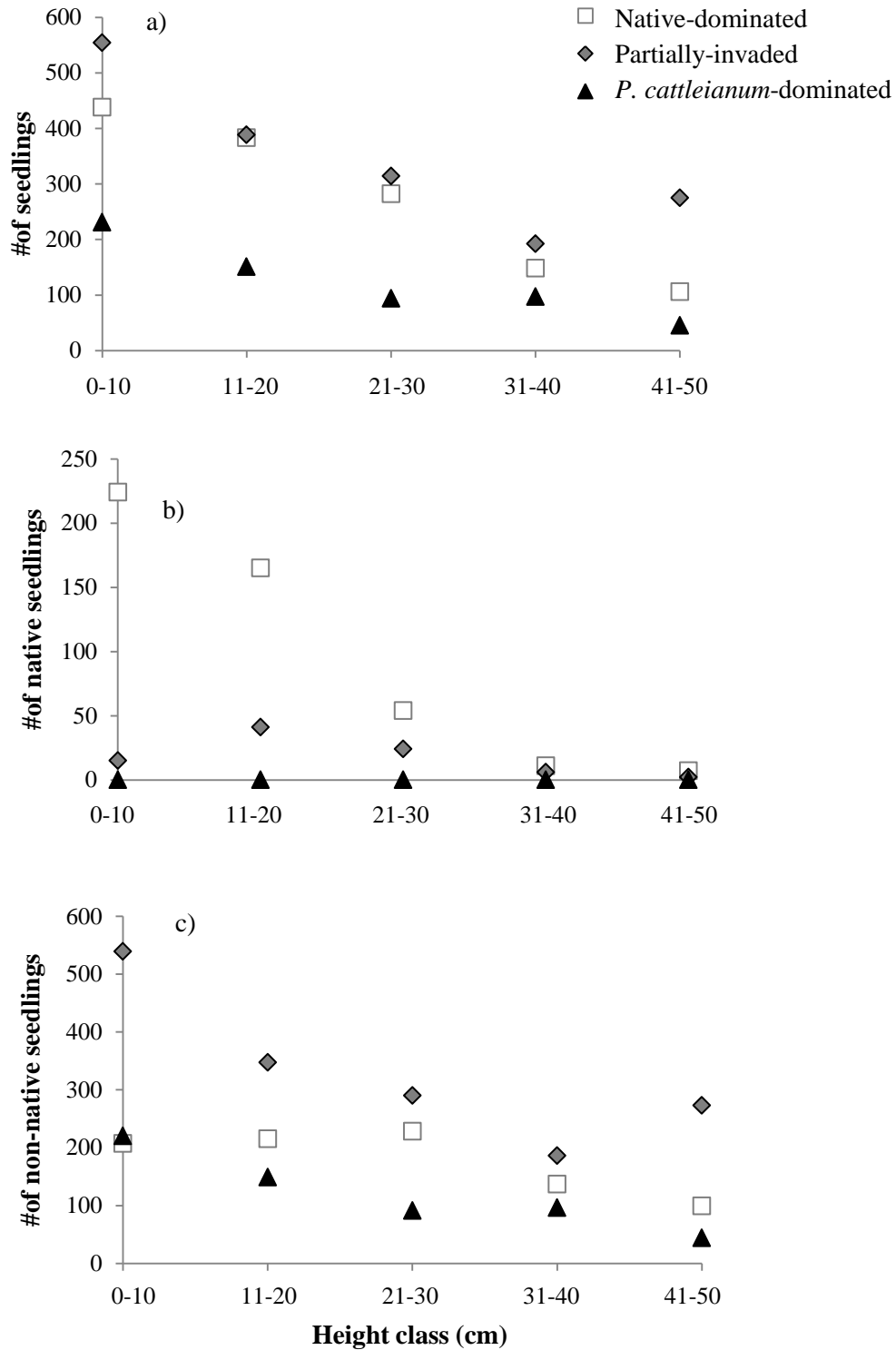


Figure 10. Number of a) all seedlings, b) native seedlings, and c) non-native seedlings in each height class across forest types



**Figure 11.**

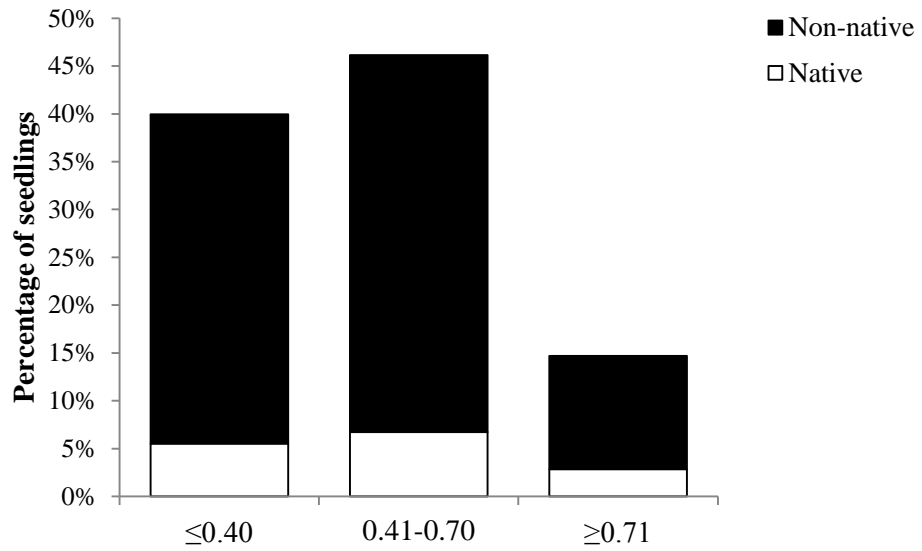


Figure 11. Percentage of native and non-native seedlings present in each red-to-far-red ratio category: low quality ( $\leq 0.40$ ), medium quality (0.41-0.70), and high quality ( $\geq 0.71$ )