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Decadal effects of thinning on understory light environments and plant community structure in a subtropical forest

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Abstract. Canopy-opening disturbance such as thinning has immediate and substantive effects on understory microclimate and therefore the establishment and growth of understory plants. A large number of studies have reported the effects of thinning on tree growth, but few studies have examined long-term effects of thinning on understory light environments and species and functional diversity of understory plants. Even less is known whether the change in understory plant community structure observed following canopy disturbance is short-lived and would diminish as the canopy closes or a long lasting due to legacy effects. We examined the effects of an experimental removal of 25% and 50% of the woody vegetation on understory light availability and variability on understory plant community structure in a subtropical *Cryptomeria japonica* plantation nine years after the treatment. Differences in availability of understory light among treatments diminished nine years after the experimental vegetation removal (thinning), but variability of understory light was still two times higher in the thinned treatments than the un-thinned control. Species diversity of dominant and common understory plants was lower in the control than in the two thinning treatments, which were not different from each other. Community species and functional composition were also different between the un-thinned control and the two thinning treatments. The thinned plots had proportionally more individuals of grasses and forbs and fewer individuals of ferns. Our results indicate that the effects of thinning on understory light variability last longer than on light availability representing an important and long-lasting alteration of resource heterogeneity. At both species and functional group levels, greater diversity and unique composition in the thinned treatments compared to undisturbed control suggest a link between resource heterogeneity and biodiversity in the forest understory or legacy effects associated with the thinning-induced changes in understory plant community.

Key words: legacy effects; species diversity; species richness; thinning; understory light.

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INTRODUCTION

The development, structure, and function of forested ecosystems are strongly linked to disturbance processes (Attiwill 1994), particularly those that increase resource availability in the forest understory (Royo and Carson 2006). Under closed forest canopy, light is generally limited, especially for species that are most often located in well-lit micro-sites such as those under canopy gaps (Denslow 1987, Dalling et al. 1998, Schnitzer and Carson 2001, Balderrama and Chazdon 2005). Increases in light availability can largely enhance the growth of shade-intolerant trees and thereby facilitate their transition into the forest canopy which would have long-lasting impacts on forest dynamics (Canham 1989).

Mechanical thinning is a common forest management practice that is conventionally applied to improve timber production (Ginn et al. 1991, Zhang et al. 2006, Roberts and Harrington 2008). Forest plantation management has increasingly moved beyond a strict focus on timber production to include a variety of ecosystem services (Chazdon 2008) such as biodiversity conservation in mechanical thinning and harvesting (Thomas et al. 1999, Wayman and North 2007, Yang and Man 2018, Yang et al. 2018). Studies have shown that if practiced properly, thinning could facilitate the development of old-growth forest characteristics (O'Hara et al. 2010) and enhance biodiversity (Pollock and Beechie 2014).

Removal of canopy trees through thinning may substantially increase light variability in the understory. Studies have suggested that enhancing spatial heterogeneity with thinning of varying intensities could help to restore biodiversity in temperate coniferous forests in northwestern USA (Carey 2003). Because trees removed in mechanical thinning are typically unevenly distributed throughout the forest, thinning may increase understory light variability by creating high-light patches in some micro-sites (where the trees are cut) while leaving light levels relatively unaffected at other micro-sites (away from the cut sites; Chiang et al. 2012). Resource heterogeneity has been considered an important driver of plant diversity (Stevens and Carson 2002, Tamme et al. 2010), and insofar as thinning increases heterogeneity of the understory light environment, it has strong potential to drive increases in understory biodiversity. Few studies have tested for links between increasing heterogeneity of the forest floor light environment and changes in understory biodiversity.

Following thinning, canopy openings gradually close by lateral growth of surrounding trees and vertical growth of trees under the openings (Drever and Lertzman 2003). Through the closing process, understory light availability gradually declines (Chan et al. 2006). Few studies have examined long-term effects of thinning on understory light environments and plant community structure (He and Barclay 2000). Canopy opening through thinning may trigger rapid growth and enhance richness and diversity of understory plants (Ares et al. 2010); however, it is not clear whether this is an ephemeral effect that will diminish following the closure of the canopy. Thinning may initiate a long-term effect on community composition if it enables the establishment of a set of shade-intolerant species which maintain their niche space due to legacy effects (Johnson and Curtis 2001, Perring et al. 2017).

Forest cover in the subtropics has been increasing since 2010 as a result of afforestation and reforestation (Keenan et al. 2015). The quality and quantity of ecosystem services provided by these forests largely depend on management practices. Compared to temperate and boreal forests, we know relatively little about ecological consequences of thinning on tropical and subtropical forest plantations. Filling this knowledge gap could facilitate improved conservation of understory biodiversity in managed tropical and subtropical forests.

In this study, we examined the effects of 25% and 50% thinning, with small-patch (10 m × 10 m) clear-cuts, on understory light environments, and understory plant diversity and community composition in Japanese cedar, *Cryptomeria japonica* (Cupressaceae), plantations in central Taiwan nine years after the thinning. We tested the following hypotheses. First, we hypothesized (H_1) that due to the thinning treatment, light availability would be highest in the 50% removal, intermediate in the 25% removal, and lowest in control stands. Second, we hypothesized (H_2) that understory light variability would follow the same pattern as availability being higher in the thinned stands and lower in the control. Third, we expected that thinning-induced increases of light availability and variability (Chiang et al. 2012) will enhance the establishment of shade-intolerant species such as grasses and suppress ferns that prefer shade and more humid habitat. Thinning likely also affected the quantity and partitioning of nutrient inputs through throughfall and stemflow, soil properties due to forest floor disturbance, and nutrient return via decomposition associated with changes in microclimate. Different groups of plants (herbaceous plant, ferns, shrub, grass, woody vines, non-woody vines, and trees) have different preferences of light availability and differ in water and nutrient use efficiency. We also expect such effects to be long-lasting due to priority effects (i.e., species that arrive first in a habitat significantly affect the establishment, growth, or reproduction of species arriving later; Fukami 2015). Thus, we hypothesized thinning would lead

to greater understory plant diversity (H_3) and divergence in the composition of understory plant community among the three treatment groups (H_4) and that the relative abundance in the number of species and relative coverage of functional groups would differ among the treatments (H_5).

Methods

Study site

The study was carried out at the Zenlun Experimental Forest, a *Cryptomeria japonica* forest plantation located in central Taiwan (23°43′ E, 120°55′ N). Elevation at the study site ranged between 1500 and 1700 m with a mean slope of ~50%. Soil textures in this area were primarily sandy loam and loamy sand with >68% sand and <14% clay (Wang et al. 2007). The natural evergreen hardwood forest in this area was clear-cut in 1960s and replaced with *C. japonica* plantation. Stem-only harvest was applied in the clear-cutting, with debris retained in the site, and was followed by site preparation (i.e., leveling and weeding) before planting seedlings of *C. japonica*. This forestry practice is not thought to substantially influence the seed bank although the piling of wood might have created some soil disruption (Taiwan Forestry Research Institute, *personal communication*). The mean annual precipitation at the site is 3800 mm, and the mean monthly temperature is 17.5°C (Wang et al. 2007). The mean tree height was ~17 m in 2006 (C. M. Chiu, *unpublished data*).

Experimental setup

In 2006, twelve 100 × 100 m stands were established at Zenlun Experimental Forest. Following the design of large forest dynamic plots at the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute, all woody plants with diameter at breast height (dbh) >1 cm were mapped, tagged, and identified to species (Losos and Leigh 2004) with nomenclature following Boufford et al. (2003). The 12 stands were evenly and randomly assigned to three treatments: un-thinned control, 25% thinning, and 50% thinning. The 25% and 50% thinning treatments were chosen to represent moderate and heavy thinning. Thinning at intensities <25% would not be cost-effective in Taiwan due to the very rough topography, while intensities >50% could lead to major erosion also due to the very rough topography.

Each stand was divided into one hundred 10 × 10 m plots, which were grouped into 25 square clusters (i.e., four plots in each cluster). Under the 25% thinning treatment, one of the four plots in each cluster was randomly assigned for stem-only harvest. Under the 50% thinning treatment, two non-adjacent plots in each cluster were randomly assigned for stem-only harvest. Thus, all thinning-created gaps were 100 m^2 in area, with all trees in 1 of 4 plots and 2 of 4 plots of each cluster felled in the 25% and 50% thinning treatments, respectively. The thinning was carried out between 1 July 2007 and 10 October 2007 by felling all trees in the assigned plots. The 100 m^2 size of the thinned sections is recognized in the literature as on the upper boundary of what is defined as a "small gap" (Runkle 1982, Gálhidy et al. 2006). A post-thinning survey indicated that 24.3 ± 2.23% and 50.1 ± 1.34% of the *C. japonica* trees were felled in the 25% and 50% thinning treatments, respectively (Chiu, *unpublished data*). All thinned trees were removed from the forest using cable skidders to minimize soil disturbance, while treetops and branches were retained on site to mimic commercial practices in Taiwan.

Measurements of understory light environments

Understory light environments were characterized using hemispherical photography (Rich 1990, Lin and Chiang 2002) between late May and mid-August 2016. We established one 100-m transect perpendicular to the elevational contours at the center of each of the 12 stands one year before the thinning. Hemispherical photographs were taken at 1.5 m above the ground, at 5-m intervals through each transect. The 5-m intervals were chosen to avoid spatial autocorrelation in understory light level among the samples (Becker and Smith 1990, Lin et al. 2003).

Hemispherical photographs (2272 × 1704 pixels) were taken using a Nikon Coolpix 4500 digital camera (Nikon, Tokyo, Japan) equipped with a Nikon FC-E8 fisheye lens (with a combined focal length equivalent to 7.2 mm and a combined F-stop [relative aperture] of 2.4). Photographs were analyzed to estimate direct and diffuse light availabilities using HemiView 2.0 (Delta-T 2000; Delta-T Devices, Cambridge, UK).

Direct and diffuse light availabilities are expressed as the proportions of direct and diffuse solar radiation reaching a given location, relative to a fully exposed location with no obstructions (Rich 1990). Direct light availability is estimated by superimposing solar tracks on the digitized images enabling the proportion of open pixels crossed by the sun's path to be calculated (Rich 1990). Diffuse light availability is determined by assessing the proportion of pixels classified as sky within the projected image of the hemisphere (Rich 1990). The direct and diffuse light availabilities can also be viewed as the proportions of direct and diffuse photosynthetic photon flux density incident on a horizontal surface above the canopy that is transmitted to the point where the photograph is taken (Rich 1990). In order to maximize the contrast between openings and foliage, all hemispherical photographs were taken at dawn or dusk or during overcast days when direct sunlight was absent. All photographs were analyzed by the same person to minimize inconsistency in the choice of thresholds for classification of images into black (canopy components) and white (canopy gaps) pixels.

Vegetation survey

Eight 1 × 1 m quadrats were evenly distributed in two randomly selected clusters in each of the 12 stands resulting in a total of 32 survey quadrats in each treatment. Within each quadrat, plants <130 cm were recorded and identified to species, with nomenclature following Boufford et al. (2003). The plants were further classified into seven functional groups: herbaceous plant, ferns, shrub, grass, woody vines, non-woody vines, and trees. The percent cover of each species was also estimated. The survey was conducted between July and August in 2016.

Data analysis

Thinning effects on understory light regimes.— Because the immediate effects (i.e., within 3 months) of thinning on understory light environments were examined by Chiang et al. (2012), we only analyzed data of understory light environments and plant diversity acquired in 2016 in this study. To ensure the independence of the thinning treatment on light environment and avoid pseudo-replication (Hurlbert 1984), individual measurements of direct and diffuse light availabilities were pooled for each 1-ha plot. In addition to the means of direct and indirect light availability, light variability of each 1-ha plot was quantified by calculating the coefficient of variation (CV; %) of direct and diffuse light availabilities. Due to the lack of enough observations for the test of normality, parametric analysis of variance was not used. Instead, we used permutation ANOVA in the coin package in R (Strasser and Weber 1999, Hothorn et al. 2008) for the tests of treatment effects on light availability (means) and variability (CVs).

Thinning effects on species diversity of understory plant community.— Alpha diversity of plant species in the understory assemblage was quantified by an incidence-based survey of the plant community. Species frequency was calculated for the 32 1-m^2 plots in each of the three thinning treatments. Although our sampling efforts were the same for each treatment, the completeness of samples (i.e., sample coverage) may be different due to the inherent differences in community structure between treatments (Chao and Jost 2012). To avoid the potential bias due to the sample coverage, we used iNEXT package in R (Hsieh et al. 2016) with Hill numbers (or the effective number of species; Hill 1973) for the comparison of alpha diversity between thinning treatments at the same level of sample coverage. In the iNEXT package, sample coverage is calculated based on functions developed from Chao and Jost (2012) and confidence intervals based on the bootstrap method were also calculated. To reveal more complete profiles of diversity, we also separate our analyses by diversity orders of $q = 0$, 1, and 2, which are equivalent or derived from three most widely used species diversity measures: species richness, Shannon diversity, and Simpson diversity, respectively (Chao et al. 2014). At $q = 0$, every species was count equally without considering the frequency of occurrence. Thus, diversity measure at $q = 0$ is the most sensitive to rare species among the three diversity orders. At $q = 1$, individual incidence of species appearing in quadrats was equally counted, and thus, species were weighted in proportion to their relative frequency. Thus, diversity measure at $q = 1$ can be regarded as the effective number of common species. Diversity measure at $q = 2$ discounts all but the dominant species and can be considered as the effective number of

dominant species in a community (Hsieh et al. 2016). We compared (1) the relative abundance of number of species, and (2) the relative coverage of individuals of understory plants of the seven functional groups among the three treatments using chi-square tests, followed by post hoc tests based on adjusted standardized residuals to examine which deviates caused the overall significant difference (Garcia-Perez and Nunez-Anton 2003).

Thinning effects on the species composition of understory plant community.—The species composition of the understory plant community for each quadrat was represented by principal component analysis (PCA). The relative abundance of each quadrat was quantified by the percent vegetation cover. In order to use ordination methods that are Euclidean-based and with community data containing many zeros (long gradients where many species are replaced by others), Hellinger transformations were applied prior to PCA (Legendre and Gallagher 2001). Although Hellinger-transformed PCA is not sensitive to rare species, it offers monotonic representation of ecological gradient among communities (Legendre and Gallagher 2001). If thinning had created changes in physical environment that lead to changes in community composition in the understory, Hellinger-transformed PCA should be an ideal measure that would reveal the differences.

To test the effects of thinning on species composition of the understory, we performed permutation test of similarities in species composition between communities under different thinning treatments. For each of the three pairwise comparisons (control. vs. 25% thinning, control vs. 50% thinning, and 25% thinning vs. 50% thinning), the observed Jaccard, Horn, and Morisita-Horn similarity indices (Jaccard 1908, Morisita 1959, Horn 1966) were calculated between treatments. Morisita-Horn index is based on the concept of Simpson's index and thus largely influenced by the *dominant* species. Compared to the Horn index, rare species have less impact on Morisita-Horn index.

Pairwise comparisons of community compositions were examined using permutation tests. The null distributions of similarity indices were created by 9999 permutation cycles. For each cycle, the identities of 64 1-m^2 quadrats (2 treatments $\times$ 4 plots/treatment $\times$ 8 quadrats/plot) were randomly re-ordered. Then, the similarity indices were calculated between treatments, based on the newly assigned quadrat identities. This permutation procedure simulates the variation of similarity indices between two groups of individuals that are randomly drawn from the same community. The *P*-values of community similarity were calculated by 2 times (two-tailed test) the sum of cycles from which the simulated similarities were more extreme (closer to the upper or lower tails of the null distribution) than the observed similarities, then divided by 10,000 (9999 permutation cycles + 1 observed case). For the test of thinning effects on community composition, the α level is adjusted to 0.017 (1/3 of 0.05) after Bonferroni correction due to the fact that three comparisons (control vs. 25% thinning, control vs. 50% thinning, and 25% thinning vs. 50% thinning) were made upon the same dataset. Other statistical tests were performed at α level of 0.05.

All statistical tests were performed using R (R Foundation for Statistical Computing, Vienna, Austria) except chi-square tests which were performed using SPSS 20 (SPSS, Chicago, Illinois, USA).

Results

Understory light availability and variability

Nine years after the thinning, availability of understory light (both diffuse and direct) was not statistically different among the three treatments (Fig. 1), refuting our hypothesis H_1, which predicted differences in light availability associated with the treatments. Treatment effects on the variability of light, represented by the coefficient of variation, were marginally significant for indirect light ($P = 0.074$) and significant for direct light ($P = 0.047$; Fig. 1) providing support for our hypothesis (H_2). Variability of light created by the thinning treatments was higher than that in the control, but statistically indistinguishable between the two thinning treatments (Fig. 1).

Plant diversity

A total of 43, 71, and 68 understory plant species were recorded in the control, 25% thinning and 50% thinning groups (Fig. 2, left panel). With the total number of 32 quadrats per treatment, the sample coverages of the understory

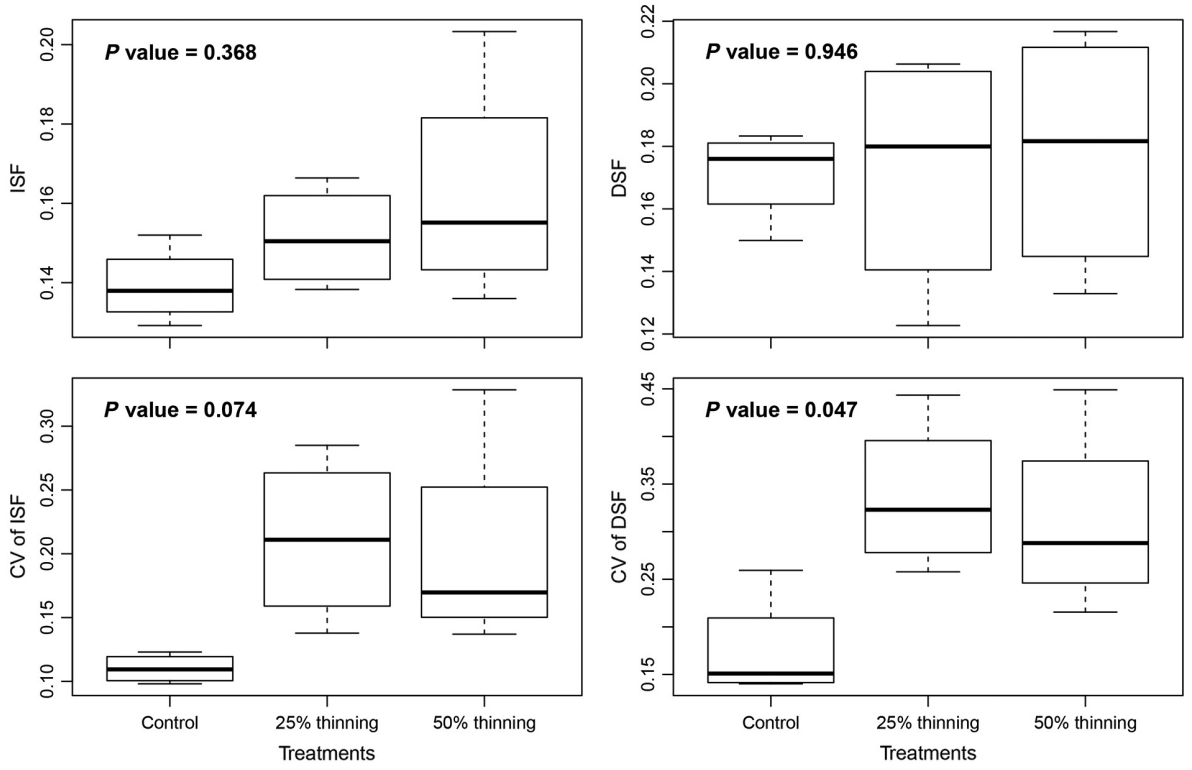


Fig. 1. The effects of thinning treatments (control, 25% thinning, and 50% thinning) on the understory light availability (ISF and DSF) and variability (CVs for ISF and DSF) in *Cryptomeria japonica* plantation in Central Taiwan. Understory light environments were quantified 9 yr after the thinning treatments. *P*-values represent the overall test results of treatment effects by permutation ANOVA. ISF and DSF are indirect (diffuse) and direct light available at a given (understory) location relative to that above the forest canopy or in the nearby open area.

vegetation were 81.1%, 84.1%, and 84.8% for control, 25% thinning, and 50% thinning, respectively. The most dominant species in the control are *Elatostema lineolatum* (42.2%) [Urticaceae] and *Diplazium dilatatum* (32%) [Dryopteridaceae], and all other species contributed to <10% of the understory cover. The two species are also the most dominant species in the 25% and 50% thinning treatments, and all other species contributed to <10% of the understory cover. However, while the dominance of *E. lineolatum* was similarly high in the 25% thinning treatment (38.3%) and the 50% thinning treatment (45.9%), the dominance of *D. dilatatum* was considerably lower in both the 25% thinning treatment (11.0%) and 50% thinning treatment (14.0%). Notably, the grass, *Piptatherum kuoi*, was absent in the control but was observed in all thinned stands and was the third most dominant species in the 50% thinning treatment contributing to 6.0% of the understory cover.

Species richness ($q = 0$) at a given sample coverage was not significantly different among treatments (Fig. 2, left panel). At $q = 1$, the effective number of common species of the control is significantly lower than that of the two levels of thinning treatments (Fig. 2, middle panel). The difference is seen throughout different levels of rarefaction and extrapolation. A similar pattern was also found for diversity measure at $q = 2$, where the effective number of dominant species is significantly lower under control treatment throughout different levels of sample coverage (Fig. 2, right panel). Our results on understory plant diversity partially supported our H_3, which predicts higher plant diversity in the thinned treatments than the un-thinned control nine years after thinning treatments.

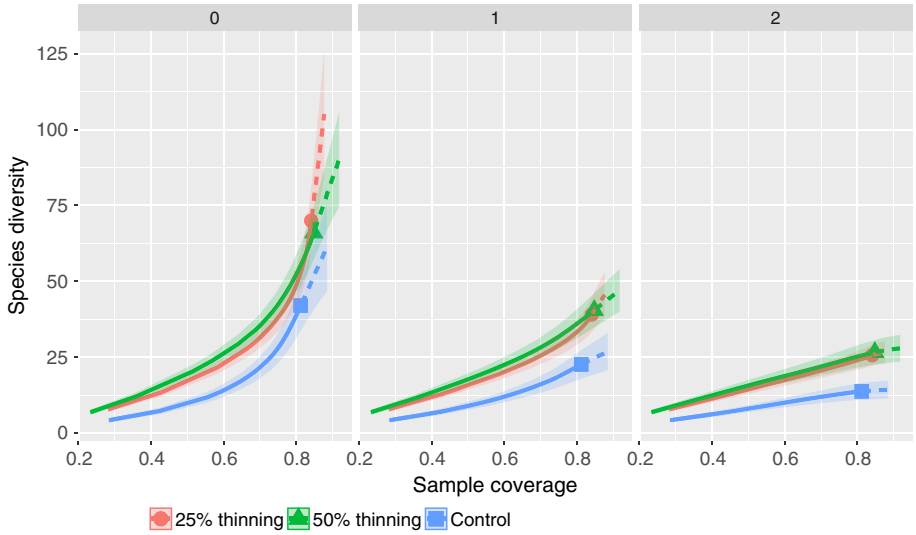


Fig. 2. Sample coverage-based rarefaction (solid line) and extrapolation (dotted line) curves of understory plant species diversity with 95% confidence intervals (shaded areas) for control, 25% thinning, and 50% thinning treatments. Understory vegetation surveys were carried out 9 yr after the thinning treatment. Analyses were separated by diversity orders of $q = 0$ (species richness, left panel), $q = 1$ (effective number of species based on Shannon entropy, middle panel), and $q = 2$ (effective number of species based on Simpson index, right panel). The solid dots, triangles, and squares represent the species diversity and sample coverage level when all quadrats were considered.

The relative numbers of species in different functional groups were not different among the three treatments ($\chi^2 = 5.20$, df = 12, $P = 0.95$; Fig. 3a), but the coverages were ($\chi^2 = 21.3$, df = 12, $P < 0.046$; Fig. 3b), partially supporting H_5. Analysis of standardized residuals indicated that the deviates between expected and observed values were significant for ferns in the control and the 50% thinning ($P < 0.001$), grasses in the 50% thinning ($P = 0.029$) and marginally significant for forbs in the control ($P = 0.054$).

Species composition

Principal component analysis based on species compositions of understory vegetation separated the quadrats into recognizable patterns representing the three thinning treatments although there was some overlap (Fig 4). The first and second principal components explained 23% and 15% of variation, respectively. In the space depicted by the first and second principal components, quadrats under control treatment exhibited little overlap with those under treatments of both thinning intensities and the separation is mainly along the first principal component (Fig. 4). Quadrats under both thinning treatments exhibited more overlap in the principal component space in the lower right quadrant; however, the 25% thinning did exhibit separation in the upper left portion of the PCA space (Fig. 4).

The observed community similarities were lower between control and thinning of both intensities than between two thinning treatments (Fig. 5). Most of the test results showed significantly lower similarity at alpha level of 0.017 for control vs. 25% thinning and control vs. 50% thinning than their respective null distributions, which were modeled assuming species and their relative abundance were randomly drawn from the same community. The only exception was for the comparison between control and 50% thinning in Morisita-Horn index that exhibited marginally significant difference at $P = 0.021$. Conversely, the observed similarities between 25% thinning and 50% thinning were not significantly different from the null distributions for Jaccard and Morisita-Horn indices (Fig. 5). Horn similarity exhibited significant difference between observed and null distribution for all pairs of comparisons.

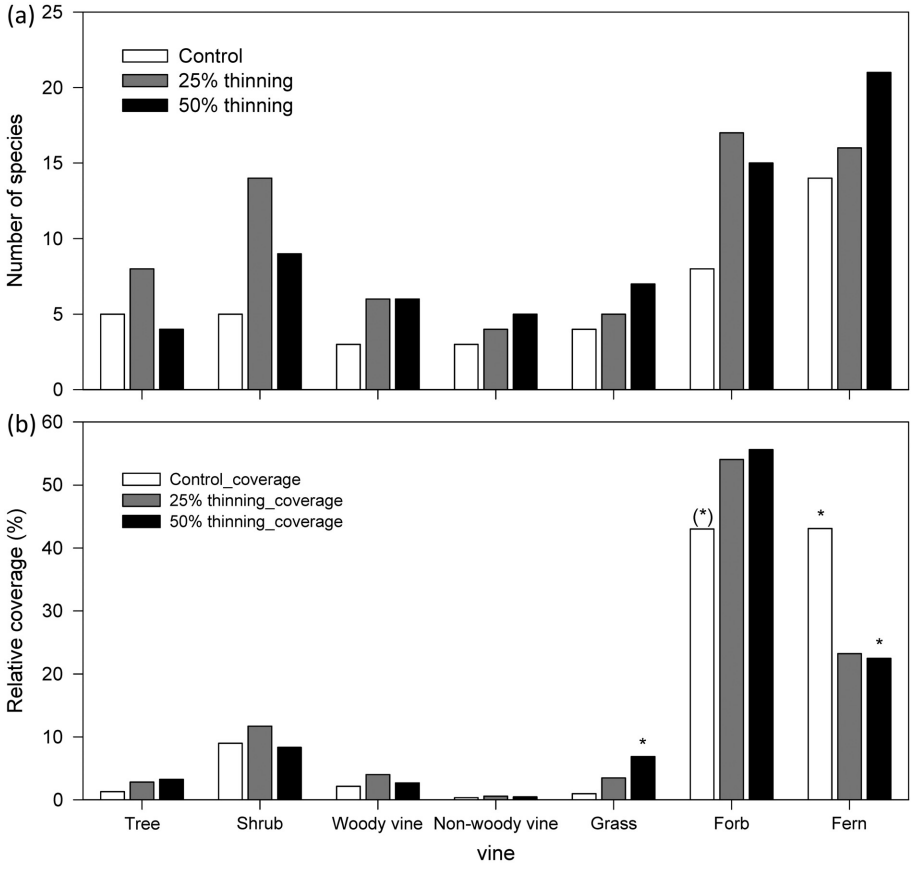


Fig. 3. The number of species (a) and relative coverage (b) of understory plants in different functional groups in the three treatments of the *Cryptomeria japonica* plantation in central Taiwan. * and (*) indicate significant deviation of the observed value from expected value at $\alpha = 0.05$ and 0.10, respectively.

Discussion

Thinning effects on understory light availability and variability

Our data indicate that the nature of the understory light environment is highly dynamic in response to disturbance. Immediately following the thinning, understory light availability was more than doubled in the thinned areas compared to the control (Chiang et al. 2012). Yet, 9 yr after thinning, there were no statistically discernable differences in light availability which refuted our hypothesis (H_1) of greater light availability in the thinned sections. These results indicate that canopy closure was relatively rapid at the 1.5 m height at which we sampled. Previous research has noted that direct light arriving at the forest floor is quite low even in large forest gaps (Canham et al. 1990) and increases in light availability generally led to rapid understory plant growth (Lieffers and Stadt 1994, Chen et al. 1996, Williams et al. 1999, Lin et al. 2014). Ritter et al. (2005) noted that the effects of a canopy gap diminish rapidly after the first year and they hypothesize that this effect is associated with "intense growth of regeneration" (p:28). Gap dynamics are a fundamental process in long-term forest dynamics and are characterized by pulses of rapid tree growth immediately after gap formation and slower growth as the gap closes (McEwan et al. 2014). Taken together, these results suggest that high-light conditions following the creation of forest gaps are an ephemeral phenomenon where high-light conditions are extinguished quickly, even in a plantation setting following the creation of openings

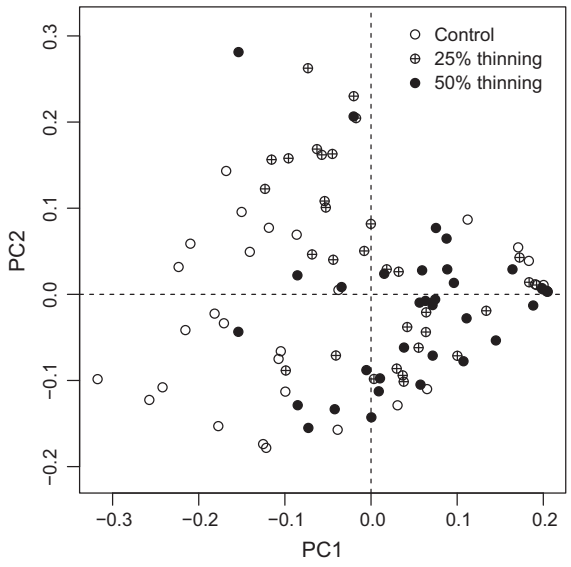


Fig. 4. Species composition of understory plant species in 1-m^2 quadrats is represented by the first two principal components (PC1 and PC2) of ordination on Hellinger-transformed species composition data. Species compositions were quantified by percent cover in each 1-m^2 quadrat. Empty circles denote quadrats under control treatment. Circles with crosses and filled circles denote quadrats under 25% and 50% thinning treatments, respectively.

through mechanical thinning removing 50% of the overstory canopy.

In contrast to a relatively brief increase in total light availability, we found that light variability remained elevated over a decadal time frame, providing support for our hypothesis of increased light variability in thinned sections (H_2). Immediately following the thinning treatment, the coefficient of variation of understory light in the 25% and 50% thinning treatments was 2.4 and 10 times of that in the control (Chiang et al. 2012). Interestingly, nine years later, the coefficient of variation of understory light in the thinning treatments was both approximately two times of that in the control groups and not different between the two thinning intensities. The thinning was conducted in a small-patch (10 × 10 m) cut manner and was practiced in one of four plots in each cluster in 25% thinning and in two non-adjacent plots in 50% thinning. Given that the treatments were spatially regular through the thinning treatments, it is unclear whether our results are applicable to natural disturbance processes where openings vary in size. Indeed, prior research suggests that gap size is an important driver of both light and plant community in the forest understory (Canham et al. 1990, Gálhidy et al. 2006). Future experiments that assess the influence of thinning on long-term patterns of light availability and variability across a range of different gap sizes would be helpful for understanding the links between the spatial layout the canopy disturbance and understory biodiversity.

Understory plant diversity

Resource heterogeneity is a key driver of plant biodiversity in forest ecosystems as postulated by the theory of gap dynamics (Watt 1947, Whitmore 1989). More heterogeneous light environments allow more species with different levels of shade intolerance to coexist in the forest understory (Levin and Pacala 1997, Bascompte and Rodriguez 2001, Valladares 2003, Liu et al. 2015). Our assessment of diversity level $q = 0$ (species richness) revealed no differences among the treatments, while both $q = 1$ (Shannon diversity) and $q = 2$ (Simpson diversity) revealed that the thinning treatments were indistinguishable but both contained higher levels of diversity than the control supporting H_3. The higher diversity in the thinned stands was associated with the much lower dominance of *Diplazium dilatatum* (<15%), relative to the control (32%). *Diplazium dilatatum* has a relatively low photosynthetic light compensation point (<20 mmol·m^{-2}·s^{-1}) making it a high competitor in low-light environments. However, its photosynthetic rate saturates quickly at light levels >200 mmol·m^{-2}·s^{-1} (Liu et al. 2015) so that it is not a good competitor in high-light environments such as those created by thinning. This is in contrast to the most dominant species, *Elatostema lineolatum* which is a shade-tolerant species with growth greatly enhanced by high-light levels (Liu et al. 2015). In the thinning plots, the space *D. dilatatum* vacated was filled by species both pre-existing in the understory and by those which colonized into the stands. The colonization of the grass, *P. kuoi*, which became the third most dominant species in the 50% thinning treatment, illustrated that opening of the forest canopy facilitated the colonization of shade-intolerant species and contributed to greater understory plant diversity in the thinned stands.

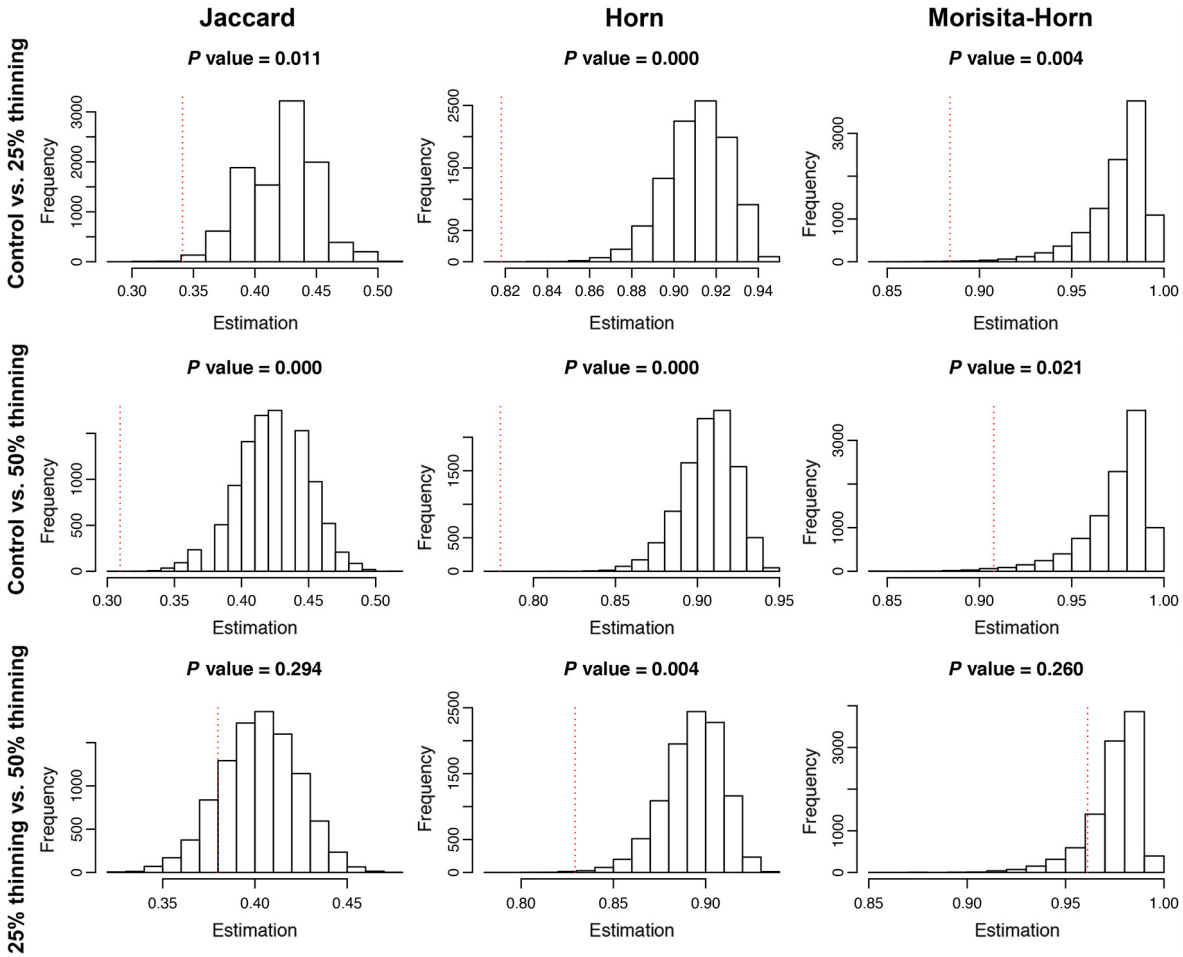


Fig. 5. Community similarities between control vs. 25% thinning (top row), control vs. 50% thinning (center row), and 25% vs. 50% thinning (bottom row), represented by observed (red dotted line) similarity in the frequency distribution of permuted similarities (9999 permutations). Similarity indices include Jaccard index (left column), Horn (center column), and Morisita-Horn (right column). *P*-values lower than 0.017 were considered significant after Bonferroni correction.

In addition, we found support that the thinning treatment would result in a unique plant community in the understory (H_4) in that similarity in community composition between the two thinning treatments was greater than between the un-thinned control and the thinned treatments (Figs. 4 and 5). Although the two thinning treatments had similar species diversity (Fig. 2), community composition focusing on common species (i.e., the Horn index) differed between the thinning intensities (Fig. 5). Thus, there were still subtle influences associated thinning of different intensities on understory community which could not be explained by the differences in understory light availability observed nine years after the thinning. Some of the differences among treatments may be associated with legacy effects from species that colonized at the time of the treatment. For example, the large decrease in the fern, *D. dilatatum,* and the high abundance of the grass species, *P. kuoi,* are likely caused by the sudden increases of light availability associated with thinning nine years ago. The regional species pool likely contains species that may establish in gaps, and through management legacies, create long-term variation in species composition (Fukami 2015).

Thinning and functional diversity

The differences in the relative coverage of plants from different functional groups among the treatments indicated that canopy opening associated with thinning suppressed fern coverage and increased grass coverage (Fig. 3b). The lack of differences in light availability among the three treatments indicates that the differences in the relative coverage of plants of different functional groups cannot be explained by the current differences in light availability. Instead, it could be the result of present differences in light variability or legacy effects from changes in the light environment that immediately followed the thinning but faded through time. Ferns generally favor shaded habitats (Watkins and Cardelús 2012) so that the large increases in light availability immediately following the thinning (Chiang et al. 2012) likely negatively affected their growth leading to their low coverage in the thinned plots. The greater proportional coverage of grasses, which typically favor high-light environments, in the thinning treatments than the control (Fig. 3b) supports the notion of legacy effects associated with increased light availability immediately following thinning (Chiang et al. 2012). Although the diminished light availability may no longer favor grasses it probably takes more than one decade for the management legacies to disappear. Legacy effects of past management practices on plant communities are widely recognized (Perring et al. 2017), and some may be even irreversible (Dupouey et al. 2002). Our results indicated that legacy effects of thinning on plant diversity, likely through changes in understory light availability, could last for at least one decade and should be taken into account if plant diversity is to be included in the management plan.

Alternatively, the differences in the relative coverage of plants of different functional groups between the control and thinned plots could be explained by the greater variability of understory light in the treated plots. The much greater variability of understory light, especially at the high-light end, in the thinned plots (Fig. 1b) means that there are some micro-sites that still had high-light availability nine years after the thinning. As a result, shade-intolerant grasses and forbs were able to maintain their niches in the thinned plots leading to their greater abundance in the thinning treatment as compared to the un-thinned control. Legacy effects and changes in understory light variability as a result of the thinning treatment may have contributed to the observed differences in the composition of functional groups between the control and the thinning treatments.

Application and summary

The findings from this study have potential application for the management of biodiversity in forestry operations in subtropical forests. Although the experimental design we employed, with high thinning intensity and defined spatial pattern may not be desirable from a forest management perspective, our findings of similar understory plant diversity between the two thinned treatments and the relationship between light variability associated with different plant diversity reinforce the importance of habitat heterogeneity in the maintenance of biodiversity. These results are likely applicable to other types and intensities of thinning. For example, our results indicate that forestry practices that increase light variability have the potential for increasing understory biodiversity and that legacy effects of thinning may last for more than a decade following the implementation.

In summary, the results of this experiment suggest that canopy openings created through thinning have the potential to alter plant communities over the long term and may be linked to alterations of the light regime. Immediately following the thinning treatment, there was strong evidence of increased light availability; however, that effect had attenuated 9 yr later and was no longer statistically discernable. Light variability remained elevated in the thinned areas, and the vegetative communities were distinguishable compared to the control both in terms of species and functional composition. Two mechanisms of interest for future research that may explain the long-term effects on understory plant diversity are (1) thinning-induced legacy effects and (2) ecological connections between the variability of the light environment and the complexity of the vegetative community. Management that includes creation of canopy gaps to mimic natural disturbance processes (Lertzman et al. 1996) may create opportunities for maintenance of biodiversity even within productive plantations. Our results indicate the influence of thinning on total light availability may rapidly diminish while influences on light

variability may be much more long lasting. Future research that explicitly considers how the spatial layout of canopy openings influence understory light heterogeneity may be advantageous for providing recommendations when enhancing biodiversity is a corollary objective of forest management.

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