The effect of typhoon-related defoliation on the ecology of gap dynamics in a subtropical rain forest of Taiwan

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Abstract

Questions: How do frequent disturbances of varying intensity affect heterogeneity of canopy openness and resulting regenerating tree diversity in subtropical rain forests? How does canopy gap pattern and regeneration time of a forest experiencing frequent but unpredictable typhoon disturbance vary over 17 yr? How is the understorey light environment influenced by canopy gaps in a forest experiencing frequent defoliation? Compared to non-gap areas, do gaps provide unique niches reflected in different seedling communities?

Location: Natural evergreen hardwood forest, northeastern Taiwan.

Methods: We examined gap characteristics, light availability and variability, and seedling diversity in both gaps and non-gaps in a subtropical forest with frequent typhoon disturbance, and compared the results to a survey at the same site conducted in 1995 following six typhoons in 1994.

Results: Gaps were smaller and covered a much smaller proportion of the forest in the 2012 survey (mean gap size 10 m^2, 3.3% of the forest) than the 1995 survey (33 m^2 and 10%). Canopy regeneration times estimated from the 2012 survey (200–400 yr) were much longer than those based on the 1995 survey (50–175 yr). Neither light availability nor variability differed between gaps and non-gaps, so gaps ostensibly did not provide a unique niche space. There were no seedling species occurring exclusively in gaps, and very high plant community similarity (>90%) between gaps and non-gaps.

Conclusions: In ecosystems with small canopy gaps resulting from frequent disturbance, gaps play a neutral role in understorey light environment and thus provide no unique niches and play a neutral role in plant diversity. Our study also suggests that measures of gap area, occurrence and forest turnover should be taken multiple times, during years with varying background disturbance rates.

Introduction

Disturbance processes have been linked to biodiversity and dynamics in a wide variety of forest ecosystems. Disturbances range across spatial and temporal scales and can have long-lasting effects on species composition (Sprugel 1991; Paine et al. 1998; Turner et al. 1998; McEwan et al. 2011). Anthropogenic and climatic factors driving shifts in disturbance regimes in some systems (Parmesan 2006; Allen et al. 2010) potentially have long-term consequences. Individual mortality of large trees and the subsequent creation of canopy gaps are thought to be important

baseline disturbance processes in forests. Gap dynamics are an essential part of most forest development models and a distinguishing feature of mature forests (Bormann & Likens 1979; Oliver & Larson 1996). The formation of canopy gaps in forests (i.e. 'holes' that penetrate the forest canopy, with plant height within the 'hole' <2.0 m; Brokaw 1982; Hubbell & Foster 1986) is thought to be a local, stochastic process; however, the role of gaps in the ecology of a forest can be strongly influenced by disturbance factors that impact the forest at larger spatial scales.

One of the fundamental effects of a disturbance in a forest is alterations of the light environment at the forest

floor. Understorey light environments are considered a critical determinant of seedling establishment and growth in forests, and therefore a driving factor in long-term forest dynamics (Caldwell & Pearcy 1994; Kitajima 1994; Niinemets et al. 1998; Nictora et al. 1999; Montgomery & Chazdon 2002). In many mature forests, low light conditions are a prevalent feature of the understorey (Canham et al. 1990), and seedlings of shade-intolerant species are limited to well-lit microsites such as those in canopy gaps (Hartshorn 1978; Denslow 1987; Whitmore 1989; Dalling et al. 1998; Schnitzer & Carson 2001; Balderrama & Chazdon 2005). Due to within-gap heterogeneity in light availability, these gaps can also benefit shade-tolerant species and play a role in 'releasing' saplings into the mid-storey (Strong 1977; Kobe 1999; Schnitzer & Carson 2001; McEwan et al. 2014). Overall, gap formation and closure are considered important processes that dictate patterns of forest regeneration and long-term succession (Jones 1945; Denslow 1987; Kern et al. 2013).

Assessments of canopy gaps as a factor in maintaining forest biodiversity have yielded inconsistent results (Lieberman et al. 1989; Whitmore 1989; Webb & Scanga 2001; Pham et al. 2004; de Römer et al. 2007; Gravel et al. 2010; Kern et al. 2013). Studies suggesting a crucial role for gaps as drivers of biodiversity are common (Elias & Dias 2009; Grandpré et al. 2011; Kern et al. 2013), although some authors have countered that gaps have little influence on biodiversity. One example of this divergence of perspective has emerged from work focused on tree-fall gaps in tropical forests of Barro Colorado Island, where Schnitzer & Carson (2001) stated that 'gaps play a strong role in the maintenance of woody species diversity,' while Hubbell et al. (1999) proposed that gaps play a 'relatively neutral role in maintaining species richness'.

Most studies of gap dynamics focus on small-scale canopy disturbances that disrupt but do not destroy the forest canopy (Dole 1981; White et al. 1985; Hart & Grissino-Mayer 2009; McEwan et al. 2014), and much of this work focused on the role of gaps within old-growth forests or other areas with infrequent larger-scale disturbances (Runkle 1982, 1998; McEwan et al. 2014). In forests that are subject to broad-scale disturbances, canopy thinning can occur without generating gaps, as commonly defined (Brokaw 1982; Hubbell & Foster 1986; Schnitzer & Carson 2001). For example, defoliation is a common type of damage caused by insect outbreak (Ehrenfeld 1980) and tropical cyclones (Walker 1991; Murphy et al. 2008; Lin et al. 2011) that limits foliar cover and increases light at the forest floor, without generating gaps *per se*. If defoliation is severe and accompanied by scattered tree falls (Lin et al. 2011), light availability in the forest will not necessarily vary between gap and non-gap environments (Lin et al.

2003). An important scientific challenge is understanding how light availability differs between gap and non-gap settings in forests where disturbance is common, and then linking light availability with distribution and growth of seedlings within and between gaps and non-gaps (Molofsky & Augspurger 1992; Gary & Spies 1997). Because natural disturbances that cause canopy gaps are unpredictable in space and time, remapping gaps in the same site is a useful technique for assessing the role of gaps within a particular forest, yet, as pointed out by Hytteborn & Verwijst (2014) '...a dynamic approach has been used in only a few studies to examine gap changes'.

This study employed a dynamic approach to assess the size, age and causes of canopy gaps in Fushan Experimental Forest, a subtropical rain forest in northeastern Taiwan. Gaps in this forest were previously surveyed in 1995 following the occurrence of six typhoon impacts in 1994. In 2012, we conducted a similar survey at the same site and, in addition, we compared light availability and variability, as well as understorey plant composition, between gaps and non-gaps. The study was guided by a series of hypotheses. First, because we assume that gap-scale disturbances are temporally stochastic, and the original sample occurred following a particularly severe typhoon season, we hypothesized that (H_1) gap size and proportion of forest area in gaps would differ between the current sampling and that in 1995. One important concept in gap theory is that canopy gaps create a high light environment in the forest understorey. Because of the occurrence of typhoon impacts in our site, we were interested in testing the role of gaps in providing high light microsites; thus this study tested the hypothesis that (H_2) understorey light availability and variability are higher in gaps than in non-gaps. As the higher resource (particularly light) environments in gap areas can generate unique opportunities for species, we hypothesized that (H_3) species richness of seedlings would be higher in gaps than in non-gaps, and also that (H_4) gap and non-gap areas would have unique seedling communities.

Methods

Study site: the Fushan Experimental Forest

This study was conducted in Watershed 1 (37 ha) of the Fushan Experimental Forest, which is a moist evergreen, subtropical hardwood forest in northeastern Taiwan (24°34′N, 121°34′E), with an area of ca. 1000 ha. Elevation in the study site is 670–1100 m a.s.l., annual precipitation is 2900–6650 mm, with a mean of 4240 mm between 1993 and 2007 (Hsia & Hwong 1999; Hsia 2008), annual mean temperature is 18.2 °C (11.8 °C in February and 24.1 °C in July; Hsia & Hwong 1999; Hsia 2008), and relative humidity is >90% throughout most of the year. Single

tree replacement has been suggested as the likely regeneration mode, but has not been rigorously tested (Lin et al. 2003).

The Fushan Experimental Forest experiences, on average, 0.74 typhoons annually, with intensities above category 1 on the Saffir–Simpson scale (Lin et al. 2011). The Saffir–Simpson scale categorizes cyclones into five categories based on the maximum sustained winds, with category 1 having maximum sustained wind speeds of 74–95 miles h^{-1} (mph), category 2 at 96–110 mph, category 3 at 111–130 mph, category 4 at 131–155 mph and category 5 at >155 mph (Simpson & Riehl 1981). However, both frequency and intensity of typhoons are highly variable, with a maximum of two consecutive years without any typhoon and a maximum of six typhoons (four of category 3) within 1 yr (Lin et al. 2011). The forest is structurally highly resistant to typhoon disturbance, with very low mortality (<5%) following even very intense (category 3) typhoons (Lin et al. 2011). It is functionally highly resilient with stream water chemistry returned within a week to pre-typhoon levels following a category 3 typhoon in 1996 (Lin et al. 2011), as compared to 500 days reported for Luquillo Experimental Forest in Puerto Rico following the 1989 hurricane Hugo (McDowell 2001).

There are 515 plant species belonging to 329 genera and 124 families within the Fushan Experimental Forest (TFRI 1989). The common tree species are *Castanopsis carlesii* var. *sessilis* Nakai (Fagaceae), *Machilus thunbergii* (Sieb. et Zucc.) Kostermans (Lauraceae), *Engelhardtia roxburghiana* Wall. (Juglandaceae), *Meliosma squamulata* Hance (Sabiaceae), *Litsea acuminata* (Blume) Kurata (Lauraceae), *Diospyros morrisiana* Hance (Ebenaceae), *Helicia formosana* Hems (Proteaceae) and *Pyrenaria shinkoensis* (Hayata) Keng (Theaceae). Most shrubs are *Ardisia quinquegona* Blume (Myrsinaceae), *Blastus cochinchinensis* Lour (Melastomataceae) and *Lasianthus fordii* Hance (Rubiaceae) (Wang et al. 2000). Based on principal components analysis of functional traits of trees in the Forest Dynamic Plot located within Fushan Experimental Forest but outside the experimental watershed, trees span a wide range of shade tolerance (Chiang unpubl. data). The forest is of short stature (10 m), possibly due to frequent typhoon disturbance (Lin et al. 2011). The forest is multi-storied, with scattered tree ferns (*Alsophila podophylla* Hook (Cyatheaceae)) and herbaceous cover (Lin et al. 2011).

Transect set-up

Seven random transects running perpendicular to the topographic contours were set up in 1995 to survey canopy gaps. The field methodology in 2012 followed the set up of seven transects in 1995 (Mabry et al. 1998); however, those transects were no longer recognizable. Seven new transects were established, ranging in length from 120 to 300 m, with a total length of 1200 m. Transects were at least 100 m apart, except for transect #1 and #2, which were 50 m apart.

Gap survey

Following the gap definition of Brokaw (1982), we located gaps as openings in the canopy resulting from branch breaks and dead, snapped or uprooted trees (Mabry et al. 1998). The location of each gap was recorded with a global positioning system (GPS; GARMIN OREGON 550t; Garmin Corp., Kansas City, KS, US), including aspect, elevation and slope.

The status of gap-makers was separated into three categories: uprooted, snapped (bole or big branches) and standing dead. The start and end points where gaps intersected the transect tape were recorded, and the resulting distance used to calculate percentage of the transect length in gaps together with canopy turnover time. Gaps were assumed to be elliptical in shape, and the area of each gap was determined using the equation $A = \pi LW/4$ (Runkle 1982), where L is length of the longest axis of the gap and W is the length of the longest axis perpendicular to the length.

Following Mabry et al. (1998), gap ages were determined based on the estimated time elapsed since damage to the gap-makers. Trees damaged within the last year were easily assessed from the presence of green leaf litter or lack of new plant growth on the soil mound created by the uprooted trees. Gap-makers with complete loss of bark and substantial decay of the bole were aged at >10 yr. Gap ages between 2–9 yr were estimated primarily by counting the number of growth rings of nearby seedlings and sprouts after the time of release (years of growth following gap formation). Due to uncertainty in age determination, gaps and damaged trees were divided into four age classes for analysis: ≤1, 2–5, 6–9 and ≥10 yr (Mabry et al. 1998).

Percentage of forest area in gaps was calculated as the total transect distance in gaps divided by the total transect length (Mabry et al. 1998). Canopy turnover time was calculated by dividing the total transect length by the transect length in gaps (Runkle 1992). In order to take into account temporal variation in gap area, canopy turnover time was estimated using gaps of different age groups (≤1, ≤5 and ≤9 yr) following Mabry et al. (1998).

Seedling survey

All seedlings <2.0-m tall located within 50 cm on both sides of each transect were identified to species, with the height measured and divided into three categories: <50 cm, 50–130 cm and 131–200 cm. We did not survey

all seedlings within gaps, only those within 50 cm on each side of the transects.

Understorey light environment

We used hemispherical photography to estimate understorey light availability and variability. Hemispherical photographs were taken at 1.3 m above the ground at 5-m intervals along the transects. Photographs were taken using a 5-megapixel Nikon Coolpix 4500 digital camera (Nikon, Tokyo, JP) equipped with a Nikon FC-E8 fisheye lens (with a combined focal length equivalent to 7.2 mm and combined F number f/2.4). All hemispherical photographs were taken just before sunrise, just after sunset but prior to dusk or on overcast days to avoid reflection of sunlight by foliage and to maximize the contrast between gaps and non-gaps (Rich 1990; Lin & Chiang 2002) between September 2012 and March 2013.

For each hemispherical photograph, we analysed direct site factor (DSF) and indirect site factor (ISF) based on the size and distribution of canopy openings using HemiView 2.15 software (Delta-T 2000; Delta-T Devices Ltd., Cambridge, UK). DSF and ISF are the proportion of direct and indirect (diffuse) solar radiation reaching a given location (i.e. where the photograph was taken), relative to a location with no obstructions (Rich 1990). Based on long-term monitoring, the contributions of direct and indirect solar radiation to total solar radiation were 35% and 65%, respectively (Lin et al. 2003); therefore, we calculated the photosynthetic photon flux density at each sampling location relative to that a location with no obstruction (RPPFD) using the following equation:

$$RPPFD = 0.65\,ISF + 0.35\,DSF$$

Data analysis

We used Pearson's correlation to examine the relationship between gap size (area and length) and number of individuals and species of seedlings in gaps. Contingency tables were used to examine the patterns of gap size distribution (three classes, ≤ 25 m^2, 26–50 m^2 and >50 m^2), damage types of gap-makers (uprooted, standing dead, bole snapped), number of gap-makers within a gap (1 and >1), and ages of gap-makers (≤ 1 and >1 yr) between the 1995 survey (Mabry et al. 1998) and the 2012 survey.

Due to the highly unbalanced sample sizes of RPPFD measurements under gaps vs non-gaps, we adjusted the number of measurements in non-gaps to that in gaps by bootstrapping 10 000 times measurements of equal sample sizes (n = number of measurements in gaps) in both environments. The bootstrapped means were calculated and level of significance (P-value) determined using a two-

tailed test of proportion of cases where bootstrapped means in gaps was more than or equal to those under the closed canopy. The same procedure was performed for bootstrapped coefficient of variation (CV) to test for differences in spatial heterogeneity of RPPFD.

Rarefaction procedures were also used to compare species diversity of seedlings in gaps vs non-gaps. According to a recent Forum in *Ecology* (Ellison 2010), there is a consensus of using number equivalents, such as Hill numbers (Hill 1973), including species richness (S), exponential of Shannon entropy (Exp(H')) and inverse Simpson concentration (1/R) in quantifying diversity. All Hill numbers are in units of 'species', with S most sensitive to rare species, followed by Exp(H') and 1/R (Chao et al. 2012). For each of the three diversity measures, a total of 10 000 bootstrapping cycles were implemented to obtain 95% confidence intervals. For each cycle, an equal number of stems (n = total number of stems in gaps) in both environments was sampled (with replacement). The level of significance in detecting the difference of each diversity measure between gap and non-gap was determined with a two-tailed test, the proportion of cases where diversity measures of bootstrapped stems in non-gaps was more than or equal to those in gaps.

The community similarity of seedlings between gaps and non-gaps were quantified using two abundance-based similarity indices. Morisita-Horn index (C_{MH}) quantifies the probability of selecting the same species from one random sample of each community (Morisita 1959):

$$C_{MH} = \frac{\sum\limits_{i=1}^{S} P_{i1} P_{i2}}{\frac{1}{2}\left(\sum\limits_{i=1}^{S} P_{i1}^2 + \sum\limits_{i=1}^{S} P_{i2}^2\right)}$$

Variable S denotes the total number of species of the two combined communities. P_{i1} and P_{i2} denote relative abundance of each species in gap and non-gap communities, respectively. Morisita-Horn index is based on Simpson's index and thus largely influenced by the dominant species. Horn (1966) developed the Horn similarity index (C_H) based on Shannon entropy:

$$C_H = 1 - \frac{\left(-\sum\limits_{i=1}^{S} \overline{P_i} \log \overline{P_i}\right) - \left(-\frac{1}{2}\sum\limits_{j=1}^{2}\sum\limits_{i=1}^{S} P_{ij} \log P_{ij}\right)}{\log 2}$$

$\overline{P_i}$ is the mean relative abundance of the ith species among two communities. P_{ij} is relative abundance of the ith species in the jth community. Compared to the Morisita-Horn index, rare species have more impact on the Horn index. The 95% confidence intervals of Morisita-Horn and Horn

indices were calculated using the 0.025 and 0.975 percentiles of both index estimates from 10 000 bootstrapped samples of seedlings in gaps and non-gaps, respectively. Both indices range from 0 (two communities with no shared species) to 1 (two communities with identical species relative abundance).

The statistical procedures for analysing RPPFD, species diversity and community similarity were performed using R (R Foundation for Statistical Computing, Vienna, AT).

Results

Gap characteristics

We recorded a total of 17 gaps with a total length of 40.2 m, or 3.3% of the total transect length, which is considerably less than the 26 gaps, or 6% of the transect area, in the 1995 survey (Mabry et al. 1998). There was a gap in transect T4, which had a 12-m high tree (>10 m) inside the gap, and another had a 3-m high tree. Because the two tree crowns were >5 m from the edge of their associated gaps in all directions and covered less than 25%, they were still considered as canopy gaps. No gap was recorded in transect T5. Gaps were widely dispersed, with the distance between two gaps being three to 100 times the length of the gaps. There were 25 gap-makers, more than half (14% or 56%) being uprooted trees, five (20%) snapped trees and six (24%) standing dead trees. The proportions of trees in different damage types were significantly different from the 1995 survey ($\chi^2 = 9.14$, $P = 0.01$; Table 1) where 58% were uprooted trees, 7% bole-snapped and 35% standing dead (Mabry et al. 1998). Ten gaps (59%) had only one gap-maker, six (35%) had two gap-makers and only one gap (5.8%) had three gap-makers. The pattern of gaps with a single gap-maker vs more than one gap-maker is significantly different from that of the 1995 survey, where 77% of gaps were caused by more than one gap-maker (Mabry et al. 1998; $\chi^2 = 5.62$, $P = 0.02$).

The largest gap covered an area of 36.4 m^2 and was associated with two uprooted trees and one snapped tree. Mean gap area was 10 m^2, which is less than a third of the mean gap area of the 1995 survey (Mabry et al. 1998). The proportions of gaps in different size categories (>50, 25–50, <25 m^2) are significantly different from the 1995 survey, with the current survey having more gaps <25 m^2 and no gap >50 m^2 ($\chi^2 = 6.40$, $P = 0.04$; Table 1).

The proportions of gaps created within 1 yr vs >1 yr ago were also significantly different between the two surveys ($\chi^2 = 19.5$, $P < 0.001$; Table 1), with a higher proportion of the gaps created within a year in the 1995 survey (46%; Mabry et al. 1998) than the current survey (17%). Canopy regeneration times based on the 2012 survey (197–398 yr) were considerably longer than those based on the 1995 survey (51–175 yr; Table 1).

Table 1. Gap characteristics of the 1995 and 2012 surveys.

Variables	1995	2012
Mean Gap Area and Range (m^2)	33, 5–110	10, 1.3–36.4
	Number of gaps	
Gap Size Class*		
≤25 m^2	16	16
26–50 m^2	3	1
>50 m^2	7	0
Total Number	26	17
Number of Gap-makers Within a Gap*		
1	6	10
>1	20	7
	%	
Gap Age (%)***		
≤1 yr	46	17
>1 yr	54	83
Type of Gap-maker (%)*		
Uprooted	58	56
Snapped	35	20
Standing dead	7	24
	Regeneration time, yr	
Gap Age		
≤9 yr	175	398
≤5 yr	154	398
≤1 yr	51	197

* and *** indicate significant difference of χ^2 tests between the 1995 and 2012 surveys at $P < 0.05$ and 0.001, respectively.

Understorey light availability and variability

Understorey light availability (RPPFD) was very high, ca. 20% of full sunlight, in both gaps and non-gaps. There was no significant difference in light availability between the two environments ($P = 0.312$; Fig. 1). Similarly, coefficients of variation of RPPFD were not significantly different between gaps (21%) and non-gaps (18%; $P = 0.311$; Fig. 1).

Understorey plant richness and community similarity

We recorded a total of 40 species of seedlings belonging to 14 families, with 12 species from six families occurring in both gaps and non-gaps, while the remaining species only occurred in non-gaps. All species found in gaps are a subset of those found in non-gaps. Only a small percentage of seedlings (7.4% for gaps and 6.7% for non-gaps) were >1.3-m high, the height at which the hemispherical photographs were taken. The three most common species are *Litsea acuminata* (Blume) Kurata, *Engelhardtia roxburghiana* Wall. and *Helicia formosana* Hemsl. (in order of dominance)
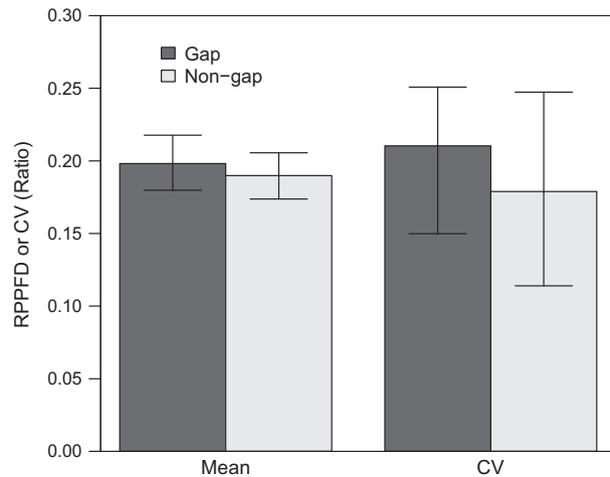
Fig. 1. Mean and coefficient of variation (CV) of relative photosynthetic photon flux density (RPPFD) in gaps and non-gaps. Neither the mean nor the CV was significantly different between gaps and non-gaps at $P = 0.05$.

Fig. 2. Species richness (S), exponential of Shannon entropy (Exp(H')) and inverse Simpson concentration (1/R) of seedling communities in gap and non-gap environments. Error bars represent 95% CI. The significance in each diversity measure between gap and non-gap is denoted by ** ($P < 0.01$) and NS ($P > 0.05$).

in both gaps and non-gaps. Among the three most common species, *E. roxburghiana* is an intermediate shade-tolerant species and the other two species are shade-tolerant (Tsui & Ying 2004; Liou et al. 2006). Neither the number of seedling species nor individuals in a gap were significantly correlated with gap area or gap length (correlation coefficients 0.07–0.45, $P = 0.07$–0.42) probably because of the low variability in gap size because all gaps were small (<40 m²; Table 1).

Both S and Exp(H') were significantly higher in non-gaps than gaps (Fig. 2). There was no significant difference of 1/R between gap and non-gap communities (Fig. 2). Species compositions of seedlings in gaps and non-gaps were very similar. The Horn index of community similarity, which is based on Shannon entropy, was 0.92 (Fig. 2); the Morisita-Horn index of community similarity, which was based on Simpson concentration and thus largely influenced by the dominant species, was 0.97 (Fig. 3).

Discussion

Disturbances that remove portions of the forest canopy are key determinants of biodiversity and forest dynamics, and are likely to be strongly altered through global change processes. Both the temporal and spatial scales of a disturbance dictate how an event will influence the ecology of a forest and, in many cases the ecology of forests is linked to multiple disturbance processes. Canopy gaps are considered a foundational disturbance in forests; however, larger-scale disturbances can potentially alter the ecology of canopy gaps and the function of gap dynamics. In the subtropical broad-leaved forests of our study site, typhoon impacts are relatively frequent and result in defoliation,
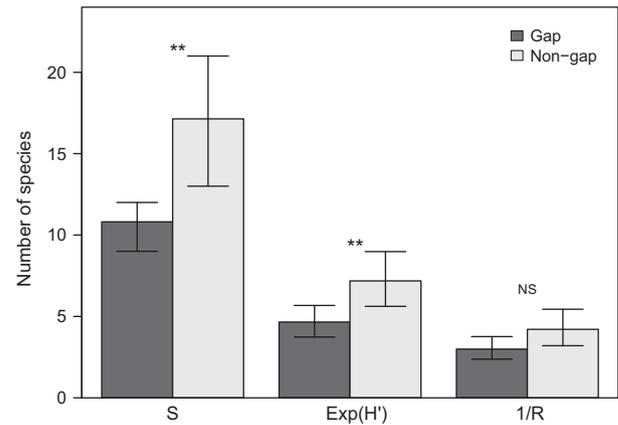

Fig. 3. Community similarity of seedlings in gap and non-gap environments. Error bars represent 95% CI.

but tree mortality is relatively infrequent. The first of our surveys documented gaps immediately following a heavy typhoon season and we hypothesized (H_1) that gap size and the proportion of forest area in gaps would differ between the two samplings. In fact, there was a higher number (26) and larger (6%) gap area in the 1995 survey than in the 2012 survey (17 gaps and only 3.3% of area). This is likely the result of much higher typhoon impact in 1994, when six typhoons affected the forest, four of which were category 3, a record number of typhoons making landfall in northeast Taiwan in 1 yr. In contrast, only one category 2 typhoon affected our study site in 2012 (Central Weather Bureau 2013). The typhoon impacts in 1994 are likely responsible for the greater proportion of gaps with multiple gap-makers and the shorter canopy regeneration time, based on comparison of the 1995 survey compared to the more recent survey. The percentage of the forest in gaps in the recent survey (3.3%) was lower than in 1995

(6%); however, both values were higher than the 0.5–2.0% reported in many temperate and tropical forests (Canham et al. 1990; Yamamoto 1992). This is likely due to more frequent typhoon disturbance in Taiwan than in other regions. If the frequency of intense tropical cyclones increases as predicted in several studies (Elsner et al. 2010; Knutson et al. 2010), our findings suggest that gap fraction will increase and forest regeneration time will decrease as a result (Lawton & Putz 1988; Liu & Hytteborn 1991). This would have major implications for biomass accumulation and carbon sequestration in forests, which have not yet been thoroughly addressed.

Comparing gap patterns from multiple surveys on the same site following periods of varying disturbance intensities/frequencies provides an important technique for measuring forest dynamics (Runkle 1998). For example, by remapping some of the same plots surveyed 50 yr ago, Hytteborn & Verwijst (2014) 'revealed that structural differences between patches did not represent a chronosequence, but rather resulted from overlying tree groups released by different disturbance events'. Our study illustrates that in regions experiencing frequent disturbance events, which are highly variable in time and intensity, results from a single survey represent only a small portion of the entire picture of gap-phase regeneration.

Understorey light availability did not differ between gap and non-gap environments in the study forest, refuting our second hypothesis (H_2), indicating that gaps are functionally equivalent to non-gaps in our system. This challenges the presumption of higher light availability in gap than non-gap environments and could be related to annual typhoon disturbance leading to canopy thinning and increased light availability in non-gaps. Understorey light levels in most tropical and temperate forests are <5% of levels in the open (Canham et al. 1990). McCarthy (2001) reported that in many tropical forests, light level in a gap may reach 9% of that above the canopy for gaps of ca. 200 m^2 and 20–35% for gaps of >400 m^2. The light level in our non-gaps was ca. 20% of that above the canopy, although our gaps were all <40 m^2 (see also Lin et al. 2011). These findings suggest that defoliation events could, in effect, homogenize the light environment on the forest floor.

The species diversity between gaps and non-gaps was significantly different in terms of species richness (S), as was Shannon entropy (Exp(H')), which were both highly influenced by rare species. In both cases, non-gap environments had higher values than gap areas, refuting our hypothesis (H_3). All species found in gaps were a subset of those in non-gaps. The exclusion of rare species in the gap environment resulted in a significantly lower S and Exp (H'). In contrast, the inverse Simpson concentration (1/R),

which is largely influenced by the dominant species, was not significantly different between seedling communities in gaps and non-gaps. This is reflected in the relatively high abundance of gap species in the non-gap environment. Indeed, we found high community similarity between seedling communities of gap and non-gap environments, refuting our final hypothesis (H_4). These findings, taken together, suggest similar environmental filters and/or biotic interactions in the two environments (gap and non-gap) resulting in similar species pools. It is likely that in this forest type with gaps in the size classes found in this study, gaps do not provide unique niches that are not available in the non-gap understorey. Further, the results suggest that gap environments are areas of lower diversity than the surrounding forest matrix. Potential ecological explanations for lower diversity within gaps include: increased soil drying from sun exposure and/or herbivory because of higher visibility of species. These findings, overall, are very different from reports from many tropical forests in which seedlings of shade-intolerant species require gaps for maintaining their niche in the forest (Denslow 1987; Whitmore 1989; Canham et al. 1990). The lack of a unique niche contributed by gaps is further supported by the fact that all gap seedling species were also found in non-gaps. The forest gap dynamics paradigm relies on the presumption that gaps represent a unique niche space with high resource availability. Our results suggest that defoliation events, particularly if they are chronic, may invalidate the assumption that gaps are a surrogate for added resource availability.

In summary, in the subtropical forest in this study, frequent typhoon-induced defoliation maintains high light availability in non-gaps, leading to a lack of difference in light availability between gaps and non-gaps. The similar light environment, in turn, leads to high seedling community similarity in gaps and non-gaps and a lack of seedling species unique to gaps. The data suggest that gaps in this forest system play a neutral role in maintaining forest plant diversity due to the neutral effect of gaps on understorey light availability and heterogeneity. Our study also refutes the generally assumed higher light availability in gaps than non-gaps. The role of gaps in forest dynamics has been challenged for several decades, and the neutral role of gaps on species diversity was proposed at the end of the last century (Lieberman et al. 1989; Hubbell et al. 1999; Gravel et al. 2010). Thus, although annual tropical cyclone disturbance in our study site may be exceptional in studies of canopy gap dynamics, the neutral role reported here is not. Rather, our study represents an unreported system in which frequent typhoon disturbance diminishes differences in resource availability between gaps and non-gaps. In an era of enhanced storms related to climate change (Knutson et al. 2010; Woollings et al. 2012) and

increasing invasions of insects capable of defoliation (Gandhi & Herms 2009; Lovett et al. 2013), one previously unstudied environmental effect may be homogenization of the environment on the forest floor. Future work is needed to test this theory using sites with a wide range of disturbance histories.

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