



Do composition and richness of woody plants vary between gaps and closed canopy patches in subtropical forests?

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Canopy gap; Density effect; Disturbance; Gap partition; Sapling; Seedling; Species accumulation curve; Species richness; Survival–growth trade-off

Nomenclature

Grierson & Long (1983–2001)

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Abstract

Questions: Do composition and richness of woody plants differ between gaps and closed canopy in subtropical forests, and does this difference vary across life stages of tree species? Is tree species richness in gaps a function of regeneration density?

Location: Subtropical *Shorea robusta* Gaertn (Sal) forest, central Nepal.

Methods: We collected vegetation data from two old-growth *S. robusta* forest stands. We sampled 128 plots of 100 m² equally spread between the two habitats: gap and closed canopy. In each plot, we recorded the total number of woody species, number of individuals of seedlings and saplings of tree species and measured the DBH of all saplings. We compared species richness and composition of total woody species, seedlings and saplings between the two habitats. We used ordination to analyse species composition, and an individual-based species accumulation curves to illustrate the effect of density on species richness.

Results: The species composition of total woody species and seedlings was similar in both habitats, but species composition of saplings differed between habitats. Total woody and seedling richness were similar between habitats at one site, but were richer under closed canopy at the other site. Sapling richness was higher in gaps at both sites and was a function of stem density at one site, but not at the other site.

Conclusions: Gaps are not always areas of higher woody species richness and therefore may be less important than expected for the overall species richness of woody plants. Instead, they are potentially important for enhancing local tree richness by increasing sapling richness. Gap disturbance is the primary driver of structural heterogeneity in forests where topographic and edaphic gradients are negligible.

Introduction

Forest canopy gaps differ from closed canopy or shaded understorey in terms of space, resources and, probably most importantly, light availability (Denslow 1987; Canham et al. 1990). Death and removal of dominant individuals also change the competitive hierarchy among the species in a forest, and different species will be favoured for growth in open areas compared to areas under a closed canopy. As a consequence, gaps and closed canopy areas are expected to support germination and growth of different suites of species, resulting in different composition and

richness between them (Denslow 1987; Swaine & Whitmore 1988; Vilhar et al. 2015).

Gaps can create higher richness compared to closed-canopy forests at different scales. At local scale a specific gap site is richer than its corresponding closed-canopy site (higher α -diversity), and at a broader scale forests with a mosaic of gaps have higher total richness than closed canopy forest (higher γ -diversity; Connell 1978; Denslow 1987; Muscolo et al. 2014). Gap partitioning *sensu* niche partitioning – a phenomenon by which species spatially partition space and resources in forest gaps from the gap centre to the edge (Grubb

1977; Denslow 1980, 1987) – is the main explanation for multispecies co-existence and consequent higher richness in the gaps. Besides niche partitioning, the disturbance creating the gaps is expected to reduce the effect of competitive exclusion by removing the canopy dominant from the forest, which may lead to higher species richness in the gaps (Connell 1978). Alternatively, it is also argued that higher richness in a gap is a positive function of the number of individuals (the density hypothesis; Brokaw & Busing 2000).

The gap partitioning hypothesis posits that gaps have a heterogeneous microenvironment due to within- and among-gap gradients in light and resources; such gradients are often associated with gap size (Ricklefs 1977; Denslow 1980, 1987; Brandani et al. 1988; Canham et al. 1990; Vilhar et al. 2015). Species with different resource requirements and competitive abilities can partition the available space according to the environmental differences along the gradients from the centre of the gap to a closed canopy, which in turn is likely to increase the species co-existence and richness in the gaps (Ricklefs 1977; Denslow 1980, 1987; Brandani et al. 1988; Lundholm 2009; Kern et al. 2013). However, prevalence of resource and microclimatic gradients within and among gaps do not necessarily lead to gap partitioning and higher richness (Hubbell et al. 1999; Brokaw & Busing 2000). Post-gap succession may also be contingent on competition between life forms (Schnitzer & Carson 2010), dispersal and recruitment limitations (Hubbell et al. 1999), and gap filling through advanced regeneration (Uhl et al. 1988). These processes may prevent gap partitioning and impede the potential richness (Hubbell et al. 1999; Brokaw & Busing 2000).

The density hypothesis asserts that gaps are sites of higher densities of individuals, and the observed higher richness is simply a function of higher density of smaller individuals (Denslow 1995; Busing & White 1997; Hubbell et al. 1999). Gap disturbance initiates gap-phase succession, which is characterized by an increase in density and growth of seedlings and saplings (Brokaw 1985; Chazdon 2014). Gap partitioning may be the most likely explanation for higher species richness in the gap, given that the richness is independent of the stem density (Brokaw & Busing 2000).

In gap-phase succession, all trees and woody species undergo rapid thinning with time after establishment of seedlings and saplings, and the thinning rate is species-specific (Runkle 2013). The species-specific thinning in the shade and the gap increase the likelihood of observing gap partitioning at the sapling stage (Dalling et al. 1998; Hart & Kupfer 2011; Runkle 2013; Cowden et al. 2014). Moreover, there are differences in the niche among life stages of trees (Grubb 1977; Poorter et al. 2005);

therefore, sapling composition may not parallel seedling composition between contrasting light regimes. It is therefore useful to analyse seedling and sapling composition separately between habitats in order to reveal whether differences in species composition are apparent only in a certain regeneration phase or life stage.

A comparison of richness between gap and closed-canopy plots is necessary to assess whether the gap plays a role in maintaining/enhancing species diversity in forests. However, there are very few studies that actually make such comparisons, as in Schnitzer & Carson (2001; but see McCarthy 2001). The few existing empirical studies making such comparisons are from either hyper-diverse tropical forest or low-diversity temperate forest (McCarthy 2001). Other studies assessing gap richness also suffer from methodological biases when they compare richness between sites that have different densities of individuals, as higher density may lead to higher richness (Kobe 1999a, b). To see if the richness differences are purely an effect of number of individuals, comparison of gaps and closed canopy should be standardized by the number of individuals (Chazdon et al. 1999). Understanding how species richness and composition across life stages vary in gaps and closed canopy is necessary for understanding how survival–growth trade-offs between regeneration stages in spatio-temporally varying environments contribute to the maintenance of woody species richness and co-existence in forests.

Subtropical *Shorea robusta* (Sal) forest is different from tropical and temperate forests in terms of diversity, light regime and canopy architecture, but has rarely been considered in gap disturbance and diversity-related studies. This paper compares plant species composition and richness between gaps and closed canopy areas in two Sal forest stands on the southern plains of Nepal. We aim to analyse: (1) differences in composition and richness of woody plants between gaps and closed-canopy plots; (2) whether the richness and composition patterns between habitats differ with the regeneration stage of trees; and (3) whether observed patterns are related to the effect of density of individuals. We propose that a compositional difference is expected due to different light regimes. We hypothesize that species richness (for the both regeneration stages of trees) will be higher in the gaps than under the closed canopy, consistent with conventional gap–disturbance theory. Richness will also be evaluated against the number of individuals using individual-based species accumulation curves to ascertain if richness in the gaps is a function of density. We do not test gap partitioning *per se*, rather we argue that if richness is higher in the gaps and is independent of stem density, it is most likely to be related to gap partitioning.

Methods

Study area

This study was conducted in the Chitwan district of Nepal. Chitwan is a dun valley between two Siwalik ranges. Dun valleys, like the Terai, are mainly flat land, made up of foreland basin deposits of Himalayan origin. Soil of the valley is largely homogenous, except for grain size variation in riverine habitats; mainly composed of quaternary alluvial deposits consisting of sandy loam, loam and clay developed over sand, gravel and boulders (Wesche 1996; Miehe et al. 2015). The climate is subtropical and monsoonal, with humid and hot summers and dry and cold winters. Average annual rainfall is 2200 mm (1971–2010), of which 80% falls during the monsoon (Jun to Aug), and average annual temperature is 24.6 °C (2000–2010; CBS 2011).

Shorea robusta (Sal) stands in the northern part of the Barandabhar Corridor Forest (BCF, site I) and the Kasara area of Chitwan National Park (CNP, site II) were sampled; these two sites are *ca.* 26 km apart. The areas of BCF and CNP are 105 and 932 km², respectively. The BCF is a north–south-oriented narrow strip of forest in the densely populated area of Chitwan and connects CNP with the Siwalik/Mahabharata range (Fig. 1). CNP – a UNESCO World Heritage site established in 1973 – is famous for the conservation of wildlife, including the one-horned rhino

and Bengal tiger. The forests at both sites are dominated by old-growth Sal stands with some riverine vegetation along streams and sand deposits. Sal is a member of Dipterocarpaceae, a tropical family mainly distributed in the Indo-Malayan region, and forms extensive mono-dominant forests in the southern part of the Himalayas, in the tropical to subtropical climate of the Indian subcontinent. Sal is a robust, gregarious and semi-deciduous tree species, and is an important high-value timber species extensively used in construction and furnishing. Sal-dominated forest, with *Dillenia pentagyna* as main subcanopy species, sandy loam soil, plain topography and similar climate are shared features of the two sites. Site I is slightly higher (220 m a.s.l.) than site II (180 m a.s.l.). *Clerodendrum viscosum* and *Lea crispa* at site I, and *Thameda arundanacea* and *Diplazium esculentum* at site II are the dominant sub-canopy species.

Forest management and disturbance

The two forests differ in management regime, and hence use and disturbance intensity. Forest at site I is used by local people for forest products, firewood, fodder and timber, and for grazing livestock (Wesche 1996). Site II is in the core area of the park, and is not used for forest biomass extraction or livestock grazing. However, people are occasionally allowed to harvest dry firewood and thatching grass, under monitoring. Rhino, deer and elephant are the

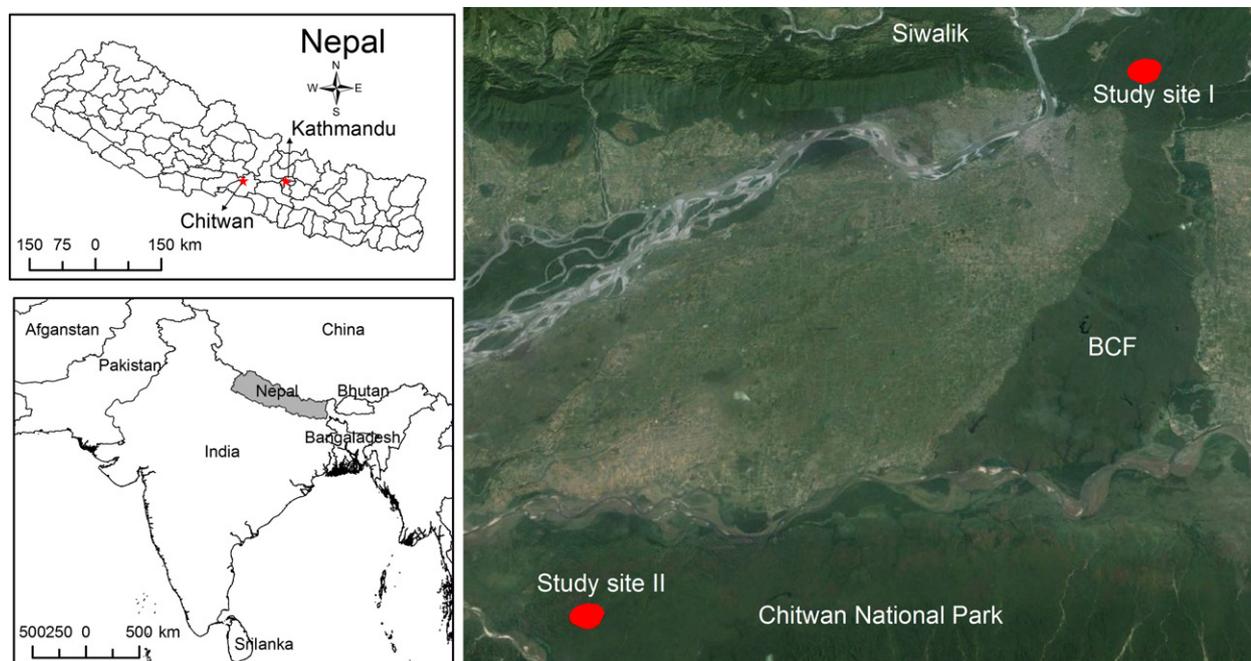


Fig. 1. Location map of the study area showing Chitwan district and the Barandabhar Corridor Forest (BCF – study site I) between Chitwan National Park (CNP – study site II) and the Siwalik mountain range in lower central Nepal. The sites are *ca.* 26 km apart.

main browsers. Fire in the ground stratum during dry season (Apr–May) is common at both sites, but the frequency is higher at site I.

Both sites have a mosaic of gaps and closed canopy patches formed by natural and anthropogenic disturbances. A gap may be formed by the death or removal of a single or multiple trees (Sapkota & Oden 2009). Sal is the exclusive gap maker at both sites. Gap formation was caused by natural death and windthrow at site II, and natural as well as anthropogenic felling at site I.

Sampling design

Sampling was designed to compare species composition and richness between the two habitats (gap and closed canopy) within a forest. We define a gap as an area where the canopy was opened by a gap $> 100 \text{ m}^2$, and we did not set an upper limit of gap size, as did McCarthy (2001). Setting the lower limit at 100 m^2 is admittedly somewhat arbitrary, but it avoids gaps caused mainly by branch breakage and smaller than the plot size. We define canopy or closed canopy as an area where crown cover is $>40\%$ and trees forming the crown cover are $>25 \text{ m}$ tall. We placed plots under the canopy where it was continuous and the canopy cover immediately above and around the plot was more or less homogenous, but avoided canopy formed by only one or two isolated trees to ensure that plots were under a 'true canopy'. We also avoided canopy formed by trees that were approaching gap-filling height of 15–20 m; this consequently excluded older gaps.

Vegetation data were collected in plots of $10 \text{ m} \times 10 \text{ m}$ (0.01 ha) laid out along two transect lines in each site, which were at least 400 m apart. In each site, we aimed to place plots (representing both habitats) along a azimuthal line at regular intervals of 100 m, but due to our definitions of canopy and gap we allowed for distances of up to 80 m left and right from the line; plots in a transect may or may not be paired. Areas with streams, marshlands, trails or unusual disturbances on the ground were avoided. An equal number of plots (32) in the gaps and in closed canopy (32) were sampled at each of the two sites, yielding a total of 128 plots.

We included only woody vegetation that encompassed all species with woody stems. In a one-time sampling design, a considerable fraction of the herbaceous species would have been missed, hence we did not include herbaceous species. We recorded all the species of trees, shrubs and woody climbers present in a plot and pooled them to obtain total richness of woody species, hereafter called 'total woody species'. Individuals of tree species were categorized into two regeneration stages: seedling (10–150 cm tall) and sapling (height $> 150 \text{ cm}$ and $\text{DBH} < 10 \text{ cm}$). We thus have three groups: total woody, seedlings and

saplings; the latter two are life or regeneration stages of trees, to compare between habitats for their composition and richness. We counted the number of individuals of seedlings and saplings for each species, and measured DBH (137 cm above ground) of saplings. We also counted the number of individuals of mature trees ($\text{DBH} > 10 \text{ cm}$) at site II; they were not considered for site I as their density/richness was influenced by illegal and preferential harvesting of mature trees. We measured the extended gap area and considered gaps to be ellipsoidal following the protocol of Runkle (1992). We also identified the gap-forming trees and the causes of gap formation by observing snags, stumps and logs. Canopy cover was measured using a spherical densiometer. Plant species were identified using Grierson & Long (1983–2001). We also estimated the ground vegetation cover as percentage (up to 1-m tall) in each plot.

Data analyses

Preliminary analyses were done to decide whether to pool the data from the two sites and to check for differences in species composition and richness between sites. The two sites were found to have different species composition in ordination space. Variance of species richness between the two sites was also different for all three metrics. Based on these exploratory analyses we decided to treat the two sites separately.

Detrended correspondence analysis (DCA; Hill & Gauch 1980), an indirect gradient analysis, with supplemental categorical environmental variables, was used to assess the difference in species composition between the two habitats. We also performed constrained ordination to evaluate more directly if the composition of the three groups differs between the two habitats. The purpose of the species composition analysis was to analyse whether gaps and closed-canopy plots had similar sets of species or not. The choice of using abundance or binary data for the analysis was an *ex-post* decision based on the preliminary analysis. Sal shares more than 40% and 50% seedling abundance in sites I and II, respectively. Sal seedling density, in turn, was three times higher in gaps than in the closed canopy at site I; while it was four times more in gaps at site II. Sal alone, therefore, can influence the species composition analysis if abundance data as such are considered in the ordination analysis. To avoid problems associated with these differences in abundance we used presence–absence data in the ordinations. We also used log-transformed abundance data after removing Sal in the ordination, and found that the result was not different from using binary data. We used redundancy analysis (RDA) for all woody species and seedlings, and CCA for saplings; this choice was based on the gradient length of the first DCA axis (RDA when <2.0 and

CCA when >2.0). The direct ordinations were performed with a single binary environmental variable, corresponding to gap or closed canopy. We tested the significance of this variable with a Monte Carlo permutation test with 499 iterations using CANOCO 5 (Šmilauer & Lepš 2014).

We compared species richness (number of species per plot) between habitat types using *t*-tests; we did not consider gap and closed canopy plots to be paired. We also used a rank-abundance curve (RAC) to compare and visualize richness and dominance of seedlings and saplings between the habitats (Magurran 2004). We used log 10 (number of individuals + 1) data to plot the RAC. The pattern of species richness along the gap size was analysed for total woody species, seedlings and saplings separately for the two sites using a GLM (McCullagh & Nelder 1989) with a log-link function. A GLM was used because the response variable (species richness) is count data and the error is assumed to have a Poisson distribution.

To account for differences in the number of individual 'density effects' when comparing species richness between the two habitats, species accumulation curves (SACs) with rarefaction were used (Denslow 1995; Kobe 1999b; Gotelli & Colwell 2001). We also compared sapling richness in gaps with tree richness in gaps and canopy using SAC to ascertain if gaps are really richer than closed canopy. We used individual-based SACs in the vegan package in R (R Foundation for Statistical Computing, Vienna, AT).

Results

General gap attributes

Gap and closed canopy plots were different in terms of tree size and ground cover. Larger-sized trees were present in all the closed canopy plots, while gaps, by definition, had only trees of smaller size. Saplings were more abundant in gap plots than under closed canopy. Total ground cover of vegetation was 35% in gaps and 52% below canopy at site I, while it was 23% and 18% in gaps and closed canopy, respectively, at site II. Mean gap size was 373 and 799 m² at sites I and II, respectively. Sal formed the canopy in 90% of the plots and *Dillenia pentagyna* was the most common sub-canopy tree. Average canopy cover in the closed canopy was 70% at both sites.

Species composition

The DCA showed no difference in species composition of total woody species and seedlings between the two habitats, whereas the composition of saplings was conspicuously different (Fig. 2a,b). Constrained ordination (RDA and CCA) verified this but explained only a small proportion of the variation for all three groups (Table 1), and only

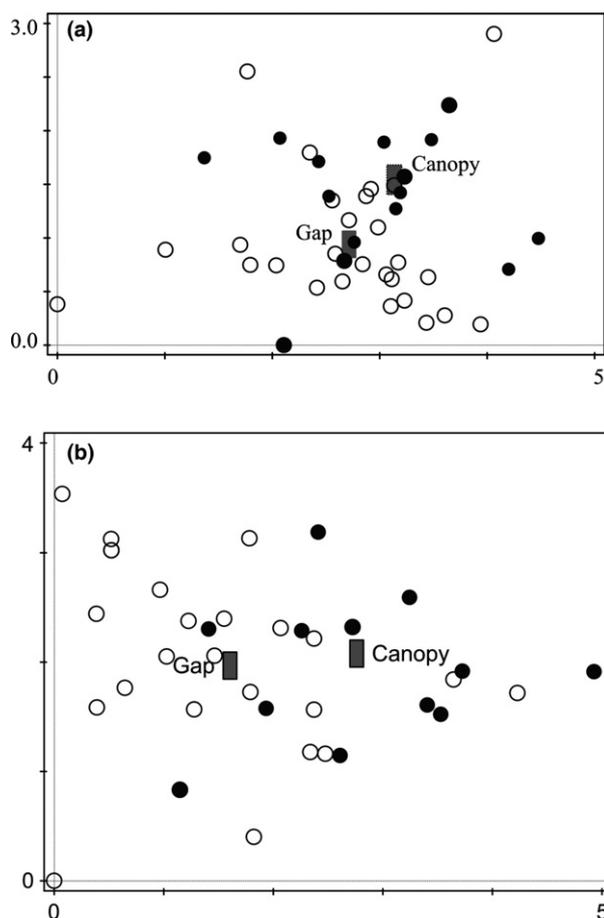


Fig. 2. DCA diagram along first and second ordination axes for saplings for (a) site I and (b) site II. Empty circles are gap plots and filled circles are closed canopy plots, boxes represent habitat types: gap and closed canopy.

Table 1. Summary statistics of the constrained ordination analyses (RDA and CCA). First ordination axis was constrained to environmental variables with gap and closed canopy as categorical variables.

	Site I			Site II		
	TW*	SI*	SP†	TW*	SI*	SP†
Var expl (%)	1.4	1.9	5.3	2.2	2.4	5.1
Pseudo F	0.9	0.9	3	1.4	1.5	2.4
P-value	0.684	0.596	0.002	0.075	0.052	0.002

Var expl, Variance explained; TW, Total woody species; SI, Seedlings; SP, Saplings.

*RDA.

†CCA.

the difference in sapling composition was significant ($P < 0.05$).

The frequency occurrence of seedlings and saplings between habitats also matched the compositional pattern visualized in the ordinations, i.e. similarities in seedlings

and differences in saplings between habitats. Most of the species in the seedling stage had more or less equal frequency of occurrence between the two habitats, and the most common species maintained the trend at both sites (Appendix S1). Contrary to the seedling pattern, almost all of the saplings had a higher frequency in the gaps, and some were restricted to gap plots only: eight out of 23 species at site I and five out of 15 at site II. Sal, the dominant canopy species as well as gap-forming tree at both sites, appeared to be subdominant as a sapling in the gaps of both sites.

Species abundance pattern, as depicted by the steepness of the RAC, also complemented the results visualized by ordination and frequency occurrence diagrams (Fig. 3a,b).

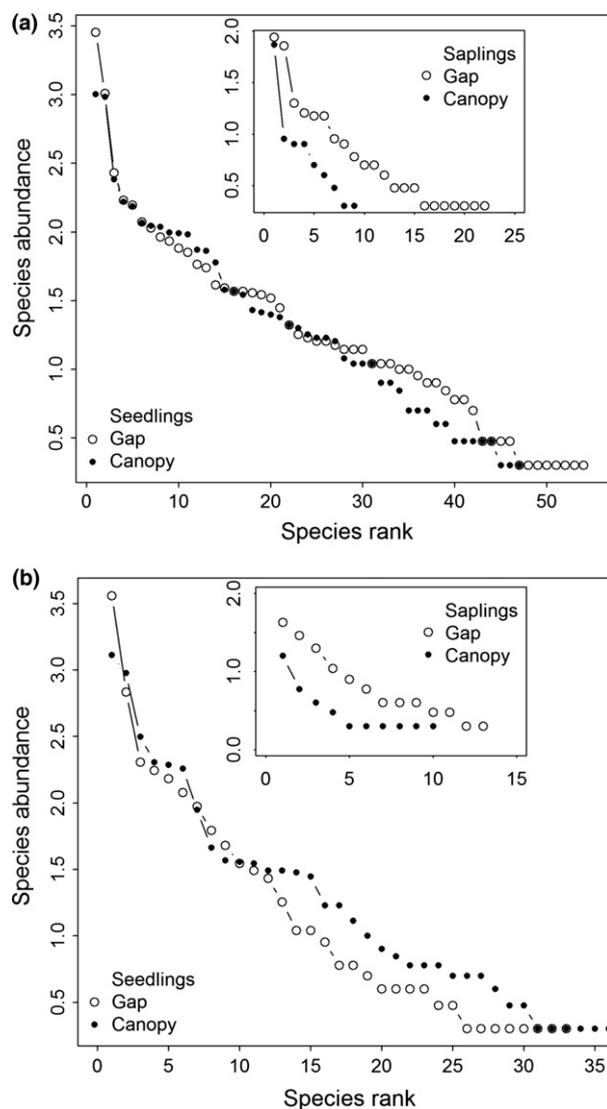


Fig. 3. Rank abundance curves for seedlings and saplings (inset) for (a) site I, and (b) site II. Species abundance is presented as $\log_{10}(\text{density} + 1)$

RAC for saplings in closed canopy plots was steeper and shorter than for the gap plots. The curve suggests that saplings in closed canopy were dominated by a single species, *Dillenia pentagyna* at both sites, and other species were relatively less abundant, while it was dominated by the two species although other species were also common in the gaps.

Species richness and abundance

At site I, we recorded 58 tree, 22 shrub and six climber species, while at site II there were 40 tree, 12 shrub and six climber species (Appendix S2). Sapling richness was a subset of seedling richness at both sites. Gaps and closed canopy plots at site I were similar in terms of total woody and seedling richness, while closed canopy plots were richer than gaps at site II (Table 2). Gaps at both sites had higher sapling richness than in the closed canopy. Total woody and seedling richness did not change along the gap size at either site. Similarly, sapling richness at site II was not a function of the gap size gradient, but at site I it declined with gap size, although the relationship was rather weak (Appendix S3). Mean seedling density (number of individuals per plot) was significantly higher in the gaps than under the closed canopy at both sites (Table 2). Similarly, the mean sapling density in the gaps was more than twice that of the closed canopy at both sites.

The rarefaction SACs between habitats for seedling richness at both sites, and sapling richness at site I, support the test results of richness (Table 2, Fig. 4a,b), i.e. the observed difference in richness between habitat types was reaffirmed after accounting for stem density. At site II, SAC for sapling richness in both habitats (Fig. 4b) ascended together, implying that for an equal number of individuals, richness is the same. Therefore, the observed difference in sapling richness at site II appeared to be a function of the density of plants. Here, saplings in the gaps were as rich as mature trees, but they outnumbered mature trees of closed canopy. Mature trees in the gaps were richer than their counterparts in closed canopy (Fig. 5).

Discussion

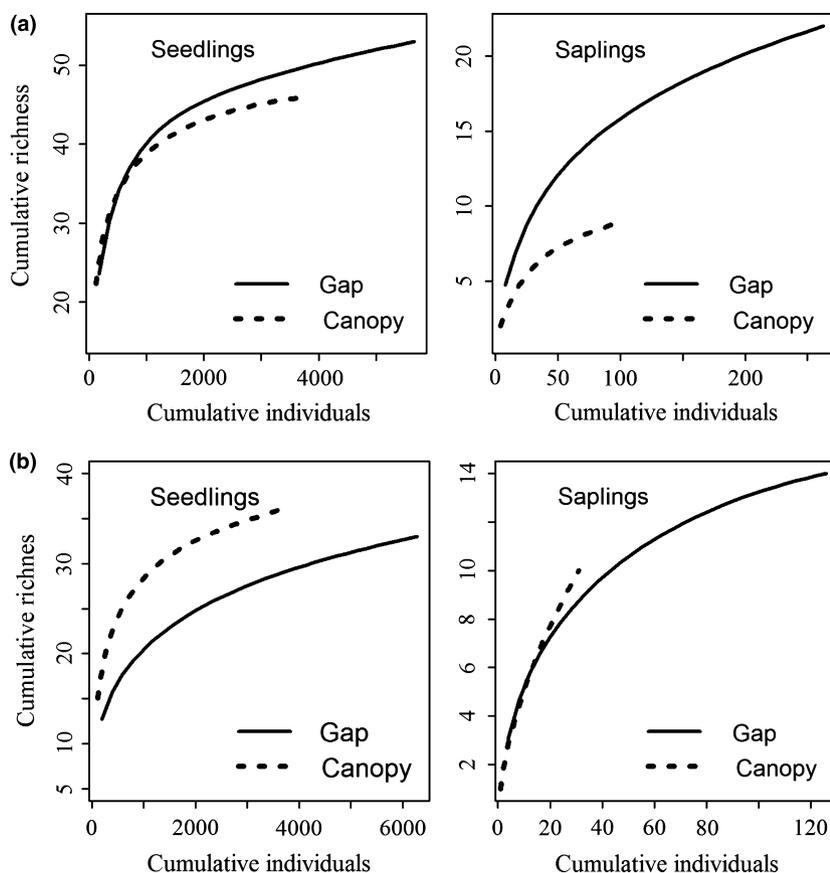
Species composition and dispersal limitations

We did not find any compositional differences in total woody species and seedlings in gaps and closed canopy, such compositional similarities in gap understorey mosaics are not uncommon (Nagel et al. 2010; Yao et al. 2015). Dispersal and recruitment limitations, in addition to the variation in light, are likely to affect species composition in the gaps and closed canopy (Dalling et al. 1998; Hubbell et al. 1999). However, the observed compositional similarity suggests that the majority of species in these forests are

Table 2. Mean and SE of mean for species richness and abundance in gap and closed canopy plots at each site (number of plots in each habitat for each site is 32). The difference in means was tested using Welch t-test.

	Site I - BCF		Site II - CNP	
	Canopy	Gap	Canopy	Gap
Total woody	24.09 ± 0.74	25.66 ± 0.79	15.43 ± 0.60	13.41 ± 0.43**
Richness				
Seedlings	16.44 ± 0.56	17.47 ± 0.68	11.75 ± 0.32	10.16 ± 0.29**
Saplings	1.69 ± 0.18	4.00 ± 0.37***	0.81 ± 0.16	2.28 ± 0.25**
Abundance				
Seedlings	117 ± 6.19	175 ± 13.94***	114 ± 8.39	196 ± 16.07***
Saplings	3.31 ± 0.56	8.22 ± 0.77***	1.0 ± 0.19	3.9 ± 0.49***

*** $P < 0.001$, ** $P < 0.01$.

**Fig. 4.** Species accumulation curves for seedlings and saplings for (a) site I and (b) site II.

not dispersal-limited. Both of the forests are grazed by herbivores, which can potentially homogenize composition in gaps and under closed canopy (Rooney 2009; Holmes & Webster 2011). Additionally, the majority of forest species can grow under varying light environments, and the fact that their juveniles can survive in shade as low-growing individuals (survival in low light) is also a likely explanation for homogeneity in composition in gaps and closed canopy. The ability of species to grow under varying light

environments suggests that the majority of the forest species are generalists rather than niche-differentiated specialists (Lieberman et al. 1995).

The compositional difference between gaps and closed canopy, however, was evident in the saplings for gaps, which had some unique sapling species and higher abundances of those species shared by both habitats. The partitioning of saplings between gaps and closed canopy in the forest may best be explained by the occurrence of spatial

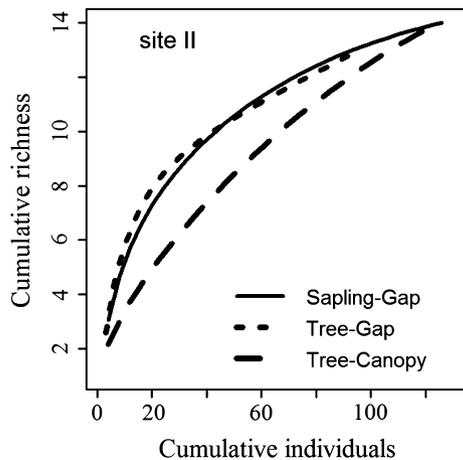


Fig. 5. Comparisons of species accumulation curves of saplings in gaps with trees in both habitats; gaps/closed canopy, at site II.

variation in light between the two habitats, the requirement of light for growth release of such plants (Kobe 1999a; Ruger et al. 2009; Philipson et al. 2012) and selective mortality of seedlings along the successional chronosequence. Light is the most limiting resource for plant growth under a closed canopy and growth spurts are apparent upon exposure to higher light (Montgomery & Chazdon 2002; Ruger et al. 2009; Philipson et al. 2012). Higher abundance of some light-demanding species, e.g. *Shorea robusta*, *Terminalia alata*, *Litsea monopetala* and *Mallotus philippensis*, in the gaps confirms their gap-dependent growth. The higher abundance of subdominant species in the gaps may increase their likelihood of establishment, thus gaps provide an opportunity for infrequent and subdominant species to establish. The most abundant species in the sapling stage at both sites – *Shorea robusta* and *Dillenia pentagyna* – are known for fire tolerance (Wesche 1996). Fire, along with light, may act as a filter in the seedling to sapling transition.

The similarity in seedling, but differences in sapling composition, in gaps and closed canopy clearly indicate that there is a life-stage trade-off between survival in low light and growth in high light (survival–growth trade-off). This segregation of life stages of trees in spatio-temporally varying environments is a plausible explanation for the observed seedling–sapling patterns in the Sal forest, and a potential mechanism for species co-existence in forest ecosystems (Wright 2002).

Total woody species and seedling richness: Gaps are not always richer

We did not find higher richness of total woody species and seedlings in gaps compared to closed canopy; instead the opposite was true for site II. However, for saplings our

hypothesis stands, as total and mean sapling richness was markedly higher in the gap plots at both sites (saplings are discussed in the following section). These findings contradict the conventional forest gap disturbance theories, which expect higher richness in the gap environment (Connell 1978; Denslow 1980, 1987); gaps are reported to be richer than closed canopy in tropical forests (Busing & White 1997; Hubbell et al. 1999; Schnitzer & Carson 2001). Our results show that species richness (total woody species and seedlings) is not related to the gap size gradient. A negative, but weak, relationship of sapling richness at one site but not the other indicates that richness and gap size relationship are not a generalizable phenomenon. Individual studies also do not confirm the relationship as a consistent pattern, as some report no relationship (Obiri & Lawes 2004; Nagel et al. 2010), while others find a positive relationship between them (Denslow 1980; Kern et al. 2013), at least for shade-intolerant species.

Competition between different plant life forms in the post-gap succession may prevent the gap from attaining its potential richness. Liana, dense shrub and high grass cover, individually or in combination, can preclude or suppress tree regeneration, and in some cases even alter the successional trajectory in canopy gaps, thus preventing canopy gaps from achieving higher richness (Royo & Carson 2006; Schnitzer & Carson 2010). At site II, the grass *Themeda arundanacea* had substantially higher cover in gap plots relative to closed canopy plots, and may have inhibited woody and tree species richness. Higher grass cover in gaps may reduce tree recruitment or seedling survivorship by acting as a biological filter (Royo & Carson 2006). However, our coarse estimation of grass cover did not allow us to draw inferences on grass cover and species richness relationships.

Compositional similarity between habitats indicates that seedlings can survive in both habitats, which is the likely explanation for similar richness of total woody species and seedlings in this study. Even in the shaded understorey, light penetrates through discrete openings between the leaves and nearby gaps, which makes some light available below the canopy (Canham et al. 1990; Yao et al. 2015), and this may be enough for species to survive at a low growth rate under the canopy (Montgomery & Chazdon 2002). Sal forest foliage density and vertical stratification allow some light through to the ground layer so the effect of shade is less strict than in more densely foliated and multi-layered tropical forests.

Gaps are richer in saplings

We found higher richness and density of saplings in the gaps. Our result contradicts the findings of Sapkota et al. (2009) from a similar forest in the region, and a few other

studies from elsewhere (Uhl et al. 1988; Busing & White 1997; Nagel et al. 2010), which report that gaps do not enhance sapling density and richness. These studies argue that gaps may be occupied by advance regeneration of shade-tolerant species. However, more species-rich gaps in the sapling stage are not uncommon (Hart & Kupfer 2011; Cowden et al. 2014).

Higher sapling richness in the gap is related to the requirement for light for growth of seedlings. Light availability in the gap increases the likelihood of seedlings establishing into saplings (growth in higher light). Gaps at both sites were not only richer but also had a higher density of saplings; this increased richness is likely to be associated with stem density. The observed high richness in gaps in tropical forests has been attributed to a higher number of individuals and is considered as 'spurious' richness (Hubbell et al. 1999). SACs suggested higher richness in the gaps at site I, but for site II richness was similar between the two habitats. Our SACs suggested there was no 'density effect' for saplings at one site, while an effect was apparent at the other site. Regardless of whether higher sapling richness is independent of stem density or not, a considerable fraction of the saplings were exclusively present in gaps at both sites, supporting the idea that gaps are important sites for tree regeneration and diversity. The comparison of mature trees between habitats, as visualized with SACs, rejects that gap richness is a function of stem density, supports that gaps are richer than closed canopy and reaffirms the importance of gap disturbance in maintaining tree richness in subtropical forests.

Conclusions

Survival–growth trade-offs between life stages of trees in gap–understorey mosaics is the most plausible explanation for similar seedling but different sapling composition and richness in the contrasting light environments. Gap partitioning as a mechanism for species co-existence in the gaps is a rather weak explanation, considering total woody species and seedling richness in our study. The higher richness of saplings in the gaps may or may not be a function of stem density; nevertheless, this higher richness and the occurrence of some gap-specific saplings supports the idea that gaps provide important regeneration niches for some tree species. Higher sapling richness in gaps and spatial segregation of tree life stages between gap and closed canopy environments indicate that gap creation could be used as a management strategy to enhance tree species richness and structural heterogeneity. We conclude that the role of gaps in enhancing overall woody species richness in subtropical forest may not be as critical as previously thought, but that gaps are important in maintaining tree richness.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species composition as depicted by the frequency of seedlings and saplings.

Appendix S2. List of all woody species (trees, shrubs and climbers) recorded in both study sites.

Appendix S3. Generalized linear model (GLM) summary statistics.