Research Article

The fate of five rare tree species after logging in a tropical limestone forest (Xuan Son National Park, northern Vietnam)

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Abstract

Rare tropical tree species are endangered due to the disappearance of old-growth forests. Although some undisturbed old-growth and formerly logged forests are protected today, the extent to which rare tree species persist and regenerate in such logged forests is often unclear. In a forested area over limestone in northern Vietnam, we studied the fate of five rare tree species after decades of logging and subsequent nine years of full protection, in comparison with an un-logged forest. Three of the studied species are largely restricted to limestone hills (*Excentrodendron tonkinense*, *Chukrasia tabularis* and *Garcinia fagraeoides*), while two of the species have a wider distribution (*Parashorea chinensis* and *Melientha suavis*). The bigger trees of the study species had lower densities and/or differences in the diameter distributions between the two forest types, indicating that these species had formerly been cut. The regeneration stem density of the study species was much lower (46% in *M. suavis* to 80% in *P. chinensis*) in the logged than un-logged forest. In the un-logged forest, we found clear relationships between ecological factors and regeneration density in four of the five study species; e.g., the regeneration of *E. tonkinense* increased with increasing rock-outcrop cover (r = 0.6, p < 0.01). Such relationships were almost absent in the logged forest. The widely distributed generalist species *Cleidion javanicum* dominated in the tree regeneration of the logged forest. Our results suggest that the studied rare tree species still existed as adults after logging and there was regeneration but at low densities. We assume that the potential for recovery remains, which further justifies the full protection of this and other restoration areas.

Keywords: Biodiversity conservation, endangered species, karst, logged forest, un-logged forest.

Introduction

With the loss of tropical old-growth forest, many tree species, and particularly rare ones, have become endangered. Rare species can be characterized by at least one of three factors: restricted geographical range, high habitat specificity, and/or small local population sizes [1]. For tropical tree species, habitat specialization and regeneration characteristics are considered to be of great importance to conservation [2].

Some remaining forest areas are protected today, many in the form of national parks. The entire conservation area often comprises near-natural vegetation as well as restoration areas on former anthropogenically disturbed sites. Among the human activities in forest transformation, selective logging is thought to cause less disturbance and impact on tropical biodiversity [3-4], although it does modify habitat heterogeneity and alters the competitive balance among tree species [5], affecting species composition and diversity of the disturbed forest [6-8]. Whether rare tree species persist and regenerate in formerly logged forests is therefore often unclear.

In the literature, we found examples of lack of regeneration [9-12] but also for regeneration success [8, 13-15] in rare tree species. Rare species are often considered poor competitors [16-19], suggesting that habitat disturbances such as logging may be advantageous to some rare species. Gaps in the canopy created by the removal of larger trees can promote both higher seedling/sapling survival rates and seed production among residual individuals of rare tree species (as e.g. discussed by Jensen and Meilby [13]). On the other hand, habitat destruction, the overharvesting of mature individuals, poor seed germination, and the lack of seed dispersal can also lead to failure of rare tree regeneration [e.g. 20].

Clearly, site conditions play an important role for regeneration, and among those habitats considered problematic, limestone karst is a prominent example. Tropical limestone forests and karsts often contain high plant diversity combined with a high degree of endemism, and are referred to as 'arks of biodiversity' [21]. Some karst species are specialists for rocky, dry and alkaline sites [21-22], while on other sites they may be less abundant due to inter-specific competition [23]. For humans, limestone areas are usually difficult to access due to their rugged topography and steep slopes, although logging and forest disturbances are still widespread [24-25].

This study was conducted in a tropical limestone forest in northern Vietnam and focuses on five red-listed tree species, which provide timber and/or non-timber forest products. Three of the species (*Excentrodendron tonkinense* [Gagnep.] Chang & M, *Chukrasia tabularis* A. Juss., and *Garcinia fagraeoides* A. Chev.) are considered specialists for limestone hills. The two other species (*Parashorea chinensis* H. Wang and *Melientha suavis* Pierre) have a wider ecological distribution range, but are commonly recorded at low population densities [26-28]. We studied fully protected, near-natural forest without signs of disturbance, as well as forest areas logged for decades and subsequently protected for nine years before we began field work for this study. We asked: 1) whether the rare tree species still exist as adults in the logged forest; 2) whether they regenerate; and 3) if so, which ecological factors control the regeneration. We hope this study will improve understanding of the ecology of the studied tree species, and also help extend fully protected zones into areas that formerly experienced logging.

Methods

Study area

The study was conducted in the Xuan Son National Park (21° 03'-21° 12 N, 104° 51'-105° 01' E), which is located in Phu Tho province, northern Vietnam (Fig. 1). The forested area of Xuan Son was established as

a nature reserve in 1986 and declared a National Park in 2002. The Park covers an area of 15,048 ha and is surrounded by a buffer zone of 18,639 ha. The topography is characterized by many steep mountains, with altitudes ranging from 200 to 1,386 m a.s.l. The area has a tropical monsoon climate, with relatively cold winters from November to March, and relatively hot summers; the mean annual temperature is 22.5 ºC and the average annual rainfall is 1,826 mm [29]. Approximately 17% of the National Park is comprised of lowland and lower montane evergreen forests on limestone, which are dominated by broadleaf evergreen tree species from the families Sapindaceae (*Amesiodendron chinense* (Merr.) Hu), Meliaceae (*Aphanamixis grandiflora* Blume) and Euphorbiaceae (*Cleidion spp.*) [29-30].
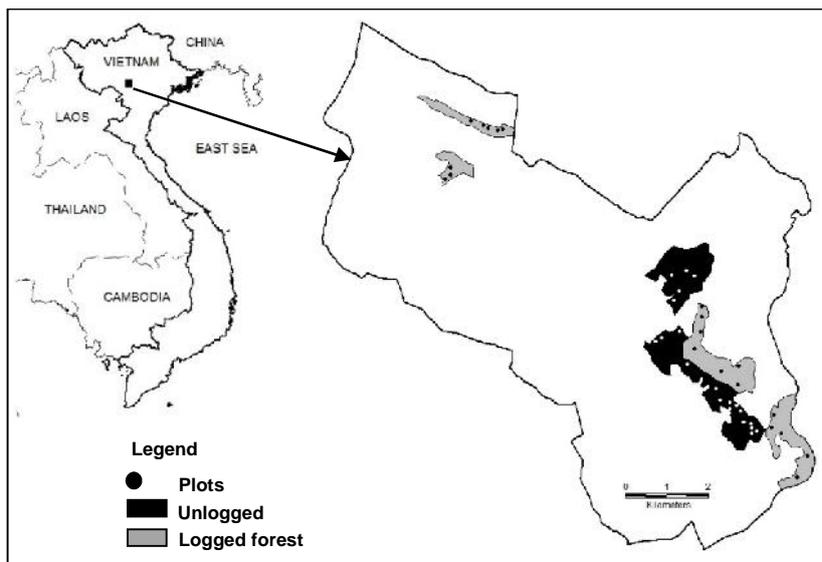

Fig. 1. Location of the study areas in the Xuan Son National Park and sample plots, northern Vietnam. The study region is surrounded by the commune boundary (bold line); the white-filled area includes non-limestone forests, limestone forests (above 700 m a.s.l.) and other land-use types.

Site selection and study species
Field work was carried out in 2010 and 2011 in un-logged and logged forest areas. The identification and delimitation of the study site were based on a map of the vegetation status [31] of the area along with a reconnaissance survey. The un-logged forest area comprised 350 ha while the logged forest covered 328 ha, and both are very similar in topography and altitude (Table 1).

The un-logged forest had experienced little or no human disturbance and was characterized by an abundance of trees of comparatively large diameter, with no stumps evident. The logged forest was intensively logged before 1992, followed by a period of small-scale illegal logging until 2002, at which point the forest was designated for conservation and became subject to strict protection [29]. The consequences of former logging activities are still evident throughout the study plots in the form of stumps, abandoned timber, and footpaths. Although there is little robust data on the intensity or extent of logging before 2002, long-term residents and former loggers recount that timber trees were logged mostly for commercial or domestic purposes and included species such as *Parashorea chinensis*, *Excentrodendron tonkinense*, *Chukrasia tabularis*, *Garcinia fagraeoides*, *Amesiodendron chinense*, *Paviesia annamensis*, *Markhamia stipulata* and *Vatica subglabra*. Some other species were subject to (partial) harvesting for food, medicines, and the construction of domestic and trade goods (e.g. *Melientha suavis*, *Canarium tramdenum*, *Michelia balansae*, *Schefflera heptaphylla*).

Table 1. General attributes of un-logged and logged forests; n = 20 plots per forest type. Lower case letters indicate significant differences in the Mann-Whitney test (p ≤ 0.05).

	Un-logged forest			Logged forest		
	Median	Minimum	Maximum	Median	Minimum	Maximum
Study area (ha) within 300-700 m asl.	350			328		
Exposure of rock outcrops (%)	76 a	45	89	60 a	48	88
Soil depth (cm)	9 a	4	20	12 a	3	24
Slope (º)	34 a	20	41	32 a	20	46
Altitude (m asl.)	504 a	350	680	542 a	300	690

Our study focused on five rare tree species, the selection criteria requiring that they be of high conservation concern (i.e. in Vietnam's Red List) and be potentially threatened by local logging activities, as well as being easily identifiable in the field. *M. suavis* is mainly used for food and medicine while the four other species are harvested for timber. The seeds of *E. tonkinense* are dispersed by ballistic explosion of the fruit; of *C. tabularis* by wind; of *P. chinensis* by wind and gravity; and of *G. fagraeoides* and *M. suavis* by gravity alone. The fruits of *M. suavis* are reportedly edible and often collected by local people [26], and *G. fagraeoides* seeds are eaten by some rodents [32]. More detailed descriptions of the characteristics and Red List categories of the species can be found in Ban [28], FIPI [33] and Chan and Huyen [34]. Some images of the study area and species are presented in Fig. 2.

Sampling
First, the study areas were overlain with a cell grid (30 x 30 m) delineated from a vegetation map for the Xuan Son. In each forest type, a total of 20 initial sample units were randomly selected from the grid for field investigation. Each initial unit consisted of an inventory plot of 30 x 30 m (900 m^2) for measuring trees with diameter at breast height (DBH) ≥ 5 cm (hereafter referred to as tree$_{\geq 5}$), with a smaller 10 x 10 m plot (100 m^2) located at the centre of the inventory plot for sampling regeneration (DBH < 5 cm and height ≥ 20 cm).

In the initial random sampling plots, DBH, height, density of target and other tree species were recorded for tree$_{\geq 5}$ individuals. As far as possible, all non-target tree species were also identified with the assistance of the National Park parataxonomist and the Xuan Son flora list [30]. Individuals that could not be determined to species level were classified by their genera or families and sorted into specimens per plot to estimate the species richness per plot. The regeneration density of target and other tree species was also recorded in the 100 m^2 plots located at the centre of the 900 m^2 plots. No standard common names are recognizable for the target species.

For each plot, rock-outcrop exposure was visually estimated in 16 systematic subplots (each 5 x 5 m). The soil depth for each plot was determined as the mean of 25 systematic measurements using a metal stake set into the ground. Slope, aspect and altitude were recorded for each plot, and five hemispherical photographs were taken at regularly-spaced points within each plot using a digital camera (Minolta Dimage Xt, 185º fish-eye lens). Automatic exposure settings were used. The devices were mounted on a leveling instrument (Regent Instruments, Canada) fixed to an adjustable tripod. Images were analyzed with the CanEye 5.0 software for canopy cover.

(a)　　　　　　　　　(b)　　　　　　　　　(c)
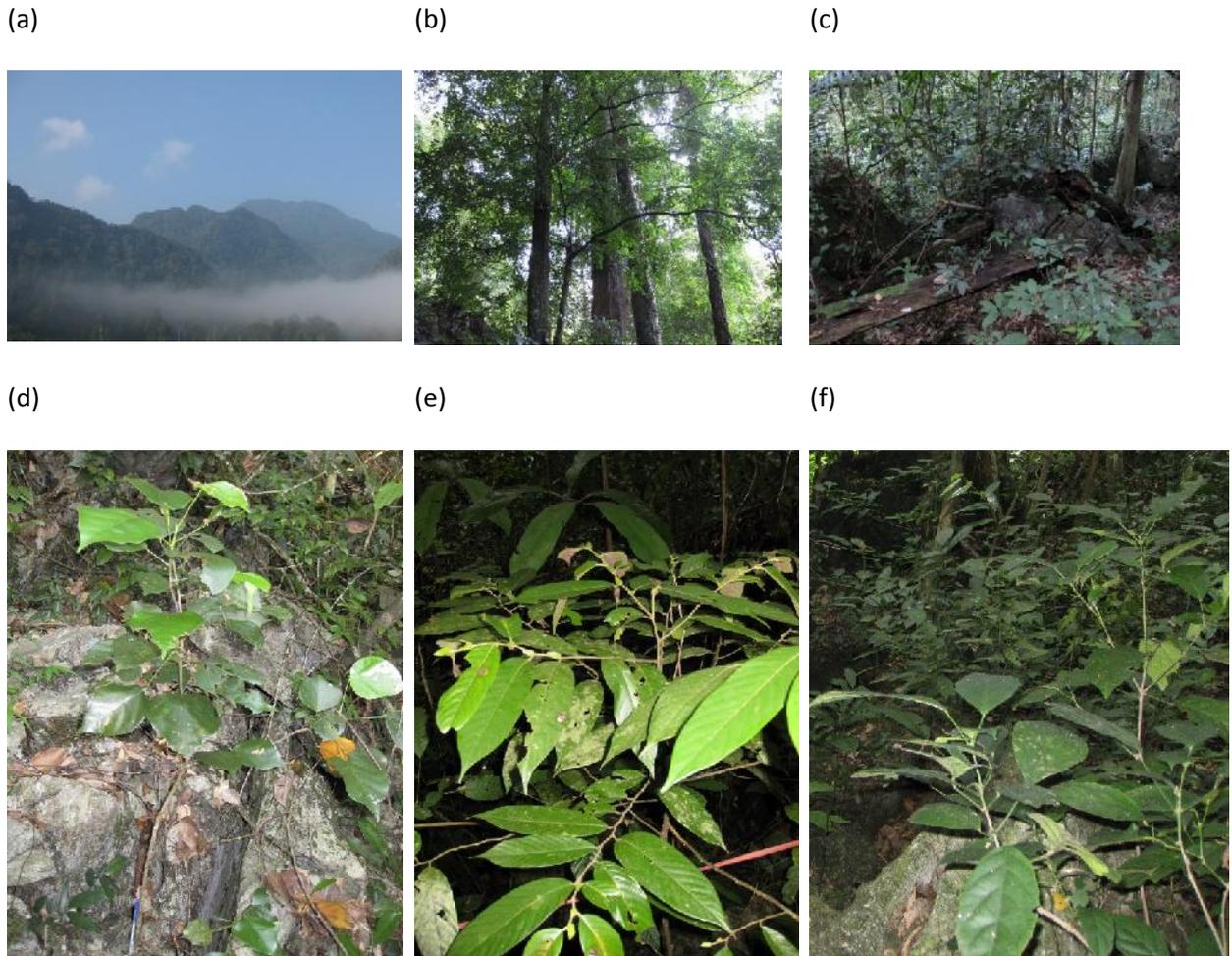
(d)　　　　　　　　　(e)　　　　　　　　　(f)

Fig. 2. The study area and the species: (a) montane limestone forest, (b) un-logged forest, (c) logged forest, (d) a regenerating individual of *E. tonkinense*, (e) a regenerating individual of *P. chinensis*, (f) two regenerating individuals of *C. javanicum*. Photos by The Long Ngo.

Based on the 20 initial plots of each forest, adaptive cluster sampling (ACS) was applied for each species, and for tree$_{\geq 5}$ and regeneration separately. The procedure for adaptive sampling depends on the presence or absence of the target species. For each initial plot, where at least one individual of the target tree$_{\geq 5}$ was found, four neighboring plots of 900 m^2 were attached to the initial plot. Next, if any of the added plots contained at least one individual of the target species, further plots were added. The procedure was stopped only when no further plots hosted the specific target species. For sampling regeneration, the same procedure was followed, but 100 m^2 neighboring plots were situated 30 m from the centre of the initial plot (Appendix 1).

On adaptively added plots, data were collected on the five studied species only and included number of individuals, DBH and tree height, as well as additional plot characteristics such as rock outcrop exposure and slope.

Both the random and adaptive sampling procedures were restricted to accessible areas due to safety concerns and to ensure sampling occurred within the stand boundaries. The inaccessible areas (e.g. cliff faces, summits) were, in most cases, rocky surfaces sparsely covered by herbs or shrubs with occasional small trees growing within crevices.

Statistical analysis

We applied the Mann-Whitney test for differences in median values of environmental variables and of tree and stand structural variables between the two forest types. The non-parametric test was applied because much of the data was not normally distributed. For a given forest type, Spearman rank correlations were performed to examine the relationship between regeneration density variables of the five studied species and potentially relevant ecological variables. The tree Shannon index was transformed to show the number of equally-abundant species of a community (based on Jost [35]). We used the modified unbiased Hansen-Hurwitz estimator [36] to calculate the mean species densities and their standard errors on ACS plots; inaccessible plots were treated as missing values.

Results

Forest stand characteristics

In un-logged forest, *Cleidion javanicum* (Euphorbiaceae) was the most dominant and frequent tree species, followed by *Amesiodendron chinense* (Sapindaceae), *Aphanamixis grandiflora* (Meliaceae) and *Terminalia myriocarpa* (Combretaceae). In logged forest, *Cleidion javanicum* was still the most frequent but less dominant tree species, while the co-dominant species were *Terminalia myriocarpa* (Combretaceae), *Linociera* spp. (Oleaceae) and *Syzygium* spp. (Myrtaceae).

Table 2. Stand characteristics of the two studied forest types; n = 20 initial plots per forest type. Lower case letters indicate significant differences in the Mann-Whitney test (p ≤ 0.05).

	Un-logged forest			Logged forest		
	Median	Minimum	Maximum	Median	Minimum	Maximum
Tree$_{\geq 5}$ density (≥ 5 cm DBH, stems/ha)	561 a	478	811	473 b	323	633
Diameter (cm)	20 a	16	24	16 b	13	17
Height (m)	11 a	9	13	8 b	7	10
Basal area (m²/ha)	28.6 a	19.8	33.2	12.6 b	8.1	14.8
Tree canopy cover (%)	75 a	67	83	73 b	59	78
Tree species richness (no. per 900 m²)	24 a	20	32	16 b	13	25
Transformed tree Shannon index (no. per 900 m²)	12 a	7	23	11 a	7	20
Overall regeneration density (< 5 cm DBH, stems/ha)	6500 a	2800	13000	5200 a	1200	11000
Regeneration density of *Cleidion javanicum* (%)	15 a	0	52	34 b	0	82

case letters indicate significant differences in the Mann-Whitney test (p ≤ 0.05).

The formerly logged sites showed lower tree$_{\geq 5}$ densities, DBH, height, basal area, canopy cover and tree species richness (Table 2). The transformed tree Shannon index per plot was similar in the un-logged and logged forests. Overall, regeneration density did not differ significantly between the two forest types, while relative regeneration density of the dominant species (i.e. *Cleidion javanicum*) was evidently higher in the logged (34%) than un-logged forest (15%).

Tree$_{\geq 5}$ individuals (trees with DBH ≥ 5 cm) of the five studied species

The five study tree species were still found as adults in the logged forest. The tree$_{\geq 5}$ densities of *E. tonkinense* (40%), *C. tabularis* (40%), *M. suavis* (44%) and *G. fagraeoides* (55%) were much lower in the logged forest than in the un-logged forest, whereas *P. chinensis* showed no difference (Fig. 3). For three specialist species, diameters and heights were clearly lower in the logged than un-logged forest, while only slightly lower median tree sizes were observed for *P. chinensis* and *M. suavis* in the logged forest (Table 3).

Table 3. Diameter and height of the tree$_{\geq 5}$ individuals (trees with DBH ≥ 5 cm) detected in adaptive cluster sampling in the two forests. Lower case letters indicate significant differences in the Mann-Whitney test ($p \leq 0.05$).

Species	Forest type	Individuals detected (n)	Diameter (cm)			Height (m)		
			Median	Minimum	Maximum	Median	Minimum	Maximum
Excentrodendron tonkinense	Un-logged	76	33 a	6	100	17 a	5	33
	Logged	40	20 b	5	71	12 b	4	23
Chukrasia tabularis	Un-logged	86	16 a	7	36	14 a	5	26
	Logged	34	13 b	5	24	9 b	5	18
Garcinia fagraeoides	Un-logged	218	30 a	6	140	17 a	5	39
	Logged	98	25 b	5	72	15 b	5	30
Parashorea chinensis	Un-logged	59	12 a	5	43	10 a	5	25
	Logged	65	11 b	5	26	9 b	4	16
Melientha suavis	Un-logged	47	11 a	5	24	8 a	4	16
	Logged	27	8 a	5	20	7 b	4	13

Compared to the un-logged forest, tree$_{\geq 5}$ individuals of four species (*E. tonkinense*, *C. tabularis*, *G. fagraeoides* and *P. chinensis*) hardly occurred in the highest DBH classes, and they showed no difference or even higher frequencies in the smaller DBH classes in the logged forest (Fig. 4a-d). However, *M. suavis* exhibited little difference in DBH class between the two forests (Fig. 4e). In the logged forest, *P. chinensis* was present mostly in diameter classes below 15 cm (82% of total individuals) and was almost absent from classes above 25 cm in DBH (Fig. 4d).
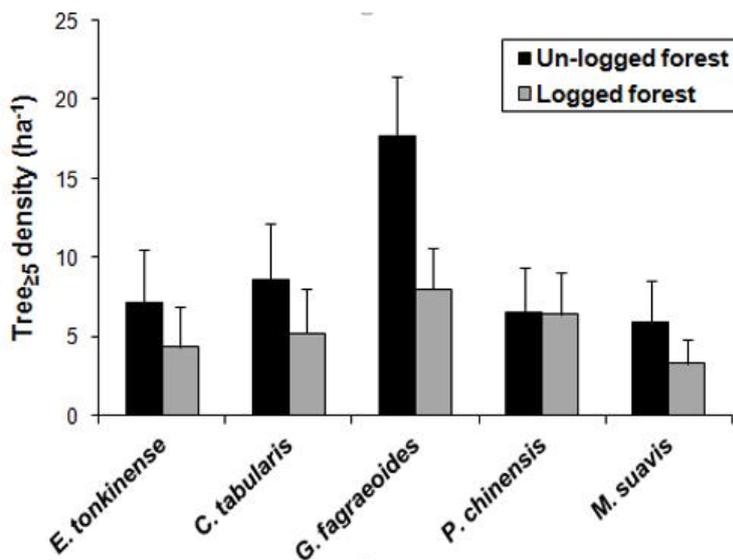

Fig. 3. Tree$_{\geq 5}$ densities (trees with DBH ≥ 5 cm) of the five study species in adaptive cluster sampling in the un-logged and logged forests (Hansen-Hurwitz estimator, means and standard errors).
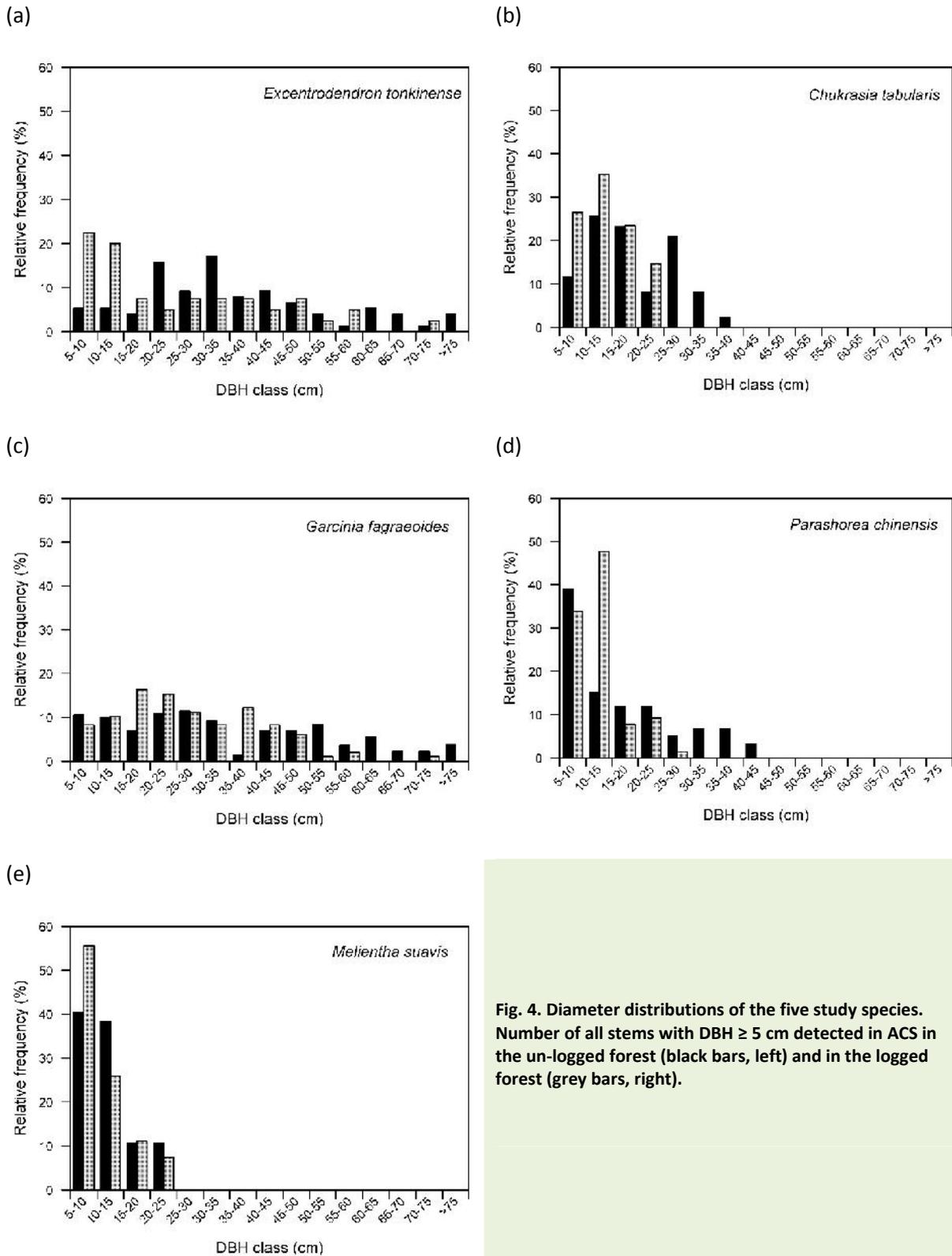
(a)

(b)

(c)

(d)

(e)

Fig. 4. Diameter distributions of the five study species. Number of all stems with DBH ≥ 5 cm detected in ACS in the un-logged forest (black bars, left) and in the logged forest (grey bars, right).

Regeneration of the five studied species

All species had much lower regeneration densities (46%, *M. suavis* to 80%, *P. chinensis*) in the logged forest than in the un-logged forest (Fig. 5). In the un-logged forest, the regeneration densities of *E. tonkinense*, *C. tabularis* and *G. fagraeoides* increased significantly with rock cover and decreased with species diversity and canopy cover (Table 4), while the densities of *P. chinensis* showed a reverse trend. In logged forest, most of these correlations were not significant. No significant correlations were found for *M. suavis*.

Table 4. Spearman rank correlations between tree regeneration densities and ecological variables in the two forests; n = 20 plots per forest type.

| | Un-logged forest | | | | | | Logged forest | | | | | |
	Rock cover (%)	Slope (°)	Soil depth (cm)	Shannon index (/900m²)	Tree species richness (no./900m²)	Canopy cover (%)	Rock cover (%)	Slope (°)	Soil depth (cm)	Shannon index (/900m²)	Tree species richness (no./900m²)	Canopy cover (%)
E. tonkinense	0.57**	ns	ns	ns	-0.45*	ns	ns	ns	ns	ns	ns	ns
C. tabularis	0.51*	ns	ns	ns	ns	-0.52*	ns	0.46*	ns	ns	ns	ns
G. fagraeoides	0.70**	0.62**	-0.66**	ns	-0.62**	-0.56*	0.47*	ns	ns	ns	ns	ns
P. chinensis	-0.49*	-0.56*	ns	0.62**	0.59**	ns	ns	ns	ns	ns	ns	ns
M. suavis	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns: not significant; *: significant at $p \leq 0.05$; **: significant at $p \leq 0.01$

Despite the low regeneration densities observed, the results of the adaptive sampling also indicate that the regeneration of three specialists (e.g. *E. tonkinense*) occurred more frequently on mostly rocky sites, while *P. chinensis* showed a reverse trend (Fig. 6). However, there was much variability in regeneration density within a given class of rock outcrop cover. In the logged forest, we found far fewer plots containing regeneration of the studied species.
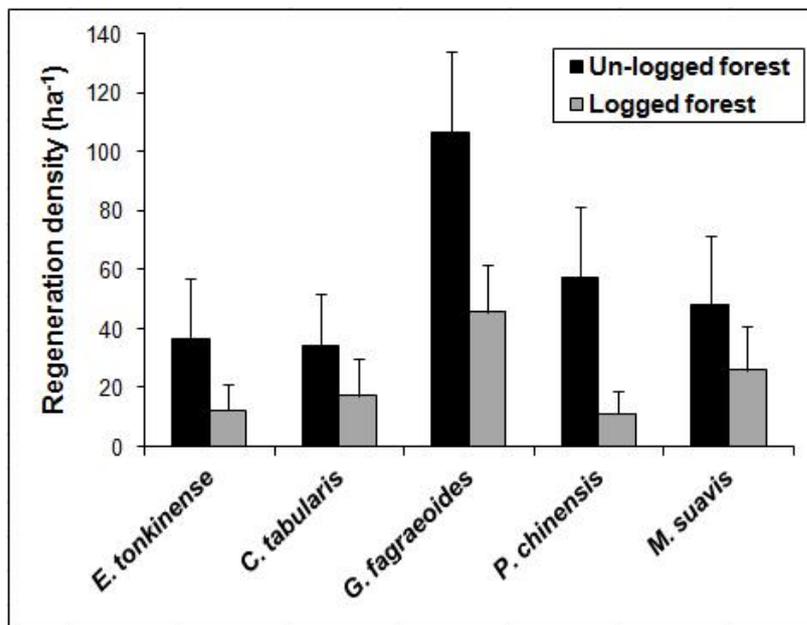

Fig. 5. Regeneration densities of the five study species in adaptive cluster sampling in the un-logged and logged forests (Hansen-Hurwitz estimator, means and standard errors).
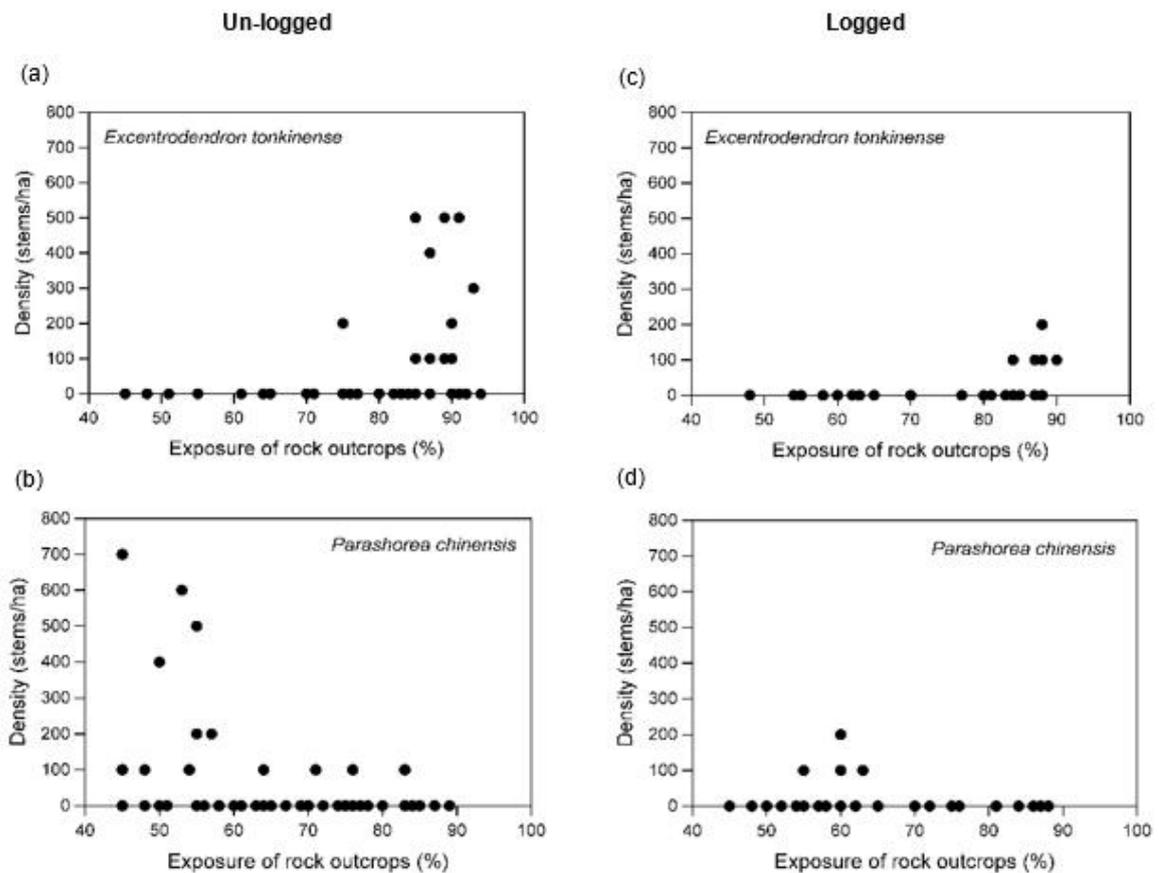
Fig. 6. Examples of the distributions of species' regeneration across rock outcrop exposures in adaptive cluster sampling. (a) and (b): un-logged forest; and (c) and (d): logged forest.

Discussion

Forest stand characteristics

Our formerly logged study forest showed clear signs of past logging, as the overall tree$_{\geq 5}$ density, mean tree diameter, basal area and tree species richness tended to be lower than that observed in the un-logged forest. The diversity index of both forest types was relatively similar, which may be explained by a reduction in the dominance structure and an increase in the evenness of the logged forest. The evenness of species was also found to be higher in disturbed than in undisturbed karst areas of southern China [37]. However, our results contrast with that of Harding and Ford [38], who reported the diversity of trees to be reduced after logging in limestone forests. Overall, regeneration densities were quite similar between the two forests, which conforms with the finding of Hoang et al. [39], who also found a considerably high density of treelets (DBH < 5 cm) in disturbed limestone forests in north-central Vietnam.

Tree$_{\geq 5}$ individuals (trees with DBH ≥ 5 cm) of the five studied species

The five study species were still present as adults in the logged forest, perhaps because logging focused on larger trees and may even have formerly supported the survival and growth of smaller trees. The

observed reductions in density, median diameter and height of tree$_{\geq 5}$individuals, along with the differences in the diameter distributions, indicate that these species were also subject to logging. In contrast, *P. chinensis* was found at similar densities and with little difference in median heights and diameters between the two forest types; however, it is considered that the species was indeed logged, but that remaining smaller trees grew larger than the 5-cm diameter threshold of our study, and many reached the 10-15 cm diameter class during the 9-year interval of restoration. Many dipterocarp species have the ability to survive for years beneath the dense, shady canopy, effectively preserving a "regeneration bank" that responds to opportunities created by logging gaps [40]. In addition, remaining dipterocarp trees may have responded to the disappearance of competitors by enhancing their growth, as suggested by Appanah [41].

Regeneration density of the five studied species
All study species also had regeneration in the logged forest, although their density was low. Density values were highest for *G. fagraeoides* (46 stems/ha), intermediate for *M. suavis* (26 stems/ha), *C. tabularis* (18 stems/ha) and *E. tonkinense* (13 stems/ha), and lowest for *P. chinensis* (11 stems/ha).

The post-harvest regeneration persistence of the study species may be a consequence of their biological characteristics and harvest regime (i.e., large tree extraction, selectively harvested products). Regenerating trees of *C. tabularis*, and particularly of *E. tonkinense* and *G. fagraeoides*, can grow on dry, rocky sites due to their strongly-developed roots, which penetrate deeply into rock fissures [32-34, 42-43]. Furthermore, *C. tabularis* and *E. tonkinense* can strongly regenerate in open places with light [33, 43-44], and larger tree extractions might benefit seedling establishment of these species. The regeneration recruitment of *C. tabularis* may also have originated from seeds dispersed into logged forest areas by wind. For *M. suavis*, its shoots and leaves are the main products harvested, thus some adult trees remained as a seed source for regeneration of the species. Nevertheless, many adult trees were still cut down to aid the gathering of leaves and shoots, as observed in the study sites.

When compared to tree$_{\geq 5}$ individuals, regeneration of the study species appeared to be more negatively impacted following logging. The low regeneration densities might be due to intensive logging of reproductive adult individuals. For example, despite being the most abundant of the five species, *G. fagraeoides* showed a significant decline in regeneration. In western Uganda, uncontrolled logging of mature and young trees lowered the potential for regeneration [6]. In addition, in another study, seeds of *E. tonkinense* and *C. tabularis* were found to be non-viable within two to three months after shedding [42, 44], and for *M. suavis*, the very short viability of seeds after falling combined with dry site conditions results in poor natural regeneration [26].

Although the densities of tree$_{\geq 5}$ stems between the two forests were similar for *P. chinensis*, regeneration in the logged forest was significantly lower. *P. chinensis* can start reproducing at an average diameter of 15 cm (22% of individuals), and the percentage of reproductive individuals increases with increasing tree diameter [45]. In our study, 46% of tree$_{\geq 5}$ individuals were larger than 15 cm DBH in the un-logged forest, while in the logged forest this value was only 18%, with individuals in the diameter classes above 25 cm being almost absent (Fig. 4d). Therefore, many *P. chinensis* trees$_{\geq 5}$ may not have reached the age of reproductive maturity in the logged forest since the cessation of logging, resulting in the much lower quantity of flowers and seeds compared to the un-logged forest. Moreover, *P. chinensis* regeneration is further hampered by its long breeding period, recalcitrant seeds, fruits consumed heavily by insects and animals, and very low seedling survival rate [27, 41, 46].

Ecological factors controlling regeneration

In un-logged forest, we found that the regeneration density of the three specialist species increased with an increase in rock-outcrop cover, while that of *P. chinensis* showed an inverse trend. The specialists can grow well on limestone, in shallow soil and on dry sites [33, 43, 47]. In contrast, sites with deep soils and high soil moisture seem to be favorable habitats for the dipterocarp species [27, 33]. The species *M. suavis* showed no significant correlation with any of the ecological variables studied; however, its abundance may be related to unmeasured variables. Its leaves, flowers, and fruits are edible [26, 33], so future studies should address the influences of seed dispersal factors and consumption of fruits by animals.

In the logged forest, there was a large perturbation in regeneration patterns that was largely unexplained. The overall regeneration densities of the two forests were not significantly different; however, the regeneration density of the study species was clearly lower in the logged forest, where the regeneration of *Cleidion javanicum*, a widely distributed generalist species, dominated.

The unexpected non-significant correlations may also be due to the small number of plots containing the target species, or it may be influenced by other unmeasured environmental variables. Seed dispersal factors and limitations of seed availability may also play a substantial role. For example, the reduction in seed trees after logging probably constrains seed supply and limits seed dispersal [48]. Wind or animal seed dispersal is assumed to be affected by forest gaps, and in tropical forests, seed arrival in gaps is found to be very different from that observed in the understory, in both quantity and functional composition [49]. Seed-dispersing animals may also enter large logging gaps less often, limiting regeneration opportunities for mammal- and bird-dispersed species [50]. Large logging gaps may promote wind-dispersed and shade-intolerant species, but not shade-tolerant timber trees [51-52]. Occupation by newly recruited trees in logging gaps also affects structure and function in tropical forests [52]. In our study sites, logging probably altered so many confounding factors that predicting where regeneration may occur is nigh impossible.

Implications for conservation

In our study, the five studied rare tree species still occurred as adults in the logged forest and regeneration was present, albeit at lower densities. From observations of the logged forest-floor and interviews with experienced former loggers, we assume that if logging is continued, it will likely have an adverse effect on regeneration of the study species due to declining seed resources as well as competition from some fast growing shrubs and liana (e.g. *Epipremmum pinnatum*). Although formerly logged limestone forests show current effects of past logging, the potential remains for further recovery, thereby justifying continuing the full protection of restoration areas. In view of former and continuing over-exploitation and degradation of limestone habitats and species of importance in Vietnam, we consider the limestone sites of the National Park to be important refuges of tropical threatened and rare tree species. The specialist species can play a significant role for restoration of sites where little fine earth is found, thus highlighting potential uses in restoration areas and outside protected areas.

Acknowledgments

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Appendix 1. Plot design of the adaptive cluster sampling. (A) The initial unit consisted of an inventory plot for tree$_{\geq 5}$ (trees with DBH ≥ 5 cm) and of a smaller plot for regeneration. (B) The procedure of adaptively adding neighborhood plots for tree$_{\geq 5}$ and regeneration. (C) The cessation of adaptive sampling when a cluster was surrounded by edge plots without target individuals.