

Research Article

Post-logging recovery of animal-dispersed trees in a tropical forest site in north-east India

Nandini Velho^{1,2*} and Meghna Krishnadas^{1,3}

¹ National Centre for Biological Sciences, Bangalore 560 065, India

² Centre for Tropical Environmental and Sustainability Science (TESS) and School of Marine and Tropical Biology, James Cook University, Cairns, Queensland 4870, Australia

³ Post-graduate Programme in Wildlife Biology and Conservation, Wildlife Conservation Society–India Program, Centre for Wildlife Studies, 1669, 31st Cross, 16th Main, Banashankari 2nd stage, Bangalore 560 070, India

*Corresponding author: E-mail address: nandinivelho@gmail.com

Abstract

Selective logging is known to alter the structural and community composition of tropical forests and may disrupt plant-fruitivore interactions. We hypothesized that even after a sufficient period of recovery, logged areas will not possess as complete a suite of species as an unlogged forest, the differences being more marked for biotically-dispersed species. Species of this functional group are expected to occur at lower densities, have lower species richness and diversity, and be smaller in logged forests. To quantify structural and functional differences in tree communities, we sampled 120 randomly placed plots, 60 each in logged and unlogged forest sites. We found significant differences in species richness and diversity between logged and intact forest. Within biotically-dispersed species, bird dispersed species showed a significant reduction in species richness. Consistent with previous studies, trees in logged forests were smaller, although overall density was not different between the two treatments. We posit that selective logging might have pervasive effects on functional aspects of tropical tree communities, which appear to persist even after two decades of logging cessation.

Keywords: selective logging, biotic dispersal, north-east India, tropical tree communities

Received: 9 August 2011; Accepted: 30 October 2011; Published: 12 December 2011.

Copyright: © Nandini Velho and Meghna Krishnadas. This is an open access paper. We use the Creative Commons Attribution 3.0 license <http://creativecommons.org/licenses/by/3.0/> - The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that the article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

Cite this paper as: Velho, N. and Krishnadas, M. 2011. Post-logging recovery of animal dispersed trees in a tropical forest site in north-east India. *Tropical Conservation Science* Vol. 4(4):405-419. Available online: www.tropicalconservationscience.org

Introduction

Tropical moist forests display large degrees of plant-animal interactions. Tree communities in many tropical rainforests are shaped by the relative roles of dispersers, seed predators, and herbivores that limit seedling growth and recruitment [1,2]. Frugivorous dispersers make up a bulk of the vertebrate population, and up to 80% of tropical rainforest trees may be dispersed by these frugivores [3,4]. Human-induced disturbances such as complete or selective logging and hunting may disrupt these interactions and affect tree community composition and diversity of tropical forests [5].

Selective logging, although considered less harmful to biodiversity [6], is known to alter the physical and community structure of tropical forests [7,8]. In addition to well-established structural changes to tree size, basal area, and biomass persisting even 12 years after logging cessation [7,9], logging may also cause pervasive changes in species composition of tropical moist forests [9]. Long-term studies (>15 years) and predictions based on the trajectory of forest recovery in these sites indicate that regeneration of the full suite of trees may take up to a century following complete termination of logging [10].

Selective logging affects the community dynamics of tropical rainforest trees by creating gaps with altered light and micro-climate conditions, facilitating the growth of small-seeded, light-loving pioneer species [11,12]. Additionally, logging is known to reduce populations of old-growth species [12]. As these species are slow-growing, they may take many years to recover [8,13]. Many old-growth trees are also important fruiting resources for animals, which in turn disperse the seeds of these species. Logging may thus reduce overall densities and alter relative abundances of frugivorous dispersers either directly or indirectly through loss of food trees [14-16]. Loss of dispersers may eventually result in reduction or loss of biotically-dispersed trees [17-19], and change the functional composition of the forest towards abiotically-dispersed species.

We examined the implications of logging for the tree-community as a whole. Specifically, our study aimed to discern the differences in tree density, species richness and diversity between an unlogged and a selectively logged forest in north-east India, after a 16-year recovery period. Further, we sought to determine if there are finer-scale differences between biotically and abiotically-dispersed species between these two treatments, and if biotically-dispersed species had lower densities, species richness, and species diversity following logging. Within the biotically-dispersed group, we examined whether richness and diversity were differentially affected within guilds of bird and mammal-dispersed tree species.

Methods

Study area

This study was done from November 2009 to May 2010 in and around Pakke Wildlife Sanctuary and Tiger Reserve (Fig. 1, 861.95 km²; 92° 36' - 93° 09' E; 26° 54' - 27° 16' N) in western Arunachal Pradesh. The main vegetation type is classified as Assam-valley tropical semi-evergreen forest [20]. The dominant tree species are *Polyalthia simiarum*, *Pterospermum acerifolium*, *Sterculia alata*, *Stereospermum chelonoides*, *Ailanthus grandis* and *Duabanga grandiflora* [19]. A high percentage of tree species (64%) are animal-dispersed, and 12% of tree species are wind-dispersed [21].

There are at least 35 predominantly frugivorous bird species [21]. The Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Rhyticeros undulatus*) and Oriental Pied Hornbill (*Anthracoceros albirostris*) are the largest avian frugivores in the area. The Mountain Imperial Pigeon (*Ducula badia*) and the Green Imperial Pigeon (*Ducula aenea*) are also important large-bodied avian frugivores. There is also a great diversity of smaller frugivores, with more than 30 species known to occur here [22]. The other species that predominantly depend on fruits and seeds are four species of viverrids (*Arctictis binturong*, *Viverra zibetha*, *Paguma larvata* and *Paradoxurus hermaphroditus*) and five species of rodents (*Hystrix brachyura*, *Atherurus macrourus*, *Niviventer* sp., *Rattus* sp., *Berylmus* sp.), excluding four species of diurnal tree squirrels [23].

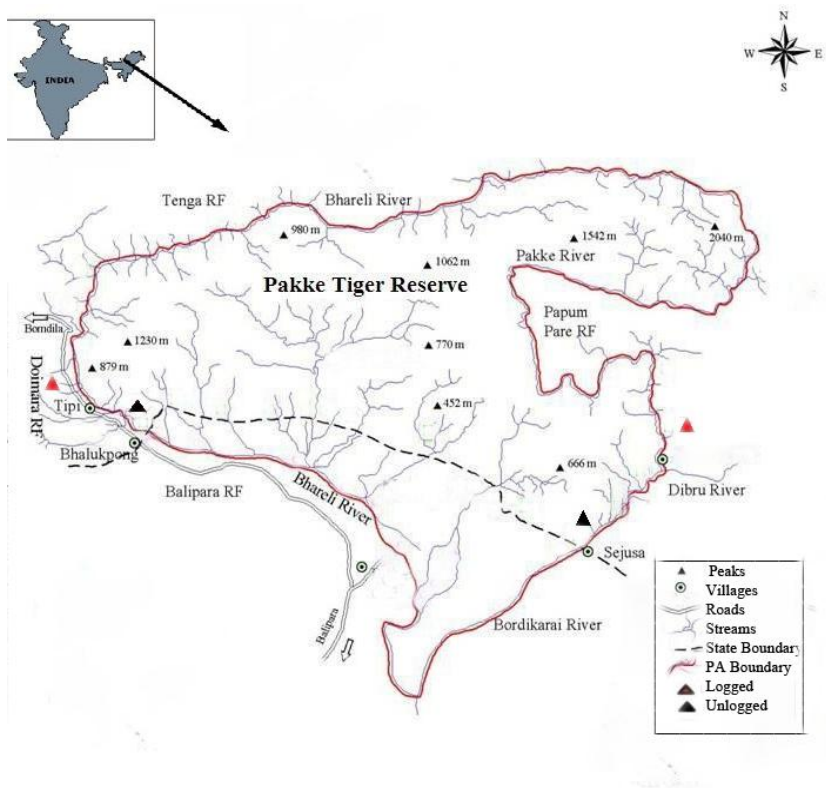


Fig.1. Map of Pakke Tiger Reserve in Arunachal Pradesh in north-east India, and the adjoining reserve forests where the study was conducted. Black triangles show sampled location in unlogged forest. Red triangles show sampled location in logged forest.

We selected two blocks (c. 10 km² each) each in logged (27° 01' N ; 92° 91' E and 27° 01' 'N; 92°57' E) and unlogged (27° 0' N, 92° 35' E and 26° 56' N; 92° 58' E) areas based on information from previous systematic records (maintained in the form of working plans of the Forest Department), Departmental Timber Operations (DTO) and published literature [13,15]. Both logged sites (27° 01' N, 92° 91' E and 27° 01' 'N, 92°57' E) were located in the adjacent peripheries of the protected area and were commercially logged. Up to the late 1970s. The Supreme Court imposed a complete ban on logging in 1996 [17]. Our study sites were about 30 km apart and broadly comparable in terms of geology, rainfall, climate, vegetation, and topography [15]. The commonly logged species were *Terminalia myriocarpa*, *Duabanga grandiflora*, *Artocarpus chaplasha*, *Amoora wallichii*, *Michelia* spp., *Dysoxylum procerum* and

Toona ciliata. Trees would be marked for felling depending on the volume sanctioned to each person by the forest department. Sawmills operating in the adjacent parts of the park were either directly supplied with timber, or residents and forest staff would sell their permits to sawmills, which led to timber being commercially exploited. Hence, although areas were largely selectively logged by the government, the irregularities in issuing permits for selective logging, also led to some amount of illegal logging.

Data collection

We set up 120 (10 × 10 m plot) vegetation plots, 60 each in logged and unlogged forest. Within each treatment (logged and unlogged), we had two blocks of 10 km², within which there were 30 plots randomly placed and separated by a distance of at least 500 m. Random selection of plots was performed using GIS software prior to undertaking fieldwork (Quantum GIS - Open Source Geographic Information System). We used the selected random points as the right lower vertex of the plot. In the protected area there was a 53 km along the east-west axis, from which plots were accessed laterally. In the adjacent reserve forests, the road segments were 18 km and 4 km in length, which we used to access our sites. There were no roads passing through our study plots, except occasional foot trails. Within these plots we enumerated all adult tree species > 25 cm diameter at breast height (DBH). We measured DBH and tree height for all species.

Statistical analyses

We used the statistical software R (version 2.11.0) [24]. We used package *Vegan* in Program R for calculating species richness, species diversity indices, and species accumulation curves.

Characterising forest structure and composition in logged and unlogged forests

We examined the changes due to logging on forest structure (DBH, tree density) and more importantly, on composition (species richness, diversity, and similarity). As tree height was positively correlated with DBH in both logged (Pearson's $R = 0.66$, $p < 0.001$) and unlogged areas (Pearson's $R = 0.48$, $p < 0.001$), we retained DBH as the response for further analyses. We used Student's *t* tests and analysis of variance (ANOVA) to compare the DBH of trees in logged and intact forest.

To examine the effects of logging on forest composition, we used ANOVA to examine differences in overall species richness between logged and intact forest. We used the respective values of the indices of diversity and evenness to compare the two treatments. We assessed this difference between two functional guilds – species dispersed by biotic and abiotic means. Within animal-dispersed species, we used one-way ANOVA to model the effects of logging on the species richness and diversity of trees dispersed by mammals alone, birds alone, and both by mammals and birds. We determined dispersal modes for trees from existing literature [21,25] and from focal tree watches [Velho et al, unpublished data].

We used Fisher's α , $S = \ln(1 + N/\alpha)$, where S is the species richness, N is the number of individuals, \ln is the natural logarithm, and α is an index of species diversity. We used Morisita-Horn index of dissimilarity to quantify extent of species overlap in logged versus unlogged plots, and between logged and intact forest. We also used the Shannon-Weiner index of diversity (H') to compare logged and intact forest for overall species composition and for differences between the entropy of species within the two functional guilds. The formula for this index is given as

$$H' = - \sum_{i=1}^S (p_i \ln p_i)$$

We used Pielou's index $J = H' / \ln(S)$, to compare evenness within the two treatments, where H' is Shannon-Weiner index and S is the total number of species in the sample.

Results

Structural differences between logged and unlogged habitats

Overall tree density did not differ significantly between the two habitats (mean logged = 601.5 ± 83.5 S.E.; mean unlogged = 598.2 ± 76.8 S.E.). Density of biotically-dispersed species, however, was higher in intact forest (mean logged = 448.4 ± 78.4 S.E.; mean unlogged = 506.9 ± 66.1 S.E.) and abiotically-dispersed species displayed the opposite trend (mean logged = 141.6 ± 62.2 S.E.; mean unlogged = 86.8 ± 35.8 S.E.), although the results were not significant ($p > 0.05$). As expected, we found a significantly lower DBH in logged forests compared to intact forests (Student's t test, $t = -6.28$, $df = 681.42$, $p < 0.001$) (Table 1). The DBH of biotically and abiotically-dispersed tree species, separately, was also lower in logged forests (Table 1). Diameter at breast height of species that were bird-dispersed (One way ANOVA, $F = 38.54$, $df = 396$, $p < 0.001$), and dispersed by both (One way ANOVA, $F = 5.05$, $df = 124$, $p = 0.03$), was significantly lower in logged forests, and DBH of mammal-dispersed species was nearly so (One way ANOVA, $F = 3.18$, $df = 47$, $p = 0.08$).

Table 1: Summary of changes in structural and compositional aspects of the tree communities in logged versus intact forest. The numbers in subscript represent the standard error (SE) of the mean values presented. The mean values for species richness are estimates. We compared species richness and tree density using ANOVA, and DBH using Student's t test. Arrows represent increase (↑) or decrease (↓) in the attributes of the two functional guilds and statistically significant differences at $p < 0.05$ are indicated as *. For diversity indices we used the magnitude of effect and not p -values for comparison.

Attribute	Intact forest	Logged forest	Abiotic (logged intact)	Biotic (logged intact)
Total trees sampled	359	361	↑	↓*
Fisher's α	42.17 ± 5.57	27.6 ± 4.01	↓	↓
Shannon-Wiener index	3.5	3.1	↓	↓
Pielou's evenness	0.87	0.93	↑	↑
Overall species richness	139.3 ± 8.6	94.7 ± 5.8	↓*	↓*
Overall tree density	598.2 ± 83.5	601.5 ± 76.8	↑	↓
DBH in cm	106.4 ± 3.6	77.5 ± 2.9	↓*	↓*
Tree height in metres	24.1 ± 1.0	18.0 ± 1.1	↓*	↓*

Overall compositional differences between logged and unlogged habitats

Species diversity was higher in intact forests (Fisher's $\alpha = 42.17 \pm 5.57$ S.E., $df = 94$) compared to logged forests (Fisher's $\alpha = 27.6 \pm 4.01$ S.E., $df = 72$). Morisita-Horn index of dissimilarity was 0.35, indicating a 35% difference in species composition between logged and unlogged sites. Shannon-Wiener index of diversity (H') was 3.96 for unlogged forest and 3.94 for logged forest. Pielou's index of evenness in composition was higher for logged forest (0.93) compared to unlogged forest (0.87).

Although the species accumulation curves were not asymptotic in either case, the curves for logged and unlogged forests indicate that the estimated species richness may be lower for logged forests (Fig. 2, mean logged = 94.7 ± 5.8 S.E.; mean unlogged = 139.3 ± 8.6 S.E.). We formally tested the relationship between felling regime and estimates of species richness (using the Chao1 for individual plots) and found significant differences between logged and unlogged forests (One-way ANOVA, $F = 9.79$, $df = 118$, $p = 0.002$).

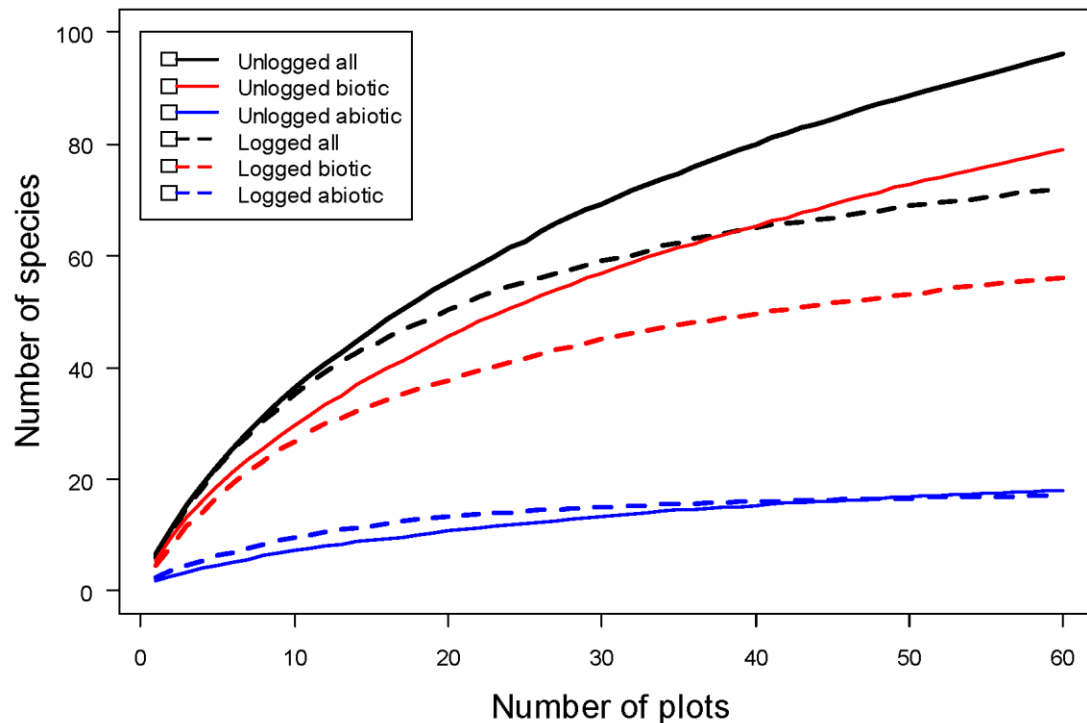


Fig.2. Species accumulation curves for all tree species and for biotically-dispersed and abiotically-dispersed species separately, in logged and unlogged forest. Overall richness was estimated using the Chao1 for individual plots. There were a total of 120 vegetation plots (10 x 10 m), with 60 vegetation plots each in logged and intact forests.

Dispersal mode: How does logging affect biotically versus abiotically dispersed plant species?

We found a lower number of biotically-dispersed species per plot in logged forests, although the results were not statistically significant (mean logged = 4.48 CI $4.22-4.77$; mean unlogged = 5.17 CI $4.66-5.51$; $p = 0.14$). The number of abiotically-dispersed individuals per plot were significantly higher in logged habitats compared to intact forests (mean logged = 1.42 CI $1.27-1.58$; mean unlogged = 0.87 CI $0.73-1.03$; $p = 0.005$). Diversity of biotically-dispersed species was higher for unlogged plots (Fisher's $\alpha = 25.1 \pm 4.3$ S.E.) compared to logged plots (Fisher's $\alpha = 11.1 \pm 2.4$ S.E.). For abiotically-dispersed species too, Fisher's α was higher for intact forest (Fisher's $\alpha = 15.8 \pm 3.2$ S.E.) compared to logged forest (Fisher's $\alpha = 19.4 \pm 3.9$ S.E.). Morisita-horn index of dissimilarity for biotic species was 0.67 indicating 67% difference in tree species composition, and for abiotic species was 0.24 , or a 24% difference in tree species composition.

Shannon-Wiener index (H') for biotically-dispersed guild was 3.1 for logged forest and 3.5 for unlogged forest. For abiotic species, the index was lower in unlogged forest ($H' = 3.2$) compared to logged forest ($H' = 3.4$). For biotically-dispersed species, Pielou's evenness index was 0.89 in logged areas compared to 0.85 in unlogged forest. Pielou's index was 0.93 in logged forest and 0.85 in unlogged forest for abiotic species.

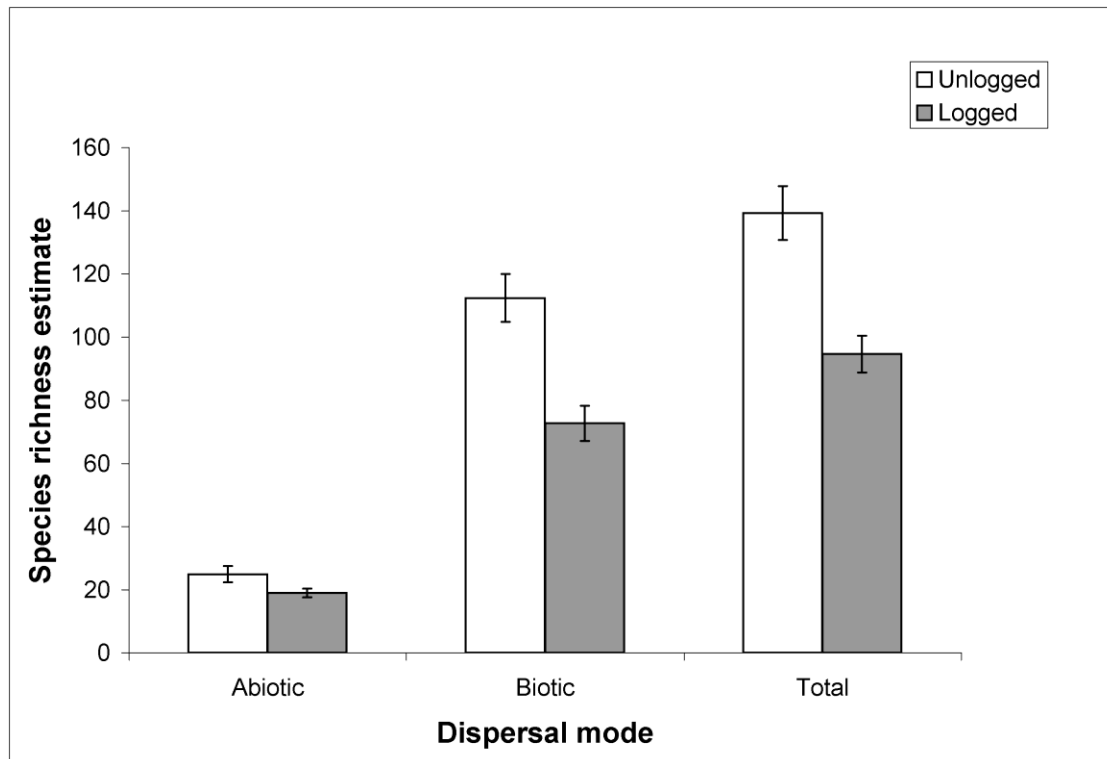


Fig.3. Species richness estimates were significantly different between logged and intact forests. Our results showed that logged forest had significantly lower overall species richness. Biotically-dispersed tree species had lower richness in logged habitats compared to intact forests. Error bars indicate S.E.

The species accumulation curves reached an asymptote only for abiotically-dispersed species within the treatments. However, the accumulation curves for biotic species (Fig. 2, mean logged = 72.7 ± 5.6 S.E.; mean unlogged = 112.4 ± 7.6 S.E.) indicate lower expected species richness in logged areas. For abiotic species (Fig. 2, mean logged = 19.0 ± 1.4 S.E.; mean unlogged = 24.9 ± 2.6 S.E.), the estimated species richness was higher in logged forest. There were significant differences between the species richness estimates (Chao1) of both abiotically (One-way ANOVA, $F = 4.98$, $df = 118$, $p = 0.03$) and biotically-dispersed tree species (Fig. 3, One-way ANOVA, $F = 4.44$, $df = 118$, $p = 0.04$). Within biotic communities, species richness of bird dispersed trees was significantly lower in logged forest (One-way ANOVA, $F = 5.84$, $df = 118$, $p = 0.02$). There were no significant differences in the species richness of trees dispersed by mammals (One-way ANOVA, $F = 0.24$, $df = 118$, $p = 0.63$) and species dispersed by both birds and mammals (One-way ANOVA, $F = 0.01$, $df = 118$, $p = 0.94$).

Discussion

Our study is one of the few that has looked at the effect of logging differentially on abiotically and biotically-dispersed tree species at a community level. We found marked changes in the functional composition of logged forest compared to adjacent and geo-physically similar intact forest. Logged forests possessed only a subset of the species found in intact forest, the difference being more marked for the biotically-dispersed guild. Canopy openness following logging is expected to favor the growth of small-seeded pioneer species, many of which are wind-dispersed, a change in community composition that persists decades after logging [26-28]. We did find a greater number of abiotically-dispersed trees per plot and greater density of this guild in logged forest. Diversity of abiotically-dispersed species was also higher in logged forest. However, our results indicate that logged forest plots were more similar in species composition with high evenness, indicating that a few species dominated the community. For the biotically-dispersed guild, logged forest was much less diverse, with a low species overlap with unlogged forest. In addition, logged forest plots were again more similar in species composition, and were dominated by a few species.

Species richness was also markedly lower in logged forest, the difference being so for both functional guilds. Within biotically-dispersed trees, species that were bird-dispersed showed a significant decrease in species richness in logged forests. However, species-area curves were not asymptotic overall or for biotically dispersed species, although estimated species richness was found to be higher in intact forest. Previous studies in the area have shown that populations of large-bodied avian dispersers are lower in logged areas [15] and this may be affecting recruitment [17]. Larger vegetation plots need to be set up on a priority basis to capture the full complement of adult trees and to understand finer scale differences for rare species (especially those dispersed by mammals and by both birds and mammals).

Structurally, our community-wide analysis on tree species showed that biotically-dispersed species occurred at lower densities. Other studies have found that stem density increased > 5 years post-logging, probably because greater canopy openness promoted the establishment and recruitment of pioneers and other competitive colonizers [26]. There was no significant difference in density of biotically-dispersed tree species between the two regimes, but there was a notable increase in abiotically-dispersed tree species. Also consistent with previous studies [9,12,19], size of trees (DBH) was significantly smaller in logged areas, unsurprising since the larger size classes are usually preferentially logged and it may take many decades for slow-growing tropical trees to reach the pre-logging size-classes.

The decrease in densities of biotically-dispersed tree species could alter the spatio-temporal availability of fruits for frugivores. In addition, many frugivores either decline in abundance or disappear from logged patches due loss of habitat or changes in the abundance and quality of food sources [12,13,18,27]. Frugivores are important seed dispersers and affect the spatial patterns of plant recruitment [2,4]. The loss of frugivorous dispersers can alter tree community composition [29], as is well documented in hunted forests [30]. However, few studies have tested for finer scale responses to selective logging in dispersal and recruitment among trees with different dispersal modes, especially comparing bird and mammal dispersed species, although studies of individual species indicate that such differences are expected [31].

Implications for conservation

The moist forests of north-east India continue to suffer high pressures from logging, hunting, and large-scale felling for agriculture. Remaining forests, especially protected areas, serve as vital population sources of biodiversity, especially plant species richness [32]. In addition to the stark loss of forests and wildlife, changes in forest composition and subtle losses of ecosystem function, as seen in our study, are likely to impact the richness of these forests in the long-run. Our study site is also representative of the conservation challenges faced by the global hotspot of the Indo-Myanmar area in dealing with timber over-harvesting [33,34]. In other parts of south-east Asia, selectively-logged and human-modified forests provide important ecosystem services and allow persistence of a wide variety of faunal species [35,36,37]. However, we find that although logged forests had marginally lower tree density overall, they had significantly lower tree species richness and diversity. Our study clearly indicates that selective logging significantly alters the functional composition of forests. Even though 16 years is a relatively short recovery period for slow-growing tropical trees, the differences in density, richness, and diversity of biotically-dispersed tree species between selectively logged and intact forests are of importance for conservation. Even amongst abiotically-dispersed tree species the community composition was more homogenous in logged areas.

The effects of dramatic habitat loss are usually clear, and populations and communities of plants and animals continue to be affected by human modification of landscapes [38]. The more insidious effects of habitat degradation, however, might be just as severe in terms of loss of ecosystem function [38,39]. Lack of post-harvest assessment presents a major impediment to monitoring species recovery in logged forests, especially with regard to functional guilds. Together with resident communities, the Arunachal forest department has instituted a variety of co-management schemes which include creation of village forest reserves and community conservation areas in many parts of the state. Given that these areas are still open to timber and firewood extraction, which directly impact local livelihoods, our study is of particular relevance and indicates that the present timber extraction patterns may be unsustainable. Additional information is required to monitor seedling recruitment and species regeneration. Further, the effects of logging on abiotic factors such as light, moisture availability, and soil characteristics and its effect on community dynamics of regenerating seedlings may also provide important insights on regenerative ability of species. Detailed information about such processes will allow us to better predict the impacts of specific management practices on tree species and communities, and scope for recovery following logging.

Acknowledgements

We obtained funding for this project from the Department of Biotechnology grant (number 6324) provided to Mahesh Sankaran at the National Centre for Biological Sciences. The Arunachal Forest Department granted research permits. We thank Putul Munda, Arun Saikia, Kishore Dorje for their help in the field. We thank Mahesh Sankaran, Jayashree Ratnam, Aparajita Datta, David Edwards, Umesh Srinivasan, Dayani Chakravarthy, Shashank Dalvi and Sachin Sridhara for ideas, discussions and help with analysis. Dr. Haridasan K identified plant specimens. George Gale and Alejandro Estrada helped improve our manuscript. For honouring our collective obligation to save Pakke Tiger Reserve, this paper is dedicated to Tana Tapi and his team of forest watchers.

References

- [1] Janzen, D.H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465-492.
- [2] Howe, H.F. and Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201:228.
- [3] Terborgh, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24:283-292.
- [4] Fleming, T.H., Breitwisch, R. and Whitesides, G.H. 1987. Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics* 18:91-109.
- [5] Corlett, R.T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* 39:292-303.
- [6] Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P, Tawatao, N.B., Ahmad, N., Magintan, D., Khen, C.V., Maryati, M., Ong, R.C. and Hamer, K.C. 2010. The value of logged tropical forests: lessons from northern Borneo. *Biodiversity and Conservation* 19:985-997.
- [7] Cannon, C.H., Peart, D.R., Leighton, M. and Kartawinata, K. 1994. The structure of lowland rainforest after selective logging in west Kalimantan, Indonesia. *Forest Ecology and Management* 67:49–68.
- [8] Heydon, M.J. and Bulloh, P. 1997. Mouse deer densities in a tropical rainforest: the impact of selective logging. *Journal of Applied Ecology* 34:484-496.
- [9] Silva, J.N.M, de Carvalho, J.O.P., Lopes, C.A., de Almeida, B.F., Costa, D.H.M., de Oliveira, L.C., Vanclay, J.K. and Skovsgaard, J.P. 1995. Growth and yield of a tropical rainforest 13 years after logging. *Forest Ecology and Management* 71:267-274.
- [10] Bonnell, T.R., Reyna-Hurtado, R. and Chapman, C.A. 2011. Post-logging recovery time is longer than expected in an East-African tropical forest. *Forest Ecology and Management* 261:855-864.
- [11] Pelissier, R., Pascal, J.P., Houllire, F. and Laborde, H. 1998. Impacts of selective logging on the low elevation dense moist evergreen forest in the Western Ghats (south India). *Forest Ecology and Management* 105:107-119.
- [12] Johns, A.D. 1988. Effects of selective timber extraction on rainforest structure and composition and some consequences for frugivores and folivores. *Biotropica* 20:31-37.
- [13] Johns, A.D. 1992. Vertebrate responses to selective logging: implications for the design of logging systems. *Philosophical Transactions of the Royal Society* 335:437–442.
- [14] Sekercioglu, C.H. 2002. Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biological Conservation* 107:229-240.
- [15] Datta, A. 1998. Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. *Oryx* 32:285-294.
- [16] Cleary, D.F.R., Boyle, T.J.B, Setyawati,T., Anggraeni, C.D., Van Loon, E.E. and Menken, S.B.J. 2007. Bird species and traits associated with logged and unlogged forest in Borneo. *Ecological Applications* 17:1184–1197.
- [17] Sethi, P. and Howe, H.F., 2009. Recruitment of hornbill-dispersed trees in hunted and logged forests of the Indian Eastern Himalaya. *Conservation Biology* 23:1-9.
- [18] Chapman, C.A. and Onderdonk, D.A. 1998. Forests without primates: primate plant co-dependencies. *American Journal of Primatology* 45:127–141.
- [19] Chapman, C. A. and Chapman, L. J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29:396-412
- [20] Champion, H.G. and Seth S.K. 1968. A revised survey of the forest types of India. Manager of Publications, Government of India, New Delhi. 404 pp.

- [21] Datta, A. and Rawat G.S. 2008. Dispersal modes and spatial patterns of tree species in a tropical forest in Arunachal Pradesh, northeast India. *Tropical Conservation Science* 1:163–185.
- [22] Datta, A. 2001. An ecological study of sympatric hornbills and fruiting patterns of a tropical rainforest in Arunachal Pradesh. Ph.D. Thesis, Saurashtra University, Rajkot. 245 pp.
- [23] Velho, N., Datta, A. and Isvaran, K. 2009. Effect of rodents on seed fate of five hornbill-dispersed tree species in a tropical forest in north-east India. *Journal of Tropical Ecology* 25:507-514.
- [24] R Development Core Team 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- [25] Kitamura, S., Suzuki, S., Chuailua, P., Plongmai, K., Poonswad, P., Noma, N., Maruhashi, T. and Suckasam, C. 2005. A botanical inventory of a tropical seasonal forest in Khao Yai National Park, Thailand: Implications for fruit-frugivore interactions. *Biodiversity and Conservation* 14:1241-1262.
- [26] Oliviera-Filho, A.T., Carvalho, D.A., Vilela, E.A., Curi, N. and Fontes, M.A.L. 2004. Diversity and structure of the tree community of a fragment in tropical secondary forest of the Brazilian Atlantic Forest Domain 15 and 40 years after logging. *Revista Brasilia Botanica* 27:685-701.
- [27] Chazdon, R.L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution, and Systematics* 6:51-71.
- [28] Chapman, C.A, Chapman, L.J., Jacob, A.L., Rothman, J.M., Omeja, P., Reyna-Hurtado, R., Haarter, J., Lewis, M.J. 2009. Tropical tree community shifts: Implications for wildlife conservation. *Biological Conservation* 143:366-374.
- [29] Bleher, B. And Böhning-Gaese K. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* 129:385–394.
- [30] Wright, S.J., Zeballos, H., Domínguez, I., Gallardo, M.M., Moreno, M.C. and Ibáñez, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* 14:227–239.
- [31] Forget, P.M., Rankin-de Merona, J.M., Julliot, C. 2001. The effects of forest type, harvesting, and stand refinement on early seedling recruitment in a tropical rain forest. *Journal of Tropical Ecology* 17:593-609.
- [32] Khan, M.L., Menon, S. and Bawa, K.S. 1997. Effectiveness of the protected area network in biodiversity conservation: a case-study of Meghalaya state. *Biodiversity and Conservation* 6:853-868.
- [33] Koh, L.P. and Sodhi N.S. 2010. Conserving Southeast Asia's Imperiled Biodiversity: Scientific, Management, and Policy Challenges. *Biodiversity and Conservation* 19:913-1204.
- [34] Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- [35] Edwards, D.P., Ansell, F.A., Ahmad, A.H., Nilus, R. and Hamer, K.C. 2009. The value of rehabilitating logged rainforest for birds. *Conservation Biology* 23:1628-1633.
- [36] Thiollay, J. 1999. Responses of an avian community to rain forest degradation. *Biodiversity and Conservation* 8:513-534.
- [37] Gomes, L.G.L., Oostra, V., Nijman, V., Cleef, A.M. and Kappelle, M. 2008. Tolerance of frugivorous birds to logging in a tropical cloud forest. *Biological Conservation* 141: 860-871.

- [38] Brook, B.W., Sodhi, N.S. and Ng, P.K.L. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* 424:420–423.
- [39] Corlett, R.T. 2002. Frugivory and seed dispersal in degraded tropical East Asian landscapes. In: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. Levey, D.J., Silva, W.R., Galetti, M. (Eds.), pp. 451-465. Wallingford, Oxfordshire, UK, pp. 451-465.

Appendix 1. List and numbers of biotically-dispersed species found in logged versus unlogged forest. The list has been divided into categories based on whether the species are only bird-dispersed, only mammal-dispersed, and dispersed by both.

Species	Logged forest	Unlogged forest
Bird dispersed		
<i>Actinodaphne angustifolia</i> (Lauraceae)	14	0
<i>Actinodaphne obovata</i> (Lauraceae)	4	14
<i>Adenantha pavonina</i> (Mimosaceae)	3	1
<i>Aglaiia</i> sp.1 (Meliaceae)	1	0
<i>Aglaiia</i> sp.2 (Meliaceae)	0	3
<i>Alseodaphne peduncularis</i> (Lauraceae)	0	1
<i>Amoora wallichii</i> (Meliaceae)	5	10
<i>Anthocephalus chinensis</i> (Rubiaceae)	0	1
<i>Beilschmiedia assamica</i> (Lauraceae)	1	0
<i>Beilschmiedia roxburghiana</i> (Lauraceae)	0	1
<i>Beilschmiedia</i> sp. (Lauraceae)	0	1
<i>Bischofia javanica</i> (Euphorbiaceae)	0	2
<i>Bridelia retusa</i> (Euphorbiaceae)	0	1
<i>Callicarpa macrophylla</i> (Verbenaceae)	0	2
<i>Chisocheton cumingianus</i> (Meliaceae)	0	32
<i>Cinnamomum glaucescens</i> (Lauraceae)	0	1
<i>Cinnamomum obtusifolium</i> (Lauraceae)	1	1
<i>Cinnamomum</i> sp. (Lauraceae)	0	1
<i>Cryptocarya amygdalina</i> (Lauraceae)	0	2
<i>Cryptocarya</i> sp. (Lauraceae)	2	0
<i>Duabanga grandiflora</i> (Lythraceae)	13	3
<i>Dysoxylum binectariferum</i> (Meliaceae)	6	11
<i>Dysoxylum hamiltonii</i> (Meliaceae)	0	2
<i>Ehretia laevis</i> (Boraginaceae)	0	1
<i>Evodia meliaefolia</i> (Rutaceae)	0	3
<i>Ficus hookeri</i> (Moraceae)	0	1
<i>Ficus</i> sp. (Moraceae)	0	1
<i>Garcinia pedunculata</i> (Clusiaceae)	17	1
<i>Garuga pinnata</i> (Burseraceae)	0	2
<i>Horsfieldia kingii</i> (Myristicaceae)	1	1
<i>Knema angustifolia</i> (Myristicaceae)	0	1
<i>Laportea crenulata</i> (Urticaceae)	2	11
<i>Leea indica</i> (Leeaceae)	7	4
<i>Litsea</i> sp. 1 (Lauraceae)	5	3
<i>Litsea</i> sp. 2 (Lauraceae)	5	1

Appendix 1 continued

Species	Logged forest	Unlogged forest
<i>Litsea</i> sp. 3 (Lauraceae)	2	3
<i>Litsea</i> sp. 4 (Lauraceae)	2	1
<i>Macaranga denticulate</i> (Euphorbiaceae)	19	0
<i>Mesua ferrea</i> (Clusiaceae)	4	7
<i>Michelia champaca</i> (Magnoliaceae)	11	9
<i>Morus laevigata</i> (Moraceae)	0	4
Paani Jamun (common name)	8	9
<i>Phoebe attenuate</i> (Lauraceae)	0	1
<i>Phoebe cooperiana</i> (Lauraceae)	0	1
<i>Phoebe goalparensis</i> (Lauraceae)	17	4
<i>Phoebe</i> sp. (Lauraceae)	0	1
Puthna (common name)	4	4
<i>Sapium baccatum</i> (Euphorbiaceae)	8	1
<i>Styrax serrulatum</i> (<u>Styracaceae</u>)	13	8
<i>Syzygium</i> sp. 1 (Myrtaceae)	3	16
<i>Syzygium</i> sp. 2 (Myrtaceae)	6	1
<i>Syzygium</i> sp. 3 (Myrtaceae)	1	8
<i>Syzygium</i> sp. 4 (Myrtaceae)	1	1
<i>Syzygium</i> sp. 5 (Myrtaceae)	0	1
<i>Trema orientalis</i> (Ulmaceae)	0	1
<i>Turpinia pomifera</i> (<u>Staphyleaceae</u>)	0	1
<i>Vitex pentaphylla</i> (Verbenaceae)	0	1
<i>Zanthoxylum oxyphyllum</i> (Meliaceae)	2	1
<i>Zanthoxylum rhetsa</i> (Meliaceae)	1	1
Total	189	209
Mammal dispersed		
<i>Baccaurea sapida</i> (Euphorbiaceae)	5	4
<i>Dillenia indica</i> (Dilleniaceae)	0	3
<i>Elaeocarpus ganitrus</i> (Elaeocarpaceae)	0	1
<i>Gmelina arborea</i> (Verbenaceae)	5	4
<i>Gynocardia odorata</i> (Flacourtiaceae)	0	6
<i>Premna bengalensis</i> (Verbenaceae)	1	2
<i>Spondias pinnata</i> (Anacardiaceae)	1	0
<i>Terminalia bellerica</i> (Combretaceae)	5	3
<i>Terminalia chebula</i> (Combretaceae)	1	1
<i>Turpinia pomifera</i> (Staphyleaceae)	2	0
Total	25	24

Appendix 1 continued

Species	Logged forest	Unlogged forest
Dispersed by both birds and mammals		
<i>Artocarpus chaplasha</i> (Moraceae)	1	1
<i>Canarium resiniferum</i> (Burseraceae)	10	3
<i>Castanopsis indica</i> (Fagaceae)	6	3
<i>Dillenia pentagyna</i> (Dilleniaceae)	0	1
<i>Ficus elastica</i> (Moraceae)	2	1
<i>Ficus maclellandii</i> (Moraceae)	0	1
<i>Mallotus philippensis</i> (Euphorbiaceae)	2	2
<i>Polyalthia simiarum</i> (Annonaceae)	10	33
<i>Semecarpus anacardium</i> (Anacardiaceae)	2	1
<i>Sterculia villosa</i> (Sterculiaceae)	7	2
<i>Talauma hodgsoni</i> (Magnoliaceae)	10	15
Tanyum (common name)	1	1
<i>Vitex peduncularis</i> (Verbenaceae)	1	2
<i>Vitex pentaphylla</i> (Verbenaceae)	3	3
<i>Zizyphus rugosa</i> (Rhamnaceae)	2	2
Total	55	71