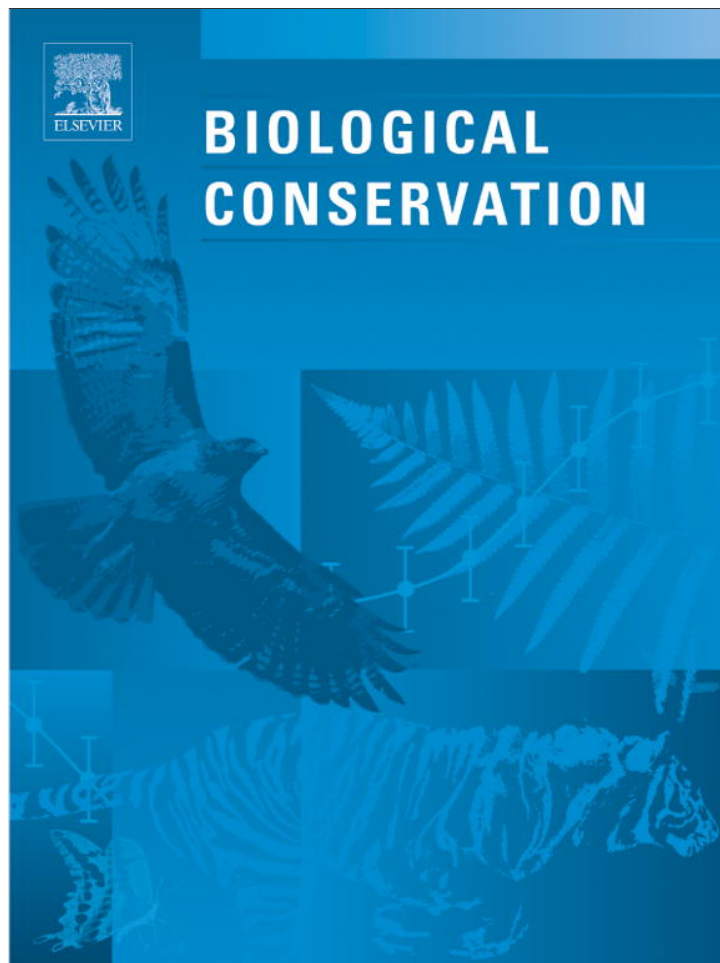


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## Shifts in community structure of tropical trees and avian frugivores in forests recovering from past logging

Nandini Velho<sup>a,\*</sup>, Jayashree Ratnam<sup>a</sup>, Umesh Srinivasan<sup>a</sup>, Mahesh Sankaran<sup>a,b</sup><sup>a</sup> National Centre for Biological Sciences, Bangalore 560 065, India<sup>b</sup> Institute of Integrative and Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

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## ABSTRACT

Logging is one of the most pervasive threats to biodiversity in tropical forests. In this study, we concurrently examined the responses of the avian frugivore community and the community of fruiting trees to past logging in a tropical forest in northeastern India. We predicted that the abundance of, and visitation by large-bodied frugivores would be lower in logged forests, resulting in reduced seed dispersal and recruitment of biotically dispersed species (especially large-seeded species). Data were collected from two logged and unlogged sites using (a) belt transects for estimating avian frugivore abundance (b) fruiting tree watches to quantify frugivore visitation and (c) vegetation plots to characterize recruitment. Our results show that differences in the abundance of bird species between logged and unlogged sites was correlated with body mass, with larger species being scarcer and smaller species more abundant in logged areas. Correspondingly, visitation rates by large avian frugivores was lower in logged compared with unlogged sites. Finally, biotically dispersed tree species, especially large-seeded species, had lower recruitment in logged forests, potentially due to lowered visitation rates and decreased fruit removal by large bodied avian frugivores. In the long term, these differences in recruitment may result in a tree community shift towards small-seeded biotically dispersed species and abiotically dispersed species in logged areas.

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## 1. Introduction

Despite evidence that logging is one of the most pervasive drivers of biodiversity loss and ecosystem disturbance (Thiollay, 1999), large areas of tropical forest continue to undergo heavy logging to this day (Koh and Sodhi, 2010). Commercial logging practices affect forest composition, structure and functioning in numerous ways (Reich et al., 2001). While clear felling leads to outright habitat loss, selective logging typically leads to habitat degradation, with associated negative impacts on both plant (Padmawathe et al., 2003; Péliissier et al., 1998), and animal communities such as primates (Felton et al., 2010), birds (Sethi and Howe, 2009), fish (Dias et al., 2009) and arthropods (Halaj et al., 2008). Even ecologically sustainable practices of selective logging such as reduced-impact logging (RIL) can have a variety of negative effects on the composition and functioning of tropical forest communities, both in the short- and long-term (Dias et al., 2009; Ernst et al., 2006; Felton et al., 2008; Pereira et al., 2002).

Logging can influence plant diversity and forest composition both directly through the process of selective removal of species,

and indirectly by altering nutrient cycling patterns, micro-climate, and soil and forest floor characteristics (Reich et al., 2001). In addition, selective logging can also disrupt key ecological interactions (e.g. plant–pollinator and plant–seed disperser interactions), which can feedback to influence community composition and functioning in the longer term (Brook et al., 2003; Corlett, 2002). In tropical forests, almost 75% of all tree species are adapted to animal-mediated dispersal, with avian frugivores playing an especially important role (Howe and Smallwood, 1982). There is often an overlap between target timber species and the diet of several frugivores in logging operations in tropical forests (Felton et al., 2010). The loss of avian frugivores from a selectively logged forest can therefore impact the recruitment dynamics of tree species, and thus, forest composition in the longer term (Kirika et al., 2008).

Amongst avian frugivores, large-bodied frugivores are expected to be especially vulnerable to habitat modifications resulting from selective logging (Gray et al., 2006; Thiollay, 1999). Their diet depends primarily on large-seeded fruit, and is relatively inflexible (Howe and Smallwood, 1982). The loss of large-bodied avian frugivores from a selectively logged forest can have a disproportionate impact on the recruitment of large-seeded tree species that depend on them as vectors for seed dispersal. As a consequence, small-seeded biotically-dispersed species may have an advantage over

\* Corresponding author. Tel.: +91 80 2366 001; fax: +91 80 6562 6304.

E-mail address: [nandinivelho@gmail.com](mailto:nandinivelho@gmail.com) (N. Velho).

large-seeded biotically dispersed species in selectively logged forests. These effects are likely to be long-term since large-bodied frugivores often have low reproductive rates and abundances and may be slow to recover from a reduction in their populations (Cleary et al., 2007). The signatures of past logging on plant and animal communities are thus likely to persist over long time periods.

While frugivory, seed dispersal and tree recruitment are processes that typically involve multiple species interactions, most studies, primarily for logistical reasons, focus either on the direct effects of logging on species populations (e.g., Datta, 1998; Sorensen and Fedigan, 2000) or on the interactions of selected frugivore species with focal tree species (e.g. Kirika et al., 2008; Sethi and Howe, 2009). Thus, while the effects of logging on the occurrence, abundance and dynamics of some selected species are well understood (Datta, 1998; Ranganathan et al., 2008), large gaps still remain in our knowledge of the community level effects of logging, and the mechanisms underlying them.

In this study of a lowland tropical forest in north-east India we scale up to explore tree-frugivore dynamics at the community level, and to identify potential mechanisms that lead to the observed patterns in tree community dynamics in logged habitats. Large sections of the forest across this landscape were historically subjected to logging. In this study, we use forest areas recovering from past logging and intact forests in protected areas as 'treatments' from a natural experiment to examine logging impacts. As in other tropical forests, hunting was also a feature of this landscape and is likely to have occurred more in logged areas. Given this history, we note that it is not possible to clearly separate the effects of hunting versus logging on the unprotected forests in this region. To minimize this confounding effect, we chose logged regions where hunting bans have been effectively enforced for the past few decades (see Section 2).

Based on our expectations of the greater vulnerability of large frugivores to disturbances and on our knowledge of their life-history traits, we predicted that in areas recovering from logging: (1) large-bodied avian frugivores would be less abundant than small-bodied avian frugivores, and (2) visitation rates of avian frugivores (hereafter referred to as interaction strengths (Bascompte et al., 2006)) would be lower, with the relative decrease being greatest for (a) large-bodied avian frugivores and (b) large-seeded trees. We also predicted that these effects would in turn cascade through to the plant community level such that (3) biotically-dispersed species would show reduced recruitment in areas recovering from logging, and (4) amongst biotically-dispersed species, small-seeded species would recruit better than large-seeded ones in logged areas.

## 2. Methods

### 2.1. Study area and study species

This study was carried out from November, 2009 to March, 2010 in and around the Pakke Wildlife Sanctuary and Tiger Reserve (861.95 km<sup>2</sup>; 92°36'–93°09'E; 26°54'–27°16'N) in western Arunachal Pradesh, India. The terrain in the study area is undulating and hilly (c. 200–1500 m asl; Datta, 1998). The main vegetation type is classified as Assam valley tropical semi-evergreen forest (Champion and Seth, 1968). The dominant tree species are *Polyalthia simiarum*, *Pterospermum acerifolium*, *Sterculia alata*, *Stereospermum chelonoides*, *Ailanthus grandis* and *Duabanga grandiflora* (Datta and Rawat, 2008).

Of the 295 bird species recorded in Pakke Tiger Reserve, about 35–40 are known to be frugivorous (Datta and Rawat, 2008). The Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Rhyticeros undulatus*) and Oriental Pied Hornbill (*Anthraceros albirostris*) are the larger-bodied 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. In addition, there is a great diversity of smaller frugivores, with eight species of bulbuls (*Pycnonotus* spp.), five species of mynas (*Acridotheres* spp.), four species of barbets (*Megalaima* spp.), four species of green pigeons (*Treron* spp.), four species of doves (*Streptopelia* sp., *Macropygia* sp. and *Chalcophaps* spp.), three parakeet species (*Psittacula* spp. and *Loriculus* sp.), two species of leaf birds (*Chloropsis* spp.), two oriole species (*Oriolus* spp.) and the Fairy Bluebird (*Irena puella*). Several species of babblers such as laughingthrushes include fruit in their diet. Species such as the rare Green Cochoa (*Cochoa viridis*) are thought to be frugivorous but we lack detailed dietary information. The other arboreal species that depend on fruits/seeds are four species of diurnal tree squirrels.

We selected two blocks each in logged and unlogged areas based on information from previous systematic records maintained in the form of Departmental Timber Operations reports – henceforth DTOs – in the working plans of the Forest Department, and from the published literature (Datta, 1998; Sethi and Howe, 2009).

All our study sites were broadly comparable in terms of geology, rainfall, climate, vegetation, and topography (see Sethi and Howe, 2009). Our two unlogged sites (c. 10 km<sup>2</sup> each) were located within the protected area. One site (92°35'E; 27°0'N) was on the western side of the park (Bhalukpong ghat – Denai area) in the Tipi range, and the other in the south-eastern part of the park in the Seijosa range (26°56'N; 92°58'E). Our two logged sites were located in the periphery of the protected area, in the Doimara Reserve Forest (245 km<sup>2</sup>; 27°01'N; 92°9'E) and the Papum Reserve Forest (1063.87 km<sup>2</sup>, 27°01'N; 92°57'E), respectively, and were commercially logged until the late 1970s (Birand and Pawar, 2004).

Forests were logged under a selection system in which trees were selectively felled and allowed to regenerate naturally. Based on the DTO records, the most commonly logged species were *Terminalia myriocarpa*, *Duabanga grandiflora*, *Artocarpus chaplasha*, *Amora wallichii*, *Michelia* spp., *Dysoxylum procerum* and *Toona ciliata*. Trees were harvested depending on the volume sanctioned to people. Each family of residents of the area and of forest staff was entitled to roughly 300 cubic feet of timber per year. Beneficiaries either sold their permit to sawmills or supplied the timber to sawmills. This commercial demand for timber led to an increase in extraction above the prescribed official volume. An order passed in 1996 by the Supreme Court of India officially banned timber harvesting, thus beginning a sustained period of regeneration which has been sporadically interrupted by illegal felling (Sethi and Howe, 2009).

A confounding factor with respect to understanding the dynamics of frugivore populations in this region is that hunting, a traditional practice in the local culture, was widespread in this region, but likely occurred more outside protected areas in recent history (Sethi and Howe, 2009). Thus the observed patterns in frugivore communities result from both past logging and hunting, with the latter likely to have impacted frugivore communities more in logged areas. Presently, the *Ghora Aabhe*, a council constituting village heads from the periphery of the park, actively enforces a wide ranging community-led ban on hunting, especially on hornbills. Nevertheless, to try and minimize the effects of hunting in logged sites, we chose study sites that were in the least accessible parts of the reserve forests, next to known anti-poaching camps, and therefore likely to be avoided by opportunistic hunters and poachers. We note that current anti-poaching efforts do not affect the legacy of past hunting.

### 2.2. Avian frugivore densities

We used belt transects to compare the abundances of avian frugivores in logged and unlogged forests. We set up 15 transects in

each of the two logged and unlogged sites, for a total of 60 transects. Transects were 400 m long and 20 m wide, and were separated from one another by a distance of at least 500 m. Each transect was sampled three times during the course of the study between 6:30 and 11:00 am, and all frugivorous birds were censused based on direct sightings and calls.

We used a generalized linear model (GLM) on species count data, with habitat type (categorical: logged or unlogged) and bird species body mass as predictor variables to model the impact of logging on frugivores of various sizes. Data on frugivore body mass was collated from Ali and Ripley (1983) and Del Hoyo et al. (2005). Where body masses were reported as a range of values, we used the mid-point of the range for statistical analyses. For the GLM, we pooled data from all transects in each habitat type to obtain species-specific counts. Since our frugivore count data were over-dispersed, we used a negative binomial GLM with a log link to model data, testing for an interaction between frugivore body size and habitat type.

### 2.3. Avian frugivore visitation rates

During winter (December to February), a fruiting scarcity of biotically-dispersed tree species occurs at Pakke Wildlife Sanctuary and Tiger Reserve (Velho et al., 2009). Since our study largely overlapped with this relatively resource poor period, we were able to sample the dominant fruiting tree species to determine frugivore visitation rates. We quantified visitation rates to six tree species that were fruiting during the period and had fruit characteristics typical of those consumed by birds (Table 1; Datta and Rawat, 2008).

At one logged (Langka) and unlogged site (Seijosa range), we randomly selected 10 individuals of each of the six fruiting tree species. We conducted focal tree watches from 6:30 to 11:00 am during peak fruiting for each tree, and noted the identity of avian frugivore visitors, numbers, time of arrival and time spent on each tree. For rare and asynchronously fruiting species such as *Ficus drupacea*, we were only able to sample six individuals each in logged and unlogged sites.

Visitation rates were computed as the number of visits by each frugivore species to each tree species for a standardized sampling period. Interaction strengths were calculated using visitation rates following Bascompte et al. (2006) and Tylianakis et al. (2007), where interaction strengths of a tree and bird species was calculated as the fraction of all visits to the tree species by a particular bird species. We used a species level analysis for each bird species across all six tree species in unlogged and logged habitats using the packages *bipartite* and *vegan* in the statistical software R (version 2.8.0; R Development Core Team, 2009). Differences in interaction strengths between habitat types (interaction strength in unlogged forest minus interaction strength in logged forest) for avian frugivores were evaluated as a function of body size, with the expectation that large-bodied frugivores would have higher interaction strengths in unlogged relative to logged habitats.

### 2.4. Regeneration patterns

At the start of each of 15 transects in logged and unlogged areas, we set up a 10 × 10 m plot to enumerate vegetation regeneration patterns. We sampled all seedlings and saplings within plots (defined as all individuals below 8 m in height) as well as adults (over 8 m in height) (Githiru et al., 2002). At the whole community level, we compared logged and unlogged sites for differences in numbers of recruits of biotically and abiotically dispersed species. We then classified biotically dispersed species as either small-seeded (<10 mm diameter) or large-seeded (>10 mm diameter; after Kitamura et al., 2005), and compared recruitment of these two categories across the two habitats. For five out of six focal bird-dispersed species for which we also had fruiting tree watches, we conducted pair-wise analyses of recruitment in logged and unlogged sites. We ran a GLM with Poisson errors and a canonical log link function to assess whether these five species showed a difference in the number of recruits in logged and unlogged areas. We excluded *F. drupacea* from these analyses because there was no recruitment recorded in both logged and unlogged plots. To examine the potential impact of adult stand structure on recruitment patterns (independent of dispersers), we compared the size distribution of biotically and abiotically dispersed recruits and compared these with adult tree distributions across logged and unlogged forests. We also report on the adult and recruit densities of the five focal species in unlogged and logged areas.

All analyses were carried out using the statistical software R (version 2.8.0; R Development Core Team, 2009).

## 3. Results

### 3.1. Avian frugivore densities

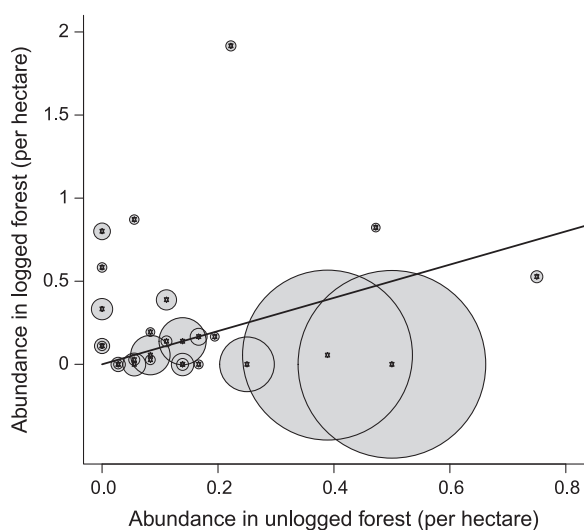
Frugivore abundances in response to logging differed by body size (significant habitat type × frugivore body mass interaction  $z_{1,56} = 2.045$ ,  $p = 0.04$ ). While the abundances of larger bodied frugivores were depressed in logged habitats, smaller bodied frugivores did not decrease, and in some cases, increased in abundance in logged habitats (Fig. 1).

### 3.2. Frugivore visitation rates

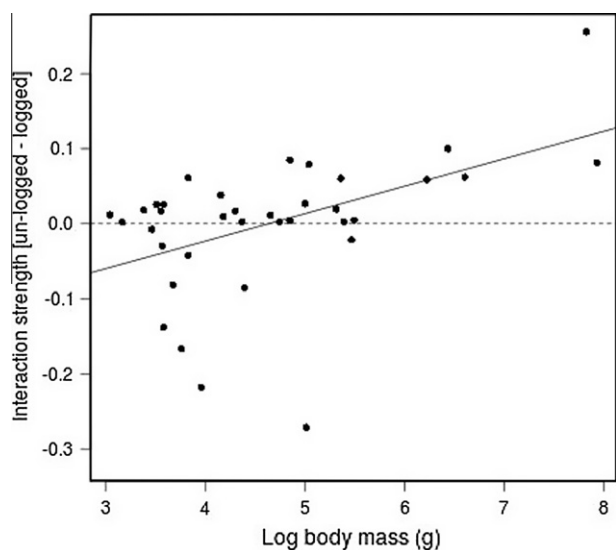
In total 42 avian frugivore species visited focal fruiting trees in both logged and unlogged habitats (30 in logged and 39 in unlogged respectively). At the species level, difference in interaction strength between logged and unlogged habitats was positively correlated with body mass (Fig. 2; Pearson's  $R = 0.48$ ;  $p < 0.01$ ), with lowered visitation rates to fruiting trees by larger bodied frugivores in logged habitats. Smaller-bodied species interacted with fruiting trees more in logged habitats. In contrast, larger-bodied species interacted more strongly with selected fruiting species in unlogged habitats (Fig. 2).

**Table 1**  
Fruit and seed characteristics of six bird-dispersed tree species selected for the study.

Tree species	Family	Fruit type	Fruiting period
<i>Actinodaphne angustifolia</i>	Lauraceae	Drupe	October–December
<i>Ficus drupacea</i>	Moraceae	Fig	January–April
<i>Litsea</i> sp.	Lauraceae	Drupe	February–March
<i>Polyalthia simiarum</i>	Lauraceae	Drupaceous carpel	December–February; May–July
<i>Talauma hodgsoni</i>	Magnoliaceae	Aggregate follicle	November–January
<i>Sterculia villosa</i>	Sterculiaceae	Follicle	February–March



**Fig. 1.** The abundance per hectare of avian frugivores in unlogged and logged habitats. The solid line indicates the line on which species would lie if their abundances in logged and unlogged habitats were equal. Species above the solid line have higher abundances in logged habitats, whereas species below the solid line have higher abundances in unlogged habitats. Each bubble denotes a single species of avian frugivore and the size of the bubble is directly proportional to body mass. As can be seen, larger species tend to occur below the line, whereas a large number of smaller species occur above it, indicating that larger species are rarer in logged habitats.



**Fig. 2.** The difference in interaction strength (see Section 2 for details) in unlogged and logged habitats for each avian frugivore species. The dotted line indicates no difference in interaction strengths between logged and unlogged habitats. Species above the dotted line interact more strongly in unlogged habitats, whereas species below the dotted line interact more strongly in logged habitats. The solid line shows the positive relationship between interaction strength and body mass.

### 3.3. Regeneration patterns

For three of the five intensively studied tree species, all of which were large-seeded, there was a significant decrease in the number of recruits per plot in logged areas (Fig. 3). For the other two focal species which were small-seeded, recruitment was uniformly low and did not differ between logged and unlogged habitats. When adult and recruit densities were compared across treatments, there was no consistent relationship between adult and recruit densities

in either logged or unlogged habitats (Figs. 3 and 4), suggesting that reduced recruitment in logged areas did not stem from a reduction in adult densities in logged areas (Fig. 4).

At the community level, logged areas had a lower number of biotically-dispersed recruits compared with unlogged areas (ANOVA  $F_{1,28} = 22.18$ ;  $R$  squared = 0.44;  $p < 0.01$  Fig. 5). This was despite the fact that the number of biotically dispersed adult trees did not differ significantly between logged and unlogged areas (ANOVA,  $t_{1,118} = 1.64$ ,  $p = 0.10$ ). Further, the size-class structure of recruits of abiotically and biotically dispersed species differed across habitats, despite adult stand structure being similar across habitats, with biotically dispersed species accounting for greater recruitment compared with abiotically dispersed species in intact habitat (Fig. 6). Finally, amongst biotically-dispersed tree species, logged areas had, on an average, fewer recruits of large-seeded species compared with unlogged areas (ANOVA  $F_{1,28} = 12.18$ ;  $R$  squared = 0.30;  $p = 0.002$ , Fig. 7).

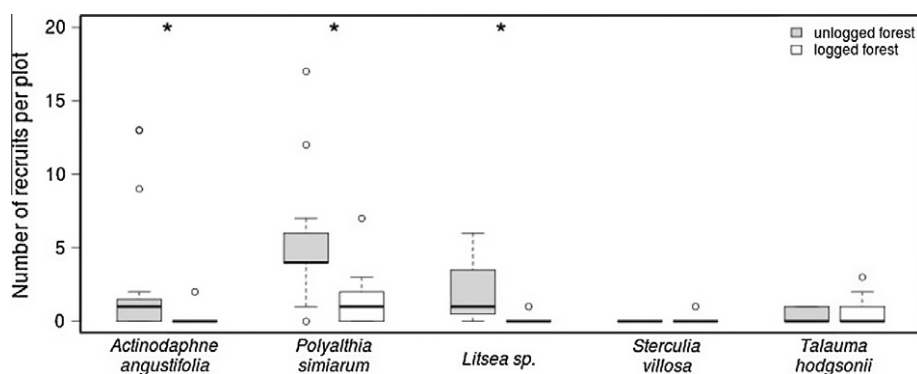
## 4. Discussion

Our results show that in this tropical forest community, both the abundances of avian frugivores and their interactions with fruiting tree species were negatively impacted in logged areas, with potential knock-on effects on plant community recruitment. Logged habitats had lower densities of large-bodied avian frugivores (Fig. 1). Logged and unlogged habitats differed in the interaction strengths of avian frugivores and fruiting trees: large-bodied frugivores such as hornbills, imperial pigeons and hill mynas had higher interaction strengths in unlogged habitats, while smaller-bodied species such as three species of bulbuls, two species of barbets and one species of parakeet had higher interaction strengths in logged areas (Fig. 2). Finally, recruitment of tree species differed in logged and unlogged areas (Figs. 3, 5 and 6), with frugivore dispersed trees with large seeds showing the greatest reductions in recruitment in logged areas (Fig. 7).

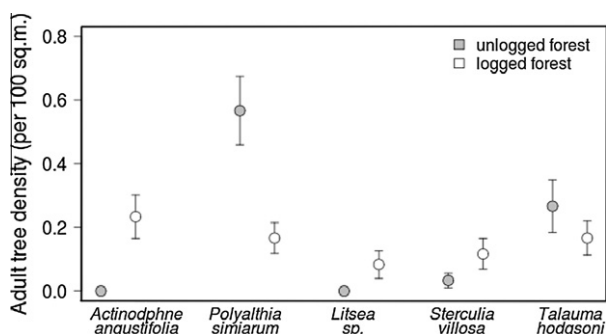
Our study expands on the scale of earlier investigations in several ways. Firstly, by including the entire cohort of frugivorous birds and fruiting trees this study provides a community-wide examination of interactions between trees and frugivores in areas modified by logging. Secondly, we take this further by comparing not just community characteristics of birds and trees separately, but also the interaction strengths between fruiting tree species and avian frugivores. Finally and most importantly, we attempt to link community level changes in tree-frugivore interactions to patterns in tree recruitment to gain insight into the mechanisms underlying recruitment patterns in logged areas.

Our results for frugivore abundance are consistent with findings from other studies that have shown that feeding guild and body size determine bird population responses to logging (Cleary et al., 2007; Edwards et al., 2009; Gray et al., 2006; Gomes et al., 2008; Thiollay, 1999; Zurita and Zuleta, 2009). Similar patterns showing declines in large-bodied frugivore species richness and visitation have been noted in response to logging in tropical Africa (Kirika et al., 2008). In this study, given that hunting was probably more prevalent in logged habitats, the lower abundances and visitation rates of large frugivores in these habitats could either be a response to the logging or it could simply be that large frugivore populations have not recovered from past hunting. Finally, the increase in overall abundance of frugivores in logged areas, observed elsewhere (Lambert, 1992; Owunji and Plumptre, 1998; Thiollay, 1999) is attributable to an increase in the abundance of smaller bodied frugivores which are capable of exploiting small-fruited plants that do well in logged habitats (Lambert, 1992).

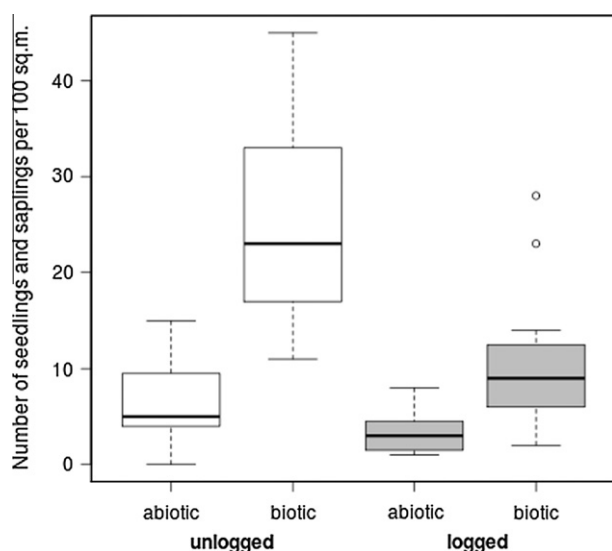
Several recent studies have examined the potential value of logged habitats in supporting biodiversity (e.g. Berry et al., 2010;



**Fig. 3.** The number of recruits of five focal bird-dispersed species per 100 m<sup>2</sup> in logged and unlogged areas. The box plot represents the 1st and 3rd quartile with the median, while the whiskers extend to the most extreme data point which is no more than range times the interquartile range from the box. For each species, a statistically significant difference in the number of recruits (Poisson GLM with a log link,  $p < 0.05$ ), is indicated with a \*. Species are arranged in order of their decreasing seed size (left to right).



**Fig. 4.** The number of adults of five focal tree species in logged and unlogged areas. Error bars indicate one standard error. Species are arranged in the same order as Fig. 3, to show that apart from *Polyalthia simiarum*, which has higher tree density and recruit density in unlogged areas, for the other tree species there is no correlation between density of adult trees and recruits.



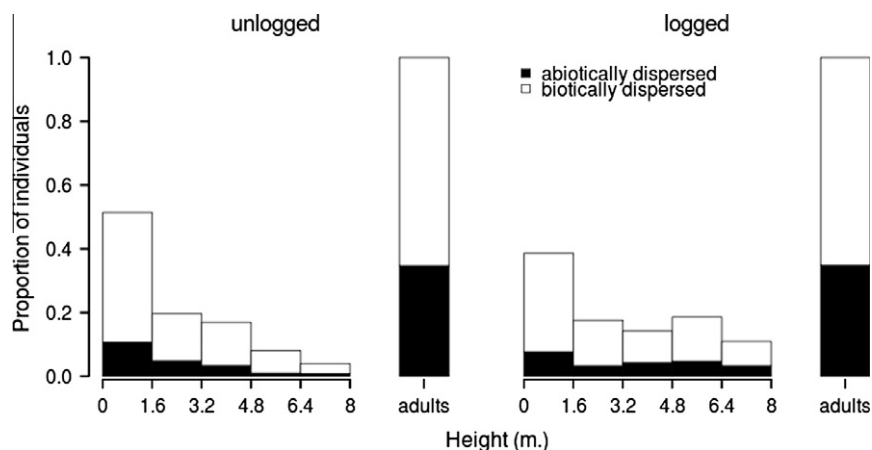
**Fig. 5.** The number of seedlings and saplings of abiotic and biotically dispersed species per 100 m<sup>2</sup> in logged and unlogged areas. The box plot represents the 1st and 3rd quartile with the median, while the whiskers extend to the most extreme data point which is no more than range times the interquartile range from the box.

Edwards et al., 2011). These studies have found that habitats subjected to reduced-impact logging often support significant biodiversity, are important for conserving certain taxa or species and

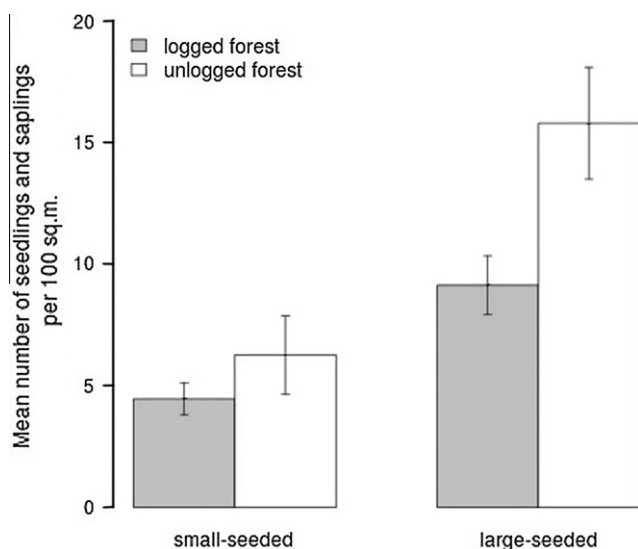
may be cost-effective options to expand the protected area network (e.g. Bertault and Sist, 1997; Wunderle et al., 2006; Fisher et al., 2011). However, Sodhi et al. (2010) caution that although some logged forests may show high tree diversity, this may not always translate to high conservation value, since logging can often facilitate the growth of abundant, early successional species while exacerbating the loss of rare, late-successional species. Although reduced-impact logging might have relatively little impact on several taxa, conventional logging practices, as seen at our study site and across this region in general, are likely to negatively impact both the abundances and interactions of key species and thereby to have a greater impact on community structures (e.g. Davis, 2000).

Not only did we find that the abundance of large-bodied frugivores was lower in logged areas, but importantly, this decreased abundance corresponded with lower visitation rates by large-bodied frugivores to fruiting trees in logged habitats. Such changes in visitation rates by a subset of potential seed dispersers need not translate to lowered levels of recruitment if other dispersers can provide compensatory seed-dispersal services, or where recruitment is not dispersal-limited (Howe and Miriti, 2004). However, we found no evidence for compensatory seed dispersal for large-seeded tree species in this community, and they were especially affected by lowered visitation rates in logged areas. For these large-seeded species, effective seed dispersal by avian frugivores may be limited by the gap width of seed dispersers, and they might consequently be constrained to dispersal mediated only by large-bodied frugivores (Holbrook et al., 2002). Consistent with this expectation, we found much lower regeneration of large-seeded species in logged habitats, compared with unlogged habitats. In contrast, although the abundance of small frugivores increased in logged habitats, the recruitment of these small-seeded species did not differ significantly between logged and unlogged sites. It is likely that recruitment in these tree species, with multiple and abundant seed dispersers, is constrained by post-dispersal abiotic or biotic factors (Sethi and Howe, 2009).

Overall, we found a lower density of biotically-dispersed recruits in logged areas when compared with unlogged areas. Similar responses of the density of recruits to disturbance have been found in other studies (Chapman and Onderdonk, 1998; Peres and Palacios, 2007). Seed dispersal services by biotic vectors are known to be very important for tree regeneration (Bleher and Böhning-Gaese, 2001; Guariguata et al., 2000; Sodhi et al., 2004). With simultaneous increases in abundance and visitation of small frugivores and reduction in visitation by large frugivores in logged habitats, small-seeded biotically-dispersed and wind-dispersed tree species may have a relative advantage over biotically-dispersed, large-seeded



**Fig. 6.** Proportion of differently-sized recruits and adults of abiotically and biotically dispersed species in unlogged and logged forest. Even though the proportion of adults from the two dispersal modes are almost identical, biotically dispersed individuals make up a larger proportion of recruits in unlogged forest, especially in the youngest size classes. For recruits and adults, heights of the bars indicate proportions relative to total number of recruits and adults respectively (separately for unlogged and logged habitats).



**Fig. 7.** Mean number of seedlings and sapling per 100 m<sup>2</sup>. Error bars indicate one standard error. Small-seeded species were classified as seeds with size less than 10 mm in diameter; large-seeded species were greater than 10 mm in diameter.

species in logged forests. Collectively, these changes might result in a tree community shift (Chapman et al., 2010) towards species that are either abiotically dispersed or dispersed by small bodied frugivores, with attendant implications for changes in the structure and functioning of logged sites. Future studies that focus on measuring structural and functional changes in these systems will generate critical insights into the trajectories of sites recovering from past logging.

Our findings of reduced visitation rates of large bodied frugivores in logged habitats ties in broadly with the observed downstream patterns of reduced recruitment of large-seeded species that they are known to disperse. As noted before, the lower visitation rates of large frugivores found in our logged sites could have resulted from either hunting or logging. However, regardless of the initial cause of decline in large frugivore abundances, one would still expect reduced visitation rates to large-seeded tree species and consequent depression in recruitment of such species to lead to a negative feedback effect on large frugivore numbers. In

the future, longer-term studies examining the relationship between visitation rates by frugivores and the dynamics of seed dispersal and recruitment would provide stronger evidence for nature of the linkages between these processes. It will also be important for future work to establish whether post-dispersal processes such as seed predation and seedling germination differ across logged and unlogged forests. Evidence from unlogged habitats shows that rodent seed-predators significantly increase seed mortality of several hornbill-dispersed tree species (Velho et al., 2009). Examining whether post-dispersal seed predators have differential impacts in logged and unlogged forests would be necessary for a complete understanding of the dispersal-recruitment loop and how this might be affected by logging.

In this study of a tropical forest recovering from past logging, we observed both reduced seed dispersal services of large-bodied avian frugivores and depressed regeneration of large-seeded tree species, with community-wide consequences for forest composition, structure and function. In particular, we note that the long persistence times of juvenile stages of tropical forest trees mean that our data on seedling and sapling stages capture a longitudinal phenomenon, and are thus a strong indicator of trends that are likely to be persistent. Across the tropics, logging remains a major conservation threat to forests. Our results suggest that banning logging alone may not always ensure a return of original forest communities. Active restoration with a focus on large-seeded species may be required in at least some regions.

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**Appendix A. Visitation rates by avian frugivores (mean number of visits per 4.5 hour observation period) on six focal tree species in unlogged forest**

Frugivore species	<i>Ficus drupacea</i>	<i>Talauma hodgsoni</i>	<i>Litsea</i> sp.	<i>Actinodaphne angustifolia</i>	<i>Polyalthia simiarum</i>	<i>Sterculia villosa</i>
<i>Hemixos flavala</i>	3.25	0	0	0	0	0
<i>Hypsipetes leucocephalus</i>	3	0	1.5	0	0	0
<i>Pycnonotus melanicterus</i>	0.25	0.625	0.125	0	0	0.125
<i>Oriolus xanthornus</i>	0.125	0	0	0	0	0
<i>Megalaima australis</i>	0.875	0	0	0	0	0
<i>Megalaima asiatica</i>	1.75	0	2.25	0	0	0.125
<i>Chloropsis jerdoni</i>	0.5	0	0	0	0	0
<i>Megalaima haemacaphala</i>	0	0	0	0	0	0
<i>Irene puella</i>	3	0	0	0	0	0
<i>Chloropsis jerdoni</i>	0.25	0	0	0	0	0
<i>Oriolus oriolus</i>	0.875	0	0	0	0	0
<i>Megalaima virens</i>	0.5	0	0	0	0	0
<i>Buceros bicornis</i>	0.375	0	0	0.5	0	0
<i>Phoenicophaeus tristis</i>	0.125	0	0	0	0	0
<i>Cochoa viridis</i>	0	0	0.125	0	0	0
<i>Ducula aenea</i>	0	0	0	0.375	1.5	0
<i>Gracula religiosa</i>	2	0	2.75	0	4.375	0
<i>Megalaima lineata</i>	3.625	0	0.375	0	0.125	0.75
<i>Heterophasia picaoides</i>	0.375	0	0	0	0	0
<i>Oriolus trailii</i>	0.875	0	0	0	0	0
<i>Ducula badia</i>	2.125	0	1.375	0.25	4.125	0
<i>Chloropsis aurifrons</i>	0	0.125	0	0	0	0
<i>Anthraceroceros albirostris</i>	0.25	0	0.125	0	0.125	0.25
<i>Treron apicuada</i>	5	0	0	0	0	0
<i>Treron pompadora</i>	2.25	0	0	0	0	0
<i>Leiothrix argenteauris</i>	0.75	0	0	0	0	0
<i>Psittacula alexandri</i>	1.625	0	0	0	0	1.625
<i>Pycnonotus cafer</i>	0	0	0	0	0	0
<i>Pycnonotus jocosus</i>	0	0	0	0	0	0
<i>Psittacula krameri</i>	0	0	0	0	0	1
<i>Treron curvirostra</i>	1.375	0	0	0	0	0
<i>Loriculus vernalis</i>	0	0	0	0	0	0.625
<i>Treron sphenurus</i>	3.125	0	0	0	0	0
<i>Alophoixus flaveolus</i>	8.125	2	1.625	0	0	0.625
<i>Rhyticeros undulatus</i>	0.875	0	0.25	1.75	1.125	0
<i>Treron phoenicoptera</i>	4	0	0	0	0	0

**Appendix B. Visitation rates by avian frugivores (mean number of visits per 4.5 hour observation period) on six focal tree species in logged forest**

Frugivore species	<i>Ficus drupacea</i>	<i>Talauma hodgsoni</i>	<i>Litsea</i> sp.	<i>Actinodaphne angustifolia</i>	<i>Polyalthia simiarum</i>	<i>Sterculia villosa</i>
<i>Hemixos flavala</i>	1.875	0	0	0	0	0
<i>Hypsipetes leucocephalus</i>	4.375	1.25	3	0	0	0
<i>Pycnonotus melanicterus</i>	2.375	0.5	0.25	0	0	0.125
<i>Oriolus xanthornus</i>	0	0	0	0	0	0
<i>Megalaima australis</i>	0	0	0	0	0	0
<i>Megalaima asiatica</i>	10.125	0.125	2.375	0	0	0
<i>Chloropsis jerdoni</i>	0.375	0	0	0	0	0
<i>Megalaima haemacaphala</i>	4.125	0	0	0	0	0
<i>Irene puella</i>	1	0	0	0	0	0
<i>Chloropsis jerdoni</i>	0.625	0	0	0	0	0
<i>Oriolus oriolus</i>	0.375	0	0	0	0	0
<i>Megalaima virens</i>	0.25	0	0	0	0	0
<i>Buceros bicornis</i>	0	0	0	0	0	0
<i>Phoenicophaeus tristis</i>	0	0	0	0	0	0



## Appendix B (continued)

Frugivore species	<i>Ficus drupacea</i>	<i>Talauma hodgsoni</i>	<i>Litsea sp.</i>	<i>Actinodaphne angustifolia</i>	<i>Polyalthia simiarum</i>	<i>Sterculia villosa</i>
<i>Cochoa viridis</i>	0	0	0	0	0	0
<i>Ducula aenea</i>	0	0	0	0.125	1.125	0
<i>Gracula religiosa</i>	0.875	0	1.875	0	7.875	0
<i>Megalaima lineata</i>	1.5	0.125	1	0	0	0.375
<i>Heterophasia picaoides</i>	2.5	0	0	0	0	0
<i>Oriolus trailii</i>	0	0	0	0	0	0
<i>Ducula badia</i>	2.875	0	1.125	0	5.125	0
<i>Chloropsis aurifrons</i>	0	0	0	0	0	0
<i>Anthraceros albirostris</i>	0	0	0	0	0.125	0
<i>Treron apicuada</i>	4.75	0	0	0	0	0
<i>Treron pompadora</i>	2	0	0	0	0	0
<i>Leiothrix argentea</i>	0.125	0	0	0	0	0
<i>Psittacula alexandri</i>	0.375	0	0	0	0	3.25
<i>Pycnonotus cafer</i>	0.25	0.875	0.875	0	0	0
<i>Pycnonotus jocosus</i>	0	0	0.5	0	0	0.625
<i>Psittacula krameri</i>	0	0	0	0	0	0.5
<i>Treron curvirostra</i>	0	0	0	0	0	0
<i>Loriculus vernalis</i>	0.25	0	0	0	0	0.75
<i>Treron sphenurus</i>	0	0	0	0	0	0
<i>Alophoixus flaveolus</i>	3.875	2.625	6.375	0	0	0
<i>Rhyticeros undulatus</i>	0.125	0	0	0.25	0.5	0
<i>Treron phoenicoptera</i>	5	0	0	0	0	0

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