Quantifying the Biodiversity Value of Repeatedly Logged Rainforests: Gradient and Comparative Approaches from Borneo

Matthew J. Struebig[*,†,1,2], **Anthony Turner**[*,‡,2], **Emily Giles**[*,§],
Felicia Lasmana[¶], **Simon Tollington**[*], **Henry Bernard**[||], **Diana Bell**[‡]
[*] Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, United Kingdom
[†] School of Biological and Chemical Sciences, Queen Mary University of London, London, United Kingdom
[‡] School of Biological Sciences, University of East Anglia, Norwich, United Kingdom
[§] World Wildlife Fund Canada, Toronto, Ontario, Canada
[¶] Daemeter Consulting, Bogor, West Java, Indonesia
[||] Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia
[1] Corresponding author: e-mail address: m.j.struebig@kent.ac.uk
[2] These authors contributed equally to this chapter

Contents

Advances in Ecological Research, Volume 48
ISSN 0065-2504
http://dx.doi.org/10.1016/B978-0-12-417199-2.00003-3

Abstract

There is substantial variation in the reported effects of logging on tropical forest fauna. In addition to inherent variation in disturbance sensitivity among taxa, another contributing factor is that most studies use comparative analyses of unlogged versus logged forests, which cannot fully account for heterogeneity in disturbance as well as underlying environmental gradients. To better understand how logging affects biodiversity, we examined changes in bat assemblages across a disturbance gradient ranging from old growth to forest logged several times. In one of the first evaluations of repeatedly logged forest, we use both comparative and gradient analyses to reveal substantial signals in assemblage change in response to habitat alteration. Despite multiple rounds of extraction in the most degraded forest, neither approach revealed a definitive effect of logging on site-based richness. However, each approach generated insight into assemblage compositional responses to forest degradation. Structural differences were evident between old-growth and repeatedly logged forest, and depauperate assemblages characterised degraded sites with low, open canopy. Ordinations identified species that best contributed to the signal of assemblage change, and also key associated forest-structure variables. Models of trap-based abundance confirmed not only the importance of forest height in determining assemblage change but also the role of tree-cavity availability in supporting forest specialists, indicating that efforts to supplement this resource could aid restoration. While highlighting the ecological importance of unlogged stands, we show that heavily degraded forests—even those that have been repeatedly logged—still hold some potential value for tropical biota and could have a role in conservation.

1. INTRODUCTION

Unprecedented levels of deforestation and forest degradation have led to major concerns regarding the fate of tropical biodiversity (Bradshaw et al., 2008; Frumhoff, 1995; Gardner et al., 2009). Throughout the tropics, forests continue to be commercially logged, resulting in considerable ecosystem degradation and fragmentation, to the point that logged-over and degraded habitats now comprise more than 50% of the tropical forest estate (Blaser et al., 2011). Nowhere is this crisis more acute than in Southeast Asia, a region where rates of forest loss and exports of tropical timber are among the world's highest (Asner et al., 2009; Cleary et al., 2007). Large densities of profitable timber species in this region serve as an incentive for logging operations to harvest multiple times, resulting in potentially high levels of disturbance (Whitmore, 1998). The resulting logged forests are often severely depleted of timber, making them vulnerable targets for conversion to other land uses (Edwards et al., 2011; Fitzherbert et al., 2008). This can have considerable implications for conservation and biodiversity management, not least of which is the loss of potential biological corridors and buffer zones around forest reserves (Chazdon et al., 2009). Nevertheless, although there have been numerous logging-impact studies, only recently have researchers begun to evaluate the biological value of forests logged multiple times (Edwards et al., 2011; Woodcock et al., 2011).

1.1. The value of degraded forests for tropical biodiversity

The rapidly expanding coverage of degraded forests across the tropics, and the concomitant scarcity of unlogged habitats, in a large part explain why ecologists have changed their views of this modified resource. By presenting an optimistic future for tropical biodiversity, Wright and Muller-Landau (2006) ignited a fierce debate regarding the ecological value of secondary forests (Laurance, 2007). A central part of Wright and Muller-Landau's argument was the equal value of these regenerating forests and those that are undisturbed (i.e. old growth, *sensu* Putz and Redford, 2010) for tropical taxa. Counter-arguments caution against this conclusion, given insufficient knowledge of the ways by which biological communities respond to forest disturbance (Gardner et al., 2007). In addition, numerous tropical species are thought to already be committed to extinction following population declines in degraded and fragmented habitat (Brook et al., 2006). While much of this debate focused on the ecological value of secondary forests regenerating from clearance, most arguments are also applicable to forests heavily degraded by commercial logging. Undisturbed old-growth forests are clearly valuable for tropical species (Gibson et al., 2011), but the conservation value of heavily logged and regenerating forests has been called into question (Didham, 2011; Edwards et al., 2011). Nevertheless, despite some discord, there is a growing recognition among ecologists and conservation planners that the future of tropical biodiversity will depend, to a large degree, on how we manage this modified resource (Chazdon et al., 2009; Clark et al., 2009; Gardner et al., 2009).

Over recent years, it has become progressively clear that large tracts of disturbed forest are more valuable to biodiversity than alternative land uses. In the Brazilian Amazon, for example, secondary forests regenerating after burning are more similar in community composition to primary undisturbed forests than they are to *Eucalyptus* plantations for the majority of taxa (Barlow et al., 2007). Across the tropics, logged forests also support higher numbers of forest specialists than plantations such as rubber (*Hevea brasiliensis*) or oil palm (*Elaeis guineensis*) (Fitzherbert et al., 2008; Gibson et al., 2011). In recognition of this, there are mounting pressures on forest managers to minimise the ecological impacts of logging activities and the inclusion in timber certification schemes of criteria aimed to enhance biodiversity is testament to this (e.g. Forest Stewardship Council; www.fsc.org). Biodiversity safeguards may also feature in payments for ecosystem services programmes. For example, the United Nations mechanism for reducing emissions from deforestation and degradation in developing countries (REDD+; www.un-redd.org) now includes provisions for biodiversity conservation as a co-benefit of protecting forests for carbon stocks, and collating data from ground-based biological inventories is proposed as one way of monitoring implementation (Gardner et al., 2012). Substantive evaluations of biological communities in disturbed forests have thus attracted renewed commercial and scientific interest, with the aim of using sound ecological science to inform tropical forest management and the design of managed landscapes (Clark et al., 2009; Gibson et al., 2011; Meijaard and Sheil, 2008).

1.2. Logging impacts on biodiversity: taxonomic variation and confounding factors

Tropical biota are thought to be highly sensitive to disturbance (Stork et al., 2009), particularly in Southeast Asia (Brook et al., 2006; Sodhi et al., 2009). Collateral damage associated with logging operations, including felling of non-harvested trees and road construction, can result in significant alterations to forest structure, including up to 80% loss in canopy cover (Fimbel et al., 2001), and a reduction of canopy height that can take substantial time to recover (Okuda et al., 2003). These changes can have considerable implications for forest fauna. For example, Wells et al. (2007) found logging to have profound effects on the prevalence of rare, small-mammal species in Borneo rainforests, a finding they attributed to reduced canopy space and altered tree composition in disturbed forest stands. Population declines of terrestrial birds in logged forests have been attributed to a reduction in leaf-litter microfauna, foraging sites and tree cavities for nesting

(Cockle et al., 2010; Johns, 1989; Lambert and Collar, 2002; Lammertink, 2004), while butterfly abundance is thought to be limited by the availability of larval host trees post logging (Cleary et al., 2009).

Nevertheless, there remains huge variation in the reported impacts of tropical forest disturbance (Chazdon et al., 2009; Foody and Cutler, 2003), which makes any synthesis of habitat value difficult and somewhat controversial (Didham, 2011). Selectively logged forest in Uganda, for example, is reported to host a more abundant and diverse small-mammal assemblage than undisturbed forest, in part due to changes to understory vegetation (Isabirye-Basuta and Kasenene, 1987). Similarly, once-logged forest in Malaysian Borneo hosts comparable levels of bird richness to unlogged forest (Edwards et al., 2011). Overall estimates of the proportion of primary forest species remaining in degraded stands range from less than 10% to more than 90% across taxonomic groups (Berry et al., 2010; Chazdon et al., 2009). Although the negative effects of logging are significant in meta-analyses at the pan-tropical level, in comparison to other disturbances faced by forests, the impact of timber extraction is relatively benign (Gibson et al., 2011).

Several reasons are reported to explain discrepancies in the logging literature. Fundamentally, species are known to differ in their sensitivity to environmental change, and so variation in responses to disturbance across taxonomic groups is evident (Meijaard et al., 2005; Meijaard and Sheil, 2008). For example, of the 15 taxonomic groups sampled in the Brazilian Amazon by Barlow et al. (2007), only four taxa (trees/lianas, birds, fruit-feeding butterflies and leaf-litter amphibians) exhibited the reduced species richness expected in *Eucalyptus* plantation compared to forest, with most groups exhibiting idiosyncratic responses even between undisturbed and regenerating forest treatments. Variation in population responses is also apparent within taxa and is most evident when regional or global datasets are collated. A synthesis of the literature on birds and butterflies in undisturbed and disturbed forests, for example, found increased and decreased diversity in response to disturbance in almost equal measure (Hill and Hamer, 2004). However, when pan-tropical analyses have partitioned bird assemblages consistently into guilds or ensembles, they reveal the abundance of granivores to increase in logged forests, insectivores and frugivores to decline, and the responses of nectarivores and carnivores to vary by tropical region (Gray et al., 2007).

While variation in disturbance sensitivity among taxa is undoubtedly central to the reported variation in logging impacts, the very nature of timber extraction in the tropics also makes robust comparisons of unlogged and logged forests difficult, and sometimes impossible. While these issues have not gone unnoticed in the logging literature (e.g. Frumhoff, 1995), only recently have ecologists voiced significant concern (Chazdon et al., 2009; Dent and Wright, 2009; Gardner et al., 2009; Lindenmayer and Laurance, 2012; Ramage et al., 2013). There is a growing recognition that at least some statistical signals, or lack of signals, in logging-effect datasets may be confounded by experimental design. The heterogeneous nature of logging in the tropics typically results in a spatial mosaic of forest types and disturbance levels, with some parts of concessions being heavily degraded, while other patches escape logging completely, despite extraction data to the contrary (Cannon et al., 1994).

Logging activities also tend to be undertaken on relatively accessible terrain, and so signals in community data can also be confounded by variation in topography, and hence forest productivity, between these sites and unlogged controls (Gardner et al., 2009). Difficulties of access and an increasing paucity of unlogged controls then raise the problem of finding sufficient numbers of replicate experimental units to undertake comparative studies. These units need to be not only appropriate to detect any response by the study organisms under question (Hamer et al., 2003; Hill and Hamer, 2004) but also large enough to encapsulate landscape-level variation in disturbance, while being sufficiently spaced apart to be considered truly statistically independent (Shea et al., 2004). Combined, these limitations have the potential to mask signals in assemblage datasets (Meijaard et al., 2005; Meijaard and Sheil, 2008), leading most researchers to make understandable and often inevitable tradeoffs between adequate scale, replication and sample sizes in study design. In addition to these problems, the most important effects of forest disturbance are likely to be more prevalent in high-intensity silviculture systems and will accumulate over multiple rounds of logging (Edwards et al., 2011; Lindenmayer and Laurance, 2012).

In summary, although taxonomic variation in sensitivity to disturbance is central to understanding the effects of logging on biodiversity, the impacts of timber extraction, as with other disturbances, are likely to vary over space, time and intensity, even within concessions with a similar management history. This makes true replication for comparative studies of disturbance treatments particularly difficult to achieve in tropical forests and has the potential to confound signals from datasets and thus contribute to some of the variation in logging effects reported in the literature.

1.3. Viewing logged landscapes as gradients

Despite methodological challenges being long recognised (Frumhoff, 1995), comparative approaches continue in the logging-impact literature and a somewhat artificial dichotomy between unlogged and logged forests prevails. Assessments of species differences solely between discrete forest management treatments risk overlooking potentially large community changes in response to environmental and/or disturbance gradients that are inherent in the study system. The simple premise of gradient analyses (*sensu* Ter-Braak and Prentice, 2004) is that species are more abundant around their environmental optimum and so successive changes in the abundance and replacement of species occurs as a function of environmental variation. Gradient approaches are well known in landscape ecology and have had a marked influence on studies of urbanisation, fragmentation and land-use change (Cushman et al., 2010; McDonnell and Pickett, 1990); yet the gradient paradigm has received relatively little attention in the logging-impact literature. Most gradient studies in the tropics to date have focused on extreme gradients of land-use change from forest to non-forest habitats (e.g. Kessler et al., 2009), habitat fragmentation (e.g. Ewers and Didham, 2006) and elevation (McCain and Grytnes, 2010) rather than forest disturbance *per se* (but see Aguilar-Amuchastegui and Henebry, 2007; Hamer et al., 2003; Lammertink, 2004). This is surprising, since viewing forest landscapes as gradients has the potential to account for spatial variation of inherent environmental parameters (Clark and Clark, 2000) as well as disturbances within otherwise preconceived logging treatments. Gradient analyses are also better equipped to detect subtle variation in population sizes and assemblage structure of forest wildlife pertinent to silvicultural management, and can provide deeper insights into biodiversity change beyond simple measures of species richness. Moreover, quantifying responses in this way also facilitates the prediction of species' responses to restoration efforts and potentially enables the identification of indicator species for biological monitoring.

1.4. Gradient and comparative approaches: a logging case study of Borneo's bats

We report on the first evaluation of tropical biota in heavily degraded logged forests based on both gradient and traditional comparative analyses. Most previous logging-impact studies have focused on the effects of a single rotation of timber extraction, and only recently has attention focused on the effects of a second round of activity (Edwards et al., 2011; Woodcock et al., 2011). One novel aspect of our study is to take these appraisals one step further by examining the biological importance of forests subject to further logging, whereby the vast majority of commercial timber is removed from the forest prior to conversion to other land uses. Our study is a product of a new large-scale experiment examining forest modification on the Southeast Asian island of Borneo, a biodiversity hotspot with some of the highest timber extraction rates in the world (Fisher et al., 2011). Central to the design of this experiment is a forest modification gradient arising from multiple rounds of logging and the eventual clearance of forest to monoculture, a process that mimics the real-world pattern of habitat conversion across much of the tropics today. The study landscape also exemplifies many of the aforementioned difficulties experienced in the design of logging-effect studies concerning replication and the influence of spatial correlation. We use both gradient analyses and comparative approaches, as well as sensitivity analyses where appropriate, to address these difficulties.

We focus on the effects of logging on insectivorous bats, which form a centre of richness in the Indo-Malayan region where they represent up to half of all forest mammal species (Findley, 1993). A number of ecological traits, such as low fecundity, longevity and high survivorship, indicate that bats are a resource-limited group (Findley, 1993), leading to recent studies promoting their utility as bioindicators (Jones et al., 2009). Nevertheless, there remains substantial variation in the reported effects of logging. To date, the majority of disturbance studies for tropical bats have been undertaken in the neotropics, where bat assemblages in forests are dominated by members of the Phyllostomidae. While some of these studies reveal predictable declines in overall bat richness and abundance in logged forest sites (e.g. Medellín et al., 2000; Peters et al., 2006), others highlight inconsistent responses among species, particularly in low-intensity extraction systems (e.g. Presley et al., 2008). In well-managed forest stands, neotropical bat assemblages are known to recover well from disturbance events (e.g. Clarke et al., 2005a,b; Willig et al., 2007).

Far fewer logging studies have focused on palaeotropical bats, assemblages of which are structured differently to those in the neotropics as they are dominated by insectivorous species not found outside the Old World. Borneo bat communities comprise at least 93 species, of which 76 are insectivorous, and up to 40 of these species can be readily captured in the forest understory (Struebig et al., 2012). Several lines of evidence suggest that a substantial number of these species use landscapes at much smaller spatial scales than is commonly perceived from their ability to fly. A recent compilation of life-history characteristics of Borneo mammals reveals the home ranges of insectivorous bats to be on average ca. 4–15 times smaller than those of larger forest mammals (median range for: 40 understory bat species = 44 ha; 13 primate species = 200 ha; 21 small carnivore species = 700 ha; Wilson et al., 2010). While the ranges of cave-roosting insectivorous bats can be substantial (median range for 14 species = 2200 ha), the ranges of those species roosting in forest trees and vegetation are comparable to those of terrestrial mammals of similar size (ca. 2 ha: 19 species of bat vs. 19 murid rodents and 10 tree shrews).

The ecological flexibility of palaeotropical bats is thought to be constrained by ecomorphological traits, roosting ecology and social organisation, which vary across taxa (reviewed in Kingston et al., 2003; Rossiter et al., 2012; Struebig et al., 2008). Combinations of these factors affect local dispersion and the capacity for movement, as indicated by differential patterns of genetic structure and gene flow across bat taxa in intact forest (Rossiter et al., 2012) and mosaic habitats (Struebig et al., 2011). Bat assemblages in this region are also known to undergo area-dependent declines in diversity following forest fragmentation (Struebig et al., 2008, 2011), structural changes following forest degradation (Furey et al., 2010) and major declines in diversity following deforestation in line with other animal groups (Fitzherbert et al., 2008). As a number of ecological traits of bats are often shared with birds and/or other mammals (e.g. wing morphology, Norberg, 1998; insectivorous/frugivorous diets and cavity-nesting tendencies, Kunz and Lumsden, 2006), examining the effects of logging on these animals may yield useful insights into the responses of other taxa.

We examine changes in bat assemblages across a habitat-disturbance gradient, ranging from pristine old growth to twice logged to forest logged several times. Our approach considers the utility of both traditional comparative analyses of forest types, as well as gradient analyses of finely resolved assemblage and forest-structure data. First, we examine patterns in species richness and abundance across forest types and sites. We then quantify variation in assemblage structure among sites using unconstrained ordination and related techniques, capable of partitioning species compositional data both as groups and in relation to gradients. Finally, we extend our gradient appraisal to the use of mixed-effects models to tease out species-abundance responses to forest disturbance at the level of sampling points and confirm the most influential forest structural variables involved in this process. By partitioning analyses in this way, and undertaking sensitivity analyses to account for potential effects of spatial pseudoreplication, we illustrate that gradient approaches can provide deeper insights into the subtle responses of biodiversity to forest disturbance than more traditional comparisons of forest treatments. Nevertheless, we conclude that both approaches are complimentary, each revealing its own element of the disturbance process that can be used to inform tropical forest management and conservation.

2. MATERIALS AND METHODS

2.1. Study area

Fieldwork was based at the Stability of Altered Forest Ecosystems Project (www.SAFEproject.net), a recently established landscape modification experiment in Sabah, Malaysian Borneo (Fig. 1). The SAFE project area encompasses 7200 ha of lowland dipterocarp rainforest in the Kalabakan Forest Reserve (4°43′N, 117°35′E), the majority of which has been long designated for conversion to plantation by the Malaysian government (Ewers et al., 2011). International sustainability standards (e.g. www.rspo.org), and indeed Malaysian law, prohibit the clearance of forest on steep

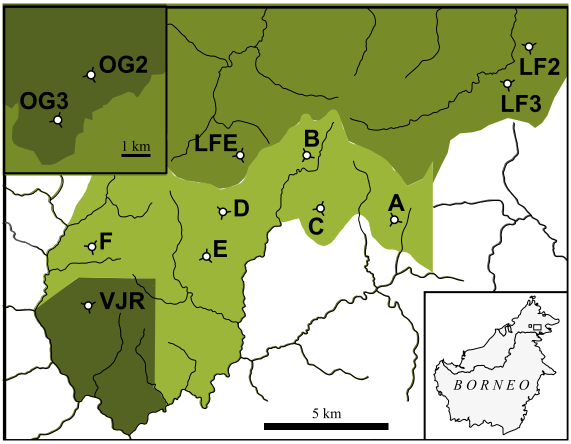

Figure 1 Location of study sites at the Stability of Altered Forest Ecosystems Project in Sabah Borneo in 2011–2012. A gradient of logging disturbance was evident; most forest sites had been logged at least two times (*twice logged*, intermediate shading), with some sites subject to additional repeatedly logging (*repeatedly logged*, light shading) ahead of clearance for plantation. *Old-growth* forest is indicated by dark shading in the experimental area (VJR) as well as at Maliau Basin (OG2, OG3), approximately 65 km away. The plantation mosaic is shown in white and lines indicate rivers.

slopes and along watercourses, characteristics shared by approximately 500 ha of the estate. In addition to these areas, the concessionaire, Yayasan Sabah, agreed to retain 800 ha for purposes of forest fragmentation research. The schedule of forest clearance provided us with a rare opportunity to survey sites across the landscape to identify pre-existing environmental gradients prior to fragmentation.

At the time of sampling, all study sites were part of a contiguous expanse of lowland dipterocarp forest (>1 million ha). Land use to the south and west of the study area comprised a mosaic of oil palm and timber (primarily *Acacia mangium*) plantations. We benefited from an exemplary study design at SAFE, defined by study sites which have been oriented to minimise factors that could potentially confound the effects of land-use change, such as latitude, slope and elevation (Ewers et al., 2011). Our sampling was undertaken between April 2011 and June 2012 at 12 forested sites that varied in the degree to which they had been logged (Fig. 1), and so the main gradient under study was that of forest disturbance from timber extraction.

The majority of logged forest sampling was undertaken in the experimental area in Kalabakan at six sites (A–F) that had been heavily logged multiple times prior to the scheduled clearance: two logging rotations under a modified uniform system, with timber restrictions lifted during the second rotation ahead of the planned clearance for plantation. Under the first rotation, ca. 113 m^3 ha^{-1} was removed (Fisher et al., 2011). Under the second rotation, the forest was actually re-logged three times, resulting in a cumulative extraction rate of 66 m^3 ha^{-1} (26, 22, then 18 m^3 ha^{-1}; D.P. Edwards, unpublished data). Forest at these repeatedly logged sites was therefore heavily degraded and characterised by a high density of access roads and skid trails, a paucity of commercial timber species, very few emergent trees, and the dominance of pioneer and invasive vegetation (e.g. *Macaranga*). We also sampled three twice-logged forest sites (LFE, LF2, LF3) in coupes within the neighbouring Ulu Segama Forest Reserve. Forest at these sites had been subject to similar timber extraction during the first logging rotation, followed by an average of 37 m^3 ha^{-1} during the second rotation. Notably, these sites were subject to timber quotas during the second rotation, during which extraction was ca. 1.7 times less than at Kalabakan. Distances between our twice-logged forest sites ranged from 1.9 to 12.4 km (mean 8.4 km) and repeatedly logged sites from 1.9 to 11.8 km (mean 5.6 km). Our remaining study sites were in the nearest topographically matched old-growth, or near-pristine, forest within the block. These sites were located within the Brantian-Tantulit Virgin Jungle Reserve (VJR) adjoining

Kalabakan, or the Maliau Basin Conservation Area (OG2, OG3), approximately 65 km northwest. Although the distances between some of these sites and those in the logged forest could potentially influence species turnover, analyses of bat inventories across little-disturbed forests of northern Borneo confirm beta diversity to be low and non-significant in the absence of environmental gradients (Struebig et al., 2012). Of these sites, OG3 and VJR had been subject to some logging for construction of access roads, but old-growth forest features remained intact. Dominant tree species in old-growth sites included *Eusideroxylon zwageri* (Belian), *Shorea parvifolia* (Meranti) and *S. curtisii* (Seraya), all highly prized for their timber.

We emphasise that logging damage and vegetation structure varied substantially across the landscape (even within coupes), therefore precluding our ability to reliably categorise sites into broad disturbance classes. However, to illustrate the benefits of gradient approaches we compare results from gradient analyses with those based on sites classified into broad habitat-disturbance treatments akin to those used in other studies. We use three broad categories pertaining to disturbance history, namely, *old growth* (OG2, OG3, VJR), *twice logged* (LFE, LF2, LF3) and *repeatedly logged* (A–F). While others have referred to twice-logged forest as 'repeatedly logged' (Edwards et al., 2011; Woodcock et al., 2011), we note that our use of this term is confined to sites that were logged more than two times. Using the ecosystem classification system promoted by Putz and Redford (2010), our twice-logged sites would be clearly defined as 'managed forest' (as would those studied by Edwards et al., 2011 and Woodcock et al., 2011), but our repeatedly logged sites would be more appropriately classified as 'degraded forest', 'derived woodland' or in transition between the two heavily disturbed states. In light of this ambiguity, we defined gradients using forest-structure variables.

2.2. Animal sampling

Bats were captured at 42 sampling points per site, 50–150 m apart, along trails used to access permanent SAFE project plots (see Ewers et al., 2011). These trails were of comparable length (ca. 3 km) and spatial arrangement across sites, and all sampling points were located in areas with vegetation exceeding trap height (>2 m). In order to minimise capture biases and methodological heterogeneity, we targeted insectivorous bats that are readily captured in the forest understory, restricted surveys to the dry season and avoided sampling in periods of heavy rain. Bats were captured using four-bank harp traps (Muzeum Zoologicum Bogoriense, Cibinong, Indonesia) using a standardised protocol employed elsewhere in Southeast Asia (Kingston et al., 2003; Struebig et al., 2008, 2009, 2011, 2012). Up to seven traps were set across transects each night and then moved to new sampling points the following day—hence, one trap set at a sampling point for one complete night constituted one harp trap night. The majority of sampling was undertaken by two teams operating at different sites at any one time, and trapping at any one site was completed within 10–12 days.

All bats were marked with wing biopsies (Stiefel Laboratories, Maidenhead, UK), and in some cases by numbered forearm bands (Porzana, Icklesham, UK), before release so that recaptured individuals could be identified and removed from analyses. We classified insectivorous species into three ensembles based on aspects of roosting and foraging ecology, as outlined in Struebig et al. (2008, 2012): (1) bats with generalist roosting habits that forage in partially cluttered edges and/or canopy gaps (hereafter *edge/gap species*); (2) bats that predominantly roost in caves, but which commute to foraging sites in the cluttered forest understory (hereafter *cave species*); (3) bats with foraging and roosting specialisations associated with ephemeral forest structures such as trees, cavities/hollows or other foliage (hereafter *forest species*).

2.3. Forest structure and microhabitat

We used forest-structure data to delineate a disturbance gradient as well as classify sites into logging treatments, because timber extraction was not uniform across the landscape. Following logging operations, forests typically become more open habitat, with a lower, broken canopy and a denser layer of shrubs, climbers and bamboos (Felton et al., 2006; Pinard, 2005). We therefore collected structural data on canopy height, openness, understory clutter and densities of standing trees, fallen (dead) wood and tree cavities/hollows—variables pertaining to timber management, and which also describe important habitat structures for forest wildlife (Meijaard and Sheil, 2008).

Canopy height (ordinal scale of 1–5: 1, 0–5 m; 2, 5–10 m; 3, 10–20 m; 4, 20–30 m; 5, >30 m), canopy openness (using a densiometer) and understory clutter (ordinal scale 1–5 ranging from no vegetation to impenetrable thick undergrowth) were estimated within a 5-m radius at 30 of the sampling points used for trapping in each site. Canopy height and openness were both correlated with an independent assessment of forest quality introduced by Ewers et al. (2011), whereby sites were scored on a qualitative scale based largely on understory and canopy density (height $R=0.94$, $p<0.001$; openness $R=-0.85$, $p<0.001$). Height and openness were themselves negatively correlated ($R=-0.817$; $p=0.001$).

Density estimates of trees and trees bearing cavities or hollows were derived from 30 m × 5 m plots established at the 30 sampling points per site (Table 1). In each plot, we quantified densities of all standing and fallen trees >1 m in length, as well as the presence of holes within them (hereafter termed *cavities* in standing trees and *hollows* in fallen trees). All standing trees >10-cm diameter were counted and classified into size categories according to diameter at breast height (DBH). We then searched each tree (standing and fallen) for the presence of cavities or hollows. These were defined as holes >5 cm in length and >3-cm deep, based on the average body size of forest insectivorous bats and birds in the region, and the roosting habits of three bat species known from the study area (Kingston et al., 2006). Tree and cavity counts were usually undertaken after trapping was completed. Due to difficulties of access at two of the sites (B and LFE), these counts were restricted to 10 sites, which were representative of the disturbance gradient. Since ordination analyses can be strongly affected by missing data, we followed recommendations by McCune and Grace (2002) for these two sites and estimated values using mean data from other sites within each forest type.

2.4. Statistical analyses

2.4.1 Site-level species diversity

Differences in the observed species richness (S_{obs}) between sites were investigated by comparing 95% confidence intervals derived by sample-based rarefaction rescaled to individuals in EstimateS v.8.2 (Colwell, 2009). Estimates of biodiversity value can be inflated by the presence of occasional species in inventories (Barlow et al., 2010), so we also repeated analyses with all singletons removed from assemblages as a precaution. To assess completeness of our site inventories, we also predicted the number of bat species at each site using the multinomial model introduced by Shen et al. (2003). Here, richness was predicted to a common sample size of 300 individuals because the majority of insectivorous bats are represented in Borneo inventories at this sampling effort (Struebig et al., 2012).

2.4.2 Site-level species composition and habitat association

To quantify variation in bat assemblage composition in relation to forest-structure variables across the disturbance gradient, we used non-metric

Table 1 Habitat characteristics of forest sites with varying degrees of logging disturbance at the SAFE project area, Sabah, Malaysia

Site	Canopy height	Canopy openness	Understory clutter	No. of standing trees[a]	No. of standing trees with cavities[a]	No. of fallen trees[a]	No. of fallen trees with hollows[a]
Old growth							
OG2	2.58 ± 0.08	4.68 ± 0.01	2.77 ± 0.13	8.7 ± 0.51	1.40 ± 0.25	1.87 ± 0.31	0.70 ± 0.16
OG3	2.50 ± 0.09	4.08 ± 0.01	5.53 ± 1.38	10.53 ± 0.56	0.80 ± 0.15	2.23 ± 0.40	1.03 ± 0.18
VJR	1.98 ± 0.09	10.20 ± 0.01	2.40 ± 0.12	7.81 ± 0.52	0.35 ± 0.1	0.32 ± 0.52	0.06 ± 0.05
Twice logged							
LFE	1.43 ± 0.09	3.08 ± 0.01	3.07 ± 0.04	9.57 ± 0.14	0.22 ± 0.07	0.93 ± 0.80	0.17 ± 0.01
LF2	2.10 ± 0.05	12.43 ± 0.01	3.14 ± 0.05	9.67 ± 0.52	0.27 ± 0.10	0.30 ± 0.52	0.13 ± 0.06
LF3	2.17 ± 0.01	9.56 ± 0.01	2.83 ± 0.01	9.47 ± 0.71	0.17 ± 0.07	1.57 ± 0.71	0.20 ± 0.09
Repeatedly logged							
A	0.95 ± 0.11	20.42 ± 0.47	2.79 ± 0.13	7.60 ± 0.70	0.23 ± 0.09	1.20 ± 0.70	0.30 ± 0.10
B	1.02 ± 0.07	19.76 ± 0.21	2.90 ± 0.12	7.30 ± 0.52	0.27 ± 0.08	0.91 ± 0.18	0.22 ± 0.06
C	0.95 ± 0.11	23.51 ± 0.73	3.41 ± 0.15	6.45 ± 0.53	0.19 ± 0.11	0.84 ± 0.53	0.13 ± 0.08
D	1.12 ± 0.05	22.77 ± 0.24	3.60 ± 0.08	7.33 ± 0.71	0.28 ± 0.10	0.72 ± 0.71	0.22 ± 0.08
E	0.73 ± 0.09	22.06 ± 1.21	3.73 ± 0.07	7.33 ± 0.62	0.23 ± 0.08	0.97 ± 0.62	0.23 ± 0.09
F	1.39 ± 0.08	11.23 ± 0.58	3.32 ± 0.09	7.80 ± 0.51	0.40 ± 0.14	0.83 ± 0.51	0.20 ± 0.10

[a] Tree density estimates based on counts in 0.015 ha plots centred on each sampling point. Due to difficulties of access, counts for sites LFE and B were estimated using the means of other sites in each forest type.

Values represent means (±1 SE) from 30 sampling points per site.

multidimensional scaling (NMDS). Ordinations based on Bray–Curtis dissimilarity coefficients using species-abundance data were undertaken in PC-Ord v.6 (MjM Software, Oregon, USA). We sought to generate an optimal ordination solution that represented the majority of assemblage variation with minimal stress (a measure of departure from monotonicity in the relationship between dissimilarity distances of the original and reduced ordination space). To determine an optimal NMDS solution, we compared ordinations with those based on randomised data matrices (abundances randomised among sites, run 250 times with real and randomised data) to assess whether our results were simply due to chance (i.e. reflecting weak pattern or structure in the original matrix) or reflected biologically meaningful structure. BIO-ENV analysis (Clarke and Ainsworth, 1993) undertaken in PRIMER v.5 (Clarke and Warwick, 2001) was used to identify the forest-structure variables that were best associated with the overall patterns of bat assemblage composition. We used weighted multi-response permutation procedures (MRPPs) to test for compositional differences in bat assemblages among forest types (i.e. old-growth, twice-logged and repeatedly logged sites) and fitted general linear models in R 2.15.1 (R Development Core Team, http://www.r-project.org/, 2012) to determine the extent to which variation in assemblage structure exhibited by axis scores was driven by forest-structure variables.

The relatively close proximity of some sites (i.e. OG2 and OG3; LF2 and LF3) could potentially influence assemblage patterns and hence skew ordination results, so we repeated NMDS analyses using subsets of sites. Ordinations were repeated by leaving out one site from each geographic pair for the four ways in which this could be done. For each of these ordinations, the linear models of axis scores versus forest-structure variables were then re-run accordingly. For the optimal ordination, the extent to which each bat species contributed to variation in assemblage structure among forest sites was determined using tau rank correlation coefficients of abundance versus NMDS axis scores. We do not report *p* values for these correlations because of constraints associated with the number of samples and covariates for analyses (McCune and Grace, 2002).

2.4.3 Trap-level responses to forest disturbance

Although the extent of our sampling was comparable to other studies in the literature, and the sites sampled were fully representative of our forest types, our analyses of 12 sites could potentially be constrained by statistical power and/or pseudoreplication within treatment. To account for these potential limitations, we also modelled abundance data at the level of individual sampling points and controlled for any variation associated with spatial correlation by fitting site localities as random effects. We used zero-inflated generalised linear mixed models (ZIGLMMs) with negative binomial error terms to identify the components of forest structure that affected the number of bats captured along the disturbance gradient. The response variable in all models was the number of individuals captured in each trap. Initial inspection of models and residual plots revealed that ZIGLMM analysis for individual species was not appropriate due to the presence of a small number of highly influential points. We therefore pooled our capture data either as all bats captured or separately for all forest bats or cave bats. Our final response variables thus represented the number of individuals (abundance) represented within these groupings. 'Site identity' was modelled as a random effect (to control for any variation associated with site-based spatial correlation—see Paterson and Lello, 2003) and forest-structure variables were coded as fixed effect covariates using spatially matched capture and habitat data. These data were derived from 272 traps in 10 sites (we were unable to safely collect habitat data from 28 sampling positions due to adverse local conditions—e.g. landslides, hornet nests).

To further account for any spatial correlation arising from the close proximity of OG2/OG3 and LF2/LF3 sites, we repeated models by coding these geographic pairs with the same site identity for each of the three ways by which this could be done (i.e. OG2 and OG3 coded as 'OG', giving 11 site identities in total; LF2 and LF3 coded as 'LF'; and the combination of these two altered codings). All explanatory variables were investigated for collinearity, which resulted in a restricted set of predictor variables in our ZIGLMMs: forest height, understory clutter, total tree density, the number of cavities in standing trees, and the number of hollows in large fallen trees (>50-cm DBH). Variables were standardised to have a mean of zero and standard deviation of 0.5 before model averaging to aid the interpretation of model-averaged parameters measured at different scales.

Global models were fitted in *R* using the *glmmADMB* package (Skaug et al., 2012) to account for the zero-inflated nature of our count data, and an information theoretic approach to model selection was applied using the *MuMIn* package (Bartoń, 2012), incorporating all possible model subsets. Model-averaged parameters were then derived from a reduced subset of models defined by Akaike's information criteria ($\Delta \mathrm{AIC} < 4$), and explanatory variables were judged to be significant if the 95% confidence intervals of the coefficient estimate did not include zero.

3. RESULTS

3.1. Forest-structure gradient

Our measures of forest disturbance—canopy height and openness—defined a clear gradient in habitat structure over the 12 sites sampled (Table 1). The canopy of old-growth forest sites was typically taller and more closed than that in logged forest. Tree density varied substantially over the forested landscape, but as expected, was greatest at sites in taller forest ($R = 0.771$; $p = 0.003$) with closed canopy ($R = -0.825$; $p < 0.001$) (Table 1). Of the 2724 trees counted in our vegetation plots, 221 (8.1%) contained cavities or hollows. Estimates of the number of cavity/hollow-bearing trees ranged from 140.0 ha^{-1} in old-growth (site OG2) to 17.8 ha^{-1} in the repeatedly logged forest (site C). Although more cavity/hollow-bearing trees were also found in taller forests ($R = 0.655$; $p = 0.021$), this was not significantly associated with high tree densities at these sites ($R = 0.307$; $p = 0.332$).

3.2. Species richness

Across the landscape, species richness varied little among forest types, but substantially among sites. We captured 1677 individuals of 31 bat species in 504 traps set over the 12 forest sites (Tables 2 and 3). Inspection of rarefied accumulation curves and confidence intervals for assemblage data pooled by forest type showed repeatedly logged forest to host similar numbers of species than old-growth forest, but significantly fewer than twice-logged forest at the same sampling effort (i.e. the same number of bats captured; Fig. 2A). However, many of the species in logged forest assemblages were occasional singletons, and when these were removed from analyses, richness levels were near-identical among forest types (Fig. 3A). A similar pattern emerged when rarefaction analyses were partitioned by ensemble, although repeatedly logged forest hosted significantly fewer cave species than twice logged or old growth (Fig. 2B and C). Site-level richness varied considerably (Table 2), indicating moderate levels of beta diversity particularly among the logged forest sites. The six repeatedly logged sites typically supported fewer bat species than sites in the least disturbed forest (Fig. 3B), but there was no decline in richness consistent with the canopy height disturbance gradient ($R^2 = 0.033$; $p = 0.267$). Again this pattern was consistent when assemblages were partitioned by ensemble and also when singletons were removed prior to analyses (Fig. 3B). Richness predictions revealed that our site inventories were 71–99% complete (Table 2), indicating that the observed patterns of richness were a reliable representation of actual patterns.

Table 2 Bat assemblage characteristics of forest sites subject to varying degrees of logging disturbance at the SAFE project area, Sabah, Malaysia

	Abundance		**Observed richness (S_{obs})**			**Predicted richness (S_{Shen})**[a]		**Inventory completeness (S_{obs}/S_{Shen})**	
Site	**All bats**	**Forest bats**	**All bats**	**Forest bats**	**Singletons**	**All bats**	**Forest bats**	**All bats**	**Forest bats**
Old growth									
OG2	214	97	19	11	4	20	14	0.94	0.81
OG3	210	93	18	10	1	18	10	0.99	1.00
VJR	113	74	12	9	3	14	13	0.84	0.67
Twice logged									
LFE	110	82	19	12	8	27	14	0.71	0.85
LF2	120	53	13	9	3	15	12	0.86	0.73
LF3	177	58	20	12	8	24	17	0.83	0.72
Repeatedly logged									
A	111	87	18	11	4	21	11	0.87	0.96
B	125	85	13	8	3	15	9	0.85	0.90
C	127	71	15	11	4	18	14	0.83	0.80
D	118	86	15	9	3	17	10	0.89	0.87
E	107	85	14	10	2	15	11	0.94	0.95
F	145	53	11	7	1	11	8	0.98	0.93

[a] Richness predicted to a common sample size of 300 individuals using the Shen multinomial model (Shen et al., 2003).

Assemblage data are based on captures from 42 harp traps set at each site.

Table 3 Abundance (*A*) and observed species richness (*S*) of bats pooled across rainforest sites classified into broad logging-disturbance classes

			Old growth		**Twice logged**		**Repeatedly logged**	
	Total		**Three sites (OG2, OG3, VJR)**		**Three sites (LFE, LF2, LF3)**		**Six sites (A–F)**	
Ensemble	***A***	***S***	***A***	***S***	***A***	***S***	***A***	***S***
All species	1677	31	537	22	407	24	733	21
Cave bats	707	8	269	7	211	7	227	4
Forest bats	924	17	264	13	193	14	467	13
Edge/gap bats	46	6	4	3	3	3	39	4

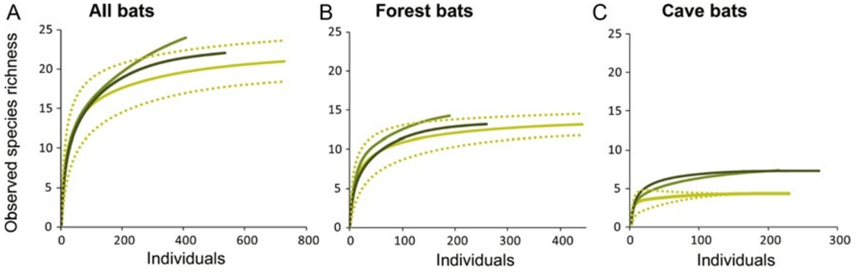

Figure 2 Rarefied species-accumulation curves for bat assemblages in old-growth (dark shading; $n = 3$ sites), twice-logged (intermediate shading; $n = 3$) and repeatedly logged (light shading; $n = 6$) forest. Curves are derived from sample-based rarefaction rescaled to individuals using pooled data from sites within each forest type. Dashed lines indicate the upper and lower 95% confidence limits of the curves for repeatedly logged forest, in which the most sites were sampled. Values outside of these confidence limits are statistically different from the main curve.

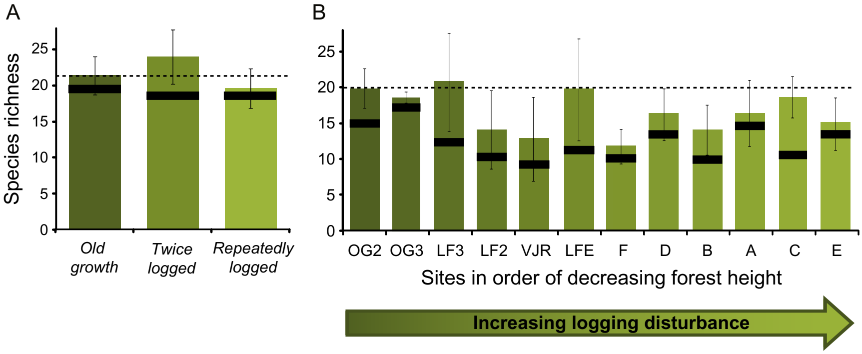

Figure 3 Rarefied species richness of palaeotropical bats across a logging-disturbance gradient. Sites are either (A) grouped into forest disturbance categories or (B) presented in decreasing order of forest height, in which case the reference richness level is the least disturbed site (OG2). Bars represent total richness (mean and 95% CIs based on rarefaction) and horizontal bars indicate richness with singletons removed.

3.3. Patterns of abundance

More bats were captured in the taller and least disturbed forest sites than at sites that had been heavily logged with a lower canopy (range 214–107 bats, sites OG2-E; $R^2 = 0.555$; $p = 0.003$). Cave bats and forest bats represented a similar proportion of all animals captured in old-growth forest (50%, 49%) and twice-logged forest (52%, 47%), but at the repeatedly logged sites, forest bats typically represented a larger proportion of the bat assemblage

(64% overall, Table 3). The majority of edge-foraging bat species over the landscape (85%) were also captured at the repeatedly logged sites (Table 3). Twelve species represented 90% of all captures across the forested landscape and the majority were present at all sites. The two most dominant species across the landscape (*Hipposideros cervinus* and *Kerivoula intermedia*) represented 39% of all bats captured.

3.4. Assemblage composition and structure

The optimal NMDS ordination of site dissimilarities performed better than that based on randomised data (Monte Carlo test of three-axis ordination based on all species: observed stress = 5.641; simulated stress = 7.438; $p = 0.032$; Fig. 4A), indicating meaningful gradient structure reflected in the bat assemblages across sites. Most (91.1%) of the assemblage variation was represented by the NMDS ordination, with 84.9% explained by two axes and the majority (53.3%) on Axis 1.

MRPPs indicated that species composition differed significantly among old-growth, twice-logged and repeatedly logged forest habitat ($T = -2.636$; $A = 0.109$; $p = 0.013$). However, pair-wise comparisons revealed that the strongest compositional differences were between assemblages at the two extremes of disturbance (old growth vs. repeatedly logged, $T = -2.318$; $A = 0.999$; $p = 0.025$), and so when data from old-growth sites were excluded from the analysis, within-group agreement (A) was notably lower and non-significant ($T = -1.465$; $A = 0.062$; $p = 0.085$). There was therefore substantial variation in compositional arrangement among sites regardless of site membership to discrete forest types.

Differences in forest structure among sites were associated with variation in assemblage composition, with the clearest signal coming from canopy height (as well as openness). Plotting vectors of forest-structure variables revealed that Axis 1 scores were associated with differences in canopy height ($R_{\text{tau}} = -0.595$; Fig. 4A, inset), tree density ($R_{\text{tau}} = -0.412$) and openness ($R_{\text{tau}} = 0.333$) between sites. Other forest-structure variables were associated with NMDS Axis 2 scores: number of cavities ($R_{\text{tau}} = 0.565$), fallen trees ($R_{\text{tau}} = 0.534$) and hollows ($R_{\text{tau}} = 0.497$). The BIO-ENV model with the highest correlation identified canopy height, cavity density and hollow density as the key factors influencing insectivorous bats, explaining 34.2% of assemblage composition over the forest landscape. Nevertheless, canopy height was the sole predictor of assemblage composition described by Axis 1, which represented the majority of assemblage variation ($R^2 = 0.728$;

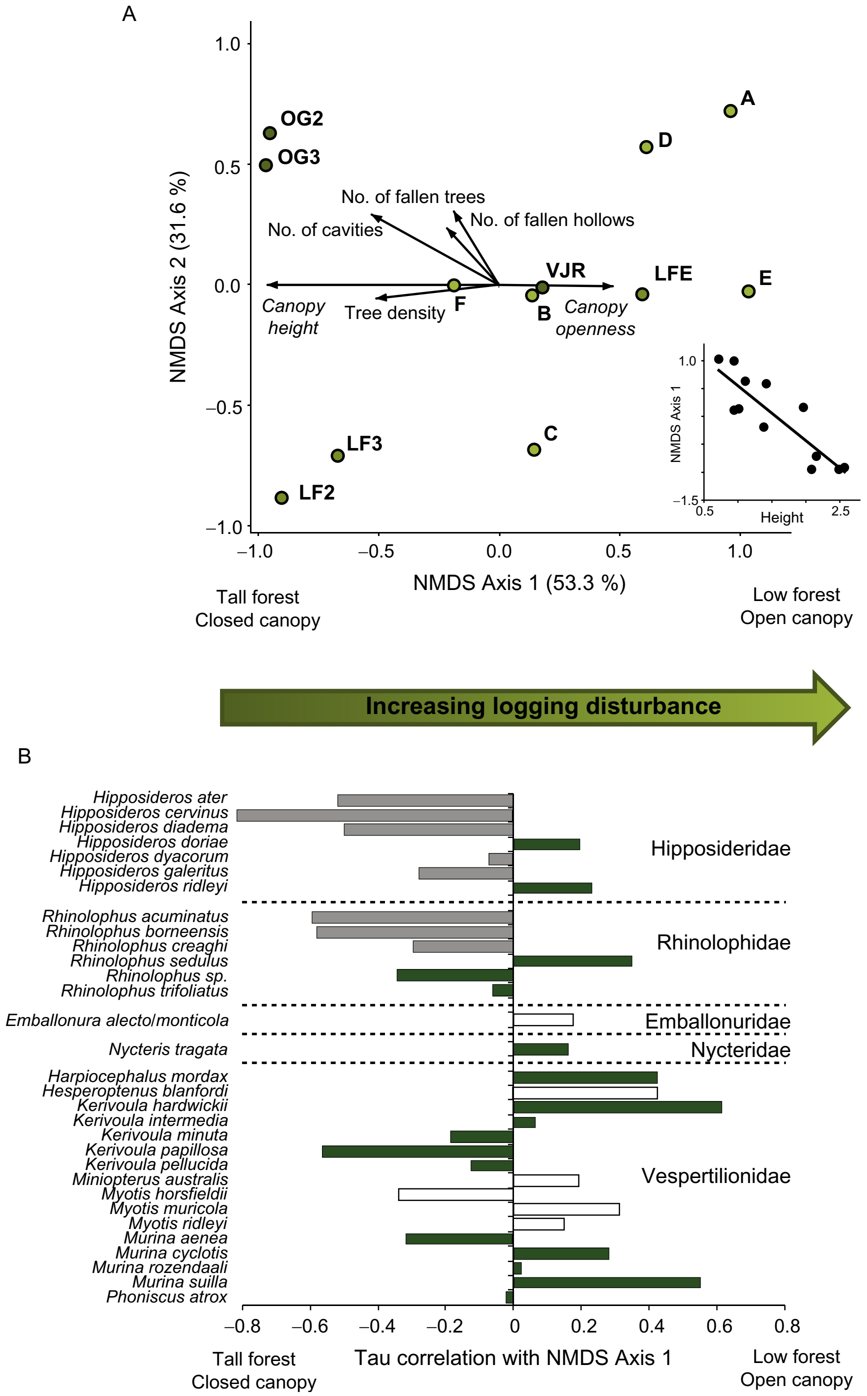

Figure 4 (A) Non-metric multidimensional scaling (NMDS) ordination of bat assemblage structure among rainforest sites with varying degrees of logging disturbance (stress = 4.527). The two axes that represent the majority of variation (84.9%) in

(Continued)

Figure 4—Cont'd assemblage structure are presented for clarity. Vectors indicate environmental correlates of assemblage structure (tau coefficients > 0.3) for macrohabitat (upper-case labels) or microhabitat (lower-case labels) variables. Sites are colour coded according to broad forest type: dark shading, *old growth*; intermediate shading, *twice logged*; light shading, *repeatedly logged*. The inset shows the significant association of canopy height with the Axis 1 site scores ($R^2 = 0.728$; $p < 0.001$). (B) Tau correlation coefficients between species abundance and the NMDS Axis 1 scores. Species are ordered according to family (upper-case labels) and shading indicates ensemble (dark shading, forest species; light shading, cave species; white, edge/gap-foraging species).

$p < 0.001$; Fig. 4A, inset). There was some reorganisation in ordination space when NMDS was repeated on subsets of non-clustered sites (see Section 2.4.2), but the overall pattern of assemblage dissimilarity and correlation of the main axis scores with forest structure was consistent across the additional four ordinations (Fig. 5).

Variation in assemblage structure was associated with changes in the abundance of several species across sites. The abundances of cave-roosting species were all negatively correlated with NMDS Axis 1 scores (Fig. 4B), indicating that these species were more abundant in assemblages at the least disturbed forest sites. Notably, two of the most abundant cave-roosting species (*H. cervinus*, *Rhinolophus borneensis*) were present at all sites, but were less abundant at logged sites ($R_{tau} = -0.791$; -0.540). This was also evident for one of the forest species, *Kerivoula papillosa*, which exhibited a decline in abundance that closely followed the logging-disturbance gradient ($R_{tau} = -0.532$). Not all species of this ensemble followed this pattern, however, and notably two forest species (*Kerivoula hardwickii*, *Murina suilla*) were much more abundant in repeatedly logged forest than in old-growth forest ($R_{tau} = 0.594$, 0.532). The majority of edge/gap species were also indicative of the most degraded repeatedly logged sites, although we note that fewer individuals of this ensemble were captured over all.

3.5. Trap-level responses to forest disturbance

Model average parameters of our ZIGLMM analyses confirmed canopy height to be the most important forest-structure variable to significantly predict overall bat abundance in traps (Table 4). Accordingly, as with those based on sites, trap-based analyses revealed that more bats were captured in the least disturbed forest localities defined by taller canopy. When models were partitioned by ensemble, height remained a significant predictor for the abundance of cave bats. However, the number of available cavities in standing trees was the single-most important and significant predictor of the

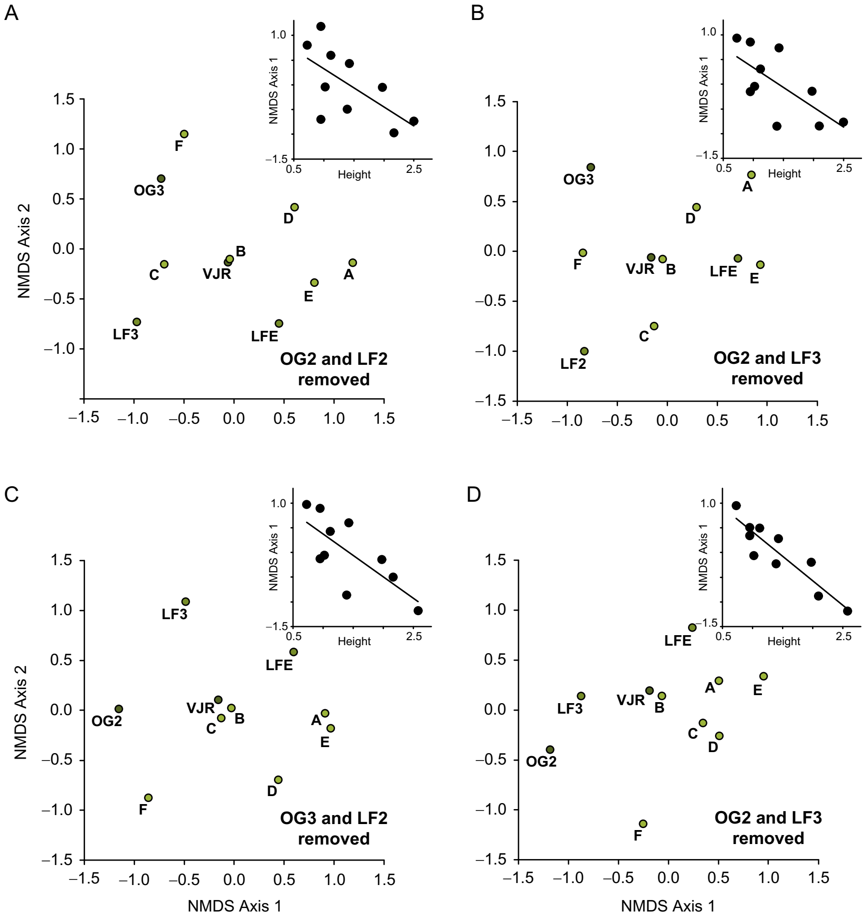

Figure 5 Non-metric multidimensional scaling (NMDS) representations of bat assemblage structure based on subsets of data with geographically clustered sites removed. The relative proximity of two pairs of sites (*old growth*, OG2 and OG3; *twice logged*, LF2 and LF3) could potentially confound the signals in assemblage change arising from forest disturbance. Ordinations were therefore undertaken after leaving out one site from each geographic pair in the four ways (A–D) that this could be done. Ordination stress (<4.611) is comparable to the optimal NMDS solution presented in Fig. 4, in which all sites were included. Sites are colour coded according to broad forest type: dark shading, *old growth*; intermediate shading, *twice logged*; light shading, *repeatedly logged*. Insets show the association of canopy height with the main axis scores for each ordination, which remains significant ($R^2 = 0.32$–0.82; $p < 0.05$) and consistent with the findings of the optimal ordination presented in Fig. 4.

Table 4 Model-averaged coefficients of forest-structure variables used to predict bat-species abundance in harp traps across the logging disturbance gradient

Response variable	Predictor	β	SE	Lower CI	Upper CI	RI
Abundance, all bats	Intercept	1.23	0.07	1.10	1.36	
	Height	**0.48**	**0.16**	**0.17**	**0.79**	**1.00**
	Tree density	0.19	0.14	−0.08	0.47	0.46
	Hollows	0.13	0.13	−0.12	0.39	0.37
	Cavities	0.06	0.13	−0.20	0.32	0.24
	Clutter	−0.05	0.13	−0.31	0.22	0.23
Abundance, cave bats	Intercept	0.48	0.30	−0.12	1.07	
	Height	**1.25**	**0.30**	**0.66**	**1.84**	**1.00**
	Tree density	0.44	0.24	−0.03	0.91	0.69
	Cavities	−0.36	0.23	−0.81	0.08	0.49
	Clutter	−0.12	0.23	−0.56	0.32	0.27
	Hollows	0.02	0.21	−0.38	0.43	0.24
Abundance, forest bats	Intercept	0.69	0.09	0.51	0.87	
	Cavities	**0.26**	**0.11**	**0.04**	**0.47**	**0.93**
	Hollows	0.13	0.11	−0.09	0.36	0.37
	Tree density	−0.08	0.12	−0.33	0.17	0.23
	Height	−0.07	0.13	−0.33	0.19	0.22
	Clutter	0.02	0.11	−0.20	0.25	0.20

Parameters are derived from zero-inflated generalised linear models with 'Site ID' fitted as a random effect: adjusted standard errors (SE), 95% lower and upper confidence intervals (CI) and relative importance factors (RI). Variables are presented in order of their relative importance, with significant predictors (i.e. those with confidence bounds not including zero) highlighted in bold. Outputs are consistent when models are re-run with spatially clustered sites coded as identical (to account for potential spatial correlation between OG and LF sites).

abundance of forest bats, with more animals being captured in plots with greater numbers of cavities. Using the results of this model to predict the bat abundance from increasing number of cavities indicated that a twofold increase in the number of tree cavities could more than double the number of bats captured (Fig. 6). Notably, model outputs were identical regardless of how sites were coded, indicating that abundance responses to forest-structure variables were not confounded by the spatial proximity of some of the sites.

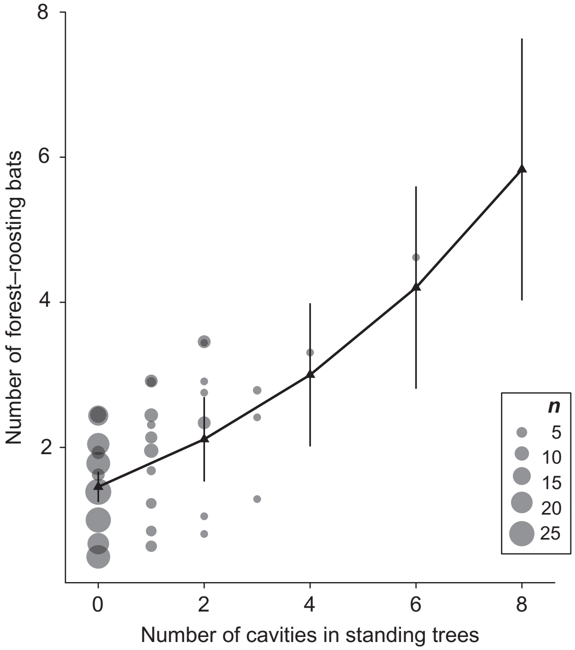

Figure 6 Increase in the abundance of forest bats (defined as those that roost in tree cavities and/or foliage) at forest localities with large numbers of cavities in standing trees. Circle size is proportional to the number of traps capturing bats at a given abundance level in a single night (maximum abundance = 6, in old-growth forest, OG2). Black triangles represent predicted bat abundance values as derived from a zero-inflated generalised linear mixed model (values are extrapolated to *n* = 8, but in principle could be extrapolated further). Error bars represent standard errors of the predicted values.

4. DISCUSSION

There remains much variation in the reported effects of logging on tropical biota. While most of this is likely due to inherent differences in the ways by which taxa respond to environmental change, another contributing factor is that many logging-effect studies evaluate impacts solely via comparative analyses of unlogged versus logged forest treatments, which brings with it methodological constraints. In our study of insectivorous bats in the heavily degraded forests of Borneo, we demonstrate the virtues of aligning assemblage data to disturbance gradients alongside more conventional comparative analyses of logged and unlogged habitats (Table 5): a straightforward practise that has been relatively little used in the logging-effect literature.

Table 5 Summary of comparative and gradient analyses of bat assemblages across the modified forested landscape

Level of analysis	**Comparative approach (forest types)**	**Gradient approach (sites/traps)**
Rarefied richness Section 3.2		
– All species included.	– Twice logged $>$ repeatedly logged $\sim$ old growth.	– Repeatedly logged sites $<$ old growth, but not associated with forest-structure gradient. Consistent at ensemble level and when singletons removed.
– Singletons removed.	– No difference in richness among forest types.	
Patterns of abundance Section 3.3	Representation of cave and forest bats: – Old growth: 50%, 49%. – Twice logged: 52%, 47%. – Repeatedly logged: 31%, 64%.	GLM: overall abundance decline in degraded forests associated with canopy height ($R^2 = 0.555$; $p = 0.003$).
Assemblage structure (ordination) Section 3.4	MRPP: variation among forest types, due to large difference between old growth and repeatedly logged forest assemblages. – All types, $A = 0.109$; $p = 0.013$. – Old growth versus repeatedly logged, $A = 0.999$; $p = 0.025$. – Twice logged versus repeatedly logged $A = 0.062$; $p = 0.085$. BIO-ENV: canopy height, cavity density and hollow density identified as main correlates of overall variation in assemblage structure.	GLM: canopy height as the sole predictor of assemblage variation on main NMDS axis ($R^2 = 0.728$; $p < 0.001$). Consistent when ordinations re-run without spatially clustered sites. Correlations and vectors: association of other forest variables with NMDS axis scores. Correlations of species abundances with NMDS axis scores identify main species driving assemblage signal.

Continued

Table 5 Summary of comparative and gradient analyses of bat assemblages across the modified forested landscape—cont'd

Level of analysis	Comparative approach (forest types)	Gradient approach (sites/traps)
Trap-level responses in abundance (ZIGLMMs) Section 3.5	N/A	Overall abundance decline predicted by canopy height for 'all bats' and 'cave bats'. Lower numbers of forest bats in traps associated with reduced availability of cavities in standing trees. Findings consistent when models re-run but coding spatially clustered sites as identical.

Each level of analysis refers to relevant section in the text.

In our study, neither approach revealed a definitive impact of intensive logging on species richness: comparative analyses indicated that repeatedly logged and old-growth forest hosted similar species numbers, and although inspection of site inventories revealed lower richness in the most degraded sites, this was not consistent across vegetation gradients. However, each approach generated insight into the structural responses of assemblages to forest degradation. Species compositional differences were evident between repeatedly logged and old-growth forest, with depauperate assemblages defining degraded sites with low, open canopy structure. Constrained ordination identified species that best contributed to the overall signal of assemblage change, and also key associated forest-structure variables. Finally, by modelling trap-based abundance data in relation to more finely resolved forest-structure data, we were able to not only confirm the importance of forest height in underlying assemblage change for cave-roosting species but also reveal the role of tree-cavity availability in supporting populations of forest specialists.

4.1. Addressing methodological shortcomings of logging-impact research

Our choice of study system in the lowlands of northern Borneo was by no means free of limitations to study design, but importantly was typical of many of the forested landscapes available to evaluate the effects of logging. Some of the main lessons learnt from logging-impact studies in recent years are the importance of controlling for scale, as well as problems associated with underlying geographic and environmental variation in study sites (Gardner et al., 2009; Hamer et al., 2003; Hill and Hamer, 2004); factors that informed the location of study sites at the SAFE project where we based our research. One potential improvement to our study, however, would be to further replicate within forest type to minimise the possibility of pseudoreplication for site-level analyses. A recent literature review revealed this problem to be pervasive in the design of logging-impact studies, with only few of the analysed investigations (7%) considered to be truly pseudoreplication free (Ramage et al., 2013). As Ramage et al. (2013) acknowledge, our ability to achieve true replication in tropical forest research is extremely difficult, making it critically important how we manage this problem and interpret data. Indeed, as with other studies (Shea et al., 2004), the high heterogeneity in topography and forest disturbance within our system precluded our ability to implement further replication reliably at the level of sites. By repeating ordinations without spatially clustered sites, we were able to assess the extent to which spatial autocorrelation could affect our dataset (see Fig. 5). Moreover, our use of trap-based mixed-effect models accounted for replication concerns in two ways. First, by increasing the number of sample units (i.e. to 272 traps), and hence statistical power of analyses, and secondly by coding site location as a random effect to control for spatial correlation within and between sites. Notably, model outcomes were consistent when the potentially autocorrelated sites were coded as identical. These approaches highlight some of the analytical solutions to the challenges faced in landscape ecology, which necessarily trade control for realism—an issue that can in part be addressed through experimental research (see Stewart et al., 2013, for a review).

Given the technical and logistical challenges involved in minimising pseudoreplication in tropical forest research, further consideration of gradient approaches is clearly warranted, perhaps across even broader disturbance gradients. Moreover, such approaches should be robust to detect signals from temporal as well as spatial gradients over the long term (e.g. as we continue to monitor faunal assemblages in sites A–F during and after habitat fragmentation at the SAFE project area). The fragmentation process brings additional environmental gradients associated with habitat area, isolation and edge effects, which are all known to confound statistical signals in disturbance research (Ewers and Didham, 2006). From the growing body of fragmentation research in Southeast Asia (e.g. Hill et al., 2011; Laidlaw, 2000; Struebig et al., 2008, 2011), we expect faunal assemblages that have already experienced substantial habitat change to become increasingly depauperate and nested in small forest patches.

Taxonomic variation in resistance, resilience and vulnerability to disturbance is particularly evident in tropical forests and remains fundamental to the variation in the reported effects of logging. For example, pan-tropical analyses demonstrate substantial variation in the sensitivity of various animal groups to forest degradation, with mammals being the most tolerant group overall (Gibson et al., 2011). Therefore, it remains to be seen whether the trends we report for Borneo's insectivorous bats are congruent with the responses of other animal groups in the SAFE project area. Gradient and comparative analyses of spatially matched data from multiple taxonomic groups, especially from our study landscape when available, could potentially help us better understand some of the causes behind the levels of taxonomic variation reported. However, although gradient analyses are well placed to detect subtle changes to populations and assemblages, it is still likely that species will exhibit different responses to habitat change.

4.2. Differences in bat assemblages between degraded forest sites/habitats

A particularly novel aspect of our research was the appraisal of heavily degraded forests that had been logged multiple times. Despite several rounds of extraction at the most heavily degraded forest, we found that logging had little effect on bat-species richness (see Figs. 2 and 3), though considerable changes to assemblage composition and abundance were evident (see Figs. 4 and 5; Tables 2 and 3). The negligible effect of logging on overall faunal richness is in broad agreement with a substantial number of previous studies (Berry et al., 2010; Meijaard et al., 2005), although a low but significant reduction of richness in logged forest is evident at the pan-tropical level (Gibson et al., 2011). Nonetheless, it is difficult to establish definitive responses to logging because the extent of disturbance typically varies between studies and is not always documented. Our findings are most appropriately compared to other studies of heavily degraded rainforests that have been logged multiple times, but the general lack of research attention to these modified ecosystems makes comparison particularly difficult. Edwards et al. (2011) and Woodcock et al. (2011) provide the only studies to date, though these were still restricted to the ecological value of twice-logged forests. In these forests, remarkably high diversity following intensive logging was documented, albeit from comparative approaches; 75% of bird and dung beetle species, and 80% of ant taxa remained in twice-logged forests, with the second round appearing most detrimental. As we examined exacerbated disturbance via additional logging in our study (at sites A–F), it is somewhat surprising that we found little effect on overall patterns of bat richness. Indeed, at the site level our results suggest that tropical forests heavily degraded by logging activities still retain some biological value.

In contrast to the patterns of richness, our examination of assemblage structure and faunal responses at the trap level revealed subtle but consistent changes in the abundance of several species over the logging-disturbance gradient. This is consistent with the results of other studies on a variety of taxa (e.g. Clarke et al., 2005a; Hamer et al., 2003; Presley et al., 2008; Wells et al., 2007) and is also to be expected, given the substantial changes to species composition frequently evident in forests regenerating from clearance or burning (Dent and Wright, 2009). Elsewhere in Sabah, Edwards et al. (2011) reported significant declines in abundance for 30% of birds and 50% of dung beetles following the first round of logging, but little change after the second rotation. Conversely, significant reductions in abundance were reported for leaf-litter ants from twice-logged forest, for nearly half of the species commonly found in unlogged forest (Woodcock et al., 2011).

The changes in the structuring of bat assemblages we documented across sites and traps were largely associated with differences in canopy height, canopy openness and the densities of cavities/hollows in standing and fallen trees. Ecologists have long considered vertical (and horizontal) complexity to be important drivers of biological diversity, by virtue of the greater variety of microhabitats and shelter that complex habitat provides (MacArthur and MacArthur, 1961). As such, efforts to manage modified landscapes for biodiversity often focus on maintaining structural complexity, and measures of canopy height and canopy density are frequently used to assess the integrity of forest ecosystems (Lindenmayer et al., 2012; Meijaard et al., 2005). Our finding that canopy height is significantly associated with the structuring of biological assemblages compares favourably with other studies (e.g. Cleary et al., 2007; Wunderle et al., 2006), and therefore supports the idea that simple measures of vegetation structure can serve as useful proxies for biodiversity in forest management. This has important implications for the application of remote technologies such as LIDAR that are increasingly used to monitor tropical forest resources, in terms of timber and, by inference, biodiversity (Müller et al., 2010; Pekin et al., 2012). It also suggests that efforts to reduce the collateral damage caused by logging operations could result in considerable biodiversity savings. For example, reduced-impact logging techniques have been shown to markedly decrease tree mortality and canopy gap fracture (Pinard and Putz, 1996), though the benefits to forest species are yet to be thoroughly demonstrated (Edwards et al., 2012).

4.3. Abundance responses of bats to forest degradation

The shift in insectivorous bat assemblage structure in response to logging in our study system mirrored broad trends found by some studies in the neotropics (e.g. Clarke et al., 2005a; Peters et al. 2006), but resulted largely from the decline of cave-roosting species and changes to the abundance of several forest-roosting taxa. Assemblages in old-growth and twice-logged forest were typically characterised by a relatively even composition of cave bats and forest bats; but far fewer cave specialists were found in the most heavily (repeatedly) logged sites (Table 3). This was most notable for leaf-nosed bats (Hipposideridae) and horseshoe bats (Rhinolophidae), echoing trends in disturbed Vietnamese karst forests, which also exhibit lower abundances of these taxa (Furey et al., 2010). Hipposiderid and Rhinolophid species that typically roost in caves tend to dominate bat assemblages in Borneo's lowland dipterocarp forests (Struebig et al., 2012), and so it is perhaps not surprising that the main signal in community change was detected in this ensemble. In Southeast Asia, cave-roosting bats can form large colonies, commute over several kilometres to foraging areas and tend to be more dominant in assemblages at localities near to major roosts (Struebig et al., 2009), yet, to the best of our knowledge, there are no major cave systems within the SAFE project area. Supporting this assertion is the fact that some cave species (e.g. *H. cervinus*, *R. borneensis*) exhibited a gradual and consistent decline in abundance from unlogged to the repeatedly logged sites, indicating that these bats were responding to disturbance effects rather than the inherent patchy distribution of caves in the landscape. Anecdotal reports suggest that some of these species roost in small boulder caves and rock formations, and will occasionally roost in sizeable hollows of large standing trees (Kingston et al., 2006): structures that our forest plot data show are in particularly low numbers at intensively logged localities. An alternative explanation for the lower abundance of cave bats in logged forest is that changes to forest structure (notably canopy height and openness) effected capture rates rather than bat abundance *per se*. We are unable to confirm this with our capture-based data, but note that acoustically derived data could potentially yield insight, as the detection range for horseshoe and leaf-nosed bats would likely exceed the range of canopy heights experienced over the landscape.

In contrast to the cave-roosting taxa in our study system, forest bat species tend to have smaller home ranges (Wilson et al., 2010) and much lower movement capabilities (Kingston et al., 2003, 2006). Nevertheless, two forest-dwelling species (*K. hardwickii*, *M. suilla*) were much more dominant in logged than in unlogged areas. One potential explanation for this trend is that these species might be more active in the midstory and/or canopy, and so would be infrequently captured in understory traps set in tall forests compared to other forest taxa, although this hypothesis has yet to be tested empirically. The significantly lower and more open structure of our repeatedly logged localities compared to those in unlogged forest might therefore bring with it a greater chance of detection for these species by our sampling protocol. Two other forest species of interest, *Hipposideros ridleyi* and *Rhinolophus sedulus*, are red-listed as vulnerable and near threatened due to habitat loss (IUCN, 2011), yet we found them to be moderately abundant in some of the most heavily logged sites. Both species exhibit small home ranges (<100 ha) and are known to roost in hollows of large fallen trees, a relatively scarce roost resource (Kingston et al., 2006). These structures, while typical of mature old-growth forest, are often left behind by logging operations because hollow trees have little commercial value (Meijaard et al., 2005). Therefore, while these bats may be able to persist in the short-term, their long-term viability in managed forests will depend largely on how well these structures are recruited back into the system. Recent research in modified forests of Australia indicates that not only are these areas losing large trees at high rates but also that cavity-bearing trees are not being recruited back into the system in sufficient numbers (Lindenmayer et al., 2012). Given the highly degraded nature of our repeatedly logged sites, it seems likely that this might also be the case in our study system, and so without adequate intervention, time lags in the manifestation of logging-disturbance effects (*sensu* Gardner et al., 2009), in particular, declines in richness, seem probable.

4.4. The importance of tree cavities for logged forest wildlife

In addition to canopy height and openness, densities of tree cavities and hollows were identified as key structural variables predicting the abundance of bats (Figs. 4 and 6; Table 4). These findings suggest that declines of at least some mammal species in logged forest are associated with a concomitant reduction in available shelter. Indeed, one forest bat species (*K. papillosa*) exhibited a substantial and consistent decline in abundance over our logging-disturbance gradient. *K. papillosa* is a colonial tree-roosting species that occurs at low to moderate population densities in undisturbed forest (Kingston et al., 2006). Patterns of local dispersion and restricted gene flow in intact forest indicate a limited capacity for movement (Rossiter et al., 2012), and the species exhibits declines in abundance and genetic diversity in small forest fragments, which are thought to be linked to a reduced availability of roosting trees (Struebig et al., 2008, 2011). The global decline in cavity-bearing trees is an emerging conservation concern for the management of forested and agricultural landscapes, because these structures provide vital nesting sites for a variety of wildlife, including mammals, birds, snakes and invertebrates (Cockle et al., 2011; Lindenmayer et al., 2012). Our finding that unlogged forest localities contained more trees, larger trees and more cavity-bearing trees than twice-logged or repeatedly logged sites is consistent with global patterns revealed by meta-analyses, although the densities quantified in our old-growth forest plots are much higher than the global average (Remm and Lõhmus, 2011). Surprisingly, there are very few studies on cavity availability in Southeast Asian forests (Cockle et al., 2011). In subtropical Atlantic forest, Cockle et al. (2010) found that logged stands had one-third the density of large trees, as well as nine times fewer cavities for cavity-nesting birds, than undisturbed forests—that is, comparable ratios to those found in our study (Table 1).

Trees with large diameters are more likely to contain cavities than smaller trees (Robles et al., 2011), in part because larger trees are typically older, with heartwood less able to resist decay (Meijaard and Sheil, 2008). Indeed, we found that very few of the pioneer trees bore cavities in repeatedly logged forest plots, especially species of *Macaranga* that are typically dominant in secondary vegetation of the region. Although preliminary studies suggest that decay processes may be central to tree-cavity development in the tropics (e.g. Boyle et al., 2008), global analyses indicate that the extent to which avian excavators are important is yet to be thoroughly demonstrated (Cockle et al., 2011). Elsewhere on Borneo, cavity-excavating woodpeckers are known to undergo substantial declines in density in logged forest (Lammertink, 2004), suggesting that the cavity-production potential of degraded forests could indeed be severely compromised by timber extraction. Given the biological importance of cavities for forest wildlife, and that relatively little research has been undertaken in the tropics, studies that identify the key factors behind cavity production and subsequent use of this resource are clearly warranted for effective biodiversity management in modified landscapes.

4.5. Applications to tropical forest management

In addition to confirming the value of undisturbed habitat for forest wildlife, our results indicate that some components of the tropical fauna persist in repeatedly logged forests. This would suggest that these degraded forests are of higher biodiversity value than is currently appreciated in conservation planning and land-use policies, which has also been proposed in the recent literature (Edwards et al., 2011; Meijaard and Sheil, 2007). A crucial caveat to this assertion is that the presence of less-disturbed forest stands over the landscape mosaic likely contributes to spill-over effects in disturbed habitats to some degree. The value of degraded forests is expected to improve over time if species from remaining patches of old-growth forest move in and accumulate (Chazdon et al., 2009). By linking assemblage change to forest-structure variables our findings indicate that, at the same time, bats could potentially recover from logging disturbance, given restoration investments to canopy structure and cavity availability.

By using gradient as well as comparative analyses, our study design served as an effective space-for-time substitution, in which the key forest-structure variables associated with disturbance and assemblage change could be identified as forests that were repeatedly logged. The unavoidable structure of our capture data precluded our ability to generate species-specific predictive models based on measures of forest structure. However, predictions based on pooled data imply that populations of tree-cavity/foliage-roosting species in heavily degraded forests could be boosted by increasing the number of cavities available for roosting (Fig. 6; Table 4). If possible, this could facilitate the post-logging recovery of assemblages akin to that seen elsewhere in the tropics in low-intensity extraction systems (e.g. for bats, Clarke et al., 2005b; Willig et al., 2007). Over the long term, this might be accomplished by enrichment planting of cavity-bearing tree species, but supplementary cavity boxes, such as those used successfully in Australia for insectivorous bats and birds (Goldingay and Stevens, 2009), would likely be necessary. Progressive forestry techniques, such as those implemented under reduced-impact logging programmes and promoted by REDD+ policies, are expected to yield more immediate cost-effective benefits to biodiversity than targeted post-logging management. For example, elsewhere in Sabah, post-extraction inventories of mammals in forest subject to sustainable management indicate that diversity and community structure remain unchanged after reduced-impact logging (Samejima et al., 2012). Such practises might include preservation of cavity-bearing trees (including those that are dead or partially dead) in addition to existing efforts to minimise collateral damage to canopy structure (Meijaard and Sheil, 2008). Although, the potential for wildlife populations to recover from tropical forest disturbance is yet to be fully realised, predictions from reviewed literature indicate that the fauna of recovering cleared land could resemble that of old-growth forest within 20–40 years (Dunn, 2004). While we note that none of the studies used to generate this prognosis were undertaken in tropical Southeast Asia, our work indicates that even forests heavily degraded by repeated logging have the potential to be of some value to tropical fauna. If the case, this could have implications for valuations of biodiversity and associated ecosystem functions and services in human-modified landscapes (see Raffaelli and White, 2013, for review). As more data become available from large-scale field experiments such as the SAFE project, the recovery potential and viability of tropical populations and assemblages in these highly degraded habitats will become increasingly clear.

ACKNOWLEDGEMENTS

We are especially grateful to the Economic Planning Unit of the Malaysian Government and the Sabah Biodiversity Council for granting permission to undertake our field research in Sabah, as well as Yayasan Sabah, Benta Wawasan Sdn. Bhd. and Sabah Softwoods Sdn. Bhd. for allowing us access to research sites. We also thank Glen Reynolds, the Royal Society Southeast Asian Rainforest Research Programme, the Maliau Basin Management Committee, Rob Ewers and the SAFE Science Committee for reviewing proposals, providing valuable feedback and greatly facilitating our research programme. Johnny Larenus, Edgar Turner and Min Sheng Khoo provided much needed logistical support, and we are indebted to the invaluable assistance of Lawrence Alan Anak Bansa and Mohd. Sallahuddin Bin Mohd. Zahid as well as the SAFE project field team (http://www.safeproject.net/personnel/field-team/). This research was supported by a Leverhulme Trust Fellowship awarded to M. J. S., as well as grants from Mohamed bin Zayed Species Conservation Fund, Bat Conservation International, Durrell Institute of Conservation and Ecology and Chester Zoo, United Kingdom. We also benefitted from funding awarded to the SAFE Project by the Sime Darby Foundation. Finally, we would like to thank the three anonymous reviewers who made suggestions that greatly improved our chapter.

REFERENCES

Aguilar-Amuchastegui, N., Henebry, G.M., 2007. Assessing sustainability indicators for tropical forests: spatio-temporal heterogeneity, logging intensity, and dung beetle communities. For. Ecol. Manage. 253, 56–67.

Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R., Emerson, R., 2009. A contemporary assessment of change in humid tropical forests. Conserv. Biol. 23, 1386–1395.

Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. 104, 18555–18560.

Barlow, J., Gardner, T.A., Louzada, J., Peres, C.A., 2010. Measuring the conservation value of tropical primary forests: the effect of occasional species on estimates of biodiversity uniqueness. PLoS One 5, e9609.

Bartoń, K., 2012. MuMIn Package Version 1.8.0: Multi-Model Inference. Model Selection and Model Averaging Based on Information Criteria (AICc and Alike). http://cran.r-project.org/web/packages/MuMIn/index.html.

Berry, N., Phillips, O., Lewis, S., Hill, J., Edwards, D., Tawatao, N., Ahmad, N., Magintan, D., Khen, C., Maryati, M., Ong, R., Hamer, K., 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodivers. Conserv. 19, 985–997.

Blaser, J., Sarre, A., Poore, D., Johnson, S., 2011. Status of Tropical Forest Management. International Tropical Timber Organization, Yokahama, Japan ITTO Technical Series 38.

Boyle, W.A., Ganong, C.N., Clark, D.B., Hast, M.A., 2008. Density, distribution, and attributes of tree cavities in an old-growth tropical rain forest. Biotropica 40, 241–245.

Bradshaw, C.J.A., Sodhi, N.S., Brook, B.W., 2008. Tropical turmoil: a biodiversity tragedy in progress. Front. Ecol. Environ. 7, 79–87.

Brook, B.W., Bradshaw, C.J.A., Koh, L.P., Sodhi, N.S., 2006. Momentum drives the crash: mass extinction in the tropics. Biotropica 38, 302–305.

Cannon, C.H., Peart, D.R., Leighton, M., Kartawinata, K., 1994. The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia. For. Ecol. Manage. 67, 49–68.

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S.E., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23, 1406–1417.

Clark, D.B., Clark, D.A., 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Manage. 137, 185–198.

Clark, C.J., Poulsen, J.R., Malonga, R., Elkan, J.P.W., 2009. Logging concessions can extend the conservation estate for Central African tropical forests. Conserv. Biol. 23, 1281–1293.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Primer-E Ltd., Plymouth.

Clarke, F.M., Pio, D.V., Racey, P.A., 2005a. A comparison of logging systems and bat diversity in the Neotropics. Conserv. Biol. 19, 1194–1204.

Clarke, F.M., Rostant, V., Racey, P., 2005b. Life after logging: post-logging recovery of a neotropical bat community. J. Appl. Ecol. 42, 409–420.

Cleary, D.F., Boyle, T.J., Setyawati, T., Anggraeni, C.D., Van Loon, E.E., Menken, S.B.J., 2007. Bird species and traits associated with logged and unlogged forest in Borneo. Ecol. Appl. 17, 1184–1197.

Cleary, D.F.R., Genner, M.J., Koh, L.P., Boyle, T.J.B., Setyawati, T., de Jong, R., Menken, S.B.J., 2009. Butterfly species and traits associated with selectively logged forest in Borneo. Basic Appl. Ecol. 10, 237–245.

Cockle, K.L., Martin, K., Drever, M.C., 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biol. Conserv. 143, 2851–2857.

Cockle, K.L., Martin, K., Wesołowski, T., 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Front. Ecol. Environ. 9, 377–382.

Colwell, R.K., 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application published at: http://purl.oclc.org/estimates.

Cushman, S.A., McGarigal, K., Gutzweiler, K., Evans, J.S., 2010. The gradient paradigm: a conceptual and analytical framework for landscape ecology. In: Cushman, S.A., Huettmann, F. (Eds.), Spatial Complexity, Informatics, and Wildlife Conservation. Springer, Tokyo, pp. 83–110.

Dent, D., Wright, J.W., 2009. The future of tropical species in secondary forests: a quantitative review. Biol. Conserv. 142, 2833–2843.

Didham, R.K., 2011. Life after logging: strategic withdrawal from the garden of Eden or tactical error for wilderness conservation. Biotropica 43, 393–395.

Dunn, R.R., 2004. Recovery of faunal communities during tropical forest regeneration. Conserv. Biol. 18, 302–309.

Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhe, M.A., Hamer, K.C., Wilcove, D.S., 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Philos. Trans. R. Soc. Lond. B Biol. Sci. 278, 82–90.

Edwards, D.P., Woodcock, P., Edwards, F.A., Larsen, T.H., Hsu, W.W., Benedick, S., Wilcove, D.S., 2012. Reduced-impact logging and biodiversity conservation: a case study from Borneo. Ecol. Appl. 22, 561–571.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81, 117–142.

Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L., Turner, E.C., 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philos. Trans. R. Soc. B Biol. Sci 366, 3292–3302.

Felton, A., Felton, A.M., Wood, J., Lindenmayer, D.B., 2006. Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. For. Ecol. Manage. 235, 186–193.

Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), 2001. The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, New York.

Findley, J.S., 1993. Bats: A Community Perspective. Cambridge University Press, Cambridge.

Fisher, B., Edwards, D.P., Giam, X., Wilcove, D.S., 2011. The high costs of conserving Southeast Asia's lowland rainforests. Front. Ecol. Environ. 9, 329–334.

Fitzherbert, E.B., Struebig, M., Morel, A., Danielsen, F., Brühl, C., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends Ecol. Evol. 23, 538–545.

Foody, G.M., Cutler, M.E.J., 2003. Tree biodiversity in protected and logged Bornean tropical rain forests and its measurement by satellite remote sensing. J. Biogeogr. 30, 1053–1066.

Frumhoff, P.C., 1995. Conserving wildlife in tropical forests managed for timber. Bioscience 45, 456–464.

Furey, N.M., Mackie, I.J., Racey, P., 2010. Bat diversity in Vietnamese limestone karst areas and the implications of forest degradation. Biodivers. Conserv. 19, 1821–1838.

Gardner, T.A., Barlow, J., Parry, L.W., Peres, C.A., 2007. Predicting the uncertain future of tropical forest species in a data vacuum. Biotropica 39, 25–30.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582.

Gardner, T.A., Burgess, N.D., Aguilar-Amuchastegui, N., Barlow, J., Berenguer, E., Clements, T., Danielsen, F., Ferreira, J., Foden, W., Kapos, V., Khan, S.M., Lees, A.C., Parry, L., Roman-Cuesta, R.M., Schmitt, C.B., Strange, N., Theilade, I., Vieira, I.C.G., 2012. A framework for integrating biodiversity concerns into national REDD+ programmes. Biol. Conserv. 154, 61–71.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.

Goldingay, R.L., Stevens, J.R., 2009. Use of artificial tree hollows by Australian birds and bats. Wildl. Res. 36, 81–97.

Gray, M.A., Baldauf, S.L., Mayhew, P.J., Hill, J.K., 2007. The response of avian feeding guilds to tropical forest disturbance. Conserv. Biol. 21, 133–141.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M., Chey, K.V., 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. J. Appl. Ecol. 40, 150–162.

Hill, J.K., Hamer, K.C., 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. J. Appl. Ecol. 41, 744–754.

Hill, J.K., Gray, M.A., Khen, C.V., Benedick, S., Tawatao, N., Hamer, K.C., 2011. Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? Philos. Trans. R. Soc. B Biol. Sci. 366, 3265–3276.

Isabirye-Basuta, G., Kasenene, J.M., 1987. Small rodent populations in selectively felled and mature tracts of Kibale Forest, Uganda. Biotropica 19, 260–266.

IUCN, 2011. IUCN Red List of Threatened Species. Version 2011.2. World Conservation Union (IUCN), Gland, Switzerland. www.iucnredlist.org. Downloaded on 8 February 2012.

Johns, A.D., 1989. Recovery of a Peninsular Malaysian rainforest avifauna following selective timber logging: the first twelve years. Forktail 4, 89–105.

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P., 2009. Carpe noctem: the importance of bats as bioindicators. Endanger. Species Res. 8, 93–115.

Kessler, M., Abrahamczyk, S., Bos, M., Buchori, D., Putra, D.D., Gradstein, S.R., Höhn, P., Kluge, J., Orend, F., Pitopang, R., Saleh, S., Schulze, C.H., Sporn, S.G., Steffan-Dewenter, I., Tjitrosoedirdjo, S.S., Tscharntke, T., 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. Ecol. Appl. 19, 2142–2156.

Kingston, T., Francis, C.M., Zubaid, A., Kunz, T.H., 2003. Species richness in an insectivorous bat assemblage from Malaysia. J. Trop. Ecol. 19, 67–79.

Kingston, T., Boo Liat, L., Zubaid, A., 2006. Bats of Krau Wildlife Reserve. Universiti Kebangsaan Malaysia Press, Bangi, Malaysia.

Kunz, T.H., Lumsden, L.F., 2006. Ecology of cavity and foliage roosting bats. In: Kunz, T.H., Brock-Fenton, M. (Eds.), Bat Ecology. University of Chicago Press, Chicago and London, p. 798.

Laidlaw, R.K., 2000. Effects if habitat disturbance and protected areas on mammals of Peninsular Malaysia. Conserv. Biol. 14, 1639–1648.

Lambert, F.R., Collar, N.J., 2002. The future for Sundaic lowland forest birds—long-term effects of commercial logging and fragmentation. Forktail 18, 127–146.

Lammertink, M., 2004. A multiple-site comparison of woodpecker communities in Bornean lowland and hill forests. Conserv. Biol. 18, 746–757.

Laurance, W.F., 2007. Have we overstated the tropical biodiversity crisis? Trends Ecol. Evol. 22, 65–70.

Lindenmayer, D.B., Laurance, W.F., 2012. A history of hubris—cautionary lessons in ecologically sustainable forest management. Biol. Conserv. 151, 11–16.

Lindenmayer, D.B., Blanchard, W., McBurney, L., Blair, D., Banks, S., Likens, G.E., Franklin, J.F., Laurance, W.F., Stein, J.A., Gibbons, P., 2012. Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. PLoS One 7, e41864.

MacArthur, R.H., MacArthur, J.W., 1961. On bird diversity. Ecology 42, 594–598.

McCain, C.M., Grytnes, J.-A., 2010. Elevational gradients in species richness. Encyclopedia of Life Sciences (ELS). John Wiley and Sons, Chichester. http://dx.doi.org/10.1002/9780470015902.a0022548.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MJM Software Design, Oregon.

McDonnell, M.J., Pickett, S.T.A., 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71, 1232–1237.

Medellín, R.A., Equihua, M., Amin, A.M., 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. Conserv. Biol. 14, 1666–1675.

Meijaard, E., Sheil, D., 2007. A logged forest in Borneo is better than no forest at all. Nature 446, 974.

Meijaard, E., Sheil, D., 2008. The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities. Ecol. Res. 23, 21–34.

Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S., O'Brien, T. (Eds.), 2005. Life After Logging: Reconciling Wildlife Conservation and Production Forestry in Indonesian Borneo. Center for International Forestry Research, Bogor, Indonesia.

Müller, J., Stadler, J., Brandl, R., 2010. Composition versus physiognomy of vegetation as predictors of bird assemblages: the role of LIDAR. Remote Sens. Environ. 114, 490–495.

Norberg, U.M., 1998. Morphological adaptations for flight in bats. In: Kunz, T.H., Racey, P.A. (Eds.), Bat Biology and Conservation. Smithsonian Institution Press, Washington, DC, pp. 93–108.

Okuda, T., Suzuki, M., Adachi, N., Quah, E.S., Hussein, N.A., Manokaran, N., 2003. Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. For. Ecol. Manage. 175, 297–320.

Paterson, S., Lello, J., 2003. Mixed models: getting the best use of parasitological data. Trends Ecol. Evol. 9, 370–375.

Pekin, B., Jung, J., Villanueva-Rivera, L., Pijanowski, B., Ahumada, J., 2012. Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. Landsc. Ecol. 27, 1513–1522.

Peters, S.L., Malcolm, J.R., Zimmerman, B.L., 2006. Effects of selective logging on bat communities in the Southeastern Amazon. Conserv. Biol. 20, 1410–1421.

Pinard, M.A., 2005. Changes in plant communities associated with timber management in natural forests in the moist tropics. In: Burlsem, D.F.R.P., Pinard, M.A. (Eds.), Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge University Press, Cambridge.

Pinard, M.A., Putz, F.E., 1996. Retaining forests biomass by reducing logging damage. Biotropica 28, 278–295.

Presley, S.J., Willig, M.R., Wunderle, J.M., Saldanha, L.N., 2008. Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. J. Appl. Ecol. 45, 14–25.

Putz, F.E., Redford, K.H., 2010. The importance of defining ‘forest’: tropical forest degradation, deforestation, long-term phase shifts, and further transitions. Biotropica 42, 10–20.

Raffaelli, D., White, P.C.L., 2013. Ecosystems and their services in a changing world: an ecological perspective. Adv. Ecol. Res. 48, 1–70.

Ramage, B.S., Sheil, D., Salim, H.M.W., Fletcher, C., Mustaffa, N., Luruthusamy, J.C., Harrison, R.D., Butod, E., Dzulkiply, A.D., Kassim, A.R., Potts, M.D., 2013. Pseudoreplication in tropical forests and the resulting effects on biodiversity conservation. Conserv. Biol. 27, 364–372.

Remm, J., Lõhmus, A., 2011. Tree cavities in forests—the broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manage. 262, 579–585.

Robles, H., Ciudad, C., Matthysen, E., 2011. Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: the role of traditional management practices. For. Ecol. Manage. 261, 1428–1435.

Rossiter, S.J., Zubaid, A., Mohd-Adnan, A., Struebig, M.J., Kunz, T.H., Gopal, S., Petit, E.J., Kingston, T., 2012. Social organization and genetic structure: insights from codistributed bat populations. Mol. Ecol. 21, 647–661.

Samejima, H., Ong, P., Lagan, P., Kitayama, K., 2012. Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management. For. Ecol. Manage. 270, 248–256.

Shea, K., Roxburgh, H., Rauschert, E.S.J., 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecol. Lett. 7, 491–508.

Shen, T.J., Chao, A., Lin, J.F., 2003. Predicting the number of new species in further taxonomic sampling. Ecology 84, 798–804.

Skaug, H., Fournier, D., Nielsen, A., 2012. glmmADMB: Generalized Linear Mixed Models Using AD Model Builder in R. http://glmmadmb.r-forge.r-project.org/.

Sodhi, N.S., Lee, T.M., Koh, L.P., Brook, B.W., 2009. A meta-analysis of the impact of anthropogenic forest disturbance on Southeast Asia's biotas. Biotropica 41, 103–109.

Stewart, R.I.A., Dossena, M., Bohan, D.A., Jeppesen, E., Korda, R.L., Ledger, M.E., Meerhoff, M., Moss, B., Mulder, C., Shurin, J.B., Suttle, B., Thompson, R., Trimmer, M., Woodward, G., 2013. Mesocosm experiments as a tool for ecological climate change research. Adv. Ecol. Res. 48, 71–181.

Stork, N.E., Coddington, J.A., Colwell, R.K., Chazdon, R.L., Dick, C.W., Peres, C.A., Sload, S., Willis, K., 2009. Vulnerability and resilience of tropical forest species to land-use change. Conserv. Biol. 23, 1438–1447.

Struebig, M.J., Kingston, T., Zubaid, A., Mohd-Adnan, A., Rossiter, S.J., 2008. Conservation value of forest fragments to Palaeotropical bats. Biol. Conserv. 141, 2112–2126.

Struebig, M.J., Kingston, T., Zubaid, A., Le-Comber, S.C., Mohd-Adnan, A., Turner, A., Kelly, J., Bożek, M., Rossiter, S.J., 2009. Conservation importance of limestone karst outcrops for Palaeotropical bats in a fragmented landscape. Biol. Conserv. 142, 2089–2096.

Struebig, M.J., Kingston, T., Petit, E., Le Comber, S.C., Zubaid, A., Mohd-Adnan, A., Rossiter, S.J., 2011. Parallel declines of species and genetic diversity in tropical forest fragments. Ecol. Lett. 14, 582–590.

Struebig, M.J., Bożek, M., Hildebrand, J., Rossiter, S.J., Lane, D.J.W., 2012. Bat diversity in the lowland forests of the Heart of Borneo. Biodivers. Conserv. 21, 3711–3727.

Ter-Braak, C.J.F., Prentice, I.C., 2004. A theory of gradient analysis. Adv. Ecol. Res. 34, 236–278.

Wells, K., Kalko, E.K.V., Lakim, M.B., Pfeiffer, M., 2007. Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia. J. Biogeogr. 34, 1087–1099.

Whitmore, T.C., 1998. An Introduction to Tropical Rain Forests, second ed. Oxford University Press, Oxford, UK, 296 pp.

Willig, M.R., Presley, S.J., Bloch, C.P., Hice, C.L., Yanoviak, S.P., Diaz, M.M., Chauca, L.A., Pacheco, W., Weaver, S.C., 2007. Phyllostomid bats of lowland Amazonia: effects of habitat alteration on abundance. Biotropica 39, 737–746.

Wilson, K.A., Meijaard, E., Drummond, S., Grantham, H.S., Boitani, L., Catullo, G., Christie, L., Dennis, R.A., Dutton, I., Falcucci, A., Maiorano, L., Possingham, H., Rondinini, C., Turner, W.R., Venter, O., Watts, M., 2010. Conserving biodiversity in production landscapes. Ecol. Appl. 20, 1721–1732.

Woodcock, P., Edwards, D.P., Fayle, T.M., Newton, R.J., Khen, C.V., Bottrell, S.H., Hamer, K.C., 2011. The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. Philos. Trans. R. Soc. B Biol. Sci. 366, 3256–3264.

Wright, S.J., Muller-Landau, H.C., 2006. The future of tropical forest species. Biotropica 38, 287–301.

Wunderle, J.M., Henriques, L.M.P., Willig, M.R., 2006. Short-term responses of birds to forest gaps and understory: an assessment of reduced-impact logging in a lowland Amazon forest. Biotropica 38, 235–255.