

Prospects for mammals in Borneo's selectively-logged tropical forests: looking beyond species richness and abundance

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Abstract

The majority of tropical forest mammal species survive selective logging, however we have only recently begun to reveal complex, variable community abundance changes. We have little detailed, long-term data, and a poor mechanistic understanding of why mammals persist or decline. Predicting resilience remains elusive. In this thesis, we aimed to fill some of these knowledge gaps by (1) Examining long-term persistence of small mammals, (2) testing whether previously-observed small mammal abundance increases coincide with reduced body condition and demographic rates, potentially reducing future resilience, (3) testing for behaviourally plastic responses in large herbivore activity patterns, and (4) investigating whether the small mammal community “spills over” edges between logged forest and oil palm plantations.

We found strongly temporally variable small mammal population dynamics in logged forest, with some evidence for extinction debt. We found no direct evidence for bottom-up control seen in unlogged forest, although this probably reflects data limitations. There was no community-wide density-dependent reduction in body condition, reduced survival or reproductive output, suggesting that prospects for community resilience are good, but more detailed data is needed for declining species.

Large herbivores showed pronounced shifts in daily activity patterns, with the largest and most hunted ungulates becoming significantly more nocturnal. However, shifts did not predict persistence, suggesting the adaptive importance of behavioural plasticity is complex and species-specific. Lastly, we found little evidence that small mammals from logged forest spill over into adjacent plantations despite the abundant food, with the edge apparently forming a formidable dispersal barrier.

Together, our results suggest that prospects are good for many mammal species in logged forests, including those adjoining agriculture. However existing richness and abundance data miss many subtle temporal and individualistic responses, and to safeguard species known to be logging-intolerant, much more detailed work is required, combined with action to rehabilitate and restore logged forests for the future.

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Declaration of Originality

Robert M. Ewers, J. Marcus Rowcliffe and Chris Carbone contributed to all stages and sections of this thesis, including the concepts, study design, and data analysis. Various further assistance to different chapters is detailed below.

Chapter One: Robert M. Ewers and J. Marcus Rowcliffe commented on earlier drafts of this chapter.

Chapter Two: Oliver R. Wearn designed the data collection programme, and both collected and provided the data from 2011, 2012, and 2014. Terhi Ruitta collected and provided the seed and fruit availability dataset. Robert M. Ewers, J. Marcus Rowcliffe, Chris Carbone, Terhi Ruitta, Oliver R. Wearn and Henry Bernard all provided extensive comments on earlier drafts of this chapter. The manuscript was also improved by the comments of two anonymous reviewers during review and publication by *Biodiversity and Conservation*.

Chapter Three: Oliver R. Wearn designed the data collection programme, and both collected and provided the data from 2011, 2012, 2013 and 2014. David Orme provided analytical advice on this chapter, while Robert M. Ewers and J. Marcus Rowcliffe provided extensive comments on earlier drafts.

Chapter Four: Oliver R. Wearn designed the data collection programme, and both collected and provided the data from 2011, 2012, 2013, and 2014. J. Marcus Rowcliffe provided analytical advice. Robert M. Ewers, J. Marcus Rowcliffe, and Chris Carbone provided extensive comments on earlier drafts.

Chapter Five: Robin Loveridge provided the step length and turning angle data for the null modelling section of this chapter. David Orme provided analytical advice. Robert M. Ewers, J. Marcus Rowcliffe, Chris Carbone, Robin Loveridge and Charlie Davison commented on earlier drafts of the chapter.

Chapter Six: Robert M. Ewers and J. Marcus Rowcliffe commented on earlier drafts of this chapter.

Apart from these contributions acknowledged above, and works fully referenced in the text, I declare that all the following work is my own in conception, execution and presentation.

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Chapter One: Introduction and Literature Review

1.1 Global deforestation of the tropics – an accelerating crisis

Tropical forest degradation and loss are now globally established issues, and are proceeding at alarming rates. While clearance of temperate forests (largely in the developed world) stabilised in the mid-20th century (Ramankutty & Foley 1999), rates of forest loss are increasing in many tropical regions (Hansen *et al.* 2008, 2013; Rosa *et al.* 2016, but see Achard *et al.* 2014).

Between 2000 and 2012, the global area of tropical forest lost increased annually by an average of over 2100 km² (Hansen *et al.* 2013), with total net loss during this period equalling some 858 500 km² (Hansen *et al.* 2013), an area over 3.5 times that of the UK. Rates of loss vary regionally: the most rapid deforestation and smallest proportions of original forest remaining are found in the Indo-Malayan region (Hansen *et al.* 2013). In the decade to 2004, Southeast Asian forests were being lost at a rate of 1.4% per annum (Sodhi *et al.* 2004), with the highest rates in the islands of Sumatra and Borneo (Miettinen, Shi & Liew 2011; Margono *et al.* 2014). This region coincides with the “biodiversity hotspot” of Sundaland (Myers *et al.* 2000), therefore levels of forest loss in this region threaten a significant portion of the tropics’ biodiversity (Sodhi *et al.* 2004, 2009, 2010b; Wilcove *et al.* 2013).

Causes and drivers of forest loss are multifarious, and are often deeply rooted in the political and socioeconomic development of tropical countries (eg. Bawa & Dayanandan 1997; Laurance 1999), as well as depending on globally deregulated trade, international investment and demand for commodities from the developed world (Laurance 1999). Among proximal causes, the expansion of agriculture is the major driver of forest loss in tropical regions worldwide (Sala *et al.* 2000; Tilman *et al.* 2001; Green *et al.* 2005; Gibbs *et al.* 2010). The precise type of agriculture driving most deforestation, and the sequence of habitat clearance varies by region. Amazonian forests are most strongly threatened by expansion of extensive systems such as pasturelands and cattle ranching, and latterly by soya plantations (Barona *et al.* 2010; Gibbs *et al.* 2010). Conversely, the rapid expansion of intensive crop systems, particularly oil palm plantations, are the major cause of deforestation in Southeast Asia (Fitzherbert *et al.* 2008; Wilcove *et al.* 2013), although oil palm conversion is accelerating globally (Pirker *et al.* 2016). Much deforestation continues despite legislation limiting clearance, for example some 40% of the forest loss in Indonesia between 2000 and 2012 occurred in nominally protected areas (Margono *et al.* 2014).

1.2. Selective logging and forest degradation

1.2.1 Background to selective logging, and its global status

Clearance and conversion to agriculture forms only the more obvious issue facing tropical forest. Millions of square kilometres of forest which remain standing and have not been converted to agriculture have nonetheless been degraded from a pristine state, often to the extent that changes in structure are visible from satellite imagery (Achard *et al.* 2002, but see Peres, Barlow & Laurance 2006). This degradation is chiefly the result of selective logging, the process of removing large, high-value hardwood canopy trees, while leaving smaller individuals and low-value species. Precise figures for logging harvests are difficult to obtain in most tropical countries (especially in the case of illegal logging, or where corruption is involved), and logging disturbances may be subtle and difficult to detect using remote sensing approaches (Peres, Barlow & Laurance 2006). Therefore we have little certainty about how much of the world's remaining forest has been logged. However, selective logging has been reported throughout the tropics (Asner *et al.* 2005, Zhang *et al.* 2005, Laporte *et al.* 2007, Sodhi *et al.* 2010), with areas affected often extremely large: Asner *et al.* (2005) estimate an area between 12,000-20,000 km² was logged annually between 1999-2002 in the Amazonian Basin. However, the greatest intensity of logging is concentrated in Southeast Asia, particularly in Indonesia and Malaysia (Curran *et al.* 2004; Sodhi *et al.* 2004; Wilcove *et al.* 2013). Lowland forests in these regions are unusual in the predominance of marketable canopy tree species (generally *Dipterocarpaceae*) which has historically led to amongst the highest rates of timber extraction in the tropics (Grieser Johns 1997; Putz *et al.* 2012). Timber obtained by selective logging from Malaysia, Indonesia and the Philippines formed 80% of global tropical timber exports in the late 20th century (Berry *et al.* 2010). As a result of this particularly high profitability, tropical forests in these areas have frequently been subjected to multiple rounds of logging between the 1950s and the 1990s, with minimum harvested trunk diameters reduced at each round, and nearly all the canopy cover being removed. In the Malaysian states of Sabah and Sarawak, intensive logging has affected over 80% of total land area since 1990, with only 8% and 3% of land area still covered with protected and intact forests, respectively (Bryan *et al.* 2013). Although protecting primary forest is pre-eminently important (Gibson *et al.* 2011), these areas are unlikely to be sufficient to maintain the enormous biodiversity of Southeast Asian forests, and any further conservation effort will have to involve the protection of logged forest on a large scale.

1.2.2 The logging – clearance – plantation sequence

Regardless of the region and intensity of logging, logged forest loses residual economic value with each extraction round: regeneration times of climax canopy tree species such as dipterocarps and mahogany are slow, and further harvesting may not be possible for decades (Snook 2003; Fisher *et al.* 2011a). Historically, logged forest has also not been perceived to be of any value for wildlife by policymakers or tourists. Combined, these factors mean that logged forest is less likely to gain legal protection than unlogged forest, and is more likely to be cleared, and converted into pastoral agriculture (particularly in South America), or into more lucrative plantation agriculture, particularly Oil Palm (*Elaeis guineensis*) (Koh & Wilcove 2007; Fitzherbert *et al.* 2008; Berry *et al.* 2010; Edwards & Laurance 2011; Reynolds *et al.* 2011). Again, this has been most severe in South East Asia: between 1991 and 2011 oil palm plantations in Southeast Asia have more than tripled in combined area from 2.7 to 10.7 million ha. Malaysia is now one of the top three global producers, with 12.2% of its land area under oil palm plantations (FAO 2012). However, oil palm expansion is now accelerating in South America and Africa, alongside other forms of plantation agriculture. New plantations are developed largely at the expense of forests, either primary forest or (in the case of heavily-logged Southeast Asia), logged-out concessions (Uryu *et al.* 2008, Vijay *et al.* 2016). Clearance for agriculture generally fragments the remaining areas of forest; this process has been most dramatic in the Atlantic Forest of SE Brazil, of which few large areas remain, and forest remnants are generally small, isolated from each other by extensive agriculture and poorly-protected (Ribeiro *et al.* 2009).

Tropical forests therefore face two possible trajectories once logging operations have finished: 1) Conversion to pastoral agriculture or plantation, perhaps with some fragmented areas remaining; or 2) retention and rehabilitation, either as strictly protected areas, as long-term investments for future logging, or as mixed-use areas involving a compromise between both. In order to weigh up these alternatives and plan an optimal future for wildlife and people in this rapidly developing region, conservation planners and practitioners need evidence as to the effects of selective logging, both on the structure and composition of logged forests, and on animal biodiversity living within them.

1.3. Abiotic and biotic features of the selectively logged forest environment

1.3.1 Changes in forest structure

Selective logging has profound effects on the structure of tropical rainforests globally (Hall *et al.* 2003; Villela *et al.* 2006; Berry *et al.* 2008, 2010; Pfeifer *et al.* 2016), which in turn affects the abiotic and biotic environment. First, removal of large canopy trees directly reduces above-ground woody biomass (AGB) (Figueira *et al.* 2008; Gatti *et al.* 2015, Pfeifer *et al.* 2016). For example, three successive logging rounds in Bornean forest reduced mean AGB from 350.4 Mt.ha⁻¹ in primary forest to 95.4 Mt.ha⁻¹ (Pfeifer *et al.* 2016). Most tree mortality is incidental: of a total 50.9% mortality in one logging round (Johns 1988), only 3.3% was attributable to the trees intentionally felled. The remainder include neighbouring trees pulled over or severely damaged when a target tree is felled, particularly where the canopy is highly interconnected by lianas and vines. Logging operations also entail clearance of areas for infrastructure, such as roads, skid trails, timber loading areas, or temporary settlements. In particular, vast networks of unpaved roads are constructed with each logging round. Estimates of road construction vary by region and mapping method (eg. Laporte *et al.* 2007; Bryan *et al.* 2013; Gaveau *et al.* 2014). Those constructed in Borneo since the 1990s probably exceed 300 000 km (Bryan *et al.* 2013), equating to a mean 1.78km per km² in Sabah, Sarawak and Brunei, a density comparable to the entire road network of the UK (1.64 km per km²), whereas those constructed in Central Africa to 2003 only averaged 0.03 km per km² (Laporte *et al.* 2007).

Successive logging rounds thus drive the thinning, and opening up of as much as 80% of the closed canopy and open midstorey layers, loss of emergent and climax canopy trees and mature woody climbers (Grieser Johns 1997; Asner *et al.* 2004a; Gatti *et al.* 2015; Villela *et al.* 2016). The existing plant community of understorey vegetation and tree seedlings responds to the gap-like conditions immediately, with enhanced growth, and leaf and fruit production (Johns 1988). Mortality of remaining trees occurs at greatly elevated rates and losses of AGB may outstrip gains from regrowth and recruitment (Figueira *et al.* 2008). This leads to the development of a dense herbaceous ground layer (Costa & Magnusson 2003; Berry *et al.* 2010) with occasional small trees, while the increased tree mortality and leftovers from logging operations contribute to a proliferation of deadwood (Keller *et al.* 2004; Pfeifer *et al.* 2015). Large bare areas inhospitable to vegetation may also persist for many years, due to soil erosion and compaction from machinery (Pinard, Barker & Tay 2000). These biophysical changes are spatially heterogeneous, because logging intensity itself varies spatially, with tree removal greatest closer to logging roads and ridge-top loading areas (Johns 1988). Less accessible areas, such as steep slopes, swampy areas and the bottoms of narrow river valleys suffer much less canopy damage. The result is a spatial patchwork of forest structure, ranging from open areas that are

bare or only support herbaceous growth to almost untouched stands, and high levels of beta-diversity in the tree community (Berry *et al.* 2008).

1.3.2 Changes in microclimate

Changes in forest structure produce strong changes in microclimatic conditions. The gradual disappearance of the forest canopy allows much more sunlight, rainfall and wind to filter downwards and reach the understorey vegetation left behind, producing conditions typical of natural treefall gaps over a wide area (Miller, Goulden and da Rocha 2007; Negrete-Yankelevich *et al.* 2007; Hardwick *et al.* 2015). This effect is further exacerbated by microclimatic edge effects, as the network of roads and skid trails allows edge conditions to penetrate laterally into adjacent logged forest stands, even where canopy cover is largely maintained (Broadbent *et al.* 2008; Laurance, Goosem & Laurance 2009). As a result, daily maximum air and soil temperatures are higher, and relative humidity is lower after logging, with logged forest being up to 2.5°C hotter than primary forest. The daily fluctuation of these parameters is also magnified (Hardwick *et al.* 2015).

1.3.3 Succession and changes in the plant community

Structural and microclimatic habitat changes generally induce plant community change due to secondary succession. Immediately after logging, community structure of forests may remain relatively similar to that of primary forests, due to the predominance of random, non-target tree mortality (Johns 1988). However, community composition changes as open country and gap-specialist “pioneer” species rapidly invade logged forests, particularly fast-growing softwood tree genera such as *Cecropia* and *Macaranga* (in the Neotropics and Southeast Asia, respectively), and vines cloak large areas of regenerating vegetation (Thiollay 1992; Heydon & Bulloh 1997; Ferry Slik, Verburg & Keßler 2002; Verburg & van Eijk-Bos 2003; Bischoff *et al.* 2005). Non-native herbaceous plants may also invade, aided by human movement along roads (Veldman & Putz 2010; Padmanaba & Corlett 2014). In contrast, recruitment of dipterocarp climax species struggles, particularly in spots with the harshest microclimates (Pillay *et al.* 2018).

Many authors have observed increases in canopy cover, AGB, and plant species richness over time, and there is some evidence that succession returns some aspects of forest structure, such as basal area and canopy height, to a primary-forest like condition over several decades (Ferry Slik, Verburg & Keßler 2002; Costa & Magnusson 2003; Verburg & van Eijk-Bos 2003; Asner *et*

al. 2004b). However, many other studies have found differences in other structural measurements, or evidence for arrested succession and suppressed recruitment of climax canopy species, leading to pronounced differences in community composition for decades after logging (Curran *et al.* 1999; Okuda *et al.* 2003; Brearley *et al.* 2004; Bischoff *et al.* 2005; Liebsch, Marques & Goldenberg 2008). There is therefore considerable uncertainty about whether regrowing logged forest will ever completely return to a “pristine” condition, with convergence estimates for some aspects of species composition, such as endemism, in the millennia (Liebsch, Marques & Goldenberg 2008).

1.3.4. Selective logging, climate change, and fires

In addition to these direct effects on forest structure and microclimate, logging frequently also interacts synergistically with forest fires. Naturally-occurring or accidental fires are more likely to occur in logged forest (Holdsworth and Uhl 1997; Nepstad *et al.* 1999; Siegert *et al.* 2001), due partly to increased presence of humans and machinery during logging operations, but also to the drier microclimate, higher temperatures, more open canopy, and abundant deadwood. Illegal loggers or farmers in adjacent plantation land may also start fires deliberately by burning debris and ground flora to clear the ground of remaining vegetation (Uhl & Buschbacher 1985). Lastly, climate change is likely to increase the severity and duration of droughts such as those caused by the El Niño Southern Oscillation (ENSO), further drying logged forest, allowing fires to catch easily, spread rapidly over large areas and complicating efforts to extinguish them (Nepstad *et al.* 1999; Laurance & Williamson 2001; Siegert *et al.* 2001; Field, van der Werf & Shen 2009; Field *et al.* 2016). Most recently, this has occurred on a large scale in Indonesia during the ENSO of 2015-16 (Field *et al.* 2016), and increased feedbacks between climate change logging and fire also threaten much of the Amazon (Nepstad *et al.* 1999).

1.4. Selective logging and animal biodiversity: multitaxon patterns and knowledge gaps

1.4.1 Species richness retention in logged forests

On a regional and global scale, many studies predict regional and global tropical extinctions in the 21st century due to a combination of selective logging, agricultural conversion, and fragmentation of forest (e.g. Turner 1996; Sala *et al.* 2000; Brooks *et al.* 2002; Sodhi *et al.* 2004, 2010a; Bradshaw, Sodhi & Brook 2009; Gardner *et al.* 2009; Wilcove *et al.* 2013; Dirzo *et al.* 2014; Newbold *et al.* 2015; Giam 2017). Only a subset of this literature explicitly focuses on the

effects of selective logging on biodiversity, however this is still a large body of ecological research. There is now a reasonably broad consensus that logged forests support a high proportion of the species richness seen in primary forest. This is often up to 70 or 80% of primary forest species, a higher percentage than any other human-modified landuse type examined, particularly oil palm agriculture, which has widely been shown to support little biodiversity (Barlow *et al.* 2007; Fitzherbert *et al.* 2008; Berry *et al.* 2010; Gibson *et al.* 2011; Putz *et al.* 2012; Edwards *et al.* 2014c; Costantini, Edwards & Simons 2016). This contrast seems to be most pronounced in Southeast Asia, echoing theoretical predictions (e.g. Phillips, Newbold and Purvis 2017), nevertheless this general pattern appears to hold true across several regions, as well as many taxa, including birds (Alexio 1999; Dunn 2004; Barlow *et al.* 2006; Berry *et al.* 2010; Edwards *et al.* 2011), dung beetles (Edwards *et al.* 2011, 2014a; Slade, Mann & Lewis 2011), small and large mammals (Fredricksen and Fredricksen 2002; Lambert, Malcom and Zimmerman 2005; Wells *et al.* 2007a; Meijaard & Sheil 2008; Bernard, Fjelds  & Mohamed 2009; Wearn *et al.* 2016), reptiles (Fredricksen and Fredricksen 2002); Lepidoptera (Willott 1999; Willott *et al.* 2000; Hamer *et al.* 2003; Dunn 2004; Dumbrell & Hill 2005, but see Hill *et al.* 1995), dragonflies (Doln y *et al.* 2013; Luke *et al.* 2017) and ants (Dunn 2004; Berry *et al.* 2010; Woodcock *et al.* 2011). Since species richness and functional diversity are closely linked, several studies of taxa with well characterised trait data, such as birds and dung beetles, have also shown that functional diversity remains high in logged forests (Edwards *et al.* 2013, 2014a; c; Chapman *et al.* 2018a).

However, there are some exceptions to this generally positive outlook, such as freshwater fish and amphibians, which seem to be much more vulnerable to logging in both species richness and functional diversity (Ernst, Linsenmair & R del 2006; Wilkinson *et al.* 2018). Even ignoring these taxa which do not fit the wider pattern, the approach of comparing species richness between unlogged and logged forest necessitates a variety of caveats, and the broad consensus that logged forests retain a proportion original diversity probably represents a considerable oversimplification for several reasons.

1.4.2 The importance of logging intensity: not all logged forests are equal

Many studies treat all logged forest as one category, with comparatively few accounting for heterogeneity in logging intensity, either using continuous measures such as above-ground biomass (Burivalova,  ekercio lu & Koh 2014); or comparing among forests subject to different numbers of logging rotations, or of more than one logging age (Edwards *et al.* 2011). Many studies simply do not explicitly define the logging intensity measured (Laufer, Michalski & Peres

2013). This is a major oversight, considering that continuous forest quality variables may be a better predictor of biodiversity responses than the unlogged/logged distinction (Kemper & Bell 1985), and that repeatedly-logged forest is now the dominant type across in many areas (Samsudin *et al.* 2010; Reynolds *et al.* 2011). Furthermore, studies in other forest regions suggest that biodiversity may show complex, non-linear responses to forest age (e.g. Ecke, Löfgren and Sörlin 2002; Moning and Müller 2009; Hu *et al.* 2013). Those studies which have explicitly compared among rotations, or used continuous intensity metrics show more variable results, with some demonstrating high resilience of species richness to intense logging (Edwards *et al.* 2011, 2014a; Woodcock *et al.* 2011), and some showing declines in richness after repeated logging (Slade, Mann & Lewis 2011; Burivalova, Şekercioğlu & Koh 2014; Ross *et al.* 2018). Many taxa appear to show a threshold effect, with species richness declining suddenly above a particular logging intensity (Burivalova, Şekercioğlu & Koh 2014). Conversely, specifically-designed strategies to reduce incidental damage such as Reduced Impact Logging (Putz *et al.* 2008) seem to exert relatively low impacts on biodiversity (e.g. Azevedo-Ramos, de Carvalho and do Amaral 2006; Wunderle, Henriques and Willig 2006, Ribeiro and Freitas 2012). Changes in diversity across a gradient are also likely to be mediated by spatial scale, with landscape scale turnover (beta-diversity) apparently counteracting lower site-level diversity in some taxa (Hill & Hamer 2004; Berry *et al.* 2008; Wearn *et al.* 2016).

1.4.3 Abundance and community composition shifts

Constant species richness over a logging gradient frequently masks pronounced and complex changes to population abundances and community structure, with subsets of the community, or individual species, decreasing or increasing in abundance (e.g. Mason 1996; Eggleton *et al.* 1997; Thiollay 1997; Peters, Malcom and Zimmerman 2006; Akutsu, Khen & Toda 2007; Cleary *et al.* 2007; Edwards *et al.* 2009, 2011; Brodie & Giordano 2012; Luke *et al.* 2017). In some cases, the whole focal group declines or increases in abundance with logging (Wilson & Johns 1982; Ghazoul 2002; Wearn *et al.* 2017). These changes in abundance have multiple conservation implications. In general, smaller and more isolated populations become more vulnerable to stochastic events and other environmental pressures. Further, not all species are of equal “value” or global threat status. Indeed, empirical evidence and model predictions suggest that those species which decline most sharply with logging or are extirpated completely (no study has reported 100% retention of primary forest species) are those with restricted global range, ecological specialisms or high evolutionary distinctiveness, while globally distributed species, invasives and generalists increase (Cleary & Mooers 2006; Meijaard *et al.* 2008; Sodhi *et al.* 2010a, Newbold *et al.* 2013, 2014) Put simply, local species richness retention

may still mask regional biotic homogenisation. Changes in abundance also affect the provision of ecosystem functions (Mason *et al.* 2005; Villéger, Mason & Mouillot 2008), meaning that inferences that logged forests support high functional diversity (Flynn *et al.* 2009; Edwards *et al.* 2013, 2014a) are of limited value without controlling for abundance. Due to threshold effects and the functional uniqueness of some species (Tylianakis *et al.* 2008), declining abundance or minor changes to species richness may abruptly cause collapse of one or more ecological processes, with species reduced to very low abundances becoming functionally extinct.

1.4.4 Short-term studies and the “snapshot” problem

Most studies evaluating the impacts of selective logging on biodiversity are carried out over a restricted time period, often after the disturbance has taken place (McGarigal & Cushman 2002). Few studies have systematically examined the effects of time since logging, and almost none have resampled the same locations over a prolonged time, with space-for-time substitutions used instead. For instance, across 78 studies covered by two recent meta-analyses (Putz *et al.* 2012; Costantini, Edwards & Simons 2016), 22 sampled plots of more than one logging age, and only 13 made direct statistical comparisons of abundance, species richness or community composition among logging ages. Only seven studies resampled locations, none more than twice, and only two studies had samples separated by more than two years (Bischoff *et al.* 2005; Akutsu, Khen & Toda 2007). The remaining 71 studies based their conclusions on a single sample of each location.

This is symptomatic of a much wider trend in ecological research (Lindenmayer *et al.* 2012) and contrasts with the apparent need for 1-2 decades of data to fully reveal complex dynamics (e.g. Jassby and Powell 1990; Magurran *et al.* 2010), and represents an important simplification which may miss both short-term and long-term changes to the “biodiversity value” of logged forest. The physical disturbance of the logging process itself is likely to cause immediate changes to abundance, such as “crowding effects” in neighbouring undisturbed areas (Bierregaard Jr & Lovejoy 1989; Ferraz *et al.* 2003; Grez *et al.* 2004). However, the “snapshot” paradigm also potentially misses more significant, long-term changes in abundance and species richness. In particular, there is mounting evidence that many species may persist for long periods following habitat disturbance, but decline to extinction after a prolonged period in “extinction debt” (Ferraz *et al.* 2003; Kuussaari *et al.* 2009; Wearn, Reuman & Ewers 2012). “Extinction debt” species eventually dwindle to local extinction after months or years, driven by stochastic losses of isolated subpopulations due to disease or natural disaster, or deterministic declines driven by reduced resource availability. These effects may take decades to play out in

long-lived species, as evidenced by declining recruitment and abundance of primates as much as thirty years after logging (Grieser Johns & Grieser Johns 1995; Chapman *et al.* 2000). Delayed loss of functionally important species such as large, seed-dispersing birds (Sekercioglu 2006) may drive even slower knock-on effects on tropical trees by impeding gene flow (Caughlin *et al.* 2014). Even in species which are not under extinction debt, habitat disturbance may drive changes in complex population dynamics, such as predator-prey cycles or bottom-up regulation by resource availability. Long-term changes in density, recruitment, health or demographics in animals following tropical forest degradation represent a major knowledge gap.

1.4.5 The challenge of a mechanistic understanding of logging impacts

Particularly in vertebrates with well-defined trait data, attempts have been made to identify traits which render some species or groups vulnerable to extirpation from logged forests. These studies generally demonstrate that vulnerable species are those with 1.) fluctuating, low-density populations, 2.) Restricted global range, 3.) trophic or habitat specialisms, 4.) high phylogenetic uniqueness, or 5) poor dispersal ability (Tscharnkte *et al.* 2002; Swihart *et al.* 2003; Henle *et al.* 2004; Sodhi *et al.* 2004, 2010a; Meijaard & Sheil 2008; Lees & Peres 2010; Uezu & Metzger 2011, Newbold *et al.* 2014; Phillips, Newbold and Purvis 2017). Some feeding guilds appear to benefit or suffer from logging more strongly than others (Lambert 1992; Eggleton *et al.* 1997; Cleary *et al.* 2007; Newbold *et al.* 2013; Hamer *et al.* 2015).

Relatively little work has been done beyond these correlative analyses to explicitly examine the mechanisms driving extinctions in modified habitat over time. Some support has been found for the hypothesis that species that are vulnerable to habitat disturbance decline deterministically due to resource limitation (Burke & Nol 1998; Zarette, Doyle & Tremont 2000) or stochastically due to natural perturbations wiping out small, isolated populations (Lima, Marquet & Jaksic 1996; Sekercioglu *et al.* 2002). However, we still know very little about the relative importance of these mechanisms for different taxa, or how species traits interact with the biotic and abiotic environment to mediate persistence over a long time period, especially in continuous, degraded habitats such as logged forest. For instance, we have seen that the logged forest environment presents animal species with frequent edges, gaps, open areas and roads. This suggests that dispersal limitation is probably an important driver of species declines, particularly for species which are strongly adapted to understorey conditions (Develey & Stouffer 2001; Laurance, Stouffer & Laurance 2004; Stratford & Robinson 2005; Moore *et al.* 2008), or which require canopy connectivity (Laurance & Laurance 1996, 1999; Laurance, Goosem & Laurance 2009).

Indeed, narrow roads and linear clearings can have strong structuring effects on species in otherwise continuous habitats (Laurance, Goosem & Laurance 2009, Lambert *et al.* 2014).

Similarly, extensive literature from fragmented tropical forest systems, such as the Atlantic Forest of Southern Brazil, suggests that many forest interior species can become isolated by a harsh matrix environment, with a variety of studies reporting species abundance declines particularly in small, isolated fragments (Laurance 1994; Chiarello 1999, 2000; Marsden *et al.* 2001; Ribon *et al.* 2003; Pardini 2004; Pardini *et al.* 2005; Giradudo *et al.* 2008). However, much of the dispersal limitation and fragmentation literature examines forest fragments embedded in a highly dissimilar agricultural matrix such as pastures or plantation monoculture, or even as islands in lake systems (e.g. Moore *et al.* 2008, Gibson *et al.* 2013). It is unclear to what extent this literature is relevant to “continuous” logged forests, as these fragmented systems are likely to present a much more intense barrier to dispersal, and at least some taxa should perceive logged forest as a single, largely connected landscape. The degree to which continuous, but degraded forest represents a fragmented habitat; or the magnitude of dispersal barriers imposed by logging gaps and clearings compared to discrete agricultural matrix habitat, should depend on the traits of the species in question (for instance, canopy-specialist species which cannot disperse readily at ground level seem particularly vulnerable even in an apparently still-contiguous logged forest; Laurance and Laurance 1996, 1999). They should also depend on the spatial scale of the structural changes wrought by logging (such as gaps and canopy damage) compared to an animal’s movements. The relationship between fragmentation *per se* and habitat degradation has hardly been investigated, and it is frequently difficult to separate these effects in fragmentation studies, where forest in smaller fragments is often in poorer, more degraded condition (e.g. Marsden, Whiffin and Galetti 2001), although da Fonseca and Robinson (1990) suggest that differences in the predator landscape due to fragment size can override effects of habitat quality.

Changes in foraging behaviour, breeding biology, dispersal and movement, body condition, survival and other individual-level variables are likely to underpin observed responses of populations and communities to logging, and may give early warning of gradual declines. For example, species in extinction debt may show reduced fecundity or survival over time compared to the same species in unlogged forest. Alternatively, individual plasticity in these parameters may be an important driver of persistence. However, very little work has been done to examine changes in these “vital rates” in logged forest or other human-modified tropical land uses (Cosset, Gilroy & Edwards 2018). Most information is on a handful of well-studied vertebrate taxa such as birds (Cosset, Gilroy & Edwards 2018).

In general therefore, we are some way from a universal, mechanistic understanding of why some species persist in logged forest, why some decline slowly or rapidly to extinction, and why others invade. While we are beginning to move beyond defining logged forest as “good for biodiversity” based on reasonably high species richness, much detail remains elusive. This is partly due to biases and inadequacies of the literature: we know too little about the basic biology of large proportions of tropical forest biodiversity. Filling these knowledge gaps is a challenge, and remains important even for “charismatic” groups, in a well-studied region, such as terrestrial mammals in Southeast Asia, which form the subject of this thesis.

1.5. Mammals in selectively-logged forest

1.5.1 General state of knowledge, and overall trends in species richness and abundance

Terrestrial and arboreal mammals are a functionally important group in tropical forests across the world. Mammals provide a range of ecological functions such as herbivory (Ickes, DeWalt & Appanah 2001; Harrison *et al.* 2013), seed dispersal and seed predation (Forget & Milleron 1991; Corlett 1998; Curran & Webb 2000; Wells & Bagchi 2005; Kitamura *et al.* 2008; Brodie *et al.* 2009; Hautier *et al.* 2010; Nakashima *et al.* 2010; Bagchi *et al.* 2011; Campos-Arceiz *et al.* 2012; Blackham & Corlett 2015), dispersal of plant mycorrhizae (Janos, Sahley & Emmons 1995), and predation (Dunham 2008; Ross *et al.* 2013; Karp & Daily 2014). Their retention in logged forests is therefore likely to help support regeneration and control seedling dynamics, while removal of mammals from tropical forests can cause trophic cascades (Wright *et al.* 2000; Stoner *et al.* 2007; Hautier *et al.* 2010; Caughlin *et al.* 2014). Although tropical forest mammals seem more vulnerable to habitat degradation and loss than several other vertebrate taxa (Sodhi *et al.* 2009; Pekin & Pijanowski 2012), they remain a relatively poorly-known group. Among the global diversity of mammal species, Southeast Asia and Amazonia in particular form major hotspots of IUCN “Data Deficient” species (Schipper *et al.* 2008). Perhaps reflecting the high intensity of logging, much of what we know about the effects of logging *per se* on mammals comes from Southeast Asian studies, and knowledge is often dominated by charismatic groups. For example, two major reviews by Erik Meijaard and coauthors (Meijaard *et al.* 2005; Meijaard & Sheil 2008) over a decade ago evaluated the state of knowledge about Bornean mammals and their responses to selective logging. These authors concluded that although some groups are comparatively well-known, such as primates (Johns 1985, 1986; Johns & Skorupa 1987; Morrogh-Bernard *et al.* 2003), the Sun Bear *Helarctos malayanus* (Wong, Servheen & Ambu 2004; Fredriksson, Wich & Trisno 2006), and to some extent civets, bats and felids, the state of our knowledge on other groups, particularly ungulates and small mammals such as murid

rodents and treeshrews is limited (Meijaard *et al.* 2005). Most studies have come from a few well-studied sites in Borneo, and a wider regional understanding is lacking, as is an understanding of how comparable Southeast Asian responses are to those seen in other ecoregions.

At a guild or whole-community level, responses of species richness and abundance to selective logging are often conflicting, with different studies showing positive or negative trends for the same species or group. Nevertheless, the wider trend of high species richness retention seems to be broadly supported, both in Southeast Asia and more broadly. (Wilson & Johns 1982; Fredricksen and Fredricksen 2002; Meijaard & Sheil 2008; Berry *et al.* 2010; Rickart *et al.* 2011; Samejima *et al.* 2012; Brodie *et al.* 2015; Wearn *et al.* 2016; Magintan *et al.* 2017, but see Wells *et al.* 2007b; Rustam, Yasuda & Tsuyuki 2012; Bernard *et al.* 2016). Further fragmentation of logged forest seems to have generally negative impacts on mammal communities, particularly in small, isolated fragments, again echoing broader trends (e.g. Chiarello 1999; Pardini 2004, Pardini *et al.* 2005). Abundance responses, by contrast, are much more variable, with many species showing contradictory responses between studies. For example, some studies have shown that Southeast Asian felids such as the Sunda Clouded Leopard *Neofelis diardi* generally persist in low numbers in logged forest (Wilting *et al.* 2012; Brodie, Giordano & Ambu 2015), others suggest that *N. diardi* may increase in density with logging (Mohamad *et al.* 2015; Wearn *et al.* 2017). While overall guilds such as browsing herbivores or small mammals may increase in logged forest (Ochoa 2000; Brodie, Giordano & Ambu 2015), this can mask complex species responses, with some species declining and others increasing, and compensatory changes within closely related species pairs. For instance, an increase in abundance of browsing herbivores after logging in Borneo probably comprises increases in Sambar Deer *Cervus unicolor*, declines in two *Tragul* mouse-deer species, and stable abundance of two *Muntiacus* muntjac species (but increased abundance of *M. muntjak* countered by declines in *M. atherodes* (Heydon 1994)). Similarly, overall increases in small mammal abundance in Venezuelan logged forest reported by Ochoa (2000) masked a homogenisation of the terrestrial small mammal community, and complex changes in feeding guilds of bats.

1.5.2 Caveats and more recent community-scale work

These uncertainties doubtless partly reflect genuine regional and local differences in responses. However, many of the knowledge gaps which we explored above, applying more generally to the literature on selective logging and biodiversity, also apply strongly to mammal studies, making comparison of trends between studies difficult. Many species are known only from one or two case studies, which are frequently old, and often do not account for heterogeneity in logging

intensity or consider heavily-logged forest (Meijaard & Sheil 2008). Poor comparability between study sites and methods, plus the lack of longitudinal studies further contribute to our fragmentary understanding. More recent community-wide studies from Sabah, Malaysian Borneo, have to some extent helped to fill these knowledge gaps for species diversity and community abundance (Brodie *et al.* 2015; Brodie, Giordano & Ambu 2015; Wearn *et al.* 2016, 2017).

The latter two studies were among the first to simultaneously sample the entire terrestrial mammal community across a logging and deforestation gradient using a unified sampling approach, controlling rigorously for detectability and other sampling biases.

These authors demonstrated that species richness and abundance patterns across the mammal community are strongly dependent on spatial scale, with landscape-scale species retention masking strong beta-diversity signals at smaller scales (Wearn *et al.* 2016), and most estimates of abundance change between primary and logged forests subject to large variability (Wearn *et al.* 2017). These results therefore underline the problems of comparability among many previous studies.

Overall, much of the mammal community proved resilient to logging, with abundances of most species increasing or remaining stable in logged forest (Wearn *et al.* 2017). However, there are still a wide variety of responses, especially when logging intensity is taken explicitly into account using a continuous scale. Many species which remained stable or increased in abundance when comparing categorical “primary” to “logged” forest (such as Sambar Deer or Bornean Orangutan *Pongo pygmaeus*) actually displayed complex non-linear relationships with aboveground biomass or landscape tree cover, showing a unimodal abundance peak at moderate disturbance levels, or other non-linear relationships (Wearn *et al.* 2017). These patterns reflect more detailed case-studies from some well-studied “flagship” species: several authors have shown that Orangutans persist well in logged forest, but either that abundance is lower in heavily-degraded forest, or that Orangutans avoid very recently-logged forest if adjacent “refuge” areas are available (Felton *et al.* 2003; Morrogh-Bernard *et al.* 2003; Ancrenaz *et al.* 2004, 2010; Johnson *et al.* 2005). Apart from this latter observation, and some evidence that abundance and recruitment of some primate species remains depressed over a decade after logging (Johns 1992; Grieser Johns & Grieser Johns 1995), we have little concept of how abundance or species richness change through time in logged forests, largely due to the dearth of long-term studies.

1.5.3 The importance of hunting, and its interactions with logging

Detecting abundance changes of mammals in selectively-logged forests is complicated by the fact that logging opens previously inaccessible forests up to humans, and increases the transient or permanent population adjacent to forests by the creation of logging camps and plantation workers' villages. This increased accessibility and demand increase the rate of hunting, often dramatically (Corlett 2007; Brodie *et al.* 2015; Harrison *et al.* 2016). While hunting has occurred for thousands of years in many tropical forests, the rapidly expanding regional and global bushmeat trade, plus the expanding market for traditional medicinal products have served to increase both the variety of species taken and the intensity of harvest (Corlett 2007; Challender & MacMillan 2014; Harrison *et al.* 2016). Technological enhancements, such as guns replacing spears, have also contributed to the increase in efficacy and intensity (Corlett 2007). It is therefore now probable that hunting is the preeminent threat to most larger mammals in many tropical forest regions, with a greater impact than logging for the 91% of species examined by Brodie *et al.* (2015), including iconic species such as the Orangutan (Marshall *et al.* 2006), and extending to near-complete loss of the whole large mammal community in fragmented systems such as the Brazilian Atlantic forest (Galetti *et al.* 2017). Nevertheless, susceptibility varies, and no-take zones or low extraction rates in indigenous reserves seem to limit the impacts for some species (Reyna-Hurtado and Tanner 2007; Mayor *et al.* 2015). Disentangling the effects of hunting from direct logging impacts at the level of a study site or a landscape is extremely difficult, as particularly in large, remote logging concessions with multiple entry points, hunters are near-impossible to monitor accurately over a wide area, or through time. This remains a knowledge gap which will remain difficult to fill, unless areas of logged forest can be studied in the complete absence of hunters.

1.5.4 Traits and processes underlying persistence – specialists versus generalists

Despite some recent progress in understanding mammalian community composition and abundance shifts in logged forest, we still have a taxonomically uneven and relatively simplistic understanding of the traits and processes underlying the observed patterns. Indeed, for most mammal species our ability to predict persistence or decline in logged forests is limited. Echoing the general patterns which we explored above (Section 1.4.5), there is some broad evidence to suggest that phylogenetically unique, range-restricted mammals are the most vulnerable to logging (Meijaard & Sheil 2008; Meijaard *et al.* 2008, although this has been challenged at a global level, see Verde Arregoitia, Blomberg and Fisher 2013). Again, this is probably due to ecological specialisation, both in terms of diet and foraging niche (Meijaard *et al.* 2008; Edwards *et al.* 2014d). Relatively generalist species, and particularly omnivores and herbivores, seem to

persist well in logged forest, suggesting that dietary plasticity is an important trait determining resilience (e.g. Ochoa 2000).

Much of our early information about the importance of dietary plasticity in logging responses comes from a handful of detailed field studies. For instance, folivorous primates persist well in logged forest, although they modify activity patterns to account for a lower availability of food of higher nutritional value (Johns 1986). Similarly, the persistence of larger ungulates and the decline of the two *Tragulus* mouse-deer appears to be largely due to the dependence of the latter on comparatively large, easily-digestible fruits such as *Ficus* figs, while the former thrive on abundant pioneer vegetation (Heydon 1994; Heydon & Bulloh 1997). Similarly, frugivorous masked titi monkeys in the Atlantic Forest partition their use of logged and unlogged forest based on food availability rather than habitat amount and disproportionately forage in remnant unlogged forest, again suggesting that dietary inflexibility confers vulnerability (Heiduck 2002). Conversely, more frugivorous civets seem less vulnerable than those which eat a more omnivorous diet with greater proportions of invertebrates (Heydon & Bulloh 1996). Isotopic analysis of small mammal diets, and bait removal experiments suggest, respectively, that many small mammals eat a greater proportion of invertebrates in logged forest (Nakagawa, Hyodo & Nakashizuka 2007), and are more important in functions such as insectivory previously dominated by other invertebrates (Ewers *et al.* 2015).

However, there is much we still do not know about diets of many tropical forest mammals, or indeed the spatiotemporal availability of different food types, before and after logging. For instance, the dipterocarp forests of Southeast Asia flower and fruit simultaneously on a sporadic basis, driven by the El Niño Southern Oscillation (Appanah 1985; Ghazoul 2016). This mast fruiting is a major dynamic process in unlogged forests, and is probably an evolutionary strategy that occurs to satiate seed predators (Curran & Leighton 2000; Wells & Bagchi 2005). Mast fruiting has pronounced effects on population dynamics and movements of mammalian seed predators, for instance causing population spikes or cycles in some small mammals (Nakagawa *et al.* 2007a; b), plus effects on body condition and mortality in Sun Bears and Bearded Pigs *Sus barbatus* (Wong *et al.* 2005). However, we know almost nothing about whether these effects continue after logging, as there have been no long-term population studies of these species in logged forest, and we only have the indirect evidence that dipterocarp mast fruiting and vertebrate seed predation still both occur in logged forest (Curran & Webb 2000; Bagchi *et al.* 2011), and some evidence from boreal systems to suggest that cycling dynamics in small mammal appear to be affected by habitat change (e.g. Hansson 1999; Ecke, Löfgren and Sörlin 2002). Despite some detailed work (Emmons 1991, 2000; Wells *et al.*

2009), our knowledge of the precise diets of many tropical forest mammals, and Southeast Asian species in particular, frequently relies on old studies (e.g. Harrison 1962) or field guides, which often print only broad feeding guild classifications, or rely largely on anecdotal knowledge (e.g. Payne & Francis 1985; Phillipps & Phillipps 2016).

1.5.5 Potential mammal responses to structural and microclimatic change

As we have seen, logging alters the availability of microhabitats and modifies microclimate. If this exerts physiological stress, modifies movement efficiency, or either enhances or reduces predator avoidance, then logging could affect species abundance separately from changes in food availability. Perhaps unsurprisingly, few detailed, labour-intensive studies have been conducted on physiology, habitat selection and ranging behaviour, which might inform how mammals response to these changes. Although precise requirements vary interspecifically and seasonally (Wells *et al.* 2004, 2006; Püttker *et al.* 2008; Naxara, Pinotti and Pardini 2009; Cusack *et al.* 2015), tropical forest small mammals largely favour dense, covered microhabitats, including the abundant logs, dead wood, vines and brush piles which characterise logged forest (Kemper & Bell 1985; Emmons 2000; Lambert and Adler 2000; Bernard 2004; Lambert, Malcolm & Zimmerman 2006; Yamada *et al.* 2016). These habitats probably enhance predator avoidance (Bernard 2004) and may also represent particularly rich food sources (Lambert, Malcolm & Zimmerman 2006). This may explain the relatively consistent increases in abundance across this group (Wearn *et al.* 2017). Altered forest structure also seems to benefit invasive rats, particularly Black Rat *Rattus rattus*, which successfully invades heavily-logged forest (Cusack *et al.* 2015), apparently because it exploits a vacant foraging niche in the dense suspended leaf litter (Loveridge *et al.* 2016). Conversely, small mammals appear to strongly avoid roads and other open gaps created by logging (Wilson, Marsh & Winter 2007; Fuentes-Montemayor *et al.* 2009; Shadbolt & Ragai 2010; Carthew, Jones & Lawes 2013).

However it is unclear if, or how, greater microhabitat availability translates into increased population density of small mammals, or to what extent gaps, roads and edges fragment populations. For instance, we do not know whether small mammals which survive in logged forests defend smaller territories, partition vertical foraging space more finely, or alter inter- or intra-specific territory overlap. Metapopulation theory, and empirical studies from fragmented systems and other taxa suggest that dispersal limitation in logged forest can structure populations spatially (e.g. Matthysen 1999; Andreassen, Hertzberg and Ims 2000; Develey and Stouffer 2001; Fuentes-Montemayor *et al.* 2009, but see Keuroghlian, Eaton and Longland 2004). This suggests that gap-avoiding species are likely to experience some population fragmentation in “continuous” logged forest, but again this has not been explicitly examined.

While many variables describing small mammal movement appear to change in logged forest, results have been inconsistent between studies (e.g. Wells *et al.* 2006, 2008), and there seems to be no pronounced increase in indicators of more intense foraging in a smaller area, such as shorter movement distances, or greater path tortuosity (Wells *et al.* 2006). We also know little about how the tropical forest small mammal community reacts mechanistically towards novel anthropogenic habitats such as intensive oil palm agriculture, which increasingly adjoins remaining forest areas. Plantations hold highly depauperate mammal communities (Bernard, Fjeldså & Mohamed 2009; Yue *et al.* 2015; Wearn *et al.* 2016, 2017), but they are rich in nutritious fruit, a potential food source for both small and larger mammals in nearby forest. Indeed, large mammals appear to “spill over” this edge to some degree, and oil palm does not appear to exert strong edge effects in nearby forests (Yue *et al.* 2015), suggesting that gap aversion might be outweighed for some species by the attractant effect of this food source. However we do not know whether observations of large mammals across a forest-oil palm edge gradient are mirrored by small mammals, and no mammal studies have investigated potential “spillover” or edge effects on the scale of individual movements.

Altered forest structure is likely to affect larger mammals such as ungulate herbivores in different ways, as operating at a larger spatial scale and featuring relatively small surface area-volume ratios, they are both more likely to experience altered microclimatic conditions in gaps, and are more likely to be physiologically affected by them (Porter and Kearney 2009, Gardner *et al.* 2011). Unungulates in particular are also exposed to intense hunting pressure, which often targets large mammals for local food consumption and regional markets (Corlett 2007; Remis and Robinson 2012; Brodie *et al.* 2015, Harrison *et al.* 2016), and can cause pervasive reductions in abundance and community simplification (Harrison *et al.* 2016; Galetti *et al.* 2017). Logging also exposes larger mammals to other nonlethal human disturbances stemming from increased human presence in logged forest. Many ungulates in other ecosystems perceive even nonlethal human disturbance similarly to heightened predation risk (Frid and Dill 2002), and a large body of research suggests that this manifests in responses such as increased vigilance, flight behaviour and altered group dynamics (e.g. Fortin and Andruskiw 2003; Manor and Saltz 2003; Stankowich 2008; Brown *et al.* 2012). Hunting, habitat degradation and fragmentation have also been shown to affect stress levels in primates (Rimbach *et al.* 2013). Together, this evidence, plus the pervasive nature of edge effects where forest borders some agricultural and urban areas (Brodie, Giordano & Ambu 2015) suggests that conditions in logged forests could impose a limiting factor on activity and behaviour of large herbivores via increased mortality from hunting, physiological stress, or tradeoffs between avoidance behaviour and foraging. However, this has not been adequately investigated in logged tropical

forests. A possible mechanism to mitigate these stressors is shifting activity patterns towards increasing nocturnality, a trend which has been observed across multiple taxa, regions and ecosystems (Gaynor *et al.* 2018). However, although degree of nocturnality has been estimated for some Southeast Asian mammals (Van Schaik & Griffiths 1996; Mohd-Azlan & Sharma 2006), no study has investigated whether activity patterns shift plastically in logged forests.

1.5.6 Summary, and the need for more individual-scale data

To summarise, we have only a fragmentary understanding of the impacts of structural and microclimatic change on tropical forest mammals, or of exactly what most species eat and how the distribution and abundance of these food resources changes after logging. Changes in these factors are likely to drive the pronounced changes to abundance and community structure seen after logging, but it is unsurprising that the relative importance of these processes is unknown. Beyond observing declines or increases in abundance, we also do not understand how logging affects animals individually, in terms of behaviour, health, or demography. This detailed information may help reveal increased competition for food resources, physiological stress, or altered predation pressure, but should definitely also shed light on the proximate causes of declines and provide early warning of extinction debt or vulnerability to future environmental change. Some evidence from primates exists: in Africa Olupot (2000) found that male grey-cheeked mangabeys *Lophocebus albigena* in logged forest were consistently lighter than analogous males in unlogged forest; while a study in Borneo found that female gibbons *Hylobates lar* and leaf monkeys *Presbytis* sp. produced fewer young in logged forest twelve years after logging (Johns 1992; Grieser Johns & Grieser Johns 1995). There is also a small body of studies examining prevalence and diversity of gastrointestinal parasites of mammals in logged and unlogged forest. Some authors have shown an increase in parasite burden with logging (Gillespie, Chapman & Greiner 2005; Helenbrook *et al.* 2017), and this appears to correlate negatively with persistence among three New World primates (Gillespie, Chapman & Greiner 2005). However at a community level in small mammals, Wells *et al.* (2007b) found complex changes, with parasite burdens increasing with logging in some species and decreasing in others, supporting evidence from fragmented systems (e.g. Puttker, Meyer-Lucht and Sommer 2008; Bordes *et al.* 2015) that effects on host-parasite interactions can play out at a complex multispecies network scale. Beyond these few studies, this information is largely lacking for most other mammal species in logged forest, either in Southeast Asia or elsewhere (Cosset, Gilroy & Edwards 2018).

1.6. Background and aims of this thesis

In this review, we have seen that although some aspects of the selective logging process are well-studied, our understanding of its effects on mammals and many other taxa are hampered by a variety of shortcomings in the existing literature. Some of these problems are difficult or impossible to control for (such as the coexistence of hunting and logging), or cannot be adequately addressed with currently available methodology (such as range overlap and territoriality of individual small mammals). However, many of the problems and inconsistencies of most published studies could be addressed by long-term projects with standardised resampling in the same locations through time, coupled with more detailed experimental work to try and unpick the individual-level processes underlying observed patterns of change in species richness and abundance.

Ideally, locations used for sampling would be controlled as much as possible for topographic, geological, edaphic and hydrological variation, and cover the full spectrum of logging intensity measured at a fine spatial scale using multiple, continuous metrics. Multiple mammal sampling methods would be used in the same locations to capture the response of the entire community, and as much demographic and population health data as possible would be collected both across the logging gradient and through time.

The Stability of Altered Forest Ecosystems project (SAFE), in Sabah, Malaysian Borneo was set up to fulfil some of these requirements, covering over 7000 ha of heavily-logged lowland dipterocarp forest. (Ewers *et al.* 2011). The majority of the SAFE Project area is eventually intended to become a fragmentation experiment, with experimental forest fragments of varying size embedded within a matrix of oil palm plantation. However, from the beginning of sampling in early 2011 up to and including 2018 the clearance of “matrix” areas had not occurred, giving potentially up to eight years of baseline data in the heavily-logged continuous forest. Mammal sampling at SAFE was begun by O.R. Wearn in 2011, and has contributed to several papers (Wearn *et al.* 2013, 2016, 2017, 2018 in press; Cusack *et al.* 2015; Loveridge *et al.* 2016). In order to complement and expand this body of work, we continued the standardised small mammal and camera trap sampling protocols across three further years, plus adapting the methods as necessary to answer a more applied question, exploring four distinct knowledge gaps in the following chapters.

In **Chapter Two**, we investigated whether the increased abundance of most terrestrial small mammals in selectively-logged forest is stable through time. Some studies have shown that on an interannual scale, abundance of multiple small mammal species fluctuates strongly in unlogged forest. This is due to a combination of the dominance of the Dipterocarpaceae in the

canopy of Southeast Asian rainforests, and the underlying bottom-up dynamics imposed by the El Niño Southern Oscillation (ENSO). ENSO causes sporadic, but pronounced droughts separated by several years, which induce mass flowering and fruiting of the entire dipterocarp tree community, and large population spikes in the small mammal community, particularly the terrestrial *Maxomys* rats, which are major seed predators. However *Maxomys* species largely survive logging and increase in abundance, despite the wholesale removal of mature dipterocarps. This suggests that this dynamic variability in community abundance is likely to weaken or disappear over time, however this has barely been investigated. Since nearly all studies of mammalian responses to logging are single-survey “snapshots”, we also do not know whether any members of the small mammal community decline gradually to extinction, so the assumption that logged forest remains a haven for small mammal communities through time is untested. We used a long-term mark-recapture dataset, with annual resampling spanning six years, to calculate population density estimates and compare landscape-scale means between years to examine these questions. We also tested whether any observed changes in population density are correlated with seed rain at a landscape scale.

In **Chapter Three**, we further explored small mammal persistence in selectively-logged forest, and addressed the absence of data on individual level changes in body condition, and demographic “vital rates”. Again, previous studies have observed that most small mammals not only persist after logging, but on average, species across the community increase in abundance by almost 200%. Only a few species decline strongly or are extirpated by logging. However it is unknown to what degree species increasing in density across the gradient pay a cost in terms of reduced body condition, interannual survival or reproductive output. If these parameters do decline in logged forest, they might provide early warning of reduced resilience to further environmental change. Conversely, these parameters might instead reveal proximate mechanisms driving declines of logging-intolerant species. We estimated body condition, reproductive output and survival of thirteen small mammal species from simple biometric and demographic data. We then modelled these parameters against a continuous measure of forest quality (aboveground biomass), controlling for temporal variability, to try and unpick complex changes with different logging intensities.

In **Chapter Four**, we turned to the larger herbivore community in selectively-logged forests. In Southeast Asia this guild, which includes browsing and digging ungulates (elephants, deer and pigs), small frugivorous ungulates (*Tragulus* mouse-deer) and large granivores (porcupines), are among the least-studied but most functionally important of all mammalian groups. These species appear to have mixed fortunes with logging: some species greatly increase in abundance, others remain stable while others decline. This includes contrasting responses

within closely related species pairs such as the muntjacs, porcupines and mousedeer. Compared to small mammals, large herbivores are more active in the daytime in unlogged forests, probably rendering them more prone to abiotic stress, as well as being strongly targeted by human hunters. This, combined with other largely diurnal anthropogenic disturbances, implies that logging exerts a strong pressure to shift activity patterns towards increasing nocturnality – a globally ubiquitous response to human disturbance. However, activity patterns of Bornean mammals have not been investigated in relation to logging. We used seven years of camera trap data to test the hypothesis that activity patterns of large herbivores in logged forest shift towards increased nocturnality between unlogged and logged forest. We also tested whether the percentage of overlap between a species' daily activity density kernels in logged and unlogged forest is related to its likelihood of decline after logging, hypothesising that shifts in activity pattern are adaptive, and therefore that species with a larger overlap (i.e. smaller shift) were more likely to decline after logging. Lastly, we tested for a trade-off between behavioural plasticity and foraging efficiency, by examining whether species with pronounced shifts towards nocturnality increased their overall activity level.

In **Chapter Five** we changed focus and tackled a more applied problem, one of major relevance as remaining selectively-logged forests increasingly exist within a plantation agricultural landscape, often directly abutting highly lucrative crop species such as oil palm trees. Plantation managers may gain many ecosystem services from adjacent forest, and dispersal of organisms providing pollination, pest control and other services have been comparatively well investigated. However, forest animals may also act as crop pests if they are able to cross the forest edge into the plantation – oil palm fruit in particular are more nutritious than nearly any wild food source, easy to reach for most animals and produced in very high densities. Forest animals may therefore increase crop damage near the plantation – forest edge, producing an additive effect to that caused by plantation-dwelling pests. Such ecosystem “disservices” pose a potential problem for conservation, even if landowners overestimate the actual threat to yields, because economic arguments for preserving large tracts of logged forest within or adjoining plantations are weakened.

However, little or no work has been done evaluating the degree to which native mammals cross forest edges into oil palm plantations. We used a dual approach to answer this question, focussing on small mammals, which exist both as invasive pest species throughout plantation and as a native community within logged forest. We used a trapping grid straddling forest edges and penetrating up to 140m into the plantation to examine the spatial distribution of native and invasive small mammal species either side of the edge. We modelled changes in abundance over the edge relative to a plantation interior control site to determine the spatial width of any

spillover effect. Secondly, we trapped native forest small mammals near the edge, and used a spool-and-line device to track individuals in their foraging movements near the edge, to observe whether any crossed the edge. We used a null-modelling approach to compare the proportion of observed edge crossers with a distribution of simulated, randomly constructed paths, hypothesising that small mammals would be more likely than expected by chance to cross the edge and feed in plantations.

Chapter Two: Inter-annual dynamics and persistence of small mammal communities in selectively logged tropical forest

2.1 Abstract

Understanding temporal change and long-term persistence of species and communities is vital if we are to accurately assess the relative values of human-modified habitats for biodiversity. Despite a large literature and emerging consensus demonstrating a high conservation value of selectively logged tropical rainforests, few studies have taken a long-term perspective. We resampled small mammals ($\leq 1\text{kg}$) in a heavily logged landscape in Sabah, Borneo between 2011 and 2016 to investigate temporal patterns of species-level changes in population density. We found that small mammal population density in heavily logged forest was highly variable among years, consistent with patterns previously observed in unlogged forest, and uncovered evidence suggesting that one species is potentially declining towards local extinction. Across nine species, population densities varied almost sevenfold during our six-year study period, highlighting the extremely dynamic nature of small mammal communities in this ecosystem. Strictly terrestrial murid species tended to exhibit strong temporal dynamics, whereas semi-arboreal foraging species such as treeshrews had more stable dynamics. We found no relationships between population density and fruit/seed mass, and therefore no evidence that our patterns represent responses to inter-annual mast fruiting of the dominant canopy dipterocarp trees. This may be due to the removal of most of the canopy during logging, and hence the dipterocarp seed resource, although it possibly also reflects spatiotemporal limitations of our data. Our results underline the importance of understanding long-term variability in animal communities before developing conservation and management recommendations for human-altered ecosystems.

2.2 Introduction

Degradation and loss of tropical forests is a global issue for biodiversity conservation. Across a large body of literature covering the comparative effects of these processes on biodiversity, there is now a broad consensus that although primary forests remain pre-eminently important (Gibson *et al.* 2011), selectively-logged and regenerating forests retain relatively high species richness (Berry *et al.* 2010; Edwards *et al.* 2014 c,d; Bernard *et al.* 2016; Costantini, Edwards & Simons 2016; Wearn *et al.* 2016). Conversely, forest clearance for intensive agriculture

generally causes large biodiversity losses, particularly accompanying pronounced structural habitat simplification, such as in the rapidly-expanding oil palm plantation landscape in Southeast Asia (Fitzherbert *et al.* 2008; Sodhi *et al.* 2010b; Gibson *et al.* 2011; Warren-Thomas, Dolman & Edwards 2015; Wearn *et al.* 2016). Nevertheless conserving all remaining areas of logged forest is probably not a practical conservation goal in the face of global agricultural expansion, and tracts will instead need to be prioritised. This should be based not only on rigorous, quantitative assessments of which taxa are most biologically irreplaceable and vulnerable to habitat modification; but also how effectively they persist in logged areas over long timescales, and how best to maintain the ecological interactions among them.

Despite this clear practical need, and the large literature on the biodiversity value of selectively logged tropical forests, there is a pronounced lack of studies examining long-term responses of ecosystems under anthropogenic change (Lindenmayer *et al.* 2012). This represents a potentially serious knowledge gap, as parameters such as abundance, species richness and community composition are unlikely to remain constant over time in forests for two reasons. Firstly, climate and rainfall in tropical forests can vary inter-annually via global-scale processes such as the El Niño Southern Oscillation (ENSO). Particularly in Southeast Asia, ENSO drives inter-annual biotic processes such as mast fruiting of trees, causing fluctuations in abundance of granivorous insects (Nakagawa *et al.* 2003) and small mammals (Curran & Leighton 2000; Emmons 2000; Nakagawa *et al.* 2007a; b; Wells *et al.* 2007a). There is some evidence that this underlying variability remains important after logging, albeit with altered intensity (Appanah 1985; Curran & Webb 2000; Bagchi *et al.* 2011).

Secondly, the plant community responds to logging over short timeframes, driven by physiological responses such as leaf flush and increased fruit production (Johns 1988); and over longer timeframes, driven by successional community turnover. For example, invasion of pioneer species increases canopy cover and structural complexity, and biotic and abiotic conditions gradually revert towards primary forest, although it is uncertain whether they ever converge fully (Curran *et al.* 1999; Brearley *et al.* 2004; Liebsch, Marques & Goldenberg 2008). Temporally changing abiotic and biotic conditions are likely to modify both trophic and non-trophic interactions over time; for example by altering the competitive landscape via availability of food and foraging niches, disrupting or rebuilding mutualisms, or mediating the spread of pathogens. Conversely, repeated logging rotations may arrest or reverse this trajectory.

Species which cannot survive the effects of logging will eventually decline to local extinction, but long-lived, slow-breeding species may decline gradually over many generations, representing an extinction debt (Ferraz *et al.* 2003; Kuussaari *et al.* 2009; Wearn, Reuman & Ewers 2012).

Background resource availability fluctuations or successional changes to vegetation may hasten, delay or reverse such declines, while causing opposing changes to highly disturbance-tolerant species. The net effect of these interacting factors may therefore be complex temporal changes to community abundance. Complex, anthropogenic changes seem to be occurring in other systems with strongly dynamic small mammal populations, such as boreal forest, where altered amplitude of rodent population cycling and increasingly chaotic dynamics appear to be due to changes in logging practices and climate change (Hansson 1999; Ecke, Löfgren and Sörlin 2002). However, short-term “snapshot” biodiversity assessments in logged tropical forests, such as the majority of those we examined in Chapter One (Section 1.4.4), generally cover at most one or two generations of the taxon in question. While such studies may be the only biodiversity assessments practicable in a threatened area and frequently offer a valuable insight into broad trends in richness and abundance, they are unlikely to capture the complexity of these temporal trends. By oversimplifying temporally variable populations, a purely “snapshot” literature may generate erroneous management recommendations, under-allocate resources to species in extinction debt, or skew long-term estimates of ecosystem processes such as seed dispersal or herbivory.

To avoid these outcomes, and capture the long-term biodiversity value of logged forest, short-term species- and community-level studies should be complemented with long-term studies, ideally measuring changes in both diversity and abundance through time. Temporal studies should ideally start before logging but at least covering multiple generations of the focal taxon, with regular, standardised monitoring techniques (Lindenmayer *et al.* 2012). Such studies are understandably rare, as the necessary sampling effort is logistically and financially challenging, however they provide insights which would otherwise be missed (Lindenmayer *et al.* 2012).

One of the most functionally important animal groups in tropical forests are small mammals, which are major seed predators (Asquith, Wright & Clauss. 1997; Curran & Webb 2000; Wells & Bagchi 2005). Despite a sizeable literature examining communities in fragmented systems (Lynam & Billick 1999; Pardini *et al.* 2005; Püttker *et al.* 2008; Vieira *et al.* 2009; Gibson *et al.* 2013), small mammals remain understudied in continuous logged forest, particularly in Southeast Asia (Meijaard & Sheil 2008). We found only two studies examining temporal patterns of abundance or species richness in continuous logged forest (Isabirye-Basuta & Kasenene 1987; Wells *et al.* 2007a). Both studies chiefly considered intra-annual reproductive trends, and did not explicitly examine patterns over longer timeframes. Isabirye-Basuta and Kasenene (1987) demonstrated intra-annual species abundance fluctuations over a four-year period in Uganda, with increasing amplitude and reduced population stability in logged *versus* unlogged forest. Conversely, Wells *et al.* (2007) found little difference in abundance fluctuations, community evenness and dominance between Bornean logged and unlogged forest. Although

both studies provide some evidence that complex temporal patterns seen in unlogged forest are retained with varying magnitude in logged forest, they are methodologically limited by small sample size and short duration respectively, and neither models abundance accounting for detection probability, a common limitation of ecological studies (Kellner & Swihart 2014). To our knowledge no study has explicitly examined population dynamics of small mammals between years in logged forest; or considered either extinction debt, or interannual fluctuations.

Here we examined population dynamics of a small mammal community over a six-year period in a continuous, heavily logged forest landscape typical of the large areas in Southeast Asia threatened by conversion to plantation agriculture. Uniquely, we resampled our communities annually, in identical locations controlling for aspect, topography and altitude. We controlled for imperfect detection using mark-recapture modelling, and tested for inter-annually variable density and long-term declines. We also tested for a likely causal factor by examining the relationship between small mammal population density and the density of seed and fruit rain. We reveal temporal patterns of community variability and persistence, and discuss the implications for landscape-scale conservation of mammal communities.

2.3 Methods

2.3.1 Study area

We collected field data at the Stability of Altered Forest Ecosystems (SAFE) project in Sabah, Malaysian Borneo (Ewers *et al.* 2011), a landscape-scale experiment situated within a 1-million ha multi-use forest concession owned by Yayasan Sabah (Sabah Foundation). The SAFE site, and the Yayasan Sabah concession in general, consists of selectively-logged lowland dipterocarp forest. Most of the area has been subject to at least two rounds of selective logging between the 1980s and the 2000s, a landscape history typical of Sabah and the wider Southeast Asian region (Grieser Johns 1997; Putz *et al.* 2012). Most large, commercially valuable timber trees were felled and removed, with an estimated cumulative 302.8 t.ha⁻¹ of aboveground tree biomass removed (Pfeifer *et al.* 2016), leaving continuous, spatially heterogeneous forest which is among the most heavily logged forest in the tropics (Burivalova, Şekercioğlu & Koh 2014). Our sites were not logged during the period of this study from 2011-2016, however some piecemeal salvage logging occurred within the wider landscape during this timeframe. Detailed locations, timings and extraction densities were not available, however no logging occurred within 100 m of our sites.

2.3.2 Live-trapping grids

We using a standardised sampling grid (Fig. 1; Wearn *et al.* 2017) to sample small mammals annually from May 2011 to July 2016, with a gap in 2013 during which no sampling was conducted for logistical reasons. These grids comprised a 4 x 12 array of sampling points with 23 m separation, and were originally designed for spatially concurrent sampling of the whole mammal community using live trapping and camera trapping (see Wearn *et al.* 2013, 2016, 2017). Grid dimensions and point spacing therefore represented a compromise between these two sampling methods (i.e. between density of coverage and covered area, respectively). Grid locations were designed to overlap with the sampling structure of the SAFE project, which is controlled as much as possible for altitude, drainage and aspect (for more details, see Ewers *et al.* (2011); Wearn *et al.* 2013). We maintained a permanent trapping effort of eight grids, which were each resampled once per year; plus eight additional grids which were trapped once, four each in 2011 and 2012 (for a map of our sampling sites, see Wearn *et al.* (2017). We trapped all grids between December-July, although matching exact dates and trapping order between years was not practical.

We placed two “Tomahawk”-style steel cage traps within a 5 m radius of each point, for a total of 96 traps covering approximately 2.1 ha, (Fig. 1; Cusack *et al.* 2015; Wearn *et al.* 2016, 2017). We sited the two traps at each sampling point on approximately 180-degree opposed bearings, but preferentially chose microhabitat features providing cover for small mammals (e.g. dense ground vegetation, fallen wood, roots, or rocks). We placed all traps at ground level, or on fallen logs ≤ 0.5 m above ground. We took care to sample at precisely the same locations during each year of the study, although there was occasional positional error, either where we resited traps due to tree falls, landslips or ant nests; or where positions were shifted accidentally due to steep topography or by large mammals. We considered these errors negligible for the purposes of this study.

2.3.3 Trapping and processing protocol

One sampling session for each grid consisted of seven consecutive trap nights annually. Each trap was covered with a black polythene wrapping to provide waterproofing and shade for captured animals, baited with one ripe oil palm fruit and left for approximately 20-24 hours before checking. We checked all traps daily in the early morning, and processed and individually marked all new small mammal captures before releasing them at the original capture location within one hour. Following the ethical trapping and handling guidelines issued by the American Society of Mammalogists (Sikes, Gannon & American Society of Mammalogists 2011), we

released highly stressed or sick animals immediately without processing, or humanely euthanised (<1% of captures) where animals were severely sick or injured. Prior to each season, our fieldwork was subject to a thorough ethical review process (via the Institute of Zoology, Zoological Society of London).

We identified individuals to species, and where possible aged and sexed all individuals using published information (Payne & Francis 1985), supporting this with biometric measurements (hind foot length, ear length, ano-genital distance, weight, head-body length, tail length) where necessary. We marked new individuals with Passive Inductive Transponder (PIT) tags (Francis Scientific Instruments, Cambridge, UK), which allowed us to uniquely identify recaptured individuals at their capture location.

2.3.4 Detectability controlled population density estimation

The value of controlling for detectability in ecological surveys is a question under debate (Banks-Leite *et al.* 2014; Guillera-Aroita *et al.* 2014), with a large majority of studies not doing so (Kellner & Swihart 2014). Accounting for correlates of detection probability by good survey design may reduce the need for detectability-controlled measures of abundance, occupancy or species richness, which are frequently data-hungry and therefore restrict authors' abilities to study rare species (Banks-Leite *et al.* 2014). In the context of our study, however, accounting for imperfect detection is advisable. Most small mammals in tropical forests are thought to be largely dietary generalists, and many are plastic in their choice of foraging strata (Payne & Francis 1985; Emmons 2000; Nakagawa *et al.* 2007b). Therefore the relative availability of seed and fruit on the forest floor compared to foods available in other strata – variability that may be particularly acute due to mast seeding – may affect foraging patterns and responses to bait (thus detection probability) independently of changes in density.

We calculated population density using spatially explicit capture-recapture modelling (hereafter SECR) using package *secr* (Borchers & Efford 2008; Efford, Borchers & Byrom 2008; Efford 2013) in R v.3.5.0 (R Core Team 2018). First, we trimmed the capture data for each grid to only include animals which were tagged and positively identified. We then converted the trap location information (polar bearing and distance from the nearest of the 48 grid points) to an X-Y coordinate system.

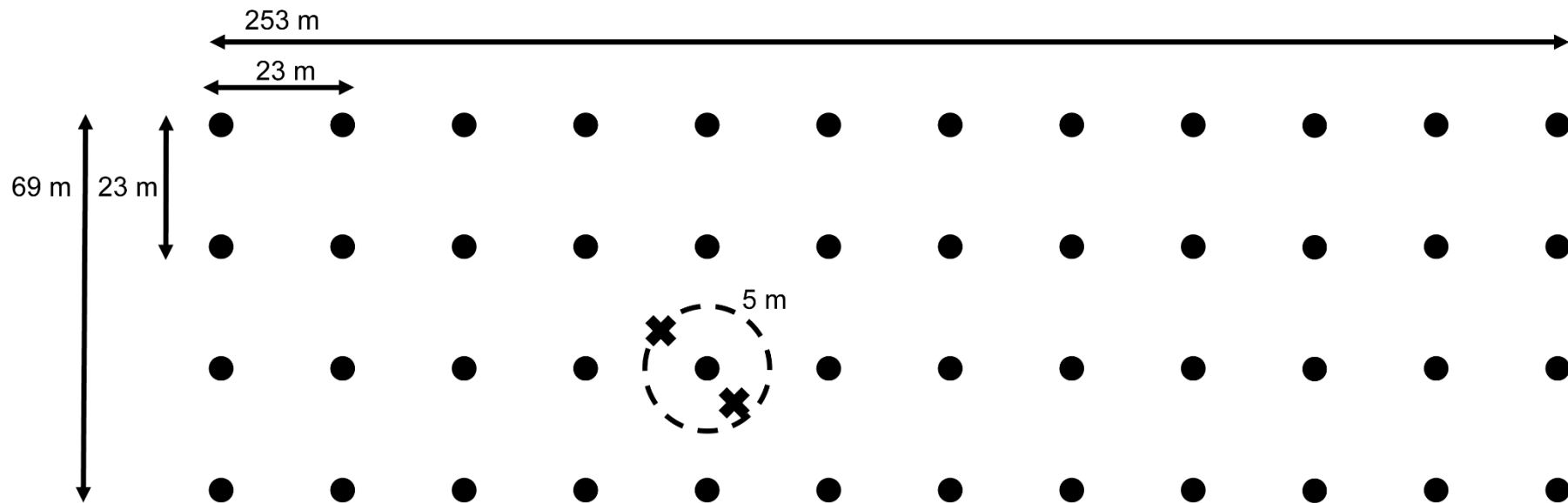


Fig. 1. Schematic of the grid trapping design, showing the arrangement and spacing of sampling points (black filled circles). The deployment of two small mammal traps (black crosses) within a 5m radius of each sampling point (black dashed circle) are shown for one point only, as an example.

SECR models require a minimum quantity of recaptures to produce a reliable estimate of population density, with an approximate minimum of five recaptures generally recommended (Royle *et al.* 2013). Our SECR models grouped the density estimates by species and sampling year, and to satisfy this assumption we therefore only included density estimates based on ≥ 5 recaptures per species per year. Where rare species did not exceed this minimum for at least four (i.e. 50%) of the grids in a given year, we excluded them from the analysis. Apart from these exceptions, SECR models were fitted to all the data for each grid, spanning all sampling sessions for 2011-2016.

We fitted maximum-likelihood SECR models using command *secr.fit*, modelling each grid separately and focusing on temporal changes in density between years. The model estimates three parameters from the data: the population density (D), the “amplitude” of the detection function curve (g_0 , the detection probability at hypothetical home range centres), and the “width” parameter of the detection function (σ , which is related to the animals’ home range radius). These parameters may be constant or related to grouping factors, in our case the species and the sampling year. Accordingly, we specified models of increasing complexity (Table 1), and used a model selection approach to select the best model for each grid (lowest Aikake’s Information Criterion [AIC]). We calculated estimates of population density for each species separately by using species identity as a grouping factor in the model. We then obtained annual community-level density estimates. We first summed the annual density estimates of all species within each grid to obtain a pooled estimate for grid-level community density, and then averaged these across grids to produce a landscape-level estimate for each year. We then compared our species-specific and pooled density estimates among years using generalized linear mixed models with Gamma error family and the inverse link function, in R v.3.5.0 (R Core Team 2018), using Package *lme4*, (Bates *et al.* 2015). Since at least *Tupaia* treeshrews appear to show defined breeding seasons in this system (Emmons 2000), month of sampling is likely to confound our annual density estimates. We therefore included month as a random effect in all our models. We controlled for multiple testing throughout, correcting our P -values using False Discovery Rates (Pike 2011).

2.3.5 Seed and Fruit Data

To investigate the link between resource availability and small mammal population dynamics, we modelled our species-level density estimates against monthly average figures for seed and fruit rain. These data originate from two sources: (1) 1 m² litter traps set once each at 96 sites across the SAFE project area during 2010-2011, and collected after two weeks; and (2) 0.25 m²

litter traps set at five permanent 1 ha carbon plots (25 per plot) during 2011-2016, collected every two to six weeks. The litter traps in (1) were located between 0 and 9.5 km from the grid locations, while the litter traps in (2) were between 0.4 and 10.2 km from the grid locations. Litter was oven-dried, sorted and weighed to give dry mass (g) of leaves, woody debris, flowers, fruit, and seeds. We pooled the fruit and seed data as the categorization is subjective and both are likely to be important to small mammals. We scaled the estimates to a uniform measure of $\text{g.m}^{-2}.\text{month}^{-1}$, and averaged across the plots to give a landscape-scale monthly estimate of seed/fruit fall, which we believe is broadly representative of local-scale seed/fruit fall, both at background levels and during mast fruiting.

We modelled the species-level small mammal density estimates for each grid against the seed/fruit fall value for the relevant month in which the mammal trapping occurred, using generalized linear models (Gamma error family and inverse link function), and removing grids ($n=12$ or 26.7% of the total data) for which fruit and seed data for that month was not available. Since inter-annual peaks in fruit/seed availability should take time to reflect in an increased abundance of small mammals, we fitted models with seven increasing lag periods from zero to six months, in each case fitting the small mammal data to the appropriate earlier month's seed and fruit data. We selected the best-fitting model in each case by comparing AIC values, and again controlled for multiple testing using False Discovery Rates.

2.4 Results

2.4.1 Trapping success, species richness and overall density

In total we ran 45 grid sampling sessions of seven days each across 2011, 2012, 2014, 2015 and 2016 (total = 30 240 trap nights). We captured 2 598 identifiable individual small mammals (mean trap success rate = 7.1%), comprising 20 species. Mean observed species richness in 2011 was 12.6 ± 0.6 ; in 2012: 11.0 ± 0.7 ; in 2014: 8.8 ± 0.4 ; in 2015: 11.3 ± 0.4 ; and in 2016: 10.6 ± 0.5 . We captured nine species in sufficient numbers (≥ 5 recaptures in ≥ 4 grids per year) to estimate density using SECR. These nine species cumulatively represented 2152 individuals, or 83% of all individuals captured (Table 2). Whitehead's Rat *Maxomys whiteheadi* was the most commonly encountered species (23.2% of individuals), with the Red Spiny Rat *Maxomys surifer* (18.6 %) also frequently encountered.

At the community-level, small mammal population density showed strong differences among years (generalised linear mixed model with inverse link, $F= 10.875$, $p < 0.0001$, Fig. 2). Density declined 34% between 2011 and 2012 ($p=0.004$, Fig. 2), and a further 30% of 2011 levels between 2012 and 2014 ($p < 0.0001$, Fig. 2). By 2015 density had partly recovered, and did not

differ significantly from 2012 levels, although it remained slightly lower in 2016 than in 2011 ($p=0.05$, Fig. 2).

Table 1. Specifications of SECR models used in the model selection process in this study. “Density” is the population density estimate, g_0 is the maximal probability of detection of an individual at distance=0 from the hypothetical home range centre, and σ is the width of the halfnormal detection function, all three of which may be held constant (~ 1) or made dependent on species or sampling year. The models were fitted separately for each sampling grid.

Model specification	Comments
Density~species, $g_0 \sim 1$, $\sigma \sim 1$	Models for grids sampled in only one year
Density~species, $g_0 \sim 1$, $\sigma \sim \text{species}$	
Density~species, $g_0 \sim \text{species}$, $\sigma \sim \text{species}$	
Density~species*year, $g_0 \sim 1$, $\sigma \sim 1$	Models for grids sampled in multiple years
Density~species*year, $g_0 \sim 1$, $\sigma \sim \text{species}$	
Density~species*year, $g_0 \sim \text{species}$, $\sigma \sim \text{species}$	
Density~species*year, $g_0 \sim \text{species*year}$, $\sigma \sim \text{species}$	
Density~species*year, $g_0 \sim \text{species*year}$, $\sigma \sim \text{species*year}$	

2.4.2 Species-specific trends

The best-performing density model for each grid is presented in Table A1 of Appendix A. The inter-annual changes in population density of individual small mammal species fell into two broad species subgroups, one of which had strongly fluctuating densities through time (Fig. 3a-c), and the second of which had more stable densities. The first, variable subgroup comprised six species that mostly had patterns that mirrored the overall trend in community-level density, as these species form the dominant component of the community (77.9% of the individuals used for density estimation, Table 2, Fig. A1). These species all declined strongly from 2011-2014, with marked synchrony between species and similar proportional losses of population density over this period. This subgroup comprised the terrestrial murids *Maxomys whiteheadi* (-74%), *M. surifer* (-73%), and *S. muelleri* (-81%), along with the treeshrews *T. longipes* and *T. tana*, which declined less severely (-61%, -66%). These species recovered to varying degrees during 2015-2016 (Fig. 3a-c), with *M. whiteheadi* recovering most rapidly, *S. muelleri* and *T. longipes* also regaining their 2011 densities by 2016, but *M. surifer* and *T. tana* had not recovered by 2016.

Table 2. Small mammals captured at SAFE 2011-16, including total unique individuals in the dataset, whether we estimated population density using SECR, and annual mean ($\pm$ SE) gross capture rate (=mean number of individuals per 7-day grid trapping session, including recaptures from previous years or other grids). See also Fig. A1. Common names follow Payne and Francis (1985).

Species	Unique individuals	Density estimated	Mean gross capture rate (individuals.grid ⁻¹) $\pm$ S.E.				
			2011	2012	2014	2015	2016
<i>Callosciurus adamsi</i> (Earspot Squirrel)	21	N	0.40 $\pm$ 0.29	0.55 $\pm$ 0.20	0.13 $\pm$ 0.12	0.63 $\pm$ 0.35	0.88 $\pm$ 0.37
<i>Callosciurus notatus</i> (Plantain Squirrel)	4	N	0	0	0	0	0.50 $\pm$ 0.47
<i>Lariscus hosei</i> (Four-Striped Ground Squirrel)	11	N	0.90 $\pm$ 0.36	0.09 $\pm$ 0.09	0	0.13 $\pm$ 0.12	0
<i>Leopoldamys sabanus</i> (Long-tailed Giant Rat)	155	Y	7.80 $\pm$ 1.21	3.73 $\pm$ 0.60	1.25 $\pm$ 0.52	2.63 $\pm$ 0.58	3.13 $\pm$ 1.12
<i>Maxomys baeodon</i> (Small Spiny Rat)	285	Y	9.80 $\pm$ 0.54	9.09 $\pm$ 0.92	4.88 $\pm$ 0.45	6.63 $\pm$ 1.62	2.38 $\pm$ 1.22
<i>Maxomys ochraceiventer</i> (Chestnut-Bellied Spiny)	3	N	0.10 $\pm$ 0.09	0	0.13 $\pm$ 0.12	0.13 $\pm$ 0.12	0
<i>Maxomys rajah</i> (Brown Spiny Rat)	6	N	0.10 $\pm$ 0.09	0.18 $\pm$ 0.12	0	0.38 $\pm$ 0.35	0.13 $\pm$ 0.12
<i>Maxomys surifer</i> (Red Spiny Rat)	483	Y	22.6 $\pm$ 2.31	11.27 $\pm$ 1.40	6.63 $\pm$ 0.73	11.38 $\pm$ 1.81	7.88 $\pm$ 0.62
<i>Maxomys whiteheadi</i> (Whitehead's Rat)	604	Y	19.40 $\pm$ 3.05	12.64 $\pm$ 2.18	5.38 $\pm$ 1.07	15.50 $\pm$ 0.92	21.25 $\pm$ 2.47
<i>Niviventer cremoriventer</i> (Dark-Tailed Tree Rat)	235	Y	5.80 $\pm$ 1.31	4.91 $\pm$ 1.23	2.75 $\pm$ 0.66	7.00 $\pm$ 1.63	7.38 $\pm$ 1.96
<i>Rattus exulans</i> (Polynesian Rat)	93	N	4.10 $\pm$ 1.05	2.09 $\pm$ 0.62	0	1.13 $\pm$ 0.48	3.00 $\pm$ 0.77
<i>Rattus rattus</i> (Black Rat)	91	N	7.30 $\pm$ 1.57	1.64 $\pm$ 0.45	0	0	0
<i>Sundamys muelleri</i> (Muller's Rat)	122	Y	5.30 $\pm$ 0.92	2.36 $\pm$ 0.45	0.63 $\pm$ 0.35	2.50 $\pm$ 0.68	4.25 $\pm$ 0.88
<i>Sundasciurus hippurus</i> (Horse-Tailed Squirrel)	8	N	0.50 $\pm$ 0.21	0.09 $\pm$ 0.09	0.13 $\pm$ 0.12	0.13 $\pm$ 0.12	0
<i>Sundasciurus lowii</i> (Low's Squirrel)	198	N	4.20 $\pm$ 0.82	5.55 $\pm$ 0.83	3.13 $\pm$ 0.62	6.00 $\pm$ 1.27	7.38 $\pm$ 1.30
<i>Tupaia longipes</i> (Common Treeshrew)	88	Y	1.50 $\pm$ 0.60	2.82 $\pm$ 0.40	2.38 $\pm$ 0.56	2.63 $\pm$ 0.53	2.13 $\pm$ 0.41
<i>Tupaia gracilis</i> (Slender Treeshrew)	86	Y	1.50 $\pm$ 0.53	1.45 $\pm$ 0.54	1.63 $\pm$ 0.39	4.13 $\pm$ 1.28	2.50 $\pm$ 0.64
<i>Tupaia minor</i> (Lesser Treeshrew)	9	N	0.30 $\pm$ 0.20	0.27 $\pm$ 0.19	0.13 $\pm$ 0.12	0.25 $\pm$ 0.23	0
<i>Tupaia tana</i> (Large Treeshrew)	94	Y	2.90 $\pm$ 0.67	2.00 $\pm$ 0.64	1.75 $\pm$ 0.42	3.38 $\pm$ 0.53	3.13 $\pm$ 0.67
Total unique individuals	2 598						
Total in density calculations	2 152						

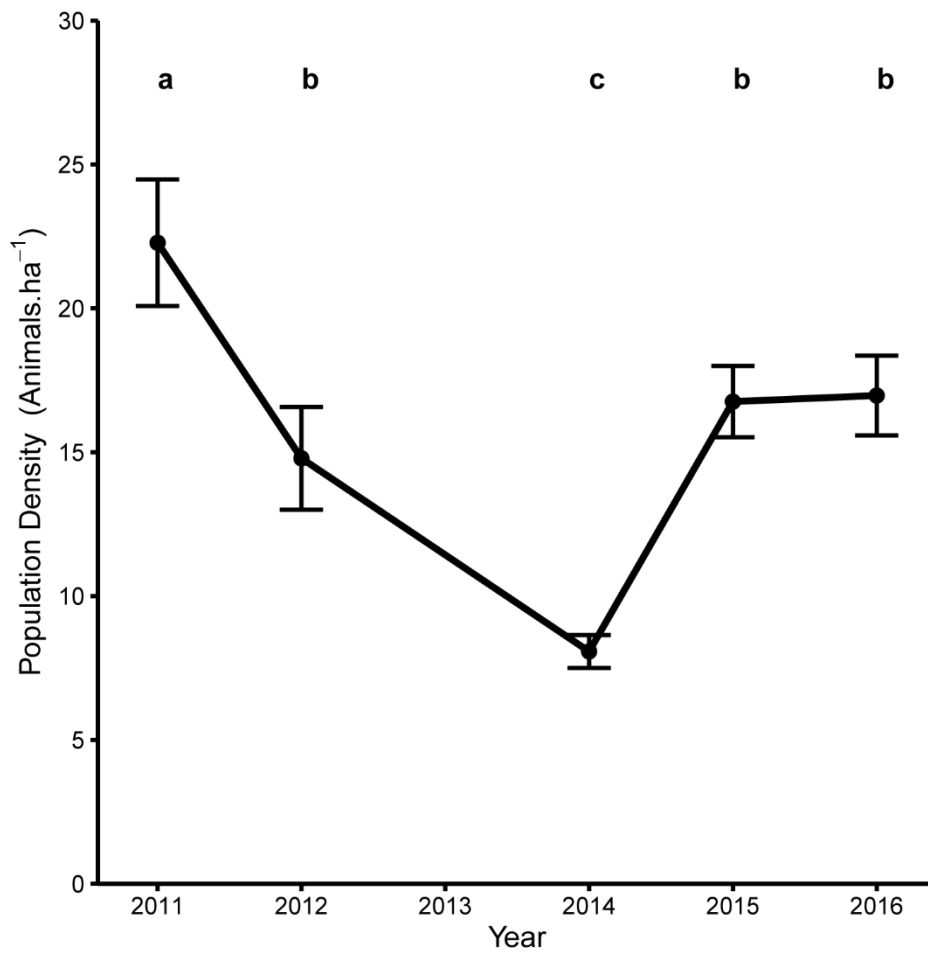


Fig. 2. Mean annual community-level population density of all small mammals from 2011 to 2016.

Error bars: ± 1 S.E. Letters denote significance groups, with significantly different means not sharing letters.

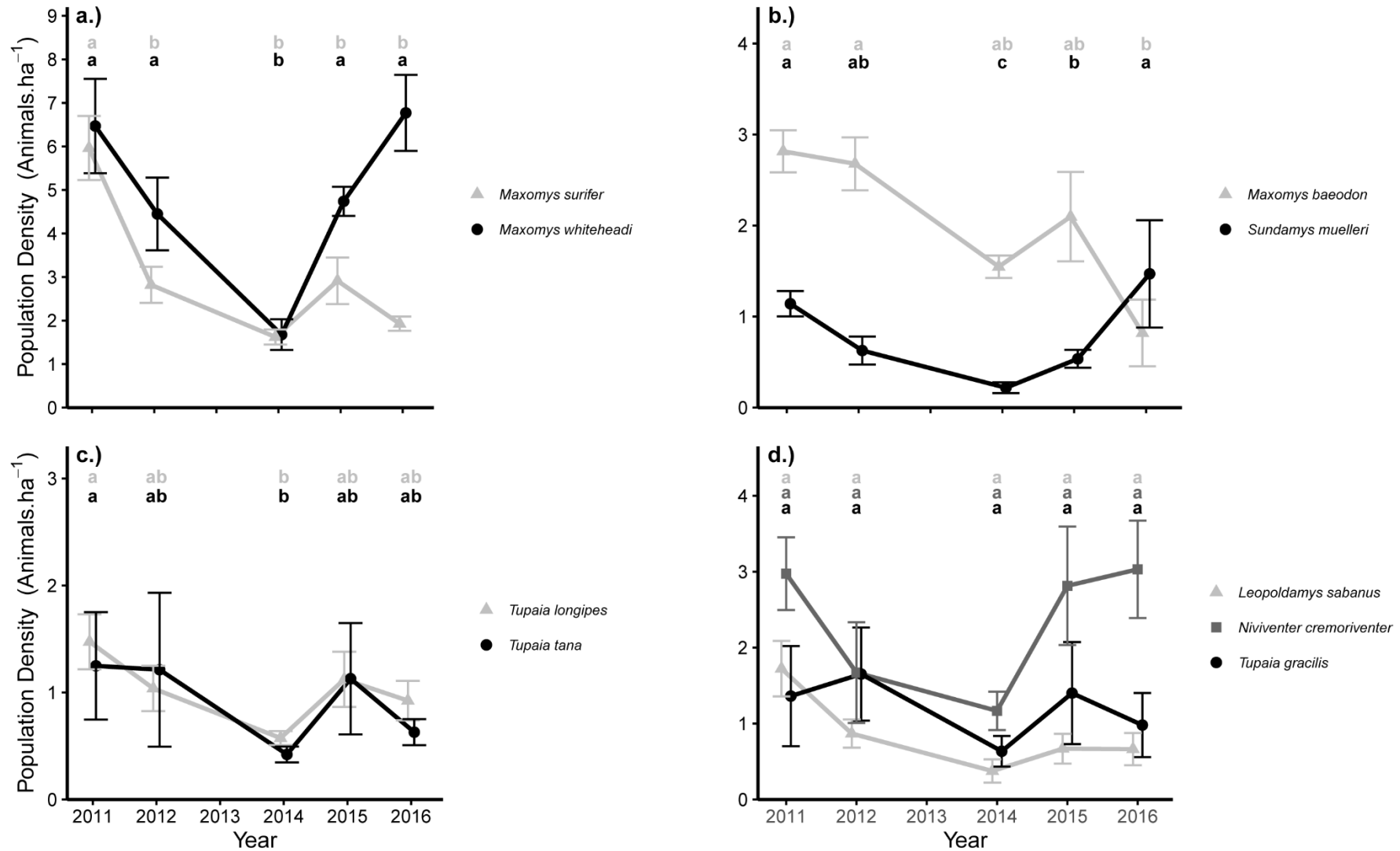


Fig. 3. Mean population density of nine small mammal species at the SAFE project 2011-2016 Error bars: ± 1 S.E. Panels a.) to c.) show species which showed variable dynamics, while d.) shows species which did not vary significantly between years. Letters denote significance groups, with significantly different means not sharing letters.

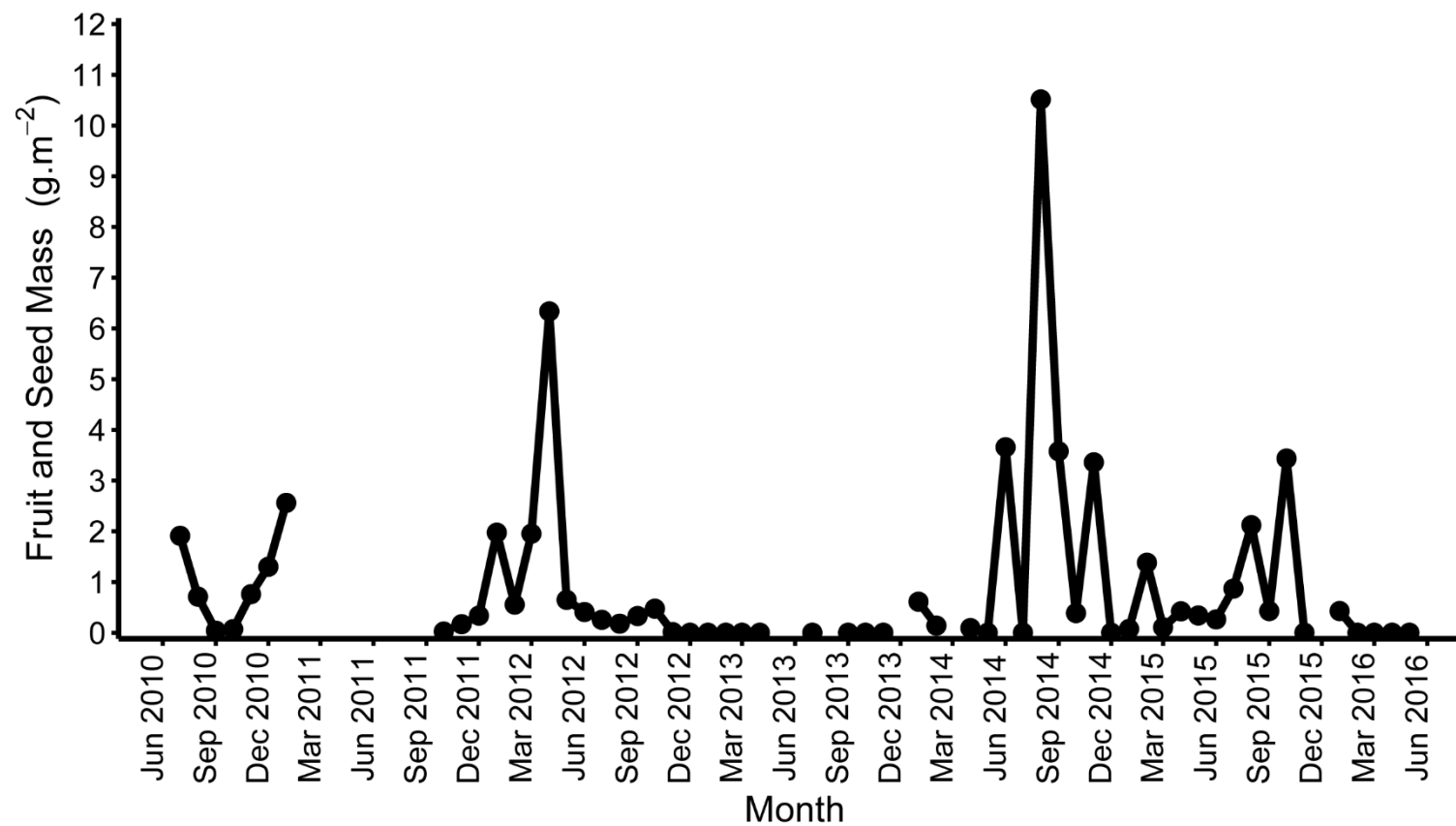


Fig. 4. Mean combined fruit and seed mass (g.m⁻²) by month, captured in litter traps at the SAFE project, 2010-2016. Gaps represent missing data.

The sixth species, *M. baeodon*, was already a comparatively rare species in 2011 and gradually declined throughout the course of study. Density was not significantly lower in 2014 than 2011, but by 2016 it had declined significantly to only 29% of the starting figure in 2011 (Fig. 3a).

The second subgroup comprised the treeshrew *T. gracilis*, and the semi-arboreal murids *Leopoldamys sabanus* and *Niviventer cremoriventer*. Although these species appeared to dip subtly in 2011-2014 (Fig. 3d), their dynamics were characterised by lower abundance, much higher between-grid variance around the annual estimates and no significant differences in population density among years.

2.4.3 Relationship with seed density

Density of fruit and seeds remained low throughout much of the time period from 2011-2016, however periodic spikes were evident in 2012, 2014 and 2015 (Fig. 4). The best fitting models of mammal population density against seed mass varied widely in their lag time from 0 to 6 months between species, with no one lag time representing the best fitting model for more than two species (Table A2). After controlling for multiple testing using False Discovery Rates, we found no significant relationship between seed density and population density for any of the species surveyed at any time lag (generalized linear models, all $p > 0.05$, see Table A2).

2.5 Discussion

As the longest-duration study of a small mammal community in continuous logged tropical forest, our results underline the importance of understanding long-term trends in parameters such as population density for assessment of the value of logged forests for biodiversity. Previous studies have observed strongly variable dynamics in small mammal communities inhabiting undisturbed forests (Nakagawa *et al.* 2007a; b; Wells *et al.* 2007a). Our results suggest that this variability persists inter-annually in intensively selectively logged forest, across two thirds of the species we examined, and in the community as a whole. We observed a high magnitude of inter-annual variation, with density reducing by up to 50% between consecutive years, and up to 80% in 2011-14. This is similar to previous evidence; for example, community-level abundance in a Bornean unlogged forest declined by approximately 90% from 1999-2002 (Nakagawa *et al.* 2007b).

The diet of Bornean small mammals is poorly known (Wells *et al.* 2007a, 2009), although the small mammal species we examined are probably relatively functionally homogenous (terrestrial/low canopy generalists and granivores, see Payne and Francis (1985)). Nevertheless, our results demonstrate a range of inter-annual dynamics, particularly during 2011-2014. This variation in dynamics seems to follow an ecological gradient from strictly

terrestrial murids (which exhibited strong temporal dynamics and dominated the community in “peak” years, see Fig. A1) to facultatively semi-arboreal foragers, including climbing murids and some treeshrews (which exhibited no strong temporal dynamics). The two treeshrew species which did vary between years (*Tupaia longipes* and *T. tana*) forage more terrestrially than *T. gracilis* (Emmons 2000), and showed intermediate variability and formed a comparatively larger proportion of the community in “non-peak” years (Fig. A1). More terrestrial small mammals are both more exposed to the vast excesses of dipterocarp seeds during mast events (Curran & Webb 2000); and are less plastic in their foraging strategies and less able to facultatively exploit food resources at other vegetation strata during inter-mast food shortages. These species may therefore be more responsive to masting than semi-arboreal foragers. Treeshrews generally have inadequate digestive systems to process dipterocarp seeds (Emmons 2000), but *T. longipes* and *T. tana* (both variable in our results) may react indirectly to masting if insect abundance at forest floor level is greatly increased during mast fruiting events (Nakagawa *et al.* 2003).

Alternatively, it is possible that these more stable dynamics in facultatively arboreal species are an artefact of our strictly terrestrial sampling design. For species which forage among several strata, detection by a terrestrial trapping grid depends on which stratum is chosen, and interannual changes in detection could be driven by interannual changes in foraging stratum selection. Indeed, the semi-arboreal species we captured may have strongly varied in density, but simultaneously increased ground-level foraging in “lean” years, dampening out observed trends. Foraging stratum selection is likely to be highly spatially variable due to the heterogeneous nature of logged forest (Section 1.3.1), and this could have contributed to the high variability in population density we observed for semi-arboreal species. Future work simultaneously trapping at multiple strata may be necessary to fully eliminate this source of bias and produce robust population trends for these species.

This apparent relationship between population density dynamics and feeding ecology, plus the fact that largely synchronous patterns were broadly shared among functionally similar species suggest that the mast fruiting-driven fluctuating patterns seen in primary forests (Curran & Leighton 2000; Nakagawa *et al.* 2007b), may persist after multiple rounds of logging. Indeed forests subjected to a single selective logging rotation may still produce sufficient fruit/seed volumes (~23% of the primary forest figure) to attract a strong response from local seed predators (Curran & Webb 2000). However, we did not find any direct evidence supporting the expected seed density-mammal density relationship, which we suggest may be due to three factors.

Firstly, the temporal extent of our data may still be insufficient to detect a relationship.

According to Sabah-wide records, ENSO-driven droughts in Sabah occurred in 2010, and to a lesser extent in 2014 and 2015 (Ghazoul 2016). While we detected the 2014 mast event (Fig. 4), for most of the rest of six-year survey period, the litter traps contained low quantities of fruit

and seed despite the variable small mammal population density. Our first litter trap collection was carried out in the second half of 2010 (Fig. 4), so it is probable that we did not detect the major 2010 mast, which might have explained the high small mammal population densities at the start of our study in 2011. We also did not find evidence for the 2015 event, suggesting it might have been too minor and localized to occur in our study area.

Secondly, unlike the West Kalimantan site studied by Curran and Webb (2000), the forest at SAFE has been subject to multiple logging rotations and the landscape retains few commercially valuable mature trees. Since logging in Borneo specifically and intensively targets the mast-fruiting Dipterocarpaceae (Grieser Johns 1997; Putz *et al.* 2012), it is possible that there are insufficient mast fruiting trees remaining in the landscape to drive significant changes in small mammal population densities, and that the variability that we observed may be regulated by other processes, such as bottom up control via other food plant taxa, or top-down control by predators.

Thirdly, even if logging damage at the landscape level is not sufficient to completely disrupt mast fruiting-driven changes to population dynamics, logging disturbance is highly spatially heterogeneous, and the forest at SAFE forms a patchwork of highly variable quality and tree cover (Pfeifer *et al.* 2015, 2016). Mast fruiting is already a spatially heterogeneous process (Ghazoul 2016), and logging undoubtedly further localizes this by leaving small “islands” of mature dipterocarp trees. This is supported by the fact that fruit/seed rain levels were very weakly correlated between the five carbon plots which supply data for our study (average $R^2 = 0.14$). These “islands” may be visited by our small mammals at some distance from the trapping locations, although the effect of habitat change on the ranging behaviour of our species is poorly known. Our seed and fruit data were collected from plots at varying distance from our small mammal grids, and we could therefore use the data only to represent a landscape-level average fruit availability, rather than to detect very localized associations between fruiting and small mammal abundance.

2.5.1 Conclusions and conservation implications

Our results reveal dynamic inter-annual variability in small mammal population densities, but not necessarily a dynamic equilibrium. Even this six-year dataset is insufficient to demonstrate inter-annual cycling of population density, with repeated peaks and troughs, which may require 1-2 decades of data, in common with “rules of thumb” regarding time-series datasets (Jassby and Powell 1990; Magurran *et al.* 2010; White 2018). Furthermore, there is some evidence to suggest that the diversity of this community is progressively declining: the Small Spiny Rat *Maxomys baeodon* continued to decline gradually throughout the course of our study, and is potentially under extinction debt since the last major round of logging in the early 2000s. This,

and the fact that the more abundant *M. surifer* failed to recover from the 2014 crash, contrast with the rapid recovery of *M. whiteheadi*, which is the most tolerant of the three to habitat degradation and the only *Maxomys* species able to persist in oil palm plantation (Chapter Five; Wearn *et al.* 2017). Together, these three trends may represent an early hint that the terrestrial *Maxomys* sub-community is simplifying over time, perhaps by *M. whiteheadi* outcompeting less disturbance-tolerant congeners. Nonetheless, although our data suggests that this is a possibility, several years of further monitoring will probably be necessary in order to confirm this. Again echoing 10-20-year “rules of thumb”, field studies of community simplification and extinction through time suggest that extinction debts in tropical forest small mammals may take 1-2 decades to become completely realized (Gibson *et al.* 2013).

Despite the fact that more data is needed to confirm cycling or extinction debt, our results nonetheless demonstrate the additional value of studies which take a long-term approach in order to assess the biodiversity value of logged forests, and of other habitats more generally. This contrasts with the bulk of existing studies, which compare between primary forests, logged forests, and oil palm plantations based on single survey periods in each habitat, often not simultaneously across habitats or resampled within habitats. Previous work implies that a short-term approach does not capture the full temporal complexity of primary forest small mammals (Nakagawa *et al.* 2007b), and our results suggest this is also true of logged forests. Indeed, a survey of our communities in any randomly selected single year may have produced density estimates varying by up to 80%. Such variation could affect conclusions and recommendations for conservation practice, which often requires prioritizing limited resources to protect the most biodiverse, resilient communities, and calculating minimum viable protected areas to support populations or communities. If the assumption that abundance remains approximately constant through time is not tested, and estimates of community abundances are drawn from different phases of the inter-annual dynamic (either due to spatial asynchrony in community dynamics, or temporal asynchrony in sampling), the data informing those decisions will not be easily comparable, and two surveys of similar communities might produce very different results, or vice versa. Errors such as these will also affect abundance-weighted functional diversity metrics (e.g. Villéger, Mason & Mouillot 2008), and comparisons of ecosystem processes driven by small mammals, such as seed predation (Curran & Webb 2000; Guariguata, Claire & Jones 2002).

Clearly, not all taxa are likely to display equally temporally variable responses across all human-modified ecosystems. Furthermore, the high costs and logistical challenges of long-term studies suggest that the subjects for such work should be chosen carefully. Realistically, a combination of “snapshots” and longer approaches will often be necessary; indeed, with time and money for conservation research often at a premium, short-term studies may prove the only option available, and we acknowledge that many “snapshots” may cover more communities and sites than one long-term study. Nonetheless, our study both underlines the insights that can be gained

from a long-term approach, and suggests that taxa likely to be variable can be often identified *a priori* from careful consideration of their ecological and functional characteristics, allowing resources to be focused on vulnerable and functionally important species. For example, the *Maxomys* rodents, which respond most profoundly to mast fruiting, and show variable population dynamics in unlogged forests, remain variable after logging. The apparent signs of decline in at least one species, and the high functional importance of the genus in this ecosystem, suggest that *Maxomys* rodents make a particularly important subject for a continued, long-term study over at least 1-2 decades.

We therefore agree with Lindenmayer *et al.* (2012) that more emphasis is needed on high-quality long-term studies which regularly resample community or population parameters of interest in order to create temporally reliable estimates of the value of human-modified habitats for biodiversity. In the face of limited resources, we suggest that long-term studies are most valuable for species whose ecological characteristics suggest a high tendency for temporal change, and in regions with strong underlying interannual processes, such as tropical forests in Southeast Asia and elsewhere. Although such studies are logistically challenging, they will prove invaluable in understanding the biodiversity potential of human-modified ecosystems globally.

2.6 Appendix A

Table A1. AIC comparison table for all the SECR models run on each of 16 grids in our data. The specification of each model is displayed: D is the modelled density, g0 is the modelled detection probability at the hypothetical home range centre, and sigma is the distance parameter for the detection probability function (for further explanation of these parameters and the model specifications, see the main text and/or Table 1). The years trapped, and the SAFE project sampling block in which each grid was located (see Fig. 2 of Ewers et al. 2011) are also shown. The raw AIC values, the difference of each value from the lowest in the comparison (dAIC) and the within-comparison weighting (AIC Wt) are displayed. For clarity, horizontal lines separate within-grid AIC comparisons, while bold text denotes the model we selected.

Grid	Block	Years	Model Specification	AIC	dAIC	wAIC
1	F	2011	D~species, g0~1, sigma~1	1202.28	0.00	0.81
1	F	2011	D~species, g0~1, sigma~species	1206.15	3.87	0.12
1	F	2011	D~species, g0~species, sigma~species	1207.26	4.98	0.07
2	F	2011	D~species, g0~1, sigma~1	1312.37	14.37	0.00
2	F	2011	D~species, g0~1, sigma~species	1298.00	0.00	0.91
2	F	2011	D~species, g0~species, sigma~species	1302.53	4.54	0.09
3	F	2011	D~species, g0~1, sigma~1	1105.34	6.16	0.04
3	F	2011	D~species, g0~1, sigma~species	1106.88	7.70	0.02
3	F	2011	D~species, g0~species, sigma~species	1099.18	0.00	0.94
4	F	2011	D~species, g0~1, sigma~1	1863.16	8.33	0.01
4	F	2011	D~species, g0~1, sigma~species	1854.83	0.00	0.94
4	F	2011	D~species, g0~species, sigma~species	1861.07	6.24	0.04
5	D	2012	D~species, g0~1, sigma~species	880.44	9.00	0.01
5	D	2012	D~species, g0~1, sigma~1	871.44	0.00	0.99
5	D	2012	D~species, g0~species, sigma~species	884.81	13.37	0.00
6	D	2012	D~species, g0~1, sigma~1	565.59	0.00	0.87
6	D	2012	D~species, g0~1, sigma~species	569.33	3.74	0.13
6	D	2012	D~species, g0~species, sigma~species	578.86	13.27	0.00
7	D	2012	D~species, g0~1, sigma~1	805.10	3.18	0.13
7	D	2012	D~species, g0~1, sigma~species	801.92	0.00	0.63
7	D	2012	D~species, g0~species, sigma~species	803.84	1.92	0.24
8	D	2012	D~species, g0~1, sigma~1	470.36	0.00	0.83
8	D	2012	D~species, g0~1, sigma~species	473.82	3.47	0.15
8	D	2012	D~species, g0~species, sigma~species	477.71	7.35	0.02
9	D	2011-12, 2014-6	D~species*year, g0~1, sigma~1	5977.35	148.98	0.00
9	D	2011-12, 2014-6	D~species*year, g0~1, sigma~species	5917.16	88.79	0.00
9	D	2011-12, 2014-6	D~species*year, g0~species, sigma~species	5828.37	0.00	1.00
9	D	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species	5981.42	153.05	0.00
9	D	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species*year	6260.76	432.39	0.00
10	D	2011, 2014-16	D~species*year, g0~1, sigma~1	3430.65	28.23	0.00
10	D	2011, 2014-16	D~species*year, g0~1, sigma~species	3415.34	12.91	0.00
10	D	2011, 2014-16	D~species*year, g0~species, sigma~species	3402.42	0.00	1.00
10	D	2011, 2014-16	D~species*year, g0~species*year, sigma~species	3615.84	213.42	0.00
10	D	2011, 2014-16	D~species*year, g0~species*year, sigma~species*year	4220.20	817.78	0.00
11	E	2011-12, 2014-6	D~species*year, g0~1, sigma~1	7539.94	131.85	0.00
11	E	2011-12, 2014-6	D~species*year, g0~1, sigma~species	7516.49	108.41	0.00
11	E	2011-12, 2014-6	D~species*year, g0~species, sigma~species	7408.09	0.00	1.00
11	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species	7476.17	68.08	0.00
11	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species*year	7609.05	200.97	0.00

12	E	2011-12, 2014-6	D~species*year, g0~1, sigma~1	7776.56	150.99	0.00
12	E	2011-12, 2014-6	D~species*year, g0~1, sigma~species	7714.27	88.69	0.00
12	E	2011-12, 2014-	D~species*year, g0~species, sigma~species	7625.58	0.00	1.00
12	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species	7720.73	95.15	0.00
12	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species*year	7830.81	205.23	0.00
13	E	2011-12, 2014-6	D~species*year, g0~1, sigma~1	6160.62	131.49	0.00
13	E	2011-12, 2014-6	D~species*year, g0~1, sigma~species	6104.62	75.49	0.00
13	E	2011-12, 2014-	D~species*year, g0~species, sigma~species	6029.13	0.00	1.00
13	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species	6188.63	159.50	0.00
13	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species*year	6441.77	412.64	0.00
14	E	2011-12, 2014-6	D~species*year, g0~1, sigma~1	4257.66	55.44	0.00
14	E	2011-12, 2014-6	D~species*year, g0~1, sigma~species	4255.38	53.16	0.00
14	E	2011-12, 2014-	D~species*year, g0~species, sigma~species	4202.22	0.00	1.00
14	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species	4330.52	128.30	0.00
14	E	2011-12, 2014-6	D~species*year, g0~species*year, sigma~species*year	4560.87	358.65	0.00
15	E	2012, 2014-16	D~species*year, g0~1, sigma~1	4882.85	64.32	0.00
15	E	2012, 2014-16	D~species*year, g0~1, sigma~species	4829.35	10.81	0.00
15	E	2012, 2014-16	D~species*year, g0~species, sigma~species	4818.54	0.00	1.00
15	E	2012, 2014-16	D~species*year, g0~species*year, sigma~species	4936.28	117.74	0.00
15	E	2012, 2014-16	D~species*year, g0~species*year, sigma~species*year	5085.65	267.11	0.00
16	E	2012, 2014-16	D~species*year, g0~1, sigma~1	4036.11	109.74	0.00
16	E	2012, 2014-16	D~species*year, g0~1, sigma~species	3980.60	54.23	0.00
16	E	2012, 2014-16	D~species*year, g0~species, sigma~species	3926.37	0.00	1.00
16	E	2012, 2014-16	D~species*year, g0~species*year, sigma~species	4052.37	126.01	0.00
16	E	2012, 2014-16	D~species*year, g0~species*year, sigma~species*year	4315.07	388.70	0.00

Table A2. AIC comparison table for models of small mammal population density against fruit and seed mass. For each species, models are fitted with increasing lag times in the fruit data, from 0 months (i.e the fitted fruit data comes from the same month as the mammal density estimate) up to 6 months. (i.e. the fitted fruit data predates the mammal density estimate by 6 months) The model we selected for each species is displayed in bold text, and for clarity, the parameter estimate, Standard error, T and P values are shown for this model only. P (adj.) denotes P-values corrected for multiple testing using False Discovery Rates (see the main text).

Species	Lag (months)	AIC	Estimate	SE	T	P	P (adj.)
Common Treeshrew (<i>Tupaia longipes</i>)	0	46.222					
	1	46.237					
	2	46.724					
	3	45.581	0.227	0.343	0.661	0.515	0.771
	4	46.376					
	5	48.221					
	6	49.933					
Dark-tailed Tree Rat (<i>Niviventer cremoriventer</i>)	0	107.916					
	1	112.191					
	2	108.882					
	3	110.725					
	4	105.386					
	5	113.216					
	6	104.446	-0.101	0.041	-2.461	0.021	0.158
Large Treeshrew (<i>Tupaia tana</i>)	0	55.308					
	1	51.454	-0.298	0.168	-1.770	0.088	0.264
	2	54.080					
	3	55.068					
	4	50.703					
	5	60.341					
	6	55.513					
Long-Tailed Giant Rat (<i>Leopoldamys sabamus</i>)	0	44.881					
	1	40.664	-0.096	0.260	-0.370	0.714	0.802
	2	43.261					
	3	46.344					
	4	50.114					
	5	49.796					
	6	57.554					
Muller's Rat (<i>Sundamys muelleri</i>)	0	41.604					
	1	43.020					
	2	44.823					
	3	47.593					
	4	30.587	-0.209	0.186	-1.120	0.273	0.49
	5	54.218					
	6	43.929					
Red Spiny Rat (<i>Maxomys surifer</i>)	0	116.088					
	1	115.161					
	2	112.709	-0.015	0.030	-0.516	0.609	0.783
	3	114.749					
	4	114.970					
	5	121.990					
	6	118.750					

Slender Treeshrew (<i>Tupaia gracilis</i>)	0	46.740					
	1	53.279					
	2	44.937	-0.565	0.249	-2.271	0.035	0.157
	3	51.377					
	4	48.792					
	5	53.289					
	6	54.249					
Small Spiny Rat (<i>Maxomys baeodon</i>)	0	110.485					
	1	111.060					
	2	111.272					
	3	109.274	-0.132	0.084	-1.573	0.126	0.284
	4	112.448					
	5	114.688					
	6	115.820					
Whitehead's Rat (<i>Maxomys whiteheadi</i>)	0	147.598	-0.006	0.026	-0.231	0.819	0.818
	1	152.862					
	2	157.111					
	3	156.888					
	4	157.867					
	5	167.684					
	6	166.384					

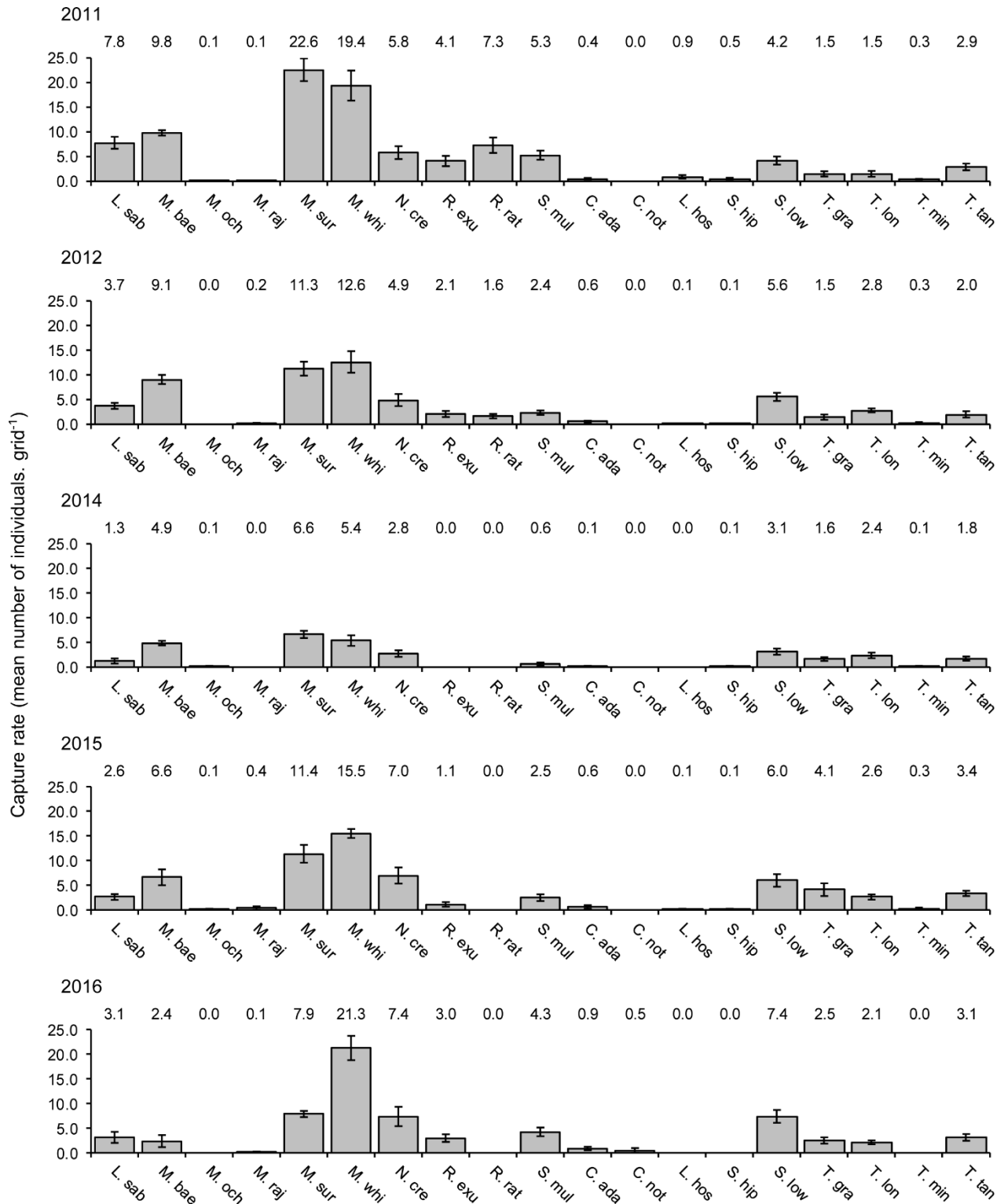


Fig. A1. Annual captures of 19 small mammal species at the SAFE project, 2011-2016. Gross mean capture rates are displayed (=mean number of individuals per 7-day grid trapping session, including recaptures from previous years or from other grids). Error bars: ± 1 S.E. Species are grouped taxonomically, with names abbreviated for brevity. **Murids:** L. sab: *Leopoldamys sabamus*. M. bae: *Maxomys baeodon*. M. och: *Maxomys ochraceiventer*. M. raj: *Maxomys rajah*. M. sur: *Maxomys surifer*. M. whi: *Maxomys whiteheadi*. N. cre: *Niviventer cremoriventer*. R. exu: *Rattus exulans*. R. rat: *Rattus rattus*. S. mul: *Sundamys muelleri*. **Sciurids:** C. ada: *Callosciurus adamsi*. C. not: *Callosciurus notatus*. L. hos: *Lariscus hosei*. S. hip: *Sundasciurus hosei*. S. low: *Sundasciurus lowii*. **Tupaids:** T. gra: *Tupaia gracilis*. T. lon: *Tupaia longipes*. T. min: *Tupaia minor*. T. tan: *Tupaia tana*.

Chapter Three: Testing for changes in biometrics and demography of a small mammal community changing in abundance across a selective logging gradient

3.1 Abstract

Recent studies of Bornean small mammals along a selective logging gradient revealed consistent, community-wide abundance increases averaging 200%, with only a few species declining or becoming locally extinct. Both the increase in the majority of species, and the sharp declines of the logging-intolerant minority suggest that associated changes in condition and demography are likely. However, we have no knowledge of whether individual body condition or population demographic parameters do in fact alter across this gradient. This knowledge gap forms part of a wider lack of understanding of how “vital rates” change with habitat disturbance in tropical forests, despite the fundamental importance of these proximal mechanisms in shaping observed occurrence and abundance patterns. We tested for changes in condition, survival and breeding success in a small mammal community across a gradient from unlogged to intensively-logged forest in Sabah, Malaysian Borneo. Apart from a decline in apparent breeding success in more heavily logged forest in the semi-arboreal murid *Leopoldamys sabamus*, we found no other changes in these parameters over the logging gradient. Our results reveal little evidence that populations of species that increase in density pay a consistent cost in terms of condition, survival or reproduction. We also find no evidence for declines in these parameters for two species of terrestrial murid which declined, although in the case of *Maxomys rajah*, this is possibly due to the near-complete disappearance of this species from even lightly-logged forest leaving inadequate numbers of individuals in logged forest to detect any effect. Our results therefore indicate that the prospects for a resilient small mammal community in Bornean logged forests are good, at least for those species which survive the first round of logging, but also underline the urgent need for more mechanistic studies of those species which rapidly decline with any disturbance of primary forest.

3.2 Introduction

Despite a large and increasing body of research, our understanding of how mammal communities respond to tropical forest degradation such as selective logging relies heavily on studies comparing species richness or abundance across a logging gradient. We know little or nothing about changes in demography or health of populations across the logging gradient – an omission which forms part of a much wider knowledge gap in tropical forests (Cosset, Gilroy & Edwards 2018).

Individual body condition, and basic demographic rates such as survival and reproductive output, are the essential processes which lead to observed patterns of abundance and occurrence of animal communities (Haridas *et al.* 2013; Srinivasan, Hines & Quader 2015). Therefore any changes in these parameters within human-modified habitats can reveal changes in vulnerability to local and regional extinction which might be missed by measurements of species richness and abundance (Cosset, Gilroy & Edwards 2018). Specifically, the retention of high species richness or abundance of animal communities after logging might mask reduced breeding success, survival or individual condition among some or all species. These subtler community changes may contribute to reduced resilience of these communities in the long term (Cosset, Gilroy & Edwards 2018). In this case, demographic or condition data may act as a valuable early warning that some apparently healthy species or communities are more susceptible to decline or local extinction, particularly in the face of future environmental change such as climate change or the arrival of invasive species. Alternatively, in the case of vulnerable species which are already declining over time in logged forest, demographic data may shed light on the proximate causes of decline, or the key life-history stages involved – an approach used extensively for conserving well-studied groups in temperate agricultural systems (e.g. Siriwardena, Baillie & Wilson 1998; Robinson *et al.* 2004).

In addition to temporal change in community resilience, changes in demographic rates with selective logging may also reveal spatial processes such as source-sink dynamics, in which populations present in suboptimal habitat are sustained by immigration from neighbouring, higher-quality areas (Gilroy & Edwards 2017). Such patterns are likely to be revealed by reduced individual condition, reproductive output or survival in “sink” habitats compared to “source” habitats. Although understudied in the tropics (Gilroy & Edwards 2017), such patterns seem highly likely to occur in logged forest, which often comprises a spatially heterogeneous patchwork of habitat quality, with heavily-degraded shrubby areas interspersed with relict high-quality areas where logging intensity has been lower (Johns 1988; Pfeifer *et al.* 2016). Indeed, recent work has suggested that this underlying heterogeneity does structure mammal communities structurally by increasing turnover (Wearn *et al.* 2016). Source-sink dynamics complicate apparent relationships between abundance and habitat quality (Gilroy & Edwards

2017), so accounting for them may modify conclusions about the value of selectively-logged forest based primarily on abundance or species richness. For instance, several studies have shown that species richness of mammals remains high in response to selective logging, even after multiple rounds of logging in many cases (Meijaard & Sheil 2008). However if populations of some species in heavily-logged areas, or in logged forest in general, rely on immigration from adjacent less-disturbed areas, the apparent “value” of these habitats may be overstated.

Despite these reasons for the importance of measuring demographic “vital rates” over a disturbance gradient, relatively few studies have done so in tropical forest. Most of these have focussed on birds, and on fragmented systems (Cosset, Gilroy & Edwards 2018). Far fewer studies have considered changes in mammal communities in response to selective logging. We found a handful of studies which have examined changes in body condition in terms of parasite burdens in small mammals or primates between logged and unlogged forest (Gillespie, Chapman & Greiner 2005; Wells *et al.* 2007b; Helenbrook *et al.* 2017) and one study demonstrating reductions in body size and condition among primates in logged forest areas (Olupot 2000). However, we found no community-level studies of body condition, reproductive output or survival over the logging gradient.

This relative scarcity of data may partly reflect the considerable difficulty of measuring these parameters accurately: many tropical forest mammals are highly cryptic and hard to detect or catch, so estimating body condition and reproductive output, or tracking survival through time can be nearly impossible. However, we suggest that estimating these parameters across a logging gradient should be relatively practical for some subgroups of the mammal community, particularly terrestrial small mammals such as murid and sciurid rodents, shrews and other Insectivora, small marsupials, and treeshrews. Although practical challenges remain (in tropical forest, many species are nocturnal and nest underground or in dense dead plant matter, (Payne & Francis 1985; Emmons 2000; Wells, Lakim & Pfeiffer 2006)), they can be caught in large numbers, and easily measured, aged, sexed, and individually marked. The resulting large volumes of basic biometric and demographic data may then be used to approximate body condition (using length/mass data, Schulte-Hostedde, Millar & Hickling 2001; Schulte-Hostedde *et al.* 2005; Peig & Green 2009), survival (apparent survival from mark-recapture observations, White & Burnham 1999; Laake & Rexstad 2008) and reproductive output (observed proportion of juveniles in a sampled population relative to survival, e.g. Beissinger 1995; Lehikoinen, Kilpi & Öst 2006; Homyack & Haas 2009).

Despite the comparative ease of collecting this data, it has not been used to examine changes in body condition or demography with selective logging in small mammals. As with mammals as a whole, most of our knowledge about responses to selective logging comprises studies of species richness and abundance (Meijaard & Sheil 2008). Many previous studies have produced

conflicting results, and probably represent oversimplifications of the logging process, often failing to properly explore the effects of logging intensity or time since logging, or to correct for underlying biotic or abiotic differences among study sites (Meijaard & Sheil 2008; Burivalova, Şekercioğlu & Koh 2014; Wearn *et al.* 2017). However a recent landscape-scale study which corrected some of these issues revealed a community-wide average increase in small mammal relative abundance of nearly 200% (Wearn *et al.* 2017). This increase followed intense selective logging over multiple rounds, with aboveground biomass (AGB) reduced from $\approx 400 \text{ Mg/ha}^{-1}$ to as little as $\leq 50 \text{ Mg/ha}^{-1}$ (Pfeifer *et al.* 2016). While species trends varied in strength, 14 of 20 small ($< 1 \text{ kg}$) mammal species studied showed a modest or strong increase with decreasing AGB (Wearn *et al.* 2017, Fig. S3.6), while the remainder declined or were extirpated.

With these pronounced changes in abundance and community structure, we might therefore expect to observe changes in “vital rates” in Southeast Asian small mammal communities for several possible reasons. First, those species which increase in abundance and population density with logging may pay a cost in terms of increased disease and parasite transmission, or increased resource limitation and inter- or intra-specific competition, which may impact condition and demography in line with theories of density dependence (e.g. Albon, Mitchell & Staines 1983; Agrell *et al.* 1995; Krasnov, Khokhlova & Shenbrot 2002; Stewart *et al.* 2005). The importance of food limitation and competition in driving changes to condition and demography should depend somewhat on the factors limiting populations before and after logging. Still, increased density will probably drive parasite-mediated declines in condition, and increase competition regardless of the relative availability of food resources. Alternatively, the species which increase in abundance may prove sufficiently adaptable and resilient to show no change in “vital rates”, and we might conversely observe reduced condition and/or demographic rates in the minority of small mammal species which decline in abundance.

Either way, declines in body condition, reproductive output or survival among small mammal species along a logging gradient are of importance for conservation, revealing potentially hidden vulnerability to future environmental change, or uncovering proximal mechanisms for observed declines in already-vulnerable species. In this study, we modelled changes in these three parameters across a small mammal community in response to selective logging in Sabah, Malaysian Borneo, using biometric, demographic and mark-recapture data from a long-term monitoring project (Wearn *et al.* 2016, 2017; Chapman *et al.* 2018b). These data are available for several thousand individuals across a broad gradient of logging intensity, from pristine unlogged forest to remnant scrub forest which has been subjected to multiple rounds of logging. To control for spatial heterogeneity in this logging intensity and avoid oversimplification, we characterised the logging gradient with aboveground woody biomass and a standardised categorical forest condition score. We tested the hypothesis that as abundance changes with

logging disturbance, body condition, reproductive output and survival change concurrently among multiple species. Lastly, since survival in particular is likely to be affected by changes in the predation landscape, which may itself change with logging as some predatory species increase or decline (Wearn *et al.* 2017), we also tested for relationships between apparent survival and predator abundance across the gradient, to establish whether predation pressure is a better predictor of survival than habitat quality.

3.3 Material and Methods

3.3.1 Study area

We collected logged forest field data for this project at the Stability of Altered Forest Ecosystems project (SAFE), a landscape-scale ecological experiment located 60 km northwest of Tawau, Malaysian Borneo (Ewers *et al.* 2011). SAFE is situated within a 1-million ha state-managed logging concession, and comprises 7200 ha of logged lowland and hill dipterocarp forest. The landscape was subjected to 2-4 rounds of selective logging between the 1970s and the 2010s, with the early rounds targeting the highest value mature dipterocarp timber trees, and successive rounds removing more trees of reduced size (Pfeifer *et al.* 2016). During the multiple rounds of logging, above-ground tree biomass declined during this process by up to 73% (Pfeifer *et al.* 2016). Combined with the topographic complexity of the landscape, this process has created a heterogeneous forest landscape, including areas of heavily degraded scrubby vegetation with relict trees, and higher quality areas with considerable remnant canopy cover (Pfeifer *et al.* 2016), allowing sampling across a wide range of forest quality typical of the region. We collected primary forest field data at the Maliau Basin Conservation Area (MBCA), a protected area of old-growth high-canopy dipterocarp forest approximately 60 km further west from the SAFE project, but situated within the same forest concession.

3.3.2 Small mammal trapping

We trapped small mammals using a standardised grid design (Wearn *et al.* 2016, 2017), with grids comprising a 4 x 12 rectangular array of sampling points with 23 m separation (For more details and a schematic, see Section 2.3.2). At each point we placed two locally-made “Tomahawk”-style steel cage traps (29 x 12 x 18 cm). Traps were placed strictly within 5 m of each point on approximately 180° opposed bearings, but were preferentially sited in association with dense ground flora cover, fallen deadwood and brush, as these microhabitats are preferred by small mammals in both unlogged and logged forest (Bernard 2004). In both sampling areas, grid locations overlaid standard SAFE sampling points, and therefore our sampling grids were

controlled as much as possible for altitude, aspect, topography and drainage (Ewers *et al.* 2011). Traps were baited with a ripe oil palm (*Elaeis guineensis*) fruit, and covered with a black plastic wrapping to act as a rain and sun shelter for captured animals. We trapped each grid once annually for seven consecutive days, checking traps and processing captures in the early morning before resetting the traps for the following day/night.

In total, we sampled in 24 heavily-logged forest sites and 12 unlogged forest sites from May 2011 - October 2017 (see Wearn *et al.* 2017, live-trapping locations in Fig. 1a, 1c). Of these, ten logged and two unlogged sites were sampled at least twice, allowing estimation of apparent survival, although logged forest sites were not sampled in 2013 and unlogged sites were not sampled in 2012 for logistical reasons. The remaining 24 sites were sampled once, chiefly during 2011-12, and provide additional datapoints for estimating age ratios and body condition.

3.3.3. Small mammal processing and biometrics

Following standard ethical procedures (Sikes, Gannon & the American Society of Mammalogists 2011), we released stressed, injured or sick animals without processing. Where an animal was moribund or severely injured, it was euthanised humanely (<1 % of captures). Apart from these exceptions, we processed all captured small mammals on the grid, before releasing individuals at the original capture locations within one hour of processing. First, we lightly anaesthetised all captured small mammals to expedite accurate biometric measurements and reduce stress from handling; following other studies in the region we used diethyl ether (e.g. Wells *et al.* 2004, 2007a, 2013, Wearn *et al.* 2016, 2017). We identified all animals to species using Payne and Francis (1985), and aged and sexed them using genital morphology. Animals of adult size were aged as adult or subadult according to reproductive maturity (descended/developed testes in males, perforation of vaginal opening in females). Animals obviously below adult size and showing identifiable pelage differences were aged as juvenile.

We took linear biometric measurements to the nearest 0.1 mm using digital vernier calipers (Proops Brothers Ltd, UK). We used hind-foot length as a proxy for body size, measuring from the heel bone to the tip of the longest toe (excluding claws or nails). Compared with direct measures of body size such as than head-body length or head-to-pelvis length, hind-foot length is more repeatable and less prone to measurement error from stretching, and other sources of measurement error (Jewell & Fullagar 1966; Blackwell, Bassett & Dickman 2006). We also took ano-genital distance as a backup sexing methodology, and recorded body mass to the nearest 1g using a spring balance (Pesola AG, Switzerland).

Table 1. Scores used to describe forest quality or condition in our analyses (taken from Ewers *et al.* 2011), plus the corresponding mean above-ground biomass values to which they correspond for our sampling areas (from Pfeiffer *et al.* 2016).

FQS	Description	Mean AGB $\pm$ S.E (Mg.ha ⁻¹)
1	No standing trees, open canopy with ginger, vines or low scrub	3.98 $\pm$ 1.41
2	Open canopy with occasional small trees over a ginger and vine layer	35.33 $\pm$ 6.22
3	Small trees abundant and canopy at least partly closed	63.04 $\pm$ 10.30
4	Lots of trees including some large trees and a closed canopy	363.08 $\pm$ 85.68
5	No evidence of logging, closed canopy with large trees	488.34 $\pm$ 67.49

3.3.4 Habitat quality metrics

In our study, body condition was estimated at the scale of a sampled individual, while juvenile-adult ratio and apparent survival were estimated at the scale of a sampled population in a grid (see Sections 3.3.5 and 3.3.6). We recorded habitat quality differently for these metrics at different scales. For the grid-scale metrics, we extracted woody plant above-ground biomass values (Mg.ha⁻¹; hereafter abbreviated “AGB”) from Pfeiffer *et al.* (2016). These values were calculated at sampling points across the SAFE project landscape in 2011-12 (see Pfeiffer *et al.* 2016 for details of the calculation). Each small mammal trapping grid overlies two AGB sampling points, so we took the grid-level AGB value to be the mean of the two values. AGB values were not available on the scale of individual trapping points. Instead, for the individual-level analysis (body condition) we assayed habitat quality using a five-point categorical forest quality score (hereafter abbreviated “FQS”) developed for the SAFE project (Ewers *et al.* 2011, see Table 1). FQS scores have been shown to correlate strongly with AGB at our study site (Table 1; Pfeiffer *et al.* 2016).

3.3.5 Analyses: Body condition and age ratio

To produce body condition indices which account for the scaling relationships between linear size and mass, and which improve on the limitations of earlier methods such as mass-size regression residuals (Green 2001), we used the Scaled Mass Index (SMI, Equation 2 in Peig & Green 2009). We first excluded individuals with incomplete biometrics (i.e. missing mass or hind foot length), and cleaned the data to remove any obviously erroneous outliers (=0.4% of individuals). To calculate apparent reproductive output, we calculated the proportion of the total individuals within a single grid x year trapping sample which were adult, having removed

all individuals where aging was uncertain (12.5% of individuals). We pooled juveniles and subadults into one category, as the abundance of juveniles in the dataset was low for most species, and in practice the distinction was frequently subjective.

3.3.6 Analyses: Survival estimates

To estimate between-year apparent survival for our captured small mammal species, we used a subset of the data comprising the twelve grids trapped over at least two consecutive years. We constructed capture history data for all individuals in this dataset, reducing multiple appearances within annual trap sessions across several years to a binary presence-absence string with one value for each trapping session on that grid. For each sampling grid, we then ran Cormack-Jolly-Seber open-population mark-recapture models (hereafter “CJS models”) on the capture history data using program “Mark” v.9.0 (White & Burnham 1999), run remotely from R v.3.5.0 (R Core Team 2018), via package “Rmark” (Laake & Rexstad 2008). Since our sampling periods were not precisely separated by one-year intervals, with a gap of approximately two years for most grids in 2012 or 2013, we constructed models with grid-specific intervals specified in decimal years, allowing the models to account exactly for temporally uneven sampling effort and return apparent survival probability estimates corresponding to annual intervals. For each species, these models produced estimates of apparent survival across each annual interval (Φ) and capture probability within each year (p). Apparent survival does not distinguish between death and emigration, which can only be achieved by parameterising dispersal (Schaub & Royle 2014) which was not possible at our sites. As well as varying by species and between years, Φ and p may depend on other covariates including age and sex. We therefore took a model selection approach, fitting CJS models of increasing complexity, with Φ and p dependent on a combination of year, age, species and sex effects. We compared between fitted models using Akaike’s Information Criterion (AIC).

3.3.7. Analyses: models of demographic parameters against forest quality

To test whether body condition, apparent reproductive output, and apparent survival decline with increasing logging disturbance we constructed generalised linear mixed models in R 3.5.0 (R Core Team 2018), using package “lme4” (Bates *et al.* 2015). Before analysis, we excluded individuals with uncertain species identification, aging or sexing. We corrected P -values for multiple testing among the species using False Discovery Rates (Pike 2011), and we use Conditional and Marginal R^2 (Nakagawa & Schielzeth 2013) to quantify the explanatory power of our models.

First, we modelled Scaled Mass Index of individuals against the five-level Forest Quality Score (Gaussian models with identity link), in each case taking the FQS value for the trap at the point of first capture. If body condition is density-dependent, it should vary inter-annually in addition to across the logging gradient, since density itself does so (Chapter 2). We might also expect body condition to vary monthly since many small mammals display monthly breeding peaks, even in this largely aseasonal environment (Emmons 2000). Therefore we controlled for this structure using capture year and month as crossed random effects. We used a model selection approach to test for effects of age and sex on body condition, fitting these terms as main effects, and in two-way interactions with forest quality score. Again, we used AIC to select the best-fitting model.

Second, we modelled the ratio of captured adults to subadults for each grid in each sampling year against log-transformed (base 10) grid-level AGB using binomial models with logit link function. Again, we controlled for month and year as crossed random effects, and also added “grid” as a third crossed random effect to control for grid-level differences not due to logging or habitat quality.

Third, we modelled our estimates of apparent survival in each grid x species x interannual interval combination against log-transformed grid-level AGB. The apparent survival estimates are proportion data bounded by zero and one, so we logit-transformed the raw data for analysis in linear mixed models with Gaussian error. We controlled for grid and survival interval as crossed random effects to account for grid-level differences not due to logging or habitat quality, and for interval-specific effects on survival. The accuracy of apparent survival estimates increases with the number of captures they are based upon, so we weighted data points for this analysis by the overall number of captures. We found that CJS models failed to converge when the total number of captures used for an estimate was less than five, so we excluded any grid x species combination where this condition was not met.

3.3.8. Analyses: Testing for underlying survival-predator abundance relationships

To test whether apparent survival is affected by variation in the abundance of predators, we calculated pooled relative abundance of predatory species in our small mammal trapping sites based on camera trap data (following e.g. Wearn *et al.* 2013, 2016, 2017; for a full description of this process, see Appendix B, Supplementary Methods B1). For logistical reasons, camera trap data was not available for every modelled survival interval, and we therefore could not use predator relative abundance as a further random effect in our main models of apparent survivorship against AGB without discarding large proportions of the data. Instead, we separately tested for an underlying relationship between predator abundance and survival

using linear models, and including only the survival intervals for which a predator abundance estimate was available. Again, we logit-transformed the survival estimates before analysis, weighted points based on the number of individuals forming the survival estimate, and controlled for multiple testing using False Discovery Rates (see Section 3.3.7). Since the degree to which most predatory vertebrates predate our species is poorly-known, we conducted this analysis twice, first with all potential predatory species included in the pooled estimate, and second including only those species which are likely to be major predators of small mammals (for further details, including how we made this distinction, see Appendix B, Supplementary Methods B1).

3.4 Results

3.4.1 Trapping success

In total, we trapped for 37632 trap-nights in logged forest and 11424 trap-nights in unlogged forest. We captured 3346 identifiable small mammals (6.82 captures per 100 trap-nights) comprising 21 species of which three were invasive (Table 2). After removing any individuals (n=395) where either age, sex, or both were uncertain, and excluding eight species due to inadequate sample size (fewer than 5 captures in any grid x year combination) we used 2891 individuals of 13 species for analysis. Of these, 2563 individuals were caught in logged forest and 328 were caught in unlogged forest (Table 2).

3.4.2 Effects of forest quality on small mammal demographics

Across all species, the best-supported body condition models were the most complex, incorporating main effects of sex and age, and interactions between these parameters and FQS (lowest AICs in each case, see Table A1). There was no significant difference in body condition between the five levels of FQS for any species, and for the models only incorporating FQS as a fixed effect, the low values of marginal R^2 indicate that very little variance was explained by this term (Table 3, Fig. 1). Age strongly predicted body condition in 10 of 13 species, with subadults displaying lower body condition while sex predicted body condition for one species, Low's Squirrel *Sundasciurus lowii* (Table 3) with males displaying lower body condition. There were no significant FQS-age or FQS-sex interactions after correcting for multiple testing using False Discovery Rates (Table 3).

Table 2. Numbers of individuals of 21 small mammal species captured in logged (L) and unlogged (UL) forest in Sabah between 2011 and 2017. Total numbers captured, and numbers with known age and sex are displayed. Crosses † denote invasive species and bold type denotes the usage of a species in the analyses (based on sample size).

Species	All individuals			Known age/sex		
	Total	L	UL	Total	L	UL
<i>Callosciurus adamsi</i> (Earspot Squirrel)	22	22	0	19	19	0
<i>Callosciurus notatus</i> (Plantain Squirrel)	2	2	0	1	1	0
<i>Lariscus hosei</i> (Four-striped Ground Squirrel)	17	16	1	16	16	0
<i>Leopoldamys sabamus</i> (Long-tailed Giant Rat)	208	172	36	189	156	33
<i>Maxomys baeodon</i> (Small Spiny Rat)	317	314	3	255	252	3
<i>Maxomys ochraceiventer</i> (Chestnut-Bellied Spiny Rat)	10	2	8	8	1	7
<i>Maxomys rajah</i> (Brown Spiny Rat)	232	6	226	208	6	202
<i>Maxomys surifer</i> (Red Spiny Rat)	552	529	23	481	461	20
<i>Maxomys whiteheadi</i> (Whitehead's Rat)	734	715	19	644	628	16
<i>Niviventer cremoriventer</i> (Dark-tailed Tree Rat)	295	276	19	256	239	17
<i>Rattus exulans</i> (Polynesian Rat)†	114	114	0	111	111	0
<i>Rattus rattus</i> (Black Rat)†	93	93	0	87	87	0
<i>Rattus tiomanicus</i> (Malaysian Field Rat)†	2	2	0	2	2	0
<i>Sundasciurus hippurus</i> (Horse-tailed Squirrel)	9	8	1	8	7	1
<i>Sundasciurus lowii</i> (Low's Squirrel)	244	227	17	216	201	15
<i>Sundamys muelleri</i> (Muller's Rat)	156	152	4	142	139	3
<i>Tupaia dorsalis</i> (Striped Treeshrew)	1	0	1	1	0	1
<i>Tupaia gracilis</i> (Slender Treeshrew)	105	104	1	91	90	1
<i>Tupaia longipes</i> (Common Treeshrew)	103	88	15	98	84	14
<i>Tupaia minor</i> (Lesser Treeshrew)	7	7	0	5	5	0
<i>Tupaia tana</i> (Large Treeshrew)	123	119	4	113	109	4
TOTAL CAPTURES	3346	2968	378	2951	2614	337
TOTAL ANALYSED				2891	2563	328

Table 3. Results of generalised linear mixed models of small mammal body condition (scaled mass index) as a function of forest quality score (FQS), age, sex, FQS-age and FQS-sex interactions, for thirteen species. Marginal and conditional R² (Nakagawa and Schielzeth 2013) are shown, as well as F and P-values for the fixed effects in each model. P-values are corrected for multiple testing using False Discovery Rates (Pike 2011). For the uncorrected values and details of the model selection, see Table A1.

Species	R ² Cond.	R ² Marg.	Fixed Effects									
			FQS		Age		Sex		FQS:age		FQS:sex	
			F	P	F	P	F	P	F	P	F	P
<i>Leopoldamys sabamus</i> (Long-tailed Giant Rat)	0.257	0.170	1.937	NS	6.206	0.022	2.240	NS	1.233	NS	0.588	NS
<i>Maxomys baeodon</i> (Small Spiny Rat)	0.323	0.178	0.595	NS	2.017	NS	1.962	NS	0.468	NS	1.009	NS
<i>Maxomys rajah</i> (Brown Spiny Rat)	0.225	0.035	0.948	NS	7.377	0.015	1.068	NS	0.443	NS	0.105	NS
<i>Maxomys surifer</i> (Red Spiny Rat)	0.250	0.146	0.197	NS	21.268	<0.001	5.625	NS	1.450	NS	2.464	NS
<i>Maxomys whiteheadi</i> (Whitehead's Rat)	0.756	0.028	1.042	NS	2.224	NS	1.840	NS	1.189	NS	0.595	NS
<i>Niviventer cremoriventer</i> (Dark-tailed Tree Rat)	0.069	0.069	0.888	NS	9.360	0.005	1.573	NS	0.497	NS	0.690	NS
<i>Rattus exulans</i> (Polynesian Rat)	0.252	0.096	0.351	NS	10.307	0.005	5.933	NS	1.209	NS	0.052	NS
<i>Rattus rattus</i> (Black Rat)	0.539	0.080	0.195	NS	0.911	NS	0.623	NS	0.740	NS	0.391	NS
<i>Sundamys muelleri</i> (Muller's Rat)	0.188	0.108	0.892	NS	6.209	0.022	2.432	NS	1.494	NS	0.502	NS
<i>Sundasciurus lowii</i> (Low's Squirrel)	0.140	0.070	0.463	NS	12.574	0.003	14.637	0.002	1.123	NS	2.514	NS
<i>Tupaia gracilis</i> (Slender Treeshrew)	0.259	0.067	0.284	NS	4.314	0.053	0.473	NS	0.908	NS	0.513	NS
<i>Tupaia longipes</i> (Common Treeshrew)	0.241	0.078	0.028	NS	6.190	0.022	0.310	NS	0.706	NS	0.707	NS
<i>Tupaia tana</i> (Large Treeshrew)	0.200	0.079	0.906	NS	12.175	0.004	5.449	NS	0.529	NS	0.396	NS

Table 4. Mean ($\pm$ S.E) interannual apparent survival estimates, status (invasive or native) and mean body mass ($\pm$ S.E.) for thirteen small mammal species. Body mass data are calculated from all identifiable individuals in the dataset (total $n = 3179$). Common names follow Payne and Francis (1985).

Species	Family	Mean apparent survival ($\pm$ S.E.)	Status	Mean body mass ($\pm$ S.E.)
<i>Leopoldamys sabamus</i> (Long-tailed Giant Rat)	Muridae (Rats)	0.197 $\pm$ 0.039	Native	293.47 $\pm$ 3.45
<i>Maxomys baeodon</i> (Small Spiny Rat)	Muridae (Rats)	0.210 $\pm$ 0.033	Native	53.04 $\pm$ 0.49
<i>Maxomys rajah</i> (Brown Spiny Rat)	Muridae (Rats)	0.148 $\pm$ 0.053	Native	93.55 $\pm$ 2.24
<i>Maxomys surifer</i> (Red Spiny Rat)	Muridae (Rats)	0.257 $\pm$ 0.025	Native	116.64 $\pm$ 1.20
<i>Maxomys whiteheadi</i> (Whitehead's Rat)	Muridae (Rats)	0.179 $\pm$ 0.030	Native	44.08 $\pm$ 0.32
<i>Niviventer cremoriventer</i> (Dark-tailed Tree Rat)	Muridae (Rats)	0.053 $\pm$ 0.011	Native	58.62 $\pm$ 0.80
<i>Rattus exulans</i> (Polynesian Rat)	Muridae (Rats)	0.028 $\pm$ 0.019	Invasive	45.64 $\pm$ 2.20
<i>Rattus rattus</i> (Black Rat)	Muridae (Rats)	0.000 $\pm$ 0.000	Invasive	99.35 $\pm$ 2.29
<i>Sundamys muelleri</i> (Muller's Rat)	Muridae (Rats)	0.177 $\pm$ 0.039	Native	174.63 $\pm$ 3.17
<i>Sundasciurus lowii</i> (Low's Squirrel)	Sciuridae (Squirrels)	0.457 $\pm$ 0.034	Native	89.34 $\pm$ 0.91
<i>Tupaia gracilis</i> (Slender Treeshrew)	Tupaiaidae (Treeshrews)	0.089 $\pm$ 0.024	Native	66.84 $\pm$ 0.89
<i>Tupaia longipes</i> (Common Treeshrew)	Tupaiaidae (Treeshrews)	0.215 $\pm$ 0.040	Native	161.65 $\pm$ 3.28
<i>Tupaia tana</i> (Large Treeshrew)	Tupaiaidae (Treeshrews)	0.386 $\pm$ 0.040	Native	183.22 $\pm$ 2.63

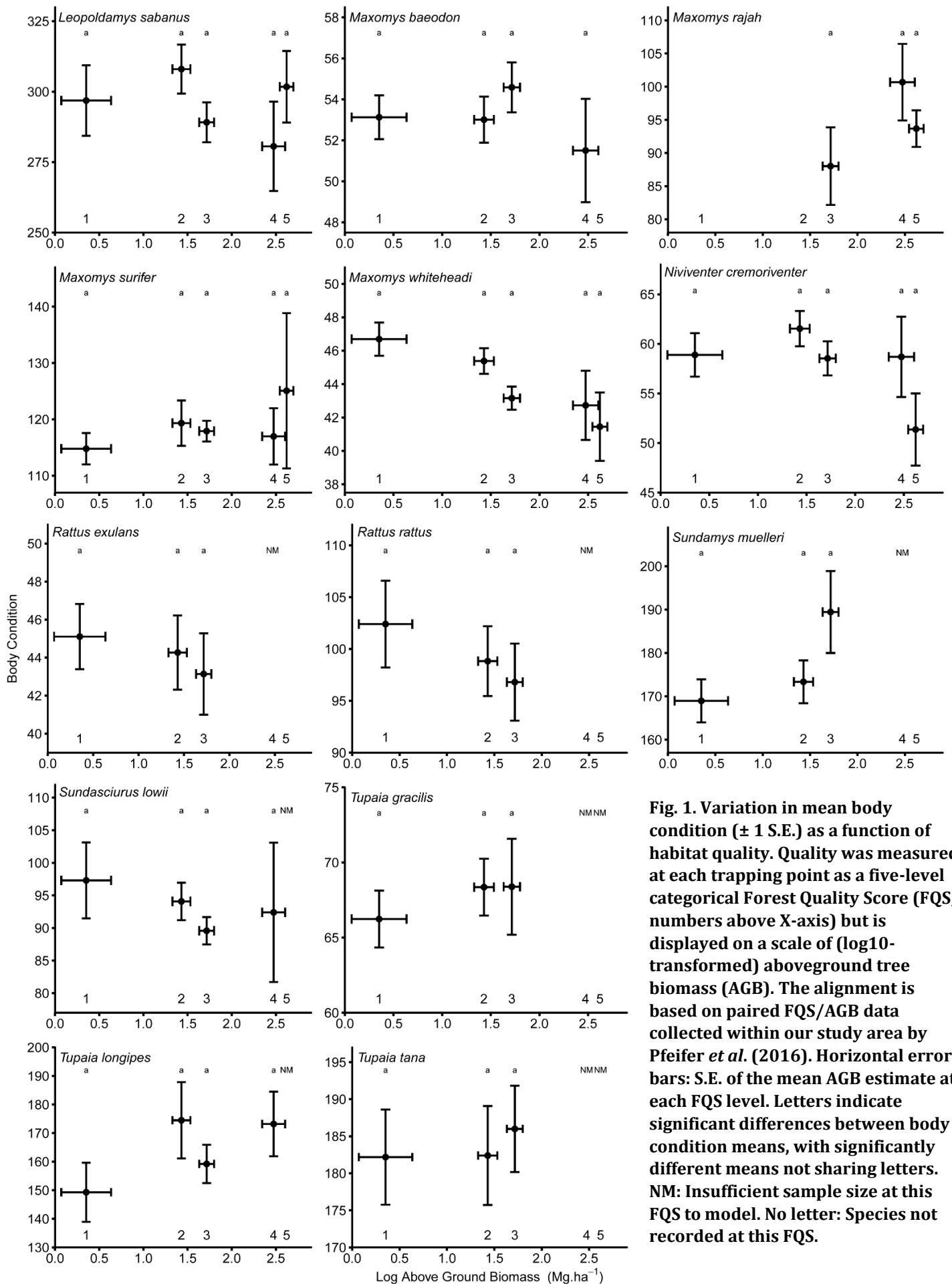


Fig. 1. Variation in mean body condition (± 1 S.E.) as a function of habitat quality. Quality was measured at each trapping point as a five-level categorical Forest Quality Score (FQS, numbers above X-axis) but is displayed on a scale of (log10-transformed) aboveground tree biomass (AGB). The alignment is based on paired FQS/AGB data collected within our study area by Pfeifer *et al.* (2016). Horizontal error bars: S.E. of the mean AGB estimate at each FQS level. Letters indicate significant differences between body condition means, with significantly different means not sharing letters. NM: Insufficient sample size at this FQS to model. No letter: Species not recorded at this FQS.

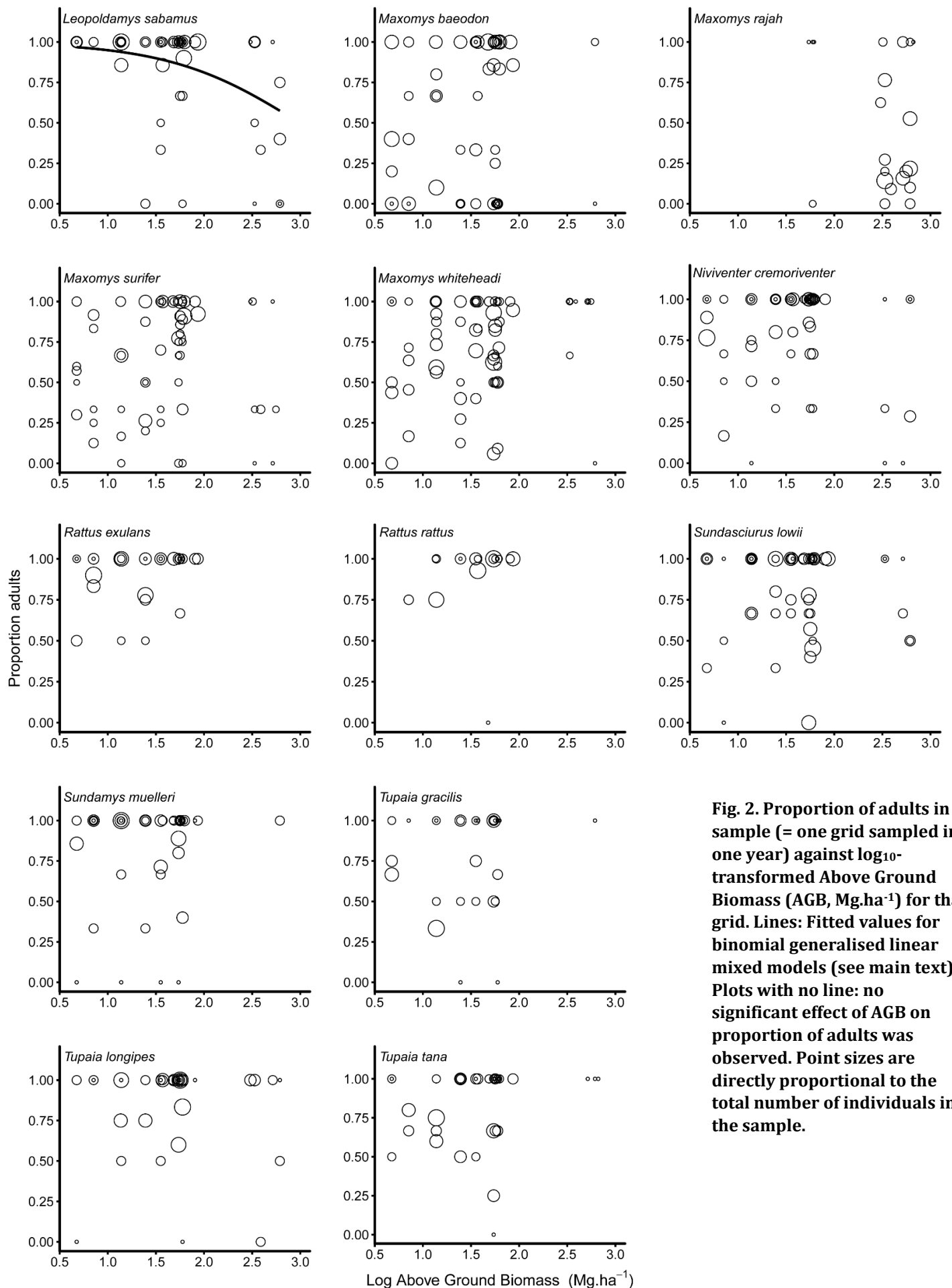


Fig. 2. Proportion of adults in a sample (= one grid sampled in one year) against log₁₀-transformed Above Ground Biomass (AGB, Mg.ha⁻¹) for that grid. Lines: Fitted values for binomial generalised linear mixed models (see main text). Plots with no line: no significant effect of AGB on proportion of adults was observed. Point sizes are directly proportional to the total number of individuals in the sample.

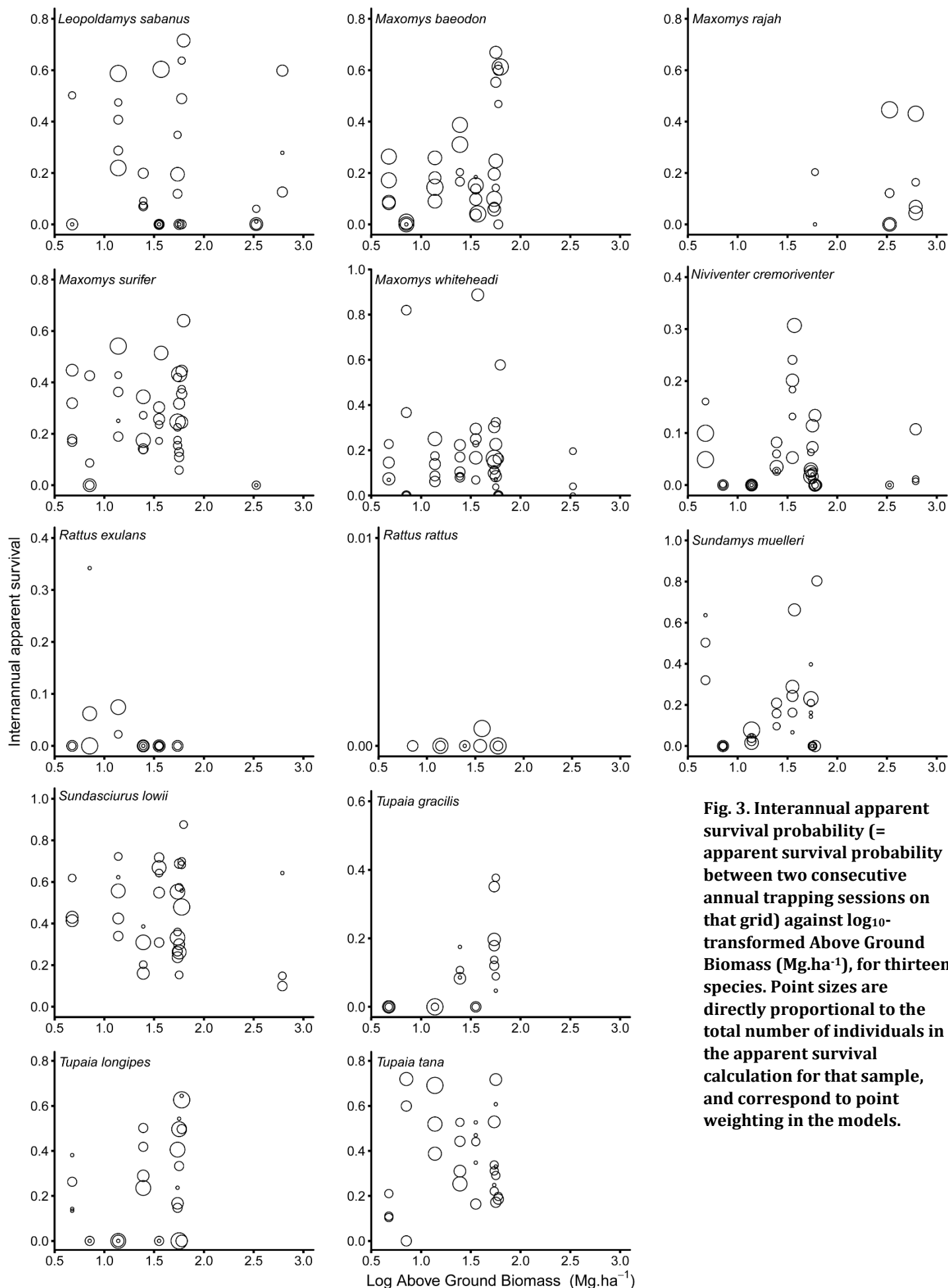


Fig. 3. Interannual apparent survival probability (= apparent survival probability between two consecutive annual trapping sessions on that grid) against log₁₀-transformed Above Ground Biomass (Mg.ha⁻¹), for thirteen species. Point sizes are directly proportional to the total number of individuals in the apparent survival calculation for that sample, and correspond to point weighting in the models.

The proportion of adults in the sampled population did not alter with AGB for any species (Table A2) except Long-Tailed Giant Rat, *Leopoldamys sabamus*, where it decreased with increasing AGB ($Z=-1.470$, $P=0.01$; Table A2; Fig. 2).

All species had a mean apparent interannual survival probability of less than 50%, however this varied across taxa, status (invasive or native) and body mass, with larger species generally having higher survival, and highest survival in Large Treeshrew and Low's Squirrel (Table 4). Both invasive rat species modelled had particularly low apparent survival: in particular, none of the 92 individuals of *Rattus rattus* were ever recaptured (Table 4). Perhaps because of the effectively zero apparent survival, our models comparing survival of this species to AGB failed to converge. However, we found no relationship between apparent survival and AGB for any other species (all $P>0.05$; Fig. 3; Table A3).

3.4.3. Relationship between predator abundance and small mammal survival

In total, our camera trap data produced 610 independent individuals of 24 predatory species, of which 268 individuals comprised the 12 species most likely to significantly predate small mammals (Appendix B, Table B1). We modelled the apparent survival-predator abundance relationship for 12 of our 13 small mammal species, omitting *Maxomys rajah* due to very low sample size (see Appendix B, Supplementary Text B1.3). While apparent survival of some small mammal species appeared to show weak relationships with pooled predator abundance, these were not significant after correcting for multiple testing using False Discovery Rates, either when all predatory species were modelled or when the analysis was restricted to “major” predators (Table B2, Fig. B1, Fig. B2).

3.5 Discussion

To our knowledge, our study represents the first investigation of changes in body condition, survival or reproductive output of a community of small mammals in tropical forest over a disturbance gradient. Despite the dramatic population increase of most small mammals with increased logging intensity reported by Wearn *et al.* (2017), we found little evidence to suggest that species with denser populations in logged forest pay a cost in terms of reduced condition or demographic rates. We also found no evidence that those species which decline in logged forest do so in association with reduced body condition, decreased reproductive output or lower survival, although we note that the species that declined most strongly were too thoroughly extirpated in logged forest for any such changes to be observable. Overall, our results suggest

that the future is positive for those small mammals which survive the initial disturbance from logging, but underline the need for a more mechanistic understanding, particularly of species which are vulnerable.

3.5.1 Little evidence for declining condition or demographic rates with increasing density

We hypothesised that the dramatic population abundance increase of most small mammals in logged forest observed by Wearn *et al.* (2017) may be accompanied by changes in body condition, apparent reproductive output or apparent survival. This might occur if those species which increase in abundance consistently pay a cost in terms of increased competition, disease transmission or other density-dependent processes which impact these parameters. However, we found little evidence to support this, with no change at all in condition and apparent survival for any of our thirteen species, and decreasing proportion of juveniles only for Long-tailed Giant Rats, *Leopoldamys sabamus*. Interannual apparent survival of *L. sabamus* did not increase over the gradient, suggesting that this trend indeed represents decreased reproductive output in logged forest, rather than reduced lifespan of adults. *L. sabamus* increased in abundance with reduced AGB (Wearn *et al.* 2017), so this decline in apparent reproductive output may represent a density-dependent impact. Since *L. sabamus* is semi-arboreal, it is possible that the lower canopy in logged forest brings it into increased interspecific competition with more terrestrial species, thus impacting reproductive output, although the evidence that logging alters space use in *L. sabamus* is equivocal (Wells *et al.* 2006, 2008). We also found no evidence to suggest that survival was more closely linked to underlying variation in predation pressure than to habitat quality, with no species showing decreasing survival with increasing relative abundance of predators, regardless of the probable strength of the trophic link (Table B2, Figs. B1-B2). While the relatively coarse temporal congruence between our camera trap and live trap datasets limits the strength of this conclusion, these results nevertheless support previous observations that top-down control in tropical forests is often of limited, or sporadic importance (Meserve *et al.* 2003, Brodie *et al.* 2013), and suggest that the lack of relationship between AGB and survival is not a result of strong confounding variation in predator abundance.

3.5.2 No evidence for altered condition or demographic rates in declining species

An alternative pattern which we might observe over the deforestation gradient is declines in demographic rates among species which decline with logging. We still know very little about the factors causing some mammal species to persist and increase after logging while others decline, although at a macro-ecological scale, phylogenetic age, which frequently correlates with dietary and other functional specialisations, appears to be a major contributing factor (Meijaard *et al.*

2008). Declining availability of foods or reduced foraging efficiency relative to more generalist competitors might drive population declines by reducing body condition, and in turn decreasing reproductive output or survival. However, we found no evidence for this in the two species in our study which decline with logging: the Brown Spiny Rat *Maxomys rajah*, which shows pronounced cross-gradient declines (Wearn *et al.* 2017), or the Small Spiny Rat *M. baeodon*, which initially survives logging in good numbers, but appears to be declining gradually through time in heavily-logged forest (Chapter 1; Chapman *et al.* 2018b).

The reasons for this are unclear. We know very little about the dietary requirements of these species, although populations of *M. rajah* fluctuate strongly with dipterocarp mast-fruiting (Wells & Bagchi 2005; Nakagawa *et al.* 2007b). While the evolutionary divergence of *Maxomys* appears to predate the last glacial maximum (Ruedas & Kirsch 1997; Gorog, Sinaga & Engstrom 2004), neither species appears to be particularly phylogenetically old, or specialised (Payne & Francis 1985). It is therefore possible that the mechanisms of decline are not strongly related to food availability and do not leave a strong trace on body condition or demography of either species.

However, in the case of *M. rajah*, we may not have observed any change in condition or demographics simply because its decline with logging in our study system was near-absolute, and too rapid to manifest itself in these parameters. Only a handful of individuals were detected in logged forest, and the species was not present at all in forest with AGB <60 Mg.ha⁻¹ (Table 2, Figs 1-3). The reverse is true of *M. baeodon*, which is present at very low density in unlogged forest. Together, these patterns highlight a more general caveat to these results: turnover of community composition with logging is very high. This realistically means that for most species, we could not sample sufficient numbers of individuals across the entire gradient of forest quality: for most species we were largely testing across varying logging intensities, with only a handful of individuals or trapping grids representing unlogged forest (Figs 2-3). Conversely, in the case of *M. rajah* we were mostly testing across the natural range of AGB found in unlogged forest. In the light of this, it is perhaps less surprising that the only change in demographic rates we found was the decline in reproductive output in *Leopoldamys. sabamus*, one of the most evenly distributed species across the gradient (Table 2).

3.5.3 Conservation implications

Despite this caveat limiting the strength of our comparisons between logged forest and unlogged forest, our results nevertheless show a remarkable lack of change in body condition and demographic rates for multiple species in logged forest of variable quality. Our logged sites covered a broad gradient of logging intensity from light damage to almost treeless scrub, and

accompany stark changes in abundance of most species across this range (Wearn *et al.* 2017). Previous predictions (Johns 1986), and some empirical evidence from primates (Grieser Johns & Grieser Johns 1995; Olupot 2000; Amato *et al.* 2013) suggest that logged forest can represent a suboptimal environment for mammals, with reduced condition, reproductive output and survival negatively impacting prospects for persistence. Other authors have suggested that intensively-logged areas can represent high-mortality “sinks” for excess individuals from higher-quality patches (Gilroy & Edwards 2017). However, our study reveals very little support for these predictions. Rather, we suggest that most species which survive the initial shock of logging are likely to persist well in logged forest, and may prove resilient in the long term, at least in the absence of further threats such as fragmentation of the remaining tracts of logged forest or conversion to plantation agriculture, both of which have severe effects on small mammal diversity and abundance (Gibson *et al.* 2013; Wearn *et al.* 2016, 2017).

However, there are several reasons for caution and further investigation. The high turnover of community abundances in general, and near-complete disappearance of *Maxomys rajah* from logged forest in particular, underline the fact that some species simply decline too rapidly and completely for condition and demographic data to provide any useful mechanistic insight. Despite being by far the most abundant species captured in unlogged forest, *M. rajah* simply disappears from all but the most lightly-logged forest (Table 2, Fig. 1), as do several other species which appeared in our dataset too rarely to analyse (such as Horse-Tailed Squirrel *Sundasciurus hippurus* and Chestnut-Bellied Spiny Rat *Maxomys ochraceiventer* (Table 2). The latter species is relatively terrestrial but generally scarce, and does seem to disappear in logged forest. However, some “rare” species, such as the larger squirrels, are strongly arboreal, so our sampling design is probably inadequate to robustly test their responses to logging. More detailed dietary and habitat selection work, perhaps trapping at multiple canopy strata, is probably essential to understand why these species are so intolerant to logging. A study of body condition and demographics which temporally straddles logging of a primary (or barely-degraded) forest, with a fine temporal grain of sampling, would improve our understanding of the proximate mechanisms driving these species to extinction. Meanwhile, the congeneric *Maxomys baeodon* appears to be declining in abundance through time (Chapter 1, Chapman *et al.* 2018b), despite retaining similar body condition, reproductive output and apparent survival, and therefore a mechanistic understanding of this species’ logging response also remains elusive.

By contrast, the invasion of the two *Rattus* species into heavily-logged forest is superficially successful with *R. rattus* particular exploiting new niches (Loveridge *et al.* 2016). However, survival of both *R. rattus* and *R. exulans* was extremely low (Table 4). It is possible that this is simply an artefact of different life-histories: if *R. rattus* and *R. exulans* are much less sedentary

than other murids in this system, the probability of recapturing individuals could be much lower. A different sampling design which allowed for spatially explicit survival estimation (Schaub & Royle 2014) would be a valuable next step to properly differentiate these scenarios; However, we suggest that the complete disappearance of *R. rattus* from our study system after 2012 is more indicative of a transient invasion and very low survival. The fact that we recaptured several of these species in oil palm plantations despite low numbers of individuals tagged (Chapter Five) also suggests that at least in agricultural habitats, they are not highly transient. Clearly, stable individual condition and demography are not always totally sufficient to predict a positive future for small mammals in logged tropical forest. Overall however, the generality with which body condition, reproductive output and apparent survival are resilient to logging intensity despite changes in abundance suggest that on the whole, species which *can* survive logging in the first place generally thrive, regardless of further logging in their environment.

3.6 Appendix A

Table A1. Results of generalised linear mixed models of small mammal body condition (scaled mass index) as a function of forest quality score (FQS, see main text), age, sex, FQS-age and FQS-sex interactions, for thirteen species. Models of sequentially increasing complexity are shown, with AIC values for comparison, as well as marginal and conditional R², and F and P-values (uncorrected for multiple testing) for the fixed effects in each model. The model we selected is highlighted in bold text in the Model Specification and AIC columns, significant fixed effects are also in bold. Species names are abbreviated for space: for a key, see footnote.

Species	Model specification	AIC	R ² Cond.	R ² Marg.	Fixed Effects									
					FQS		Age		Sex		FQS:age		FQS:sex	
					F	P	F	P	F	P	F	P	F	P
BIR	~FQS only	724.04	0.466	0.004	0.606	0.550								
BIR	~FQS +age	717.57	0.481	0.013	0.715	0.493	2.528	0.116						
BIR	~FQS +sex	720.11	0.479	0.037	0.818	0.445			1.134	0.291				
BIR	~FQS +age +sex	713.95	0.511	0.062	0.903	0.410	2.167	0.145	0.832	0.365				
BIR	~FQS+age +sex +FQS:age	700.68	0.528	0.076	0.158	0.854	1.161	0.285	0.537	0.466	0.834	0.438		
BIR	~FQS+age +sex +FQS:sex	703.93	0.514	0.064	1.242	0.295	2.115	0.150	0.963	0.330			0.508	0.604
BIR	~FQS+age+sex+FQS:age+FQS:sex	690.85	0.539	0.080	0.195	0.824	0.911	0.343	0.623	0.433	0.740	0.481	0.391	0.678
BSR	~FQS only	1979.4	0.233	0.011	0.667	0.514								
BSR	~FQS +age	1963.6	0.232	0.011	0.684	0.506	13.618	<0.001						
BSR	~FQS +sex	1976.2	0.247	0.025	0.707	0.494			0.762	0.384				
BSR	~FQS +age +sex	1959.9	0.246	0.026	0.728	0.484	14.195	<0.001	1.312	0.253				
BSR	~FQS+age +sex +FQS:age	1949	0.228	0.029	1.077	0.343	7.325	0.007	1.143	0.286	0.531	0.589		
BSR	~FQS+age +sex +FQS:sex	1949.9	0.248	0.031	0.621	0.538	14.139	<0.001	1.427	0.234			0.189	0.828
BSR	~FQS+age+sex+FQS:age+FQS:sex	1939.2	0.225	0.035	0.948	0.389	7.377	0.007	1.068	0.303	0.443	0.643	0.105	0.900
CoT	~FQS only	961.41	0.145	0.005	0.956	0.417								
CoT	~FQS +age	945.1	0.157	0.044	1.358	0.261	11.939	0.001						
CoT	~FQS +sex	955.39	0.263	0.052	0.866	0.462			1.724	0.193				
CoT	~FQS +age +sex	939.76	0.233	0.066	1.246	0.298	11.169	0.001	1.129	0.291				
CoT	~FQS+age +sex +FQS:age	915.15	0.243	0.074	0.050	0.985	8.519	0.005	0.464	0.498	1.264	0.292		
CoT	~FQS+age +sex +FQS:sex	917.21	0.229	0.068	0.935	0.428	9.210	0.003	1.156	0.286			1.276	0.288
CoT	~FQS+age+sex+FQS:age+FQS:sex	893.94	0.241	0.078	0.028	0.994	6.190	0.015	0.310	0.580	0.706	0.551	0.707	0.551
DTR	~FQS only	2121	0.006	0.006	0.837	0.503								
DTR	~FQS +age	2106.5	0.008	0.008	0.447	0.775	13.188	<0.001						

DTR	~FQS +sex	2118.8	0.038	0.038	0.810	0.520			1.083	0.299				
DTR	~FQS +age +sex	2105.2	0.044	0.044	0.443	0.778	12.163	0.001	0.192	0.662				
DTR	~FQS+age +sex +FQS:age	2087.1	0.051	0.051	0.856	0.491	10.264	0.002	0.271	0.603	0.500	0.736		
DTR	~FQS+age +sex +FQS:sex	2088.2	0.059	0.059	0.429	0.788	11.438	0.001	1.656	0.199			0.698	0.594
DTR	~FQS+age+sex+FQS:age+FQS:sex	2070	0.069	0.069	0.888	0.472	9.360	0.002	1.573	0.211	0.497	0.738	0.690	0.599
LaT	~FQS only	1062.5	0.084	0.001	0.185	0.832								
LaT	~FQS +age	1047.9	0.092	0.004	0.403	0.669	10.884	0.001						
LaT	~FQS +sex	1053.6	0.149	0.045	0.235	0.791			5.118	0.026				
LaT	~FQS +age +sex	1037.7	0.164	0.053	0.374	0.689	12.414	0.001	6.612	0.012				
LaT	~FQS+age +sex +FQS:age	1024.8	0.188	0.071	0.838	0.436	12.242	0.001	6.297	0.014	0.531	0.589		
LaT	~FQS+age +sex +FQS:sex	1026.1	0.171	0.062	0.460	0.633	12.397	0.001	5.509	0.021			0.403	0.670
LaT	~FQS+age+sex+FQS:age+FQS:sex	1013.1	0.200	0.079	0.906	0.408	12.175	0.001	5.449	0.022	0.529	0.591	0.396	0.674
LoS	~FQS only	1893.4	0.088	0.014	0.558	0.644								
LoS	~FQS +age	1880.7	0.108	0.028	0.365	0.778	10.206	0.002						
LoS	~FQS +sex	1888	0.155	0.042	0.610	0.609			3.361	0.068				
LoS	~FQS +age +sex	1870.2	0.162	0.050	0.320	0.811	15.569	<0.001	8.595	0.004				
LoS	~FQS+age +sex +FQS:age	1854.3	0.169	0.059	0.413	0.744	12.341	0.001	8.267	0.004	0.621	0.602		
LoS	~FQS+age +sex +FQS:sex	1851.7	0.139	0.064	0.215	0.886	14.346	<0.001	13.983	<0.001			2.022	0.112
LoS	~FQS+age+sex+FQS:age+FQS:sex	1834.2	0.140	0.070	0.463	0.708	12.574	<0.001	14.637	<0.001	1.123	0.341	2.514	0.060
LTR	~FQS only	2063.5	0.095	0.011	1.801	0.131								
LTR	~FQS +age	2050.4	0.178	0.085	1.433	0.225	8.352	0.004						
LTR	~FQS +sex	2059.1	0.190	0.114	1.780	0.135			0.170	0.680				
LTR	~FQS +age +sex	2045.2	0.243	0.160	1.393	0.238	9.211	0.003	1.022	0.313				
LTR	~FQS+age +sex +FQS:age	2012.1	0.238	0.158	1.593	0.178	6.531	0.011	1.081	0.300	1.073	0.371		
LTR	~FQS+age +sex +FQS:sex	2017.9	0.259	0.171	1.369	0.247	8.135	0.005	1.878	0.172			0.424	0.791
LTR	~FQS+age+sex+FQS:age+FQS:sex	1983.9	0.257	0.170	1.937	0.106	6.206	0.014	2.240	0.136	1.233	0.299	0.588	0.671
MuR	~FQS only	1460.1	0.114	0.037	2.767	0.066								
MuR	~FQS +age	1450.1	0.137	0.051	1.990	0.141	5.561	0.020						
MuR	~FQS +sex	1453.9	0.143	0.072	2.699	0.071			2.328	0.129				
MuR	~FQS +age +sex	1443.7	0.170	0.088	1.907	0.153	5.853	0.017	2.640	0.107				
MuR	~FQS+age +sex +FQS:age	1428.2	0.169	0.093	0.853	0.429	6.049	0.015	2.474	0.118	1.416	0.246		
MuR	~FQS+age +sex +FQS:sex	1431.9	0.188	0.102	1.759	0.176	5.840	0.017	2.563	0.112			0.410	0.665

MuR	~FQS+age+sex+FQS:age+FQS:sex	1416.3	0.188	0.108	0.892	0.412	6.209	0.014	2.432	0.121	1.494	0.228	0.502	0.606
PoR	~FQS only	850.7	0.213	0.032	0.577	0.563								
PoR	~FQS +age	836.2	0.205	0.032	0.389	0.678	12.628	0.001						
PoR	~FQS +sex	840.05	0.207	0.070	0.474	0.624			9.456	0.003				
PoR	~FQS +age +sex	827.99	0.196	0.076	0.317	0.729	10.161	0.002	7.008	0.009				
PoR	~FQS+age +sex +FQS:age	817.59	0.211	0.081	0.391	0.677	10.484	0.002	6.507	0.012	1.186	0.310		
PoR	~FQS+age +sex +FQS:sex	821.64	0.237	0.088	0.266	0.767	9.910	0.002	6.005	0.016			0.006	0.994
PoR	~FQS+age+sex+FQS:age+FQS:sex	811.13	0.252	0.096	0.351	0.705	10.307	0.002	5.933	0.017	1.209	0.303	0.052	0.949
RSR	~FQS only	4688.4	0.125	0.003	0.179	0.949								
RSR	~FQS +age	4668.3	0.167	0.048	0.309	0.872	18.899	<0.001						
RSR	~FQS +sex	4685.3	0.196	0.090	0.167	0.955			1.158	0.282				
RSR	~FQS +age +sex	4662.8	0.236	0.140	0.298	0.880	21.521	<0.001	3.618	0.058				
RSR	~FQS+age +sex +FQS:age	4638.3	0.248	0.140	0.280	0.891	20.784	<0.001	3.288	0.070	1.420	0.226		
RSR	~FQS+age +sex +FQS:sex	4635.2	0.238	0.145	0.216	0.929	21.488	<0.001	6.424	0.012			2.438	0.046
RSR	~FQS+age+sex+FQS:age+FQS:sex	4610.5	0.250	0.146	0.197	0.940	21.268	<0.001	5.625	0.018	1.450	0.217	2.464	0.044
SIT	~FQS only	711.79	0.212	0.011	0.246	0.782								
SIT	~FQS +age	706.66	0.216	0.014	0.237	0.789	2.972	0.088						
SIT	~FQS +sex	709.61	0.257	0.056	0.233	0.793			0.196	0.659				
SIT	~FQS +age +sex	704.09	0.257	0.056	0.224	0.800	3.336	0.071	0.581	0.448				
SIT	~FQS+age +sex +FQS:age	694.76	0.260	0.062	0.170	0.844	3.571	0.062	0.389	0.534	0.759	0.471		
SIT	~FQS+age +sex +FQS:sex	696.07	0.253	0.061	0.247	0.782	3.866	0.053	0.642	0.425			0.356	0.702
SIT	~FQS+age+sex+FQS:age+FQS:sex	686.3	0.259	0.067	0.284	0.754	4.314	0.041	0.473	0.494	0.908	0.407	0.513	0.601
SSR	~FQS only	1916.2	0.203	0.029	0.503	0.681								
SSR	~FQS +age	1908.7	0.214	0.043	0.437	0.727	7.509	0.007						
SSR	~FQS +sex	1904.9	0.277	0.137	0.415	0.743			11.210	0.001				
SSR	~FQS +age +sex	1899.9	0.283	0.145	0.357	0.784	4.732	0.031	8.835	0.003				
SSR	~FQS+age +sex +FQS:age	1891.4	0.316	0.170	0.364	0.779	2.283	0.132	8.181	0.005	0.299	0.826		
SSR	~FQS+age +sex +FQS:sex	1889.9	0.315	0.166	0.538	0.657	5.048	0.026	2.831	0.094			0.845	0.470
SSR	~FQS+age+sex+FQS:age+FQS:sex	1880.9	0.323	0.178	0.595	0.619	2.017	0.157	1.962	0.163	0.468	0.705	1.009	0.389
WhR	~FQS only	4850.7	0.756	0.002	2.254	0.062								
WhR	~FQS +age	4840.1	0.747	0.003	1.975	0.097	11.226	0.001						
WhR	~FQS +sex	4851	0.772	0.024	2.253	0.062			0.150	0.698				

WhR	~FQS +age +sex	4839.6	0.762	0.027	1.974	0.097	12.046	0.001	0.982	0.322					
WhR	~FQS+age +sex +FQS:age	4825.1	0.762	0.028	1.036	0.388	1.453	0.228	1.261	0.262	1.086	0.362			
WhR	~FQS+age +sex +FQS:sex	4829	0.756	0.028	1.629	0.165	12.229	0.001	1.468	0.226			0.486	0.746	
WhR	~FQS+age+sex+FQS:age+FQS:sex	4813.6	0.756	0.028	1.042	0.384	2.224	0.136	1.840	0.176	1.189	0.314	0.595	0.666	

Key to species codes: BLR=Black Rat, *Rattus rattus*. BSR= Brown Spiny Rat, *Maxomys rajah*. CoT: Common Treeshrew, *Tupaia longipes*. DTR: Dark-Tailed Tree Rat, *Niviventer cremoriventer*. LaT: Large Treeshrew, *Tupaia tana*. LoS: Low's Squirrel, *Sundasciurus lowii*. LTR: Long-Tailed Giant Rat, *Leopoldamys sabamus*. MuR: Muller's Rat, *Sundamys muelleri*. PoR: Polynesian Rat, *Rattus exulans*. RSR: Red Spiny Rat, *Maxomys surifer*. SlT: Slender Treeshrew, *Tupaia gracilis*. SSR: Small Spiny Rat, *Maxomys baeodon*. WhR: Whitehead's Rat, *Maxomys whiteheadi*

Table A2. Results of generalised linear mixed models of small mammal age ratio (proportion of adults in an annual grid sample) against log aboveground biomass (AGB) for thirteen species. Marginal and conditional R^2 are shown, as well as parameter estimates, standard errors, Z-statistics and P-values (corrected using False Discovery rates, see main text) for the fixed effect of log AGB in each model. Bold type: species with significant effect of AGB.

Species	R^2 cond.	R^2 marg.	Fixed effect: Log AGB			
			Estimate	S.E	Z	P
<i>Leopoldamys sabamus</i> (Long-tailed Giant Rat)	0.337	0.201	-1.470	0.445	-3.302	0.012
<i>Maxomys baeodon</i> (Small Spiny Rat)	0.623	0.001	-0.257	0.528	-0.487	0.732
<i>Maxomys rajah</i> (Brown Spiny Rat)	0.686	0.039	1.701	1.164	1.461	0.588
<i>Maxomys surifer</i> (Red Spiny Rat)	0.447	0.001	0.106	0.532	0.199	0.843
<i>Maxomys whiteheadi</i> (Whitehead's Rat)	0.306	0.022	0.468	0.532	0.880	0.588
<i>Niviventer cremoriventer</i> (Dark-tailed Tree Rat)	0.255	0.004	-0.371	0.447	-0.829	0.588
<i>Rattus exulans</i> (Polynesian Rat)	0.184	0.061	1.268	1.062	1.193	0.588
<i>Rattus rattus</i> (Black Rat)	0.233	0.233	3.207	1.445	2.220	0.172
<i>Sundamys muelleri</i> (Muller's Rat)	0.108	0.013	0.247	0.591	0.419	0.732
<i>Sundasciurus lowii</i> (Low's Squirrel)	0.259	0.013	-0.499	0.411	-1.215	0.588
<i>Tupaia gracilis</i> (Slender Treeshrew)	0.014	0.014	0.563	0.651	0.864	0.588
<i>Tupaia longipes</i> (Common Treeshrew)	0.274	0.009	0.342	0.771	0.444	0.732
<i>Tupaia tana</i> (Large Treeshrew)	0.088	0.025	0.572	0.580	0.986	0.588

Table A3. Results of generalised linear mixed models of logit-transformed small mammal interannual survival against log aboveground biomass (AGB) for thirteen species. Marginal and conditional R^2 are shown, as well as parameter estimates, standard errors, T-statistics and P-values (corrected using False Discovery rates, see main text) for the fixed effect of log AGB in each model. NB: The model for *Rattus rattus* failed to converge, thus results are uninformative and have been excluded.

Species	R^2 cond.	R^2 marg.	Fixed effect: Log AGB			
			Estimate	S.E	T	P
<i>Leopoldamys sabamus</i> (Long-tailed Giant Rat)	0.002	0.481	0.287	1.670	0.172	0.974
<i>Maxomys baeodon</i> (Small Spiny Rat)	0.067	0.266	2.167	1.323	1.639	0.609
<i>Maxomys rajah</i> (Brown Spiny Rat)	0.042	0.230	2.795	2.186	1.279	0.669
<i>Maxomys surifer</i> (Red Spiny Rat)	0.000	0.379	-0.037	0.503	-0.073	0.974
<i>Maxomys whiteheadi</i> (Whitehead's Rat)	0.001	0.084	-0.362	0.973	-0.372	0.974
<i>Niviventer cremoriventer</i> (Dark-tailed Tree Rat)	0.001	0.545	-0.186	1.114	-0.167	0.974
<i>Rattus exulans</i> (Polynesian Rat)	0.075	0.942	-2.395	2.444	-0.980	0.828
<i>Rattus rattus</i> (Black Rat)			N/A			
<i>Sundamys muelleri</i> (Muller's Rat)	0.000	0.950	0.091	2.688	0.034	0.974
<i>Sundasciurus lowii</i> (Low's Squirrel)	0.025	0.220	-0.467	0.370	-1.262	0.669
<i>Tupaia gracilis</i> (Slender Treeshrew)	0.346	0.930	4.764	2.467	1.931	0.609
<i>Tupaia longipes</i> (Common Treeshrew)	0.036	0.460	2.102	2.704	0.777	0.866
<i>Tupaia tana</i> (Large Treeshrew)	0.027	0.202	1.131	0.744	1.519	0.609

3.7 Appendix B

Supplementary Text B1: Assessing the relationship between predator relative abundance and small mammal survival

B1.1 Introductory note

While selective logging and other habitat degradation pressures may impact body condition and demographic rates of mammals directly (due to changes in food availability, disease transmission, abiotic stress, etc), we might also expect an indirect effect on survival driven by predators, if abundance of the latter also varies with logging. Predator abundance seems likely to track prey abundance to a large extent, however it may also be driven by extrinsic changes related to logging such as increased anthropogenic disturbance (e.g. Gaynor *et al.* 2018), hunting of the predators themselves or of alternative prey (Brodie *et al.* 2015), or structural changes to forest altering hunting efficacy (e.g. Cooper and Francis 1998). Changes in survival driven by predator abundance might therefore be complex and unpredictable, and mask changes to survival driven by habitat quality *per se*.

Controlling for spatiotemporal variation in abundance of predators in estimates of prey survival at a landscape scale requires large amounts of high-quality data measured simultaneously for both predators and prey. For this study, we were able to partly achieve this due to combined camera and small mammal trapping at the Stability of Altered Forest Ecosystems project in Sabah, Malaysian Borneo, started in 2011 by O.R. Wearn (see Wearn *et al.* 2013, 2016, 2017) and continued by the current author in 2015-2017. Logistical constraints meant that it was not possible to collect camera trapping data in every year and every location that small mammals were sampled, and camera trapping did not always directly precede the small mammal trapping, as is ideal for relating survival during an interannual interval with predator abundance at the outset of that interval. We therefore could not use predator abundance as a random effect in our main models of small mammal apparent survival against habitat quality (grid-level aboveground biomass) without discarding large proportions of the latter data. We also could not test for individual relationships between abundance of particular predator species and individual small mammal species, as most predators were sampled at very low abundances and were spatiotemporally patchy in occurrence.

However we did test for a general underlying relationship between pooled predator abundance and apparent survival, separately fitting linear models using the subset of the data where estimates of both were available. These Supplementary Methods outline the collection of the camera trap data, and the procedures we used to process it before modelling against the previously-calculated apparent survival estimates (Section 3.3.6).

B1.2 Camera trap data

Following the small mammal data collection (Section 3.3.1), we conducted camera trapping in two locations in Sabah, Malaysian Borneo: unlogged lowland dipterocarp forest at the Maliau Basin Conservation Area (N4°44.68' E116° 57.42'), and repeatedly-logged forest at the Stability of Altered Forest Ecosystems (SAFE) Project (N4° 43.27' E117° 35.94, Ewers *et al.* 2011). Camera traps were deployed using the same 4 x12 grids used to sample small mammals (Section 3.3.2), with camera trap locations randomly assigned to a subset of these points (following Wearn *et al.* 2016, 2017, see also Section 4.3.2) in order to reduce any potential sampling bias in encounter rates (Wearn *et al.* 2013). We deployed variable numbers of traps (4-12, mean=7) according to serviceability. In total across the whole permanent sampling programme, camera trapping was carried out at 36 sites (24 in logged forest and 12 in unlogged forest) between 2011 and 2017. Of these, 12 sites (11 logged and one unlogged) coincided spatiotemporally with small mammal trapping that was repeated in subsequent years (i.e. allowing calculation of interannual apparent survival). Several grid sites featured multiple rounds of camera trapping each paired with an interannual small mammal survival interval, and in total 23 such intervals (22 in logged and one in unlogged forest) had associated camera trap data. This corresponded to 10,455 trapnights of data.

At each randomly selected camera location we deployed one camera trap (Reconyx HC500, Holmen, Wisconsin, USA), attaching each camera to a tree strictly within 5 m of the point and ≈ 30 cm above ground level. To avoid creating trails and influencing animal detection, we cut the minimum of vegetation, and instead maximised field of view by siting and angling the camera. Cameras were left for a variable number of days according to logistical constraints (15 -105 days, mean = 47 days), and when the motion sensor was triggered, they recorded 10-image burst mode sequences to maximise the number of identifiable sequences.

B1.3. Metadata processing

We processed the metadata of recorded images in several stages. First, we manually added keywords to the EXIF metadata describing trapping location and species observed, using photo cataloguing software (Adobe Lightroom 6.0, Adobe Systems, California, USA). Then, we automatically extracted the metadata to .csv format using ExifTool v.10.90 (Harvey 2018), and used the keyword structure to subset the metadata records to those containing predatory species. Following Wearn *et al.* (2013), we assumed that individual images records were independent if they featured identifiably different individuals, or occurrences were separated by an arbitrary 1-hour period. We produced Relative Abundance Indices by dividing the count of individuals for each species in each grid by the number of trap-nights during that camera trapping session to account for varying sampling effort.

Next, we identified predatory species of vertebrate based on identification guides (Payne and Francis 1985, Das 2010, Phillipps and Phillipps 2014, 2016). Information on which species prey on particular Southeast Asian tropical forest small mammal species, or on the relative importance of small mammals in diets of predatory species is frequently lacking: a wide variety of carnivorous or omnivorous species could potentially prey on small mammals, but only a subset of these probably do so regularly. Therefore, we produced two pooled counts of predators to use as an explanatory variable in our models. First, we split all species in our camera trap data into three categories based on the descriptions of diet across our identification guides: 1: any species specifically described as preying on “small mammals”, “small vertebrates”, “rodents”, etc. 2: Any species generally described as “predators”, “omnivores” or mentioning “small animals” without being more specific, and 3. Any species for which the description did not include any mention of animals, or specifically referred to invertebrates only. We then produced a count of all potential predators (categories 1 and 2 combined) and probable or “major” predators (category 1 only, for lists of our predatory species, see Table B1).

We then used these pooled predator abundance indices as predictors in linear models against our survival estimates for the sampled small mammal species. Two grid-year combinations we sampled in logged forest did not contain any records of species in category 1, so we excluded these two datapoints, leaving 21 grid-year combinations (=9925 trap-nights). Furthermore, Brown Spiny Rats (*Maxomys rajah*) were almost exclusively confined to primary forest, and we only had one survival interval with associated camera trap data in this habitat, so we excluded this species from the analysis on the basis of low sample size. However we fitted models for the remaining twelve species, as described in Section 3.3.8.

Table B1. Predatory species tagged in our camera-trap data. Species are divided according to their likely interaction with small mammals, based on dietary classifications from field guides (Payne and Francis 1985; Phillipps and Phillipps 2014, 2016): Major predators are specifically listed as predators of small mammals, while occasional predators are those listed as “omnivorous”. The number of unique individuals from the grids which we analysed against small mammal survival is also displayed. For further details, including those of the camera-trapping procedures, see Supplementary Text B1.

Species	Predator type	Individuals in dataset
Binturong (<i>Arctictis binturong</i>)	Occasional	1
Small-Toothed Palm Civet (<i>Arctogalidia trivirgata</i>)	Occasional	1
Bay Cat (<i>Catopuma badia</i>)	Major	8
Cat sp. (<i>Felidae</i>)	Major	1
Sun Bear (<i>Helarctos malayanus</i>)	Occasional	50
Banded Civet (<i>Hemigalus derbyanus</i>)	Occasional	172
Hose's Civet (<i>Hemigalus hosei</i>)	Occasional	1
Short-Tailed Mongoose (<i>Herpestes brachyurus</i>)	Occasional	14
Collared Mongoose (<i>Herpestes semitorquatus</i>)	Occasional	12
Long-Tailed Macaque (<i>Macaca fascicularis</i>)	Occasional	11
Yellow-Throated Marten (<i>Martes flavigula</i>)	Major	23
Malay Weasel (<i>Mustela nudipes</i>)	Major	1
Stink Badger (<i>Mydaus javanensis</i>)	Occasional	28
Sunda Clouded Leopard (<i>Neofelis diardii</i>)	Major	9
Wallace's Hawk-Eagle (<i>Nisaetus nanus</i>)	Major	1
Masked Palm Civet (<i>Paguma larvata</i>)	Occasional	17
Common Palm Civet (<i>Paradoxurus hermaphroditus</i>)	Major	1
Marbled Cat (<i>Pardofelis marmorata</i>)	Major	7
Orangutan (<i>Pongo pygmaeus</i>)	Occasional	33
Leopard Cat (<i>Prionailurus bengalensis</i>)	Major	15
Banded Linsang (<i>Prionodon linsang</i>)	Major	3
Owl sp. (<i>Strigidae</i>)	Major	1
Monitor sp. (<i>Varanus</i>)	Occasional	2
Malay Civet (<i>Viverra zibetha</i>)	Major	198
Subtotal: major predators		268
Total: all predators		610

Table B2. Results of linear models of logit-transformed small mammal interannual survival against pooled relative predator abundance at the start of the survival interval, for twelve species. R² values are shown, plus parameter estimates, standard errors, T-statistics and P-values (corrected using False Discovery rates, (see main text) for the fixed effect of predator relative abundance in each model. Models are fitted for two groups of mammal predators: all potential small mammal predators, and confirmed major predators of small mammals (see Supplementary Text B1 and Table B1).

Species	Predator grouping	R ²	Fixed effect: Log AGB			
			Estimate	S.E	T	P
<i>Leopoldamys sabamus</i> (Long-tailed Giant Rat)	All	0.082	-35.572	31.763	-1.120	0.520
	Major	0.132	-116.445	86.309	-1.349	0.520
<i>Maxomys baeodon</i> (Small Spiny Rat)	All	0.003	4.406	17.165	0.257	0.835
	Major	0.026	-27.746	39.683	-0.699	0.623
<i>Maxomys surifer</i> (Red Spiny Rat)	All	0.159	32.647	19.355	1.687	0.520
	Major	0.310	96.876	38.600	2.510	0.300
<i>Maxomys whiteheadi</i> (Whitehead's Rat)	All	0.122	14.696	10.178	1.444	0.520
	Major	0.044	19.191	24.910	0.770	0.623
<i>Niviventer cremoriventer</i> (Dark-tailed Tree Rat)	All	0.084	-32.694	26.907	-1.215	0.520
	Major	0.016	-30.506	62.624	-0.487	0.760
<i>Rattus exulans</i> (Polynesian Rat)	All	0.077	29.228	23.898	1.223	0.520
	Major	0.038	-44.628	56.187	-0.794	0.623
<i>Rattus rattus</i> (Black Rat)	All	0.051	-18.932	23.654	-0.800	0.623
	Major	0.007	15.217	56.653	0.269	0.835
<i>Sundamys muelleri</i> (Muller's Rat)	All	0.243	-4.931	3.291	-1.498	0.520
	Major	0.601	-16.669	5.543	-3.007	0.300
<i>Sundasciurus lowii</i> (Low's Squirrel)	All	0.025	10.538	14.856	0.709	0.623
	Major	0.005	11.553	38.649	0.299	0.835
<i>Tupaia gracilis</i> (Slender Treeshrew)	All	0.124	33.670	28.319	1.189	0.520
	Major	0.083	78.990	87.294	0.905	0.623
<i>Tupaia longipes</i> (Common Treeshrew)	All	0.184	29.098	14.856	1.959	0.520
	Major	0.111	55.887	40.837	1.369	0.520
<i>Tupaia tana</i> (Large Treeshrew)	All	0.001	1.651	15.130	0.109	0.914
	Major	0.065	-42.170	36.568	-1.153	0.520

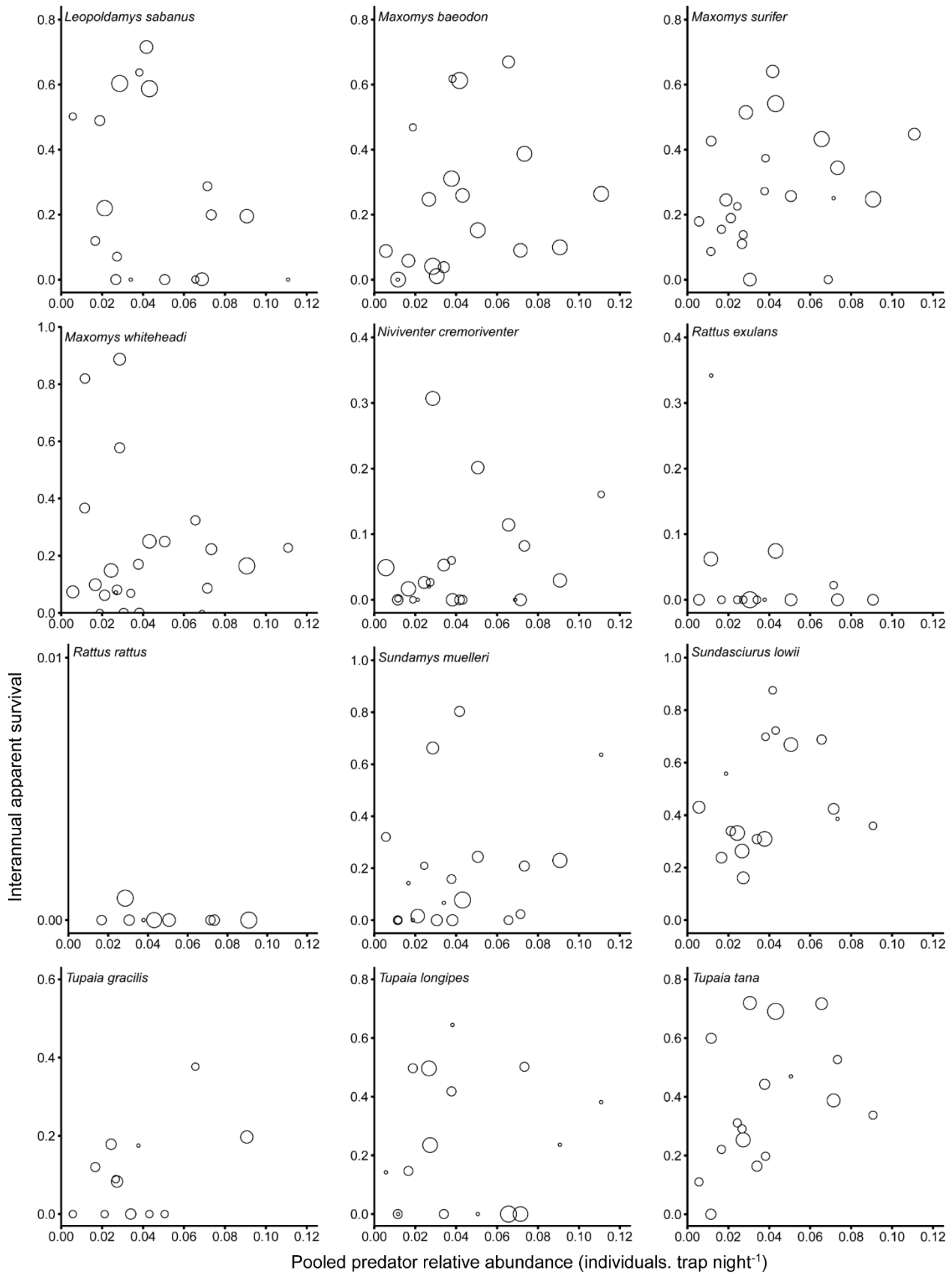


Fig. B1. Interannual apparent survival probability (= apparent survival probability between two consecutive annual small mammal trapping sessions on one grid) for 12 small mammal species, against pooled relative abundance of all potential predator species (individuals per trap night), measured in the same grid during the year of the first trapping session. Point sizes are directly proportional to the total number of individuals in the apparent survival calculation for that sample, and correspond to point weighting in the models.

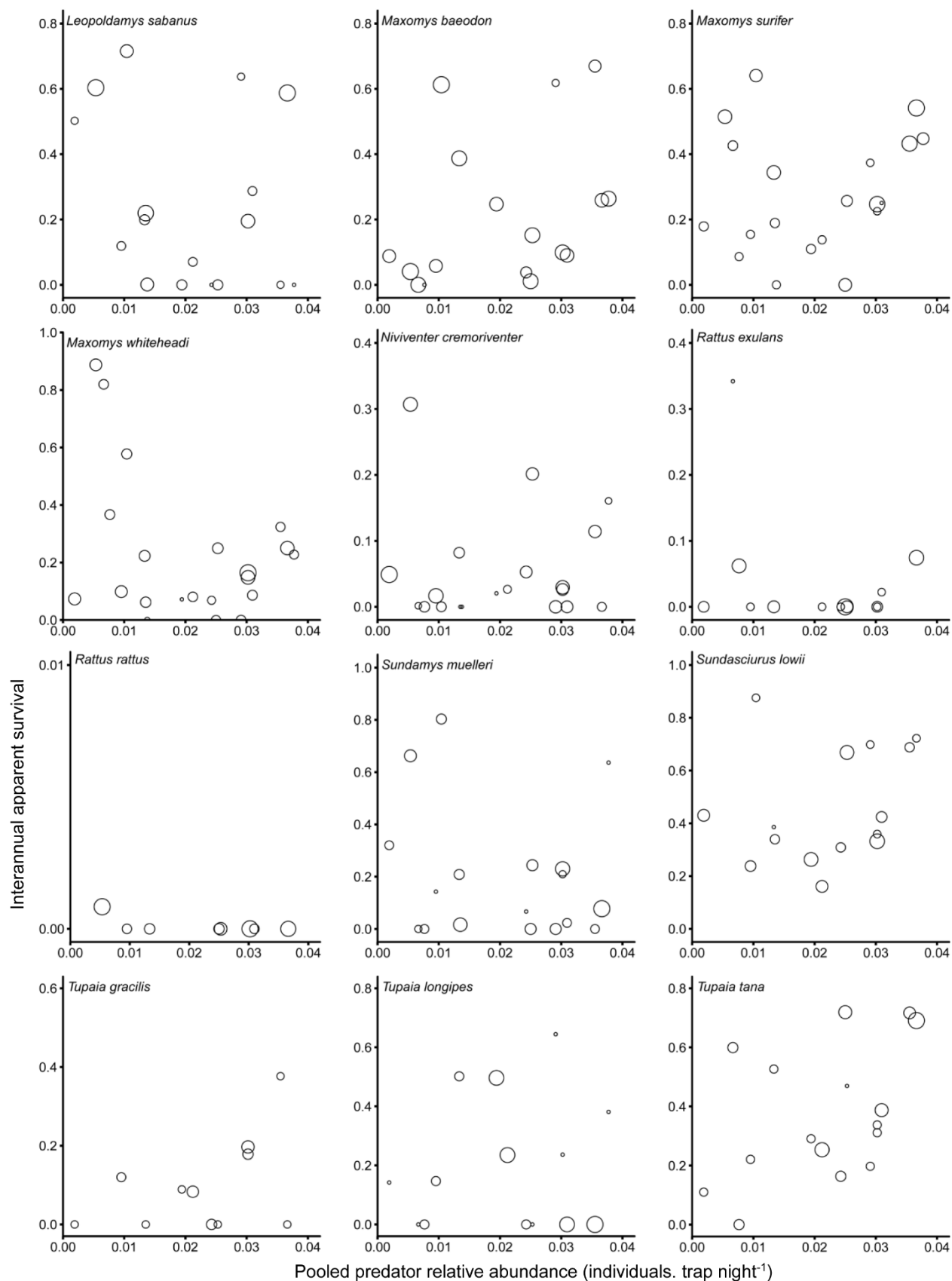


Fig. B1. Interannual apparent survival probability (= apparent survival probability between two consecutive annual small mammal trapping sessions on one grid) for 12 small mammal species, against pooled relative abundance of major predator species (individuals per trap night), measured in the same grid during the year of the first trapping session. Point sizes are directly proportional to the total number of individuals in the apparent survival calculation for that sample, and correspond to point weighting in the models.

Chapter Four: Activity pattern shifts and persistence among ungulates and other large herbivores in Bornean selectively-logged forests

4.1 Abstract

Understanding mechanisms of species persistence in human-modified ecosystems such as selectively-logged tropical forests is crucial for safeguarding vulnerable species as these habitats become increasingly common. One possible mechanism is altering of activity patterns in order to minimise exposure to anthropogenic pressures. Indeed, shifts towards increased nocturnality were recently shown to be a globally ubiquitous response to human disturbance, particularly for the understudied ungulates and other large herbivores. In logged forest, we would expect several concurrent pressures to increase nocturnality, particularly among the largest ungulate herbivores. These could include abiotic stress in larger animals from higher and more variable daytime temperatures and dryness, plus hunting and other human disturbances. Nevertheless, the degree to which tropical forest ungulates shift activity pattern with logging, and the adaptive significance of any shifts, remain unknown. We tested for shifts in activity pattern of the whole large herbivore community in Sabah, Malaysian Borneo, comparing between unlogged and repeatedly logged dipterocarp forests using an established random camera trapping methodology. We found cross-community evidence for this form of behavioural plasticity, with six of eight species shifting activity significantly in logged forest. Confirming our predictions, the most pronounced shifts towards nocturnality occurred in the larger ungulates, while smaller species such as mouse-deer and porcupines showed more variable responses. There was no overall relationship between magnitude of activity pattern shift and probability of persistence, implying that although behavioural plasticity in activity patterns among Bornean ungulates is high, it does not appear to represent a universally successful strategy for survival in logged forest.

4.2 Introduction

With the great majority of extant primary forest in Southeast Asia already protected (Bryan *et al.* 2013), attention has shifted to conserving the remaining forest areas, mostly comprising logged-out timber concessions of low residual economic value and little legal protection (Reynolds *et al.* 2011). These areas are at risk of conversion to plantation agriculture,

particularly oil palm (*Elaeis guineensis*), a process which has strongly negative effects on biodiversity (Fitzherbert *et al.* 2008; Wilcove *et al.* 2013; Wearn *et al.* 2017). However, the low land value of these areas also makes them potentially easy to acquire for conservation (Fisher *et al.* 2011b), and there is an increasing consensus that they remain valuable for biodiversity (Putz *et al.* 2012; Edwards *et al.* 2014d; Costantini, Edwards & Simons 2016).

The responses of different animal taxa to selective logging remain unevenly studied. In the case of mammals, changes in species richness and abundance with logging have received considerable attention (Meijaard & Sheil 2008; Bernard *et al.* 2016; Wearn *et al.* 2016, 2017). These studies have suggested that logging has limited impact on species richness, but revealed strong interspecific variation in abundance responses. The main drivers for this variation probably include body size, evolutionary distinctiveness and trophic specialisation (Meijaard & Sheil 2008), but responses can vary strongly within trophic groups. For example, Wearn *et al.* (2017) found overall abundance of most groups except frugivores remained similar or increased in logged forest, but 20 of 57 species had a $\geq 50\%$ chance of declining in abundance. Together, this pattern suggests that the overall high abundance of each group in logged forest is driven by disproportionate increases of some species, particularly small mammals.

Our understanding of the mechanisms causing functionally similar species to show contrasting abundance responses to logging remains limited. Most detailed mechanistic studies of mammalian responses to logging have focused on taxa which are charismatic, such as primates and carnivores; or easily-trapped and relatively abundant, such as small mammals (Lambert, Malcolm & Zimmerman 2005; Wells *et al.* 2006; Meijaard & Sheil 2008; Loveridge *et al.* 2016). Medium-sized and large herbivores, frugivores and granivores (hereafter “large herbivores”) such as ungulates and hystricid rodents (porcupines) have received much less attention. This belies their disproportionately high functional importance in tropical forests, where they act as seed dispersers, seed predators and browsers, and thus mediate tree recruitment and community structure (Curran & Webb 2000; Wright *et al.* 2000; Paine & Beck 2007; Harrison *et al.* 2013).

Wearn *et al.* (2017) suggested that some Southeast Asian large herbivores are relatively resilient to logging (particularly Sambar Deer *Cervus unicolor*, Red Muntjac *Muntiacus muntjac*, Bearded Pig *Sus barbatus*, and Banteng *Bos javanicus*). Conversely several others appear more vulnerable, with three species having a $>75\%$ chance of declining in logged forest (Thick-spined and Long-tailed porcupines *Hystrix crassispinis* and *Trichys fasciculata*, and Yellow Muntjac *Muntiacus atherodes*). The factors underlying this variation remain poorly known, although one extensive study (Heydon 1994; Heydon & Bulloh 1997) suggested that declining fruit availability and increased abundance of leafy vegetation may be important. The resilient

ungulate species tend to be omnivorous (Beaded Pig), obligate browsers (Sambar Deer), or facultatively able to increase browsing (Red Muntjac). Conversely the smaller ungulate species, particularly the mouse-deer, are much more dependent on fruit, which becomes scarcer and more patchily distributed after logging (Heydon 1994).

Another potential factor affecting persistence is the tolerance of large herbivores to altered microclimatic conditions resulting from logging-induced changes to forest structure. These include higher mean temperature, reduced relative humidity, and greater daily range in both temperature and relative humidity (Hardwick *et al.* 2015). The continuous cool, dark, humid understorey changes particularly starkly, being largely replaced by a hotter, drier and brighter herbaceous shrub layer (Johns 1988; Broadbent *et al.* 2008; Pfeifer *et al.* 2016). Although relatively modest in magnitude (Hardwick *et al.* 2015), these changes might be expected to place some physiological stress on animals adapted to understorey conditions. While this is particularly likely for ectotherms (Tewkesbury, Huey & Deutsch 2008; Stork *et al.* 2009; Logan, Fernandez & Calsbeek 2015; Nowakowski *et al.* 2018), understorey endotherms, particularly those with large body sizes, may also inhabit restricted thermal niches and thermoregulate less adequately, or experience enhanced rates of moisture loss in gap-like conditions (Porter & Kearney 2009; Gardner *et al.* 2011). Furthermore, sensory adaptation to the gloomy understorey, particularly light-sensitive, high acuity vision (Veilleux & Lewis 2011) may also impede animals' ability to orient and navigate in microhabitats with somewhat increased light levels (Prevedello, Forero-Medina & Vieira 2011). Together, these constraints, although understudied, could potentially impede foraging and ranging behaviours, restrict dispersal and fragment populations.

One mechanism that may help herbivorous mammals tolerate these altered conditions is behavioural plasticity in activity patterns. Shifts in activity pattern have been observed in several mammal species in response to other anthropogenic pressures (Kitchen, Gese & Schauster 2000; Tigas, Van Vuren & Sauvajot 2002; Paviolo *et al.* 2009; Norris, Michalski & Peres 2010; Gaynor *et al.* 2018), and represent a surprisingly universal response to many forms of human disturbance, particularly among large herbivores (Gaynor *et al.* 2018). We might therefore expect large herbivores to change their daily activity patterns to avoid the altered microclimatic conditions, with diurnal, crepuscular or cathemeral (active throughout the day and night, Tattersall 2006) species becoming increasingly nocturnal. Temperature and humidity attain greater daily extremes in logged forest and begin to increase and decrease, respectively, earlier in the morning (Hardwick *et al.* 2015). Obligately nocturnal animals may therefore also shift activity towards the earlier or middle parts of the night to avoid this.

Several other factors should also exert pressure on activity patterns, leading to increased nocturnality among large herbivores in logged forest. Firstly, as prey animals these species can use behavioural plasticity as an anti-predator strategy. For example, in the absence of the obligately nocturnal Sunda Clouded Leopard (*Neofelis diardi*), the diurnal Bearded Pig *Sus barbatus* displayed significant shifts towards increased nocturnality, while the nocturnal Greater Mouse-deer *Tragulus napu* became proportionately more active earlier in the night, a time period when leopards were particularly active when present (Ross *et al.* 2013). Clearly, the direction of predator-driven activity pattern shifts depends on the balance of nocturnal and diurnal predation risk. However, logging and associated anthropogenic disturbance can strongly reduce abundances of Southeast Asia's felid apex predators such as Clouded Leopards and the Sumatran Tiger *Panthera tigris sondaica* which display nocturnal or crepuscular activity patterns and are the main predators of large herbivores (Ridout & Linkie 2009; Ross *et al.* 2013). We would expect, then, that any release from predation by these species would reduce the net cost of increased nocturnality in large herbivores.

Similarly, animals may shift activity patterns in response to human hunters (Kitchen, Gese & Schauster 2000) and other nonlethal disturbances (Frid and Dill 2002). Logging operations create large road networks (Gaveau *et al.* 2014), dramatically increasing the accessibility of forest to humans. Consequently hunting is now a major threat to tropical forest mammals in many areas of the world, including Southeast Asia, where efficient commercial hunting for markets is replacing subsistence hunts by local and indigenous people (Corlett 2007; Brodie *et al.* 2015; Harrison *et al.* 2016). Hunting is therefore frequently inseparable from other impacts of logging, making the effect of hunting pressure *per se* hard to quantify.

The effect of hunting on the activity patterns of a focal species should depend on the intensity of hunting pressure, and its timing relative to the species' underlying activity patterns, which in turn is probably dependent on the hunting method used. Both these parameters are spatially and socioeconomically variable (e.g. Bennett, Nyaoi & Sompud 2000), and quantitative data is frequently difficult to obtain, particularly on illegal hunting. However, the most comprehensive study we could locate covering Southeast Asian forests suggests that large ungulates, particularly the Bearded Pig and Sambar Deer are generally among the most heavily-targeted species, mostly by active hunters using guns (Bennett, Nyaoi & Sompud 2000; Brodie *et al.* 2015). Such hunting may be practiced diurnally or nocturnally (Caldecott 1988; Bennett & Gumal 2001), with unknown relative efficiency, so the net directional effect on activity patterns is uncertain. Still, these species seem to be chiefly diurnal or crepuscular in the absence of logging, suggesting that hunters should predominantly target them at these times (Heydon 1994; Van Schaik & Griffiths 1996; Mohd-Azlan 2006; Ross *et al.* 2013). Furthermore, other

forms of human disturbance related to logging are also generally diurnal, including mortality from traffic collisions on logging roads (a significant impact on large herbivores, see Corlett (2007)), and general noise from traffic, logging operations and local human foragers. Nonlethal human disturbance can elicit analogous responses to heightened predation risk (Frid and Dill 2002), and have also been shown to elicit a wide variety of behavioural responses across many regions and taxa (e.g. Manor and Saltz 2003; Stankowich 2008, Brown *et al.* 2012). Globally, human nonlethal disturbance forms a major driver of shifts towards nocturnality (Gaynor *et al.* 2018).

Combined, we might expect that these drivers have additive effects, precipitating a shift towards increased nocturnality in large herbivorous mammals after selective logging of tropical forests. However, no studies have investigated whether this occurs. We also do not know whether shifting activity patterns is universally adaptive: shifts may incur energetic costs to diurnal animals if foraging efficiency is suboptimal, and energy expenditure is increased in lower light levels. In this instance, we might expect compensatory increases in overall activity level, with longer periods spent actively foraging. Therefore, behavioural plasticity potentially imposes a balance of costs and benefits, and may either actively promote persistence in logged forest, or represent animals being forced into a suboptimal temporal niche.

In this study, we examined activity patterns among communities of large herbivorous, frugivorous and granivorous mammals in unlogged and heavily logged forest in Malaysian Borneo, to test the hypothesis that anthropogenic pressures in logged forest drive shifts towards increased nocturnality, and that this affects persistence in logged forest. We focussed on ten species with a variety of observed abundance responses to logging (Table 1; Wearn *et al.* 2017). We examined: (1) to what degree the species shifted their activity patterns towards greater nocturnality, (2) whether the degree of shift varies with body size, (3) whether species with shifted activity patterns in logged forest are more or less likely to decline in local abundance, and (4) whether species showing increased nocturnality counteract potentially reduced foraging efficiency, by becoming more active overall.

4.3 Methods

4.3.1 Study area

We conducted fieldwork for this study at two locations in Sabah, Malaysian Borneo, comparing unlogged and repeatedly-logged lowland dipterocarp rainforest. We sampled unlogged forest at the Maliau Basin Conservation Area (N4°44.68' E116° 57.42'), which was characterised by high-

canopy dipterocarp forest with mean above-ground biomass $\approx 350 \text{ t.ha}^{-1}$ (Pfeifer *et al.* 2016). We sampled repeatedly-logged forest at the Stability of Altered Forest Ecosystems (SAFE) Project, a 7000ha forest modification experiment some 60km to the east ($\text{N}4^{\circ} 43.27' \text{ E}117^{\circ} 35.94$, Ewers *et al.* 2011). This forest forms part of the 1 million hectare Yayasan Sabah logging concession, and had been subjected to two or more rounds of selective logging between the 1980s and 2000s, leaving $\approx 120 \text{ t.ha}^{-1}$ of aboveground tree biomass (Pfeifer *et al.* 2016). This forest was heavily degraded but highly heterogenous, with a dense cover of vines and pioneer vegetation on flatter, more heavily logged areas, and patches of relict canopy tree cover on steeper, more lightly-logged slopes. This landscape history is typical of Sabah and the wider Sundaland region. An unpublished survey of local loggers and plantation workers (Fitzmaurice 2014) suggested that hunting of Bearded Pigs, birds and unspecified deer occurs within the landscape at unknown intensity, echoing the Sabah-wide results of Bennett, Nyaoi and Sompud (2000).

4.3.2 Grid design and camera trap placement

We sampled in 24 logged forest sites and 12 unlogged forest sites from May 2011 - May 2017 (see Wearn *et al.* 2017, Fig. 1a, 1c). Our sites overlie the sampling structure of the SAFE project, which is largely controlled for topography, altitude and aspect (Ewers *et al.* 2011). At each site we constructed a 4×12 grid of sampling points with 23 m separation, and randomly assigned camera trap locations to a subset of these points (following Wearn *et al.* 2016, 2017, see also Section 2.3.2). Placing traps randomly with respect to landscape features such as trails and gaps helps to reduce any potential sampling bias, both in encounter rates (Wearn *et al.* 2013) and in temporal patterns of microhabitat use (for instance, crepuscular or diurnal animals may disproportionately use trails and gaps earlier in the day when abiotic stress is lower). Numbers of traps deployed varied from 4-12 (mean=7) according to serviceability, however this variation in sampling effort is unlikely to bias our activity pattern estimates. Of the 36 sites, 22 logged and five unlogged sites were sampled more than once during the total sampling period, with a total trapping effort comprising 37,153 trap-nights (unlogged forest: 12,843 trap-nights; logged forest: 24,310 trap-nights).

At each randomly selected point we deployed one camera trap (Reconyx HC500, Holmen, Wisconsin, USA), attaching each camera to a tree strictly within 5 m of the point and $\approx 30\text{cm}$ above ground level. To avoid creating trails and influencing animal detection, we cut the minimum of vegetation, and instead maximised field of view by siting and angling the camera.

Cameras were left for between 15 and 105 days (mean = 47 days), and recorded 10-image sequences in burst mode upon triggering of the motion sensor, which maximised the number of identifiable sequences.

4.3.3 Metadata processing

We processed the metadata of the images in two stages. First, we used photo cataloguing software (Adobe Lightroom 6.0, Adobe Systems, California, USA) to manually append keywords denoting location and species to the EXIF metadata of all images. Second, we extracted the metadata automatically using the metadata management tool ExifTool v.10.90 (Harvey 2018). Using the keyword structure, we trimmed out all non-target sequences (i.e. images not containing an animal) and sequences containing non-focal animals; before finally reducing the remaining images to the first image in each sequence (or the first image where the animal(s) is present, if different).

4.3.4 Activity pattern estimation

We fitted activity pattern kernels using package *activity* (Rowcliffe 2016) in R v. 3.5.0 (R Core Team 2018). We used the time-of-day information encoded in each image's metadata to fit circular kernel probability density functions (PDFs) for each species, thus producing a daily activity pattern model (function *fitact*). We did this separately for each species in unlogged and logged habitats, and derived 95% confidence intervals for the kernels by bootstrapping. To test whether each species displayed different overall activity levels between unlogged and logged forest, we derived overall activity level estimates from the circular kernel PDFs, and compared these using a Wald chi-squared test to determine whether the observed difference differed significantly from zero (function *CompareAct*).

To evaluate the overlap of the circular kernel PDFs between forest types, and therefore test whether each species significantly shifted its activity pattern (as distinct from its overall activity level) in logged forest, we calculated the overlap index (equation 3.3 in Ridout & Linkie 2009) for our observed kernels in unlogged and logged forest. We then generated a null distribution of overlap indices by bootstrapping from the combined, randomised data, in order to estimate the probability that the observed overlap index arose by chance (Function *CompareCkern*). Significantly non-overlapping circular kernel PDFs and low overlap indices between forest types may not necessarily translate into biologically meaningful, directional shifts in activity. Therefore, we also estimated the net percentage of the 24-hour period over which activity

patterns were specifically shifted towards nocturnality. We divided the 24-hour period into day (06:00 – 18:00) and night (18:00-06:00). We then summed the proportion of the day in which activity in logged forest was lower than in unlogged forest (95% confidence intervals around the fitted circular kernel PDFs did not overlap), and the proportion of the night in which activity in logged forest was higher than in unlogged forest. We then expressed this as a percentage of the total 24-hour period. To account for shifts in the opposite direction, we calculated the proportions of day and night where the reverse was true, and subtracted the resulting percentage to give a net percentage of the 24 hours showing a shift towards nocturnality.

To explore the effect of body size on activity pattern shifts, we compiled body mass figures from the literature (Van Weers 1976, 1979; Payne & Francis 1985; Heydon 1994; Yasuma, Apin & Yu 2003; Phillipps & Phillipps 2016), taking the mean of all published figures between sources. Where sources only published a range of mass, we took the mean of the two extremes as the value for that source. We then modelled the net percentage shift against the overall mean mass for each species using linear models with Gaussian error, first log-transforming (base 10) our estimates of net percentage shift and body mass.

Lastly, to assess the relationship between activity pattern shifts and persistence in logged forest, we modelled the log net percentage shift for each species against the probability of its local decline from primary to logged forest in this study system, extracted from Wearn *et al.* (2017) (Linear models with Gaussian error).

4.4 Results

4.4.1 Camera images captured

Our camera traps recorded a total of 788 179 images, comprising 18 163 unique sequences which corresponded to an identifiable species. Of these, 10 975 sequences corresponded to our target species (Table 1). Two species, the Bornean Elephant (*Elephas maximus borneensis*) and the Thick-Spined Porcupine (*Hystrix crassipinis*) were effectively absent from one forest type (Table 1) and were excluded from subsequent analyses.

4.4.2 Overall activity levels compared between unlogged and logged forest

Of the eight species, five did not increase or decrease their overall activity level in logged forest (Fig. 1). The activity level of Sambar Deer (*Cervus unicolor*) decreased approximately 31 % (Wald chi-sq test, $W=4.00$, $p=0.05$), as did overall activity of Long-tailed Porcupine (*Trichys*

fasciculata, approximately 30 % decline; $W=6.13$, $p=0.01$). Conversely, overall activity of Greater Mouse-deer increased in logged forest by approximately 114% ($W=13.16$, $p=0.0002$, Fig. 1).

Table 1. Detections of medium-sized and large herbivorous, granivorous and frugivorous mammals in our dataset, separated by forest type. Common names follow Payne & Francis (1985).

Species		Unlogged Forest	Logged Forest	Total detections
Red Muntjac	<i>Muntiacus muntiacus</i>	1549	1867	3416
Bearded Pig	<i>Sus barbatus</i>	409	2791	3200
Sambar Deer	<i>Cervus unicolor</i>	101	881	982
Greater Mouse-deer	<i>Tragulus kanchil</i>	910	67	977
Malayan Porcupine	<i>Hystrix brachyura</i>	182	439	621
Yellow Muntjac	<i>Muntiacus atherodes</i>	540	73	613
Lesser Mouse-deer	<i>Tragulus napu</i>	319	276	595
Long-tailed Porcupine	<i>Trichys fasciculata</i>	354	133	487
Thick-spined Porcupine	<i>Hystrix crassispinis</i>	75	1	76
Borneo Elephant	<i>Elephas maximus</i>	0	8	8
Total		4439	6536	10975

4.4.3 Activity patterns and overlap between forest types

The eight species showed a variety of different activity patterns and degrees of overlap between logged and unlogged forest, although activity patterns generally overlapped by $\geq 75\%$. (Fig. 2). Only two species (Malayan Porcupine and Lesser Mouse-deer) showed differences in overlap that were not greater than expected by chance.

Two species, Bearded Pig *Sus barbatus* and (to a lesser extent) Sambar Deer, were relatively diurnal in unlogged forest but became strongly more nocturnal in logged forest (75.7% and 19.73% shift respectively, Table 2). These species showed reduced activity approximately between 08:30 and 16:00, and 09:30 and 14:30 respectively (95% confidence intervals do not overlap between these periods, Fig. 2a-b). Conversely, activity was increased from approximately 17:30-06:00, and from 03:00-05:30 respectively (Fig. 2a-b). The two muntjac species also showed a broadly crepuscular/diurnal pattern in unlogged forest, with activity peaks around dawn and dusk (Fig. 2c-d).

However, these two species altered their activity patterns in logged forest in different ways. Activity of Red Muntjac *Muntiacus muntjak* was generally very similar in logged forest (overlap

index=0.926), differing chiefly in an earlier decline in activity during the dusk period, and reduced activity until approximately 19:30, with a minimal net shift towards diurnality (Fig. 2c, Table 2). Yellow Muntjac *M. atherodes* showed a more strongly variable activity pattern both within and between forest types. However, activity was slightly higher before dawn, and both lower after dawn and around midday in logged forest, with an 11.85% shift towards nocturnality (Fig. 2d, Table 2).

Table 2. Net percentage shift towards nocturnality between unlogged and logged forest for eight species of large herbivorous, granivorous and frugivorous mammals. Shifts are calculated by comparing the 95% confidence intervals around circular kernel probability density functions fitted for the two forest types. Where the confidence intervals did not overlap, activity levels were taken to have differed. The net shift is the summed length of non-overlapping time periods in the expected direction, minus the summed length of non-overlapping periods in the opposite direction, expressed as a percentage of the total 24 hours. Positive percentages indicate a shift towards nocturnality, while negative values indicate a shift away from nocturnality. For further details, see Section 4.3.4. Common names follow Payne & Francis (1985).

Species		Percentage shift
Bearded Pig	<i>Sus barbatus</i>	75.7
Sambar Deer	<i>Cervus unicolor</i>	19.73
Red Muntjac	<i>Muntiacus muntiacus</i>	-2.36
Yellow Muntjac	<i>Muntiacus atherodes</i>	11.85
Greater Mouse-deer	<i>Tragulus kanchil</i>	0.25
Lesser Mouse-deer	<i>Tragulus napu</i>	0
Malayan Porcupine	<i>Hystrix brachyura</i>	-0.65
Long-tailed Porcupine	<i>Trichys fasciculata</i>	-5.09

The two mouse-deer displayed predominantly bimodal, crepuscular activity patterns in unlogged forest, with peaks around 06:00 and a more pronounced peak at 18:00, although Greater Mouse-deer *Tragulus napu* was largely inactive from late morning to mid-afternoon while activity of Lesser Mouse-deer *T. kanchil* remained relatively high between the dawn and dusk peaks (Fig. 2e-f). Logging had no effect on the activity pattern of Lesser Mouse-deer, but a strong and complex effect on the activity pattern of Greater Mouse-deer. The activity of this species changed from the strongly bimodal pattern to a more constant level, with decreased activity around dusk, but increased activity around both midday and midnight. Both species showed little or no directional shift towards nocturnality (Fig. 2e, Table 2).

The two porcupine species were strictly nocturnal in both unlogged and logged forest, with little or no activity between 07:00 and 17:00 (Fig. 2g-h). However, logging altered the portion of the

night at which Long-tailed Porcupine was most active. In unlogged forest, this species displayed a strong activity peak around 04:00, with lower, relatively constant activity for the remainder of the night. Conversely, Long-tailed Porcupines in logged forest were significantly more active between 17:30 and 20:30, but less active between 02:30 and 06:00, with a minimal net decrease in nocturnality due to earlier onset of activity at dusk (Fig. 2h, Table 2).

4.4.4 Overlap, body size and response to logging

Herbivores with increasing log body size showed larger net shifts in activity towards nocturnality (Fig. 3; Linear model, $R^2=0.59$, $T= 3.36$, $p =0.02$). Conversely, although species with larger net shifts appeared to be less prone to decline with logging (Fig. 4), this relationship was not significant (linear model, $R^2=0.19$, $t=-1.62$, $p=0.16$).

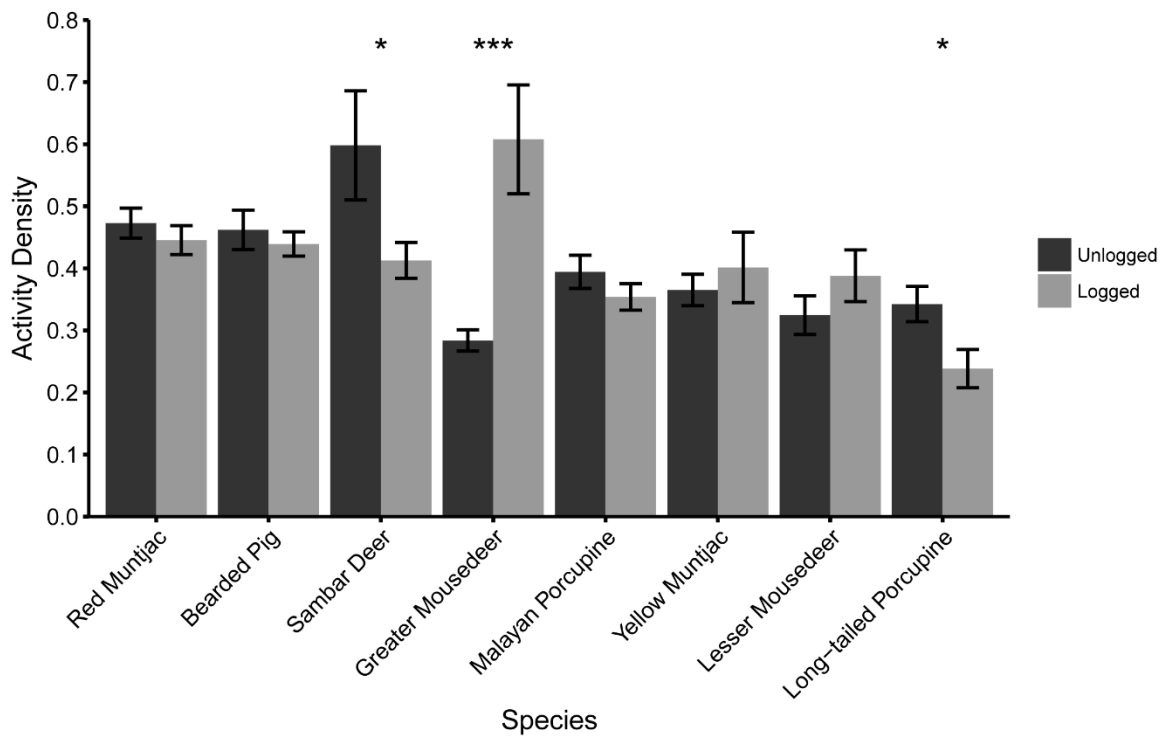


Fig. 1. Overall activity levels ($\pm$ S.E.) of eight large herbivore species in unlogged and logged forest. Asterisks represent significantly different activity levels between the habitat types, (Wald test: * $p=0.05$. * $p=0.001$)**

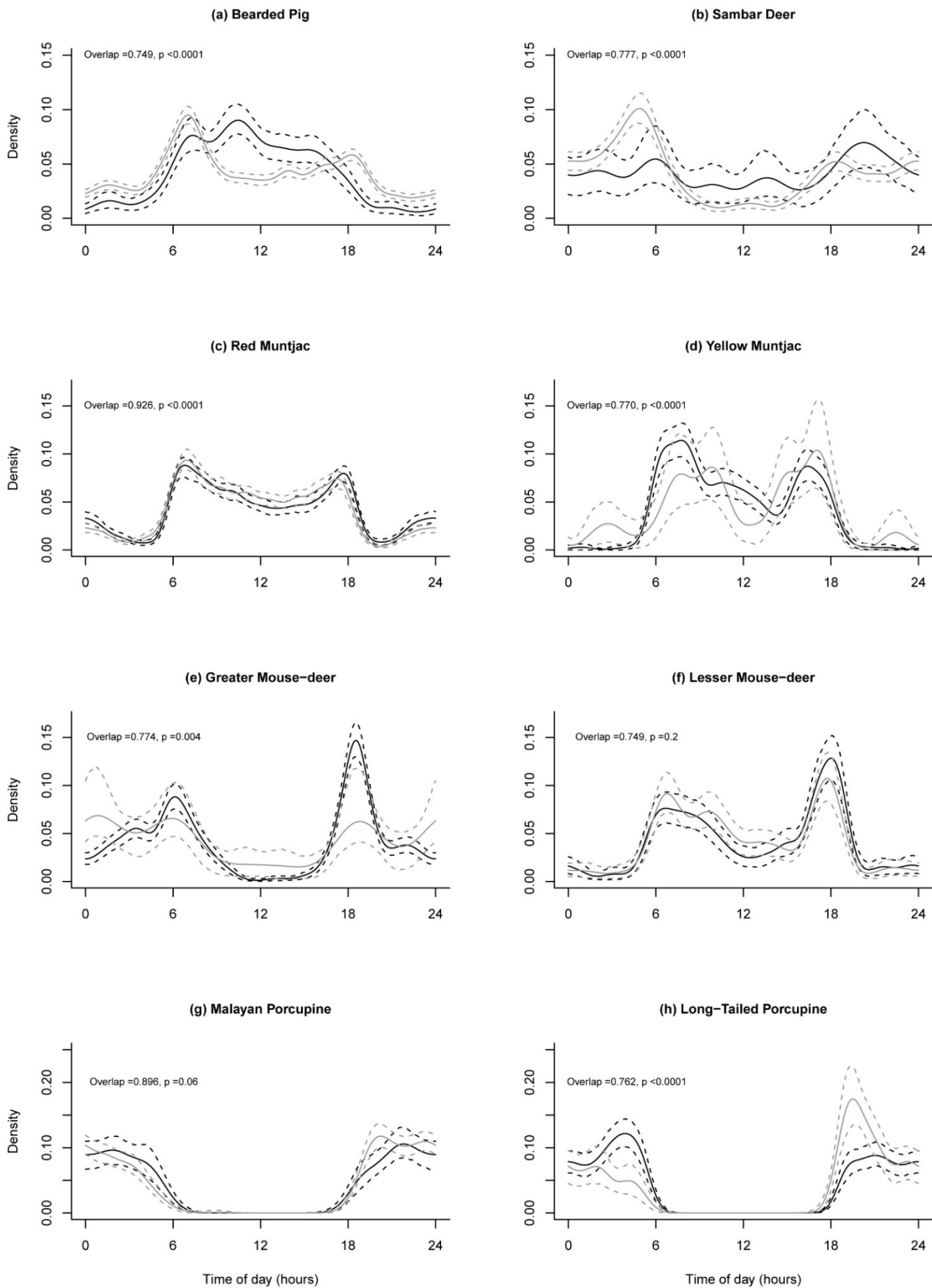


Fig. 2. Activity patterns as fitted circular kernel probability density functions, for eight species of large herbivorous mammals in unlogged (black) and logged (grey) forest. Dotted lines: 95% confidence intervals. Overlap estimates and p-values are displayed.

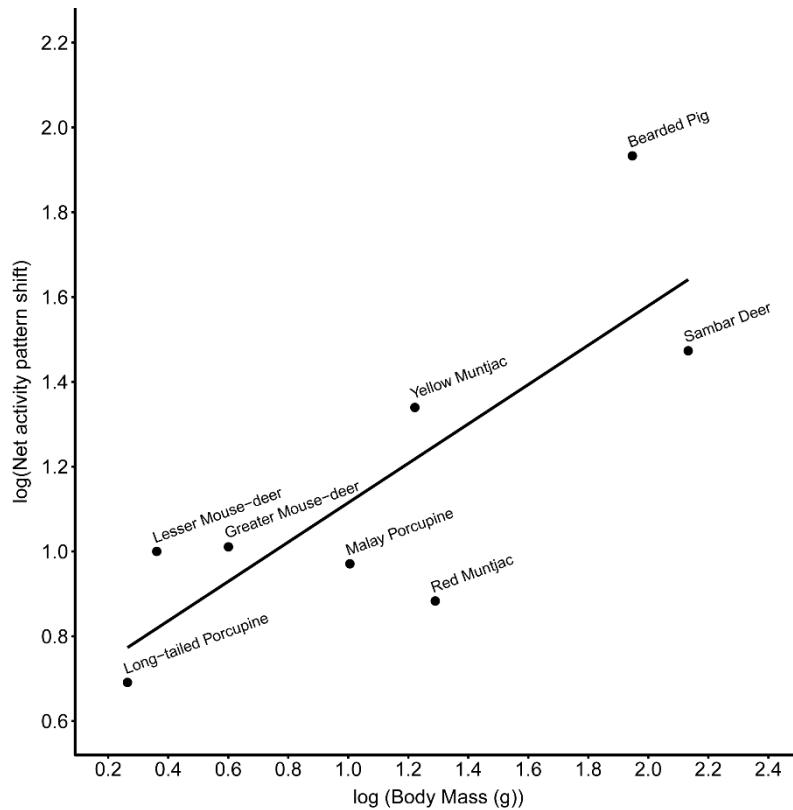


Fig. 3. Log net shift in activity pattern of eight species of large herbivorous mammals between unlogged and logged forest, plotted against mean body size.

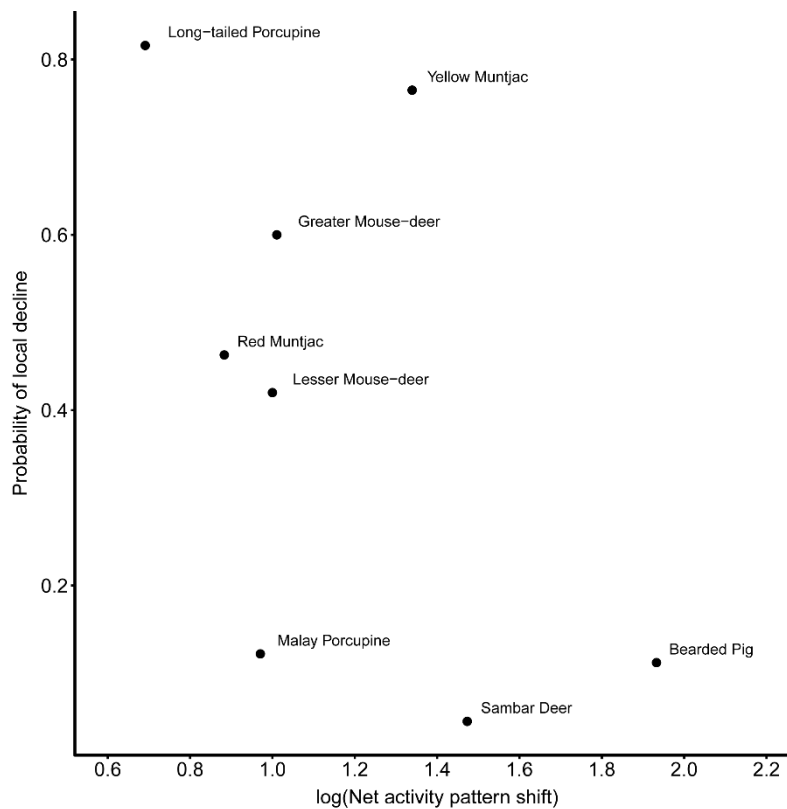


Fig. 4. Log net shift in activity pattern of eight species of large herbivorous mammals between unlogged and logged forest, plotted against the probability of that species declining in local abundance between unlogged and logged forest (from Wearn *et al.* 2017).

4.5 Discussion

To our knowledge, this is the first community-level study examining large herbivore activity patterns in response to tropical forest selective logging. Our results reveal a broad cross-community effect of logging on activity patterns, with shifts in activity patterns observed across six of eight mammal species studied. This suggests that behavioural plasticity in Bornean large herbivores is high, at least among those species which still inhabit logged forest. However, species-level changes in activity patterns at different times of day were idiosyncratic, and the strength and direction of activity pattern shifts appear to depend on underlying activity pattern in the absence of logging.

4.5.1 Increased nocturnality in the largest ungulates

Of six species which shifted activity pattern significantly, three confirmed our predictions by exhibiting a pronounced shift towards nocturnality through either increased activity during the night, decreased activity during the day, or a combination of both. These species (Sambar Deer, Bearded Pig and Yellow Muntjac) were generally comparatively diurnal or cathemeral in unlogged forest, agreeing with broad classifications of these species in the literature (Van Schaik & Griffiths 1996; Grassman *et al.* 2006; Kitamura *et al.* 2010; Gray & Phan 2011). The species showing the most directional shifts towards nocturnality tended to be larger (Fig. 3), with the two most pronounced shifts seen in the largest two species, Sambar Deer (c.80-200 kg, 19.72% shift) and Bearded Pig (c. 55-120 kg, 75.7% shift), and a smaller but distinct shift in Yellow Muntjac (c. 15-28 kg, 11.85% shift). The fourth “larger” ungulate, the Red Muntjac, also showed significantly non-overlapping activity patterns, but the main decline in activity in its activity in logged forests fell either side of around dusk, and so showed little net directional shift (Table 2).

The relative consistency of these shifts towards nocturnality among three larger ungulates suggests that logging exerts similar pressures on these species. Large-bodied species are likely to be more affected by abiotic stress than smaller bodied species, as their lower surface area-volume relationships reduce metabolic rate, impacting heat dissipation and loss, and reducing the optimal temperature for minimising energetic and water costs (Porter & Kearney 2009; Speakman & Król 2010; Gardner *et al.* 2011). This suggests that the larger ungulates in our study may be reacting to the increased maximum temperature, reduced relative humidity and increasingly variable conditions in logged forests. However, these large ungulate species with the most pronounced shifts towards nocturnality are also among the most heavily-hunted in Southeast Asia (Corlett 2007; Harrison *et al.* 2016). Indeed the Bearded Pig, the species showing the strongest shift towards nocturnality, can account for $\approx 75\%$ of hunted animals by biomass in

Borneo and is often also dominant in terms of abundance (Bennett, Nyaoi & Sompud 2000; Bennett & Gumal 2001). If active hunters with guns arrive after logging and find that these large ungulates are initially more frequently encountered and easily targeted during daylight hours (consistent with their behaviour in unlogged forest), hunting activity could also drive the observed shifts towards nocturnality. Other forms of human disturbance in logged forest such as traffic noise and logging operations are also chiefly diurnal, and may represent a further concurrent pressure driving nocturnality. Conversely, predator release, the third possibility discussed in the Introduction, is unlikely to be a major factor, as our logged study areas retained healthy population sizes of predators including Clouded Leopards *Neofelis diardi* (Wearn *et al.* 2013, 2017), the main threat to large ungulates (Ross *et al.* 2013; Wearn *et al.* 2013). Unpicking the possible mechanisms for these changes will probably prove difficult, and it is not clear why they do not apply to the same degree Red Muntjac, which is probably frequently hunted in logged forests in our study system (Bennett, Nyaoi and Sompud 2000, Fitzmaurice 2014), and is of a comparable body mass and shape to Yellow Muntjac (Fig. 3). It is possible that Red Muntjac is less behaviourally affected by other diurnal disturbances than the other ungulates, although to our knowledge this has not been tested.

4.5.2 *More variable responses in smaller species*

In contrast to the larger species, smaller-bodied species tended to display more variable responses, with overlap of activity patterns not significantly greater than expected for two of four species, and all four species showing minimal directional shifts in activity patterns (Fig. 2, Table 2). The diurnal-crepuscular activity pattern of Lesser Mousedeer agrees with previous observations in unlogged forest (Matsubayashi, Bosi & Kohshima 2003) and was not affected by logging. In contrast, Greater Mouse-deer became more cathemeral. As responses of both species enhance exposure to elevated daytime temperatures and reduced humidity in logged forest, abiotic stress seems unlikely to be an important driver. The small body size of mouse-deer gives them higher upper limits to the thermoneutral zone and potentially greater physiological plasticity (Gardner *et al.* 2011); and may also allow mouse-deer to avoid intense abiotic stress by plastically selecting more sheltered microhabitats.

Instead, we suggest that the observed pattern in Greater Mouse-deer is more probably due to underlying resource availability constraints. Heydon (1994) and Heydon and Bulloh (1997) concluded that Greater Mouse-deer in particular decline in logged forest chiefly due to their dependence on *Ficus* figs, which become increasingly scarce and spatially patchy. The activity shift we observed, with the “spreading out” of the dusk activity peak, plus the increase in overall

activity level, are consistent with the mouse-deer ranging further over longer portions of the day to visit more spatially patchy resources, rather than making a short dusk commute to nearby fruiting trees.

The two porcupine species were already obligately nocturnal in unlogged forest and therefore could not become significantly less active during daylight hours (Fig. 2g-h). However Long-tailed Porcupine shifted the peak of its nocturnal activity strongly from the later night to the earlier night. Malayan Porcupine also showed a hint of this shift, although not significantly so (Fig. 2g). The reasons for this are unclear: although it is possible that porcupines are impacted by earlier onset of higher temperatures and lower humidity in logged forest, the major reduction in activity of Long-tailed Porcupine occurs between approximately 03:00 and 06:00 (Fig. 2h), which is largely before the daily onset of temperature increases (Hardwick *et al.* 2015).

4.5.3 Relationships with persistence

We found no relationship between decreasing overlap in activity pattern and probability of decline with logging (Fig. 4). Furthermore, the large herbivore community generally showed null, or inconsistent changes in overall activity level, instead of consistent decreases as might be expected if shifting activity patterns is universally adaptive and increases foraging efficiency; or consistent increases as might be expected if shifts are maladaptive and decrease foraging efficiency. Together, this suggests that activity pattern shifts, while prevalent, do not represent a universal strategy for survival in logged forest. It is possible that the lack of a pattern is because the logged forest mammalian herbivore community already represents a filtered subset of the primary forest community: we could not analyse several larger herbivores such as Thick-Spined Porcupine *Hystrix crassispinis*, Banteng *Bos javanicus* and Bornean Elephant *Elephas maximus borneensis*, as they were too scarce within our study area in general, or confined to one habitat type. A further species, Bornean Rhino *Dicerorhinus sumatrensis harrisoni* is already effectively extinct from the entire region (Havmøller *et al.* 2016)(Havmøller *et al.* 2016).

4.5.4 Conclusions

Overall, our results show a high level of behavioural plasticity in Bornean herbivorous mammals, which bodes well for their survival in the face of future anthropogenic disturbance and environmental change, and supports the global pattern described by Gaynor *et al.* (2018). Nevertheless, the patterns we observed are relatively species-specific, and we found no

relationships between activity pattern shifts and persistence. The largest changes in activity patterns we observed, with the most pronounced shift towards nocturnality, were among the largest ungulate species that form the major hunting targets in the region (Bennett, Nyaoi & Sompud 2000). However, further work to separate the effects of hunting pressure from other potential drivers of increased nocturnality, such as abiotic stress, may prove difficult. Logging and hunting frequently accompany each other (Robinson, Redford & Bennett 1999; Bennett & Gumal 2001), not least because of the increased access to humans resulting from creation of thousands of kilometres of logging roads (Gaveau *et al.* 2014), and increased local populations (eg. at logging camps, sawmills and newly-cleared plantations). Nevertheless, conservation measures to reduce hunting, and those to rehabilitate and regenerate logged forests (thereby reducing abiotic stress) require different strategies and allocation of resources. Our results thus suggest that disentangling these drivers, as well as gaining a more general understanding of species activity patterns and their responses to logging, are important avenues for future research if we are to mitigate future negative impacts of logging on mammal diversity in tropical forests.

Chapter Five: Minimal spillover of native small mammals from Bornean tropical forests suggests limited impact on adjacent oil palm plantations

5.1 Abstract

In the face of rapid tropical agricultural expansion, preservation of tropical forest remnants is vitally important. Forest remnants requiring conservation often directly adjoin the edges of new or established plantations, so landscape-level conservation requires a good understanding of the balance between ecosystem services and disservices provided by forest, including potential yield reductions caused by pest species inhabiting forest remnants. Currently we know very little about the scale of any spillover effect at forest edges, or to what extent native, forest-dependent species are involved. Sampling across an edge gradient between logged tropical forest and oil palm plantations in Sabah, Malaysian Borneo, we examined the distribution and behaviour of small mammals, an important pest group in oil palm plantations. We took a dual approach, using a trapping grid to reveal patterns of community distribution and species relative abundance across the forest-plantation edge, and tracking individuals of forest species using a spool-and-line. Although two invasive small mammal species were found across the whole edge gradient, we uncovered little evidence that the native forest small mammal community crosses the edge and uses the plantation. Of 10 forest species detected, we found only the adaptable murid *Maxomys whiteheadi* in the plantation, where it appeared to persist at low abundances at all distances from forest, including the plantation-interior control site. Our observed abundance patterns reveal no evidence for a spill-over of *M. whiteheadi* populations from forest fragments. On the forest side of the edge, observed species richness of small mammals increased with distance into the interior, suggesting a negative edge effect may exist within forest remnants. Of 23 successfully tracked small mammals, only one *M. whiteheadi* crossed the forest-plantation edge, with null modelling suggesting that animals were significantly repelled from crossing into plantation habitat. Our results suggest that spillover of native small mammals contributes little or nothing to oil palm damage close to forest-plantation edges, but rather that oil palm may negatively impact small mammal populations within adjacent forest remnants.

5.2 Introduction

Maximising the remaining area of tropical forest amid agricultural expansion is a priority for conservation (Green *et al.* 2005; Barlow *et al.* 2007; Sodhi *et al.* 2010a; Gibson *et al.* 2011), especially in Southeast Asia where the expansion of oil palm (*Elaeis guineensis*) continues to threaten one of the world's great biodiversity hotspots (Fitzherbert *et al.* 2008; Wilcove *et al.* 2013; Yue *et al.* 2015; Vijay *et al.* 2016). With most remaining primary forest already preserved, extant areas in need of conservation are generally logged-out timber concessions with limited residual value for logging and poor legal protection (Reynolds *et al.* 2011).

A key challenge in creating and maintaining protected areas adjacent to plantation agriculture is understanding and managing spillover of plants and animals between the two habitat types. Spillover may involve transient dispersal and foraging movements in either direction across the habitat boundary, and involve species providing ecosystem services such as pest control (Koh 2008; Lucey *et al.* 2014; Nurdiansyah *et al.* 2016); or ecosystem "disservices" such as crop damage to the forest or to the plantation, which harms yields and therefore profits (Zhang *et al.* 2007). Therefore, depending on the organisms involved, there may exist a range of ecological effects from net benefit to net cost on either habitat close to the boundary (Rand, Tylianakis & Tscharncke 2006; Blitzer *et al.* 2012; Edwards *et al.* 2014b). The way that plantation workers, landowners and policymakers perceive this service-disservice balance is important, as ecosystem services provided may be subtle and complex. Even if there is a net positive effect of retaining forest remnants in plantations, if stakeholders regard them as pest reservoirs they are likely to resist efforts to conserve those remnants, contributing to local and global losses of biodiversity from tropical deforestation (Bradshaw, Sodhi & Brook 2009; Wilcove *et al.* 2013).

Forest remnants may act as a source of pests in two different ways. First, the remnants may harbour increased abundance of generalist, sometimes invasive pests. Such species are often already prevalent in the wider landscape, and remnants may provide them with undisturbed breeding space and favourable microhabitats that shield them from pesticide control (White, Wilson & Horskins 1997; Tweheyo, Hill & Obua 2005; Valantin-Morison, Meynard & Doré 2007; Amici *et al.* 2012). Second, forest-dependent species might cross the forest-plantation edge and forage in plantations, thus adding novel pest species to the plantation community (Hill 1997, 2000; Naughton-Treves 1998; Saj, Sicotte & Paterson 2001; Strum 2010). Where forest species do cross into plantations and are susceptible to pre-existing intensive pest control measures, their populations may be reduced near the edge and thus the plantation can act as a sink habitat and an "ecological trap" (Forbes & Theberge 1996; Woodroffe & Ginsberg 1998; Lamb *et al.* 2017). In a landscape where most forest remnants are small and isolated, this could contribute to extirpation of vulnerable species at a landscape scale. The identity of communities spilling

over at the forest-plantation edge is therefore important from both a conservation and an economic standpoint.

Despite these practical questions, evidence for the contribution of tropical forest species to agricultural ecosystem disservices remains lacking. Among the most economically significant pests of Southeast Asian oil palm are murid rodents (Puan *et al.* 2011). To quickly gauge the perception of their economic importance, we informally surveyed nine oil palm plantation managerial staff from three companies in Sabah, Malaysian Borneo. All reported that rats caused at least moderate damage to oil palm trees, with seven respondents linking this to yield reductions. Five respondents identified greater damage at forest-plantation edges, while two respondents said that damage was reduced at edges.

This diversity of views coincides with a lack of studies examining the spillover of small mammals across forest-plantation edges. Most available literature on oil palm pest species focuses on economic impacts and chemical control (Wood 1984; Wood & Liao 1984a; b; Wood & Chung 1990; Hafidzi & Saayon 2001; Andru *et al.* 2013) rather than broader aspects of their ecology (but see Buckle *et al.* 1997). The literature is also heavily biased towards established pest species, generally a handful of invasive, open-country generalists of the genus *Rattus*, particularly the Malaysian Field Rat *R. tiomanicus* (Wood 1984; Wood & Liao 1984a; b; Buckle *et al.* 1997; Wood & Fee 2003; Puan *et al.* 2011). Conversely, spillover of forest small mammal species into plantations has hardly been investigated. These species remain at high abundances within heavily-logged forest adjoining oil palm landscapes (Wells *et al.* 2007a; Bernard, Fjeldsø & Mohamed 2009; Wearn *et al.* 2017; Chapman *et al.* 2018b; Chapter Two), and are easily trapped using oil palm fruit as a bait (pers. obs.). Therefore there is potential for the forest community to spill over into adjacent plantations and increase existing levels of fruit predation and yield damage, although the opinions of plantation managers are split on whether this actually happens or not. Such a split in opinion may arise if the spatial scale and duration of any spillover depends on the microhabitat characteristics of the plantation, which can vary even within individual oil palm estates. Key variables that might influence spillover patterns include whether sufficient ground cover is available for small mammals to avoid predators, and the spatial availability of oil palm fruit.

Nevertheless, we found only two studies which reported spillover of forest small mammal species. Bernard, Fjeldsø and Mohamed (2009) captured one *Sundamys muelleri* and three *Maxomys whiteheadi* individuals 200 m inside a plantation, plus one *Maxomys surifer* 30 m inside the plantation. Rajaratnam *et al.* (2007) captured *Niviventer cremoriventer*, *M. surifer*, and *M. whiteheadi* at unspecified distances into the plantation, with the latter occurring at a comparatively high density. Neither study caught any invasive *Rattus* species, but it is unclear

whether this represents native species competitively excluding invasives, or greater susceptibility of invasives to control measures. Although poorly-studied, the home ranges of most Southeast Asian small mammals are probably small, with mean observed movement distances around 20–60m (Nakagawa *et al.* 2007a; Wells, Lakim and Pfeiffer 2008). We might therefore expect relatively high volumes of spillover (consistent with animals siting home ranges mostly within a plantation) over only 50–100m into plantations. However, variance in movement distances appears to be high, with some species occasionally ranging above or beyond 200m (Wells, Lakim and Pfeiffer 2008). This supports the observations of Bernard, Fjeldså and Mohamed (2009) mentioned above, and suggests that limited spillover might occur over large spatial scales. Nevertheless, we found no study explicitly investigating the spatial scale of this spillover of forest-derived small mammal populations, or testing whether spillover is dependent on characteristics of the plantation environment.

We also found no studies examining how forest-plantation edges affect movement behaviour of individual forest small mammals, including whether they regularly cross edges or are impeded by them. If edge crossing occurs regularly, we also do not know how they select microhabitat within plantations. In both unlogged and logged Southeast Asian rainforest, small mammal species forage at various vegetation strata and differ in scansorial tendencies. The community therefore partitions habitat vertically (Wells *et al.* 2006; Loveridge *et al.* 2016), although most species prefer densely sheltered microhabitats (Bernard 2004). Much of the available fruit in an oil palm plantation occurs at tree crown level; therefore the yield damage caused by forest small mammals may depend on species identity and foraging niche, as well as plantation age. For instance, Puan *et al.* (2011) found that the relationship between abundance of invasive rats and fruit damage in plantations weakened with increasing plantation age, presumably because lower, younger palm crowns were more accessible to rodents than older, taller ones. Furthermore, younger plantations exhibit reduced canopy closure but increased herbaceous ground cover (Luskin & Potts 2011), which may further encourage shelter-dependent forest species to cross the habitat boundary and forage.

In this study, we investigated the distribution and behaviour of forest small mammals at forest-plantation edges in Sabah, Malaysian Borneo, using a dual approach. Firstly, we used a live-trapping grid spanning from forest to oil palm plantation to examine broad patterns of community distribution across the edge. We tested the hypothesis that most or all forest small mammal species will occur in the plantation, but that capture rates of all species will decline with increments of distance into the plantation from the edge, and that the distance at which species disappear will vary interspecifically. We related the abundance of different small mammal species in the plantation to key structural variables describing the oil palm plantations

to examine whether plantation management affects the scale of the spillover effect and the species involved. Secondly, we used spool-and-line tracking of individual forest small mammals captured at the edge, or just inside the forest, to examine edge crossing behaviour and movement patterns within plantations. We compared observed paths against species-specific random null paths generated from data on movement within continuous logged forest (Loveridge *et al.* 2016) to test whether individuals cross the edge more or less than expected by chance. Filling these knowledge gaps will help to quantify the effects of forest small mammals at the edges of plantations, and the effects of oil palm edges on neighbouring forest small mammal communities. Therefore our findings should serve to inform both economic and biodiversity arguments as to the costs and benefits of retaining forest remnants in an oil palm landscape.

5.3 Methods

5.3.1 Study areas

We collected field data within the 1 million hectare Yayasan Sabah Forest Management Area in Sabah, Malaysian Borneo, which comprises a patchwork of protected primary dipterocarp forest, selective logging concessions and oil palm plantations (Reynolds *et al.* 2011). We sampled forest-plantation edges in two locations: the experimental landscape at the Stability of Altered Forest Ecosystems (SAFE) project, a landscape-scale deforestation experiment (Ewers *et al.* 2011; N4° 41' 58", E117° 37' 40"), and a second area of forest approximately 23 km west-southwest (N4° 38' 26", E117° 26' 09"). At both edge locations, the forest comprised >1000 ha tracts of heavily-logged forest, with continuous cover extending for ≥1 km behind the edge, and featured a structure typical of logged forest in the region, with few large trees and a dense understorey of vines and herbaceous plants (Pfeifer *et al.* 2016). Our forest study areas directly adjoined oil palm plantations (managed by Benta Wawasan Sdn. Bhd.), which were planted between 2004 and 2013, and therefore ranged from young but established plantations (c. four years old) to mature plantations (c. 13 years old). Oil palm trees were planted at an average density of 120-140 palms .ha⁻¹, and we chose plantations that were managed with moderate intensity, typical of the wider region. This was defined by control of ground flora: epiphyte cover had been allowed to persist on palm trunks, and unplanted areas such as stream gullies had been allowed to develop extensive ground cover of kudzu (*Pueraria* sp., young plantations) or native herbs (older plantations) to limit soil runoff.

5.3.2 Sample sites

We sampled small mammal communities at nine sites spread between the two edge locations: six at the SAFE project edge, and three at the second edge to the west-southwest. We also sampled at one plantation-interior control site (at the west-southwest area), which was >1.5 km from the forest edge at the second location. Within a study area, sites were located along the same forest edge, however we spaced neighbouring sites ≥ 300 m apart (308-761m) to minimize interactions between sampled communities and maintain independence between sites. This distance is several times the maximum home range radius of *Leopoldamys sabanus*, the largest and widest-ranging murid likely to be encountered (Wells *et al.* 2008), and thus minimises interactions between communities within the area. We preferentially selected sites with a straight forest edge, as this minimised error in the measurement of distance from the edge to the trapping points inside the forest. We also chose sites with a cleared, herbicide-treated buffer strip separating the herbaceous forest understorey vegetation (or the base of the trees) from the ground flora in the area covered by the plantation. This strip varied from 2-5 m wide, and invariably contained a small two-strand electric livestock fence, and minimal or no ground vegetation. We selected this feature because: (1) this management technique was predominant in our study system and the landscape as a whole; (2) the measurement of the position of the forest-plantation edge is relatively discrete and unambiguous, allowing us to precisely locate traps at a defined edge position; and (3) we could control for the presence and density of “bridges” of ground vegetation linking the ground cover of the forest remnant and the oil palm plantation. To further control for the physical structure of the edge, we rejected sites where the strip was >5 m wide, included an active access track, or was significantly eroded into gullies by rainwater runoff, as these features may bias movement of individuals near the edge.

5.3.3 Trapping

Before starting fieldwork, all trapping and handling procedures were approved by two ethics committees (Imperial College London’s Animal Welfare and Ethical Review Body, and the Zoological Society of London’s Ethics Committee). At each edge site, we set up a live-trapping grid comprising 36 trap points in nine lines of four with 23 m spacing between lines, spanning the edge from 46 m inside the forest to 138 m inside the plantation, with one trap line at 0 m, i.e. directly on the forest-plantation edge (total area covered = 6072 m², see Fig. 1). We designed the grid carefully to avoid biasing animal movement towards the edge, and particularly avoided cutting access trails perpendicularly into the forest toward each trap, as this potentially provides an easy route from interior to edge. Instead, we made a single perpendicular access

trail to one side of the grid, and accessed traps via side trails parallel to the edge, with the first trap appearing >5 m from the perpendicular access trail. We took care to cut the minimum vegetation required to access traps. At each trapping point we placed one locally made “Tomahawk” style wire mesh cage trap (28 x 18 x 12 cm), placing traps preferentially in dense ground cover or undergrowth, and baiting with a ripe oil palm fruit. Although this bait is clearly abundant in the environment, previous experience in this study system has shown that palm fruit is still effective at capturing small mammals in oil palm plantations as well as forest (e.g. Wearn *et al.* 2017). This is possibly due to the preference of small mammals to feed in sheltered spaces, meaning that bait inside an enclosed trap remains more attractive than bait in the wider environment. We therefore covered traps with a black plastic wrapping, which also sheltered captured animals from rain and excess heat. The control site did not straddle an edge, but we designed it to cover the same area with equal trap density (one trap per 3.78 m²).

We ran traps for three days and nights, with checking carried out daily in the early morning to avoid exposing animals to excess heat. Captured animals were handled in accordance with the guidelines proposed by the American Society of Mammalogists (Sikes, Gannon & American Society of Mammalogists 2011), and sick or injured animals were released without processing. We anaesthetised all other newly captured animals using diethyl ether, identified to species, aged and sexed where possible, and uniquely marked them with a Passive Integrated Transponder (PIT) tag (Francis Scientific Instruments, Cambridge, UK) to enable individual ID of recaptures. To support uncertain ID, aging and sexing, we also took biometrics (hind foot and ear length, ano-genital distance and weight). We recorded the ID and location of all recaptures, then released all animals at their capture location.

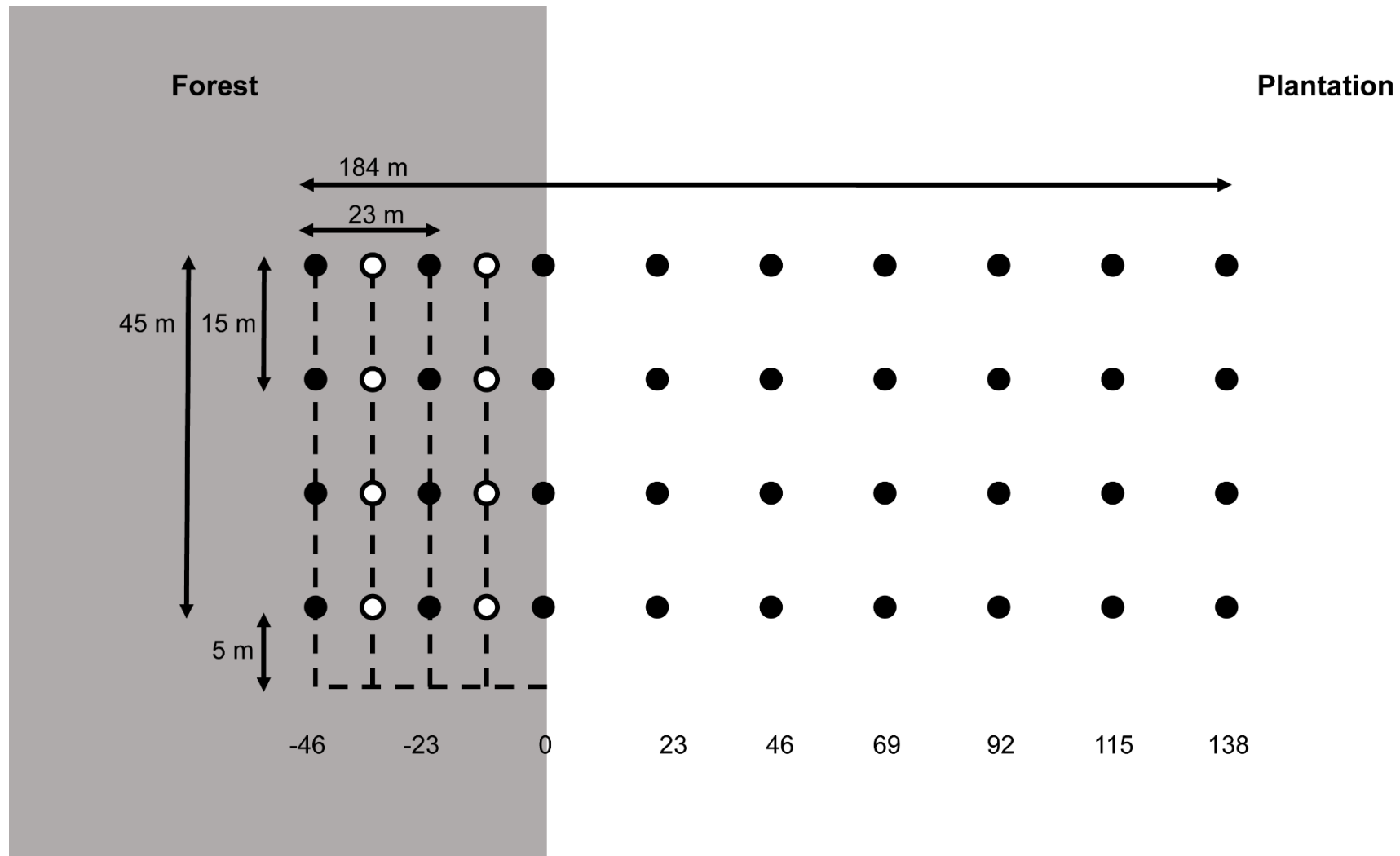


Fig. 1. Schematic of the grid trapping design, showing the arrangement of trapping points (filled circles) in the forest (grey shaded area) and plantation (white area). Distances of trapping lines from the edge (in metres), as referred to in the text, are shown at bottom, with the line at 0 m being situated exactly on the edge. Open circles: extra trapping lines used for the individual movement portion of the study, interspersed between the forest trapping lines at -11.5m and -34.5m. Dashed lines: Access trails (see text).

5.3.4 Spool-and-line tracking

To examine patterns of individual movement at edges, we trapped on the three trap lines of each grid covering the forest and edge (i.e. the lines at 0, 23, and 46 m into the forest, see Fig. 1) for an additional three nights. To maximise capture rates, we added two extra trapping lines interspersed between the existing lines (at 11.5 and 34.5 m into the forest, see Fig. 1) to maximise capture rates. Since most Bornean small mammals are nocturnal, we processed captures and released them for tracking with several hours of night remaining in order to capture representative space use behaviour. We set traps at dusk, and processed captures between 21:00 and 22:00, remaining >50 m away from the grid during the intervening period to minimise disturbance. To track released small mammals, we used a spool-and-line device following Loveridge et al. (2016). We covered an industrial nylon cocoon bobbin (Danfield Ltd, Lancashire, UK) with a cling film wrapping to ensure that it unravels and detaches cleanly, and then wrapped it with cloth tape and attached it to the back of the small mammal using cyanoacrylate glue. Following established procedures for radio tracking (e.g. Kenwood 2000) we unwound each spool so that the total mass including wrapping did not exceed 5 % of the animal's body weight. This left approximately 120 m of line. Once each animal had fully recovered from anaesthesia, we released it, having first tied the loose bobbin end to the trap or adjacent vegetation at the trapping site. The bobbin is coreless and unravels freely from the inside outward, so the animal moves with minimal resistance and the outside end detaches easily once the animal has moved the entire length of the thread (Miles, de Souza & Póvoa 1981). We took considerable care to release animals as simultaneously as possible on the grid and exit the area quietly and rapidly in order to avoid disturbing previously-released individuals, and we did not spool more than three animals per night.

The following morning we followed and collected the spool threads, measuring the total tracked distance, and recording whether animals crossed the edge. For animals which did not cross, we recorded whether they approached within five metres of the edge (defined as moving towards the edge from within the forest and remaining less than five metres from the edge for at least five metres travelled distance). Since animals can only cross the edge if they move further than the distance from their release point to the edge, and because small animal movements are seldom linear, we only retained for analysis those paths where the animal had travelled at least the distance from its release point to the edge, plus 20% extra. In the case of animals released at 0 m, we discarded paths where the animal travelled <20 m overall.

5.3.5 Vegetation covariates

To investigate whether plantation characteristics affect the spillover of forest-dependent small mammals, we measured habitat variables at each of the 24 trap points of the grid covering the plantation side of the edge (Fig. 1), ensuring that this coincided with trapping. First, for all trap locations we recorded a categorical trap location variable, describing whether the location was in a stand of oil palm trees (at least one trunk within five metres), open bare ground, or open ground with ground covering vegetation. For the subset of locations on each grid (mean = 20.9 ± 0.81) which fell within a stand of palms, we measured four characteristics of the closest palm to the trap: 1.) Trunk height (to the underside of the branches level with the crown), using a laser rangefinder (Bosch GmbH, Stuttgart, Germany). 2.) Ground vegetation cover within a five-metre radius of the trunk base, using a four-level categorical index, corresponding to 25 % increments (1= 0-25% cover, 2= 25-50% cover, 3= 50-75% cover, and 4= 75-100% cover); 3.) The number of visible infructescences; and 4.) Presence/absence of ripe fruit at ground level. On several occasions, harvesting was occurring in our study sites during trapping. Since harvested fruit will have been previously available to small mammals, our count of infructescences included obviously fresh cut scars where infructescences had been removed within the preceding 24 hours.

5.3.6 Analyses

We carried out all modelling using R v.3.5.0 (R Core Team 2018). To investigate the extent of the spillover effect, we first identified which species that were trapped in forest were also trapped in oil palm. We defined the spillover extent of each species as the distance from the edge over which abundance is elevated above that species' background abundance in the oil palm plantation (following conceptually similar approaches in e.g. Chen, Franklin & Spies 1992; Brand & George 2001; Hylander 2005). We used capture rate of each species as a proxy for abundance, pooling captures of individuals (i.e. discarding subsequent recaptures) over the three trapping nights at each trap point. To statistically test spillover extent of each species, we tested for the difference between mean capture rate at each trap line and capture rate in the interior oil palm control plot using a generalised linear mixed model (Poisson error, log link) fitted in package *lme4* (Bates *et al.* 2015). Where capture rates ceased to differ from that within the control plot, we took this distance to represent the limit of the species spillover into the plantation. Where a species was trapped at our edge sites but not at the control site, we took the species spillover limit to be the distance at which capture rates ceased to differ from zero. To

account for our sampling structure, and thus for potential site-specific differences in capture rates, we included “site” as a random effect in our models.

To test whether the characteristics of oil palm plantations predicted capture rates of each species within the plantation, we subsetting the trapping data to only include captures from the 24 traps in each grid on the plantation side of the edge (see Fig. 1). We then modelled pooled capture rates of each species against our plantation structure variables, using generalised linear mixed models (Poisson error, log link) in two stages, again controlling for site-specific variation in capture rates using “site” as a random effect. First, we modelled capture rates across all plantation traps against the categorical trap location variable (oil palm stand/open bare ground/ground cover vegetation) to test whether this basic plantation characteristic predicted capture rates. Then, we subsetting further, to only include trap points within a stand of oil palm trees (mean = 20.9 ± 0.81 locations per grid). We modelled pooled capture rates at each trap point against the detailed habitat quality variables (oil palm tree height, ground cover, fruit bunch count and presence/absence of ripe or fallen fruit). We took a model selection approach, fitting models of increasing complexity. First, we fitted each variable separately, then models with the terms added sequentially, then models with all combinations of two-way interactions. We selected the best-fitting model for each species based on Akaike’s Information Criterion (AIC).

To investigate whether edges impede individual small mammal movement behaviour, we used a null modelling approach to compare the observed proportion of individuals crossing edges with null proportions derived from simulated random small mammal paths. First, we grouped our observed small mammal paths by species and distance released from the edge. For each species, at each release distance, we recorded the observed proportions of individuals which crossed the edge. We assumed that small mammal movement trajectories can be simplified to a series of step lengths in centimetres, connected by relative turning angles in degrees (following e.g. Almeida *et al.* 2015; Loveridge *et al.* 2016). To simulate random paths and generate null crossing proportions, we extracted species-specific distributions of these step lengths and turning angles from Loveridge *et al.* (2016). These authors made detailed measurements of small mammal paths in continuous selectively logged forest within our study landscape. This forest was >1 km away from the nearest forest-plantation edge, but was analogous in logging intensity and vegetation structure to the forest at our study edges (Loveridge *et al.* 2016). We then iteratively constructed null paths by sampling randomly from these distributions of step lengths and turning angles.

For each of the observed species $\times$ distance groups, we constructed 1000 null groups, each composed of null paths exactly corresponding in number and total travelled distance to the individuals in the observed group.

We then plotted these null paths in Cartesian x-y space, and calculated the proportion of the paths which crossed the edge at the relevant distance from the release point. For example, given an observed group of five individuals released 23 m from the edge, we constructed a group of five null paths exactly matching the observed paths in travelled distances, then iterated this 1000 times, recording for each group of five null paths the proportion which moved ≥ 23 m along one axis from the release point. To eliminate any directional bias in the starting heading of the null paths, we randomly varied the orientation of the axis along which the path should exceed the critical distance, switching between x, y, -x, and -y. This process produced a distribution of null crossing proportions for each species $\times$ distance group: we then calculated significance by comparing the observed proportion of edge crossers with the 0.025% and 97.5% quantiles of this null distribution, to determine whether there was less than a 5% chance that the observed proportion of crossers was drawn from the expected distribution.

5.4 Results

5.4.1 Trapping success and community distribution across the edge gradient

Across our ten trapping grids, we ran 36 traps per grid for three days each, giving a total trapping effort of 1080 trap-nights. In 230 identifiable capture events, we captured 215 individual small mammals comprising 12 species (20 % trap success rate, see Table 1). All 12 species occurred inside the forest, and included 10 native murids, squirrels and treeshrews, plus two invasive murids (*Rattus rattus* and *R. exulans*). In the plantation, we only caught these two invasive species, plus the native murid *Maxomys whiteheadi*. We therefore caught no species which were confined to the plantation, but nine that were confined to the forest. With the exception of *M. whiteheadi*, no native forest-dependent small mammal species were trapped at any distance into the plantation. Of the remaining nine native species captured in forest, four were captured immediately at the forest-plantation edge (0 m), a further three were only captured 23 m into the forest and two species were not captured closer than 46 m to the edge (Table 1).

5.4.2 Abundance of murids across the edge gradient relative to the plantation interior control site

The three murid species which were present in plantation showed different patterns of abundance across the forest-plantation edge (Fig. 2). At all forest trap lines including at 0 m, *Maxomys whiteheadi* was more abundant (higher catch rate) than in the oil palm control site (generalised linear mixed model with Poisson error and log link, all $P < 0.05$). However, abundance of *M. whiteheadi* did not differ from the control value at any plantation distance (Fig. 2a). By contrast, *Rattus exulans* had similar abundance in forest and oil palm, and did not differ from the control value at any distance along the edge gradient (Fig. 2b). *R. rattus* was scarce and patchily distributed across the whole gradient, and its abundance also did not differ from the control value at any point (Fig. 2c).

5.4.3 Habitat variables as predictors of murid abundance in the oil palm plantation

The presence or absence of oil palm trees surrounding each trap did not predict capture rates of any of the three species occurring within the plantation. However, for the subset of traps within a stand of oil palm trees, the height of the nearest oil palm tree did negatively predict the capture rates of both *Maxomys whiteheadi* (generalised linear mixed model with Poisson error and log link; $z = -2.91$, $p = 0.004$; Table A1), and *Rattus exulans* (generalised linear mixed model with quasipoisson error and log link, $z = -2.272$, $p = 0.023$, Table A1). The abundance of *Rattus rattus* was not significantly predicted by any habitat variables.

Table 1. Total unique small mammal captures across our edge gradient by species and distance from the edge. The edge is at 0m, while negative distances denote forest trap lines and positive distances denote plantation trap lines (See Fig. 1). Crosses † denote invasive plantation generalist species. Common names follow Payne and Francis (1985).

Species	Forest			Plantation							Total
	-46m	-23m	0m	23m	46m	69m	92m	115m	138m	Control	
Four-Striped Ground Squirrel, <i>Lariscus hosei</i>	1	-	-	-	-	-	-	-	-	-	1
Long-Tailed Giant Rat, <i>Leopoldamys sabanus</i>	1	-	-	-	-	-	-	-	-	-	1
Red Spiny Rat, <i>Maxomys surifer</i>	3	2	-	-	-	-	-	-	-	-	5
Whitehead's Rat, <i>Maxomys whiteheadi</i>	16	23	18	5	3	7	5	9	5	2	93
Dark-Tailed Tree Rat, <i>Niviventer cremoriventer</i>	1	1	3	-	-	-	-	-	-	-	5
†Polynesian Rat, <i>Rattus exulans</i>	5	4	8	3	4	8	8	13	5	2	60
†Black Rat, <i>Rattus rattus diardii</i>	4	3	2	1	1	5	1	3	-	1	21
Horse-Tailed Squirrel, <i>Sundasciurus hippurus</i>	-	2		-	-	-	-	-	-	-	2
Low's Squirrel, <i>Sundasciurus lowii</i>	3	2	1	-	-	-	-	-	-	-	6
Slender treeshrew, <i>Tupaia gracilis</i>	-	-	1	-	-	-	-	-	-	-	1
Common Treeshrew, <i>Tupaia longipes</i>	8	4	3	-	-	-	-	-	-	-	15
Large Treeshrew, <i>Tupaia tana</i>	2	3	-	-	-	-	-	-	-	-	5
Total	44	44	36	9	8	20	14	25	10	5	215

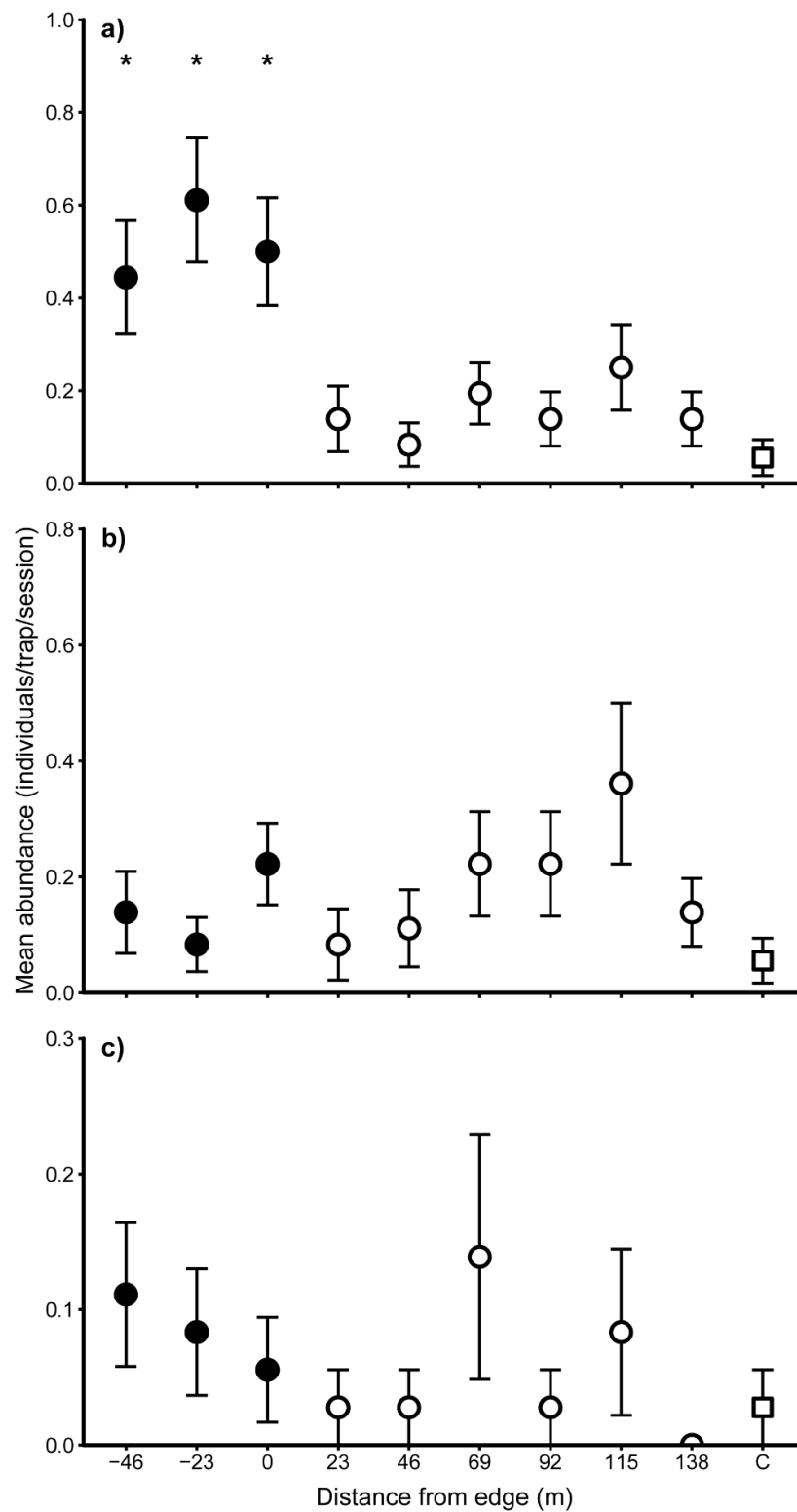


Fig. 2. Mean pooled abundance $\pm$ S.E. (individuals. trap⁻¹. session⁻¹) of three small mammal species at 23 m intervals across a gradient between forest (filled circles) and oil palm plantation (open symbols): a) *Maxomys whiteheadi*; b) *Rattus exulans*; and c) *R. rattus*. Asterisks denote significantly different abundance between each distance increment and the plantation interior control site (open square): * indicates $P < 0.05$.

5.4.4 Individual edge crossing frequency, edge use behaviour and null modelling

We attached spools to 39 individual small mammals (of which 14 had previously been captured and PIT-tagged in the community distribution section of the study). Of these, 23 individuals were tracked for a distance at least 120 % of the distance to the edge, including 18 *Maxomys whiteheadi*, three *Rattus rattus*, one *Niviventer cremoriventer*, and one *Maxomys surifer*.

Ten of the 23 individuals approached the edge from within the forest (defined as moving towards the edge to within five metres, and remaining less than five metres from the edge for at least five metres travelled distance). Six *M. whiteheadi* and one *Niviventer cremoriventer* made apparent foraging or ranging movements to the extreme edge of the forest vegetation (i.e. to 0 m) for an apparently prolonged period (> 10 travelled metres). Only one *M. whiteheadi* crossed the edge, an adult female, which was released at 11.5 m into the forest. This animal made c. 40 m of apparent foraging movements within the forest, before penetrating the plantation to a total straight-line distance of 11.5 m (covered distance = 27.85 m) before shedding the spool.

Due to the low sample sizes of most tracked species, we could only apply null modelling to *M. whiteheadi* (n=18 individuals). Sample sizes were also too low at most distances from the edge to separately construct quantiles and estimate significance for the difference between the observed and expected proportions of edge crossers. Therefore, after simulating the random path groups at each distance from the edge, we pooled these into an “interior” group of 12 simulated individuals (caught and released ≥ 23 m from the edge) and a “near-edge” group of eight individuals (caught and released at ≤ 11.5 m from the edge). Small mammals in the “interior” group were no more or less likely than random expectation to cross the edge (Observed proportion = 0; 2.5% and 97.5% quantiles of simulated distribution = 0, 0.0833). However, small mammals from the “near-edge” group were significantly less likely than random expectation to cross (Observed proportion=0.125; 2.5% and 95% quantiles = 0.25, 0.75).

5.5 Discussion

5.5.1 Distribution of the native small mammal community around the edge

Our results reveal little evidence that native small mammal communities spill over from forest into adjacent oil palm plantations, and we reject our hypotheses that the majority of native small mammals use the plantation with elevated abundance near the edge, but declining abundance with distance into the plantation. In our oil palm traps we did not capture the three native species (*Maxomys surifer*, *Sundamys muelleri*, and *Niviventer cremoriventer*) observed at

trace abundances in Sabah oil palm plantations by previous studies (Rajaratnam *et al.* 2007; Bernard, Fjeldså & Mohamed 2009), despite a higher number of individuals caught in plantation (n=91, Table 1) than these two studies. Of the 10 native species trapped in our forest plots, only the small terrestrial murid *Maxomys whiteheadi* (Whitehead's Rat) occurred in the plantation, being present throughout our distance gradient and plantation-interior control site. This supports previous observations which demonstrate that *M. whiteheadi* appears to be a successful and resilient native competitor to the invasive *Rattus exulans* and *R. rattus*, with populations persisting over long timescales in both heavily-logged forest and plantations (Cusack *et al.* 2015; Wearn *et al.* 2016, 2017; Chapman *et al.* 2018b). No studies report *M. whiteheadi* in oil palm plantations outside Sabah, which we suggest may reflect the scarcity of small mammal community studies in Southeast Asian plantations. Plantation murids have been shown to exhibit rapid shifts in community composition, for example the near-replacement of *R. tiomanicus* by *R. rattus* in peninsular Malaysia during the 1980s (Wood & Fee 2003). This change was probably mediated by evolution of resistance to chemical rodenticides (Wood & Fee 2003), so the emergence of *M. whiteheadi* as one of the dominant small mammal species in our studied plantations is potentially both recent and temporary. *M. whiteheadi* populations may also be relatively transient within individual plantations: We found that oil palm tree height (a proxy for plantation age) negatively predicted capture rates for this species and for *Rattus exulans*. Whether this is due to lower accessibility of oil palm fruit (eg. Puan *et al.* 2011), or increased mortality in older plantations (due to enhanced poisoning or decreased vegetative ground cover) is unclear, although capture rates of these species were not predicted by either our measures of ground cover or of fruit availability.

5.5.2 Abundance of *M. whiteheadi* across the edge gradient

Our data suggest that *M. whiteheadi* remains at high abundance near the edge of forest but declines to a lower constant abundance a mere 23 m into the plantation. Clearly, direct comparison of abundance between plantation and forest trap lines is subject to the caveat that we baited our traps with oil palm fruit, a bait which is abundant in the wider plantation, but absent in the forest. Therefore detectability is likely to be lower within the plantation. Our trapping in this habitat probably underestimated absolute abundance of all species, and possibly altogether missed native species making very occasional feeding forays. Using an alternative bait would not satisfactorily solve this problem, as palm fruit is the most effective available small mammal bait for forest or plantation in this study system (O.R. Wearn, pers. comm.). Detectability would therefore be similar or lower in a fruit-rich plantation environment if an alternative, less attractive trap bait was used. However, even if absolute abundance

changes between forest and plantation are hard to measure, if a significant spillover effect occurred over ≥ 23 m into the plantation we would still expect increased abundance in trap lines close to the edge, relative to the control value. The fact that this did not occur for *M. whiteheadi* suggests that any undetected spillover effect either occurs over distances < 23 m, or represents an extremely minimal increase in abundance. Similarly, the absence of any other native species in the plantation indicates that any undetected spillover of these species is also negligible.

The lack of an observed spillover pattern in *M. whiteheadi* could reflect two different population-level scenarios: (1) comparatively unconnected plantation and forest populations, with the edge acting as a significant dispersal barrier; or (2) one interconnected population, with relatively free dispersal across the edge countered by high mortality at any distance into the plantation. We suggest that the former scenario is more likely, for two reasons. First, we recaptured no individuals of *M. whiteheadi* (or any other species) on the other side of the edge from their capture location, which suggests that dispersal between populations either side of the forest-plantation edge is probably infrequent. Second, only one of our 18 tracked *M. whiteheadi* crossed the edge, despite multiple individuals approaching it closely before returning to the forest interior. While this is a low sample size to make reliable inferences about the behaviour of individuals throughout a population, our null modelling nonetheless demonstrated a significant barrier effect of edges. The proportion of edge crossers was no greater than random expectation across any original capture locations, and for individuals captured ≤ 11.5 m from the edge, crossing was significantly less likely than chance expectation. We therefore demonstrated that *M. whiteheadi* from inside forest were not significantly attracted to nearby plantations, and are more probably actively repelled by them.

5.5.3 Invasive small mammals across the gradient

Although we focussed on the distribution and behaviour of native small mammal species at the forest-plantation edge, we also found no evidence that forest harbours elevated abundance of the invasive *Rattus exulans* and *R. rattus*. Both species were present in all our forest lines, which supports previous evidence that they can competitively invade logged forest (Cusack *et al.* 2015; Loveridge *et al.* 2016; Wearn *et al.* 2016, 2017). However, abundance of both species did not differ from the control site at any distance. Assuming that differences in detectability underestimate abundance within the oil palm plantation, this suggests that if anything, true abundances of these species are probably lower in forest than in the adjacent plantation. Our results from Chapter Three (Table 4 in Section 3.4) suggest that survival of *Rattus* spp. in logged forest is extremely low. We therefore suggest that these species' persistence in forest adjacent

to plantations may depend on extensive spillover from plantations to forest, i.e. the opposite direction to that we investigated here.

5.5.4 Conservation implications

Our results have important implications for reconciling palm oil agriculture and conservation. First, we show that under current plantation management strategies (such as existing rodenticide regimes and cleared edge strips), the forest-plantation edge represents a largely sufficient barrier to ensure minimal spillover of native small mammals from forest into adjacent plantations. This component of forest biodiversity is therefore not a valid justification for the removal of native forest remnants in oil palm landscapes.

Second, we found no evidence that plantations act as a sink habitat for the native small mammal community by attracting individuals out into a high-mortality environment. Rather, most forest species appear to be impeded from entering the plantation at all. The pattern of our captures on the forest side of the edge, with several species not caught within 23 m of the edge, is also not consistent with a spillover of the native small mammal community into plantations. Rather, this pattern indicates the presence of an edge effect in the opposite direction. Although not yet documented for a forest-oil palm plantation edge (Yue *et al.* 2015), this phenomenon has been observed by small mammal studies within other forest-agricultural systems (Stevens & Husband 1998; Pardini 2004). Our results suggest that forest remnants embedded in plantations are likely to host small, isolated populations of native small mammals. This edge effect may be species-specific however, and not necessarily correlate with known responses to deforestation: for example, we captured the specialist squirrels *Sundasciurus hippurus* and *Lariscus hosei*, both of which are highly forest dependent and thought to be threatened by habitat degradation and loss (Meijaard & Sheil 2008). Neither the immediate proximity of an established oil palm plantation, nor the heavy logging at our sample sites, has led to the extirpation of these species from the area.

Third, the persistence in plantations of one native species (*Maxomys whiteheadi*) is positive news for conservation, and indicates that despite its Vulnerable IUCN classification (IUCN 2018), *M. whiteheadi* is unlikely to be at significant risk from anthropogenic habitat change. Nonetheless, *M. whiteheadi* represents just one out of the 21 terrestrial forest small mammal species in adjacent logged forests (Wearn *et al.* 2017), so this result should be viewed in context. With a home range radius of ≈ 52 m (Nakagawa *et al.* 2007a), populations persisting in our control site >1.5 km into a plantation are probably self-sufficient rather than sustained by dispersal from a forest-plantation edge. Nevertheless, it is possible that presence of *M.*

whiteheadi in plantations is tied to forest cover at a regional scale, particularly if it represents the result of a recent invasion, or if breeding success is marginal and persistence requires occasional long-distance immigrants from forests. We also do not know whether *M. whiteheadi* exploits a novel foraging niche in plantations (and potentially causes novel forms of yield damage), or simply displaces the invasive *Rattus* species. Our expectation is that because *M. whiteheadi* is largely terrestrial (Wells *et al.* 2004) and appears to be a dietary generalist (Wells *et al.* 2009), the latter may be more likely.

5.5.5. Management recommendations and conclusions

Although this study was predominantly aimed at assessing native small mammal spillover in plantations, the apparent edge effects we observed inside the forest deserve further investigation. The strong barrier effects of edges indicate small mammal populations inhabiting forest fragments are probably isolated, and the apparent edge effects indicate the effective fragment area available for small populations is much lower than the actual forest area (Ewers & Didham 2007). We also suggest that under current plantation management routines, oil palm managers have little cause to worry that native terrestrial small mammal populations from forest increase yield damage at forest-plantation edges. Indeed, the “sharp” edges along which we sampled form a sufficiently strong barrier to dispersal to effectively separate populations of terrestrial small mammals living only tens of metres apart. However, further research on other potential pest taxa may reveal different results, and as a precaution we recommend managers avoid canopy connectivity between forest and plantation by several metres to deter squirrels and other canopy frugivores from crossing the edge. For example, on several occasions during our fieldwork we observed the canopy-dwelling Plantain Squirrel (*Calliosciurus notatus*) crossing the edge by this means. *C. notatus*, which was not trapped during this study, has been observed to predate oil palm fruit (CABI 2017). Another potential mammalian pest, Bearded Pigs (*Sus barbatus*), left visible trails crossing the edge at several of our sites and are known to persist inside plantations (Love *et al.* 2017; Wearn *et al.* 2017). For this species, electrified boundary fences, especially of a more substantial design than those used in our sampling areas, may be a viable management approach. Overall however, we believe our results are an important information source for oil palm managers. Delivering this information to them is the next step to influencing their management actions and, ultimately, towards helping reconcile agricultural expansion with conservation of Southeast Asian tropical forest on a local scale.

5.6 Appendix A

Table A1. AIC comparison table for generalised linear mixed models of small mammal capture rates for three species against plantation characteristics. Mean pooled capture rates at a particular trap location are fitted against height of the nearest oil palm tree (height), a four-level categorical index of ground cover around the nearest tree (g. cover), the number of infructescences on the nearest tree (bunches) and the presence or absence of fallen ripe fruit at the base of the nearest tree (ripe). Models of increasing complexity are fitted, with each predictor fitted separately, then with the predictors added sequentially, and lastly with all predictors present and all combinations of single oneway interactions. The model we selected for each species is displayed in bold text, and for clarity, the parameter estimate, standard error, Z and P values are shown for this model only.

Species	Model specification	AIC	Estimate	SE	Z	P
Whitehead's Rat (<i>Maxomys whiteheadi</i>)	~height	153.250	-0.411	0.141	-2.910	0.004
	~g. cover	160.617				
	~bunches	159.990				
	~ripe	159.172				
	~height +g. cover	155.522				
	~height +g. cover +bunches	157.337				
	~height +g. cover +bunches +ripe	158.867				
	~height +g. cover +bunches +ripe +height :g. cover	162.661				
	~height +g. cover +bunches +ripe +height :bunches	160.849				
	~height +g. cover +bunches +ripe +height :ripe	160.307				
	~height +g. cover +bunches +ripe +g. cover :bunches	160.314				
	~height +g. cover +bunches +ripe +g. cover :ripe	159.882				
Polynesian Rat (<i>Rattus exulans</i>)	~height	187.001	-0.306	0.135	-2.272	0.023
	~g. cover	191.436				
	~bunches	187.116				
	~ripe	190.414				
	~height +g. cover	189.707				
	~height +g. cover +bunches	189.129				
	~height +g. cover +bunches +ripe	189.740				
	~height +g. cover +bunches +ripe +height :g. cover	192.920				

Black Rat (<i>Rattus rattus</i>)	~height +g. cover +bunches +ripe +height :bunches	191.699				
	~height +g. cover +bunches +ripe +height :ripe	191.646				
	~height +g. cover +bunches +ripe +g. cover :bunches	192.097				
	~height +g. cover +bunches +ripe +g. cover :ripe	191.513				
	~height +g. cover +bunches +ripe +bunches :ripe	191.572				
	~height	52.332				
	~g. cover	54.012				
	~bunches	51.512				
	~ripe	48.907	-17.57	387.036	-0.045	0.964
	~height +g. cover	55.994				
	~height +g. cover +bunches	57.065				
	~height +g. cover +bunches +ripe	55.103				
	~height +g. cover +bunches +ripe +height :g. cover	58.826				
	~height +g. cover +bunches +ripe +height :bunches	56.829				
	~height +g. cover +bunches +ripe +height :ripe	57.103				
	~height +g. cover +bunches +ripe +g. cover :bunches	55.799				
	~height +g. cover +bunches +ripe +g. cover :ripe	59.103				
	~height +g. cover +bunches +ripe +bunches :ripe	57.103				

Chapter Six: Context and implications of this thesis - the importance of a holistic, long-term approach to biodiversity conservation in logged forest

6.1. Summary of aims and research questions

The literature reviewed in Chapter One comprises a taxonomically broad, but not particularly detailed knowledge base about the impacts of selective logging on animals in general, and mammals in particular. Specifically, we understand that logged forests generally retain high species richness, but the variable, complex changes in abundance and community composition which have been observed suggest that all species, and all logged forests, are not equal. Species vary in their sensitivity to the profound changes in biotic and abiotic conditions, with some thriving and some declining or becoming extirpated. However, beyond simple categorical comparisons we have little consistent idea of how species respond to variable logging intensity, while our mechanistic understanding of these species-specific abundance changes varies from patchy to non-existent.

From these broad issues, we identified significant knowledge gaps in our understanding of how and why some mammal species persist better than others in logged forests. We focussed on small mammals and large herbivores: despite their functional importance, and the relative ease of collecting large live-trapping and camera-trapping datasets, their basic biology and logging responses are among the most poorly-understood of any mammal groups. We chose four research questions to address these knowledge gaps:

1. Is the “high biodiversity value” of logged forest for small mammals sustained over time? Does abundance remain constant, fluctuate, increase or decline?
2. Previous studies have observed increases in small mammal community abundance with increasing selective logging intensity. However, does this conceal declining body condition and demographic rates, limiting community resilience to future change?
3. Do larger mammals in logged forests plastically shift activity patterns toward increasing nocturnality, as might be expected from the increasingly harsh microclimatic conditions and potentially elevated hunting pressure?
4. How do small mammal communities react to the edges between areas of selectively-logged forest and plantation agriculture? Is there a “spillover” effect potentially detrimental to agricultural yields?

6.2 Main findings of this thesis in relation to our research questions

In Chapter Two, six of the nine common small mammal species we studied over six years did display variable dynamics after heavy selective logging. Population densities varied by a factor of more than six, with pronounced synchronous declines from 2011-2014, and a general, more gradual recovery in 2015-16, apart from the apparently consistently declining *Maxomys baeodon*. The three species not significantly differing among years visually appeared to mirror these dynamics, but large spatial variability among sites negated any annual differences. The data requirements of our models precluded studying several much rarer species which we captured at low abundances, and it is possible that these species display quite different dynamics. However, this synchronicity among the most abundant species, plus the tendency for pronounced dynamics among terrestrial granivores, and less pronounced dynamics among semi-arboreal and more insectivorous species, implies a common underlying driver. As in unlogged forests, this is probably bottom-up population control characterised by intense resource availability spikes and long famines driven by El Niño-induced droughts and the mast fruiting cycle. We did not find a relationship between population density and our seed availability data. However we suggest that this analysis is probably insufficient to reject mast fruiting as the driver of our observed dynamics. The available data on seed and fruit availability were not closely linked spatiotemporally to our small mammal sampling, and were only available at a relatively coarse spatial scale. Rather, the landscape-wide mast fruiting process is probably filtered in intensity by the pronounced heterogeneity of logged forest, with access of animals to dipterocarp seeds varying greatly on a fine scale depending on logging intensity.

In Chapter Three, we found that body condition, survival and apparent breeding success of small mammals were largely unchanged by logging. Despite the previously observed abundance increases across most species, and the community as a whole, we found little evidence that species which increase in abundance exhibit reduced health or demographic rates. We also found no contrasting signal in species which decline with logging in this system, either in *Maxomys baeodon*, which declined slowly through time (Chapter Two), or *M. rajah*, which declined rapidly to very low abundance. We suggest that the disappearance of *M. rajah* is probably too rapid and absolute to be detectable in altered condition or demographic parameters, although the lack of a pattern with *M. baeodon* is less easily explained. Again, it is possible that species at very low abundances across the gradient respond differently. Overall however, there was no clear evidence to suggest that small mammal communities in logged forest are vulnerable to future environmental perturbations, such as climate change or invasive species.

In Chapter Four, we found pronounced logging-induced shifts in circadian activity patterns among six of eight large herbivores and granivores studied. There was a significant positive relationship between degree of shift towards nocturnality and body size, with the most pronounced shifts towards increased nocturnality occurring in the two largest species, Bearded Pigs and Sambar Deer. These species are probably the least vulnerable to mammalian predators but the most widely-hunted regionally, suggesting that this response may be driven by harsher microclimatic conditions, human avoidance, or both, and echoing globally-observed patterns in larger ungulates. Yellow Muntjac, a medium body size species, also showed a pronounced increase in nocturnality. However, the remaining five medium or smaller body size species showed contrasting responses, and while Red Muntjac and Greater Mouse-deer showed one or more responses consistent with avoidance of microclimate or humans: (reduced activity at dawn and/or dusk, increased activity around midnight, or reduced activity around midday) these did not translate into a pronounced shift towards nocturnality. The Long-Tailed Porcupine, already highly nocturnal in unlogged forest, shifted activity from the late to the early part of the night. We found no evidence that shifts in circadian pattern were universally adaptive or maladaptive, nor imposed costs of reduced foraging efficiency: there was no relationship between activity pattern overlap and probability of decline in abundance, nor a consistent trend of compensatory increases in overall activity level. Rather, we suggest that the relative costs and benefits of shifting activity patterns may differ according to species' life histories.

In Chapter Five, we found that despite the abundance of food in oil palm plantations, the native small mammal community in logged forests is remarkably partitioned by forest-plantation edges. For some species, a "classical" edge effect may exist: although we did not design our sampling to test for it, observed species richness appeared to increase further into the forest. Nevertheless, most native small mammal species were found right up to the forest edge, including several spool-tracked individuals apparently foraging for prolonged periods at the outer limits of the forest vegetation. Despite these observations, we found no evidence that any native species crosses into the plantation apart from the Whitehead's Rat *M. whiteheadi*, which together with two invasive *Rattus* species was found throughout our forest and plantation trapping areas, including the plantation interior control site. However, compared to the control site, we found no elevated abundance in plantation areas nearer the forest edge, even at the first trap line only 23m from the edge. This suggests that no noticeable spillover of these three species from forest "refuges" occurs, either via transient foraging visits or permanent dispersal and settlement in the matrix. Spillover extending less than 23m is unlikely, as this was approximately the distance across the cleared buffer strip to the nearest line of palm trees. Our

tracking of *M. whiteheadi* also revealed little to suggest routine edge crossing, with animals caught and released closest to the edge being significantly less likely to cross than expected by random chance. These results add to an extensive body of literature showing that small mammals can easily become isolated in forest remnants surrounded by an inhospitable matrix environment. We emphasise the need to maximise landscape connectivity and minimise edge effects to maximise persistence of biodiversity in agricultural landscapes.

6.3. Knowledge gaps in temporal trends and individual-scale responses addressed by this thesis

The findings of this thesis add to our knowledge about community responses to selective logging, and help towards a more mechanistic understanding of these changes in several ways. Firstly, our findings in Chapter Two help to fill an important knowledge gap, as interannual population dynamics had been investigated only in unlogged forest for some of our species (Emmons 2000; Nakagawa *et al.* 2007b; Wells *et al.* 2007a), while post-logging dynamics of small mammals had only been measured in a more limited way by two studies (Isabirye-Basuta and Kasenene 1987; Wells *et al.* 2007a). Indeed, we know of no study which combined annual abundance estimates for so many mammal species over such a long period in logged forest, while controlling for detectability. Similarly in Chapter Three, our results showing constant body condition, survival and apparent breeding success between logged and unlogged forest are among the first estimates of these parameters in vertebrates over a logging gradient (Cosset, Gilroy & Edwards 2018). Although it remains challenging to determine exactly what combination of factors limits populations and drives observed abundance responses to logging, we provide a baseline for further, more detailed investigations into these mechanisms.

In Chapter Four, our results uncover an understudied behavioural response to the stresses imposed on larger mammals by logging: changes in diel activity patterns, which are generally consistent with increased activity at night, particularly among the largest ungulates. While the potential for activity pattern shifts has been comprehensively demonstrated by Ross *et al.* (2013) in relation to predation pressure, to our knowledge our results are the first attempt to evaluate the direct effects of logging, in a landscape where large predators remain comparatively abundant before and after logging (Wearn *et al.* 2013, 2017). Again, further work is required to conclusively demonstrate which factor, or combination of factors drive these responses, and our results demonstrate that the effects of activity pattern shifts on persistence are species specific. Nevertheless, our results demonstrate a high degree of behavioural plasticity among large mammals and add to a broader global literature, both in terms of the

diverse ungulate behavioural responses to human disturbance, and the broad tendency of mammals to avoid humans by becoming more nocturnal.

Lastly, our results from Chapter Five provide a valuable and timely addition to the literature on small mammals in oil palm plantations, and bridge the gap between the largely pest control-oriented literature covering small mammals in this habitat, and our ecological understanding of this group in tropical forests. We directly addressed a prominent if little-understood concern of plantation managers, and our results help quantify the balance of ecosystem services and disservices at plantation forest edges. Our observation that *Maxomys whiteheadi* is significantly impeded from crossing edges also adds to the large and growing literature on the impacts of edges, fragmentation and matrix impermeability on limiting movements of small mammals and structuring their populations (Pardini *et al.* 2005; Laurance, Goosem & Laurance 2009; Carthew, Jones & Lawes 2013; Lambert *et al.* 2014). The generally depauperate community in our plantations also underline the low value of oil palm plantations for mammalian biodiversity (Fitzherbert *et al.* 2008; Rustam, Yasuda & Tsuyuki 2012; Wearn *et al.* 2017).

6.4 Emergent themes: The importance of resource availability

6.4.1 The importance of diet in moderating persistence

A prominent thread running through our results, particularly those of Chapters Two and Three, is the likely importance of dietary plasticity and changes in resource availability for moderating species' responses to selective logging. Two ostensibly differing, but probably concurrent processes seem to be occurring. First, the temporally variable mammal abundance observed in Chapter Two, which strongly resembles the fluctuations observed by other authors in unlogged forest in its amplitude, synchrony, and irregular periodicity (Nakagawa *et al.* 2007a; b; Wells *et al.* 2007a). As we have argued (Chapter Two; Section 6.2), the unlogged forest pattern of mast fruiting-induced resource "spikes" and intervening "famines", probably continues to drive population dynamics after logging. Second, baseline abundances of most small mammal species also increase in addition to these variable dynamics being retained (Wearn *et al.* 2017). This increase should logically be due to a relaxation of population-limiting factors, probably including microhabitat space, food resources, or predation. Our results in Chapter Three imply that populations of most species do not suddenly become intensely food-limited in logged forest, a scenario which should reduce body condition, reproductive output, and/or survival. Instead, these parameters remain stable, perhaps suggesting that baseline food abundance increases. Furthermore, under a scenario of intensified food limitation in logged forest, we might also expect many species to spill over the forest edge into oil palm, risking elevated

mortality risk for supplementary food. However we observed remarkably little such spillover in Chapter Five.

What is the most likely mechanism driving increased food availability for small mammals after logging? One possibility is that the dipterocarp mast fruiting cycle itself alters, lessening the severity of famines or boosting the population peaks during mast fruiting. Theoretically, this could occur if more fruit is produced in logged forest landscapes than unlogged, or if mast-fruiting peaks become more frequent or less synchronous, making inter-peak famines shorter and less intense. However, there is no evidence for either possibility, and neither seems likely. Although residual small dipterocarp trees left after logging continue to fruit (Appanah & Manaf 1990, 1991), the pronounced reduction in overall tree biomass (Pfeifer *et al.* 2016) means that overall mast fruit abundance becomes much lower (Bagchi *et al.* 2011) and probably more spatially heterogeneous (hence, perhaps, our lack of a fruit-population density relationship in Chapter Two). We also found no studies suggesting that El Niño-driven droughts and mast fruiting events increase in frequency or decrease in synchrony after logging. Instead, we suggest that in logged forest, mast fruit peaks are probably heavily supplemented by the seeds and fruit of pioneer and early-successional trees and ground flora plants, forming an abundant, and more stable food supply than is readily available at ground level in unlogged forest. Another potential alternative, or complementary driver is reduced granivory and increasing insectivory (Nakagawa, Hyodo & Nakashizuka 2007; Wells *et al.* 2009; Ewers *et al.* 2015). If surviving species can digest a wider range of more abundant seeds and fruit, and/or shift diet to invertebrates in between mast fruiting peaks, this may explain the general increase in community abundance, and apparent lack of negative effects on demography and body condition.

6.4.2 Diet as a knowledge gap, and new research directions

These conclusions about the role of diet in mediating persistence are nevertheless speculative, and will remain so until detailed dietary data are available. A handful of primate studies from other tropical regions (e.g. Fairgrieve & Muhumuza 2003; Pinto, Azevedo-Ramos & de Carvalho Jr. 2003) suggest changes in diet with logging, but these are mostly observational. We found no studies that have comprehensively quantified diet of our studied species, or linked diet to food availability before and after logging to predict persistence. The most useful data comes from one study of the two *Tragulus* mousedeer (Heydon & Bulloh 1997). These authors concluded that both species are predominantly frugivorous, but tentatively linked the sharper decline with logging of *T. napu* than *T. kanchil* to its greater dependence on larger fruit such as *Ficus* figs (Heydon & Bulloh 1997), which seem to be strongly impacted during logging operations (Johns

1988). *T. napu* was among our species which shifted activity pattern strongly, becoming less crepuscular and more cathemeral (Chapter Four), but was nevertheless strongly likely to decline. These patterns might be consistent with wider ranging in search of increasingly scarce and spatially patchy *Ficus* trees, so our results appear to provide tentative support for this hypothesis.

Among small mammals, we found only two dietary studies: one showing a shift in trophic position using stable-isotope analysis (Nakagawa, Hyodo & Nakashizuka 2007) and one suggesting changes in seed abundance within murid faeces (Wells *et al.* 2009). Neither author was able to positively identify foods to species, or relate the proportion of foods eaten to that available in logged or unlogged forests. As we have seen, this reflects a broader problem with mammal studies in tropical forests. Some authors have made relatively detailed observations of mammal diet in primary forest (Emmons 1991, 2000; Heydon & Bulloh 1997), but most rely on broad categorisations such as “granivore” or “herbivore”. Conversely, several authors have quantified the effect of logging on seed predation and dispersal from the perspective of vegetation dynamics, without directly linking this to diet and differential vulnerability of the mammalian seed predators (e.g. Guariguata, Clare and Jones 2002; Babweteera and Brown 2009, Hautier *et al.* 2010; Bagchi *et al.* 2011). Without explicitly quantifying mammalian diet and relating it to plant (and invertebrate) community composition before and after logging, it will remain extremely difficult to unpick population limitation, understand the cost-benefit balance of shifting activity patterns, or predict community spillover into plantations.

This knowledge gap also limits our ability to understand why despite the general logging tolerance of mammals, some species largely or completely vanish, often being too scarce to include in our analyses. These include cryptic species rare even before logging, such as the Tufted Ground Squirrel *Rheithrosciurus macrotis*, a species which is phylogenetically and morphologically distinctive (Payne & Francis 1985; Pečnerová & Martínková 2012), and probably highly ecologically specialised. However, some declining species are relatively easily captured or photographed in unlogged forest (Brown Spiny Rat *Maxomys rajah* and Chestnut-Bellied Spiny Rat *M. ochraceiventer*, or the Thick-spined Porcupine *Hystrix crassispinis*), and are no more obviously specialised than their close relatives which persist successfully in logged forest (other *Maxomys* species, and Malayan Porcupine *H. brachyura*, respectively). Clearly, dietary information would fill the gaps in our understanding of vulnerable species, help to robustly attribute abundance patterns to changing resource availability, and perhaps identify specific food resources which should be protected during logging operations. We therefore

underline the need for comprehensive community dietary studies for mammals in logged forests, both in Borneo and elsewhere. Modern techniques will be crucial, as manually identifying seeds from faeces presents daunting practical challenges (Wells *et al.* 2009), while stable-isotope analyses can only provide limited resolution on shifts of diet among plant species. Instead, we suggest a comprehensive metabarcoding study, covering both faeces from as wide a sample possible of the mammal community, and a spatiotemporally matched sample of seeds, fruit and arthropods around the relevant capture locations. We could then reconstruct both available food resources and mammalian diets in multivariate space, and potentially match changing dominance of dietary components to changing plant community abundance over the logging gradient.

6.5. Emergent themes: The importance of ranging and movement

6.5.1 The importance of ranging and movement in moderating persistence

Our results also suggest the need for more detailed data on mammal movement and ranging behaviour, and how mammal species perceive the “continuous” selectively-logged forest environment. These data would, for example, help us to understand whether the increase in sheltered microhabitats with logging opens up more forest floor area for small mammal territories and helps to drive observed abundance increases. Conversely, if we could map small mammal territories at the plantation-forest edge we might expand on the observations of Chapter Five, and perhaps understand the structuring effect of the edge or better capture sporadic crossing movements. Understanding how territories map to key food resources such as fruiting trees, combined with more detailed dietary data, could shed light on spatiotemporal importance of mast fruiting in logged forests and help us unpick the drivers for the dynamics we observed in Chapter Two. Lastly, if we could discover whether large herbivores avoided areas with the harshest microclimates, we might uncover the drivers behind the activity pattern shifts in Chapter Four.

6.5.2. Emergent themes: Movement as a knowledge gap, and new research directions

Movement of tropical forest mammals in relation to anthropogenic pressures has been better-studied than diet, however much of what we know concerns the often quite pronounced impacts of fragmentation, or road building (Pires *et al.* 2002; Keuroghlian, Eaton & Longland 2004; Pardini *et al.* 2005; Nasi *et al.* 2008; Shadbolt & Ragai 2010; Carthew, Jones & Lawes 2013; Lambert *et al.* 2014; Brodie, Giordano & Ambu 2015). It is unclear to what extent different mammal species in selectively-logged forest perceive their environment as continuous or fragmented, and therefore we do not know how broadly these conclusions apply. Compared

to fragmented forest in an agricultural matrix, logged forest seems likely to impose less harsh effects on mammal movement: as we saw in Chapter One, a shrubby, interconnected ground flora layer rapidly regenerates after logging as succession begins. However, as with fragmented systems (Pires *et al.* 2002) species will likely vary in the degree to which they perceive the selectively-logged landscape as “continuous” or “fragmented”, according to life-history and body size.

Several studies have tested the effects of logging *per se* on movement efficiency, often showing null, or contradictory results rather than a general decline in efficiency (Johns 1986; Colón 2002; Wells *et al.* 2006, 2008). However, almost no authors have mapped home ranges or quantified partitioning of habitat space across the logging gradient, apart from one study of Malay Civets (Colón 2002) and one of primates (Johns 1986). The one extensive study of treeshrews in unlogged forest by Emmons (2000) remains the most successful attempt to map home ranges of tropical forest small mammals, probably because doing so accurately is extremely challenging. Radio tracking (Emmons 2000; Colón 2002) or mark-recapture data (Nakagawa *et al.* 2007a; Wells, Lakim & Pfeiffer 2008) can be used to map home ranges, but the latter is inevitably crude and limited to the area of the trapping grid, while the former is expensive, prone to interference from the dense undergrowth, and extremely labour-intensive. Unlike Emmons’ treeshrews, most of the remaining small and larger mammals in our study system and elsewhere are nocturnal, and larger herbivore species are much more challenging to catch and tag. Together, these issues mean that collecting sufficient accurate real-time fixes, from enough individuals, to construct ranging patterns and calculate overlap with other individuals or abiotic features such as gaps remains a formidable challenge.

However, the trend towards increasing miniaturisation, interconnectedness and open-source availability of tracking and monitoring tags (e.g. Clark *et al.* 2006; Gandra, Seabra & Lima 2015; Cain & Cross 2018; MATAKI 2018), plus recent-developments in networked, autonomous data gathering systems (e.g. Sethi *et al.* 2017) mean that we may soon be able to track a whole community autonomously, synchronously and remotely in real-time, using simple animal-mounted radio or GPS tags which share data among individuals, together with an autonomous fixed sensor network triangulating radio signals and/or uploading GPS data. If and when such a system does emerge, we suggest that it would alleviate the problems with existing methods, and tackle this important knowledge gap for the entire mammal community, plus a wide variety of other taxa in selectively-logged forest.

6.6 Conservation implications and conclusions

As we have seen, our results contribute to a large body of research on selectively-logged forests and other anthropogenic landuses in tropical Southeast Asia, and more generally in tropical regions around the world. We do not contradict the general observation that selective logging (even the repeated and high-intensity logging typical of Southeast Asia) has comparatively limited effects on species richness, especially compared to clearance for intensive agriculture. However, our research emphasises that mammals show much more complexity and subtlety in their responses when we move beyond species richness and consider changes in abundance and community composition, as well as individual behaviour, condition, demography or movement. Other less well-known animal taxa, with similar or greater levels of behavioural complexity and often more stringent physiological requirements, are likely to show even more variable responses. To conserve functioning and resilient forest ecosystems, conservation managers and planners need to look beyond species richness retention and towards a more holistic, long-term approach wherever possible. In particular, our results from Chapter Two demonstrate that measuring abundance and community composition changes with logging is complicated by underlying variation and, potentially, extinction debt. This is a conclusion with wide generality: while the precise form of the interannual dynamics we observed are probably specific to the dipterocarp forests of Sundaland, the need for a long-term perspective is probably universal.

Despite the interannual variability of our study system, this thesis generally paints a positive picture for the small and large mammal communities in heavily selectively-logged forests. The lack of apparent density-dependent effects on demographic rates and body condition, despite the increased baseline community abundance suggest a high degree of resilience, as does the apparent behavioural plasticity of large herbivores in Chapter Four. Furthermore, our results from Chapter Five demonstrate that there is little scientific basis for conflicts between conservation of logged forest and agriculture along the edges where they meet, at least in terms of small mammals threatening oil palm yields. Overall, we suggest that with appropriate management to limit hunting pressure (such as the targeted closing of logging roads and perhaps surveillance of likely entry and exit points), as well as targeted reforestation in gaps, roads and skid trails, the majority of the generalist mammal community in logged forest can be expected to remain healthy through time.

Of more concern are the species which have become, or are becoming too scarce in logged forest for us to model in our analyses. As we have seen, our current understanding of their traits may not reveal why they are so vulnerable. Our discovery in Chapter Four that plasticity in herbivore activity patterns does not correlate with persistence underlines this problem: we are still some

way from a mechanistic understanding of how and why specialist species decline, and what can be done to sustain them in the logged forest environment. Scarce, cryptic species are inherently harder to study, but if we want to rehabilitate selectively-logged forest towards a primary forest-like state and conserve the maximum percentage of Southeast Asia's imperilled biodiversity, it is important to understand their ecological needs. With further work building on the results of this thesis, such as that outlined in Sections 6.4.2 and 6.5.2, we argue that it should be possible to increase our understanding of how and why species persist or decline in logged forests – an imperative course of action if we are to save Southeast Asia's astonishing biodiversity from the potential disaster awaiting it.

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