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Tropical Rainforest Food Webs in the Anthropocene

By

Matthew Scott Luskin

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

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of the

University of California, Berkeley

Committee in charge:

Professor Matthew D. Potts, Chair

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Tropical Rainforest Food Webs in the Anthropocene

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By Matthew Scott Luskin

Abstract

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Tropical forests throughout the world are rapidly being converted to agriculture. Remaining forests are often fragmented, threatening area-demanding species, such as apex predators and mega-herbivores (e.g. elephants). The loss of predators can trigger trophic cascades, whereby prey species increase in abundance, altering food web dynamics. Fragmentation also increases hunters' and poachers' access to previously remote areas, adding an additional threat to megafauna. A pressing challenge in conservation biology is to understand where, why, and over what time scales these unintended secondary processes are degrading remaining forests. My dissertation seeks to address this challenge by exploring how forest loss, predator loss, hunting, and rapid oil palm agricultural expansion are affecting tropical forest floral and faunal communities in Southeast Asia.

My first chapter, an introduction, discusses the process and theories on how land use change affects species and drives ecological cascades. In my second chapter, I grapple with the approaches used to study the impacts of agricultural expansion on biodiversity, and how different methods can shape outcomes for conservation planning. In this chapter, I explore the land sparing versus land sharing framework for conservation planning. Land sparing advocates meeting production targets through increasing yields on existing farmland (intensification) in order to protect natural areas from further conversion (set asides). Land sharing promotes conservation within agricultural landscapes using wildlife-friendly farming practices. Using a literature review, I argue that there is an emerging consensus of ecological theory, empirical data, and direct case studies supporting the "land sparing" approach to conserve biodiversity in tropical forested landscapes. Studies of land sharing landscapes routinely report the complete absence of over 50% of forest species, even in wildlife-friendly agroforestry systems. This indicates most species are sensitive to any farming activities, and so conservation should focus on minimizing forest loss. I conclude by exploring three important considerations to effectively implement a land sparing strategy: (i) the tradeoffs and synergies with other ecosystem services (e.g. carbon, water quality); (ii) the economic benefits of forest offsets (e.g. from REDD+ carbon payments) and; (iii) the sociopolitical obstacles to insuring effective forest offsets are created.

In the third chapter, I turn to the abiotic impacts of agricultural expansion, comparing and contrasting the microclimate of agricultural lands and forest. Specifically, I examine how abiotic conditions in oil palm plantations vary throughout the life cycle of a plantation. I present a chronosequence study on microclimate and vegetation structure in protected forest and its surrounding oil palm plantations surrounding in Peninsular Malaysia. My results indicate that understory vegetation is twice as tall in young plantations, but leaf litter depth and total epiphyte abundance is twice as high in old plantations. Plantations are also substantially hotter (+2.84 C) and drier (+0.80hPa vapor pressure deficit) than forests during the day, but there are no nocturnal microclimate differences between the two. These findings are important to revealing the habitat heterogeneity throughout the 25-year plantation lifecycle. Based on these results, I develop environmental guidelines to improve the spatio-temporal planning of oil palm plantations for wildlife, drawing heavily on timber management practices. I conclude that oil palm plantations can be developed to create a permeable matrix in order to connect remaining forests habitats and increase the conservation value of the landscape.

In Chapter 4, I explore how agricultural expansion is affecting faunal communities, focusing on predators. Accurately monitoring predator populations is an essential but difficult challenge for conservation biologists. Until very recently, many of the methods employed by conservationists overestimated population densities and sizes. This is particularly true for apex predators like tigers, which are important to maintaining ecosystem function and are especially sensitive to habitat loss and poaching. To accurately and defensibly estimate current Sumatran tiger populations, in this chapter, I present new data collected from camera trap arrays across three expansive landscapes (843-999km²), which together make up the UNESCO Tropical Rainforest World Heritage Sites of Sumatra. I use these data to estimate tiger densities using the spatial-capture-recapture approach. Then, to compare my results with other studies, I develop a new approach to correct for biases in previous research and conduct a meta-analysis to draw inferences about the determinants of densities. I find that traditional mark-recapture techniques published before 2010 inflated estimates of tiger densities by 63.3% on average. Controlling for this bias, tiger densities increased 4.2%/yr from 1999 to 2014 and primary forest densities were 58% higher than disturbed forests. Based on my study, I estimate there are 734 ± 304 tigers within or connected to source landscapes. These results highlight that Sumatran tiger densities in remaining forest may be increasing. However, forest loss, fragmentation, and poaching have reduced the total population and threaten the subspecies with extinction.

In Chapter 5, I delve deeper into the impacts of agricultural expansion by focusing on changes in faunal and floral community dynamics. There has been significant debate over whether herbivores are regulated from the “top-down” by predators or from the “bottom up” as plants adapt and limit herbivores’ consumption. In altered ecosystems, such as forests fragmented by agriculture expansion, the widespread loss of predators is thought to be the main destabilizing force. I challenge this status quo by examining the effect of bottom-up agricultural resource subsidies (palm oil fruits) in controlling forest faunal populations as well as the effect on tree communities. To determine these impacts, my fifth chapter takes advantage of a landscape-scale manipulation of agricultural resources adjacent to a 2500 ha forest reserve in Peninsular Malaysia. First, I evaluate whether resource subsidies affect forest wildlife populations by compiling two decades of wild boar (*Sus scrofa*, a crop-raiding species)

abundance data at the Pasoh Research Forest in Peninsular Malaysia. Second, I evaluate if altered wild boar abundance had cascading impacts on the vegetation community by re-censusing seven wildlife exclosures established in 1996. Finally, I evaluate how wild boar predation shaped tree sapling diversity using 24 years of tree census data from the Smithsonian Institute's Center for Tropical Forest Science 50-ha research plot at the Pasoh. I find that the forest density of wild boar was 100 times higher when palm oil plantations were fruiting (1996-2000 and 2007-2014) than when plantations were cleared and fruit was unavailable (2001-2006). Second, wild boars' predation of tree saplings (100-200 cm in height) led to a 46% reduction in the density of 1-2cm dbh saplings over a 23-year period. Third, while all species of tree saplings had lower abundances, there was a 13% increase in tree diversity as measured by the Fisher's alpha diversity index. This suggests wild boars exhibit density dependent selective mortality on trees that disproportionately reduces the abundance of common tree species.

My final chapter turns to the role of humans in these new forest-plantation landscapes. In this chapter, I examine how the immigration of farmers alters hunting practices. Using information from in-depth interviews with hunters, agricultural workers, and wild meat dealers in Jambi province, Sumatra, I first describe how plantations have affected local human demography. Then, I explore how wildlife hunting and consumption rates vary between different indigenous and immigrant ethnic groups. I also uncover how hunting near palm oil plantations has become primarily a commercial endeavor for managing crop-raiding wild boars. These results also indicate that wild boars may be experience ecological release, either from the loss of predation by tigers, or increased food available in agricultural fields. I discuss how proper management could reduce crop damage and also yield large amounts of wild boar meat with relatively little by-catch of threatened wildlife.

Taken together, these studies indicate that oil palm habitat is unsuitable for most forest species, and that forest fragments in oil palm landscapes are undergoing a loss of predators and thus potentially suffer from trophic cascades and subsidy cascades. I found that cross-border agricultural resource subsidies shape wildlife communities and devastate tree sapling communities. These results also suggest that predator loss and agricultural expansion can lead to combined trophic and subsidy cascades with heightened effects, and that this form of indirect forest degradation may be widespread in the region and globally. As such, my results indicate that protecting large continuous forests is necessary to preserve functioning Southeast Asian food webs. This conclusion has direct applicability across the tropical rainforests regions where oil palm agriculture is rapidly expanding, and more generally informs the discussion on how to achieve conservation goals.

Dedicated to the memory of Pak Barisan

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Chapter 1

Introduction

Conservation biology is tasked with preserving biodiversity and ecosystem function. The field arose in response to the immense scale of disturbances in the current era, the Anthropocene, with 40% of the world's arable land converted to agriculture within the last century (Ramankutty *et al.* 2008). However, conservation is especially difficult in hyper-diverse rainforests because biologists are still trying to describe and document their biodiversity and then learn how that diversity is maintained. One way to meet both challenges is to take advantage of already existing human-caused changes to test ecological theories. In my dissertation, I study the ecology of natural and disturbed ecosystems and try to understand changes from a community ecology perspective. I focus on the cascading impacts of land use change in Southeast Asia resulting from habitat fragmentation, hunting, and agriculture. I develop new approaches to studying wildlife, conduct empirical field studies of both plants and animals in Peninsular Malaysia and Indonesia, and synthesize existing bodies of work to draw conclusions.

For tropical forests, the most important disturbance of the Anthropocene has been their conversion to agriculture. Tropical forests have been the source of 83% of new agricultural land globally (1980-2000). I focused my studies on the ecologically fascinating tropical rainforests of Peninsular Malaysia and the island of Sumatra, which have suffered the highest global deforestation rates in recent decades. Here, the main driver of deforestation is the creation of oil palm plantations, which now represent >50% of the agricultural area and >25% of the land areas of both study regions. In my second and third chapters I evaluate the broader issues associated with agricultural expansion, including how to study them, and then specifically evaluate the value of oil palm plantation habitat for Southeast Asian wildlife.

To reconcile the needs of agriculture and biodiversity conservation, conservation biologists have argued in favor of two disparate strategies (Green *et al.* 2005). The first strategy is called 'land sparing' which involves increasing yields (intensification) in order to spare additional land from needing to be converted. The second strategy is called 'land sharing' and promotes wildlife-friendly farming practices in order to increase biodiversity on the farm and within the farmland matrix. In Chapter 2 of my thesis, I examine the relative merits of these two strategies through quantitative review of previous work. Then, in my third chapter, I compare the abiotic conditions within oil palm plantations to the conditions in surrounding forest and examine how plantation habitat changes over the 25-year production period. Finally, I discuss how farm and landscape scale planning could improve plantation habitat quality for wildlife.

The impacts from agricultural expansion extend far beyond the immediate reduction of forest area. For example, wildlife communities in remaining forests are affected by fragmentation, which disproportionately affects area-demanding apex predators and mega-herbivores. The roads built for agriculture also allow poachers to easily access and kill wildlife (Robinson and Bennett 2002). Farmers also hunt for wild meat, and in extreme cases can eliminate all large species from a forest. Finally, croplands often possess large quantities of food, such that crop-raiding species like wild boar may actually increase following agricultural expansion. The relative importance of different disturbances in shaping remaining communities

is unknown, and disturbance type and hunting intensity varies between sites. As a result, similar sized tropical forests can contain a variety of wildlife conditions ranging from intact to complete defaunation of all large species (Laurance *et al.* 2012, Harrison *et al.* 2016). The selective removal of predators has been noted in many areas (Estes *et al.* 2011, Ripple *et al.* 2014), while other forests have become supersaturated with a subset of species (Ickes *et al.* 2001; Luskin 2010). My fourth, fifth, and sixth chapters use fragmentation and agricultural expansion as a natural experiment to understand the forces that shape wildlife communities.

For decades the field of ecology has been engaged in a lively debate about whether ecosystems are regulated from the “top-down” by predators or by “bottom up” plant defenses that inhibit herbivores’ consumption (Estes *et al.* 2011). In farmed landscapes, the widespread loss of predators is thought to be the main destabilizing force for herbivores. Trophic cascade theory emphasizes that the loss of predators releases prey species, which then cause tertiary effects on the vegetation. The potential effects from trophic cascades are far reaching throughout food webs and across spatial scales. More nuanced studies also shows that effects of trophic cascades on ecosystem dynamics can be nonlinear, delayed, and unpredictable (Estes *et al.* 2011).

Southeast Asia is an important region for trophic cascade research because the apex predator, tigers, have seen a >90% decline in their historic range over the last century. This indicates that trophic cascades are potentially a widespread phenomenon in the region. However, current tiger population levels and trends remain unclear, largely due to difficulties in monitoring such rare, cryptic species. To examine if trophic cascades may be an issue in Asia landscapes, in my fourth chapter I develop a variety of new quantitative methods to increase our ability to accurately monitor predator populations and apply these methods to estimate the tiger population and the threats of top-down trophic cascades in Sumatra.

While ecologists’ focus on trophic cascades is justified, resource subsidies may also lead to higher herbivore populations, which in turn can have secondary impacts on other species. The subset of animals that forage in farmland or pastures clearly benefit from resource subsidies, but may alter normal food web dynamics when they return to natural areas (Polis 1998). Ecologists remain unclear about whether the cross-border flow of animals and nutrients from cultivated areas initiates positive or negative “cascading impacts” in natural areas. Further, in areas where top predators have already been locally extirpated, subsidies may amplify the ecological release of herbivores or mesopredators. A key challenge is understanding how subsidy cascades operate and whether trophic cascades and subsidy cascades interact in disturbed landscapes.

My fifth chapter investigates the role of agricultural subsidies in shaping forest wildlife dynamics. I explore three interrelated potential impacts of agricultural subsidies: first I evaluate whether agricultural subsidies have a meaningful effect on forest wildlife dynamics, or if wildlife are responding to fragmentation, edge habitat, hunting, or predators. I take advantage of a landscape-scale addition and removal of oil palm plantations around the Pasoh Forest Reserve in Peninsular Malaysia to partially control for the effects of fragmentation, edge habitat, hunting, and predators. Specifically, I focused on the extent to which forest wild boar (*Sus scrofa*) populations track palm oil fruit production.

Second, I evaluated if altered wild boar abundance had cascading impacts on the vegetation community by re-censusing seven wildlife exclosures established in 1996 and using 24 years of tree census data from the Smithsonian Institute's Center for Tropical Forest Science (CTFS) 50-ha research plot at the Pasoh. Wildlife is an important filter for trees because they disperse, consume, and kill seeds, graze and browse foliage, and can re-engineer their whole environment (e.g. elephants). In this way, wildlife is largely responsible for adult tree communities having strikingly different composition than initial seed production. The seedling and sapling stage is a powerful selection period because these stems spend decades slowly growing in the understory, during which time sporadic or seemingly small-scale disturbances can accumulate. For example, wild boar (*Sus scrofa*) and bearded pigs (*Sus barbatus*) are tree predators because they use tree saplings to construct their nests (Ickes *et al.* 2001).

Finally, I evaluated how wild boar predation shapes tree sapling diversity using the CTFS 50-ha plot data. Predation could support diversity through two mechanisms: first, predation usually causes density-dependent mortality, meaning more abundant species suffer higher rates of direct consumption and indirect predation (e.g. parasites and diseases; this can be viewed as the Janzen-Connell Hypothesis). The selective removal of common species means that rare species represent a higher percentage of the community, which increases diversity by most metrics. High predation reduces stem densities generally, and this opens niche space and reduces competition between stems, so that even locally poor competitors can persist. Indeed, as Terborgh (2015) argues, high predation may be the secret to tropical forest tree hyperdiversity. The exception is when predators become super-abundant and locally consume all individuals of a species, which clearly decreases local diversity. I adopt this framework to examine if the subsidy cascade benefiting wild boars increased or decreased tree sapling diversity.

My sixth chapter brings the thesis full circle, returning to humans, the ultimate cause of these altered landscapes, and exploring how we are using these new landscapes. I specifically evaluate how widespread oil palm plantation agricultural expansion is altering the demographics of frontier landscapes, and whether this influences hunting outcomes. Agriculture expansion is accompanied by a massive influx of humans, who often hunt wildlife in remaining forests. However, hunting is a culturally-dependent activity, both in terms of people's relationship with the forest itself, the reasons people hunt (e.g. sport, economic gain or for subsistence wild meat), and preferences for different species. The diversity of potential outcomes is particularly true in Southeast Asia, where the Malay (a Muslim majority in Malaysia and Indonesia) generally avoid forests and hunting, the Dayaks of Borneo value forests and hunting, and the large Chinese populations use rare species for medicines. I focus on the hunting of wild boar, which is the primary species benefiting from subsidy cascades in the region. Wild pig species (Suidae species) are also important to people and dominate the harvestable forest biomass. There is notable love of pork by the Dayaks and Chinese, and a complete aversion by the Malay because the Islam Halal diet forbids its consumption. Based on my findings, I discuss how human hunting could be managed to mitigate trophic cascades and subsidy cascades through direct wildlife management of wild boars.

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Chapter 2

Land sparing or land sharing for tropical forest species?

Abstract

Population growth and increasing per-capita consumption are requiring huge increases in food and biofuel production, particularly in the tropics, urgently requiring coordinated approaches to reconcile agriculture and biodiversity conservation. Progress to this end has been long-stymied arguments about the relative merits of different production strategies, often termed the “land sparing debate.” The “land sparing” approach seeks to maximize yields on existing farmland so that less habitat needs to be converted, while “land sharing” seeks to conserve more species on farmland and within the landscape matrix. My review highlights that empirical research in tropical forest landscape routinely reports >50% of forest species are never recorded wildlife-friendly tree crops farmland (generally considered land sharing systems), and that annual cropland support even fewer species. At the same time, 89% of studies focused on tree crops, often agroforestry, while annual crops accounted for 87% of area expansion from 2000-2010. I discuss how three methodological issues also obscure conclusions: (i) the failure of biodiversity research to provide sufficient and robust data to make informed decisions, (ii) a variety of biases when sampling species in different habitats, (iii) biases in study locations and different production systems, both in terms of scale and geography. To improve inferences on the land sparing debate, I discuss what new research will most constructive, but in the mid-term, suggest tropical landscape policies adopt a land sparing farmland intensification paired with defensible forest offsets and implemented within spatially-designed landscapes. In the longer term, I explore three real-world considerations to effectively implementing a land sparing strategy: (i) the tradeoffs and synergies with other ecosystem services (e.g. carbon, water quality); (ii) the economic benefits of accrued by forests offsets (e.g. from REDD+ carbon payments) and; (iii) the logical obstacles to insuring effective forest offsets are created.

Keywords: Agricultural expansion, Wildlife-friendly farming, Land-use change, Intensification versus extensification, Agroecological matrix, Deforestation

Introduction

Current projections show that from 2005 to 2050 the global demand for agricultural production will double due to population growth and the increasing per capita consumption of meat, edible oil, and other agricultural commodities (Tilman *et al.* 2011). Consequently, conserving biodiversity while also producing more food, fiber, and fuel has become a global priority (Balmford *et al.* 2012). Two opposing production strategies to reconcile food production and biodiversity conservation have been hotly debated for nearly a decade. The first strategy, land *sparing*, involves increasing yields (intensification) in order to spare additional land from needing to be converted, while the second strategy, land *sharing*, involves farming with comparatively wildlife-friendly practices in order to increase biodiversity on the farm and within the farmland matrix (Green *et al.* 2005). A consensus about the tradeoffs between strategies has yet to emerge, greatly hindering the development of effective conservation policy (Ramankutty & Rhemtulla 2013). Notably, this debate is most poignant for tropical forests, which have been

the source of the 83% of new agricultural land (1980-2000) and which hold the highest levels of terrestrial biodiversity (Bradshaw *et al.* 2009; Gibbs *et al.* 2010).

Today, governments, agribusinesses, international development agencies, and a host of other stakeholders are making important decisions about whether to adopt land sparing or land sharing agricultural production strategies in tropical forest landscapes. Publicized examples of land sparing include Brazil's forest retention laws on private farms and certification schemes that require the preservation of small patches of forest within cropland (e.g., the "high conservation value forest" clause in the guidelines for the Roundtable for Sustainable Palm Oil (RSPO); SEACOMM 2010; Edwards and Laurance 2012). Likewise, there are numerous market-driven land sharing schemes such as shade grown coffee and cacao, organic produce, and other environmentally certified crops. While it is clear that a diversity of well-intentioned approaches are being implemented, each with its intuitive merit, I argue there is mounting consensus that land sparing is the best approach to conserve tropical biodiversity.

In this paper, I present a cohesive body of evidence based on ecological theory, empirical research, and case studies that supports land sparing as the best strategy to conserve biodiversity in tropical forested regions. Following on from this conclusion, I discuss the practical considerations to executing a land-sharing approach in the tropics. I identify major hurdles, tradeoffs, and opportunities with respect to ecosystem services and economics.

Approach

To reconcile agriculture and conservation, given a production target from a landscape, the overarching goal is to maximize the total population size of each native species (e.g. the sum of all individuals in both farmland and forest). The key-farming objective of land sparing is to more conserve natural habitats by increasing yields on existing land to meet production targets. The land-sparing approach is most often typified by large monocultures applying conventional "green revolution" technologies, including high-yielding crop varieties and synthetic fertilizers, herbicides, and pesticides, in order to increase yields (Tilman *et al.* 2002; 2011). However, there are varieties of methods to increase yields and to improve farmland for biodiversity. For example, very high yielding organic or "ecologically intensification" farms that replace unnatural or damaging inputs could also be part of a land sparing strategy (Foley *et al.* 2011; Bommarco *et al.* 2013).

The primary land sharing farming objective is to increase biodiversity on the farm through wildlife-friendly farming methods, even if lower yields require more forest be converted to meet the production target. The land sparing approach is typified by smaller farms or polycultures that use of fewer inputs and often retain natural features, such as trees (Fischer *et al.* 2008; Figure 1). Land sharing includes low-yielding "extensive systems" like upland rice, which is characterized by long fallows, as well as intensively managed farms like commercial shade grown coffee polycultures, where high-yielding coffee varieties are planted underneath uniform mono-specific tree canopy. Nonetheless, wildlife-friendly farming practices are assumed to produce substantial yield-penalties, although this not a steadfast rule (Badgley *et al.* 2008; discussed below).

The key decision point for adopting a land sparing intensification approach is whether the individuals living in newly protected forested land (or *forest offsets*) outweighs the decline of farmland individuals. However, if a species is only found in forests and never found in wildlife-friendly farmland, land sparing to retain forests is the only effective conservation option (Phalan *et al.* 2011a).

Results

Fundamental ecological principles developed over the preceding decades, such as niche theory, habitat requirements and suitability analysis, emphasize that farmland's capacity to benefit native species largely depends on its similarity to the natural habitat (Sutherland & Hill 1995; Benton *et al.* 2003; Schroth *et al.* 2004). Most tropical forests have dense overlapping foliage often reaching over 50 m in height, often blocking over 98% of light from reaching the forest floor (Figure 1, 2; Carson and Schnitzer 2008). There are also few natural disturbances, primarily just tree fall gaps, which are comparatively rare and of small spatial and temporal scale (e.g. as opposed to fires; Carson and Schnitzer 2008). Thus, when forests are clear-cut and converted to agriculture, nearly all habitat features, and the species reliant on these niches, are lost during the planting phase. Even fully-grown tree plantations do recreate forest habitat conditions because they rarely reach over 15m in height, then, after a few decades they are clear-cut and replanted, essentially resetting the successional process for most forest species (Figure 2; Luskin and Potts 2011). Thus, annual croplands are particularly inhospitable habitat for forest interior species, especially for arboreal species, regardless of whether or not wildlife-friendly farming methods employed.

In multi-use landscapes, species are conserved within cropland and remaining forests, with most studies assessing biodiversity levels in farmland. Reviewing this empirical work, I first became aware of many methodological biases, including ecological sampling flaws as well as interpretation pitfalls when comparing forests and agriculture (Table 1). I found that most these flaws would produce results that overstate the value of farmland to species conservation- a research bias against land sparing.

Notwithstanding the potential methodological biases, to evaluate general trends of tropical forest species persistence within farmland, I reanalyzed data in Gibson *et al.*'s (2011) meta-analysis of 138 studies that spanned 28 countries and 92 study landscapes by crop type (enabling 2,200 pairwise comparisons). I found significant biodiversity impacts in all agriculture types but more deleterious effects in annual crops (mean effect size 1.04) than in tree plantations (mean 0.50; $p < 0.01$; Figure 3). This indicates that annual crops such as soybeans, maize, rice, and sugar cane generally retain lower levels of forest biodiversity than tree crops such as cacao, coffee, rubber, and oil palm. Another finding was that forest specialists, which generally are greater conservation concern, were also more sensitive to all types of disturbances than the community as a whole, indicating that land sparing benefits are pronounced for this group.

The significant variation between the conservation values of different crops led us to evaluate how researchers' study systems may influence general results. Most research on tropical

forest species' responses to agriculture has focused on comparatively biodiversity-friendly tree crops. A prime example is coffee, which is not one of the 20 largest tropical crops nor globally expanding, yet has been the focus of much biodiversity research, probably due to its potential to be grown in shaded polycultures. In fact, of the 59 studies published between 1975 and 2010 comparing tropical biodiversity in primary forests to agriculture that met our *a priori* selection criteria, 89% of the studies included tree crops (Figure 4; supplementary materials *Methods*). In contrast, only 32% studies comparing tropical forest biodiversity in agriculture included annual cropping systems, yet annuals constituted 87.4% of total tropical cropland in 2010 (supplementary materials Table 1; FAO 2013). This shows a strong research bias towards a small subset of biodiversity-friendly tree crops.

Finally, evaluating how farming affects species within remaining forest fragments, I found there is evidence that a wildlife-friendly farming matrix has a small effect on species' persistence within fragments (Prevedello and Vieira 2010). However, habitat corridors appear comparatively more efficient at connecting fragments to benefiting isolated populations (Gilbert-Norton *et al.* 2010). Further, in some cases, wildlife-friendly farming can cause some generalist species become overabundant due to their utilization of adjacent farmland resources, for example, native wild boars that feed on oil palm fruit in Southeast Asia become hyper-abundant and then also negatively impact remaining forests (Fitzherbert *et al.* 2008; Luskin *et al.* 2013). Thus, there does not seem to be a significant advantage of "softer" matrix in comparison the alternative land sparing strategies of adding corridors or more total forest habitat (e.g. Perfecto and Vandermeer 2010).

In the largest and most robust study to date, Phalan *et al.* (2011b) found land sparing to be advantageous to conserve birds and trees across landscapes that included a variety of annual and tree crops in India and Ghana. Hulme *et al.* (2013) also found land sparing was most beneficial for the majority of bird species in Ugandan banana-coffee landscapes. In Brazil, Mahood *et al.* (2012) found that 70% of the 560 regional bird species were completely absent from the Amazonian countryside and concluded land sparing would be optimal for the majority of species. Likewise, in a global analysis, Wright *et al.* (2012) found that only 28% of threatened bird species in developing countries (mostly tropical) even temporarily used any sort of farmland. In Sulawesi, Indonesia, the conversion of primary forest to cacao agroforestry also reduced forest species richness by ~60% across a wide variety of taxonomic groups (Steffan-Dwenter *et al.* 2007). The complete loss of most species from both annual and tree cropland indicates land sparing would be beneficial for majority of forest species.

In Costa Rica, Chandler *et al.* (2013) found that "integrated open canopy" (IOC) coffee plantations, which resembles "small-scale land sparing" because they pair 1-3 ha of farmed land with equal-sized patches of forest, conserved more bird species than "land sharing" shade grown coffee. Edwards *et al.* (2010) also found land sharing to be advantageous for bird species in oil palm landscapes in Borneo; however, they specifically advocated larger forest offsets because abundances of imperiled bird species were 200 times lower in oil palm and 60 times lower in fragments than in contiguous forest. Further, Edwards *et al.*'s fragments were substantially larger than Chandler *et al.*'s (mean = 21.1 ha versus 1-3 ha, respectively), thus, it is probable that larger-scale land sparing approach, where the individual IOC forest patches in Costa Rica would be combined into fewer larger patches, would yield even higher total population sizes across the

landscape.

Discussion

Implementing production strategy in the real world requires a balance between conserving tropical forest biodiversity and other societal goals. Below I discuss the practical considerations to implementing a land sharing approach in the tropics. I focus on (i) the tradeoffs and synergies with other ecosystem services (e.g. water quality); (ii) the economic benefits of accrued by forests offsets (e.g. from carbon payments, ecotourism, or non-timber forest products) and; (iii) the logical obstacles to insuring forest offsets occur.

Sustainable ecological intensification methods may help create win-win high-yielding and wildlife-friendly farming systems (Bommarco *et al.* 2013). Kremen and Miles (2012) discuss a variety of methods to intensify with labor and knowledge (sometimes termed “precision” or “resource conserving” agriculture), as well as the benefits of growing a variety of crops together (“diversified farming”). For example, over the 25-30 year oil palm plantation life cycle, livestock grazing can be conducted in early years when the canopy is open, and then shade-tolerant crops can be intercropped when palms are tall, likely with negligible effects on palm oil yield (Luskin & Potts 2011). However, while sustainable intensification methods may benefit aquatic species due to reduced pollution and runoff (Tilman *et al.* 2002), most do not significantly increase farmland’s structural habitat complexity and thus provide few added niches for forest species. I urge scientists to recognize the benefits and limitations of sustainable intensification.

Increasing yields to spare forests also promotes other important ecosystem services and some forest-based livelihood resources. For example, land sparing maximizes carbon storage in the tropics, and there is substantial geographic overlap between the highest carbon and biodiversity-laden areas (Venter *et al.* 2008; West *et al.* 2010). Forests also provide many livelihood benefits, such as wild meat, a critical resource to millions of people.

Third, in addition to provisioning ecosystem services, land sparing forest offsets can accrue value themselves from REDD+ carbon schemes, ecotourism, or non-timber forest products. It is also foreseeable that sustainably managed production forests, spared from agriculture but still selectively harvested for timber, may be included as offsets in a pragmatic land sparing portfolio (Fisher *et al.* 2011; Putz *et al.* 2012). In these cases, the combined value of the land sparing landscape would include the high agricultural output on intensified farms and values generated from spared forests, an attractive development approach.

Finally, choosing the optimal crop for a desired outcome, such as biofuels, may lead to net gains for both biodiversity and yields. For example, biodiesel can be produced from both oil palm and soybeans, but oil palm is a comparatively more wildlife-friendly tree crop, has higher oil yields, and sequesters significantly more carbon (Fargione *et al.* 2008).

Tradeoffs and challenges to implementing land sparing

Land sparing can deliver many benefits but conventional land sparing intensification farming methods also negatively affect some critical ecosystem services. For example, soil and

water quality, pollination, pest control, and erosion control are favored by land sharing systems (Kremen and Miles 2012). Further, some land sparing intensification methods may not be feasible in some ecologically fragile areas due to the potential for soil degradation, limiting the maximum sustainable yields in these marginal areas (Tilman et al. 2002; Fisher et al. 2008). Here, the best approach may be wildlife-friendly farming or conservation set-asides, which could potentially be included as “spared land” under a regional-scale land-sparing approach.

Another challenge for land sparing arises in situations where gross yield from a landscape is not the stakeholders’ decision-making currency. For example, lower yielding land sharing systems may actually be more profitable if they have lower production costs (e.g. less inputs) and/or their products can fetch a premium (e.g. when certified as organic; Bolwig and Gibbon 2009).

Forests are not automatically spared following yield intensification, particularly in frontier landscapes (Barretto *et al.* 2013). In fact, yield increases that increase profitability may actually incentivize further crop expansion (Lambin and Meyfroidt 2011). Promisingly, for developing countries over past 20 years, agricultural output increased by 3.3% annually, while new deforestation’s contribution to the cultivated area only increased by ~0.3% per annum, indicating most of production gains have come from intensification (Angelsen 2010). There are also large yield gaps that can be easily closed, which some would call the lowest-hanging fruit (Licker *et al.* 2010). However, demand often outpaces yield gains from intensification (e.g. palm oil), incentivizing additional conversion (Ewers *et al.* 2009), and forests are often comparatively cheaper or easier to access, particularly for large agribusiness (Gutiérrez-Vélez *et al.* 2012). Thus, like many worthy development models, to achieve its goal of reducing natural habitat conversion, land sparing will need to be part of comprehensive set of forest-protection and development policies, including protected forest offsets.

Once a robust land sparing agreement with forest offsets has been approved, conservationists can begin the process of designing and implementing an effective strategy. The first step is locating new forest offsets, which requires landscape-scale conservation planning, including more research to devise species and ecosystem-specific recommendations (Margules and Pressey 2000). Important considerations include whether offsets should be targeted for the largest remaining forests (Edwards *et al.* 2010), small fragments on each farm (e.g. Brazil’s forest code; Chandler *et al.* 2013), habitat corridors to connect existing patches, or to regenerate previously cleared forests. It is also important for set-asides to target habitat suitable for the species being directly displaced by agriculture (e.g. if peat-forests are cleared for agriculture, they should also be targeted as forest offsets).

Conclusion

Ifound land sparing was the best strategy to conserve tropical forest species in the face of rising agricultural demands. These findings contradict a recent emphasis on biodiversity-friendly farms and landscapes (Bhagwat *et al.* 2008; Melo *et al.* 2013); even in exemplary wildlife-friendly farmlands over 50% of forest species were routinely absent. However, biodiversity conservation is just one ecosystem service affected by agriculture, and there is an outstanding need to quantify

tradeoffs *between* services and assess how society values different services. Moving forward to implementing a land sparing approach, I am optimistic about synergies between ecosystem services (e.g. sequestering carbon in spared forests), and added economic returns from forest offsets (e.g. REDD+ carbon payments or ecotourism). However, specifically including defensible forest offsets is imperative to avoid green-washing further expansion (Edwards & Laurance 2012). I conclude that a land sparing approach with clear and defensible forest offsets within carefully spatially designed landscapes can provide substantial returns for agriculture, conservation, and other ecosystem services.

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Tables

Table 1: Potential methodological biases affecting empirical tests of the land sparing debate.

Study species or habitat biases		
1	Species' conservation values	Special consideration should be given to native threatened species (Barlow <i>et al.</i> 2010). For example, the immigration of non-indigenous species into farmland may actually increase richness or abundance compared to forests, but does not contribute to most conservation goals (exotic or invasive species can even detract from conservation efforts; Fitzherbert <i>et al.</i> 2008). Simple biodiversity metrics, such as total species richness, that do not appropriately weight species of concern, are inappropriate for estimating the true "conservation value" of a habitat.
2	Over or under sampling specific micro-habitats	The systematic omission of difficult to sample habitats may conceal important losses in forest diversity. For example, canopy-dwelling specialists may show high sensitivity to habitat modification, but are systematically left out of surveys due to the difficulty of sampling in a 50-70m canopy.
3	Different effective sampling intensities	There may be differences between the effective sampling intensities in different habitats due to structural habitat complexity. For example, sampling in open agricultural fields may lead to better accessibility, visibility and higher collection rates compared to dense forests (Gardner <i>et al.</i> 2008). Point-counts used to study birds are particularly susceptible to different collection rates between, for example, a 60m primary forest canopy and 15m plantation canopy.
4	Guild-specific or morphological-specific responses	Using easy to sample species or indicator species that do not represent other species of concern can obscure important differences. For example, birds are particularly mobile group and thus more prone to temporarily utilizing or dispersing through cropland than most other groups of organisms.
Biases interpreting species' presence in farmland		
5	Interpreting presence as equivalent to population density	The use of simple biodiversity metrics, such as species richness, where presence alone in farmland, versus population densities, is gauged as indicative of equivalent population levels between habitats, can conceal a large decline in a species' density.
6	Transient farmland fauna interpreted as resident	Species dispersing through or temporary using farmland resources can be misinterpreted as persisting within farmland (Anand <i>et al.</i> 2008; Sridhar 2009). Even seemingly resident farmland biodiversity may periodically require forest for critical resources (e.g. for breeding; Luskin 2010).
7	Not sampling across the crops' lifecycle	The conservation value of a habitat must be considered (integrated) over the entire crop lifecycle. For example, most studies of coffee, oil palm, and cacao sample in mature plantations (5-25 years post-planting), not during years of site preparations or planting when many more species are completely absent (Luskin and Potts 2011).
8	Interpreting species presence as long-term viability	Farmland may be a "sink habitat" where reproductive success is low and populations are continually decreasing or must be rescued. To date, however, there is little research on demographics within tropical cropland.
Landscape or community-wide changes		
9	Difficulty measuring community-level or tropic structure changes	Heterogeneous landscapes with "soft matrixes" commonly advocated by land sharing proponents often lose area-demanding keystone species (e.g. top predators), potentially causing widespread but overlooked ecological cascades. This may affect the entire wildlife community across large expanses, including within the remaining forests (Terborgh & Estes 2010).
Using inappropriate forest baselines		
10	Using historically fragmented or disturbed forest baselines	Using historically fragmented or disturbed forest as "natural habitat" reference system is inappropriate because even though it likely already lost many forest specialists (many Costa Rican countryside studies; Ranganathan <i>et al.</i> 2008). Even large forest fragments can suffer from pervasive edge effects or ecological cascades, shifting down the baseline against which farmland biodiversity is measured and obscure true species declines.
11	Spatial pseudo-replication of baseline forest sites	Primary forests are noted for their beta-diversity (significant natural species turnover even at large spatial scales; Ramage <i>et al.</i> , 2013) while farmland communities are comparatively homogenous (Gardner <i>et al.</i> , 2008). Spatial pseudo-replication of forest sites thus leads to lower forest baselines, biasing results towards showing smaller differences in farmland.
12	Comparing across different biophysical or ecological gradients	Farmland systematically replaces lowland and gently slopping areas. Higher elevation and steeper forest sites could naturally hold different species or lower overall richness or density than the original lowland forests.

Figures

Figure 1: Forest versus different agricultural land uses in Peninsular Malaysia. (A) Primary lowland rainforest, (B) land sparing monoculture paddy rice (C) land sharing small-scale wildlife-friendly agriculture (dragon fruit, sugarcane) and agroforestry (rubber) (D) land sharing mixed small scale wildlife-friendly agriculture (paddy rice, ginger) and agroforestry (coconut, teak) (E) land sparing industrial oil palm- 8 years since planting (F) land sparing industrial oil palm- 23 years since planting (photos by M Luskin).

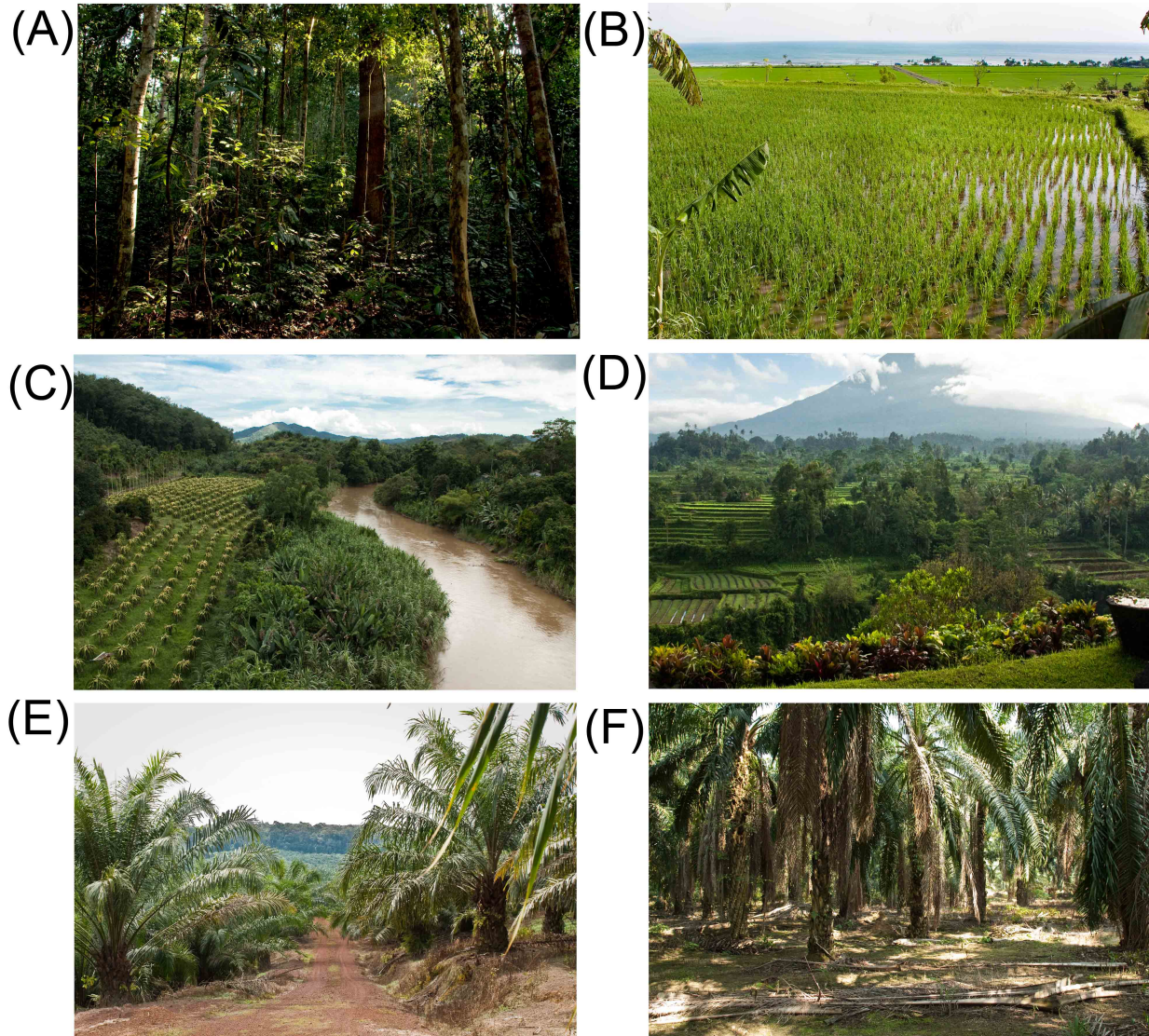


Figure 2: Lateral sections of various forms of agroforestry, plantation and annual cropland relative to primary forest.

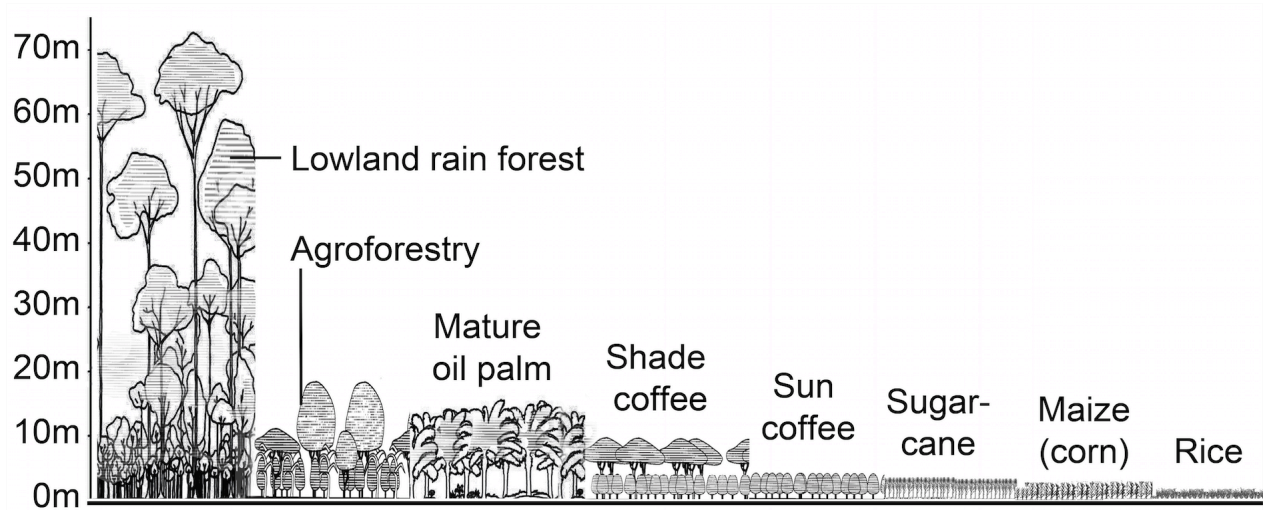


Figure 3: Effect size of different agricultural systems on forest species. Plotted are median values and box plots showing 95% confidence intervals. Sample sizes of paired comparisons are shown in parentheses. Annual cropland is statistically different from all plantations and agroforestry ($p < 0.01$); plantations and agroforestry are not statistically different from each other.

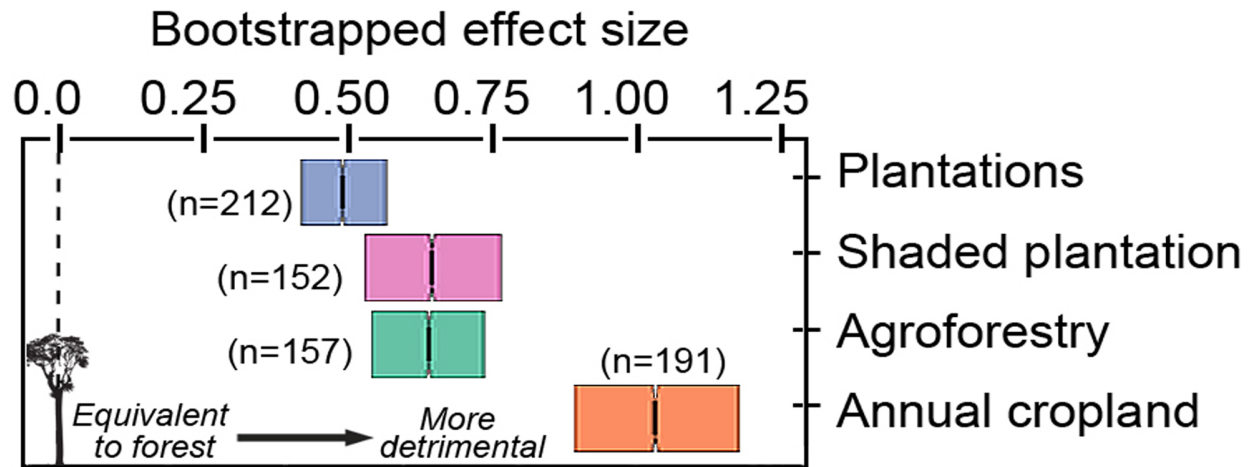
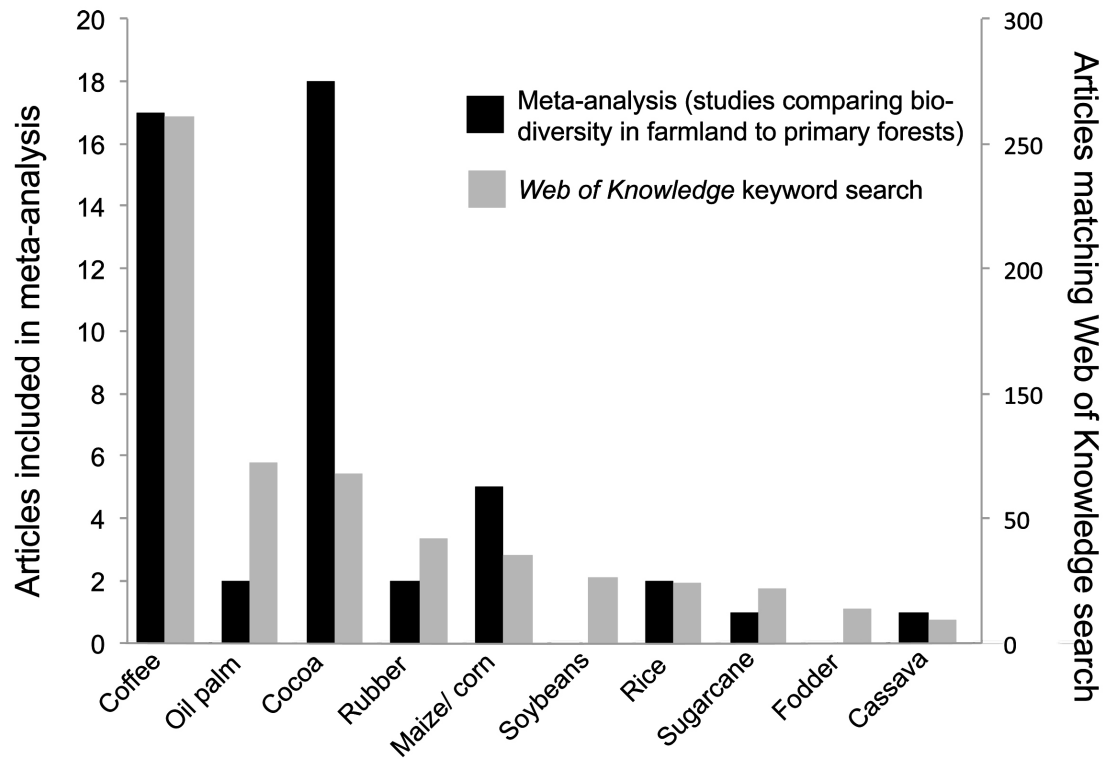


Figure 4: Research on tropical biodiversity responses to agriculture by crop from 1975-2010. The left y-axis shows the number of articles used in the meta-analysis on biodiversity impacts from tropical agriculture relative to primary forests (Gibson *et al.* 2011 and Figure 2) and the right y-axis shows returns from a more general literature search in *Web of Knowledge*.



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Chapter 3

Microclimate and habitat heterogeneity through the oil palm lifecycle

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Abstract

The rapid expansion of oil palm cultivation and corresponding deforestation has invoked widespread concern for biodiversity in Southeast Asia and throughout the tropics. However, no study explicitly addresses how habitat characteristics change when (1) forest is converted to oil palm, or (2) through the dynamic 25–30-year oil palm lifecycle. These two questions are fundamental to understanding how biodiversity will be impacted by oil palm development. Our results from a chronosequence study on microclimate and vegetation structure in oil palm plantations surrounding the Pasoh Forest Reserve, Peninsular Malaysia, show dramatic habitat changes when forest is converted to oil palm. However, they also reveal substantial habitat heterogeneity throughout the plantation lifecycle. Oil palm plantations are created by clear-cutting forests and then terracing the land. This reduces the 25 m-tall forest canopy to bare ground with a harsh microclimate. Eight- year-old oil palm plantations had 4 m open-canopies; 22-year-old plantations had 13 m closed-canopies. Old plantations had significantly more buffered microclimates than young plantations. Understory vegetation was twice as tall in young plantations, but leaf litter depth and total epiphyte abundance were double in old plantations. Nonetheless, leaf litter coverage was patchy throughout the oil palm life cycle due to the stacking of all palm fronds. Overall, oil palm plantations were substantially hotter (+2.84 C) and drier (+0.80hPa vapor pressure deficit), than forests during diurnal hours. However, there were no nocturnal microclimate differences between forests and plantations. Finally, we describe how the variable retention of old palm trees during crop rotation can retain habitat features and maintain more stable microclimate conditions than clear-cutting senescent plantations. We discuss the implications of habitat changes for biodiversity and introduce three methods to utilize temporal habitat heterogeneity to enhance the quality of the oil palm landscape matrix.

Keywords: Tropical rain forest; Biodiversity; Landscape ecology; Plantation crop; Agroforestry; Agricultural matrix; Vegetation structure; Southeast Asia; Malaysia

Introduction

Large-scale deforestation for oil palm, *Elaeis guineensis*, within the Southeast Asian “biodiversity hotspot” has emerged as a paramount global conservation issue (Myers et al. 2000; Sodhi, Koh, Brook, & Ng 2004; Koh & Wilcove 2008; Sodhi et al. 2010). Palm oil has recently

become the world's most-consumed vegetable oil, and oil palm plantations have become the largest perennial cropland on earth, their exponential growth partly driven by unparalleled oil yields compared to other crops (Corley 2009; FAO 2009). Oil palm's rapid expansion has fueled widespread concern over how and where oil palm production is occurring and its impacts on the environment and biodiversity (Curran et al. 2004; Fitzherbert et al. 2008; Koh & Ghazoul 2010).

Ecologists argue that a growing number of studies on diverse taxa demonstrate native biodiversity is undoubtedly negatively impacted when oil palm replaces forests because few native species can persist in oil palm plantations (Fitzherbert et al. 2008; Wilcove & Koh 2010). Meanwhile, the oil palm industry maintains that plantations grow into "forests" that can support high biodiversity (MPOC 2008; RSPO 2008; Butler 2011). Indeed, current research does indicate that oil palm plantations can sustain high abundances and a diverse array of species. However, these species assemblages are distinct from those in natural forests and lack most native species (Danielsen et al. 2009). The magnitude of current oil palm expansion and controversy surrounding its consequences has sent ecologists scrambling to increase research efforts to quantify the biodiversity impacts (Turner, Snaddon, Fayle, & Foster 2008).

An essential preliminary step to exploring *in situ* and landscape-level biodiversity responses to oil palm expansion is understanding the biotic and abiotic habitat characteristics that are central to shaping species distributions. Important habitat conditions for native species in plantations include tolerable microclimate conditions, leaf litter depth and coverage, and the structure, composition and complexity of the herbaceous understory and canopy (Lawton et al. 1998; Tews et al. 2003; Schroth et al. 2004). Minimizing the differences between forest and plantation habitat conditions can increase the ability of native species to live within plantations or to periodically use plantations for foraging or other resources (Brockerhoff, Jactel, Parrotta, Quine, & Sayer 2008). Increasing the permeability of the agricultural matrix with favourable habitat conditions also facilitates native species movement between remaining forest patches, bolstering native species persistence in the landscape (Fischer, Lindenmayer, & Manning 2006).

Habitat features change throughout the plantation lifecycle, such as forage availability and continuity of canopy cover. As oil palm trees grow and gain structural complexity, native species may be more likely to utilize resources or disperse through plantations (Schroth et al. 2004; Brockerhoff et al. 2008). For example, ants, currently the best-studied taxonomic group within oil palm, exhibit marked shifts in diversity and abundance in relation to local habitat features such as microclimate, ground cover, leaf litter, and extent of epiphytes within plantations (Room 1975; Taylor 1977; Dejean, Djieto-Lordon, & Durand 1997; Pfeiffer, Tuck, & Lay 2008; Brühl & Eltz 2010; Turner & Foster 2009; Fayle et al. 2010). However, despite the fundamental role that habitat plays in determining biodiversity, little is currently known about specific habitat differences between oil palm plantations and native forests. Similarly, there is sparse data on habitat variations throughout the plantation lifecycle or at different spatial scales. Understanding how habitats change over time is especially important for oil palm plantations due to their prolonged lifecycles. Moreover, a thorough understanding of spatio-temporal habitat idiosyncrasies is vital to suggesting plantation management practices that are relatively biodiversity-friendly.

Converting forests to establish oil palm plantations dramatically alters habitat features. It

requires clearing all vegetation mechanically and/or with fire, then terracing soil, building roads and drainages, and finally planting exotic oil palm seedlings (Butler 2011). A plantation has a 25–30-year lifecycle with palms beginning to fruit after just 3–5 years (Butler, Koh, & Ghazoul 2009). Plantations go through a small tree phase with high solar radiation and wind exposure before the canopy closes (Wilson & Ludlow 1990; Corley & Tinker 2003; Fig. 1). Finally, plantations are rotated by clear-cutting existing palms when yield diminishes and trees become too tall to harvest economically (Butler et al. 2009). Slash is either reduced mechanically, by fire, or leaving it to decompose, the land is then prepared and new oil palm seedlings are replanted (Corley & Tinker 2003). Beyond the lifecycle-related effects on plantation habitat, spatial heterogeneity emerges within the oil palm landscape due to different plantation sizes and shapes. For example, oil palm cultivation ranges from smallholder plots of 1–10 ha to international corporations and government-operated mega-plantations exceeding 10 km² (Corley & Tinker 2003). The size, shape, layout and management of plantations ultimately determine much of the important landscape-scale biological processes such as connectivity, permeability and edge effects (Forman 1995).

Oil palm is continually managed in evenly spaced monocultures without overstory shade trees, which limits the capacity of characteristic forest habitat features to develop. At the local scale, periodic herbicide applications commonly maintain easy access to the palms for harvesting and inhibit competition between the palms and other plants (Corley & Tinker 2003). Alternatively, beneficial groundcover such as small ferns or leguminous nitrogen-fixing species may be cultivated to minimize erosion and hold water close to the palms (Corley & Tinker 2003; Koh 2008). Trimmed palm leaves are stacked in large piles beneath the oil palms, which creates a patchy environment of leaf litter. The process of trimming leaves to harvest fruit bunches creates stubs that protrude 10–30 cm upwards from palm trunks. These stubs act as “pots” that collect organic matter where epiphytes then grow. Epiphytes are ubiquitous in oil palm plantations and can support epiphyte-associated species. However, the majority of epiphytes in plantations are exotic species (Danielsen et al. 2009; Fayle et al. 2010).

This study’s primary aim was to enumerate the habitat differences between forests and oil palm that affect biodiversity responses to conversion. Next, we sought to describe how habitat conditions in oil palm change over the course of the 25–30-year plantation lifecycle. Finally, due to the vast scales which oil palm is grown, we sought to understand how habitat changes at different distances from forests. In order to account for changes due to management, we also compare our results from plantations using herbicides to published results from plantations that cultivate an understory of beneficial plants (Koh 2008).

Methods

Study location

Sampling was conducted from June to August 2010 across oil palm plantations and late-successional lowland dipterocarp forest of the 2450 ha Pasoh Research Forest, Peninsular Malaysia (lat 2°5’N, long 102°18’W; Okuda et al. 2003; Fig. 2). At the landscape scale, the Pasoh Research Forest is bordered on three sides by monocultures of oil palm plantations that extend 4–10 km in each direction and forest on the fourth side (Sun, Chen, Hubbell, Wright, &

Noor 2007). All plantation land was clear-cut over 30 years ago, terraced, and planted with oil palm (Naoki, Nur Supardi, Mazlan, Mahdan, & Toshinori 2001). No riparian areas or High Conservation Value Forest (HCVF) were spared and there was no intercropping. In 2010, the majority of area was in its second oil palm rotation while 22-year-old plantations were at the end of their first rotation (Fig. 2). Malaysia's largest oil palm developer, the Federal Land Development Agency (FELDA), operated the plantations using standard techniques advocated by the Malaysian Palm Oil Board (MPOB 2010). All plantations practiced identical 9 m $\times$ 9 m palm spacing in a triangular formation by offsetting every other row. Herbicides were periodically applied in plantations, but no applications occurred for at least 3 months prior to sampling. Groundcover and epiphytes were otherwise left unmanaged unless they became obstacles to harvesting.

Sampling design

We measured microclimate in: (i) *clear-cut*, as might be found during standard plantation establishment or rotation; (ii) *young plantations*, 8 years since planting, characterized by short palm trunks (<3 m) and an open canopy; (iii) *old plantations*, 22 years since planting, characterized by tall palm trunks and a closed canopy; (iv) “*variable retention*” regeneration, an experimental rotation where every other row of 22-year-old palms was selectively thinned and an understory of new palms was re-planted 6 years prior to the study; and (v) *forest*, mature rainforest including both primary forest and forest selectively logged ~50 years earlier (Okuda et al. 2003). Vegetation was only sampled in young and old plantations. Finally, due to the vastly different scales at which oil palm production is grown, we sampled young and old plantations at both 100 m and 1 km from the forest edge. Within the forest, young plantations, and old plantations, we randomly located 6 sites, three of which were 100 m from the forestplantation edge and three of which were 1 km from this edge. The three “variable retention” regeneration sites were opportunistically located 100–500 m from forests, and the one bare ground site was located in a 15 m $\times$ 15 m clearing at about 500 m from forest (Fig. 2).

Data collection

Temperature and relative humidity were sampled at 10 cm above the ground at 20-min intervals using 15 iButton sensors (model DS1923) rotated among all sites for 10 weeks (42,609 total observations collected for both temperature and humidity). The iButton sensors took readings accurate to 0.0625 C and 0.04% relative humidity (Maxim Integrated Products 2009). Sensors were housed in small open microclimate stations to allow for the measurement of ambient conditions while being shielded from direct sunlight and rain. For all analyses, relative humidity was converted to vapor pressure deficit (VPD) using simultaneous temperature readings (World Meteorological Organization 2008). VPD is a more biologically meaningful measure of potential water-stress, with 0 hPa representing the water vapor saturation point for a given temperature and positive values showing drier conditions.

Vegetation structure data was collected in young and old plantations along 12, 50-m transects, but not in forests, variable retention, or clear-cut sites (but see Okuda et al. 2003 for forest description). Canopy height was measured with a telescoping pole, and canopy density was measured by counting the number of separate leaves directly overhead at every meter. Trunk height (m), trunk diameter at breast height (dbh; cm), epiphytes (abundance and size per m²) and

the number of palm stubs per m² were measured for closest tree at 5-m intervals along transects, including at the first and last meter (132 observations for each variable). The depth of leaf litter, height of live understory vegetation, or presence of *bare ground* were measured at every metre point along the 50-m transects (600 observations; the mean vegetation height and leaf litter depth reported excludes zeros). *Percent area covered* represents mean presence of vegetation, leaf litter, or bare ground for all data points.

Epiphytes were quantified by creating vertical plots (1 m × 1 m) at 0.5–1.5 m above the ground on tree trunks yielding 132 plots and 2373 total epiphyte observations. The size of each epiphyte was measured as length from base to the end of the longest leaf, and only epiphytes originating within the vertical plot were counted. Epiphytes were identified into five broad groups: (i) ferns (phylum: *Pteridophyte*); (ii) palms (family: *Arecaceae*); (iii) grasses (family: *Poaceae*); (iv) vines and climbers (distinctive functional group of Angiosperms); and (v) leafy plants (all other Angiosperms). When a vertical plot could not be established, every epiphyte on the palm was counted and then transformed into a per m² value based on trunk surface area.

Statistical analyses

All microclimate analyses used generalized linear mixed models (GLMM) and controlled for the known effect of time of day (blocked by hour; (R-Cran lme4 package). We allowed for random site and day variation. In order to highlight diurnal and nocturnal microclimate differences without washing out daily fluxes, for each site we grouped 6 diurnal hours from midday (12:00 to 18:00) and 6 h following midnight (00:00 to 06:00). These were the two time periods separated by 12 h that showed the greatest statistical difference. Variable retention regeneration and bare ground sites were analyzed separately unless specifically noted. We also used GLMMs to explore differences between each type of plantation (young or old and 100 m or 1 km from forest). Vegetation analyses allowed for random site and tree variation. There were no significant temperature or VPD differences within forests at 100 m and 1 km from plantation edge, which is consistent with results from the Amazon where microclimate edge effects became undetectable at 100 m (Didham & Lawton 1999). Thus, all forest sites were grouped for the remainder of the comparisons with plantation sites.

Finally, to compare our results with results from plantations with understories actively managed for beneficial fern and nitrogen-fixing leguminous species, we ran the same analyses on vegetation data from the oil palm plantations in Malaysian Borneo reported by Koh (2008). We combined all ground vegetation types reported in Koh (2008) together and ran GLMMs for the response variables total abundance of ground vegetation and epiphytes. Fixed effect predictors consisted of plantation age and two covariates (forested area in the landscape and sampling effort, which were the only other significant predictors) and allowed for random variation between each plantation.

Results

Microclimate results

In forests, the mean diurnal temperature was 26.33°C and the mean VPD remained near the saturation point (0.00hPa). After controlling for normal diurnal flux in forests, plantation

conditions were +2.84 C hotter and +0.80hPa drier (Table 1). For comparison, the daily forest microclimate flux was less than +4 C and +0.20 hPa, so plantations produced large deviations from forests conditions (Fig. 3). There were no nocturnal microclimate differences between forests and any treatments and thus we only report diurnal results for the remainder of analyses. The microclimate in old plantations showed less deviation from forest conditions than young plantations, being -1.20 C cooler and +0.19 hPa more humid than young plantations ($p = 0.01$ and $p = 0.06$, respectively). Spatial effects from the distance from forests had low statistical significance with the most pronounced effect being young plantations +0.22hPa drier at 1km from forest than young plantation at 100 m ($p = 0.099$). Variable retention sites showed much less deviation from forest conditions than both clear-cut and young plantations (-1.28 hPa more humid and -3.73 C cooler than clear-cut, both $p < 0.01$; -0.30 hPa more humid than young plantations, $p = 0.045$). The clear-cut site was substantially hotter and drier than all other sites (Table 1; Fig. 3).

Vegetation results

Leaf litter was twice as deep in old plantations as in young plantations (mean 9.84 cm depth in young plantations compared to 20.61 cm in old plantations), while the live vegetation understory was twice as high in young plantations (mean 11.46 cm in old plantations compared to 21.77 cm in young plantations; Fig. 4). However, the percentage of ground area occupied by bare ground, vegetation, and leaf litter did not vary between old and young plantations. Old plantations had taller trees and increased canopy depth but fewer frond stubs remaining per m² on trunks. Distance from forest had no detectable effects on vegetation characteristics. Epiphyte density in young plantations was twice that in old plantations (mean 12.35 epiphytes m⁻² compared to 23.50 epiphytes m⁻² in young plantations), yet total epiphyte abundance was still much greater in old plantations due to vastly greater trunk surface area (Table 2). In old plantations, there was a fourfold decrease in the density of ferns and palms, while grasses were more abundant. Leafy and climbing epiphytes showed no differences between young and old plantations. Overall, ferns dominated the epiphytic community, climbers were the largest and most rare, and grasses were the smallest.

The analysis of the Koh (2008) vegetation data from plantations in Borneo with managed understories showed a similar decreasing trend for epiphyte density with plantation age (1.29% *less* “epiphyte coverage” per year; $p < 0.05$), yet a positive trend for understory vegetation coverage through time (1.19% *more* ground coverage per year; $p < 0.05$).

Discussion

There are complicated and sometimes opposing habitat trends through the oil palm plantation lifecycle. Overall, there is a shift from taller ground vegetation in open young plantations to a more buffered microclimate, increased leaf litter, and a closed-canopy in old plantations (Fig. 5). The diurnal microclimate was dramatically altered during plantation establishment (clear-cut), became increasingly buffered though time as palms grew and the canopy closed, but never regained the stability of forest conditions (Fig. 5). Leaf litter depth increased as plantations aged, but more importantly, the percentage of area covered by leaf litter was always low (47%), with the vast majority neatly stacked into even patchier piles (for

comparison, leaf litter coverage is >90% in forests). The understory vegetation height and epiphyte density were greater in young plantations where the open canopy allowed more sunlight to penetrate (Wilson & Ludlow 1990), yet the ground area covered with vegetation remained constant between old and young plantations. We anticipated nocturnal conditions to be colder, windier and drier in plantations due to less standing biomass and less structural complexity to trap and re-radiate heat and moisture than forests (Siles & Harmand 2009). However, there were no microclimate differences between forests and plantations or between plantation types during the night.

Spatial effects were less pronounced than lifecycle-related changes but suggested young plantations might be drier further from forests ($p = 0.099$; Fig. 3). We anticipated microclimate would be more extreme at 1 km away due to less spillover from forests and greater all-around exposure; however, our results showed only small changes that may require increased sampling to detect with statistical certainty. Similarly, we hypothesized that epiphyte abundance and ground vegetation would decline further from forest source populations, yet there were no detectable spatial effects on any vegetation parameter (but note that species composition was not studied).

Habitat changes and biodiversity

The substantial microclimate differences in all plantations relative to forests confirm ecologists' concern that forest-dependent species will be threatened by oil palm expansion (Fitzherbert et al. 2008). Hot and dry diurnal conditions observed throughout the plantation lifecycle present a microclimatic barrier to sensitive native species that are adapted to moist, buffered rainforest climates (Perfecto and Vandermeer 1996; Porter & Kearney 2009). This effect would be reduced for nocturnal species, as plantation conditions were indistinguishable from forests at night. A species' ability to live or move through plantations will also change through time as plantations grow. For example, the dramatically drier conditions in clear-cut and young plantations could preclude understory herbaceous plants or amphibians that require stable, moist conditions for recolonizing. By contrast, these species may survive later when the plantation canopy closes and microclimate is more buffered. Thus, old plantations with smaller microclimate differences from forests will be relatively more hospitable to native species in this niche dimension. Nonetheless, predicting species-specific impacts requires significantly more research (Jackson, Betancourt, Booth, & Gray 2008; Tewksbury, Huey, & Deutsch 2008).

More ground vegetation in young plantations may attract herbivores to forage (Lawton et al. 1998; Tews et al. 2004). Wahab (2000) similarly showed a decreasing trend in total understory vegetation biomass through the oil palm lifecycle, led by declines in grasses, legumes, and edible dicots (see Appendix A). However, old plantations possess other habitat features including epiphyte abundance, leaf litter depth, increased ferns and non-edible dicots, and a closed canopy that may provide cover and support wildlife movement (see Appendix A, Armbricht, Perfecto, & Vandermeer 2004; Hilty, Lidicker, & Merenlender 2006). A closer examination of wildlife usage of large leaf litter piles is warranted, as we opportunistically observed passerine birds, birds of prey, snakes, monitor lizards, small lizards, rodents, macaques, pigs, a civet, and leopard cats within or on top of piles.

Management implications

Habitat heterogeneity through the plantation lifecycle should be integrated into planning more biodiversity-friendly oil palm landscapes (Pimentel et al. 1992; Tews et al. 2004; Perfecto, Vandermeer, & Wright 2009; Fig. 5). First, reducing patch/field size and creating a patchwork of different-aged plantations can increase the total habitat variety and complementarity in the landscape (Fig. 6, “Increased Heterogeneity”). This also reduces the contiguous size of major disturbances and increases the availability of features through time. Even massive plantations could designate “blocks” for rotation/replanting at different time periods, a widespread biodiversity-friendly tactic used in timber production forests throughout the world, including parts of Southeast Asia (Thang 1987; Smith, Larson, Kelty, & Ashton 1997; van Kuijk, Zagt, & Putz 2009). Furthermore, increasing landscape-scale heterogeneity could have social and economic benefits by more evenly distributing costs, oil production, income, and labor requirements through time. A detailed cost-benefit analysis is warranted.

In addition to creating a patchwork of different aged plantations, planting schedules could be augmented to increase permeability and connectivity between remaining forests. Planting in progressive strips between remaining forests would create a multitude of continuous plantation “corridors” of the same habitat types (Fig. 6, “Increased Connectivity”). Also, special attention to maintain continuous oil palm canopy cover and shade could increase wildlife propensity to traverse between forest patches (Perfecto, Rice, Greenberg, & Van der Voort 1996). These methods could complement, not replace, natural habitat corridors, riparian corridors, and High Conservation Value Forest, to increase the quality of the landscape matrix (Hilty et al. 2006; RSPO 2008).

Clear-cutting old palms to regenerate senescent plantations creates a barren landscape and harsh microclimate (Figs. 3 and 5). This eliminates most *in situ* biodiversity, restarting the process of biodiversity colonization and accumulation within plantations. On the other hand, a “variable retention” method leaves mature palm trees during the initial conversion (usually every-other row), and then converts the rest after 5–10 years when the new crop has started fruiting (Fig. 6, “Variable Retention”). This incurs less severe disturbance and retains a more hospitable microclimate and vegetation structure that native species are more likely to utilize and traverse (Smith et al. 1997; van Kuijk et al. 2009). However, local FELDA managers complain that retained old palms can serve as disease and pest reservoirs, and the Malaysian Palm Oil Board advises against this method, citing disease and efficiency reasons (Corley & Tinker 2003; MPOB 2010). Nonetheless, smallholders often practice variable retention due to logistical, personal, and economic reasons, such as maintaining consistent fruit production and revenue streams over the rotational period (FELDA, pers. comm.). The biodiversity responses, yield effects, economics, and disease-related dimensions of variable retention regeneration should be a research priority, as currently available data suggest it may be a relatively easy method to reduce the severity of continued disturbances within plantations.

At the local scale, agricultural land with unmanaged understory can support greater plant diversity, including more weedy species that host additional associated biodiversity (Légère, Stevenson, & Benoit 2005). Our analysis of Koh’s (2008) data from managed plantations shows vegetation coverage increasing through time, yet this likely reduces floral diversity (De Chenon

& Susanto 2006). Thus, in young plantations where sunlight is abundant, allowing the understory to develop naturally by minimizing herbicide application may promote high floral diversity and abundance (see Appendix A). In old plantations, more research is needed to weigh the relative benefits of floral diversity and total ground vegetation coverage provided by managed understories.

Overall, these management suggestions echo the calls of other ecologists for careful spatial design of oil palm landscapes to minimize impacts on biodiversity (Koh, Levang, & Ghazoul 2009). However, we further this discussion by introducing another layer, the temporal scales associated with the oil palm lifecycle, which can be manipulated at both the field level (variable retention rotations) and landscape level (reduced field size and altering planting/rotation times; Fig. 6). Spatio-temporal landscape design should be integrated with improved management within plantations, and most importantly, traditional conservation efforts (HCVF, riparian corridors, et cetera) to improve the quality of oil palm landscapes for biodiversity.

Conclusion

Continued high intensity disturbances make oil palm plantations poor habitat compared to the stable forests they replace. These conditions likely present a barrier to sensitive rainforest species and oil palm should never be considered a substitute for natural forests. Ongoing conservation efforts should therefore continue to focus on slowing deforestation by limiting oil palm expansion to existing degraded areas, of which there are plenty (Koh & Ghazoul 2010). While oil palm plantations never regain the microclimate or vegetation structure of forests, specific habitat characteristics evolve following different trajectories, creating a heterogeneous habitat through time. Our discussion highlights several potential methods to utilize temporal habitat heterogeneity to create a higher-quality landscape matrix. Specifically, the oil palm matrix may be improved by (1) reducing field sizes and creating a patchwork of different aged plantations, (2) increasing connectivity by maintaining continuous tracts of same-age plantations through the landscape, and (3) minimizing the intensity of continued disturbances by using the variable retention method of rotating senescent plantations instead of clear cutting. These tools should be incorporated into landscape planning to improve the oil palm matrix quality, but cannot replace traditional conservation efforts.

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Figures

Figure 1: Major oil palm plantation lifecycle stages relative to forest, shown with stacked palm fronds and understory vegetation. Far left is a young, 8-year-old plantation with an open canopy with a mean canopy height of 4.3 m, the middle shows an 22-year-old plantation with a closed canopy and a mean height of 13.4 m, and the far right shows adjacent forest with mean canopy height of 24.8 m (forest height from Okuda et al., 2003). Initial site preparation including clear-cutting, terracing and planting of oil palm seedlings is not shown.

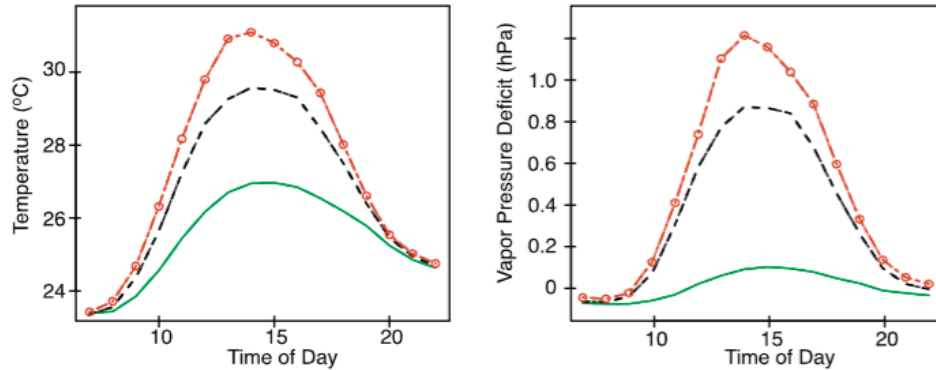


Figure 2: Map of sampling design. F = Forest, OP = Old Plantation, YP = Young Plantation, VR = Variable Retention Regenerating Plantation, CC = Clear-Cut. Top right photo shows a young plantation at 8 years since planting, the center right photo shows a 22-year-old plantation, and lower right photo shows a plantation being rotated using the “variable retention” method (22-year-old palms have been thinned and a new cohort planted 6 years ago).

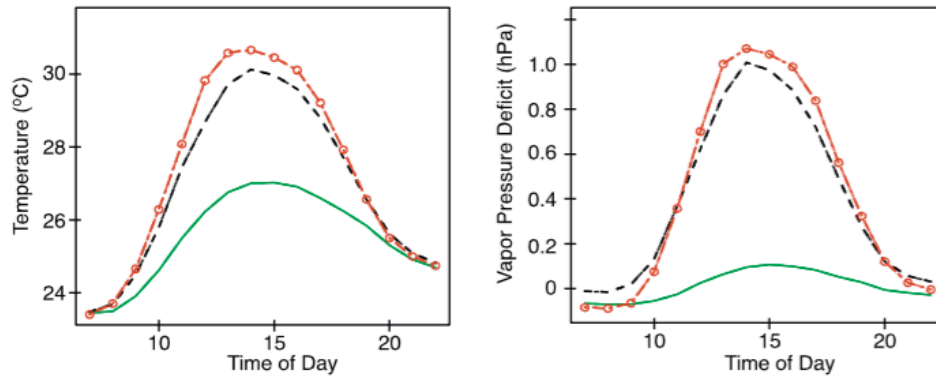


Figure 3: Microclimate conditions in forests and different oil palm plantations. Graphs on the left show temperature (degrees Celsius); graphs on right show vapor pressure deficit (hPa). Panel (A) shows young plantations are hotter and drier than old plantations, panel (B) shows plantations further from forests are only slightly hotter and drier, and panel (C) shows clear-cut sites are considerably hotter and drier than the “variable retention” method of rotating plantations.

(A) Forest (solid green), old (dashed black), and young plantations (red open circles)



(B) Forest (solid green), plantations at 100m (dashed black), and 1km (red open circles)



(C) Forest (solid green), variable retention (dashed black), clear-cut (red open circles)

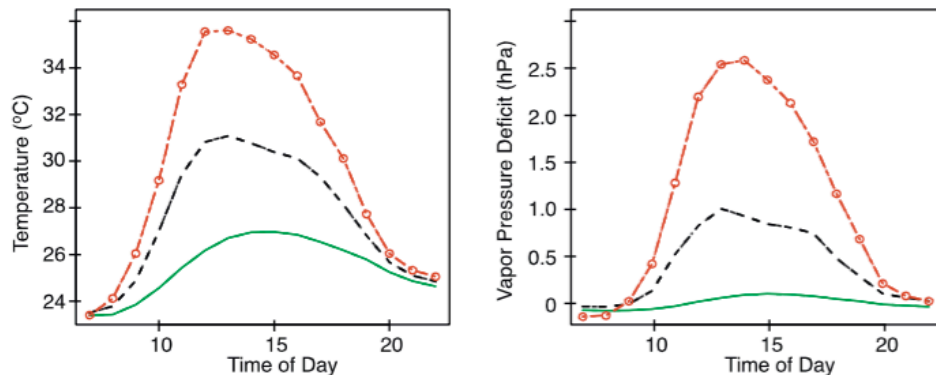


Figure 4: Vegetation structure of oil palms, ground vegetation and leaf litter in plantations. Young plantations are 8 years since planting, old plantations are 22 years since planting. Statistical significance between old and young plantations indicated by *** for $p < 0.01$, ** for $p < 0.05$, and * for $p < 0.10$.

Palm Structure	Young	Old	
Canopy Top (m)	4.31	13.38	***
Trunk Height (m)	1.31	9.63	***
Canopy Bottom (m)	2.21	8.17	***
Leaves Overhead	2.20	2.76	
Trunk DBH (m)	0.77	0.61	***
Trunk Surface Area (m ²)	3.16	18.49	***
Frond Stubs (per m ²)	30.82	19.42	***
Ground Structure			
Height Live Veg (cm)	21.77	11.46	**
Leaf Litter (cm)	9.84	20.61	**
Bare Ground Coverage	22%	22%	
Live Veg Coverage	46%	45%	
Leaf Litter Coverage	47%	47%	

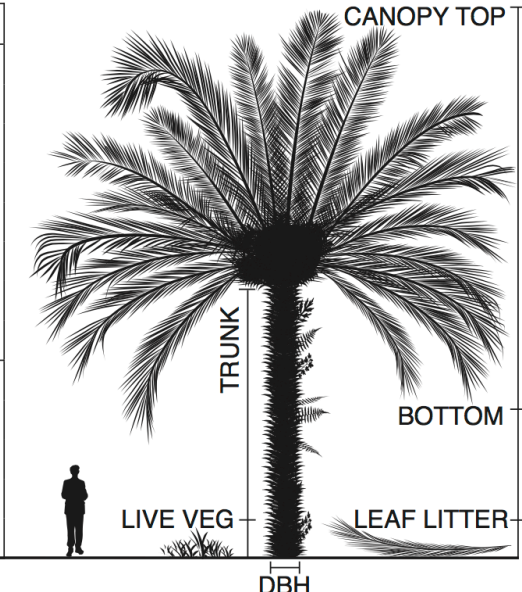


Figure 5: Diurnal microclimate changes over the oil palm plantation lifecycle relative to forest conditions. Points denote where data was collected, lines between points estimate interim conditions. Forest values are standardized to 0 (no change from natural conditions). Plantations are hotter ($^{\circ}\text{C}$) and drier ($+\text{hPa}$) relative to forests. VPD is shown offset 1-year back to differentiate overlapping points. In this scenario, forest is clear-cut in year -2 , oil palm seedlings are planted in year 0, and the senescing plantation is rotated by clear-cutting in years 25–30 (replanting not shown).

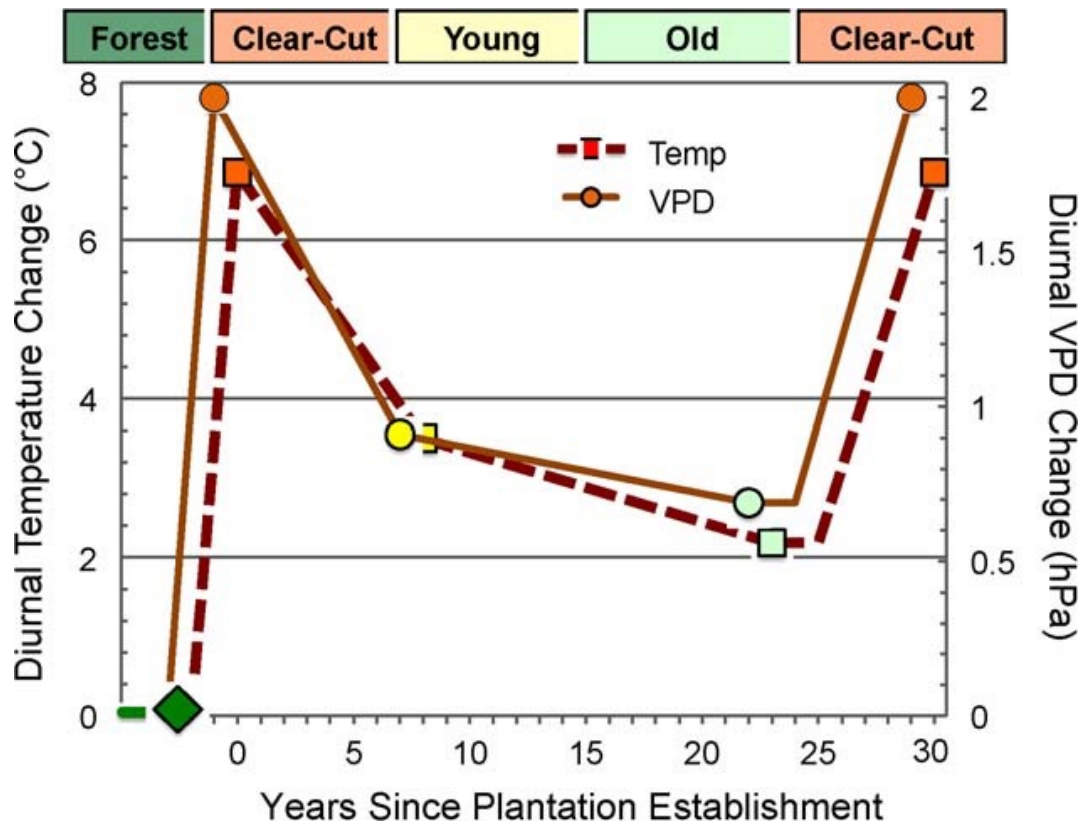
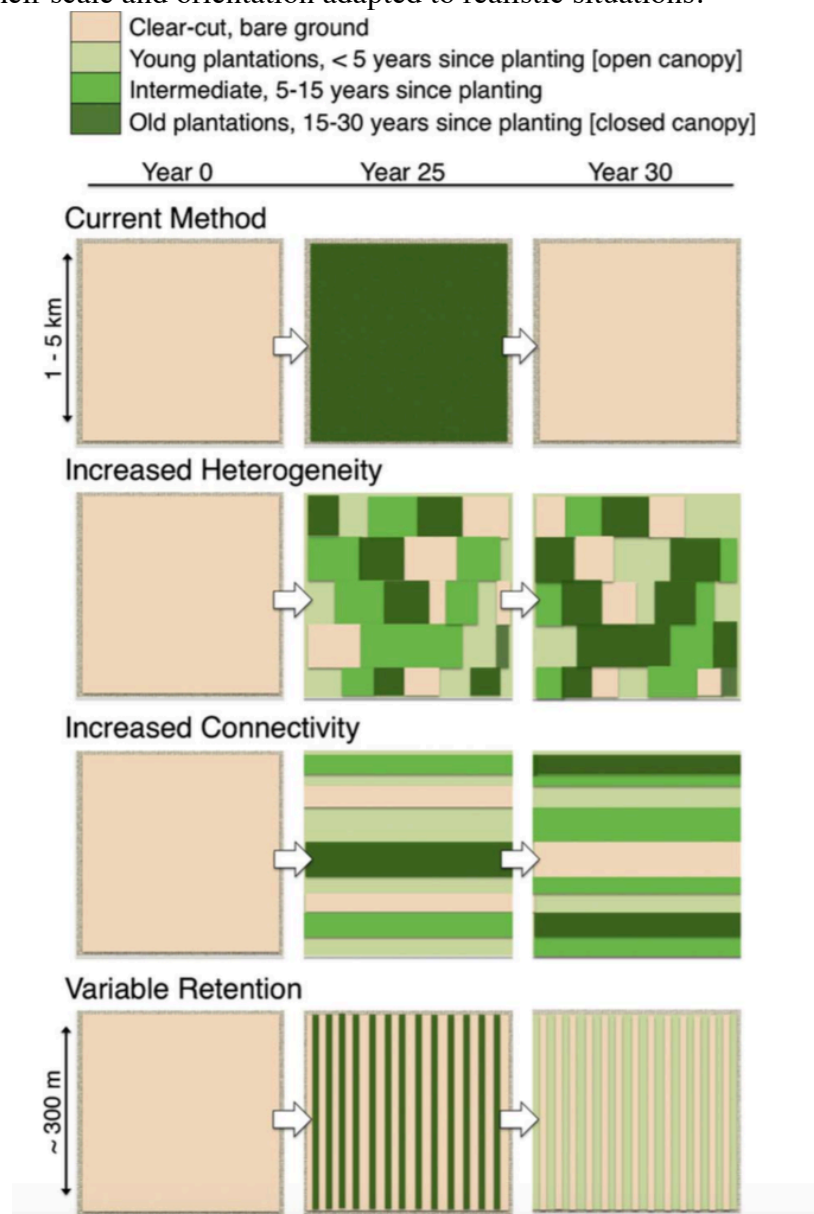


Figure 6: Conceptual models to increase field and landscape-level plantation habitat heterogeneity. The prevalent “Current Method” is to plant single-aged mega-plantations. This creates large tracts of monotonous habitat and periodic large-scale high-intensity disturbances during clearing and replanting. The “Increased Heterogeneity” scenario shows the same landscape when smaller patches of oil palm are planted at intervals. This creates a patchwork of different fields and reduces the area clear-cut at a given time. The “Increased Connectivity” scenario provides a continuous habitat-type (i.e. a closed canopy) between remaining forests by planting in successive strips. These “corridors” of continuous oil palm habitat can enhance forest species movement through the matrix. The “Variable Retention” of palms during crop rotation reduces the severity of disturbance. First, *every other row* is cleared and replanted after 20–25 years, and then 5–10 years later the remaining rows are replanted. These three methods can be combined and their scale and orientation adapted to realistic situations.



Tables

Table 1. Mean microclimate conditions in forest and relative differences (effect size) in plantations. Values show mean changes during the 12:00 to 18:00 time period. In the lower portion of the table, the relative difference of the latter category is shown (e.g. young plantations are +1.20 ° C hotter and +0.19 hPa drier than old plantations). Statistical significance between groups indicated by *** for $p < 0.01$, ** for $p < 0.05$, and * for $p < 0.10$.

	Temp (°C)	VPD (hPa)
Forest means	26.33	0.00
Forest vs	Mean Diurnal Plantation Effect Size	
All old and young	+2.84***	+0.80***
Old 100 m	+2.03***	+0.72***
Old 1 km	+2.34***	+0.66***
Young 100 m	+2.97***	+0.80***
Young 1 km	+4.03***	+1.02***
Variable retention	+3.18***	+0.73***
Clear-cut	+6.86***	+2.00***
Within Plantation Differences		
All: Old vs young	+1.20**	+0.19*
All: Near vs. far	+0.72	+0.09
Young: Near vs. far	+0.92	+0.22*
Old: Near vs. far	+0.31	+0.07

Table 2. Epiphyte density (number of individuals per m² of stem surface), total epiphyte abundance per tree, and mean size of each epiphyte (length from base to tip measured in cm) in 22-year-old and 8-year-old oil palm plantations. Statistical significance between old and young plantations is indicated by *** for $p < 0.01$.

	Epiphyte density (per m ²)		Epiphyte abundance (per plant)		Epiphyte length (per tree)	
	Old	Young	Old	Young	Old	Young
Fern	4.24	14.7***	78.40	46.45***	15.6	12.3
Climber	0.26	0.48	4.81	1.52	107.9	105.7
Leafy	4.09	5.55	75.62	17.54***	14.2	16.2
Grass	3.24	0.02***	59.91	0.06***	7.6	8.8
Palm	0.52	2.76***	9.61	8.72	27.5	15.1
Total	12.35	23.50***	228.35	74.26***	15.5	16.0

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Chapter 4

Accurately monitoring predators: Higher densities may not reduce the threat of extinction

Abstract

Accurately monitoring elusive predators is essential for their conservation but difficult because field studies often produce very little data with which to make inferences. Further, until very recently, the primary analytical approach employed for predators (capture-mark-recapture), was susceptible to underestimating home range sizes, which in turn leads to an overestimation of their population densities and sizes. To remedy these issues, in this chapter I develop a new approach to re-calculate density from previously published biased estimates by using larger animal movements. I apply this approach to a case study of critically endangered tigers in Sumatra (*Panthera tigris sumatrae*). I found that studies published before 2010 inflated tiger densities by 63.3% on average due to underestimating home range sizes. I was able to effectively control for this bias in subsequent analyses and then conducted a meta-analysis of all published density estimates, including new estimates I derived from camera trap arrays set across three expansive landscapes (843-999km²) that make up the UNESCO Tropical Rainforest World Heritage Sites of Sumatra. I found that tiger densities increased 4.2%/yr from 1999 to 2014 and primary forest densities are 58% higher than disturbed forests. I estimate there are 734 ± 304 Sumatran tigers within or connected to source populations with >50 breeding females. These results indicate that although ongoing deforestation has reduced the number of source populations on the island, but also that tigers may be increasing in well-protected forests. However, the success of anti-poaching programs should not obscure the importance of reducing forest loss and fragmentation in preventing the extinction of Sumatran tigers.

Introduction

Predators' role structuring food webs is vital to ecosystem health and biodiversity across a variety of biomes, providing strong incentive for their conservation (1). However, accurately monitoring dwindling populations of rare and elusive predator species has been an challenge for scientists (1)(2). This is because field studies often produce very little data with which to make inferences and analytical methods have been fraught with bias (3)(4)(5)(6). For example, until recently, many studies systematically underestimated predator home range sizes, which in turn caused densities to be inflated by over 30% (6) (7) (8). The general lack of accurate information has raised concerns that we are missing important thresholds or windows for their recovery and limits our ability to assess the success of previous conservation efforts (1).

Apex predators are notoriously difficult to study because they have low densities and travel very large distances to hunt and secure their territories (9). Fortunately, for some species individually distinctive markings (e.g. tiger stripes and leopard spots) allow for the use of invasive capture-mark-recapture (CMR) analyses. The primary method to collect data for CMR is to use noninvasive camera trapping arrays and analyze the sets of individual animal capture histories using hierarchical models that account for their probability of being detected (10)(11).

To get density from traditional CMR, the abundance is divided by the effective area surveyed (EAS), which is the camera trap array convex polygon plus a buffer width. The buffer width is derived from home range size, which CMR infers as function of the mean maximum distance moved (MMDM) for animals capture at multiple traps (11). Since it is unlikely traps are set at each animals home range boundary, and because detection probabilities are lowest away from home range centers, the MMDM approach has been shown to systematically underestimate buffer widths, leading smaller EAS and densities inflated by 20-60% (6). This finding indicate that predators may be more threatened than previously thought, with wide ranging consequences (1).

Over the last five years, spatially explicit capture-mark-recapture (SECMR) have been developed as an improvement on traditional CMR approach. A key advance in SECMR models is that the detection probability λ_0 , animal movement σ (also used to estimate home range size), and density are all estimated simultaneously in a single model, eliminating the use of subjective buffers (12). SECMR is considered substantially more accurate than CMR (mean values), albeit not necessarily more precise (wide confidence intervals) (6). In order to monitor predator population dynamics through time, a central goal of this chapter is developing a method to make comparisons between older estimates made with CMR and newer SECMR estimates. By standardizing results between CMR and SECMR studies, there are opportunities to conduct longitudinal analyses of population trends, and meta-analyses between sites, to understand the drivers of predator densities, evaluate protected area success, and develop the most appropriate conservation interventions.

I then apply this approach to tigers (*Panthera tigris*), which are Asia's apex predator and a focal point of decades of CMR and SECMR studies and conservation in the region (13). In order to conserve tigers requires understanding the drivers of their declines, but these often situation and remain unclear, as does the success of many existing protected areas (1)(7)(14)(15). For example, should a country- or park- focus on halting forest loss, poaching, or both simultaneously (15)? The remainder of this chapter seeks to address this question for the island of Sumatra, Indonesia, using the approach described above.

There is been special attention on preventing the critically endangered Sumatran tiger (*Panthera tigris sumatrae*) from going extinct as the Balinese and Javanese tiger sub-species did in the 20th century (16) (17) (18). Robust population monitoring is critical to identifying population strongholds, understanding threats, and designing effective Sumatran tiger recovery programs (2)(19). The conservation strategy is focused on maintaining a network of source populations in protected areas (PAs) that have >25 breeding females that "are embedded in a larger landscape with the potential to contain >50 breeding females" (13). Tiger monitoring programs aim to specifically track the individuals in source populations in PAs, which constitute the backbone of the global tiger conservation movement, as well as individuals occupying logged or fragmented forests outside PAs since these are important for regular gene flow and creating a network of metapopulations (13)(20)(21)(22)(23).

In this chapter, we estimate the density and abundance of critically endangered Sumatran tigers across the island. I implemented camera-trapping surveys and estimate density using SECMR methods for three source populations Sumatran tigers in UNESCO Heritage Site parks.

To account for the tigers traveling outside the forest, we included a “soft edge” to explicitly model tiger densities in primarily forested areas versus primarily non-forest areas. I also apply a multi-site pooled data approach to improve estimates of detection probability λ_0 and home range size σ . I sampled across large ($>800\text{km}^2$) landscapes to reduce the known bias from using smaller scale sampling protocols (6). Then I conducted a literature review of all published Sumatran tiger CMR studies and SECMR studies and extracted data relevant to how they estimated density. I manually re-calculated the effective study area for CMR studies, then applied a single buffer length derived from SECMR studies. This buffer value is substantially larger than derived using a $\frac{1}{2}$ MMDM approach, and thus lowered all the traditional CMR density estimates (6). Using the standardized set of densities, I conduct a meta-analysis to examine if there were longitudinal trends in tiger densities or differences relating to disturbance (*i.e.*, primary versus selectively logged forest) or forest type (*i.e.*, lowland versus hill forest). Finally, I combine the best density model results with the tiger distribution map and a detailed land cover map from the Indonesian government to estimate population parameters of the island-wide tiger population.

Methods

Study sites

We established camera trap networks at Gunung Leuser National Park (GL), Kerinci Seblat National Park (KS), and Bukit Barisan Selatan National Park (BBS) during 2013-2014 (Figure 1A). These national parks are the three largest in Sumatra and together constitute UNESCO’s “Tropical Rainforest Heritage of Sumatra,” which is nationally and internationally protected (24). The vegetation at all sites is wet evergreen tropical rainforests with a mixture of lowland and hill forests, and includes canopies dominated by the *Dipterocarpaceae* tree family that exhibits mast fruiting phenology. Rainfall is seasonal and ranges from 2500 mm to 4700 mm with temperatures between 22 - 35°C (Table 1). All sites are bordered by a mix of industrial and smallholder plantations of oil palm, rubber, rice, coffee, and cacao, in order of decreasing abundance.

Data collection

We used passive infrared camera traps set across areas of $\sim 500\text{km}^2$ in each park to collect information on tigers and prey species (Figure 1B). I deployed 90-100 cameras for a 2-3 month period of intensive sampling at each park (Table 1). Cameras were placed within pre-mapped 1.5km x 1.5km grids, and all cameras were spaced $>1\text{km}$ apart, except in three fragments. To increase detection probability and standardize deployment between teams, all cameras were placed along ridgeline wildlife trails at elevations 50-1200m asl (Table 1). Sampling was conducted at distances of 0-15km from forest edges into forest interiors, as well as in 11 forest fragments ridgelines remaining in the converted landscapes (Table 1).

We used a single camera at each trapping location. Using single cameras reduces the probability that all captured animals can be identified using both flanks, but with a sufficient number of captures, the two flanks can be analyzed separately as two samples of the same population or together with a pooled multi-site approach (39,(12). New cameras offer the ability to collect multiple photos per capture event (*e.g.*, sequences or videos), which increases the probability of recognizing non-flank-specific features (*e.g.*, facial, chest, legs, or tail markings).

As a result, we identified and analyzed both sets of flank photos together at GL and KS forests, while at BBS, right and left flank photos were analyzed separately.

Spatially-explicit density estimates

We used a spatial capture-recapture model to estimate the density of tigers in GL, KS, and BBS from our camera trap data (12)(26). I analyzed our models in a maximum-likelihood framework using the *secr* package in R (27). To overcome the limitation of small sample sizes, new approaches combine data from multiple sites or seasons of sampling to improve estimates of key parameters that are relatively consistent, such as movement (the σ parameter) and detection probability (λ_0). Though both movement and detection could be influenced by covariates like habitat type, our sampling protocol was highly standardized and our model fitting did not support the inclusion of habitat covariates for either parameter. The multi-site pooled analysis did allow us to evaluate models with sex and habitat (forest versus non-forest) covariates on density.

We combined data from all three study areas into a single model and compared different models using the AIC to test if σ and λ_0 were different for male and female tigers or between parks. Model selection did not support a model with a sex-specific σ or λ estimates so we used a single σ and λ_0 for all study areas. Our tiger σ value was 4.59 ± 0.95 km, which was similar to that found in other SECMR studies (mean $\sigma = 5.33$; 42). For BBS, we analyzed left and right flank datasets separately. To modeled densities in forest versus non-forest habitat and excluded water bodies (i.e., the Indian Ocean nearby BBS) using a recent land use map (IMoF 2011)

Meta-analysis of tiger density estimates

To compare our results with previous studies, we compiled all published density estimates and details of their study design and analysis approach (SM Table 1). For SECMR studies, we calculated the effective buffer length for a 95% the home range size ($2.45 * \sigma$ for density estimates using a half-normal detection probability distributions). To correct CMR estimates for their buffer and study area bias, we manually recalculated effective study area by digitizing published trapping grids using ArcGIS and adding a buffer of 11.24 km corresponding to the mean diameter of the 95% home range derived from SECMR studies and finally calculating effective study area as the grid MCP + buffer. I calculated density by dividing the estimated number of tigers by our standardized effective study area.

We constructed mixed effects models to evaluate the influence of specific study design and analysis variables on density estimates. The following variables were included: year, forest size, study area, deforestation rate, camera days, number of cameras deployed, tiger captures, the number of tiger individuals (M_{t+1}), effective study area, and the buffer length (SM Table 1). To avoid spatial or temporal pseudo-replication, we accounted for multiple estimates from the same tiger landscape by including a random effect for “landscape” in all analyses. Mixed effects regression models were constructed in R using the lme4 package (29). Model selection was evaluated with an ANOVA Chi-squared test, and model fit was evaluated by R^2 (Table 2, (30). To supplement the 17 density estimates from eight landscapes in Sumatra, we included six rainforest estimates from four parks in Peninsular Malaysia (SI Table 1, Figure 2B).

Population estimates

To estimate the total tiger population of Sumatra, we took the modeled density for each habitat type in 2014, and used also used the only published estimates for montane and peatland forests (0.30 and 0.45, respectively (43, 42). I identified tiger occupied forested areas following (29)(32), and mapped forest cover for 2010 using a high-resolution land cover map (30), Fig. 1, Table 4).

To estimate the population in source tiger landscapes, we defined source tiger landscapes as those with a large core forested areas ($>4000\text{km}^2$) likely holding >25 breeding females that are embedded within a forest landscape whose total forest area likely holds >50 breeding females (13). Tigers usually have sex ratios favoring females, and so we conservatively estimated the number of breeding female population as half the total population size based on forest cover (15). In defining tiger landscapes, we included forested areas that were $>100\text{-}4000\text{km}^2$ and within >20 km of the core forest because these are likely connected by regular dispersal events.

Calculating forest area and deforestation for the meta-analysis

For the meta-analysis, we used the forest area reported for studies whenever possible, and where this was not recent, we interpreted based on deforestation rates. we calculated deforestation rates based on remote sensing analyses reported in Joshi et al. (2016). This calculated the average forest loss per year in tiger landscape (including protected and unprotected forest) from 2002-2014. I used the single deforestation rate for the “Taman Negara – Belum” landscape for all connected areas in northern Peninsular Malaysia (e.g. the Temengor and Gunung Basor forest reserves).

Method to derive a buffers used in CMR studies

To derive density, traditional CMR methods use identified animals' capture histories to estimate detection probability and the number of individuals in a study area. To convert these numbers to population density, the number of animals is divided by the effective study area; the effective study area is estimated as the minimum convex polygon (MCP) around cameras plus a buffer (Karanth & Nichols 1998). Buffers are intended to recognize that animals captured may have a home range center outside the MCP. Buffer lengths are typically estimated as half of the mean maximum distance moved ($\frac{1}{2}\text{MMDM}$) for individuals detected multiple times, but full MMDM and the absolute maximum distance moved have also been used. These methods usually underestimate actual movement because it is unlikely cameras will capture an animal at the two furthest distances from its home range center.

Results

We camera trapped for 5759, 5246 and 3531 days in Bukit Barisan Selatan (BBS), Kerinci Seblat (KS), Gunung Leuser (GL) national parks, and our effective study areas were 911, 999, and 842 km^2 , respectively (Figure 1, Table 1). I obtained 50 independent captures of tigers across all three sites and identified 26 unique individuals. Density in forest habitat was estimated as 1.94 ± 0.91 tigers/ 100km^2 , 0.74 ± 0.65 tigers/ 100km^2 , 1.31 ± 0.81 tigers/ 100km^2 at BBS, KS, and GL, respectively. Densities in non-forest habitats were 0.56, 0.21, and 0.38 tigers/ 100km^2 for GL, KS, and BBS, respectively (71% lower than forest on average). The movement parameter σ for the combined dataset was 4.59 ± 0.95 km, corresponding to a 95% home range size of 397

km². Pooling data across sites was important for deriving density estimates from our limited number of recaptures. Without this, we would not have been able to estimate densities at Kerinci Seblat or Gunung Leuser.

In our meta-analysis of all tiger density estimates from rainforests, buffer lengths were significantly smaller in traditional capture-recapture (CR) studies (mean 6.30 km) than for spatially explicit capture-recapture (SECR) studies (mean 11.24 km, $p=0.0005$, Fig 2A). I found that tiger density estimates were negatively related to the estimated buffer length (e.g., Conditional $R^2 = 0.576$, F-statistic: 36.38 on 1 and 25 DF, $p<0.0001$; (33); Figure 2B). Therefore, we standardized all previous CMR and SECMR estimates by digitizing the published camera grids in ArcGIS, adding the mean SECMR estimate (11.24 km), and calculating the true effective study size. I refer to the corrected densities as $\hat{D}^*$ (Figure 2C). I found that originally reported CMR densities were inflated by an average of 63.3% (original mean 2.161 versus corrected mean of 0.794 tigers/100km², Welsh 2-sample t-test, $df=12$, $p<0.001$).

Using the standardized $\hat{D}^*$ from the meta-analysis, we constructed mixed models that account for multiple estimates from the same tiger conservation landscape and evaluated the effect of site and study design covariates using AIC model selection. The top model included disturbance (primary versus disturbed forest, the latter including fully and partially selectively logged areas), and year when sampling occurred (anova, $\text{Pr}(>\text{Chisq})<0.001$; conditional $R^2 = 0.352$; (33); Table 2). This model shows tiger densities in primary forests are 58.0% higher than disturbed forests and there has been mean annual density increase of 4.2% from 1999 to 2014 (Welsh 2-sample t-tests on model coefficients, $df=8$, $p=0.0173$ and $p=0.093$, respectively). To evaluate if these trends are unique to Sumatra, we added the six rainforest estimates from four parks available in Peninsular Malaysia and corrected the CMR estimates for effective study area using the same procedure (SI Table 1, Figure 2B). This led to the model predicting tiger densities in primary forests are 44.4% higher than disturbed forests and there has been mean annual density increase of 5.0% from 1999 to 2014 (Welsh 2-sample t-tests, $df=12$, $p=0.0098$ and $p=0.00767$, respectively). The following variables did not have support for including the models: size of forested area (Figure SI 1), effective study area (Figure 2B), habitat types (e.g. lowland versus hill forest, $p=0.126$; Figure 3B), or deforestation rate (Figure 3D).

To estimate the total tiger population size we multiplied the modeled habitat-specific densities by the extent of forest in each category for each tiger conservation landscape, based on the most recent landcover map from the Indonesian government (30). I report error as the mean standard error (se^A) for the proportion of standard error (se^A) on $\hat{D}^*$ (0.48) and also from the modeled density estimates ($se^B = 0.33$). This procedure led to a total 2014 adult Sumatran tiger population estimate of 1093 ($se^A \pm 524$ tigers or $se^B \pm 362$). By comparison, multiplying the general 2011 forest cover layer by the uncorrected mean of all Sumatra tiger density estimates (including CMR and SECMR studies), the naïve population estimate would be 1922 tigers.

Our analysis identified that only five of the eight previously defined source populations of Sumatran tigers currently meet the inclusion criteria described in (13). However, we also support Batang Gadis landscape being added as a source population (including the Barumon and Pasaman forested areas) because together it may contain >50 breeding females and is

experiencing comparatively little encroachment (<1% annual forest loss). Taken together, we consider that was a reduction from nine to six source populations. Bukit Tiga Puluh and Bukit Balai Rejang were downgraded because we estimate there are <50 breeding females and both have forest loss exceeding 2% annually. Kerinci North and Kerinci Central were merged because both face high forest loss (>2% annually) and selective logging, such that independently it is unlikely they contain >50 breeding females. Bukit Balai Rejang was added to the Bukit Barisan Selatan (BBS) landscape, which has robust enforcement in the national park and in the remote forested areas south of the park (<1% annual forest loss). Thus, we retained BBS as a source population even though there may be <50 breeding females because it is secured.

The islands source populations are now (1) the north half of Ulu Masen in Aceh province (100-200 tigers), (2) Gunung Leuser national park and southern half of Ulu Masen (150-250 tigers), (3) Batang Gadis landscape (50-150 tigers), (4) the northern half of Kerinci Seblat landscape (including Batang Hari; 100-200 tigers), (5) the southern half of Kerinci Seblat national park (100-200 tigers), and (6) Bukit Barisan Selatan landscape (50-150 tigers). I estimate the total 2014 island-wide source population at 779 tigers ($se^A \pm 373$ tigers; $se^B \pm 257$).

Discussion

Density and population size are crucial parameters for predator conservation and management efforts; our results represent a new standard in creating transparent, defensible estimates. For the purposes of conservation, we follow others in advising that animals in source be used for monitoring trends, and not the total population estimate (13). Our value of 779 tigers ($se^B \pm 257$) closely matches that reported by the IUCN assessment (mean = 670 tigers, range: 371 to 1273; (14)), but incorporates methodological advancements to facilitate a consistent, repeatable, and defensible monitoring program for the future. I also want to stress that any projection incorporates large uncertainty and assumptions, including homogeneity in prey in each habitat type, equivalent levels of poaching, and that forests considered occupied are actually still occupied. For Sumatran tigers, island wide occupancy study has not been conducted since 2009 (32). Thus, the precautionary principal should be applied when using population estimates for monitoring threat levels (i.e. the low end of the estimate range, which in our study is 406 tigers in source populations).

Our analysis of source populations indicates that deforestation caused the downgrading of four of the eight remaining Sumatran tiger populations as independent sources over the last decade. This was primarily caused by expansion of palm oil plantations that drove annual deforestation rates of >2% in the tiger conservation landscapes of Jambi, Riau, South Sumatra and Bengkulu provinces (34)(27). Further, non-forest tiger densities were 71% lower than forests and these are likely to be poached, supporting other studies indicating plantations contribute little to tiger habitat (36)(35). The fact that disturbed forest have 44.4% lower densities echoes other findings that primary forests are irreplaceable for biodiversity conservation (37) and logging should be avoided in important tiger landscapes (Fig 3A). I fear that the contraction and continued fractioning of remaining source populations has substantially increased the probability of extinction over the last decade.

The mean published Sumatran tiger density has decreased 63.3% since 2010 when the spatially explicit capture recapture analyses (SECR) became available (Figure 2; SI Table 2). If interpreted naively, this could indicate a sudden change and heightened extinction risk. However, our method of correcting pre-SECR estimates, followed by our meta-analysis, highlights the opposite trend: tiger densities in forests represented increased 4.2% annually from 1999-2014, while the mean deforestation rate in these forests was 2.9% from 2002-2014 (34); SI Methods A; SI Table 1). This indicates the density and actual tiger population in these core study areas increased during from 2001-2014, indicating conservation programs are effective at reducing poaching and modestly growing the tiger population in the core areas (38). However, sites represented in this study are thought to have comparatively higher tiger densities due to researcher sampling biases in favor known tiger occupied areas, larger forests, and protected areas with less poaching, disturbance, and encroachment. The presence of researchers themselves conducting camera trap surveys could be a strong deterrent for poachers. These biases, in addition to the downgrading of three source populations and the increasingly fractured structure of remaining sub-populations, still lends strong support the claim that the island-wide population declined from 2002-2014.

We echo recent recommendations that forest protection should be the primary focus in order to double the population and maintain long-term persistence of Sumatran tigers (27, (34)). Our study highlights support for the effectiveness of the source population strategy in growing tiger numbers, and fortunately, tigers have relatively high reproductive rates and dispersal capabilities, and persist in a range of forest and non-forest habitats (20) (7). A recent Sumatran-wide occupancy surveys confirms that tigers are present in many disturbed landscapes (31). Even if these landscapes are “population sinks” over long time horizons, those tigers still contribute to the total population size, genetic pool, and genetic connectivity (40). Moving forward, to prevent the last Indonesian tiger from extinction, we advocate increased pressure on curtailing Sumatra’s ongoing forest loss in order to retain the possibility that tigers could rebuild a robust meta-population.

The loss of apex predators threatens food webs by initiating trophic cascades, whereupon prey species are released from predation control (1). I show that tiger densities in disturbed forest are 44.4% lower than primary forest (Fig 3A), and the proximate drivers of this trend are likely higher prey abundances and reduced poaching (41). Sumatra’s fragmented forests may already be seeing the local and/or functional extinction of tigers; this could be resulting in trophic cascades, as evidenced by exceptionally high densities of wild boars (*Sus scrofa*) and pig-tailed macaques (*Macaca nemestrina*) in fragments (42). The ecological release of these generalist pest species causes severe damage to forest ecology and to local farms (42). Tiger presence and predation in forest edges and fragments has the potential to support tiger populations, buffer the impacts from trophic cascades, and reduce pest species and crop damage. This could represent a rare opportunity for a win-win scenario in conservation (32, 31). However, tigers living in fragments and non-forest habitat increase the threat of human-wildlife conflict, including livestock depredation or attacks on humans (44) 35). There is already a high rate of tiger attacks in Sumatra, and most of these occur outside of forests (36, 37). The survival of Sumatran tigers may depend on effectively mediating conflict in forest edges, fragments, and in the expansive forest-plantation habitat matrixes.

Finally, we hope an important contribution of this project will be the robust method of correcting biases in traditional mark-capture-recapture (MCR) studies by re-calculating the effective area sampled from the original study designs. I foresee our meta-analysis approaches becoming widely used to re-assess other species previously studied using traditional MCR approaches, and to draw inferences across sites.

Acknowledgements

Mathias Tobler helped with the analyses and Wido Albert helped conduct the fieldwork.

Figures

Figure 1: (A) 2010 forest cover in Sumatra, Indonesia, (B) close up of each study site with placement of cameras.

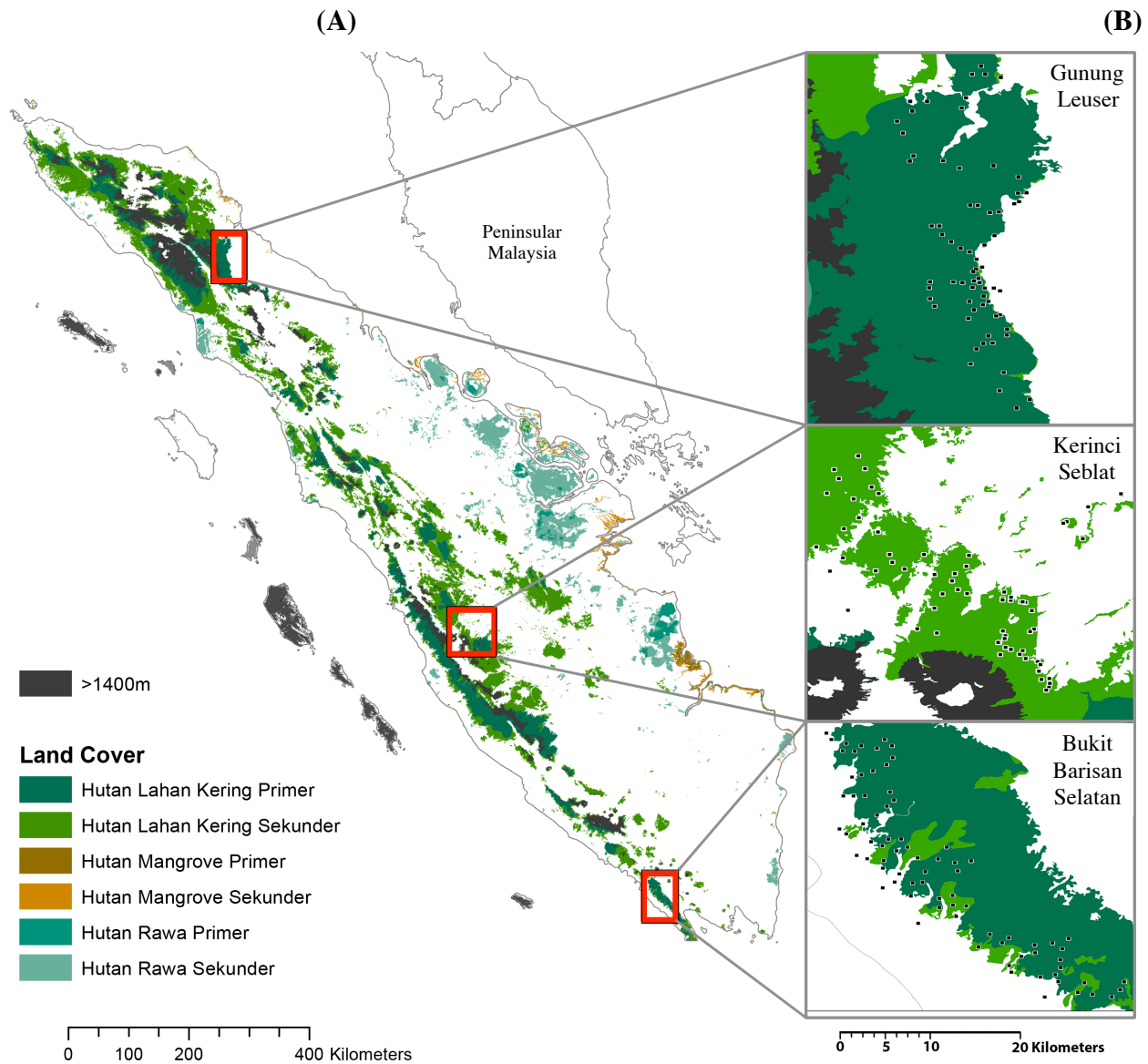


Figure 2: Tiger densities reported in rainforests as a function of the originally reported buffer length used to calculate the effective study area ($n = 27$ estimates from 12 forests (including Malaysian sites)). Data points denoted by the analysis method used to estimate density (CR = tradition capture-recapture, SECR = spatially explicit capture recapture). (A) shows originally reported densities, (B) shows recalculated CR densities based on new effective study areas using a standard buffer length of 11.24 km, and (C) shows corrected densities as a function of the originally reported density. Statistical tests are Welsh 2-sample t-tests of regression slopes in mixed model with a landscape random effect ($n=23$ estimates from 12 landscapes).

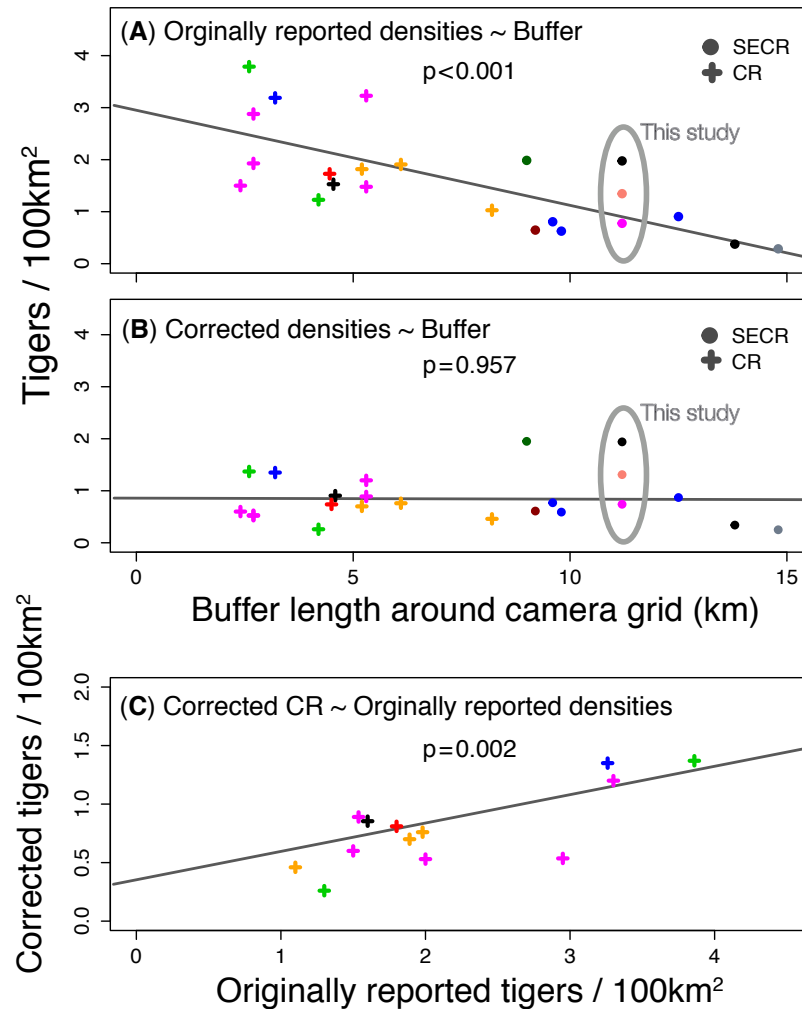
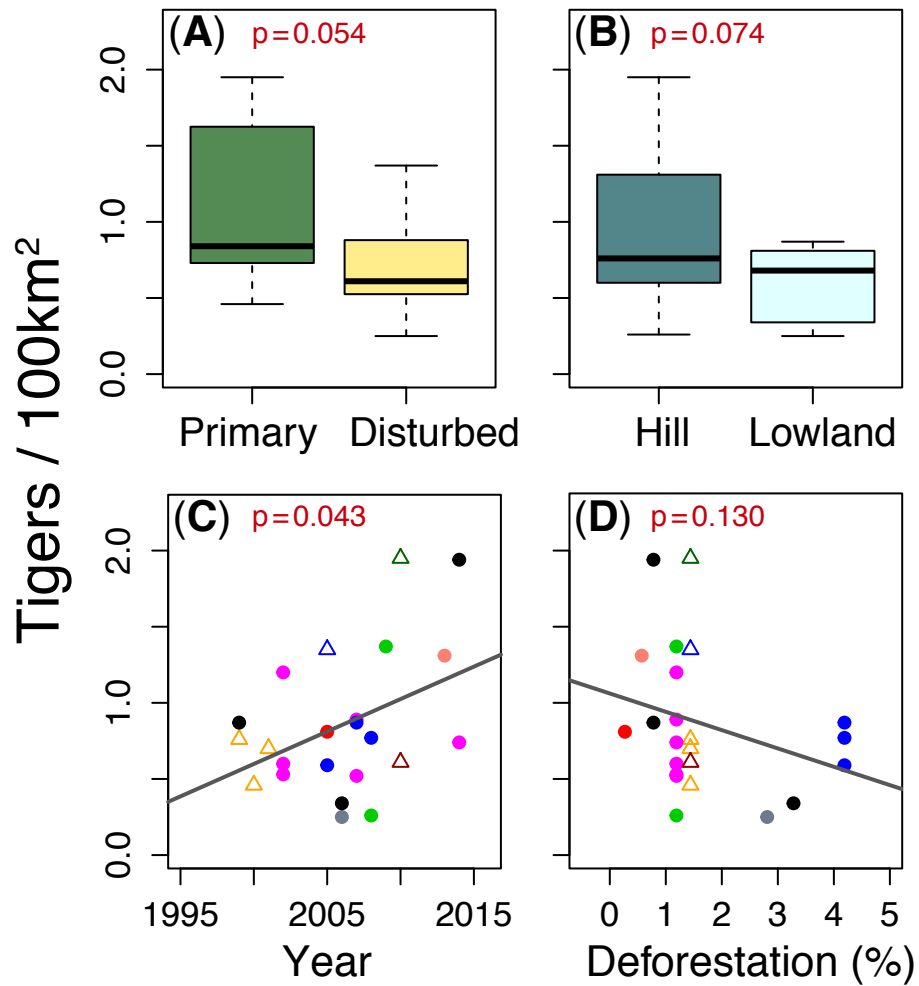


Figure 3: Tiger density comparisons after applying effective study area correction: **(A)** primary versus disturbed (secondary and mixed primary and logged forests; best mixed effects model coefficient t-test: $p = 0.0098$). **(B)** Lowland (mean elevation <400m asl) versus hill forest (>400m asl). **(C)** Year that sampling was conducted (best mixed effects model coefficient t-test: $p = 0.00767$). **(D)** Deforestation rate in the study area (methods in SI). All statistical tests are Welsh 2-sample t-tests in mixed model with a landscape random effect ($n=23$ estimates from 12 landscapes). In (C) and (D) colors correspond to site, circles show Indonesian study sites, and triangles show Malaysian study sites.



Tables

Table 1: Study sites, sampling effort and area, tiger captures, and human and prey activity in the three national parks that make up the UNESCO Tropical Rainforest Heritage of Sumatra where fieldwork was located.

	<u>Gunung Leuser</u>	<u>Kerinci Seblat</u>	<u>Bukit Barisan Selatan</u>
Sites characteristics			
UNESCO protected area (km ²)	8630	13753	3568
Contiguous forest 2010 (km ²)			
Rainfall (mm)	3000-4650	2500-3500	3000-4000
Data collection			
Cameras collected [lost]	69 [13]	73 [23]	78 [5]
Camera days	3531	5246	5759
Trap elevation (mean +/- SD)	313 +/- 248	614 +/- 197	369 +/- 185
Elevation covered (range in m)	27 to 882	256 to 1152	114 to 934
Start of 3-mo survey	December 2013	March 2014	July 2014
Number of fragments (cameras ⁺)	3 (4)	8 (24)	4 (4)
Tiger captures (individuals)	10 (5)	12 (3)	28 (10R, 8L)
Minimum Convex Polygon (MCP) km ²	516	813 ^z	474
Effective study area km ²	911	999	842
Capture frequency of humans and main prey species¹			
Human	2.10	2.37	1.96
Pig-tailed macaque (<i>Macaca nemestrina</i>)	8.40	20.58*	8.47
Muntjak deer (<i>Muntiacus Muntjak</i>)	3.00	3.99	7.00*
Wild boar (<i>Sus scrofa</i>)	5.00	12.08*	5.95
Bearded pig (<i>Sus barbatus</i>)	0.00	14.98*	0.00
Sambar deer (<i>Cervus unicolor</i>)	1.18	0.66	1.83*
Tapir (<i>Tapirus indicus</i>)	0.00	0.59	1.40*
All prey ²	27.6	71.1*	38.6
⁺ total number of cameras placed within forest fragments ^x core trapping area + 2.45*the σ movement parameter using the model excluding [*] significantly higher than the other two parks at the P<0.05 level using Wald test. ^z Highly irregular shape and uneven camera distribution due to sampling in distant fragments ¹ Capture frequency is the mean number of independent captures per 100 camera days. Independent capture events are photos separated by >30min intervals. Values shown are the mean of all cameras at each site. High values for pig-tailed macaques at Kerinci were due to larger number of cameras in fragments, where these generalists thrive. ² All prey includes animals shown, plus the following rare or smaller species: Argus (<i>Argusianus argus</i>), mouse deer (<i>Tragulus napu</i> and <i>T. kanchil</i>), serow (<i>Capricornis sumatrensis</i>), long-tailed macaque (<i>Macaca fascicularis</i>), pangolin (<i>Manis javanica</i>).			

Table 2: AIC model selection results for mixed model of covariates for 24 estimates of tiger density originating from 12 rainforest landscapes. Response variable is tigers/100km² after being corrected for different methods of estimating effective study area. Not shown is the random landscape effect in all models to account for multiple estimates from a landscape. The best model based on the lowest AIC value is bolded. Coefficients for this model are reported in Table 3.

response = tigers/ 100 km ²	Df	AIC	Chis q	Pr(>Chis q)
~ Primary_Disturbed	4	40.7		
~ Primary_Disturbed + Area_sampled	5	41.2	1.57	0.21
~ Primary_Disturbed + Forested_area	5	42.7	0	1
~ Primary_Disturbed + Country	5	42.7	0	1
~ Primary_Disturbed + Year_sampled	5	35.7	6.99	< 2e-16
~ Primary_Disturbed + Year_sampled + Forested_area	6	37.6	0.08	0.77
~ Primary_Disturbed + Habitat_type	7	42.2	0	1
~ Primary_Disturbed + Year_sampled + Habitat_type	8	38.2	5.96	0.015

Table 3: Mixed-effects model results of the best model explaining 24 estimates of tiger density originating from 12 rainforest landscapes. Response variable is tigers/100km² after being corrected for different methods of estimating effective study area. Not shown is the random landscape effect in all models to account for multiple estimates from a landscape. Coefficient estimates denote change in tiger density for disturbed sites (secondary and mixed primary and logged forests) relative to primary forest sites, and change per year, relative to 1999 when the first study was conducted.

	<i>Estimate</i>	<i>Std. Error</i>	<i>t-value</i>	
Fixed effects	<i>e</i>	<i>r</i>	<i>e</i>	<i>Pr(> z)</i>
(Intercept)	0.79	0.18	4.43	9.5E-06
Disturbed	-0.44	0.17	-2.58	0.0098
Year	0.050	0.019	2.67	0.0077

Table 4: Sumatra's forest cover and estimated tiger population in 2010. Predicted tiger densities described in text. Standard error (*se*) for tiger densities derived as the mean *se* from the 24 estimates in meta-analysis as a percentage of the estimate (0.4373). Forest cover information shown in black, tiger information shown in blue.

Tiger landscape		Montane (km ²)	Primary		Degraded		Total forest x1000	Tigers 2010	se (tigers 2010)
			Lowland & Hill (km ²)	Peat (km ²)	Lowland & Hill (km ²)	Peat (km ²)			
<i>Predicted density</i>		<i>0.300</i>	<i>1.34</i>	<i>0.89</i>	<i>0.90</i>	<i>0.45</i>			
¹	Gunung Leuser - Ulu Masen - Tana Karo	9318	14780	85	18619	1056	43.9	399	132
²	Batang Toru - Dolok Surungan - Parmonangan - Asahan	629	1462	0	4561	50	6.7	63	21
³	Batang Gadis - Barumon - Pasaman-Maninjau	1191	4070	40	5990	248	11.5	113	38
⁵	Senepis - Buluhala - Giam Siak Kecil -Kuala Kampar (KK) - Kerumutan (KER) - Bramitam - Berbak - Sembilang	0	0	2120	24	12369	14.5	75	25
⁶	Rimbang Baling (RB) - Tesso Nillo (TN) - Bukit Tiga Puluh - Bukit Betabuh / Bukit Sosa	28	1443	0	8071	411	10.0	94	31
⁷	Kerinci Seblat (KS) - Batang Hari - Bukit Kaba	3986	10642	0	12310	152	27.1	266	88
⁸	Bukit Dua Belas - Harapan Rainforest - Dangku	0	0	0	1300	11	1.3	12	4
⁹	Bukit Barisan Selatan (BBS) - Bukit Balai Renjang	1319	3058	0	2720	0	7.1	69	23
¹⁰	Way Kambas	0	0	0	0	450	0.5	2	1
Totals		16.5	35.5	2.2	53.6	14.7	122.5	1093	362

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Chapter 5

Subsidy cascades from oil palm alter forest tree dynamics

Abstract

There has been significant debate about whether herbivores are regulated from the “top-down” by predators or “bottom up” plant adaptations to limiting herbivores’ consumption including chemical defenses and infrequent fruiting. In altered ecosystems, such as forests fragmented by agriculture expansion, the widespread loss of predators is thought to be the main destabilizing force for herbivores. We use a landscape scale manipulation of agricultural resources adjacent to a 2500ha rainforest in Peninsular Malaysia to examine the role of bottom-up agricultural resource subsidies (palm oil fruits) in controlling herbivore populations. We found the forest density of a crop raiding species, wild boar (*Sus scrofa*), was >100 times higher when palm oil plantations were fruiting from 1996-2000 and 2007-2014 than when plantations were cleared and fruit was unavailable from 2001-2006. Using an 18-yr wildlife exclosure experiment and tree census of >200,000 small saplings monitored for 24 years, we show that this led to a 44% decline in sapling density and a 13% increase in diversity (Fishers Alpha). Our results provide evidence that the bottom-up effects from cross-border subsidy cascades can shape wildlife communities, devastate tree communities, and that higher saplings predation may favor rare species and lead to higher diversity at large scales (>1ha). Our results also suggest that predator loss and agricultural expansion can lead to combined trophic and subsidy cascades with heightened effects, and that this form of indirect cryptic forest degradation may be widespread in the region and globally.

Manuscript

There is growing body of research on how land use change can alter species interactions in remaining natural areas, potentially degrading ecosystems over long time horizons (Dirzo 2014). The focus has been on trophic cascades, the secondary effects following the loss of predators that cascade from the “top-down” through food webs (Estes 2011, Ripple 2014). There has been less attention on the “bottom-up” pathway whereby changes in the plant community can lead to secondary changes in the abundances of herbivores and predators. This could be important because the conversion of 40% of the world’s arable land to agriculture has widely increased wildlife access to cultivated foods (Ramankutty 2008). The subset of animals that forage in farmland or pastures clearly benefit from resource subsidies, but may alter normal food web dynamics when they return to natural areas (Polis 1998).

Ecologists remain unclear about whether the cross-border flow of animals and nutrients from cultivated areas initiates positive or negative “cascading impacts” in natural areas (Robb 2008). If subsidies support a keystone species that might otherwise be lost, such as seed dispersers or top predators, this may maintain ecosystem function or prevent trophic cascades (Fig. 1A, Polis 2004, Robb 2008, Luskin 2010). Alternatively, in areas where top-predators have already been locally extirpated, subsidies may amplify the ecological release herbivores or mesopredators (Prugh 2009). A key challenge is understanding how subsidy cascades operate

and whether trophic cascades and subsidy cascades interact in disturbed landscapes.

To evaluate the direction and magnitude of subsidy cascades, we took advantage of a landscape-scale natural experiment of palm oil agriculture subsidy additions and removal at the Pasoh Research Forest (PRF) in Peninsular Malaysia (Fig. 1). We monitored wildlife populations and tested for cascading impacts on vegetation using wildlife exclosures over 18 years, as well as tracking the fate of 423,000 trees for 24 years spanning the time before, during, and after palm oil subsidies were added. We tested whether palm oil fruit production explained wildlife dynamics in the forest, and if there were cascading effects from wildlife consuming subsidies for the forest tree community.

The natural resources available to wildlife are patchily distributed in space and time, so the effect of subsidy cascades should be greatest where and when wildlife populations are resource limited (Powers 2004, Robb 2008, Fryxell 2014). We hypothesized that the expansion fruit in palm oil plantations may buffer wildlife in Southeast Asia from “bottom up” resource limitation imposed by the regional mast fruiting dynamics. Naturally, forest fruit levels remain low for years and then during sporadic, punctuated supra-annual events the majority of tree species and individuals synchronously fruit (Curran 2000, Sun 2007). On the contrary, palm oil plantations produce fruit continuously for 20-25 years (Luskin 2010). This could be an important resource subsidy allowing a subset of species to increase, such as the native wild boar, *Sus scrofa*, an opportunistic omnivore and well-documented crop raider of palm oil (Fig 1A, Luskin 2014). Alternatively, if wildlife is not fruit-limited, but instead primarily controlled by predators, parasites, disease, or competition for non-fruit resources (e.g. nesting sites), then palm fruit subsidies would not increase wildlife abundances.

To investigate the link between wildlife and agricultural subsidies at PRF, we collected data on wild boar populations before, during, and after >95% (>15km²) of palm oil plantations surrounding the PRF where cleared and replanted (Luskin 2001). We used wild boar birthing nest density as a proxy for their populations, and estimated their density along transects located 1.5-2.5km from the forest edge. We found that variability in wild boar populations was primarily explained by palm oil fruit production in neighboring plantations (Fig. 2, $r^2 = 0.65$, $n=12$, $p<0.0003$). Wild boar populations also peaked concurrently with oil palm fruit production (>36-56 animals/km² and ~6.0 nests ha⁻¹ yr⁻¹ from 1995-1998). Wild boar dropped 100-fold when plantations were cut down and replanted from 2001-2004, then rebounded 100-fold when palm oil resumed fruiting from 2006-2010 (Fig. 1B). Alternative hypotheses to explain the wild boar fluctuations include natural fruiting cycles and release from predation (Ickes 2001). However, wild boar predators at PRF are primarily tigers, which have been locally extinct since the plot was established. Leopards and clouded leopards also remained exceedingly rare throughout the duration of the study (23, S2). While predators may have dampened the boar explosion at PRF, their role appears to be minor, either due to naturally low-densities as a result of territoriality, avoidance of forest edges, or due to poaching. Finally, the role of forest resources in shaping wild boar populations is strongly discredited because their population crash (2001-2002) coincided with a forest-wide “general mast fruiting” event from January-March 2002 (Fig S4).

The pronounced magnitude of the subsidy-driven ecological release of wild boars documented at PRF is likely due to perennial palm oil fruit subsidies that starkly contrasts the

infrequent mast fruit phenology of “bottom-up regulated” Southeast Asian forests. This is intensified by the enormous quantity of fruit that palm oil plantations produce; tropical forests’ fruit production generally averages $<1\text{Mg ha}^{-1}\text{ yr}^{-1}$ and palm oil plantations produce $>10\text{ Mg ha}^{-1}\text{ yr}^{-1}$ ha of fruit/ha (Curran and Webb 2000, Sun 2007, Butler 2009, Chave 2010). Palm oil’s disruption of the regional phenology is most immediately concerning in Malaysia, Southern Thailand, and Indonesian Borneo and Sumatra, where its growth has doubled to over $200,000\text{km}^2$ and covers $\sim 30\%$ of the lowlands (FAOSTAT 2014; Figure 1B). Palm oil is also expanding exponentially in Africa and Central and South America (FAOSTAT 2014).

The release of wild boars is likely higher than other large species because they efficiently convert resources into population growth. This is a social problem because wild boars cause substantial crop damage, and their movement increases the risk of spreading diseases to livestock, as well as zoonotic diseases to people (Ruiz-Fons 2008, Naranjo 2008, Boadella 2012, Luskin 2014). For example, in 1999, pigs were the primary vector for Nipah virus between forest bats and people in Malaysia and Singapore (Chua 2003). Strategies to control wild boars in that region, and globally, include limiting access to farmland resource subsidies through fencing or patrols and direct lethal management (e.g., culling). However, large-scale fencing and patrolling have logistical, ecological, and effectiveness issues, and may not be a desired component of a landscapes (Luskin 2014). Direct human control (e.g., through bushmeat hunting) is possible where crop raiders are easily hunted or are valuable for bushmeat. However, this is not the case in Peninsular Malaysia and Indonesia where the majority religion, Islam, and the Halal diet that its devotees follow, prohibits the consumption of wild boar (Luskin 2014). One incentive to increase direct lethal control of wild boar is trade to urban areas where there is demand from non-Muslim groups (Luskin 2014). This could improve forest conservation if managed carefully (Luskin 2014), or paradoxically could lead to defaunation if hunting is left unregulated (Dirzo 2014, Harrison 2016).

The secondary cascading impacts from subsidies are thought to be greatest for species with numerous direct and indirect food web associations (Terborgh and Estes 2010). Wild boars play important roles shaping tree dynamics through seed predation and their practice of uprooting or snapping sapling trees for nest construction (Fig 1A, Ickes 2001a, 2001b, 2005). To test the hypothesis that wild boar populations were impacting tree dynamics within forests, and to determine through which behaviors, we conducted an 18-year wildlife exclosure experiment at PRF. We monitored seven 49 m^2 fenced exclosures and 14 paired controls established 2.3km from forest edges from 1996 until 2014. This experiment was designed to isolate impacts from megafauna versus background environmental conditions or impacts from arboreal and small animals ($<1\text{kg}$). We posited that if control plots had lower densities across all understory tree size classes, this would indicate the importance of megafauna seed predation or inhibited seedling establishment (e.g., through soil disturbances). Alternatively, if only specific sapling size classes were reduced in control plots, this would indicate the importance of megafauna herbivory or physical damage. We found that saplings in the size class specifically preferred for wild boar nests were $220\% \pm 100$ more abundant in wildlife exclosures than controls (mean $\pm 1\text{SD}$, saplings sized $125\text{-}275\text{cm}$ height and $<2\text{cm}$ diameter at breast height, hereafter “dbh”; Fig. 3B, $n = 7$, t-test, $p < 0.01$). However, there were no significant differences for other size classes.

Next, we evaluated whether the cascading impacts on tree dynamics that we documented with exclosures were also important over larger spatial and temporal scales, and if the cascading impacts affected tree diversity. We analyzed data spanning 24 years and 435,591 trees within a 50-hectare forest dynamics plot at PRF. The 50-ha plot study area is located adjacent to the exclosure experiment and 1.5-2.6km from any forest edge. All tree stems over 1cm dbh were identified and measured during censuses in 1986, 1990, 1995, 2000, 2005, and 2010. Strengthening the exclosure results, we found that each census had progressively lower densities of saplings 1-2cm dbh, totaling a forest-wide 44% reduction after 24 years (Fig. 2C, t-test, $p < 0.01$). Sapling density loss was greatest for their preferred size class (1.0-1.5cm dbh) versus larger stems (1.5-2 cm dbh; Fig 2E, t-test, $p < 0.001$).

These results show that palm oil-fed wild boars can significantly alter tree reproduction >2km into forests. They also highlight the unusual importance of a reproductive activity, nest building, as opposed to direct consumption, in altering forest tree recruitment dynamics. This finding is supported by previous work at PRF from 1995-1998 that estimated boars removed a minimum of 1602 $\pm$ 516 (mean $\pm$ 1SD) saplings $\text{ha}^{-1} \text{yr}^{-1}$ for their nests and accounted for 25.4-58.9% of all sapling damage and mortality (Ickes 2005). The pronounced cumulative effects may be due to saplings remaining vulnerable to boars for decades while in the forest understory. Wild boar soil disturbances have been linked to the establishment of an invasive herbaceous species at PRF, *Clidemia hirta* (Fujinuma 2011). Wild boars are also a generalist omnivore and mesopredator and feed on a range of small vertebrates and invertebrates, likely suppressing numerous small animals in the forest understory (Bieber 2005). Finally, we fear that the greatest cascading impact may be through the exploitative competition associated with boars thinning the forest understory because this severely reduces food and habitat available to other terrestrial species.

Next, we asked whether the temporary removal of palm oil altered wild boars impact on the forest tree community. If wild boars remained present and readily substituted palm oil subsidies with forest resources when plantations were cleared, this could increase forest degradation. Alternatively, if wild boars vanished when the palm oil was cleared, forests could recover. To assess this, we evaluated whether boar damage changed when palm oil subsidies were removed from 2001-2006 by looking at the rate of sapling stems being snapped. We found that stem breakage decreased 22.28% compared to the mean breakage during the two census periods before and after clearing (t-test, $p = 0.0015$, Fig 1B, S4). This is supported by observations that wild boars were uncommon at Pasoh when plantations were cleared. There was no evidence of high mortality (e.g. no obvious presence of carcasses or skulls were found, which infers wild boars left area and did not stay and starve). The inversely correlated dynamics of palm oil trees and forest trees suggests that wild boars are mediating apparent competition.

Our final question was whether wild boar predation of tree saplings altered their sapling diversity. If wild boars act as 'normal predators' that selectively remove the most dominant species (e.g., through prey switching), rarer species will increase relative densities and overall diversity would increase, as measured by the Fishers Alpha metric. Alternatively, if wild boars are non-discriminatory in their destruction of saplings, Fishers Alpha should remain unchanged, or rare species will be lost due to sampling effects (Terborgh 2015). We found that at the 1ha scale, all measures of sapling 1-2cm dbh diversity increased, with the Fishers Alpha diversity

metric showing a 13.4% increase in diversity ($p=0.001$, Fig 4B). This supports theoretical models that predict that higher predation can increase local alpha diversity (Terborgh 2015).

Collectively, the case documented at PRF, and the greater significance of subsidy-driven cascades globally, serves as a warning that we are severely underestimating the net impact of agricultural-driven land use change on biodiversity, food webs, and ecosystem services. In particular, we demonstrate how the ecology of mixed landscapes can be affected by native wildlife populations being released from natural resource constraints from agricultural subsidies, particularly in naturally bottom-up controlled ecosystems. This can then trigger ecological cascades that devastate remaining habitats >2km from an edge. The result illustrates how native tree species that are spatially separated from cultivated crops (palm oil) can still be linked through apparent competition. Finally, we highlight how reproductive activities, and not seed predation or herbivory, can be the dominant mechanism perpetuating wildlife-driven cascades, and also shape diversity. To limit subsidy-driven cascades in Asia and globally, our findings echo prevalent calls to support planning for large-scale forest protection wherever possible (Gibson 2011, Phalan 2016). In lieu of expansive protected forests remaining in a landscape, we suggest new management techniques to limit wildlife access to agriculture subsidies. There are many options for new research to contribute to our understanding of agricultural subsidies' impacts on food webs in mixed-use landscapes and there is an urgent need for methods to mitigate subsidy-driven cascades in protected areas.

Figures

Figure 1: (A) Simplified food web with direct interactions (consumption) shown with solid arrows, indirect interactions (apparent competition) shown with dashed arrows. (B) Wild boar activities in forest and oil palm plantations. Left shows wild boars consuming forest tree seeds, middle shows them breaking saplings to build nests (background) and right shows them consuming palm oil fruits in plantations. (C) Area of plantation crop expansion in Malaysia and Indonesia from 1970-2012 (data from FAOSTAT).

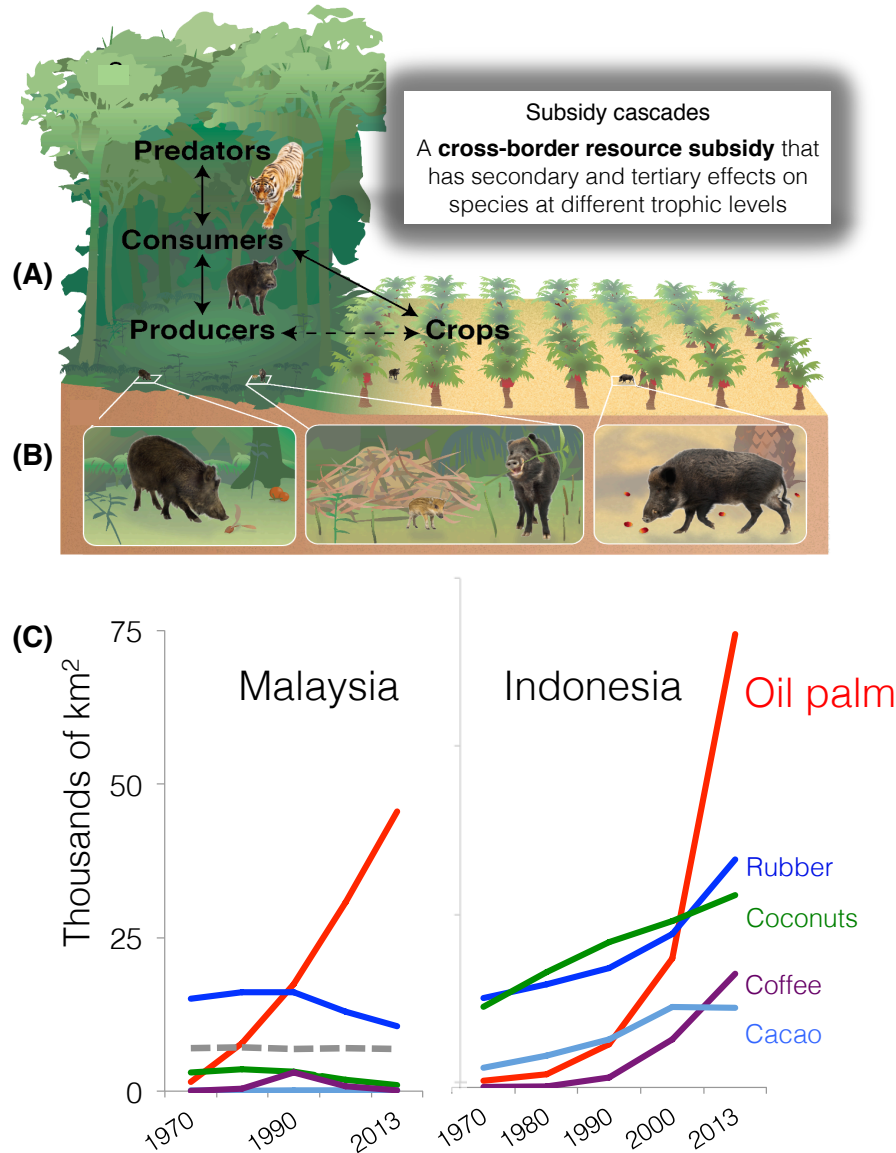


Figure 2: Palm oil fruit production, wild boar nests in forests from 1990-2013. Forest wild boar nests (shown on log scale) within the 50-ha research plot at PRF and yellow shows fruit production in plantations in tons/ha/yr (Table S1). During the study period from 1995-2014, oil palm plantations were cut down in early 2001, replanted in May 2004, and began fruiting again in 2006. The solid red line shows wild boar nests.

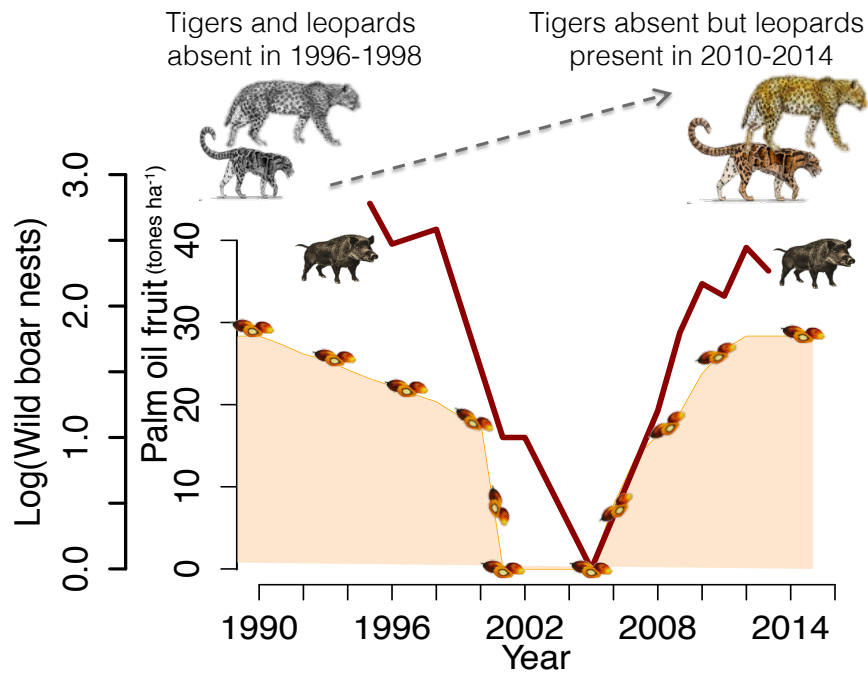
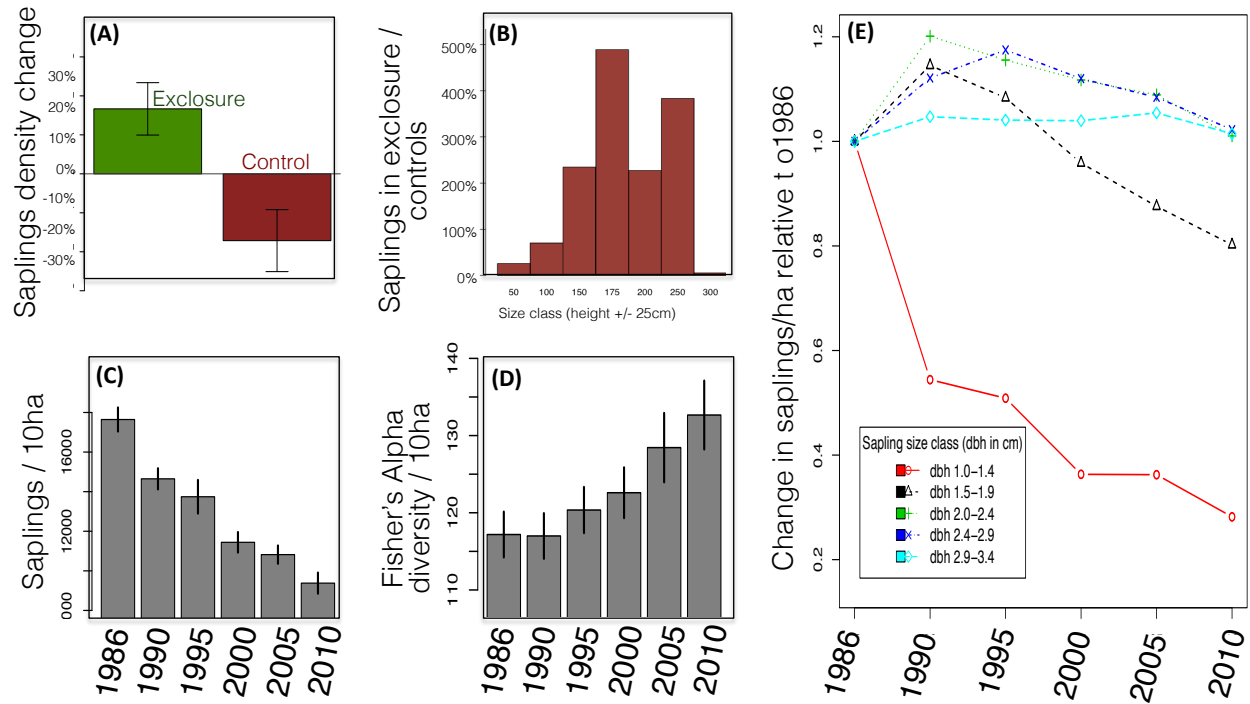


Figure 3: (A) Change in density of sapling from 1996-2014 in exclosures (green) and controls (red). (B) Relative abundance of saplings in 7 wildlife exclosures compared to 14 control plots after 18 years (1996-2014) based on size class. [Will re-do to show overlap b/w this and sapling sizes in nests] (C) Saplings 1-2cm dbh/ha in the 50 plot in each census. (D) Fishers Alpha diversity metric for saplings 1-2cm dbh/ha in the 50 plot in each census. (E) Size-specific change in sapling density over 23 years.



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Appendices

Methods

Study Site

The Pasoh Forest Reserve protects 13,000 ha of natural forest for timber production in the state of Negeri Sembilan in Peninsular Malaysia. Within the forest reserve is the 1840-ha Pasoh Research Forest (PRF; 2°58'47"N, 102°18'29"E), which is composed of 1,240 ha that was logged once in 1974 and protected since, and a central core research area of 600 ha of primary forest (SI Fig 1). Soils on hills are predominantly Ultisols, and the flats are Entisols (Amir Husni et al 1991). The PRF is hyper-diverse, aseasonal, humid lowland (80-130m asl) tropical forest, with the 40-60m tall canopy dominated by the Dipterocarpaceae family (Ashton *et al.* 1988). Dipterocarps are also notable for their phenology, whereby a majority of the tree species and adult tree individuals flower gregariously and fruit synchronously, a phenomenon known as general flowering and mast fruiting (GFMF; Medway 1972; Appanah 1985; Ashton *et al.* 1988; Sakai *et al.* 1999; Yasuda *et al.* 1999). GFMF events are triggered by the drought conditions associated with the ENSO climatic cycles and happen irregular multi-year intervals. Detailed site descriptions are provided in Okuda et al (2003).

The PRF is managed by the Forest Research Institute of Malaysia (FRIM) and there has been nearly continuous research at PRF since 1975 (Kato et al 1978). In 1985, a 50-ha forest dynamics plot (FDP) was initiated within the PRF primary forest area through a collaboration between FRIM and the Smithsonian Tropical Forest Research Institute's (STRI) Center for Tropical Forest Science (CTFS). The main FDP activities are locating, identifying, and measuring the size (diameter at breast height, or dbh) of all tree stems ≥ 1 cm dbh at five year intervals. The 50-ha FDP uses the same data collection procedures as dozens of other plots located around the globe as part of the Forest Global Earth Observatory (CTFS-ForestGEO; STRI 2016).

The PRF is bordered on three sides by monocultures of oil palm plantations that extend 4–10 km in each direction and forest on the fourth side (Figure SI 1, Sun et al 2007). The fourth side is connected to the Pasoh Forest Reserve production forest. A GIS study by Naoki et al (2001) reported for a 60km x 60km area encompassing Pasoh, forest cover decreased from 65.6% in 1976 to 36.3% in 1985, and then 29.4% in 1996. Oil palm increased from 4.9% to 20.6% over the same period, including completely bordering the PRF. The flat lowland areas immediately surrounding PRFs were cleared in 1970-1971 and terraced, and planted with oil palm in 1976-1978 (Manokaran et al 2004). Malaysia's largest oil palm developer, the Federal Land Development Agency (FELDA), operates the plantations using standard techniques advocated by the Malaysian Palm Oil Board (MPOB 2010). All plantations practiced identical 9 m x 9 m palm spacing in a triangular formation by offsetting every other row. Herbicides were periodically applied in plantations and ground- cover and epiphytes were otherwise left unmanaged unless they became obstacles to harvesting. No riparian areas or "High Conservation Value Forest" were spared and there was no significant inter-cropping. These monocultures were harvested for fruit from 1981-2001. In 2001, >95% of the plantations within a 2km buffer surrounding PRF were clear cut, and then replanted in 2003-2004, and began fruiting again in 2006. They have again been continuously harvested for fruit from 2016 through today.

Mammal community and hunting

More than 90 mammals (including rodents and bats), 166 birds, 489 ants, and 75 species of herpetofauna have been recorded at Pasoh (Okuda et al 2003). Both species of rhino and the gaur, *Bos gaurus*, were extirpated in early 1900s (Medway 1983), and the last elephants, *Elephas maximus*, were removed by the Malaysian Wildlife Department in the 1989 (SI Table 1). As of 1998, the effects of fragmentation and the hunting of muntjac and sambar deer left wild boar and the lesser mouse deer, as the only common terrestrial herbivorous or omnivorous species >1kg that was ever recorded with any frequency (Ickes et al 2001). However, hunting decreased markedly after 2006 and recent camera trapping has shown many larger wildlife species recolonized (e.g. Malayan sun bear, *Helarctos malayan*) but remain rare (TEAM 2016). It is notable that tapirs are now common and muntjac present.

Religious and ethnic customs shape hunting decisions and these follows similar patterns described by Luskin et al (2014) in Sumatra. The most important notes being that the Muslim majority adheres to a strict Halal diet and doesn't consume wild boar meat, but will opportunistically kill wild boar for pest control. The local Chinese minority actively hunts wild boars for meat using shotguns within plantations by spotlighting at night along the forest edges. All groups occasionally hunt muntjac and sambar deer for meat within forests. Unlike Sumatran oil palm landscapes or areas with high levels poaching, the use of snares is very uncommon, while the use of shotguns is widespread. Hunting increased (as judged by the number of shotgun being heard fired) from 2002-2006. This coincided with the local economic issues associated with the oil palm plantations being rotated. During this time, no income is gained from selling fruit bunches and the replanting process is expensive, particularly purchasing new high-yielding varieties. There are few other employment opportunities in the areas near PRF. Throughout the study period, there has been a healthy primate community despite light traditional blowgun hunting by the few *Oran Alsi* forest dwelling groups remaining in the area.

Wild boar methods

To compile the relative abundance index of wild boar nests in the CTFS-ForestGEO 50-ha plot between 1996 and 2014 we collected data in three separate ways, then standardized to 50-ha plot area. First, K. Ickes censused 25 ha of the 5-ha plot in 1995, 1996, and 1998 (described in detail in Ickes et al 2005). Then, from 2001-2006 when oil palm plantations were not fruiting and wild boars became rare, nest abundance in the entire 50ha plot was estimated in 2001-2002 and 2005 as part of a different project that required extensive fieldwork periods (e.g. Chen 2007, Sun et al 2007). S.J. Wright conducted three 1.5km transects for visual counts that corroborate the timing and magnitude of the wild boar decline in 2001, 2002, and 2003. After oil palm plantations resumed fruiting in 2006, I.F. Sun and his undergraduate field biology course counted all wild boar nests within 6m x 1000m strips within the 50-ha plot each July from 2008-2014. The total area surveyed during successive years was 12.44ha, 6.33ha, 4.38ha, 8.38ha, 3.048ha, 4.32ha, and 4.xx ha between 2008 and 2014, respectively. Wild boar nests decompose within a year so all estimates are independent (Ickes et al 2001).

50-hectare tree census methods

The FRIM and CTFS-ForestGEO 50-ha FDP plot was first censused in 1986/1987, 1990, 1995, 2000, 2005, and 2010. All free-standing trees and shrubs >1 cm in diameter at breast height (DBH; 1.3 m) are mapped to the nearest 0.5 m, measured to the nearest mm, and identified to species following. Condit (1998) and Losos & Leigh (2004) provide detailed explanations of the data collection methods.

The initial census included 335,347 stems belonging to 814 tree species, 294 genera, and 78 families (Kochummen et al. 1990). By 2010 a total of 435,591 total stems had been measured. In the initial 1986/1987 census there were 177,725 (53.00%) were in the 1.0-2.0 cm dbh “small sapling” size class (including dbh =1.0 and 2.0). Of this initial 1.00- cohort of small saplings, 54.68% survived until 2010, and those survivors’ mean dbh was 26.44 cm in 2010 (se = 0.00444, n= 97174), with a mean growth of 1.287 cm dbh / yr over the 23yr period.

To create a relative index of wild boar damage, we identified snapped but living saplings in the 50-ha FDP census data, which is primarily caused by wild boars snapping saplings for their nests (Ickes et al 2004). Specifically, when stems >1cm dbh in a census one were broken, the dbh in the next recensus were marked 0 cm, but the tree was also evaluated to be dead or alive. If the same stem regrew it could re-enter >1cm dbh it would reenter the next re-census, or if a separate new resprouted stem grew to be >1cm dbh, this was recorded as a separate stem (Manokaran et al 2004).

Wildlife-exclosure experiments

To test experimentally the impact of wild boars on the plant community, eight 49m² exclosures were constructed in 1996 in primary forest immediately adjacent to the 50-ha FDP. To slow decomposition the posts were made from solid 4in x 4in x 2.5m dipterocarp timber, and enclosed with a 1.5m tall heavy gauge 4cm² mesh metal chain-link fencing. To ensure that pigs did not root under the fence, up to four rows of barbed wire encircled each fence, from ground level to 60 cm in height. Exclosures were open above. Because of this open-top design and the wide mesh size, it did not appear that the exclosures altered light, wind speed, rainfall or other microclimate conditions. However, only large (>1kg) animals that were strictly terrestrial would have been excluded. Until 2006 this was thus primarily only excluding wild boar and lesser mouse deer, and after 2006 this would have also excluded the rare tapir, muntjac, sambar, or porcupine. More detailed description provided by Ickes et al (2001). Two control plots were paired with each exclosure in a block design. These were placed 1m outside of the exclosures on the two sides that subjectively most closely resembled the vegetation structure within the paired experimental plot in 1996.

All woody free standing stems (including lianas) >30cm height were tagged, identified and measured in 1996 and 1998 in a 25m² area within exclosures (n=8) as well as in 25m² paired control plots (n=16) in August-September 1996 and August 1998. In August 2014, seven of the eight exclosures remained effective and all stems >30cm were censused in the exclosures. An equivalent total of 25m² was measured in the 14 controls adjacent to seven remaining exclosures. Identical 12.5m² portions of both controls were censused at each exclosure. Additionally, in 1998 only, all seedlings of woody plants < 30 cm tall were also counted but not identified in 1m² plots

in the corners of the eight 25m² experimental and 16 control plots. In 1996 and 1998, plant species were identified by K. Ickes, primarily based on prior identification of species for the 50-ha permanent plot at Pasoh. Unknown species were collected and identified at the herbarium of the FRIM with assistance from herbarium staff and visiting specialists. The recruits into the 2014 census have not been identified and thus diversity is not reported for exclosure data, only for the 50-hectare tree census.

There were 3223 total tree and liana stems measured in exclosures and controls, 1414 in 1996 and 2236 in 2014. Of the sapling-sized stems (height 30-300cm), 80.8% were trees in 1996 and 79.0% were trees in 2014. The relative abundance of trees in exclosures was 81.9% of stems in 1996 and 82.0% of stems in 2014. There was an absolute abundance increase of 83.9% for trees and 90.2% for lianas, but the increase was significantly different. The relative abundance of trees in controls was 79.7% in 1996 and 74.7% of stems in 2014. There was an absolute abundance increase of 14.6% for trees ($p>0.10$) and 62.7% for lianas ($p<0.01$). The controls and exclosures gained both increased their abundances seedlings and saplings (30-300cm height, 0-0.25cm dbh) from 1996 to 2014, likely due to the temporary absence of wild boars from 2001-2006 when palm oil plantations were removed. Nonetheless, abundance changes were higher in exclosures than controls for all stem size classes <4m height and <2cm dbh (SI Figure xx). A likely rationale for the relative increase in lianas in control plots is their being comparatively difficult for wild boars to break for their nests.

To compare exclosure and 50-hectare results requires examining dbh. The total number of tree saplings 1-2cm dbh in all exclosures rose 58.1% and in controls decline 81.4% from 1996 to 2014. This is larger decline in controls than reported in the 50-hectare plot over the entire 24-year period (Figure 3B). A likely explanation is local displacement wild boar use of saplings from exclosures to adjacent controls. This is supported by the fact that wild boars uprooted or snapped 53% of all free-standing woody plants >70 cm tall and <2.0 cm dbh in the immediate 250m² area around their nest (~9m radius; Ickes et al. 2005). Thus, the inability to access 49m² area in exclosures could significantly increase extraction from nearby control plots.

There were 287 trees 30-300cm tagged in exclosures in 1996 that survived and were re-measured in 2014. Using this subset of stems, we calculate that the average growth of tree saplings was 104.34cm from 1996 to 2014 (Figure SI XX). Based on this rate, the mean time for a 30cm seedling to grow to 249cm, the mean height of for 1cm dbh stems entering the 50-hectare tree census, is 49.8 years (Figure SI XX). For stems that were snapped but alive in 1996 at the onset of the exclosures, their growth rate was 18.74cm (18.0%) lower than un-snapped stems over the 24-year period.

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Figure 1: Top shows study site within Southeast Asia. Bottom shows the Pasoh Research Forest, CTFS 50ha plot location, and exclosure (east of the plot).

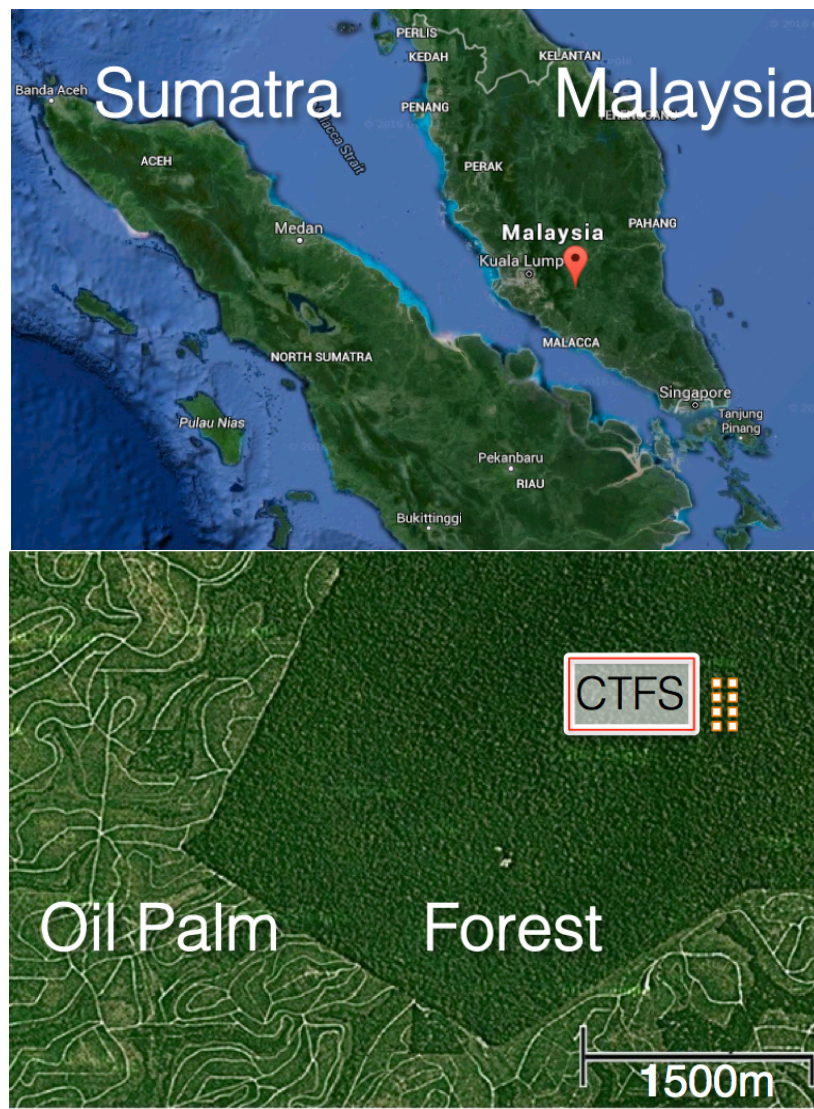


Figure 2: Exclosure results from the Pasoh research forest (n=7). Lines show standard errors.

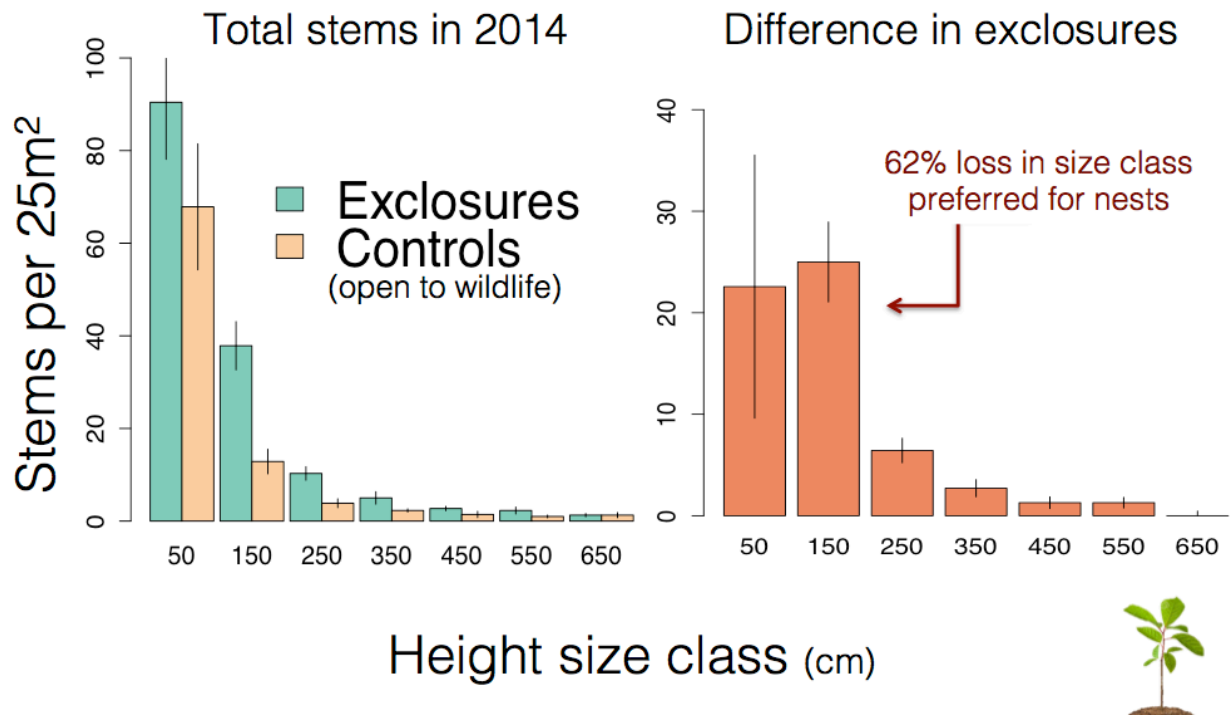


Figure 4: (A) Sapling dbh to height comparison for trees in control plots in 2014. Orange lines show mean height at 1cm dbh (height = 249cm) whereupon saplings enter the 50-ha tree census data. (B) Sapling growth based on starting height for tagged stems in exclosures that survived from 1996 to 2014.

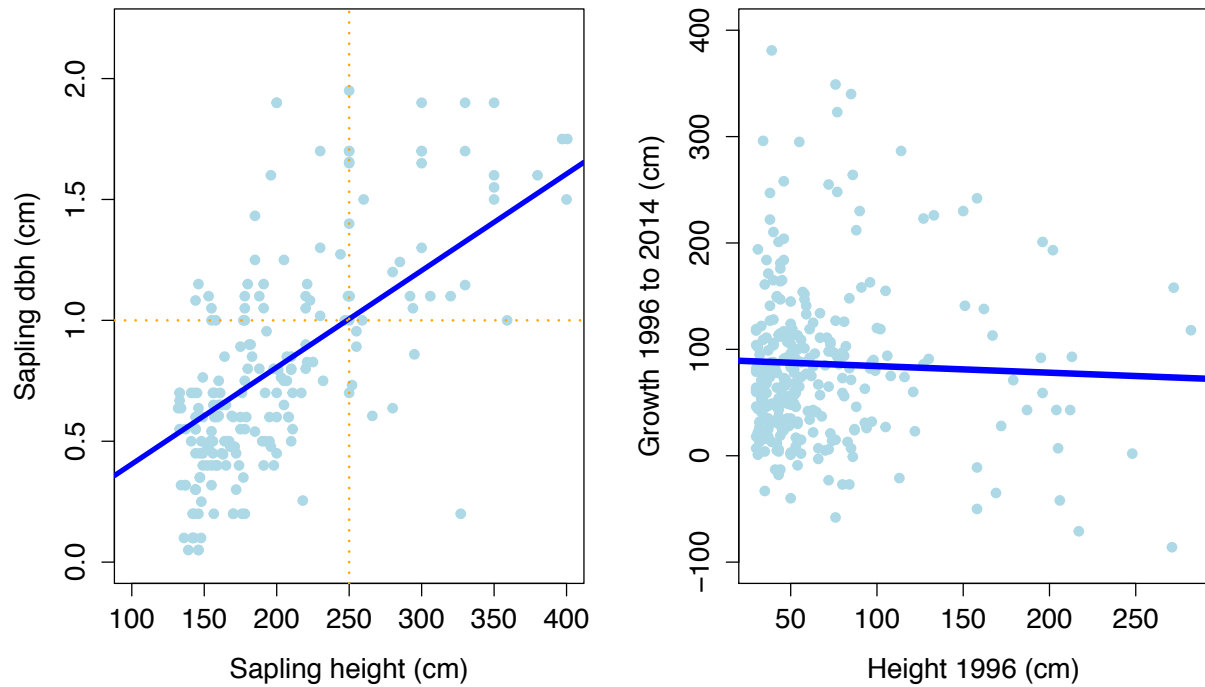


Table 1: Wildlife species in the PRF in 1986 and 2010.

Species	Status in 1986	Status in 2010
<i>Large herbivores/omnivores (>100kg)</i>		
Asian elephant (<i>Elephas maximus</i>)	Extinct	Extinct
Javan rhinoceros (<i>Rhinoceros sondaicus</i>)	Extinct	Extinct
Tapirs (<i>Tapirus indicus</i>)	Absent	Uncommon
Sambar deer (<i>Rusa unicolor</i>)	Absent	Rare
Sumatran rhinoceros (<i>Dicerorhinus sumatrensis</i>)	Extinct	Extinct
<i>Medium herbivores/omnivores (10-100kg)</i>		
Muntjak/barking deer (<i>Muntiacus muntjak</i>)	Rare	Uncommon
Bearded pig (<i>Sus barbatus</i>)	Extremely rare	Extinct
Malayan sun bear (<i>Helarctos malayan</i>)	Absent	Rare
Pangolin (<i>Manis javanica</i>)	Unknown	Extremely rare
Wild pig (<i>Sus serofa</i>)	Common	Hyperabundant
<i>Small herbivores/omnivores (<10kg)</i>		
Lesser mouse-deer (<i>Tragulus kanchil</i>)	Common	Common
Greater mouse-deer (<i>Tragulus napu</i>)	Absent	Extremely rare
Malayan porcupine (<i>Hystrix brachyura</i>)	Rare	Common
Binturong (<i>Arctictis binturong</i>)	Extremely rare	Extremely rare
Pangolin (<i>Manis javanica</i>)	Extremely rare	Extremely rare
Brush-tailed porcupine (<i>Atherurus macrourus</i>)	Extremely rare	Extremely rare
<i>Large predators (>10kg)</i>		
Tiger (<i>Panthera tigris</i>)	Extinct	Extremely rare*
Clouded leopard (<i>Neofelis nebulosa</i>)	Absent	Extremely rare
Leopard (<i>Panthera pardus</i>)	Absent	Rare
Dhole (<i>Cuon alpine</i>)	Extremely rare	Extremely rare
Marbled cat (<i>Neofelis marmorata</i>)	Extremely rare	Extremely rare
<i>Small predators (<10kg)</i>		
Leopard cat (<i>Prionailurus bengalensis</i>)	Unknown	Common
Yellow-throated marten (<i>Martes flavigula</i>)	Absent	Extremely rare
Short-tailed mongoose (<i>Herpestes brachyurus</i>)	Unknown	Extremely rare
Flat-headed cat (<i>Prionailurus planiceps</i>)	Unknown	Extremely rare
<i>Primates</i>		
Pig-tailed macaque (<i>Macaca nemestrina</i>)	Abundant	Hyperabundant
White-handed Gibbon (<i>Hylobates lar</i>)	Common	Common
Banded Leaf Monkey (<i>Presbytis melalophos</i>)	Common	Common
Dusky Leaf Monkey (<i>Presbytis obscura</i>)	Common	Common
Long-tailed macaque (<i>Macaca jascicularis</i>)	Unknown	Uncommon
Siamang (<i>Hylobates syndaetylus</i>)	Rare	Rare

*One confirmed presence of a tiger in 2007, which lasted <1 month.

Table 2: Sapling breaks or deaths 1-2cm dbh per hectare within the 50ha plot (n=50 per census), with results standardized to inter-census duration.

Census	Breaks or deaths / ha
86-90	344 +/- 18.63
90-95	377 +/- 10.20
95-00	460 +/- 22.54
00-05	366 +/- 20.53
05-10	355 +/- 10.86

Table 3. Sapling fate in each census period as a percent of saplings in starting census period, with results standardized to inter-census duration.

Census	Breaks or deaths	Remained in 1-2 cm dbh	Grew to >= 2 cm dbh	Total stems per subplot
86-90	0.15 +/- 0.008	0.56 +/- 0.015	0.29 +/- 0.013	2823.24 +/- 76.44
90-95	0.16 +/- 0.004	0.69 +/- 0.023	0.16 +/- 0.005	2344.14 +/- 67.83
95-00	0.21 +/- 0.010	0.66 +/- 0.026	0.13 +/- 0.005	2199.84 +/- 80.67
00-05	0.20 +/- 0.011	0.60 +/- 0.023	0.19 +/- 0.006	1819.84 +/- 62.31
05-10	0.20 +/- 0.006	0.63 +/- 0.024	0.17 +/- 0.005	1733.12 +/- 49.93

Chapter 6

Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia

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Abstract

The ongoing expansion of plantation agriculture has changed the ecological, demographic, and social conditions of Southeast Asia's forested areas, yet little is known about hunting practices in these novel landscapes. Using information from 73 in-depth interviews with hunters, agricultural workers and wild meat dealers in the Jambi province of Sumatra, Indonesia, we describe contemporary hunting practices, including how hunting methods, wildlife harvest and consumption rates vary between different indigenous and immigrant ethnic groups. Hunting is now primarily a commercial endeavor for harvesting wild boar (*Sus scrofa*) meat; over 7500 wild boars were sold in Jambi City alone in 2011. The Muslim majority avoids wild boar for religious reasons, but there is substantial local and export demand driven by Chinese and Christian Batak. We conclude that hunting within oil palm plantations may reduce crop damage from wild boar and also yield large amounts of wild meat with relatively little by-catch of threatened animals.

Keywords: Wildlife harvest; Bushmeat; Tropical rain forest; Human-wildlife conflict; Palm oil; Rubber; Wild boar (*Sus scrofa*); Livelihoods; Jambi; Southeast Asia; Sustainable hunting

Introduction

Southeast Asia's forested regions are undergoing a period of rapid environmental and social change, largely driven by plantation agriculture (Sandker *et al.* 2007; Bradshaw *et al.* 2009; Sayer *et al.* 2012). Socially, there are higher population densities made up of a diverse set of immigrants (Hirawan 2011). Economically, livelihood options are now largely market-based rather than forest or subsistence-based (Rigg 2006). Ecologically, forests have been reduced in area, fragmented and often also disturbed (e.g. selective logging), with myriad cascading effects on the remaining floral and faunal communities (Sodhi *et al.* 2004). These changes occur in inter-connected ways and coalesce to shape new human-environment relations, one of the most direct articulations of which can be seen through hunting practices.

To date, most research on hunting in Southeast Asia has focused on traditional peoples with forest-based livelihoods living in areas with extensive forest cover (Caldecott 1988; Rye 2000; Robinson and Bennett 2000; Corlett 2007; Pangua-Adam *et al.* 2012). However, as 'new

frontiers of land control' emerge, including plantation agriculture development, they bring with them a complex array of political, social and cultural changes (Peluso and Lund 2011). These changes are often manifested in changing patterns of access to, and use of, forest resources (Cramb *et al.* 2009; Fox *et al.* 2009). Despite this, research has only begun to explore hunting conditions in developed plantation landscapes that now dominate the region. For example, Pangau-Adam *et al.* (2012) recently described the emergence of commercial hunting practices following new oil palm plantation establishment in Papua, Indonesia. Building on this work, in this paper, we describe hunting practices across a variety of indigenous groups (i.e. groups that historically have lived in a region), as well as immigrant ethnic groups, in extensively developed agricultural landscapes in Sumatra, Indonesia.

Two plantation crops, oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*), dominate recent agricultural development in Southeast Asia and drive the world's highest deforestation rates in the region (Achard *et al.* 2002; Koh and Wilcove 2008; Gibbs *et al.* 2010; FAO 2012). Both oil palm and rubber are labor-intensive to cultivate, harvest, and process, and require larger labor forces than are usually available locally (Sayer *et al.* 2012). In Indonesia, the large-scale immigration that regularly accompanies plantations is often encouraged by government transmigration programs (Hirawan 2011; Li 2011). Further, even where sufficient labor is locally available, immigrants are often preferred by companies who seek an easily disciplined labor force (Li 2011). Developed plantation landscapes are thus often associated with large-scale demographic change (Sandker *et al.* 2007; Cramb *et al.* 2009; Hirawan 2011).

Parallel to biophysical and demographic changes, wildlife communities (e.g. species composition and relative abundances) are also changing in plantation-dominated landscapes (Mohd. Azlan and Sharma 2006; Maddox *et al.* 2007; Fitzherbert *et al.* 2008; Luskin 2010; Luskin and Potts 2011). In areas characterized by a forest-plantation mosaic, there is often an increase in generalist or edge-adapted species and a decrease in forest-interior and area-demanding species (Gibson *et al.* 2011; Laurance *et al.* 2012). In Southeast Asia, wild boar (Ickes 2001), monitor lizards, pythons, and cobras (Shine *et al.* 1999), and other edge or generalist species have been observed to become hyper-abundant in and around oil palm plantations (Bennett and Dahaban 1995; Fitzherbert *et al.* 2008), while larger species like tigers, gaur, Asian elephants and Sumatran rhinos have often been found to be absent (Sodhi *et al.* 2004; Nyhus and Tilson 2004; Corlett 2007; Fitzherbert *et al.* 2008; Maddox *et al.* 2007; Alfred *et al.* 2012). In Indonesia, these wildlife conditions have led to the commercial harvest of wildlife from plantations (e.g. reptiles; Shine *et al.* 1999) and the construction of expensive fencing systems to reduce crop damage from wild pigs and elephants (Alfred *et al.* 2012).

Changing socio-ecological conditions in plantation landscapes also affect hunting practices and wildlife harvest. Immigrants often bring culturally distinctive wildlife preferences and hunting methods, potentially leading to the over-hunting of preferred game or economically valuable species (Redford and Robinson 1991; Wilkie and Curran 1991; Koster 2008; Pangau-Adam *et al.* 2012). Simultaneously, hunting practices may adapt to capture or deliver important ecosystem services (e.g. to reduce crop damage) and new economic opportunities to sell wildlife (Robinson and Bennett 2000; Corlett 2007). Exploring how hunting practices change in association with changing socio-ecological landscapes is thus integral to broader understandings of contemporary conservation efforts and livelihood strategies.

Our objective is to describe contemporary hunting practices in a characteristic plantation-dominated region of Indonesia in the Jambi province of Sumatra. We conducted semi-structured in-depth interviews with knowledgeable professional and sport hunters, local plantation agriculture workers and managers, government officials from relevant departments, and wild meat market dealers in Jambi City. In this paper, we explore four important aspects of hunting in detail: (1) motivations for hunting, (2) modern practices, with specific consideration of how practices differ between ethnic groups, (3) species harvested and extraction rates, and (4) wildlife consumption patterns and trade.

Methods

Study area

Our study area of Jambi province is located in central Sumatra, Indonesia, extending from the eastern coast to the Barisan mountains in the west. Our respondents primarily lived, worked and hunted within the central regencies of Muara Jambi (5,246 km²), Batang Hari (5,180 km²) and parts of Tebo (6,461 km²), which surround the Jambi City regency (01°37'S, 103°36'E; Fig. 1). The total population of Jambi province was 3,088,618 in 2010 with the capital of Jambi city having a population of 531,857 (BPS, 2010).

The dominant forms of land use in Sumatra have evolved considerably over the past 50 years. Prior to 1960, smallholder rice was the predominant human land use, along with small areas of rubber, coffee, tea, tobacco, cinnamon, and *Agathis* plantations (Rye 2000; Tomich *et al.* 2000; Margono *et al.* 2012). Beginning in early 1970, this shifted to large-scale logging concessions, timber plantations, and rubber, cocoa and coffee estates, often in association with transmigration programs (Margono *et al.* 2012). Since the early 1990s, oil palm has dominated agricultural expansion, with new plantations often coming at the expense of previously forested land (Miettinen *et al.* 2011). Today, Sumatra is a primary growing region for oil palm, accounting for 73% of Indonesia's palm oil production, which is the world's largest producing country (Table 1; Colchester *et al.* 2006; FAO 2012). Jambi is a microcosm of Sumatra, losing 32% of its forest cover from 1990 to 2000, and another 17% from 2000 to 2010 (Margono *et al.* 2012). During that time, oil palm and rubber grew by 85% and 19% from 2000 to 2010 in Jambi, respectively (Table 1).

Despite this rate of development, Jambi is still known for its forests and biodiversity. Jambi is home to part of the Kerinci Seblat National Park, Sumatra's largest national park, which supports a plethora of threatened wildlife including tigers (*Panthera tigris sumatrae*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), Asian elephants (*Elephas maximus sumatrensis*), malay tapirs (*Tapir indicus*), Sunda pangolins (*Manis javanica*), serows (*Capricornis sumatraensis*), dholes (*Cuon alpinus sumatrensis*), gibbons (Hylobatidae spp.), and Sunda clouded leopards (*Neofelis diardi*; IUCN 2012). Some wildlife species are protected under Indonesian law, but hunting is loosely regulated and many species, such as wild boar (*Sus scrofa*), are completely legal to hunt and sell (Government Regulation PP No. 7 1999; ICUN 2012). However, firearms are tightly controlled and expensive (Corlett 2007). There are also numerous smaller protected areas in Jambi, as well as scattered production and secondary forests (Margono *et al.* 2012; Fig. 1).

As elsewhere in Indonesia, substantial recent social and demographic change in Sumatra has been strongly associated with transmigration programs enacted to encourage agricultural development (Sandker *et al.* 2007). Jambi's population has tripled in the last 40 years (BPS 2010) and immigration consistently accounts for 15-20% of population growth (Suryadinata *et al.* 2003; Colchester *et al.* 2006; Table 2). Immigration into oil palm producing regions is widespread across Indonesia (Table 2). Immigrants then supply the large year-round workforces in rubber and oil palm plantations by tapping rubber trees, harvesting oil palm fruits by hand, processing these commodities, and building supporting infrastructure (Li 2011). In 2004, for example, 4.5 million people on Sumatra and Kalimantan were employed in oil palm production alone (Sandker *et al.* 2007).

The largest ethnic group in central Jambi is the indigenous Malays, who are primarily Muslim, and made up 38% of Jambi's population in 2000 (Suryadinata *et al.* 2003). The second largest group is Muslim Javanese immigrants who constitute 30% of the population (Suryadinata *et al.* 2003). The largest minority groups are Batak (collective term for related ethnic groups) who are indigenous to North Sumatra and primarily Christian (6% of the population), the Minangkabau who are indigenous to West Sumatra and are predominately Muslim (5% of the population), and the Chinese (3% of the population), who are predominately Buddhist but also Confucianists, Taoist or Christian (Suryadinata *et al.* 2003). The Batak and Minangkabau also retain some of the historical "adat" animist traditions (INRN 2003). Across all ethnic groups in Jambi, about 91% of the population is Muslim, 5% are Christian, and 3% practice either Buddhism or Confucianism (Suryadinata *et al.* 2003). The 2000 ethnic-specific census is most current available, and Jambi's specific demographic makeup continues to change.

Interview methods

We conducted 73 in-depth semi-structured interviews that lasted between 30 minutes and one hour each with hunters, plantation laborers, owners and managers, and wild meat dealers from May through August 2011. One of the authors (EDC), a native of Jambi City, conducted the interviews in Indonesian. Respondents were first identified through conversations with plantation owners and managers, smallholder farmers, police and forestry officials, wild meat dealers, hunting equipment vendors, and the hunting organizations *Persatuan Olah Raga Buru Babi Indonesia* (PORBBI; translated to *Pig Sport Hunting Association of Indonesia*) and *Persatuan Menembak Sasaran dan Berburu Seluruh Indonesia* (PERBAKIN; translated to *Target Shooting and Hunting Association of Indonesia*). We used a combination of targeted subjects and referral sampling where existing study subjects recruited future subjects from among their acquaintances. Referral sampling allowed us to find a large number of knowledgeable respondents and engage them with a higher level of trust due to shared intermediary acquaintances. A weakness of referral sampling is that it is non-random and thus does not necessarily reflect the entire hunting population, which prevents some statistical analyses and limits population-wide conclusions. By targeting active, experienced and knowledgeable informants, we were able to more efficiently accumulate a wealth of collective expert knowledge stratified by ethnic group and occupation than if had we randomly sampled the population or used standardized surveys (Table 3; Bewley 2002). This method was appropriate

for our study sites given the results of our initial interviews, which suggested that a low percentage of the population engages in hunting.

Our respondents were representative of the five main ethnic groups, Javanese, Malay, Batak, Chinese and Minangkabau, as well as of the primary religious groups, Islam, Christianity, Buddhism and Confucianism found in Jambi City and the neighboring regencies (Table 3). Of the 73 interviewees, fourteen worked in oil palm plantations (wage laborers), eight worked in rubber plantations (wage laborers), ten were smallholder farmers (often growing oil palm or rubber), eight were professional hunters, ten were wild meat vendors and 23 worked other non-agricultural jobs.

From each interviewee, we collected a diverse range of quantitative and qualitative data encompassing demographics and livelihood strategies, hunting practices and harvest rates as well as wildlife consumption and trade. We recorded each respondent's background information (i.e. ethnicity, religion, cultural practices, immigration history) and economic information (i.e. employment, earnings, family status, and farming activities). To avoid potential biases stemming from closely related "circles of influence," we also inquired about relationships among our subjects to other groups to triangulate and corroborate inferences about how and why different groups hunted. This included stratified sampling across different hunting groups, and when hunters were part of larger organizations (e.g. PORBBI), we interviewed people from chapters in different cities and regencies.

Interviewees were asked about their hunting effort (frequency, duration, hunting sites, distance traveled and hunting group size), locations and habitat (forest, oil palm, rubber, etc.), methods (weapons, traps, strategies), motivations (cultural, subsistence, commercial), and wildlife species harvested (quantity and frequency). We also directly observed hunts by accompanying hunters and hunting groups on hunts. We informally interviewed leaders of two hunting organizations (PERBAKIN and PORBBI) as well as local police, and officials at the forestry, agriculture, and conservation/resource management authorities (Dinas Kehutanan Jambi, Dinas Perkebunan, Dinas Pertanian dan Pangan, and Balai Konservasi dan Sumber Daya Alam).

Interviewees were also asked about their domestic and wild meat consumption (the frequency with which they had consumed different wildlife or domestic meat over the past week, month or year), wildlife trade (what was sold, for how much, to whom, and for what purpose), and agricultural pests (i.e. to rank species by damage incurred). In addition to respondents' perceptions of agricultural pests, we analyzed accounts of pest species' damage from government reports obtained from the agricultural department in Jambi (Dinas Perkebunan Provinsi Jambi 2012). These reports quantified the types of losses and associated costs caused by wildlife pest species in plantations from January-March, 2011. The reports were compiled from 471 km² of oil palm and 740 km² of rubber plantations monitored within Jambi province. Finally, respondents were asked about their perceptions of short and long-term wildlife population trends (what animals were increasing or decreasing, when, where, and why), as well as to speculate about other people's practices, which yielded reports of poaching of protected animals that respondents may have avoided describing in their personal practices.

Wild meat vendors were asked about the species they sold, quantities sold per week (animals and weight), price, customers, and trends in demand. We also asked about the source of meat including characteristics about the hunter and method of hunting, when possible. Regional wild meat off-take was calculated from the number of animals sold in markets per week multiplied over the year, but this was only possible for wild boar (*Sus scrofa*) due to low frequency and highly variable presence of other wildlife species in meat markets. Of the 10 wild meat dealers interviewed, nine were located in Jambi City and were visited multiple times, and one was located in Muara Tebo, 200km east in the Tebo Regency, and only visited a single time. Regardless, our four-month study period was too short to capture potential seasonal variations. This study also concentrated on hunting for wild meat, not the illicit wildlife trade; however, poaching is known to an issue in Jambi, often undertaken for international export of pets, exotic foods and Chinese traditional medicines (Corlett 2007; Nijman 2010).

Results

Hunting motivations, methods, and harvest rates

Hunting methods and motivations corresponded closely to specific ethnic groups. Acquiring meat for personal consumption (“subsistence” hereafter) was reported as the primary motivation for hunting by 12.2% of respondents (primarily Javanese immigrants and Malays) followed by 40.8% hunting primarily for sale (primarily Chinese and Batak) and 46.9% hunting for social/cultural reason (primarily Minangkabau). The five hunting methods commonly employed (in order of total number of estimated annual hunter-days) were (1) weekly large social day hunts by ethnic Minangkabau’s that primarily utilized dogs, (2) herding wild boar (*Sus scrofa*) from within oil palm plantations into wire net traps, done by professional Chinese hunters at night twice-weekly, (3) snare hunting, usually done by Malay smallholder farmers in forest fragments and unkempt rubber plantations, (4) air rifles used by Malays primarily seeking mouse deer (*Tragulus spp.*) in rubber plantations or forest, and (5) vehicular hunts using firearms, conducted by wealthy members of the sport hunting group, PERBAKIN.

The Minangkabau dog-hunts were comprised of 10-300 people hunting together for social reasons and were organized through the PORRBI hunting association. Large dog-hunts occurred each Sunday in areas containing a mix of forest, rubber and oil palm plantations and covered an area 5-15 km². The atmosphere at these hunts was leisurely and hunts lasted the entire day. There were even mobile vendors who accompanied the hunters to sell food and drink along the road. Upwards of 1000 hunters join for special hunts, sometimes in conjunction with festivals (FFI 2005, Rizali *et al.* 2007). The Minangkabau sought deer for personal consumption, and wild boar for pest control. Wild boars were either given to the Batak helpers who joined hunts for this purpose, or the hunting dogs were allowed to eat wild boars on the spot. Dogs also rounded up a wide variety of other animals that were killed but not always eaten (for example, a agile gibbon (*Hylobates agilis*)), and even tiger cubs (FFI 2005).

Professional Chinese hunters targeted wild boar within oil palm plantations and sold the meat. They hunted in groups of four to six people at night, herding wild boar from oil palm plantations into wire net traps, locally called *lapun babi*, which were placed at the plantation edge. *Lapun babi* wire traps are a type of circular snare approximately 1-2m in diameter that

entangle passing animals until they can barely move. A team of hunters set 50 to 150 traps on oil palm plantation borders late at night (~ 02:00) after wild boars had entered the plantations to forage on fallen palm fruits. At ~ 04:00 the hunters chase the wild boar out of the oil palm plantations and into the traps. An entire hunt can take 10-24 hours when travel time, trap set up and break down are included and thus only one to three hunts were undertaken per week.

Malay farmers and plantation managers hunted with air guns, often carrying the guns throughout the work day. They reported most often shooting macaques (*Macaca nemestrina*) from within plantations, with the purpose of reducing crop damage, and wild boar for both pest control and for sale. Farmers with air guns would sometimes hunt mouse deer (*Tragulid spp.*) in rubber plantations or nearby forests at night for personal consumption (less than one hunt per week). Air guns are relatively expensive (more than USD 100) and are often modified to kill large animals such as wild boar, thus partially substituting for firearms.

Malay farmers and some Batak snared in forests patches (often selectively logged or secondary forests) or rubber plantations with undergrowth. They targeted wild boar for pest control and sale as well as deer species for personal consumption. However, snares also captured a variety of other wildlife (“by-catch” hereafter). Snares were usually set close to homes or farms where they could be conveniently checked. There were also commercial hunters who placed snares in forests along rural roads, primarily to catch and sell wild boar to prearranged vendors.

Wealthy hunters (those making more than 5 million IDR per month) who could afford the cost of guns and licenses used firearms and were most often also members of the PERBAKIN hunting association. Firearms were then used to hunt by shooting animals out of the back of pick-up trucks at night for sport. Hunters kept preferred species for personal consumption (e.g. deer) and gave wild boar to hired helpers who most often sold the meat. The Batak often hunted with other groups, accompanying Muslim hunters (e.g. the Minangkabau) to collect wild boar and sometimes set snares in forests along rural roads. Javanese were the least involved in hunting, but would occasionally kill and consume macaques and porcupines.

Among the methods, snares and Minangkabau dog hunts were the most non-discriminate with the highest levels of by-catch (non-pig or deer species). Both practices occasionally led to the capture of all deer species, sun bears (*Helarctos malayanus*), tapirs (*Tapirus indicus*), pangolins (*Manis javanica*), bearded pigs (*Sus barbatus*; which were only locally present seasonally), and porcupines (Hystricidae spp.). Even arboreal species like binturong (*Arctictis binturong*), and primates such as gibbons (Hylobatidae spp.) and macaques (*Macaca nemestrina* and *Macaca fascicularis*) were sometimes captured in snares or by dogs. However, hunters reported that only wild boar was captured in oil palm plantations at night. Further, only wild boar – the target species of several hunting methods – was harvested consistently enough across different methods to estimate harvest rates for different methods (Fig. 2).

Wild meat trade and consumption

The majority of hunters preferred deer meat for their personal consumption, but took other animals for commercial purposes, pest control or sport. Wild boar was the most harvested species (both numerically and in terms of biomass). Deer species were the second most harvested

(mouse deer (*Tragulus* spp.), muntjak (*Muntiacus muntjak*), and sambar (*Cervus unicolor*), respectively). Deer species were unanimously reported to have declined in the area while respondents reported that wild boar populations were stable or increasing. People were broadly aware that some species were protected, which might have affected whether they reported hunting protected species.

Data from wild meat vendors showed that wild boar was often the only wild meat routinely sold at local rural and urban markets, although deer (usually sambar, which are too large for one family to consume) was occasionally available. The current widespread availability of wild boar meat in markets stands in stark contrast to a decade ago when Meijaard (2002) only found wild boar meat for sale in North Sumatra (home to the Batak). Wild boar meat was sold in two ways: “raw” and “pumped.” The latter involves pumping water through the animal pre-butchered to add weight to the meat and turn it a lighter pink color, which was reported to more closely resemble domestic pork. This “pumped” wild boar meat is sold at a ~25% lower price by weight than “raw” wild boar meat. Hunters earned ~ 5,000 Rp/kg (~0.58 USD/kg) for selling dressed wild boar; dressed adult carcasses generally weighed between 30 and 40 kilos. Vendors then sold wild boar meat for ~15,000-20,000 Rp/kg (1.75- 2.34 USD/kg), which is substantially higher than estimates from Jambi in 2001 of 0.10-0.20 USD/kg (Linkie and Sadikin 2003). For reference, when our fieldwork was undertaken, domestic pork sold for 3.51-4.09 USD/kg, wild sambar deer (*Cervus unicolor*) sold for 4.09-4.68 USD/kg and domestic beef (cow) sold for 4.09-5.26 USD.

Each wild meat dealer sold 400 kg to 1100 kg of wild boar meat per week (10-30 wild boars). Together, the nine wild meat dealers in Jambi City sold more than 7500 wild boars and 250 tonnes of wild boar meat in 2011, while a single dealer in Maura Tebo (one of many) sold another 1400-1500 wild boars and 50 tonnes of wild boar meat. This equates to a minimum harvest density of 0.71 wild boar/km²/year for the three regencies surrounding Jambi City. Wild boar is also personally consumed by hunters or traded outside of markets. Further, we did not speak with every dealer in the area (e.g. there were export meat dealers, other wild meat dealers in Maura Tebo, as well as dealers in many smaller towns). Thus, the true harvest density is likely more than double our minimum estimate of 0.71 wild boar/km²/year .

Wild meat dealers reported that their largest customers were local Batak or Chinese restaurant owners who frequently purchased wild boar. However, wild meat dealers outside urban areas also exported their meat, primarily via refrigerated trucks that regularly travel to Medan, a city in North Sumatra that is home to a large Batak population. Wild meat exporters also reported selling meat to Jakarta where there is a demand from Chinese, and Batam Island in Riau to meet demand from Batak there. Dealers and other interviewees reported that the wild boar meat export trade was expanding, made possible by improved road infrastructure associated with the development of the timber and agricultural sectors. However, except for wild boar, trade in wild meat was reported as declining; supplanted by an increasing availability of cheap domestic meat, which is also often preferred for taste.

The meal recall data showed 71% of respondents reported eating wild meat over the past year. Domestic meat consumption (including domestically raised meats, eggs and seafood) was present in 55.1% of meals across all respondents based on three meals per day, with little

variance between ethnic groups. Wild meat was present in 3.9% of meals, representing 6.7% of all meat servings. Across all respondents, 82% of all wild meat servings were wild boar, but this was almost exclusively consumed by non-Muslim Batak and Chinese. Muslim Javanese and Malay inhabitants were the only groups that frequently consumed other wildlife, primarily macaques, mouse deer, and porcupines (Javanese 19.7 times per year, Malay 8 times per year).

Crop raiding perceptions and damage

The reports from the Jambi government's agricultural department (Dinas Perkebunan Provinsi Jambi 2012) showed that in 2011, wild boar caused the most damage to oil palm (4.5 million Rp/ha; 526 USD/ha), rubber (7.6 million Rp/ha; 889 USD/ha) and coconut plantations (0.8 million Rp/ha; 94 USD). Corroborating these statistics, 100% of respondents listed wild boar as causing the most damage to farms when explicitly asked about wildlife pests. Oil palm and rubber crop damage by wild boar was primarily due to their destruction of young trees. Farmers and hunters reported that wild boar exhibit a diurnal habitat shift, living and nesting in forest fragments or unkempt rubber plantations during the day and feeding in oil palm plantations at night. Corroborating this, hunters only reported to have captured wild boar within oil palm plantations at night and farmers only reported damages from wild boar at night. Further, when questioned, hunters reported that the stomach contents of the wild boar caught in all habitat types, including forest, often contained oil palm fruit. This indicates that wild boar are obtaining an important food source from oil palm plantations and are freely moving between habitats. To minimize damage, it was common for smallholder farmers to hunt in and around their property and for oil palm plantation managers to request hunting in their area and large oil palm estates, occasionally even paying hunters per boar killed.

Perceptions of the second most significant source of farm damage from wildlife species differed between rubber and oil palm plantations. Rats (*Muridae* spp.) were ranked second for oil palm and indeed caused the second most costly damage in government reports (2.2 million Rp/ha; 257 USD/ha). Macaques (primarily *Macaca fascicularis*, but also *Macaca nemestrina*) were perceived as the second-most damaging pest in rubber plantations, but their damage was not significant enough to be included in any agricultural reports. Elephants (*Elephas maximus sumatrensis*) were never listed by our respondents, but accounted for the third most costly source of damage to oil palm plantations in the agricultural reports (0.8 million Rp/ha; 94 USD/ha); while elephant damage is rare it is severe when it occurs (WWF 2004; Alfred *et al.* 2012). Porcupines and squirrels were reported as occasional but insignificant pests in both oil palm and rubber. Deer were never mentioned as pests.

Discussion

Jambi's 85% increase in oil palm plantation land from 2000-2010 has been accompanied by a 17% decline in forest cover, 28% rise in total population, new immigrant populations representing 15-20% of population growth, and widespread infrastructural improvements and a growing market economy with cheap domestic meats (Tomich *et al.* 2000; Angelsen and Kaimowitz 2001; Hirawan 2011; Margono *et al.* 2012). Our data suggest that these new socio-ecological conditions are shaping hunting strategies and wildlife harvest. First, commercial and cultural hunting were more common within Jambi than subsistence hunting, with wild meat

present in just 3.9% of our respondents' meals. Second, a relatively small proportion of Jambi's rural and urban residents were engaged in hunting; this was indicated by interviewees' responses as well as by the difficulty we faced in locating people who hunted. Third, our results demonstrate that different ethnic groups consistently practiced distinct forms of hunting, preferred different types of wild meat, and consumed different quantities of wild meat. Fourth, our results showed that hunters are overwhelmingly harvesting one species, wild boar, and that there is a thriving local and export trade in wild boar meat. This stands in stark contrast to previous reports from Jambi that describe almost no market for wild boar meat, that it was primarily consumed by hunting dogs, and when sold, was an order of magnitude cheaper in 2001 than in 2011 (Meijaard 2002; Linkie and Sadikin 2003; FFI 2004; Rizaldi *et al.* 2007). Fifth, the demand for wild boar has emerged from non-Muslim Chinese and Batak immigrant groups, both locally and outside Jambi. Finally, hunting motivations were multiple and inter-connected. For example, farmers hunted themselves and also requested that commercial hunters or Minangkabau social hunts to their plantations to remove wild boar in order to reduce crop damage. Hunters then consumed harvested deer meat but usually sold wild boar meat. Thus, the same hunting activity was simultaneously undertaken for pest control, subsistence, social reasons, and economic gain.

Muslim groups (e.g. Javanese, Minangkabau, and Malay) did not consume wild boar for religious reasons, but would hunt and sell it. Batak prefer the taste of wild boar to domestic pork for cultural dishes, while Chinese prefer the taste of domestic pork. Chinese people reported using wild boar as a cheaper alternative to domestic pork, particularly in restaurants. Demand from Chinese and Batak populations in other Sumatran provinces was reported as the reason underlying a substantial export of wild boar meat from Jambi, particularly to Batak in Medan. Clayton and Milner-Gulland (2000) describe a similar situation among adjacent but religiously distinct districts in Sulawesi where Christians hunted more actively and consumed more wildlife than their Muslim neighbors, instigating a cross-district wildlife trade.

The low proportion of wildlife consumption by respondents (just 3.9% of meals) indicates that wild meat is not a critical component of people's diets in the study area. This finding is especially interesting since hunters may be expected to eat more wildlife than the general population. One explanation for apparently low levels of engagement in hunting and wild meat consumption may be the widespread availability of domestic meat in Jambi's rural and urban areas, since this constituted the vast majority of meat consumed across all ethnic groups. This mirrors development trends from other studies in region; for example, in remote forested areas of Malaysian Borneo, Bennett *et al.* (2000) found that between 67.1% and 90.0% of meals contained wild meat. As they sampled in increasingly market-connected areas, the same study reported that 49.1% of loggers' and 36.8% of traditional hunter-cultivators' meals contained wild meat, while only 4.1% of plantation workers meals contained wild meat. Bennett *et al.* (2000) also found that all communities hunted primarily for subsistence, only also engaging in commercial or sport hunting in areas with oil palm plantations. An important distinction however is that Borneo's Dayak groups are not predominantly Muslim, and thus do not face the same religious restrictions against consuming wild or domesticated pork. In Papua, where oil palm plantations are a recent addition to the landscape, more than half of meals still contained wild meat and 26% of hunters primarily sought subsistence (Pangau-Adam *et al.* 2012). In comparison to results from these studies, it seems that the low levels of subsistence hunting and

wild meat consumption we observed in Jambi reflect a decreasing reliance on forest products in developed plantation landscapes. This hypothesis is consistent with broad development trends in the region and elsewhere (Shively 1997; Angelsen and Kaimowitz 2001; Brashares *et al.* 2011).

Among the hunters we interviewed, those from different ethnic groups used different hunting methods with appreciably different harvest efficiencies. Malays most often hunted with snares for wild meat, which was the most efficient method because it only takes a single hunter a few hours daily to check snares. Minangkabau dog hunts in contrast were the least efficient because they were comprised of 10-300 men (and up to 1000 men) hunting all day for social and cultural reasons rather than meat harvest (FFI 2004, Rizaldi *et al.* 2007). Full-time Chinese hunters who sold the meat as their primary income source consistently harvested the most wild boar, although their method of herding animals from within oil palm required a substantial total time investment (12-24 hours). The Javanese immigrants we interviewed who primarily worked in plantations seemed the least involved with hunting and consumed the least wildlife. This mirrors Bennett *et al.*'s (2000) finding that oil palm laborers in Borneo (also often immigrants) were the least involved in hunting. With the exception of traditional Minangkabau dog hunts, our results may also indicate a modernization of hunting technologies since some historical methods, such as blowguns, which are commonly used in Malaysian Borneo (Bennett *et al.* 2000), and bows and arrows, which were still the most common hunting method used in Papua, were never reported by our respondents (Pangau-Adam *et al.* 2012). Shotguns were the primary method used by Malaysian hunters in Borneo, but air rifles were more common in Jambi (Bennett *et al.* 2000). This is due to firearms being more strictly regulated in Indonesia, causing their usage to be limited to the military or wealthy sport hunters that can afford to obtain guns and licenses (Corlett 2007).

Respondents reported that the novel ecological conditions in Jambi's oil palm plantation landscapes affected the contemporary wildlife community. Specifically, wild boar was reported to be the most abundant large wildlife species in plantation landscapes and the primary source of crop damage to plantations. This result is corroborated by camera trapping study from Jambi, which reported that wild boar accounted for 42% of wildlife photographs in forests adjacent to oil palm plantations and 82% of photographs within plantations (Maddox *et al.* 2007). Similarly, high wild boar densities were also reported in Peninsular Malaysia where a forest fragment surrounded by oil palm plantations had 27 boars/km² and 47 boars/km² in two different estimates (Ickes 2001), while natural densities ranged from 3 to 5 pigs/km² (Kawanish and Sunquist 2004). Such facts are consonant with what might be expected from the feeding habits and reproductive strategies of wild boar; unlike strict herbivores, wild boar are generalists that consume palm fruits and their reproductive rate is higher than other large mammals (e.g. wild boar sexually mature as early as 8 months old and give birth to one or two litters per year, each with 4-12 piglets; Bieber and Ruf 2005).

Related to this, our study captures how the shift in wildlife towards more wild boar is informing farming practices, hunting practices, and livelihood strategies. Oil palm farmers reported that they have adapted their management in response to the new wildlife conditions by more actively hunting (primarily wild boar) to reduce crop damage as well as investing significant resources in digging trenches and erecting fences (even electric fences; WWF 2004; Alfred *et al.* 2012). In Jambi, oil palm plantation owners have also encouraged hunting around

their property and even paid hunters to kill wild boar. Likewise, hunters have developed novel methods tailored towards hunting within oil palm plantations, namely by herding wild boar into nets. The new demand for wild boar meat has enabled hunting to be a full-time commercial enterprise. Finally, hunting wild boar can provide an alternative “safety net” resource for communities during crop failures or employment shortages (Brashares *et al.* 2004). In this vein, we wonder what happens when large oil palm and rubber estates replant plantations and there is a temporary (3-5 year) loss in harvesting jobs. Will this lead to a dramatic increase in hunting activity and will there be sufficient stocks of wildlife locally available?

Changing wildlife populations and hunting practices in oil palm landscapes also affects the ecology of remaining forests. For example, wild boar disturb the soil when grubbing, rooting and wallowing, and also consume a large percentage of the seed bank and kill seedlings to build nests (Ickes *et al.* 2005). In excess, these disturbances are associated with the establishment of invasive species and suppressed tree recruitment (Curran and Webb 2000; Ickes *et al.* 2005; Fujinuma and Harrison 2012). At the other extreme, in Borneo, excessive hunting led to defaunation and instigated dramatic changes in tree recruitment dynamics, likely largely due to the loss of wild pigs (Harrison *et al.* 2013). At the same time, hunting within plantations can potentially serve as a “buffer zone” to core natural areas (Wilkie and Lee 2004). Similarly, hunting pigs may divert hunting pressure from more threatened wildlife species (Naughton-Treves *et al.* 2003). Thus, from a conservation perspective, managing for a natural density of native wild boar is advantageous to maintaining healthy forest ecosystems.

We found that the different hunting methods and locations resulted in different species captured and harvest rates. In particular, hunting wild boar within plantations resulted in the capture of few threatened species. This method may thus be preferable to more indiscriminate methods used in forests, such as snares or dogs. To better identify specific causes and impacts of changing hunting practices, we recommend research that quantifies hunting intensities across forest-plantation landscapes, longitudinal studies, and research in a variety of different locations with different ethnic groups.

Conclusion

Our findings show how changing biophysical and demographic conditions in plantation-dominated landscapes influence contemporary hunting practices and wildlife harvest. First, oil palm development has led to better road networks, increasing access to forests and the potential to bring wild meat to market. Then, the influx of non-Muslim groups has created a substantial rural and urban demand for wild boar meat and thus the ability to earn income from hunting. Hunting motivations, methods and wildlife consumption were closely tied to different ethnic groups and thus affected by immigration. Overall, we found that hunting is no longer primarily a subsistence activity, but done to commercially trade wild boar meat inside and outside Jambi province, as well as to reduce crop damage, and as a cultural activity by the Minangkabau and social or sport activity by wealthy hunters.

In the wake of widespread deforestation, hunting poses a serious threat to wildlife in Southeast Asia’s remaining forests (Sodhi *et al.* 2004; Corlett 2007). Promisingly however, our results demonstrate that the specific hunting methods and locations being used in Jambi may

offer clear management opportunities. With many wild boars (*Sus scrofa*) but few threatened wildlife species utilizing oil palm plantations, policies that limit hunting to within plantations may minimize the harvest of threatened wildlife while maximizing the benefits obtained via hunting. If sustainably managed, hunting wild boar in plantations may satisfy cultural practices, provide meat and income to local people, and reduce damage to crops.

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Figures

Figure 1: Landcover map of Sumatra showing the study region and Jambi City (adapted from Margono et al. 2012 with permission).

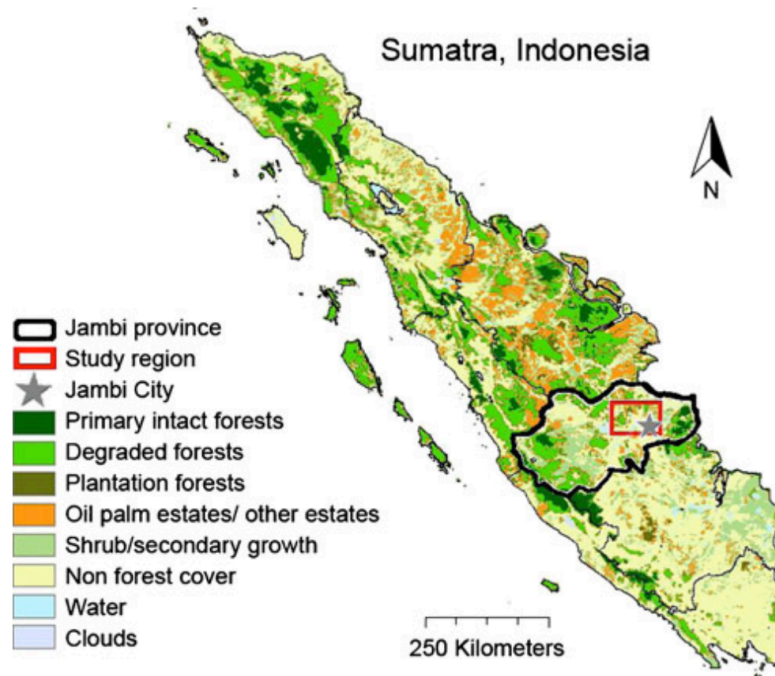
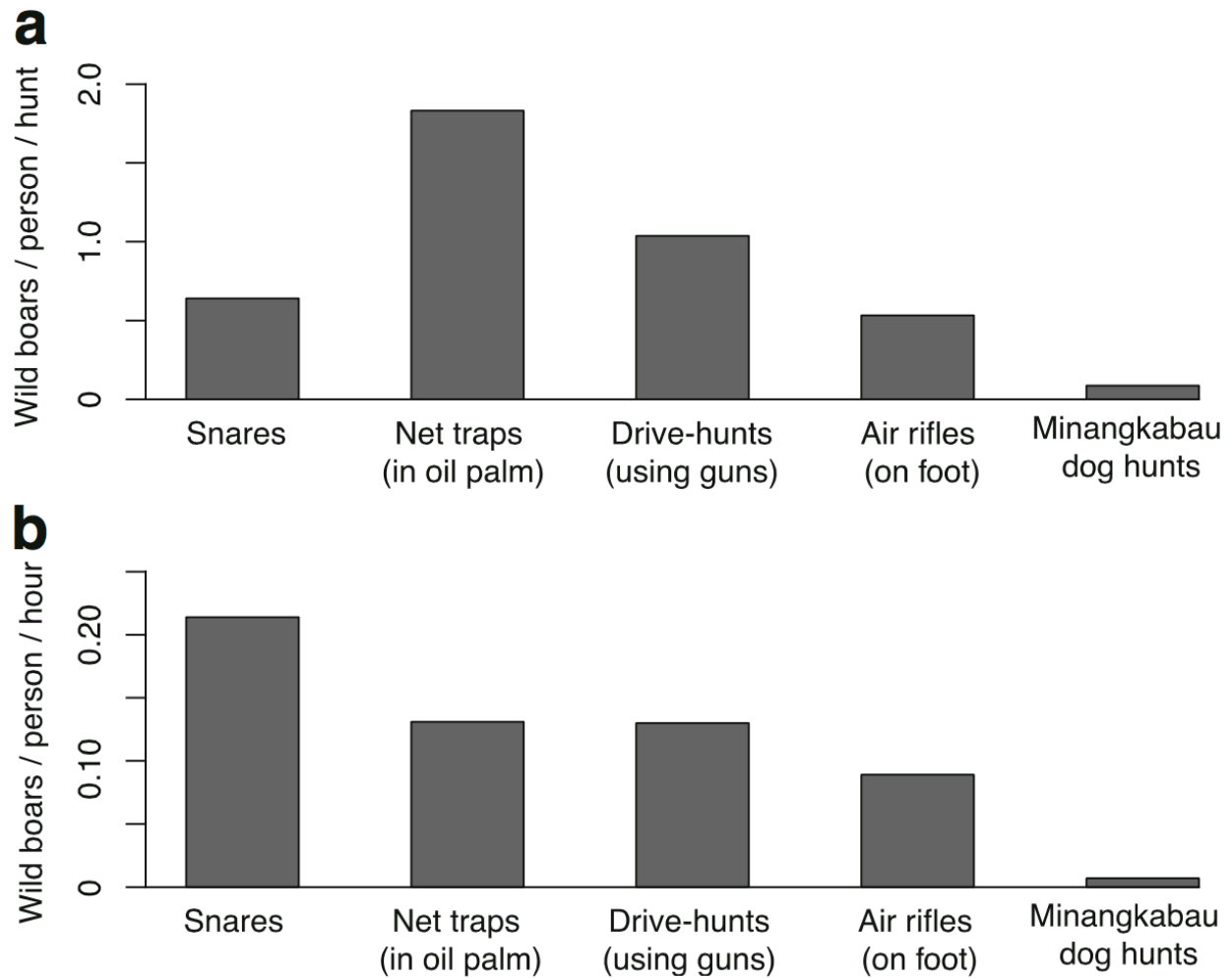


Figure 2: Wild boar harvest rates by hunting method (n=48). **a** Mean wild boar harvest per person per hunt. **b** Mean wild boar harvest rates per person per hour (affected by hours spent hunting).



Tables

Table 1: Change in area between 2000 and 2010 of intact and disturbed forests, and major plantation crops in Jambi and Indonesia. Forest cover data from Margono et al. (2012) for Jambi and Miettinen et al. (2011) for all of Indonesia, agricultural data from Dinas Perkebunan Provinsi Jambi (2011) for Jambi and FAO (2012) for all of Indonesia.

	Jambi		Indonesia	
	Km ² in 2010	Change (2000–2010)	Km ² in 2010	Change (2000–2010)
Forest	15,100	–17 %	86,039	–9.3 %
Oil palm	4,894	+85 %	53,700	+167 %
Rubber	6,451	+19 %	30,646	+28 %
Coconuts	1,186	–15 %	30,807	+19 %
Coffee	249	–15 %	11,660	–8 %
Cocoa	13	–61 %	10,260	37 %

Table 2: Net migration from 1980 to 2005 for selected Sumatran provinces, Java, and all Indonesian oil palm producing provinces versus non-oil palm provinces ('+' denotes in-migration and '-' denotes out-migration). West Sumatra is the historical center of the Minangkabau; North Sumatra is historical center of the Batak. Oil palm producing provinces contained more than 35 km² of plantations in 2005. Data compiled from Hirawan 2011 and BPS 2010.

Island(s)	Province(s)	Net migration (1980–2005)
Sumatra	Jambi	+ 209,476
	West Sumatra	– 313,332
	North Sumatra	– 764,543
Java	All provinces	– 4,478,859
All Indonesia	All oil palm producing provinces	+ 4,842,719
	All non-oil palm producing provinces	– 4,245,343

Table 3: Respondents' self-identified ethnicity and religion. The Minangkabau are indigenous to West Sumatra, the Malay are indigenous to East Sumatra, including Jambi province, and the Batak are indigenous to North Sumatra.

Religion	Ethnicity					Totals
	Javanese	Minangkabau	Chinese	Malay	Batak	
Muslim	17	18	1	9	1	46
Buddhist	0	0	16	0	0	16
Christian	1	0	2	1	6	10
None	0	1	0	0	0	1
Totals	18	19	19	10	7	73

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Chapter 7

Conclusions

Tropical forests throughout the world are rapidly being converted to agriculture. In Chapter 1, my introduction, I familiarized the reader with the different ways that agricultural expansion could affect forest species. Then, in my subsequent chapters, I explored the secondary effects of oil palm agricultural expansion in Southeast Asia, focusing on how forest loss and fragmentation, predator loss, and hunting can affecting tropical forest food webs.

In Chapter 2, I examined how deforestation and agriculture expansion affect biodiversity in general. I began by reviewing the literature assessing whether the negative effects of agricultural expansion can be best mitigated through intensifying existing farmland in order to set aside land for protection (“land sparing”), or by implementing more wildlife-friendly practices on farms to encourage conservation. My review showed that land sparing is best if strictly considering biodiversity and not other ecosystem services. Empirical research in tropical forest landscapes routinely reported that >50% of forest species were never recorded in wildlife-friendly tree-crop farmland (generally considered land sharing systems), and that annual-crop farmland supports even fewer species. At the same time, 89% of the studies I reviewed focused on tree crops, often agroforestry, while annual crops accounted for 87% of recent area expansion (2000-2010). Together, these findings indicated that despite the study system (crop) and methodological biases, intensification to spare land for nature is the optimal strategy to conserve forest species.

In Chapter 3, I moved to a smaller spatial scale and explored the role that farmland habitat quality plays in limiting forest species. I specifically looked at microclimate and habitat structure of tree plantations. My fieldwork was located in Peninsular Malaysia and focused on oil palm plantations, which are widespread in Southeast Asia where they are primarily grown to produce the palm oil, the world’s biggest source of vegetable oil. I found that oil palm plantations were substantially hotter (+2.84 C) and drier (+0.80hPa vapor pressure deficit), than adjacent forests during diurnal hours, but there were no significant nocturnal microclimate differences. Through the 25–30-year oil palm lifecycle, habitat quality ranged from being clear cut in years 1-2, having substantial understory vegetation from years 2-10, and then shifting to less understory but high epiphyte loads from years 11-25. Finally, I developed farm and landscape level management suggestions that incorporate temporal habitat heterogeneity to enhance the quality of the oil palm landscape matrix.

In Chapter 4, I turned my investigation to wildlife communities themselves, with a specific focus on how agricultural expansion could alter predator-prey dynamics and lead to trophic cascades. The loss of predators is thought to have wide-ranging cascading impacts on food webs, but there is little information about the status of the regional apex predator, tigers. I studied tigers in forest and non-forest habitats using camera trap arrays across three expansive landscapes (843-999km²) in Bukit Barisan Selatan (BBS), Kerinci Seblat (KS), Gunung Leuser (GL) national parks, which together make up the UNESCO Tropical Rainforest World Heritage Sites of Sumatra. I obtained 50 independent captures of tigers across all three sites and identified 26 unique individuals. Using spatially explicit mark-capture-recapture models, I estimated

density in forest habitat to be 1.94 ± 0.91 tigers/100km², 0.74 ± 0.65 tigers/100km², 1.31 ± 0.81 tigers/100km² at BBS, KS, and GL, respectively. To draw larger inferences across the island, I conducted a meta-analysis wherein I applied a novel method of standardizing densities between studies to account for different methodological approaches. This revealed that traditional capture-mark-recapture techniques (pre-2010) overestimated densities by 63.3% ($p < 0.001$) compared to new spatially explicit techniques. After correcting for this bias, I found that tiger densities in primary forests are 42.0% higher than disturbed forests ($p = 0.0642$), and there has been a mean annual increase of 5.3% from 1999 to 2014 within the forests that do remain ($p = 0.0385$). Lastly, I conducted a spatially explicit calculation of the island-wide tiger population using a 2011 landuse map for Sumatra, and estimate the tiger source population to be 734 tigers (± 362 , 1se). These results highlight that Sumatran tiger densities in remaining forest may be increasing. However, forest loss, fragmentation, and poaching have reduced the total population and threaten the subspecies with extinction. This result indicates a high threat of trophic cascades that would lead to increased prey abundance.

In altered ecosystems, such as forests fragmented by agriculture expansion, the widespread loss of predators is thought to be the main destabilizing force for herbivores. However, an unrealized indirect of agricultural expansion on forest food webs could be resource subsidies for forest-dwelling wildlife species that raid crops. I evaluated the direction and magnitude of subsidy cascades by tracking the wild boar population at the Pasoh Research Forest (PRF) in Peninsular Malaysia for 18 years. When crop subsidies were temporarily removed from the landscape, wild boar abundance dropped 100-fold, then rebounded 100-fold when palm oil resumed fruiting from 2006-2010.

Cascading impacts are known to occur following large changes in wildlife abundances, such as those documented in wild boar. At the PRF I tested for cascading impacts on the vegetation using wildlife exclosures over an 18-year period, as well as tracking the fate of 200,000 saplings across 24 years using the Center for Tropical Forest Science's (CTFS) tree census data. I found that tree saplings in the size class specifically preferred for wild boar nests were 220% $\pm$ 100 more abundant in wildlife exclosures than controls (mean $\pm$ 1SD, saplings sized 125-275cm height and < 2 cm diameter at breast height, hereafter "dbh"; $n = 7$, t-test, $p < 0.01$). However, there were no significant differences for other size classes. Likewise, the CTFS census data showed progressively lower densities of saplings 1-2cm dbh, totaling a forest-wide 44% reduction after 24 years (t-test, $p < 0.01$). Fishers Alpha diversity metric for tree saplings in the CTFS census also increased 13.4% over the 24-yr period ($p = 0.001$). These findings support the claim that palm-oil fed wild boars cause substantial damage to the tree community, primarily through their reproductive activities, and provide support for theoretical models predicting that higher predation can increase local alpha diversity (e.g. negative density-dependence).

My sixth chapter investigates how hunting practices change in the wake of palm oil expansion and increasing wild boar abundance. Using information from interviews with hunters, agricultural workers and wild meat dealers in Sumatra, I describe how contemporary hunting practices vary between different indigenous and immigrant ethnic groups. Specifically, hunting has shifted from subsistence to the primarily commercial endeavor of harvesting crop raiding wild boars (*Sus scrofa*). The Muslim majority in Malaysia and Indonesia avoids wild boar for

religious reasons, but there is substantial local and export demand driven by the Chinese in urban areas. Hunting within oil palm plantations may thus reduce crop damage from wild boar and also yield large amounts of wild meat with relatively little by-catch of threatened animals. This could also be an effective method for mitigating negative impacts on forests.

In conclusion, my dissertation results strongly indicate that the forest loss from initial agricultural expansion is just the tip of the iceberg when it comes to conservation concerns. Within plantations, habitat is so distinct from forests that few interior species are likely to persist in or traverse the agricultural matrix, further isolating species in remaining forests. Adjacent to plantations, crop-raiding species become hyperabundant and disturb the native vegetation. Humans are also changing their hunting behaviors in response to abundant pest species, with their impact ranging from sustainable control of crop raiding species to defaunation. At the landscape scale, the loss of apex predators may be instigating trophic cascades. Together these results echo other recent work highlighting the irreplaceable role of large contiguous forests in protecting tropical rainforest food webs in the Anthropocene.