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Maintaining ecosystem function and services in logged tropical forests

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Running head: Managing tropical logging

Abstract

Vast expanses of the world's tropical forests are being impacted by selective logging. We evaluate the environmental impacts of such logging and conclude that natural timber-production forests typically retain most of their biodiversity and associated ecosystem functions, as well as their carbon, climatic and soil-hydrological ecosystem services. Unfortunately, the value of production forests is often overlooked, leaving them vulnerable to further degradation, including post-logging clearing, fires and hunting. Because logged tropical forests are extensive, functionally diverse, and provide many ecosystem services, efforts to expand their role in conservation strategies are urgently needed. Key priorities are improving harvest practices to reduce negative impacts on ecosystem functions and services, and preventing the rapid conversion and loss of logged forests.

Industrial timber production from the world's tropical forests

Selective logging has emerged as one of the most prevalent land uses in the tropics. At least 20% of the tropical forest biome was selectively logged at some level between 2000 and 2005 [1]. More than 400 million hectares of natural tropical forest are now in permanent timber estates [2], some of which contribute to a network of multiple-use protected areas [3]. Consequently, logged tropical forests are now more widespread than intact old-growth (primary) forests across most of the tropics [4], with the notable exception of the vast Amazon rainforest and Papua New Guinea—yet even this is rapidly changing.

For centuries, colonial governments established forestry services in their outposts, in which trained foresters often practiced a precautionary approach to management, with both conservation and the permanence of the production system as primary roles [5]. Early scientific guidelines for harvesting tropical forests suggested that at least a quarter of a production area be protected to ensure the maintenance of ecological processes on which the forest depends [6]. Forestry's less-than-green reputation developed after WWII when the use of heavy-tracked vehicles became widespread in the expansion of large-scale, industrial timber cutting [7]. However, much of this activity was focused on one-time harvesting and land-clearing – not the selective logging investigated here.

Forests of the wet tropics are typified by tall canopies with even taller emergents and dark, humid interiors. The felling and removal of trees fragments the forest canopy, damages neighboring vegetation, opens up the forest-interior to sunlight and creates gaps that either facilitate regeneration and growth of the remaining trees and saplings, or are choked by vigorous growth of non-tree species including climbing vines and bamboos [8, 9]. What remains after large-scale mechanized logging is a disturbed tropical forest, typically dissected by extraction roads and skid trails [10] along which heavy machinery has compacted soils, impeding forest regeneration [8] and long-term productivity [11]. Even so, there remains no consensus about the impacts of logging on wildlife, ecosystem functions and services.

Some logged forests can have surprising value. Uganda's famed mountain gorilla (*Gorilla beringei beringei*) (Fig. 1b) is a global conservation icon and a major tourist attraction, generating much of the revenue on which Uganda's national parks depend. Like many generalist herbivores, these gorillas prefer logged forest because canopy openings increase the abundance of succulent herbs and other food plants [12] (Fig. 1a). The Bwindi Forest (Fig. 1a), where around half of the surviving gorillas persist, was previously a production forest safeguarded for its hydrological value and exploited for timber until its designation as a national park in 1992.

At present, however, the conservation value of production forests globally remains contentious: Some argue that logging is almost invariably unsustainable, and ultimately results in deforestation and loss of services and wildlife [7, 13-15]. Others suggest that, because logged areas are (and will be) so extensive and harbor so many species, they have high conservation value, retain most functions and services, and must play an increasingly important role in protection [16-18].

Here we explore the impacts of tropical logging on ecosystem functioning within biological communities and on the key forest services of carbon storage, evapotranspiration, and water. We find evidence and theory to suggest that production forests retain most ecosystem functions and services, and that they have far greater value to ecosystem conservation than other land-uses, including agriculture and even old-growth forest fragments isolated by farmland. Such fragments, though they contain old growth, might contribute less to ecosystem function and have reduced resilience compared with large contiguous production forests because key ecosystem processes are disrupted by the loss of connectivity with other wildlife habitats in the same landscape. Unfortunately, production forests are often susceptible to various threats, including conversion, hunting (defaunation), and fire. Given these facts, we outline recent scientific advances in the management of production forests so as to enhance ecosystem functions and services, and for a research and conservation agenda to better understand and safeguard the critical functions and services of tropical forests managed for timber production.

Impacts on ecosystem functioning

Tropical organisms differ in a number of important ways from temperate organisms, including their evolutionary history, demography, dispersal ability and sensitivity to climatic fluctuations (**Box 1** [19, 20]). These factors make many components of tropical biodiversity more vulnerable to habitat loss, fragmentation and degradation than their temperate counterparts, with implications for food webs and the provision of ecosystem functions.

Many forest species are linked by interactions across trophic levels. These include sometimes-tight associations between plants and animals that depend on each other for food or reproduction, as in the case of co-evolution between particular flowers and their specialized nectarivores [e.g., 21]. Interactions among species, some specialized and others diffuse, make up the complex architecture of food webs that maintain forest structure via processes such as pollination, seed dispersal, nutrient decomposition, and predation, with broad implications for ecosystem functioning [22]. For example, many tree species are dispersed by animals in tropical forests, such that the loss of frugivorous animals can reduce seed dispersal and alter the demography and composition of tree communities [23].

Discerning the impacts of logging on species diversity, food webs and ecosystem functioning can be challenging. First, most research has focused on just a few taxonomic groups, such as birds, mammals, ants and dung beetles. Second, different species within a particular functional group can show contrasting responses, making simple generalizations challenging [24]. Third, methodological limitations are common, with most studies lacking a pre-logging baseline or being conducted very shortly after logging [25, 26]. Finally, when studies focus on species and functional composition, changes following logging can be conflated with pre-existing natural species turnover across space (beta-diversity) [26, 27].

Two meta-analyses that each considered over 100 scientific studies reveal that logged forests in the Amazon, Africa, and Southeast Asia retain a similar species richness of animals, insects and plants to that found in nearby old-growth forest

[18, 28], although disturbance-sensitive species often decline and edge-tolerant species increase in abundance, resulting in shifts in species composition [e.g., 17]. Logged forests generally retain far higher species richness than competing land uses, including various agricultural and agroforestry systems [28] (Fig. 2), indicating major shifts in the local communities [e.g., 29]. Logged forests thus harbour important wildlife and plant populations (**Box 2**). An example is the endangered Bornean Orangutan (*Pongo pygmaeus*; Fig. 1c), which has 42% of its range within active or former production forests and only 22% in protected areas [30].

Simply assessing the impacts of logging on species richness can hide dramatic shifts in vulnerable wildlife and plant groups with particular life histories, functional traits or ecological requirements. Among these sensitive or vulnerable species are long-lived, old-growth tree species [31]; forest-interior amphibians [32]; large-bodied vertebrates that require tall, emergent trees for nest sites [33]; phylogenetically old or morphologically diverse lineages [34]; those with narrow ecological niches [34], including specialists of dark, forest-interior microhabitats [9]; and those in certain foraging guilds, such as insectivorous birds [35]. Large-bodied species are often sensitive to hunting [36], which often increases in logged areas, meaning that logging and hunting effects tend to be confounded [37]. Species traded as cage birds, such as the straw-headed bulbul (*Pycnonotus zeylanicus*), can also be susceptible [9, 38]. In contrast to these vulnerable groups, plant and wildlife species associated with forest-gap and edge microhabitats [31], such as early successional trees, weedy species (including alien exotics, e.g., *Piper aduncum* [39]), and disturbance-loving vines, and those animals with generalized diets or that feed on nectar [35, 40], tend to do well in logged forests, typically increasing compared to their pre-logging abundance or invading from non-forest ecosystems.

Changes in entire groups of species exhibiting particular functional traits indicate potentially far-reaching consequences of logging for food-web structure and ecosystem function [41]. The use of stable isotopes of nitrogen provides a mechanistic approach for detecting how logging impacts the flow of energy through food webs—and thus whether there are trophic cascades of secondary extinctions, as found in some fragmented forests [42]. The ratio of N15 to N14 isotopes increases with each trophic level as energy is transferred up the food chain. Recent results from Borneo suggest that many species of understorey birds and leaf-litter ants exhibit dietary flexibility, operating *higher* up the food chain after logging [24, 43] (Fig. 3). This indicates a shift from more frugivory to more insectivory in the case of birds; and for predatory ants, the consumption of more predatory types of insects.

Another approach to understanding logging impacts is to use functional diversity, which combines the array of functional traits played by species within communities, such as predation, body size, and foraging mode, into a single numerical value that can be used to infer impacts of logging on ecosystem functioning. Functional diversity reveals that Amazonian tree and Bornean bird and dung beetle communities provide similar numbers of ecological functions both before and after logging [31, 44, 45], whereas amphibians in the Neotropics and Africa lost functional groups after logging, especially those that rely on flowing water and large or permanent pools for reproduction [32]. Retention of functional diversity does not necessarily mean that there is no change in ecosystem functioning after logging, because the component functions can differ. For instance, Amazonian tree communities had lower wood density and softer leaves in logged than unlogged forest, despite having similar functional diversity [31], with implications for carbon storage and the abundance of herbivorous insects.

Crucially, the decay of ecosystem function can be less under logging, in comparison with other human land-uses. For example, large production forest areas retain more insectivorous and seed-dispersing birds, pollinating bees, nocturnal and dung-rolling beetles, and army-ant raiders than do small forest fragments or plantations [40, 44, 45]. This will influence ecosystem processes—for instance, because insectivorous birds and army-ant raiders play important roles in controlling insect herbivores [46]—with implications for leaf and plant growth, photosynthesis and biogeochemical cycling. Furthermore, while production forests help to retain functional connectivity in the landscape (**Box 2**), forest conversion and fragmentation isolate habitat patches within frequently inhospitable agricultural lands, disrupting movements and dispersal of species [47].

Impacts on ecosystem services

The maintenance of ecosystem processes reliant on functioning food webs and interactions among animals and plants is not merely important for preserving biodiversity, but underpins the provision of services important to humans.

Carbon storage – As the most productive terrestrial habitats on Earth, tropical forests store billions of tons of carbon. Most undisturbed tropical forests have been carbon sinks for the last three or more decades, absorbing more carbon than they emit [48]. Tropical forest clearance for agriculture or plantations is a major source of atmospheric carbon emissions [49], especially in peat lands [50]. In contrast, the emissions per hectare from selective logging are much lower than those from conversion [49]. Shortly after the first timber harvest, logged forests still contain on average 76% of the carbon stored in old-growth forest [18]. While the full recovery of above-ground biomass after logging can require several decades [51-53], reduced-impact logging can speed production forest recovery. In the southern Amazon, reduced-impact logging allowed 100% of original above-ground biomass to be recovered in just 16 years (conventionally logged forests recovered 77% of their original biomass in the same time) [53].

Evapotranspiration and temperature regulation – There is mounting evidence that tree cover plays a major role in influencing local temperature and rainfall [54]. Local and regional climates are largely driven by cycles of rainfall, evaporation, and cloud formation within rainforest biomes. As forest cover declines, this cycle can be disrupted, with the number of rain days declining and interannual variability in rainfall increasing [55]. However, forest conversion and fragmentation apparently have much bigger impacts than selective logging on rainfall and temperature. In the Amazon, large-scale areas without tree cover have higher temperatures and lower rates of evapotranspiration [56, 57], resulting in less rainfall [58] and potentially longer dry seasons [56, 57]. In the Brazilian Atlantic forest, increasingly fragmented forests similarly have fewer rain days [55]. On Sumatra, oil palm has higher air temperatures than logged or old-growth forest [59], while rural communities on Borneo consider increased temperatures the most detrimental environmental impact of deforestation [60]. Although controversial, it has been suggested that continuous forests might help generate winds that carry rainfall far into continental interiors and stabilize rainfall [54]. More studies are required but it appears likely that contiguous areas of selectively logged forests could function more like continuous forests, better helping to sustain regional rainfall, than does a matrix of agriculture and forest fragments.

Watershed services – Old-growth tropical forests provide watershed services including maintaining stream flows during dry periods, moderating flash floods, recharging groundwater, enhancing water quality, and conserving soils [61]. Selective logging increases water runoff [62]. In two catchments in Indonesian Borneo, this primarily stems from ten-fold higher runoff from skid trails and roads than from harvest or control plots, which differed in runoff only marginally [63]. In Southeast Asia, the additional runoff after logging was insufficient to produce detectable flooding downstream [64]. Forest conversion, however, results in 100–800% increases in annual water flow [62], because of enhanced run-off in rainstorms, with peak flows 185% higher and water levels rising nearly twice as quickly than under forest cover [65], and greatly reduced evapotranspiration. In Indonesian Borneo alone, such floods displaced 1.5 million people between 2009 and 2012, especially in the deforested middle reaches of rivers [66].

Forest soils are prone to erosion after logging, causing sedimentation of rivers and reduced water quality [61]. As a consequence of water runoff, soil erosion is most severe on skid trails and roads, often in association with landslides [67, 68]. In Borneo this resulted in 100 to 3,000 times the soil loss compared to forested control plots [63]. Despite the initial pulse of erosion and sediment runoff, by several years after logging, total soil runoff (including skid trails) was similar to that of primary forest [65]. In contrast, the clearance of logged forests results in a massive pulse of soil erosion: in Southeast Asia, soil loss increased from ~20 t km^{-2} yr^{-1} to between 1,100 and 8,940 t km^{-2} yr^{-1} [65]. Further, on steep hills or mountainsides, forest conversion to cropland or plantations permanently reduces rooting strength, increasing landslide potential [67]. As a result, forest clearance markedly decreases water quality [61], with annual sediment loads in streams rising from ~28 to 125 t km^{-2} [65], though actual values will vary greatly with topography, geology and soils.

The vulnerability of logged forest

Despite providing important ecosystem functions and services, many logged tropical forests are vulnerable. The biggest threat is that over-harvesting reduces the residual timber value so much [38], and logging roads so greatly increase forest accessibility [10, 69], that it becomes tempting to clear the remaining forest for agriculture or for profitable plantations, such as monocultures of fast-growing timber or oil palm. Globally, timber extraction followed by clearance has resulted in the loss of over 50 million ha of natural forests between 1990 and 2010 [70]. However, in assessing the role of logging in promoting forest clearing, we need to distinguish between cases where harvesting proceeds planned forest clearing, versus cases where logging promotes illegal clearing or post-logging reclassification for clearance. Unfortunately such key distinctions are seldom recorded.

In the Amazon, at close (<5 km) and far (>25 km) distances from roads, production forests were no more likely to have been cleared than primary forests in the first four years after logging [71]. At intermediate distances (5–25 km) from roads, however, production forests were 2-4 times more likely to have been cleared than old-growth forests, but whether this was planned conversion is unclear [71]. In Indonesian Borneo, forest loss from protected areas between 2000 and 2010 could not be distinguished statistically from that in production forest concessions, at locations matched in terms of elevation, terrain and distance to major roads and towns, indicating that timber extraction does not enhance rates of illegal forest clearance. However, when logging concessions were reclassified and allocated for conversion to agriculture and paper-pulp plantations, forest clearance was significantly higher in production forests [72]. In Indonesia, at least 33 million hectares of production forests were recently excluded from a major REDD+ initiative with Norway, leaving them open to conversion [73].

In many cases, production forests appear vulnerable to illegal invasions from small-scale farmers and hunters as a result of the extensive road networks created by logging [10, 37, 69] (Fig. 1d). Major trunk roads, in particular, fragment the forest understory and can impede movements of some sensitive (generally small-bodied) forest-interior animals [69] (Fig. 1e). In addition, the use of trunk roads and skid trails by large-bodied vertebrates increases hunting risk [74]. Many guidelines exist for reducing hunting in production forests [9], with the designation, recognition and enforcement of no-hunting zones crucial to ensure that wildlife is not hunted out [37]. However, local people and loggers themselves often engage in hunting and the live-animal trade. Commercial opportunities for selling meat increase when timber concessions are present, making hunting and wildlife trade a more severe threat in easily accessible production forests than in protected areas [9, 38].

Fire is another threat to production forests, especially following desiccation from sustained droughts [38]. The canopy disruption and trail networks that result from logging promote forest desiccation, while fine slash from logging is highly flammable when dry. Burnt, production forests are also vulnerable to further disturbances, such as subsequent fires, “salvage” logging [75], invasion by grasses [76], and even conversion to persistent *Imperata* grasslands [75]. Fortunately, if a logged forest is not burnt soon after extraction, then susceptibility to fire can diminish within a few years [77].

Managing for improved conservation of functions and services

Much remains poorly understood about tropical logging. Key research priorities are to devise forest management practices to improve biodiversity and associated functions in production forests (**Box 3**); and to understand the impacts of logging over time and space, of restoration after logging, and the circumstances under which logging might be desirable (**Box 4**). By far the most important step is to ensure that managed concessions are designated and retained as part of the permanent timber estate, rather than simply being converted after logging [e.g., 72]. Beyond this, some of the strategies to improve biodiversity and environmental outcomes in production forests are obvious—such as an effective presence to protect the forest, control hunting, stop conversion and fight fires [9].

Here we restrict ourselves to strategies for optimising ecosystem services within permanent timber landscapes. These include leaving sufficient time between cutting rotations for post-harvest regeneration, imposing stringent cutting-diameter limits and retaining large emergent trees [78], and using reduced-impact-logging techniques to limit forest damage (reviewed in [8, 38]). Realistically, however, most production forests will have lower biomass than old-growth forests, because there will be insufficient time for giant emergent trees to grow before a further logging rotation [51, 52]. Set-asides within production forests are therefore important to ensure that ecological services, functions and biodiversity associated with old-growth forests are maintained in the wider landscape [79], and these should include some flat lowlands where the biggest trees occur.

Various 'incentives' exist for timber companies to engage in conservation-friendly practices, including government regulations, maintaining good public relations and market access, the existence of market premiums for eco-certified timber, and certain tax breaks [80]. Increasingly, tropical timbers must be verifiable, with policy initiatives such as the USA Lacey Act and European FLEGT agreements restricting trade in timber of unverifiable or illegal origin. Such schemes help to reduce corruption that has historically meant that many countries are defrauded of royalties, via underreporting, bribery, and price fixing [7]. In turn, a growing number of timber-consuming firms will only purchase certified timber from sustainably managed forestry to protect their 'green' credentials from negative publicity.

Of particular interest are financial incentives for increasing logging sustainability. Payments for ecosystem services schemes, such as REDD+, could levy reduced carbon emissions via less destructive logging or the retention of production-forest cover for watershed protection. Sustainability labels, such as that from the Forest Stewardship Council, increase the market value of timber, resulting in a 5–77% price premium [81]. Unfortunately, the demand for certified timber and ecosystem services has thus far been to small to provoke a major shift in forest management practices, especially in the tropics [82].

Concluding remarks

The common strategy of protected area establishment tends to create islands of intact habitat in a highly disturbed matrix [83]. Habitat fragmentation is a primary concern, because many species need larger areas of habitat and/or connectivity across the matrix to survive, with the importance of bigger protected areas having been highlighted previously (**Box 2**, [84]. Consequently, while it is vital to continue protecting old-growth forests [28], global conservation needs cannot be met solely via this approach.

Logged tropical forest is the next best alternative to old-growth habitat, offering the potential of conserving the majority of ecosystem services, functions, and species within huge expanses of habitat, but with lower opportunity costs than fully protecting old-growth forest [38]. Production forests also generate higher revenues than protected areas in similar geographic contexts, thus providing economic incentives for maintaining forested landscapes. There are various ecological reasons why production forests can play a role in supplementing protected networks. Production forests suffer reduced edge effects compared to fragments, they allow connectivity among patches of intact forest even if they themselves sometimes function as population sinks, and they can maintain meta-community processes key to population survival, such as gene flow and recolonization after stochastic extinction (**Box 2**). Several studies suggest that forest species will navigate gallery or logged forest but not agricultural lands [e.g., 85].

Finding ways to protect large tracts of old-growth forests for their intrinsic (non-economic) values remains a core conservation priority, and we are not advocating the opening of old-growth forests for predatory or illegal logging. However, when national socio-economic and development pressures dictate that primary forest must be exploited for timber, we argue that it is vital that such lands be maintained as timber concessions rather than subsequently converted to agriculture or plantations [16, 20]. Perhaps the greatest obstacle to integrating production forests into effective conservation strategies has been the common perception that they are no longer important environmentally. This is an enormous misperception. Acknowledging their myriad values is the first step towards incorporating them fully into the global conservation framework, a process gaining traction with the expansion of multiple-use forests in a protected-area framework [3]. Retaining logged tropical forests must be seen as one of the most pressing priorities for the future.

Glossary

Conversion: clearance of forest for agriculture, settlements and other human development.

Concession: an area of forest granted by governments for timber extraction, typically to a single company which then manages the logging and sale of timber, from which it pays the government royalties (fees).

Coupe: each logging concessions is divided into multiple blocks, each of which is harvested on rotation, i.e. at different times.

Ecosystem function: the biological, geochemical and physical processes that operate within an ecosystem, sustaining it and enabling it to supply ecosystem services. Key ecosystem functions include nutrient cycling, seed dispersal, and many other interactions within and between the structural components of an ecosystem (e.g., water, soil, atmosphere and biodiversity). Also termed 'ecological processes'.

Ecosystem service: the provision of a natural resource or process that is valued by humankind (e.g., carbon storage and rainfall).

Forestry: the management of a forest for multiple outcomes, including timber harvest, ecosystem services, and biodiversity conservation.

Logging: the process of timber harvesting, including the cutting and removal of trees.

Logging intensity: the amount, manner and frequency of wood removal. Logging intensity varies greatly across the tropics, depending on extraction methods, re-cutting frequencies, the density of timber trees, topography, and on local regulations and economic factors [9].

Opportunity cost: the cost of forgoing an alternative economic activity

Permanent timber estate: land that is designated for logging but that will remain under permanent forest cover.

Post-harvest regeneration: the process of natural forest regeneration following a logging rotation. Regeneration includes gap closing by early successional trees and vines, and the rapid growth of unharvested trees beneath the threshold size of trees harvested.

Production forest: natural forest officially designated and managed for generating timber.

Rotation: a single logging event, including opening of roads, timber cutting and extraction, and post-logging management to close the coupe. Rotations should be several decades apart, but the time between rotations is frequently reduced to 15–20 years in early re-entry logging [17].

Selective logging: targets only certain species and stems, typically above a minimum trunk diameter (typically 40–60 centimeters, depending on the species), leaving other species and stems unharvested. Selective logging contrasts with clear-cutting of all trees, as frequently occurs in temperate regions.

BOX 1: The sensitivity of tropical species to anthropogenic disturbance

Organisms vary in life history and ecology across latitude, largely as a result of increased climatic and thus resource stability in the tropics [19]. In comparison to ecologically similar species in the temperate zone, many tropical species have longer lifespans and generation times, lower reproductive output, patchier distributions and lower population densities [19, 20]. As a result, tropical species can require a far greater area of intact habitat—estimated as 4–12 times larger on average in birds [20]—to protect viable populations and to maintain ecosystem processes.

Many tropical organisms also exhibit extreme dispersal limitation, including numerous species unable or unwilling to cross relatively small gaps such as roads [19, 69], and a limited tolerance of microclimatic variation. Old-growth lowland rainforests are typically characterized by complex structure and dark understory, with relatively stable humidity and temperature. Forest-interior species are thus often constrained by narrower environmental niches, light sensitivity and reduced tolerance of thermal stress [19].

These life history and ecological constraints create a combination of attributes that make numerous tropical forest organisms highly sensitive to anthropogenic disturbances, particularly habitat fragmentation and hunting [19, 20, 86]. The same issues may also limit persistence of sensitive species in production forests, given that (a) they tend to be warmer and brighter than intact forests, (b) logging roads and skid trails create barriers and provide access to hunters, and (c) patches of old-growth or higher-quality logged forest are fragmented within a matrix of disturbed forest. Sensitive species tend to be clustered in particular feeding groups or body-size categories, meaning that extinction following disturbance is typically non-random, with implications for seed dispersal, herbivore control and other functions in tropical forests [86].

BOX 2: Why do production forests retain biodiversity and ecological functioning?

Given that many tropical species are sensitive to anthropogenic disturbance (**Box 1**), why do production forests retain so many species and ecosystem functions? First, the intensity of logging varies regionally. In many areas of Africa and South America, logging is at very low intensities, with just 1-2 trees harvested per hectare [9, 18]. Within individual concessions, logging intensity is often patchy because of varying topography and the patchy distribution of large marketable timber trees. Harvest guidelines generally prevent cutting on steeper slopes (typically over 25–30 degrees) or in riverine strips (often 20–50 m in width) [9]. More stringent management plans can also require the protection of features such as saltlicks, caves, and high concentrations of fruit trees. What remains across logged landscapes, therefore, are often-substantial patches of old-growth forest, plus areas that have only been lightly logged. The retention of such patches is promoted as a key mechanism for allowing species retention within logging concessions, particularly immediately after timber extraction [9].

Second, treefall gaps like those created by logging are a conspicuous and common part of forest dynamics. For instance, 9% of mature and unlogged Malaysian rainforests are in gap phase at any one time [87]. Similarly, some tropical forests, especially those in the cyclonic and hurricane zones from 7–20° latitude, are periodically disturbed by intense windstorms, creating abundant large gaps [88]. Gaps are not only a normal component of the forest landscape, but also provide important microhabitats that are critical for the maintenance of tropical diversity. Among these are various ‘edge’ species adapted to treefall-gap microhabitats, including a host of understorey fruiting shrubs and fruit-eating birds [89].

Finally, although logging creates a dynamic and patchy landscape of more disturbed and better-quality patches of habitat, the landscape is still under a mostly connected tree canopy (Figure I). The broad extent and relative contiguity of production forests permits the dispersal of organisms between suitable patches, effectively connecting subpopulations. This connectivity is crucial in maintaining subpopulations of sufficient size and viability, and in sustaining a range of meta-community processes linked to gene flow and reproductive success, all of which are essential for long-term species persistence [90] and ecosystem functioning [86]. In contrast, connectivity is much reduced in fragmented patches of old-growth forest [47].

Figure I. Please see attached high resolution file

Figure I. Impacts of logging on forest connectivity. **(A)** *Koompassia excelsa* tree remains uncut in the Yayasan Sabah logging concession, Malaysian Borneo. Despite some of the highest intensities of timber harvest in the tropics, equating to 8–10 trees cut per hectare, a near-continuous forest canopy exists two decades later. Reproduced, with permission, from David Edwards. **(B, C)** Schematic diagram of population viability and rescue effects in fragmented **(B)** versus selectively logged **(C)** forests. Mature forest patches (dark green) are either embedded in a non-forest matrix (e.g., agriculture; white, **(B)**) or logged forest (pale green **(C)**), and the rate of dispersal and gene flow between patches is indicated by the arrow thickness. A large proportion of forest-dependent organisms can either survive in or disperse across logged forest, whereas agriculture harbours few forest species and is often a barrier to dispersal between forest fragments. Theoretically, this process results in lower population sizes, higher levels of extinction, and thus loss of functions in fragmented versus production forest landscapes. This effect is accentuated in smaller patches, which lose many species over time through area effects in fragmented landscapes, but are likely to retain high species and functions in logged forest through rescue effects (i.e. immigration after local extinction).

BOX 3: Managing timber concessions for improved biodiversity outcomes

Despite the persistence of much biodiversity within logged forests, some species and corresponding ecosystem functions are negatively affected even when hunting and fire are effectively controlled. Reducing such negative impacts, and ensuring the maintenance of specific values, are the goals of the High Conservation Value concept applied by timber concessions certified by the Forest Stewardship Council, while it could take on further importance in obtaining biodiversity or sustainability funds under REDD+.

Given a particular investment in conservation, the key question is how to maximize conservation benefits. One possibility is to retain old-growth features within logging concessions. This could be via the 'retention approach', which reduces the intensity of logging to retain small patches of old growth, some large trees and decaying logs dotted across entire concessions [78]. Alternatively, a single larger block of old growth could be protected within the logging concession [79]. This dichotomy maps onto the land-sharing versus land-sparing framework developed for farming. In Southeast Asia, simulations suggest that a land-sparing approach of protecting a single large old-growth block and logging intensively elsewhere would benefit bird (Figure IA), dung beetle and ant species [79]. This is because species that are either rare or absent in logged-over forest can persist in the old growth 'reserve'. This framework needs empirical testing in other regions (e.g., the Amazon), where much old-growth forest is slated for timber production.

Another possibility is to better manage the spatial arrangement of logging across concessions. Harvest plans can be designed to minimize species extinctions by maintaining a matrix of different aged patches in close proximity or by creating habitat blocks of similar successional stage. In simulation models of trees in a concession that is entirely logged, harvest plans with large contiguous harvest units yield high extinction probabilities for dispersal-limited species with clustered pre-harvest distributions (Figure IB) [91]. These results suggest that small, randomly located harvest units can reduce extinction rates in tropical production forests. The key question is how protecting old-growth features (blocks, riparian strips, etc.) impacts these predictions.

Finally, reduced-impact logging (RIL) could benefit biodiversity because it decreases the residual damage incurred by tropical forest across multiple logging rotations [reviewed in 8, 38]. A first rotation of RIL compared to old-growth forest has minimal negative impacts on many taxa including fish, birds, mammals and ants [92, 93], but negative impacts for arachnids [93] in the Amazon. A second rotation of RIL (following a first rotation via conventional logging) had no negative impacts on Bornean mammals compared to areas not yet re-harvested [94], and no difference in bird, dung beetle and ants compared to areas re-harvested via conventional logging [95].

Figure I. Please see attached high resolution file

Figure I. Impacts of harvest management on biodiversity. **(A)** The frequency of bird species richness recorded in 1000 simulations of land-sparing versus land-sharing logging in Southeast Asia. **(B)** Mean species-level persistence probabilities for tree species of different dispersal abilities under block, strip and random harvest plans. Tree species included are those that exhibit clustered distributions pre-logging and that are of conservation concern (defined as any species that went extinct in at least one random harvest plan replicate). Data from [79] **(A)** and [91] **(B)**, photos reproduced, with permission, from David Edwards.

BOX 4: Outstanding questions

(1) Logging impacts over space and time

Animal and plant communities in forests fragmented by agriculture continue to decline decades or even centuries after human impacts have occurred, such that young fragments still have to pay an “extinction debt” (**Fig. I, Box 2**; [96]). The fact that most studies take place shortly after timber extraction [25, 26], and thus rarely assess rates of species loss or recovery over time, might conceal a slow decay of biodiversity or ecosystem function. We still lack a basic understanding of these longer-term effects, raising important questions from individual movement patterns to population growth rates and functional provisioning. We also still know little about the breeding ecology of harvest trees and retaining viable populations.

Many logging studies are conducted in close proximity to blocks of primary forest: the apparent functional value of production forests could thus be inflated if spillover from ‘source’ populations in old-growth forests sustains ‘sink’ populations in production forest [28]. The key management question is at what distance and at what ratio between old-growth and production forest does any breakdown in value render protecting logging concessions a poor conservation strategy? We also need to understand how connectivity can be improved across production forests, perhaps via inclusion of stepping stone primary habitats.

(2) The value of forest ‘restoration’

Aggressive silvicultural techniques, such as strip cutting or thinning of lianas and non-harvestable trees, can aid the recovery of timber harvests [97]. Enrichment planting, where saplings of desirable timber species are planted in production forest and sometimes tended for several years, has only mixed success and high costs [6]. This makes it uneconomic as a blanket choice, but it remains beneficial in heavily degraded areas to restore canopy cover and populations of rare species [98]. Key questions remain, including: (i) what is the cost-effectiveness of sequestered carbon in production forests?; (ii) does enhancement of future timber stocks promote premature re-logging of forests or help to prevent forest conversion to agriculture?; and (iii) what are the long-term impacts of active forest restoration on fauna, flora, and ecosystem services [99]?

(3) When is a logged forest desirable?

The choice between logging and protection depends on the effectiveness of these two land uses in avoiding forest loss [71, 72]. How effectiveness can be modified by sustainable management, conservation, and carbon-payment schemes [e.g., 100] is thus a key research frontier. One of the benefits of logged over unlogged forests is the revenue and employment they provide—to many politicians this can justify the maintenance of at least some forests because they “pay their way”. Yet estimates of the size of these economic benefits vary widely and need to be better calculated across space at regional and global scales.

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References

1 Asner, G.P. *et al.* (2009) A contemporary assessment of change in humid tropical forests. *Conserv. Biol.* 23, 1386-1395

2 Blaser, J. *et al.* (2011) Status of tropical forest management. *ITTO Technical Series 38. International Tropical Timber Organization, Yokohama, Japan.*

3 Leroux, S.J. *et al.* (2010) Global protected areas and IUCN designations: Do the categories match the conditions? *Biol. Conserv.* 143, 609-616

4 Laurance, W.F. *et al.* (2014) Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* 29, 107-116

5 Wiersum, K.F. (1995) 200 years of sustainability in forestry - lessons from history. *Environ. Manag.* 19, 321-329

6 Dawkins, H.C. (1958) The management of natural tropical high-forest with special reference to Uganda. *Imperial Forestry Institute, University of Oxford*

7 Shearman, P. *et al.* (2012) Are we approaching 'peak timber' in the tropics? . *Biol. Conserv.* 151, 17-21

8 Putz, F.E. *et al.* (2008) Reduced-impact logging: Challenges and opportunities. *Forest Ecol. Manag.* 256, 1427–1433

9 Meijaard, E. *et al.* (2005) Life after Logging: Reconciling wildlife conservation and production forestry in Indonesian Borneo. *Center for International Forestry Research (CIFOR), Bogor, Indonesia*

10 Laporte, N.T. *et al.* (2007) Expansion of industrial logging in Central Africa. *Science* 316, 1451-1451

11 Hawthorne, W.D., *et al.* (2012) Logging scars in Ghanaian high forest: Towards improved models for sustainable production. *Forest Ecol. Manag.* 271, 27-36

12 Blumenthal, S.A. *et al.* (2012) Detecting intraannual dietary variability in wild mountain gorillas by stable isotope analysis of feces. *Proc. Natl. Acad. Sci. U.S.A.* 109, 21277-21282

13 Michalski, F. and Peres, C.A. (2013) Biodiversity depends on logging recovery time. *Science* 339, 1521-1522

14 Bowles, I.A. *et al.* (1998) Logging and tropical forest conservation. *Science* 280, 1899-1900

15 Zimmerman, B.L. and Kormos, C.F. (2012) Prospects for sustainable logging in tropical forests. *Bioscience* 62, 479-487

16 Chazdon, R.L. *et al.* (2009) Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica* 41, 142-153

17 Edwards, D.P. *et al.* (2011) Degraded lands worth protecting: The biological importance of Southeast Asia's repeatedly logged forests. *Proc. R. Soc. B* 278, 82-90

18. Putz, F.E. *et al.* (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conserv. Lett.* 5, 296-303

19 Stratford, J.A. and Robinson, W.D. (2005) Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. *Frontiers Ecol. Environ.* 3, 91-98

22 Tobias, J.A. *et al.* (2013) Bird conservation in tropical ecosystems: challenges and opportunities. *Page 258-276 in Key Topics in Conserv. Biol. 2, John Wiley & Sons.*

23 Muchhala, N. and Thomson, J.D. (2009) Going to great lengths: selection for long corolla tubes in an extremely specialized bat-flower mutualism. *Proc. R. Soc. B* 276, 2147-2152

22 Dobson, A. *et al.* (2006) Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* 87, 1915-1924

23 Terborgh, J. *et al.* (2008) Tree recruitment in an empty forest. *Ecology* 89, 1757-1768

24 Edwards, D.P. *et al.* (2013) Trophic flexibility and the persistence of understory birds in intensively logged rainforest. *Conserv. Biol.* 27, 1079-1086

25 Laufer, J. *et al.* (2013) Assessing sampling biases in logging impact studies in tropical forests. *Trop. Conserv. Sci.* 6, 16-34

26 Lindenmayer, B.D. and Laurance, W.F. (2012) A history of hubris – Cautionary lessons in ecologically sustainable forest management. *Biol. Conserv.* 151, 11-16

27 Ramage, B.S. *et al.* (2013) Pseudoreplication in tropical forests and the resulting effects on biodiversity conservation. *Conserv. Biol.* 27, 364-372

28 Gibson, L. *et al.* (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378-381

29 Edwards, D.P.*, et al.* (2010) Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. *Conserv. Lett.* 3, 236-242

30 Wich, S.A. *et al.* (2012) Understanding the impacts of land-use policies on a threatened species: Is there a future for the Bornean Orang-utan? *PLoS ONE* 7, e49142

31 Baraloto, C. *et al.* (2012) Contrasting taxonomic and functional responses of a tropical tree community to selective logging. *J. Appl. Ecol.* 49, 861-870

32 Ernst, R. *et al.* (2006) Diversity erosion beyond the species level: Dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biol. Conserv.* 133, 143-155

33 Velho, N. *et al.* (2012) Shifts in community structure of tropical trees and avian frugivores in forests recovering from past logging. *Biol. Conserv.* 153, 32-40

34 Meijaard, E. *et al.* (2008) Phylogenetic age is positively correlated with sensitivity to timber harvest in bornean mammals. *Biotropica* 40, 76-85

35 Gray, M.A. *et al.* (2007) The response of avian feeding guilds to tropical forest disturbance. *Conserv. Biol.* 21, 133-141

36 Cardillo, M., *et al.* (2005) Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239-1241

37 Poulsen, J.R. *et al.* (2011) Decoupling the effects of logging and hunting on an Afrotropical animal community. *Ecol. Appl.* 21, 1819-1836

38 Wilcove, D.S. *et al.* (2013) Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends Ecol. Evol.* 28, 531-540

39 Padmanaba, M. and Sheil, D. (2014) Spread of the invasive alien species *Piper aduncum* via logging roads in Borneo. *Trop. Conserv. Sci.* 7, 35-44

40 Schleuning, M. *et al.* (2011) Forest fragmentation and selective logging have inconsistent effects on multiple animal-mediated ecosystem processes in a tropical forest. *PLoS ONE* 6, e27785

41 Reiss, J. *et al.* (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24, 505-514

42 Terborgh, J. *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science* 294, 1923-1926

43 Woodcock, P. *et al.* (2013) Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. *PLoS ONE* 8, e60756

44 Edwards, F.A. *et al.* (2013) Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis* 155, 313-326

45 Edwards, F.A., *et al.* (2014) Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Anim. Conserv.* 17, 163-173

46 Van Bael, S.A. *et al.* (2003) Birds defend trees from herbivores in a Neotropical forest canopy. *Proc. Natl. Acad. Sci. U.S.A.* 100, 8304-8307

47 Pavlacky, D.C. *et al.* (2012) Anthropogenic landscape change promotes asymmetric dispersal and limits regional patch occupancy in a spatially structured bird population. *J. Anim. Ecol.* 81, 940-952

48 Lewis, S.L. *et al.* (2009) Increasing carbon storage in intact African tropical forests. *Nature* 457, 1003-1006

49 Asner, G.P. *et al.* (2010) High-resolution forest carbon stocks and emissions in the Amazon. *Proc. Natl. Acad. Sci. U.S.A.* 107, 16738-16742

50 Hergoualc'h, K. and Verchot, L.V. (2011) Stocks and fluxes of carbon associated with land use change in Southeast Asian tropical peatlands: A review. *Global Biogeochem. Cy.* 25, GB2001

51 Bonnell, T.R. *et al.* (2011) Post-logging recovery time is longer than expected in an East African tropical forest. *Forest Ecol. Manag.* 261, 855-864

52 Huang, M.Y. and Asner, G.P. (2010) Long-term carbon loss and recovery following selective logging in Amazon forests. *Global Biogeochem. Cy.* 24, GB3028

53 West, T.A.P., *et al.* (2014) Forest biomass recovery after conventional and reduced-impact logging in Amazonian Brazil. *Forest Ecol. Manag.* 314, 59-63

54 Makarieva, A.M., *et al.* (2014) Why Does Air Passage over Forest Yield More Rain? Examining the Coupling between Rainfall, Pressure, and Atmospheric Moisture Content. *J Hydrometeorol* 15, 411-426

55 Webb, T.J. *et al.* (2005) Forest cover-rainfall relationships in a biodiversity hotspot: The Atlantic forest of Brazil. *Ecol. Appl.* 15, 1968-1983

56 Wang, K. and Dickinson, R.E. (2012) A review of global terrestrial evaoptranspiration: Observation, modeling, climatology and climatic variability. *Rev. Geophys.* 50, RG2005

57 Mahmood, R. *et al.* (2013) Land cover changes and their biogeophysical effects on climate. *Int. J. Climatol.* 10.1002/joc.3736

58 Spracklen, D.V. *et al.* (2012) Observations of increased tropical rainfall preceded by air passage over forests. *Nature* 489, 282-286

59 Ramdani, F. *et al.* (2014) Local surface temperature change due to expansion of oil palm plantation in Indonesia. *Climatic Change* DOI 10.1007/s10584-013-1045-4

60 Meijaard, E. *et al.* (2013) People's perceptions about the importance of forests on Borneo. *PLoS ONE* 8, e73008

61 Lele, S. (2009) Watershed services of tropical forests: from hydrology to economic valuation to integrated analysis. *Curr. Opin. Environ. Sustainability* 1, 148-155

62 Bruijnzeel, L.A. (2004) Hydrological functions of tropical forests: not seeing the soil for the trees? *Agr. Ecosyst. Environ.* 104, 185-228

63 Hartanto, H. *et al.* (2003) Factors affecting runoff and soil erosion: plot-level soil loss monitoring for assessing sustainability of forest management. *Forest Ecol. Manag.* 180, 361-374

64 Chan, N.W. and Parker, D.J. (1996) Response to dynamic flood hazard factors in peninsular Malaysia. *Geogr. J.* 162, 313-325

65 Douglas, I. (1999) Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: a review. *Phil. Trans. R. Soc. B* 354, 1725-1738

66 Wells, J. *et al.* (2013) Forests, floods, people and wildlife on Borneo. *UNEP, Bangkok, Thailand.*

67 Sidle, R.C. *et al.* (2006) Erosion processes in steep terrain - Truths, myths, and uncertainties related to forest management in Southeast Asia. *Forest Ecol. Manag.* 224, 199-225

68 Walsh, R.P.D. *et al.* (2011) Long-term responses of rainforest erosional systems at different spatial scales to selective logging and climatic change. *Phil. Trans. R. Soc. B* 366, 3340-3353

69 Laurance, W.F. *et al.* (2009) Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24, 659-669

70 FAO (2010) Global forest resources assessment 2010. Progress towards sustainable forest management. *FAO Forest Paper 163. Food and Agricultural Organization of the United Nations, Rome, Italy.*

71 Asner, G.P. *et al.* (2006) Condition and fate of logged forests in the Brazilian Amazon. *Proc. Natl. Acad. Sci. U.S.A.* 103, 12947-12950

72 Gaveau, D.L.A. *et al.* (2013) Reconciling forest conservation and logging in Indonesian Borneo. *PLoS ONE* 8, e69887

73 Sloan, S. *et al.* (2012) Does Indonesia's REDD+ moratorium on new concessions spare imminently threatened forests? *Conserv. Lett.* 5, 222-231

74 Bennett, E.L. and Gumal, M.T. (2001) *The interrelationships of commercial logging, hunting, and wildlife in Sarawak: recommendations for forest management*.

75 Van Nieuwstadt, M.G.L. *et al.* (2001) The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. *Conserv. Biol.* 15, 1183-1186

76 Veldman, J.W.*, et al.* (2009) Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. *Forest Ecol. Manag.* 258, 1643-1649

77 Blate, G.M. (2005) Modest trade-offs between timber management and fire susceptibility of a Bolivian semi-deciduous forest. *Ecol. Appl.* 15, 1649-1663

78 Lindenmayer, D.B. *et al.* (2012) A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conserv. Lett.* 5, 421-431

79 Edwards, D.P. *et al.* (2014) Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Glob. Ch. Biol.* 20, 183-191

80 Dennis, R.A. *et al.* (2008) Biodiversity conservation in Southeast Asian timber concessions: a critical evaluation of policy mechanisms and guidelines. *Ecol. Soc.* 13, 25

81 Kollet, W. and Lagan, P. (2005) Do certified tropical logs fetch a market premium? A comparative price analysis from Sabah, Malaysia. *XXII IUFRO World Congress Proceedings, Session 163.*

82 Meijaard, E. *et al.* (2011) Report on barriers and constraints to ecosystem services certification. *CIFOR Occasional Paper No. 66.*

83 DeFries, R. *et al.* (2005) Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecol. Appl.* 15, 19-26

84 Peres, C.A. (2005) Why we need megareserves in Amazonia. *Conserv. Biol.* 19, 728-733

85 Gillies, C.S. and Clair, C.C.S. (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proc. Natl. Acad. Sci. U.S.A.* 105, 19774-19779

86 Bregman, T.P.*, et al.* (2014) Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. *Biol. Conserv.* 169, 372-383

87 Poore, M.E.D. (1968) Studies in Malaysian rain forest. I. Forest on Triassic sediments in Jengka Forest Reserve. *J. Ecol.* 56, 143-&

88 Laurance, W.F. and Curran, T.J. (2008) Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecol.* 33, 399-408

89 Levey, D.J. (1988) Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69, 1076-1089

90 Elkin, C.M. and Possingham, H. (2008) The role of landscape-dependent disturbance and dispersal in metapopulation persistence. *Am. Nat.* 172, 563-575

91 Ramage, B.S. *et al.* (2013) Conserving tropical biodiversity via strategic spatiotemporal harvest planning. *J. Appl. Ecol.* 50, 1301-1310

92 Dias, M.S. *et al.* (2010) Effects of reduced-impact logging on fish assemblages in Central Amazonia. *Conserv. Biol.* 24, 278-286

93 Azevedo-Ramos, C. *et al.* (2006) Short-term effects of reduced-impact logging on eastern Amazon fauna. *Forest Ecol. Manag.* 232, 26-35

94 Samejima, H.*, et al.* (2012) Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management. *Forest Ecol. Manag.* 270, 248-256

95 Edwards, D.P., *et al.* (2012) Reduced-impact logging and biodiversity conservation: a case study from Borneo. *Ecol. Appl.* 22, 561-571

96 Ferraz, G., *et al.* (2003) Rates of species loss from Amazonian forest fragments. *Proc. Natl. Acad. Sci. U.S.A.* 100, 14069-14073

97 Gourlet-Fleury, S., *et al.* (2013) Tropical forest recovery from logging: a 24 year silvicultural experiment from Central Africa. *Phil. Trans. R. Soc. B* 368, 20120302

98 Kettle, C.J. (2012) Seeding ecological restoration of tropical forests: Priority setting under REDD+. *Biol. Conserv.* 154, 34-41

99 Rey Benayas, J.M., *et al.* (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325, 1121-1124

100 Venter, O., *et al.* (2013) Using systematic conservation planning to minimize REDD plus conflict with agriculture and logging in the tropics. *Conserv Lett* 6, 116-124

Figure legends (high resolution files attached separately)

Figure 1. The impacts of logging on forest structure and biodiversity. **(A)** The Bwindi forest is a former logging concession and is home to the mountain gorilla **(B)**, which thrives on the succulent herbs growing in logging gaps. **(C)** Orangutan in a timber concession in Borneo, where 42% of the total population live within logged or formerly logged forests. **(D)** Logging roads to extract timber. If entrance points are not guarded then logging roads permit easy access to remote forests by bushmeat hunters. **(E)** Logging roads inhibit movement of forest-interior specialists, such as the ant-following scale-backed antbird (*Willisornis poecilinotus*) of the Amazon. Reproduced, with permission, from Douglas Sheil (A,B), Nardiyono (C), Erik Meijaard (D); and Susan Laurance (E).

Figure 2. The biological value of selectively logged forests is much higher than other disturbed habitats. Each habitat is weighted against the species richness of an old-growth forest (black dashed line), such that increasing values indicate more detrimental impacts of a habitat disturbance. Median values are plotted (central line), with notch width of median value representing 95% confidence intervals and with coloured bars representing interquartile ranges of 10,000 resampled effect sizes. Selectively logged forests have by far the smallest negative impact compared to old-growth forest and they are far better for species richness than all other forms of disturbed environment. The logged forest bar is divided by region and taxonomic group: it is only in Asia (As) where impacts are apparently very detrimental compared to old-growth forest. By contrast, in South America (SA) or Central Africa (CA), and when focusing on mammals (m) or birds (b), there is a minor positive impact of logging on species richness, and for plants (p) and amphibians (a) a minor negative impact. Data from [28].

Figure 3. Elevation of bird trophic levels after logging. Mean (±SE) tropic levels are plotted for ten species commonly recorded in both old-growth (unlogged)

and logged forest. From left, species are *Arachnothera longirostra*, *Stachyris erythroptera*, *Trichastoma bicolor*, *Malacocincla sepiaria*, *Macronous ptilosus*, *Malacocincla malaccensis*, *Hypogramma hypogrammicum*, *Sasia abnormis*, *Alophoixus phaeocephalus*, *Prionochilus maculatus.* All $P<0.05$, except *Prionochilus maculates*, which is not significant. Data from [24]. Image is a little spiderhunter (*Arachnothera longirostra*), which feed from higher up the food chain in logged versus old-growth forest. Image reproduced with permission from David Edwards.

Figure 1

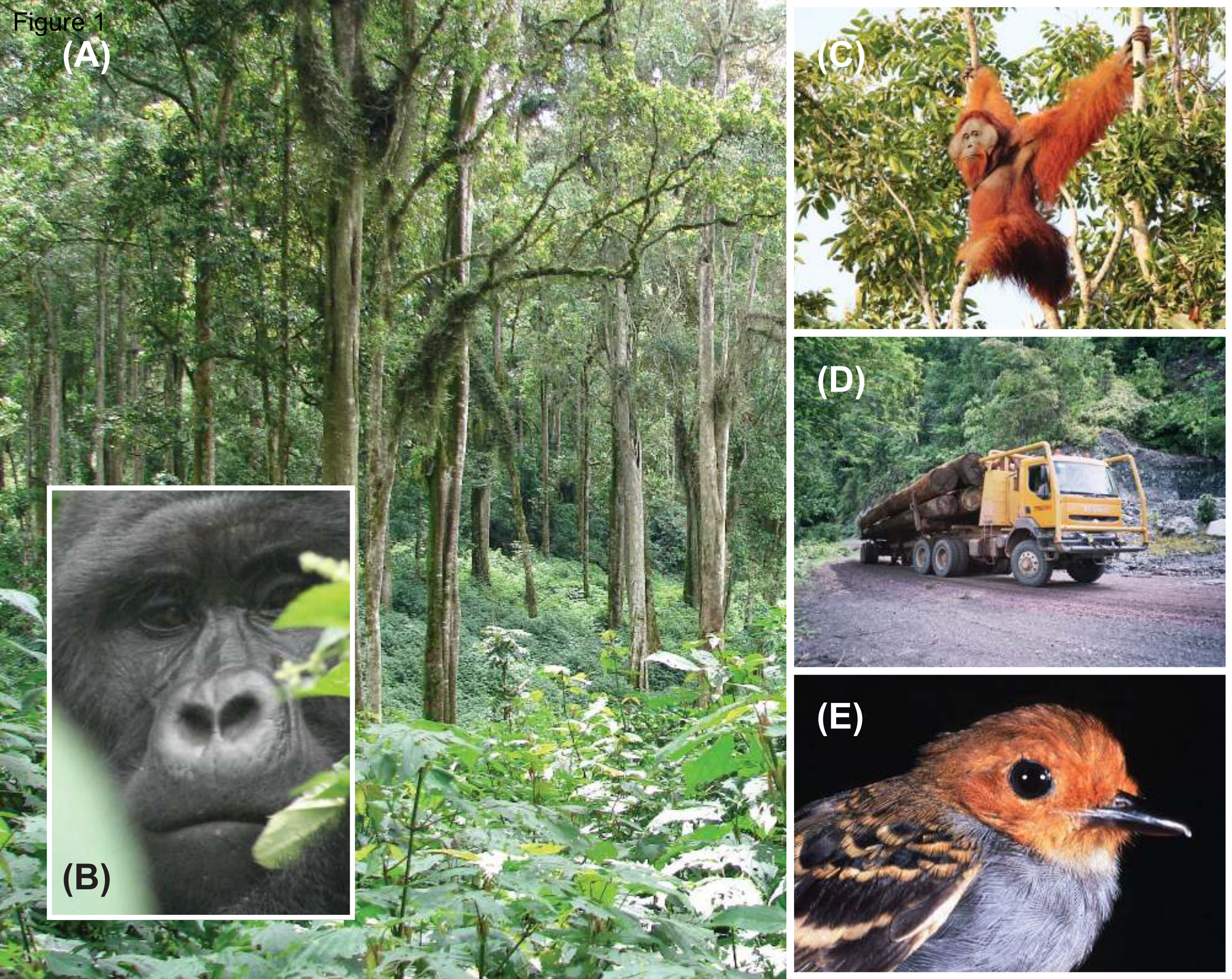
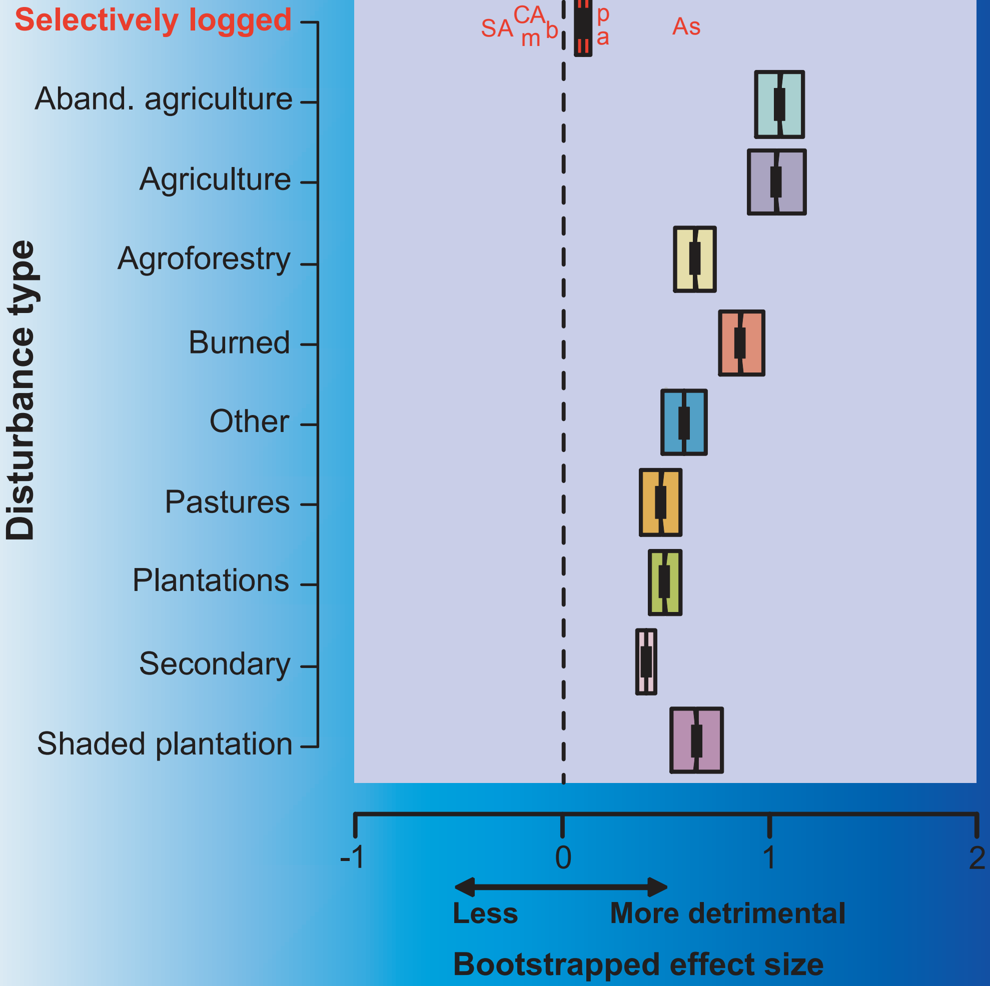
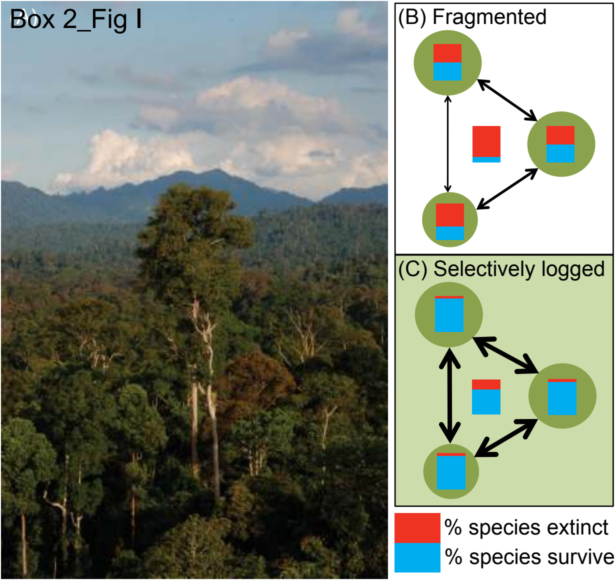


Figure 2


Selectively logged
SA
CA
m
b
p
a
As
Aband. agriculture
Agriculture
Agroforestry
Burned
Other
Pastures
Plantations
Secondary
Shaded plantation
Disturbance type
-1
0
1
2
Less
More detrimental
Bootstrapped effect size

Box 2_Fig I


(B) Fragmented
(C) Selectively logged
🟥 % species extinct
🟦 % species survive

Box 3_Fig I

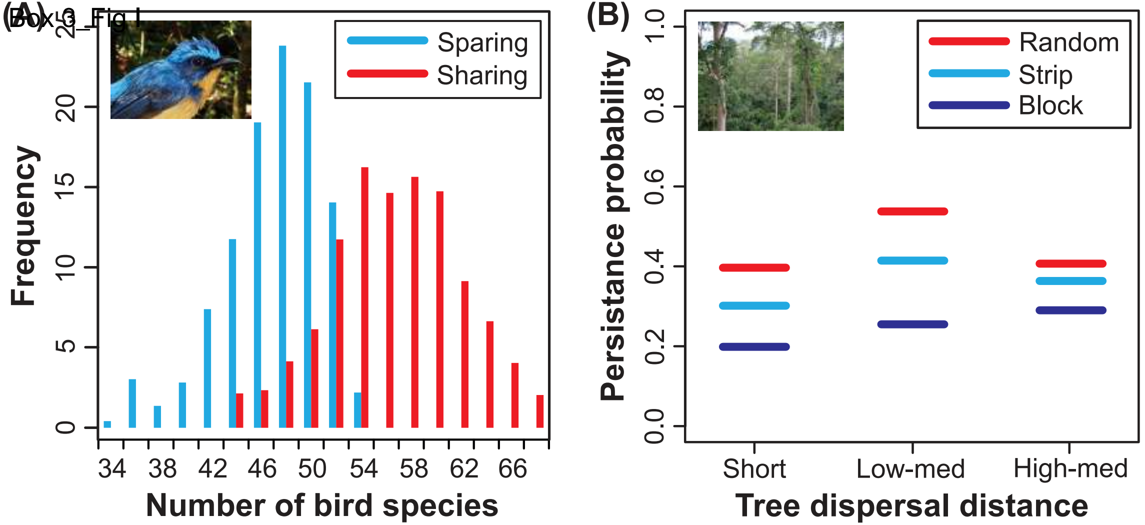
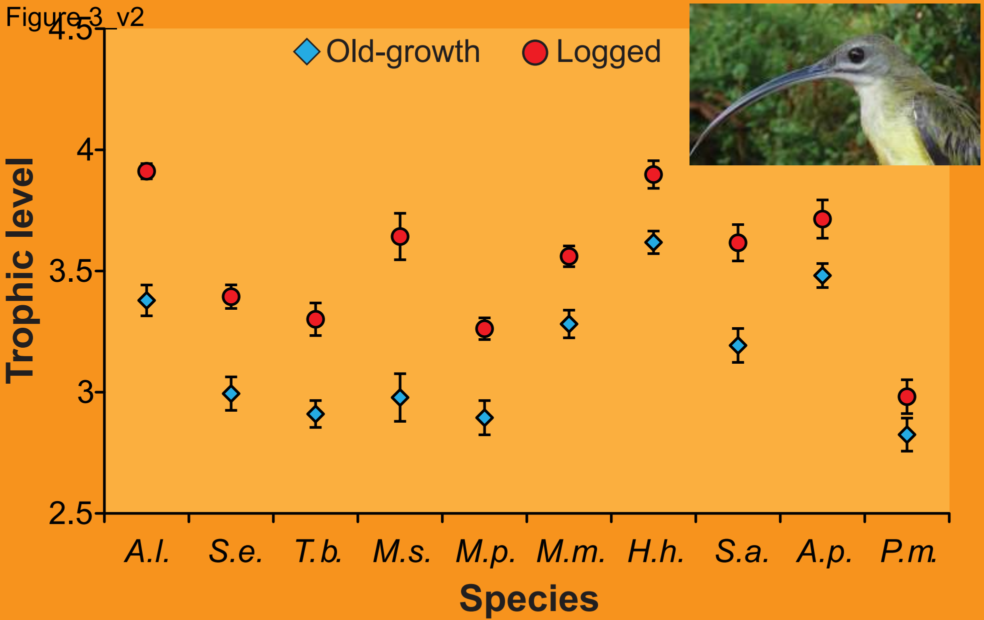

(A)
Frequency
0
5
10
15
20
25
Number of bird species
34
38
42
46
50
54
58
62
66
Sparing
Sharing
(B)
Persistance probability
0.0
0.2
0.4
0.6
0.8
1.0
Random
Strip
Block
Short
Low-med
High-med
Tree dispersal distance

Figure_3_v2


Old-growth
Logged
Trophic level
4.5
4
3.5
3
2.5
A.l.
S.e.
T.b.
M.s.
M.p.
M.m.
H.h.
S.a.
A.p.
P.m.
Species