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Human-Altered Mesoherbivore Densities and Cascading Effects on Plant and Animal Communities in Fragmented Tropical Forests

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1. Introduction

Rainforest loss and fragmentation are proceeding at an alarming rate, and having demonstrable consequences for the relevant plant and animal communities. Between 1984 and 1990 6.5 million hectares of humid tropical rainforest were lost annually worldwide (Hansen & DeFries, 2004). This rate increased to 7.3 million hectares annually between 1990-1997, due largely to accelerating deforestation rates in Asia. Though the pantropical deforestation rate slowed to 5.5 million hectares annually between 2000-2005 due to slowing in much of Asia and Latin America, deforestation continues to increase in Brazil (Hansen et al., 2008). As of 2005, half to two-thirds of humid tropical regions have <50% tree cover, with an additional 20% undergoing selective logging between 2000 and 2005 (Asner et al., 2009; Table 1).

Much of the remaining original forest persists as small, isolated fragments. The highest rates of forest fragmentation are found in North and South America, respectively (Riitters et al., 2000). In the Amazon, the amount of forest in fragments or within 1km of forest edge exceeded the extant forest area by 150% (Skole & Tucker, 1993), and between 1999 and 2002 over 30,000 km of new forest edge was created there annually (Broadbent et al., 2008). Asia and Africa currently have the lowest levels of tropical rainforest fragmentation, although with the rapidly accelerating Southeast Asian deforestation rates this is likely to change (Sodhi et al., 2010a).

Such loss and fragmentation of tropical forest, coupled with other global change phenomena, have profound and diverse effects on the remaining forest fragments. The very complexity of these synergistic effects is only beginning to be documented and comprehended. Recent studies show that tropical forest fragmentation disproportionately affects the largest vertebrates (Henle et al., 2004; Stork et al., 2009; Wilkie et al., 2011). Large predators experience the strongest fragmentation effects, with cascading consequences for the small- and intermediate-sized herbivores regulated by vertebrate predators (Duffy, 2003; Purvis et al., 2000; Redford, 1992). Altered populations of these herbivores, which we term "mesoherbivores" (after Soulé et al.'s (1988) term "mesopredator" referring to small- and intermediate-sized predators), in turn cascade down to affect plant growth and recruitment via altered seed predation and dispersal (Duffy, 2003; Redford, 1992).

	Annual deforestation rate (x10^6 hectares)			Selective logging[3] (%)
	1984-1990[1]	**1990-1997[1]**	**2000-2005[2]**	**2000s**
Latin America	4.31	4.28	3.31	17.2%
Tropical Asia	1.81	2.57	1.88	19.2%
Tropical Africa	0.43	0.37	0.30	27.2%
Pantropical	6.50	7.30	5.50	20.3%

[1] Data from Hansen & DeFries, 2004
[2] Data from Hansen et al., 2008
[3] Percent of regional forest area experiencing selective logging. Data from Asner et al., 2009

Table 1. Annual deforestation rate and selective logging extent in humid tropical forests.

Herein, we review both the direct and indirect effects of fragmentation on tropical forest communities. We review the literature on vertebrate herbivores both because few reviews are available for tropical forests and the pervasiveness and diversity of their ecological effects remain largely undocumented. We begin by reviewing the substantial tropical literature on human overhunting of mesoherbivores and the consequences this has for tropical forest plant communities, in an effort to understand the magnitude of the effects of human-perturbed mesoherbivore populations on tropical forest plant communities.

Ultimately, however, we are particularly interested in the poorly-studied phenomenon wherein loss of vertebrate predators without compensatory human hunting may result in dramatic increases in mesoherbivore populations, which we call "mesoherbivore release." This phenomenon has been observed in multiple temperate systems, as well as tropical savanna and grassland systems (see review in Salo et al., 2010), yet it is poorly studied in tropical forests. This section of the review will synthesize for the first time the sparse and scattered literature involving putative tropical examples of mesoherbivore release, making the case that the cascading consequences of increased mesoherbivore abundance can be as widespread and ecologically destructive as those resulting from mesoherbivore decline. Finally, we address the most pressing conservation and management implications of the research on perturbed mesoherbivore populations, both decline and release. We also identify topics in need of further investigation, in terms of both ecology and conservation.

2. Direct effects of fragmentation

Predictably, rainforest loss and fragmentation are dramatically altering tropical forests, both directly and indirectly. Loss of forest area and, to a lesser degree fragmentation, directly drive population decline and extinction of myriad plant, invertebrate, and vertebrate species pan-tropically (Beier et al., 2002; Fahrig, 1997, 2002, 2003; Laurance, 1999; Laurance et al., 2011; Michalski & Peres, 2007; Newmark, 1991; Sodhi et al., 2008, 2010b; Yaacobi et al., 2007). Pervasive edge effects further alter the microclimate and vegetation structure of remnant fragments, affecting still more species (Fletcher et al., 2007; Laurance, 2000; Laurance et al., 2002, 2011; Lindell et al., 2007; Manu et al., 2007; Norris et al., 2008; Pardini, 2004; Tabarelli et al., 2008). Synergistic interactions between fragmentation and other global change drivers, notably climate change with its concomitant increased drought and fire frequency, and

exploitation of wildlife, further exacerbate loss and degradation of remnant tropical rainforest and their plant and animal communities (Brook et al., 2008; Ewers & Didham, 2006; Laurance & Useche, 2009; Laurance & Williamson, 2001; Tabarelli et al., 2008). Roads and other infrastructure also contribute to accelerating declines of mammals, birds, and other organisms in both fragments and intact forests (Benítez-López et al., 2010), e.g., by increasing hunting pressure (Peres, 2001).

Even if a species persists temporarily in fragmented forest, it is likely to experience reduced genetic diversity, inbreeding depression, reduced adaptive potential, and accumulation of deleterious mutations (Keyghobadi, 2007). Inbreeding depression and reduced genetic diversity combine with dispersal limitation, competitive disadvantages, fragment area and isolation effects, and other species- and fragment-level traits to create an "extinction debt," wherein extinctions proceed for decades post-fragmentation (Brooks et al., 1999; Ewers & Didham, 2006; Ferraz et al., 2003; Laurance et al., 2008; Metzger et al., 2009; Tilman et al., 1994), if not at the rate once thought (He & Hubbell, 2011). These high short- and long-term extinction rates, combined with the rapid and accelerating loss and fragmentation of remnant tropical forest, have led many scientists to warn of a tropical biodiversity crisis resulting in a potential mass wave of extinctions rivaling historical extinction events, resulting in an era of novel secondary tropical forests (Bradshaw et al., 2009; Brook et al., 2008; Dirzo & Raven, 2003; Gardner et al., 2007; Laurance, 1999, 2006; Lugo, 2009; but see Wright & Muller-Landau, 2006a,b).

Species declines following rainforest loss and fragmentation are highly non-random. Fragmentation-sensitive species typically share a common suite of traits, including small population size/rarity, large body size, and specializations (see Table 2). Many of these traits (e.g., "slow" life-histories, dietary and habitat specialization) are unique to, or relatively prevalent in tropical species, thus rendering many paradigms (e.g., edge effects) and conservation strategies developed for temperate and boreal forests largely irrelevant when developing conservation plans for tropical forests (Stratford & Robinson, 2005).

Common traits of fragmentation-sensitive species	
Small population size / rarity	High sociality
Large body size	Disturbance- and competition- sensitivity
High trophic position	Specialized diet (e.g., insectivorous and large frugivorous birds)
Fluctuating population dynamics	Specialized habitat use (especially forest interior)
"Slow" life-histories (low fecundity, high annual survival)	Location near edge of altitudinal or biogeographical range
Low dispersal capability	Involved in mutualistic interaction

Table 2. Common traits of fragmentation-sensitive species (from Henle et al., 2004; Kattan et al., 1994; Laurance, 1991; Laurance et al., 2011; Lees & Peres, 2008; Sigel et al., 2006, 2010; Stork et al., 2009)

Tropical forests also tend to harbor diverse, pervasive mutualistic interactions, notably plant-animal interactions (Terborgh & Feeley, 2010). Between 70 and 90% of tropical trees rely on animals for seed dispersal (Muller-Landau & Hardesty, 2005), and >95% of lowland

tropical trees are animal-pollinated (Bawa et al., 1985). Thus, habitat loss and fragmentation also alter many important plant-animal interactions, including pollination, seed dispersal, seed predation, and herbivory (Herrera et al., 2011; Laurance, 2005). Some of these altered interactions result from direct effects of habitat loss and fragmentation on plants and animals involved in mutualisms, e.g., extirpations of forest-interior butterflies following loss of their host plants (Brown & Hutchings, 1997; Koh et al., 2004). However, in many cases plant-animal interactions change in response to indirect effects of other animals declining higher in the food chain, in what is known as trophic cascades.

3. Indirect effects of fragmentation: Trophic cascades

Fragmentation effects are particularly strong on large predators, due to their high trophic position, "slow" life-histories that preclude rapid population response to disturbances, large home ranges, and other traits characteristic of fragmentation-sensitive species. Apex predators such as jaguars, pumas, tigers, leopards, large raptors, and large snakes are amongst the first species to disappear from tropical rainforest fragments (Duffy, 2003; Pimm et al., 1988; Purvis et al., 2000; Ray et al., 2005; Redford, 1992; Terborgh, 1992). Moreover, the cascading consequences resulting from apex predator loss can dramatically affect ecosystem structure and function in ways we are just beginning to understand, and thus far exceed the effects of loss of species from lower trophic levels (Dobson et al., 2006; Duffy, 2003; Estes et al., 2011; Schmitz et al., 2010; Terborgh et al., 1999).

Trophic cascades, wherein perturbations of apex predator populations cascade down to affect lower consumer (e.g., herbivore) and producer (i.e., plant) levels (Paine, 1980), were once thought not to occur in tropical forests as a result of their high species diversity and high intraguild predation, leading to functional redundancy and weak links between individual predator and prey species (Polis & Holt, 1992; Polis & Strong, 1996; Shurin et al., 2002; Strong, 1992; Van Bael et al., 2003; Vance-Chalcraft et al., 2007). Terborgh (1992) first presented evidence suggesting a carnivore (jaguar, *Panthera onca*; puma, *Puma concolor*) – large seed predator (peccary, *Pecari* spp.; paca, *Cuniculus* spp.; agouti, *Dasyprocta* spp.) – large-seeded tree (*Dipteryx, Protium*) trophic cascade at Barro Colorado Island, Panama. Three years later, Dial and Roughgarden (1995) published one of the first experimental studies of trophic cascades in tropical rainforest, showing that insectivorous *Anolis* lizards limit herbivorous insects and in turn, herbivory on canopy trees. Shortly thereafter, Letourneau and Dyer (1998) were the first to experimentally show a four-level (beetle – ant – herbivore – plant) trophic cascade in tropical rainforest understory. Within the next few years, a flurry of exclosure experiments demonstrated that insectivorous birds and bats limit arthropod herbivores and herbivory in rain forest canopy and understory (review by Van Bael et al., 2008; Kalka et al., 2008; Michel et al., in review; Williams-Guillén et al., 2008).

Additionally, a number of experimental and observational studies have shown effects of mesopredator release (reviews by Brashares et al., 2010; Prugh et al., 2009). Mesopredator release is a phenomenon wherein small to mid-sized predators increase in abundance following declines of their own predators, resulting in declines in their prey, which are typically small herbivores and insectivores, especially birds and small rodents (Fig. 1; Soulé et al. 1988, Crooks and Soulé 1999). Though first documented in fragmented temperate habitats, Laurance (1994) noted increases in rodents - including one species, *Uromys*, known

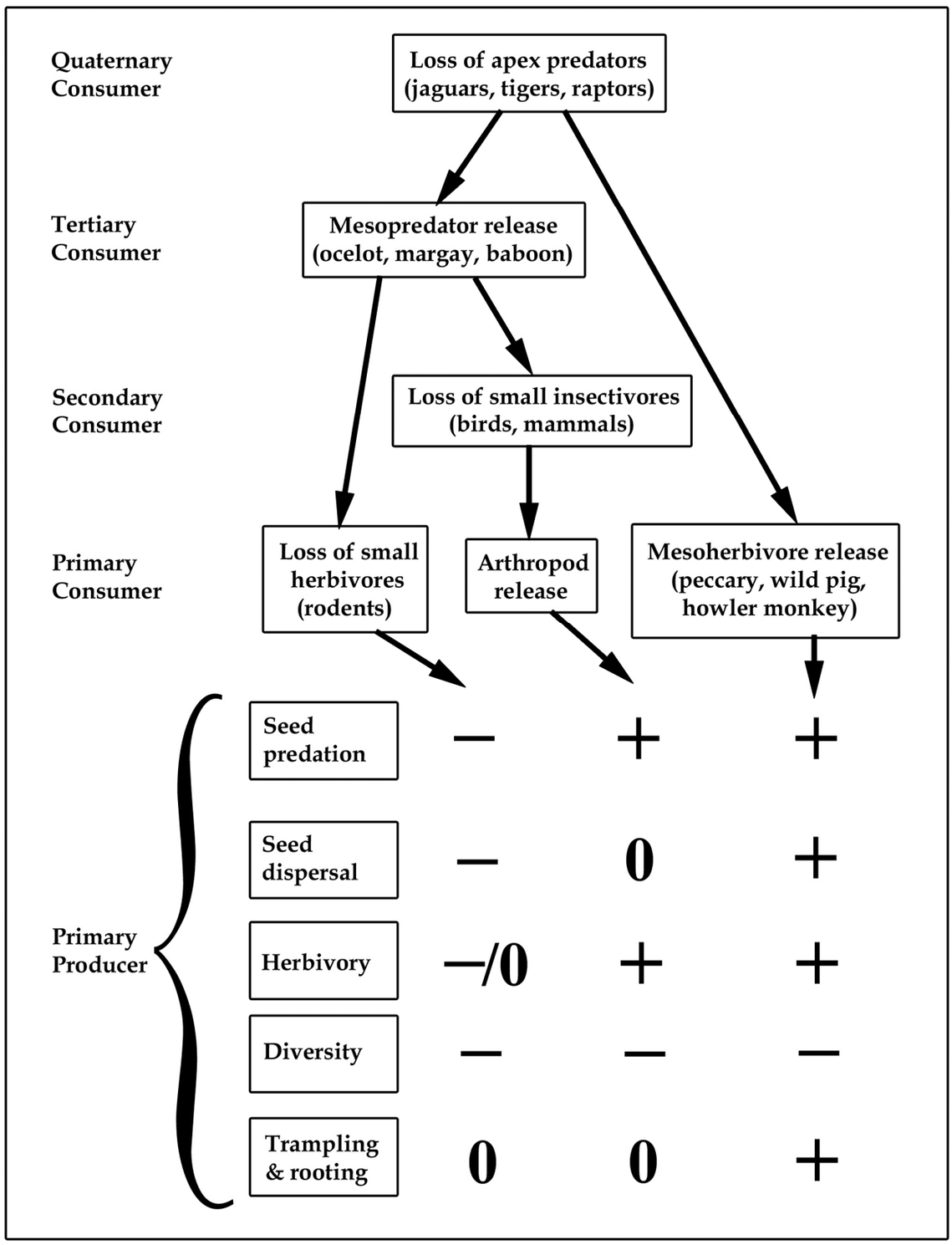


Fig. 1. Diagrammatic representation of the potential cascading consequences of apex predator loss via mesopredator and mesoherbivore release.

to depredate bird nests and consume small vertebrates - in Australian rainforest fragments missing large predators. Increases in other small, generalist predators (e.g., barn owls, red-bellied blacksnakes, and white-tailed rats) were also observed in fragments without large, specialist predators (Laurance, 1997). Elsewhere in Australia, declines and extirpations of dingoes, an apex predator, resulted in continent-wide collapse of native marsupials due to release of invasive house cats and red foxes from predation (Johnson et al., 2007). On Barro Colorado Island, Panama, high avian nest predation has been attributed in part to increased small mammalian nest predators such as white-nosed coatimundi (*Nasua narica*), white-faced capuchin monkeys (*Cebus capucinus*), and opossums following isolation from the mainland, and subsequent loss of large carnivores, when the Panama Canal was built (Loiselle & Hoppes, 1983; Sieving, 1992; Wright et al., 1994). On the Lago Guri islands in Venezuela, former hilltops isolated from nearby mainland by a hydro-electric reservoir, anomalously low bird densities were associated with abundant olive capuchin monkeys (*Cebus olivaceus*), which depredated all artificial nests (Terborgh et al., 1997). Olive baboons (*Papio anubis*) also dramatically increased in Ghana following steep declines in lions (*Pantera leo*) and leopards (*Pantera pardus*), negatively impacting smaller ungulates, primates, rodents, and birds, as well as human livestock, pets, and crops (Brashares et al., 2010).

In summary, strong trophic cascades, resulting in increases in arthropod herbivores and mesopredators, have been repeatedly demonstrated to occur in tropical rainforest despite the functional redundancy and potentially weak links between predators and prey (Terborgh & Feeley, 2010). However, very few experimental studies have focused on the potential cascading consequences of loss of large terrestrial predators on vertebrate herbivores (i.e., of mesoherbivore release), and subsequent plant community effects, despite the fact that large predators have been shown to effectively limit vertebrate herbivores in a variety of habitats worldwide (Estes et al., 2011; Salo et al., 2010). This is likely due, in large part, to logistical, methodological, and financial constraints, including the large scale of impacts and the long generation times of vertebrate herbivores and the trees they frequently impact; responses may not be apparent for years or even decades following perturbations to predator and herbivore populations (Terborgh & Estes, 2010). Furthermore, in many cases, apex predator populations were decimated decades or centuries prior to the development of the theory of trophic cascades (Estes et al., 2011). Moreover, across much of the tropics, the lost ecological services attributable to prey regulation (Dobson et al., 2006, Schmitz et al., 2010) once provided by predators such as jaguars, leopards, and tigers have been compensated - and often overcompensated - for by a new apex predator: human hunters.

4. Humans, herbivores, and tropical tree germination and recruitment

By far the majority of studies documenting cascading effects of altered vertebrate herbivore densities on rainforest plant communities have focused on consequences of extirpated or greatly reduced herbivore populations. Herbivores, especially larger herbivores, often experience declines due to simple area effects of habitat loss and fragmentation (MacArthur & Wilson, 1967; e.g., Dalecky et al., 2002; Laurance et al., 2011), as well as edge effects (Norris et al., 2008; Restrepo et al., 1999), altered vegetation structure, local climate (e.g., droughts), and/or microclimate within fragments (Chiarello, 1999; Fleury & Galetti, 2006; Laurance, 1994; Laurance et al., 2008; Laurance & Williamson, 2001). But tropical forests are rarely impacted by habitat loss and fragmentation alone. Many anthropogenic factors, including logging, fires, introduction of invasive species or disease, and hunting, interact

synergistically to exacerbate fragmentation effects on tropical forest residents (Brook et al., 2008; Laurance, 2005, 2008; Laurance & Useche, 2009; Wright 2005, 2010).

Synergistic effects of fragmentation and hunting are particularly strong, as fragmentation - also commonly associated with increased road-building - both a) allows hunters easier access to prey species and to markets, and b) subdivides remnant forest into patches below the minimum area requirement to support sustainable hunting (Peres, 2001). As a result, hunting is having dramatic effects on vertebrates, including herbivores and the plants dependent upon them for pollination and dispersal, resulting in what has come to be known as the "bush meat crisis" (Milner-Gulland et al., 2003; Wright et al., 2007a). Humans have been implicated in extinctions of large vertebrates as far back as 46,000 years ago, when extinctions of Australia's megafauna coincided with human arrival (Roberts et al., 2001). Similarly, humans are partially, if not predominantly, responsible for the North American megafauna extinction, including loss of herbivorous mammoths and mastodons, over 12,000 years ago (Alroy, 2001; Johnson, 2002). The impact of human hunters on large herbivores have only increased as the human population grew exponentially over the last 2,000-3,000 years, and also as it developed modern hunting techniques and weapons, including firearms and traps (Corlett, 2007). Their relative abundance (compared to cats and other apex predators) often makes vertebrate herbivores a prime target for human hunting.

Today human hunting is decimating herbivore populations pan-tropically in intact as well as fragmented forest. In the Congo, 60% of mammals are unsustainably harvested, including 93% of herbivorous ungulates, suggesting catastrophic losses of herbivores and their dependent plants in the near future (Fa et al., 2002). While Fa et al. (2002) estimated that only 20% of Amazonian mammals are unsustainably hunted, Peres and Palacios (2007), using slightly different methods, found that 22 of 30 large mammals, birds, and reptiles significantly declined under high hunting pressure, at rates of up to 74.8%. Large-bodied vertebrates and seed dispersers experienced greater declines than seed predators and browsers. As a result, hunted Amazonian forests will likely experience altered plant communities as large-seeded trees and lianas are no longer able to escape and recruit away from the parent tree (Peres & Palacios, 2007). Indeed, tree species richness is already 55% lower, and density of large-seeded, primate-dispersed trees is 60% lower, in hunted sites near Manu National Park, Peru, where large primates were exterminated and midsize primate populations reduced 80% by hunters (Nuñez-Iturri & Howe, 2007). Another study from the same hunted site found 50-60% lower sapling densities, and declines amongst 72% of tree species, particularly among large-seeded species (Terborgh et al., 2008). Within the Biological Dynamics of Forest Fragments Project (BDFFP) reserves, the large-seeded, mammal-dispersed *Duckeodendron cestroides* experienced a 300% reduction in seed dispersal, 500% reduction in maximum dispersal distance, and 5000% reduction in the number of seeds dispersed 10m beyond the crown in hunted fragments relative to continuous forest (Cramer et al., 2007). Overall, up to one third of Amazonian plants may suffer failed dispersal due to losses of vertebrate seed dispersers (da Silva & Tabarelli, 2000).

Similarly, in the Atlantic coastal forest of Brazil, large-seeded *Astrocaryum aculeatissimum* palms in fragments with low agouti density faced a collapse in seed dispersal, as agoutis disperse more seeds than they predate, and smaller rodents are unable to compensate for the agouti's absence (Donatti et al., 2009). In southern Mexico, fragments <30ha lack most to all large frugivores, and as a result dispersal and recruitment of large-seeded species

declined ~50% (Melo et al., 2010). Large frugivorous seed dispersers have also declined in Australian rainforest fragments, affecting 12% of all plant species, particularly large-seeded species (Moran et al., 2009). In Asia, commercial hunting threatens mass extinctions of mammals greater than 1-2 kg, particularly the major seed dispersers – elephants, tapirs, deer, primates, and large birds and bats, all of which face greater hunting pressure than seed predators. As a result, future Asian forests are likely to be dominated by small-fruited and –seeded, fast-growing trees at the expense of large-seeded species (Corlett, 2007).

While all the studies cited above found declines in large-seeded tree species in hunted fragments due to loss of seed dispersers, a number of studies have found the opposite: large-seeded species increase in abundance and diversity due to the loss of hunted vertebrate seed predators. In Panama, hunters favor large-seeded tree species by removing seed predators (e.g., Central American agoutis, *Dasyprocta punctata*, and collared peccaries, *Pecari tajacu*), and thereby increasing seedling survival (Wright et al., 2007b), resulting in 300-500% higher seedling density of two large-seeded palms at heavily hunted sites (Wright et al., 2000). Lianas also benefit from hunting, as most liana seeds are wind-dispersed, then escape competition from small-seeded species that have lost their seed dispersers (Wright et al., 2007b). This effect is particularly pronounced in Los Tuxtlas, Mexico, where thick monospecific carpets of large-seeded seedlings result from heavy rodent predation of small-seeds (Dirzo et al., 2007). In northeastern Costa Rica, large-seeded *Dipteryx panamensis* escaped predation in fragments due to heavy hunting of squirrels (*Sciurus* spp.), agoutis, and peccaries, resulting in higher seedling densities (Hanson & Brunsfeld, 2006). However, even where seed and seedling survival is increased due to the loss of seed predators, the concurrent loss of seed dispersers often results in monospecific seed and seedling carpets clustered underneath conspecific parent trees, eventually resulting in lower tree species diversity (Figure 2; Wright et al., 2000; Wright & Duber, 2001).



Fig. 2. Collared peccary (*Pecari tajacu*; top left), Central American Agouti (*Dasyprocta punctata*; bottom left), and a carpet of undispersed *Attalea butyraceae* fruits at a heavily hunted site in Parque Nacional Camino de Cruces, Panama (all photos by Nicole L. Michel).

Relative seed dispersal and predation rates between hunted fragments and protected forest tend to be highly plant species-specific (Guariguata et al., 2000, 2002; Wright et al., 2000). Regardless of which species are impacted or favored by increased hunting pressure on seed dispersers and predators, it is clear that the loss of large herbivores and frugivores is having dramatic effects on density and diversity of the remnant plant communities (Wright, 2010; Wright et al., 2007a). There is some hope, however, that negative density dependence may allow once declining plant species to rebound as the forest is protected, and once seed disperser and predator populations to return to their historical levels (Muller-Landau, 2007).

5. Mesoherbivore release

The previous section focused on the consequences of excessive human predation on midsize and large herbivores and frugivores, the so-called mesoherbivores. However, large non-human predators also effectively limit vertebrate herbivores in diverse natural systems (Fig. 1; Estes et al. 2011; Salo et al., 2010). What happens when large non-human predators are removed in the absence of human hunting? Terborgh (1992) first suggested that the loss of large carnivores (jaguars, pumas) from Barro Colorado Island, Panama could explain the seemingly higher densities of mesoherbivores such as peccaries, pacas, and agoutis relative to Cocha Cashu, Peru. Yet, very few studies have since followed up with experimental or observational studies documenting increased mesoherbivore abundance in tropical forests following losses of large predators. The few studies that do exist, however, suggest that mesoherbivore release may have consequences just as catastrophic as their decline.

The best-known and most clear-cut cases of mesoherbivore release occur at temperate latitudes. In North America, white-tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus*) populations have exploded following the disappearance of wolves and mountain lions, with catastrophic effects on plant cover and diversity, nutrient and carbon cycling, and forest successional rates, with rebounding effects on insects, birds, and other mammals (see reviews by Côté et al., 2004; McShea et al., 1997). In Yellowstone National Park, in the western United States, elk (*Cervus canadensis*) populations increased and altered their foraging behavior when wolves (*Canis lupus*) were extirpated, causing collapses in aspen and cottonwood (*Populus* spp.) recruitment that did not recover until wolves were reintroduced (Beschta, 2005; Halofsky & Ripple, 2008a,b; Ripple & Larsen, 2000). Less well-known in the literature is the eradication of dholes (wild dogs; *Cuon alpinus*) in Bhutan that allowed wild pig (*Sus scrofa*) densities to increase thirty-fold, resulting in extensive crop losses and even direct attacks on humans and livestock (Wang et al., 2006; Wangchuk, 2004).

In tropical forests, mesoherbivore release was first suggested at Barro Colorado Island (BCI), Panama. Terborgh (1992) compared mesoherbivore densities at BCI, with ocelots persisting but not jaguars and pumas, versus Cocha Cashu (CC), Peru, with all large cats. He reported mesoherbivore densities 8 to 20 times greater on BCI than CC, and predicted that this could have a detrimental impact on large-seeded tree species via increased seed predation. However, this result is controversial, as Wright et al. (1994) pointed out multiple problems with both the data and its proposed implications. Mesoherbivore densities at BCI may have been overestimated due to human habituation, and densities at CC may be anomalously low due to seasonal flooding; indeed other Neotropical sites with large predators have mesoherbivore densities similar to BCI. Further, predation on and recruitment of the large-seeded *Dipteryx panamensis*, commonly predated by agoutis, was similar at BCI and CC

despite an order of magnitude difference in agouti abundance between the sites (Terborgh & Wright, 1994). Seed survival of three large-seeded species was also similar at BCI and the nearby mainland after poaching was greatly reduced, and seedling herbivory was lower on BCI (Asquith et al., 1997). Additionally, calculations of total herbivore consumption rates by predators indicates that Manu's jaguars, pumas, and ocelets do not eat sufficient herbivore biomass to effectively limit their populations (Leigh 1999). This led Wright et al. (1994) to conclude that, in comparison to the effects of hunting-driven meso-herbivore loss, "There is, however, no evidence to support the hypothesis that the relatively subtle increases in abundances that may follow the extirpation of large felids are of similar importance."

However, release of tropical mesoherbivores from predation does not always result in "relatively subtle increases in abundance," especially when combined with other factors (e.g., increased food availability) that may amplify mesoherbivore population growth. At Pasoh Forest Reserve, an aseasonal tropical forest in Malaysia have, native wild pig (*S. scrofa*) densities exploded to an estimated 47/km^2 in 1996, due to a combination of lost natural predators (tigers, leopards) and increased food supply provided by nearby oil palm plantations (Ickes, 2001). These densities are one or two orders of magnitude greater than the observed wild pig densities of 0.1 – 4.2/km^2 in tropical forest with predators present, and are similar to densities found on Peucang Island, coastal dipterocarp forest with no natural predators (27-32/km^2; Ickes, 2001). The hyperabundant pigs had dramatic effects on the natural forest vegetation structure and diversity. Within experimental pig exclosures, the number of seedling recruits increased 3 times, stem density increased by 56%, liana density increased 18%, plant species richness increased by 10%, and height growth increased 52.5% for trees 1-7m tall, though mortality was not affected (Ickes et al., 2001). Female pigs damage an estimated 170,000 saplings/km^2 annually by snapping the stems to build woody nests (Ickes et al., 2003). Pigs build 6 nests/ha annually, causing an estimated 29% of observed tree mortality and 43% of sapling mortality and damage (Ickes et al., 2005). Pigs preferentially select saplings of the dominant and ecologically important Dipterocarpaceae for nest building (Ickes et al., 2005). Yet, tree species have differential ability to regenerate following snapping; the dominant dipterocarps have particularly poor regrowth rates (Ickes et al., 2003). The wild pigs are also implicated in Pasoh's recent invasion by *Clidemia hirta* (Melastomataceae), an invasive shrub colonizing recent treefall gaps and pig-disturbed soil (Peters, 2001). Thus, the ecological release of feral pigs in Pasoh, due to a combination of artificial food inputs (i.e., oil palm) and lost native predators (Ickes, 2001; Ickes & Williamson, 2000), is having and will continue to have dramatic cascading effects on forest structure and tree community composition.

In Gunung Palung National Park in Borneo, recruitment of the dominant dipterocarp canopy trees collapsed during the 1990s, purportedly due, in part, to release of vertebrate seed predators (Curran et al., 1999). Dipterocarps exhibit mast fruiting during El Niño-Southern Oscillation events, and the large extent and synchronous production allow some seeds to escape predation. However, forest fragmentation due to logging and human-induced wildfires has reduced the extent and intensity of the mast fruiting events; and masting events at Pasoh Forest Reserve in Malaysia also have been highly variable in recent years, for unknown reasons (S.J. Wright, pers. comm.). Nonetheless, vertebrate seed predators (including bearded pigs, *Sus barbatus*; primates, rodents, and birds) and seed predation increased dramatically in 1998, particularly in logged and degraded land (Curran

et al., 1999; Curran & Leighton, 2000). The combination of high predation, logging, and wildfires contributed to a complete collapse in dipterocarp reproduction: not a single seedling was found following the 1998 masting event, compared to 150,000 seedlings/ha following the previous masting event (Curran et al., 1999).

At Lago Guri in Venezuela, herbivorous howler monkeys (*Alouatta seniculus*), common iguanas (*Iguana iguana*), and leaf-cutter ants (*Acromyrmex* spp. and *Atta* spp.) occur at densities 10-100 times greater than nearby mainland sites (reviewed by Terborgh & Feeley, 2010). As a result, seedling and sapling densities have dramatically decreased due to high mortality and low recruitment, creating "ecological meltdown" (Terborgh et al., 2001, 2006). Mortality and recruitment of both small and large saplings on these islands exceeded comparable rates on the mainland by a factor of 2, primarily due to leaf-cutter ant herbivory (Lopez & Terborgh 2007; Terborgh et al., 2006). Though leaf-cutter ants are clearly not mesoherbivores, this example demonstrates the magnitude of the effects herbivores can have on tropical forest plant communities. Furthermore, hyperabundant mesoherbivores also had species-specific effects on nutrient cycling: iguanas and howler monkeys increased the carbon/nitrogen ratio and, in turn, tree growth, while leaf-cutter ants had the opposite effect (Feeley & Terborgh, 2005). This altered nutrient regime drove a ricocheting bottom-up effect, in which the positive indirect effects of howler monkey density (and concomitant increased nutrient availability) on bird species richness exceeded the negative, direct effects of island area on bird species richness (Feeley & Terborgh, 2008). Indeed, birds maintained territories 3 to 5 times smaller on islands with abundant howler monkeys than on the adjacent mainland (Terborgh et al., 1997). While the herbivore hyperdensities are commonly attributed to the absence of all large and mid-sized predators from the islands (Terborgh et al., 2001, 2006), the very small size of the islands, extensive edge effects, and refuge effect during reservoir inundation also likely contributed (S.J. Wright, pers. comm.).

In each of the previous examples, hyperabundant mesoherbivores were shown to have dramatic, cascading consequences on the rainforest plant communities, yet release from predation may have accounted only in part for the altered herbivore densities. On the contrary, La Selva Biological Station in Costa Rica presents a more clear-cut case of mesoherbivore release. Collared peccaries (*Pecari tajacu*) have increased from a density of ~0/km^2 of trail in the 1970s (T.W. Sherry, pers. obs.) to 14/km^2 in 1993 (Torrealba-Suárez & Rau, 1994), and likely higher today (Romero et al., unpubl. data). While some herds forage in neighboring croplands (Torrealba-Suárez & Rau, 1994), peccaries had similar effect sizes (i.e., no block effects) on vegetation density at 5 paired mammal exclosures located far from any station boundary. This suggests that peccary densities are consistent across the station and thus not dependent on food inputs or experiencing a refuge effect, leaving release from predation a likely driver of the current high peccary densities (Michel et al., unpubl. data).

The question of whether collared peccaries at La Selva are over- or hyperabundant is under debate, and accurate current density estimates are greatly needed. However, the most recent available estimate (14/km^2 in 1993) is itself over double the mean 6.6/km^2 density estimated at 26 unhunted Amazonian sites (Peres & Palacios, 2007), despite some hunting occurring at La Selva (N.L. Michel, pers. obs.). It also exceeds reported densities of 9.6/km^2 at BCI, Panama, despite similar area, hunting pressure, and soil nutrient levels to La Selva (Powers et al., 2005; Wright et al., 2000). Known peccary densities elsewhere in Central America are all lower (3-7.5/km^2; Michel et al., unpubl. data). Furthermore, effect sizes of mammal

(primarily collared peccary) exclosure on vegetation metrics at La Selva exceed effect sizes from exclosures at BCI and Gigante Peninsula, Panama by 200-400%, despite sturdier exclosures in Panama that exclude more terrestrial mammals (Michel et al., unpubl. data). Thus all evidence suggests that La Selva's collared peccaries occur at unusually high densities that could be considered overabundant (McShea et al., 1997).

High-density peccaries at La Selva consume 98.6% of *Mucuna holtonii* (liana) seeds on the forest floor (Kuprewicz and García-Robledo, 2010), and reduce seedling densities at La Selva vs. nearby sites with greater hunting pressure (Chazdon et al., in press; Hanson et al., 2006). Peccaries consume stilt roots of *Socratea exorrhiza*, causing high mortality in these once-abundant trees, effects rarely observed at other Central American sites (Lieberman & Lieberman, 1994; N.L. Michel, pers. obs.). Seedling abundances of 30 focal species in exclosures versus controls were significantly different, presumably due to differences in seed predation pressures and herbivory rates (A. Wendt et al., unpubl. data). Peccaries have also reduced woody and herbaceous stem density, canopy cover, and vine and liana density and cover at La Selva (based on mammal exclosures, Fig. 3). Moreover, six sites from Costa Rica-Panama show liana tangle frequency varies inversely with peccary density, and liana tangles are 133% more abundant within mammal exclosures than paired controls at La Selva. This research suggests that the hyperabundant collared peccaries at La Selva are having dramatic effects on understory, and even canopy, vegetation. This is particularly troubling, given that vines and lianas provide important foraging and nesting substrate for many organisms, including understory insectivorous birds, a guild that has experienced significant declines at both La Selva and BCI over the past 40 years (Sigel et al., 2006, 2010).



Fig. 3. Understory vegetation density at La Selva Biological Station, Costa Rica, is lower in areas exposed to collared peccaries (left) than within experimental peccary exclosures (right; photos by Nicole L. Michel).

6. Conclusion

6.1 Conservation and management implications

It is clear from this review that fragmentation-induced trophic cascades are having catastrophic impacts on tropical forests worldwide. Regardless of whether mesoherbivores are increasing due to the loss of large predators, over-protection in some ecological reserves (e.g., La Selva), and/or food inputs, or decreasing due to human hunting pressure, it is clear that the cascading effects of perturbations in mesoherbivore populations on tropical forest plant communities and the animals reliant on them are catastrophic, diverse, and pervasive. Indeed, trophic cascades and increased mesoherbivore abundances are considered to be as serious threats to tropical biodiversity as climate change (Terborgh & Feeley 2010).

The solution to the problem is clear: large extents of continuous, or at least connected, forest must be protected and carefully managed to keep populations of both apex predators and mesoherbivores within natural ranges (Soulé, 2010). However clear the solution, its implementation is far from simple for many reasons:

- Large predators have large home ranges and are highly edge-sensitive. In Central America, female jaguars have home range sizes of 10-18.8 km², whereas male jaguars roam over 28-40km² (Rabinowitz & Nottingham, 1986; Woodruffe & Ginsberg, 1998). As a result, jaguars require a minimum "critical reserve size" of 69 km², or 6,900 hectares, to maintain a 50% probability of population persistence (Woodruffe & Ginsberg, 1998). This far exceeds the size of most Central American forest reserves. Tigers, with a female home range size of 16.9 km², require even more space: 135 km² is the minimum required to maintain a 50% probability of population persistence (Woodruffe & Ginsberg, 1998). Where mesoherbivores are also hunted by humans and prey is thus scarce, predators are likely to need even more space (Cramshaw & Quigley, 1991).
- Human phobias associated with large predators and their impacts on domesticated animal herds contribute to resisting reintroduction of predators to areas from which they have been extirpated, and heavily persecuting predators even beyond reserve borders (Soulé, 2010). Conflict with humans along reserve borders is one of the major causes of predator mortality within protected reserves (Woodruffe & Ginsberg, 1998).
- Many tropical forests are found in countries with limited funds to protect and effectively manage forest reserves (Bruner et al., 2004). The corruption endemic to many national governments in tropical regions further complicates matters (Wright et al., 2007c). Even in Costa Rica and Panama, two of the wealthiest (International Monetary Fund, 2010) and least corrupt (Transparency International, 2010) countries in Central America, poaching is endemic. In Panama, poachers are altering seed dispersal, predation, and recruitment via limitation of mesoherbivores (Wright & Duber, 2001; Wright et al., 2000, 2007b). In Costa Rica, poaching continues to affect vertebrates such as white-lipped peccaries even in the relatively well-protected Corcovado National Park (Carrillo et al., 2000, 2002), and the 260 km² Tortuguero National Park was often patrolled by fewer than five forest guards as recently as 2005 (N. Michel, pers. obs.).
- Many people in tropical countries rely upon hunting for either their own subsistence or to trade for food and other necessities (Corlett, 2007). If patrolling forest reserves effectively limits hunting, many neighboring people would need other means of support. This could result in increased slash-and-burn agriculture with its concomitant negative effects on tropical biodiversity (Naughton-Treves et al., 2003).

Many scientists and conservationists argue that simply setting aside land in forest reserves is sufficient to preserve biodiversity, regardless of connectivity or management (e.g., Fahrig, 1997). Yet, others argue that connectivity, i.e., developing biological corridors to connect nearby reserves, is sufficient to preserve biodiversity (e.g., Soulé, 2010). However, if proposed reserves do not already have apex predators, or have degraded habitat unable to support apex predators, or if heavy hunting pressure is limiting mesoherbivore and/or predator populations, the reserve will function in reality as an "Empty Forest" (Redford, 1992; Wilkie et al., 2011). This is a serious problem, as much of the land remaining in tropical regions is either degraded, or in suboptimal habitat, and/or heavily impacted by hunting, and – as discussed above – government funding of reserve protection is often insufficient to control poaching. In order for conservation to succeed, it is imperative that reserves of sufficient size and/or connectivity not only be set aside, but these reserves must also contain sustainable populations of both apex predators (whether extant or reintroduced) and mesoherbivores, i.e., balanced populations to which the natural vegetation and other organisms are adapted. Furthermore, adequate protection needs to be instituted and continued monitoring of predator and herbivore populations, perhaps using a Footprint index (de Thoisy et al., 2010), is crucial in order to prevent destructive trophic cascades and the subsequent loss of tropical biodiversity.

6.2 Future research needs

In terms of future research, we need intensive study of not only what are "normal" and sustainable abundances of mesoherbivores, but also how to maintain these abundances through a combination of vegetation, predator, and/or hunting management. We need better information on all the consequences, both long- and short-term, of human-altered mesoherbivore abundances on native tropical forest communities. There is an urgent need for better information and models on how altered trophic dynamics, especially mesoherbivore abundances, will be affected by other global phenomena, especially climate destabilization. Finally, it is essential to determine the effectiveness of various conservation actions, in order to determine which techniques can best prevent a mass extinction of tropical biodiversity (Brooks et al., 2009).

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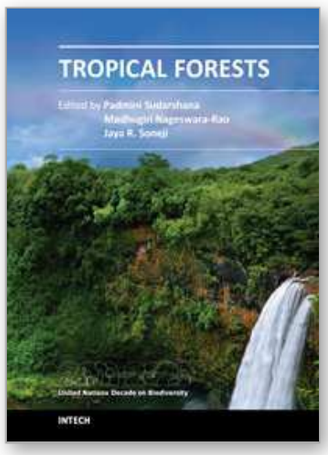
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The astounding richness and biodiversity of tropical forests is rapidly dwindling. This has severely altered the vital biogeochemical cycles of carbon, phosphorus, nitrogen etc. and has led to the change in global climate and pristine natural ecosystems. In this elegant book, we have defined "Tropical Forests" broadly, into five different themes: (1) tropical forest structure, synergy, synthesis, (2) tropical forest fragmentation, (3) impact of anthropogenic pressure, (4) Geographic Information System and remote sensing, and (5) tropical forest protection and process. The cutting-edge synthesis, detailed current reviews, several original data-rich case studies, recent experiments/experiences from leading scientists across the world are presented as unique chapters. Though, the chapters differ noticeably in the geographic focus, diverse ecosystems, time and approach, they share these five important themes and help in understanding, educating, and creating awareness on the role of "Tropical Forests" for the very survival of mankind, climate change, and the diversity of biota across the globe. This book will be of great use to the students, scientists, ecologists, population and conservation biologists, and forest managers across the globe.

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