



## Review

## Does hunting threaten timber regeneration in selectively logged tropical forests?



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## ABSTRACT

Avoiding the conversion of tropical production forests to non-forest land uses is a forestry and conservation priority, and is contingent on successful regeneration of commercially important species. The underlying ecological processes that facilitate regeneration, however, are poorly understood. Perhaps as a result, timber yields after regeneration can be lower than expected. Hunting is widespread in timber concessions, and may threaten regeneration by disrupting the various processes facilitated by wildlife. Vertebrate seed dispersers are often heavily hunted, resulting in reduced seed movement for many species and a shift in community composition to favor those plants dispersed by small animals and abiotic means. Timber species with large seeds and fleshy fruit are at particular risk for dispersal and recruitment failure. Hunting also alters granivore communities, resulting in increased predation on species favored by insects and small rodents, and changing the spatial template of seed predation, with detrimental effects on many timber species. Large vertebrate herbivores decline with hunting pressure, resulting in the modification of plant competitive interactions. This is disadvantageous to several traits that are common among timber trees, including relatively slow growth and high wood density. A lack of appreciation for – and management of – these interactions could threaten forest biodiversity, limit future timber production, and increase the likelihood of forest conversion for other land uses. In this review, I highlight the plant-animal interactions that could influence timber regeneration in tropical forests, as well as how these processes might be expected to change under hunting pressure. The review concludes with recommendations for management and future research priorities.

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## 1. Introduction

Timber production represents a major land use for tropical forests worldwide, encompassing 403 million hectares (Blaser et al.,

2011) – roughly half the area of the contiguous United States. Though logging can have various detrimental impacts on tropical forests (eg Johns, 1988; Bawa and Seidler, 1998; Fimbel et al., 2001), there is mounting evidence that timber concessions are not without environmental merit, potentially meeting both forestry and conservation goals (Johns, 1985, 1997; Putz et al., 2000; Meijaard et al., 2005; Clark et al., 2009; Berry et al., 2010).

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Selectively logged forests under responsible management represent a valuable “middle way” between deforestation and absolute protection (Putz et al., 2012, but see also Rice et al., 1997). Avoiding the conversion of production forest to non-forest land uses is thus critical, and relies on continued regeneration of commercially important species.

Most selective timber systems with sustained yields (Putz et al., 2012) use one form or another of natural forest management (see reviews by Baur (1964) and Buschbacher (1990), but see also Bawa and Seidler, 1998). These management schemes rely to varying degrees on the natural regeneration of target timber species, often with simple silvicultural treatments. Reproduction under close-to-natural forest conditions – for eventual harvest in future cutting cycles – is less labor intensive and expensive than other methods, and is thus a favored forestry scheme across much of the tropics (Weetman and Vyse, 1990; Gómez-Pompa and Burley, 1991).

Recent evidence shows that the post-harvest regeneration of timber species can be lower than expected (Fredericksen and Mostacedo, 2000), highlighting the need to understand the ecological requirements of these tree species and identify the causes of regeneration failure. Plant-animal interactions are increasingly recognized as critical to maintaining tropical forest integrity and composition, particularly the processes of seed dispersal (eg Terborgh et al., 2008), seed predation (eg Asquith et al., 1997), and herbivory (eg Clark et al., 2012). These processes may play a role in timber regeneration, given the extensive interactions between timber species and tropical forest wildlife (see Tables 1 and 2). Disruptions to plant-animal interactions can have consequences both for biodiversity and forest carbon production (Wright, 2003; Brodie and Gibbs, 2009; Jansen et al., 2010; Poulsen et al., 2013), though the specific effects on the regeneration of timber are largely unknown. As a result, logging companies generally lack any practical management of these processes, despite their apparent importance (Terborgh, 1995; Hammond et al., 1996; Guariguata and Pinard, 1998; Sheil and Van Heist, 2000; Putz et al., 2012).

A major threat to the integrity of plant-animal interactions is the increasing impact of hunting for subsistence and the commercial wild meat trade (Redford, 1992). Hunting is widespread in tropical forests (Robinson and Bennett, 2000; Fa et al., 2002), and is further facilitated by logging through the creation of road networks and increased access to frontier forests (Wilkie et al., 2000). Hunting within concessions can be particularly intensive, as extractive industries promote immigration and timber companies rarely provide supplemental protein to their workers' diets (Robinson et al., 1999; Auzel and Wilkie, 2000; Poulsen et al., 2009). Overall, hunting within concessions affects animal distributions more strongly than do the direct effects of logging (van Vliet and Nasi, 2008; Poulsen et al., 2011).

Hunting alters ecological processes in many ways (see reviews by Wright (2003), Stoner et al. (2007), Abernethy et al. (2013) and Kurten (2013)). If these processes are important for the regeneration of timber, disruptions to them may threaten continued production and must be managed appropriately. In this review, I highlight the plant-animal interactions that could influence timber regeneration, as well as how these processes might be expected to change under hunting pressure, with a focus on seed dispersal, post-dispersal seed predation, and herbivory. I identify specific interactions between hunted wildlife and prominent timber tree species, with attention to the world's three main regions of tropical forest. The review concludes with recommendations for management and future research priorities.

## 2. Seed dispersal

Dispersal confers several potential reproductive advantages to the seed. Dispersed seeds may benefit from colonizing novel and

uncompetitive environments, landing in sites suitable for establishment, and escaping the vicinity of the parent (Howe and Smallwood, 1982; Willson and Traveset, 2000; Muller-Landau and Hardesty, 2005). Escape through dispersal reduces the incidence of attack on seeds and seedlings by host-restricted natural enemies near the parent tree, as described by the Janzen–Connell model (Janzen, 1970; Connell, 1971). This model of distance- and density-responsive mortality mechanisms is well-supported scientifically (see reviews by Hammond and Brown (1998) and Terborgh (2012)), and dictates a major role of seed dispersal in regeneration success. Indeed, there is strong evidence that nearly all sapling recruits arise from seedlings of dispersed seeds (Howe and Miriti, 2000; Terborgh and Nuñez-Iturri, 2006; Terborgh, 2013). Any disruption to the dispersal process may have impacts on individual trees, species, and communities. In particular, hunting threatens the integrity of animal-mediated dispersal, with potential consequences for timber regeneration in forests subject to such pressures.

The majority of tree species in humid tropical forests produce seeds with fleshy fruit or aril and are dispersed by animals (Howe and Smallwood, 1982; Willson et al., 1989; Jansen and Zuidema, 2001; Beaune et al., 2013). Many species producing a hard pericarp are also dispersed by vertebrates through caching and other pathways (Janzen, 1971; Forget, 1990; Jansen and Forget, 2001; Hulme, 2002; Beck, 2005). Dispersal by animals is thus widespread, and is probably as common for potential timber species as for tropical forest tree species in general (Jansen and Zuidema, 2001). Trees with vertebrate-dispersed seeds account for 72% of the 95 timber species in the Guianas (Hammond et al., 1996), and 74% of the 46 timber species in Bolivia (Jansen and Zuidema, 2001). Although this over-represents animal dispersal among the few timber species most desired by current world markets (see Table 1), proportions of animal-dispersed timber trees are expected to increase with depletion of high-value, wind-dispersed timbers and growing demand for lesser-known species (Jansen and Zuidema, 2001; Putz et al., 2001).

Dispersal by animals is clearly important for many timber species (see Tables 1 and 2), though few studies have determined its specific role in regeneration success. As noted above, dispersal which increases seed distance from the parent tree may be critical for timber regeneration. Pulp removal and gut passage may also improve survival and germination of animal-dispersed seeds (Traveset, 1998; Traveset and Verdu, 2002; Levi and Peres, 2013). To assess the value of dispersal for the timber tree *Virola surinamensis* in Panama, Howe et al. (1985) monitored seeds and seedlings located near the parent, noting over 99% mortality by insects and mammals within 12 weeks; seeds dropped 45 m from the fruiting tree were at an advantage of up to 44-fold compared to their undispersed counterparts. Similarly, undispersed seeds and seedlings of the timber species *Pycnanthus angolensis* and *Canarium schweinfurthii* in Cameroon faced substantially greater mortality by invertebrates and rodents than those that had been dispersed by primates (Mbelli, 2002). Poor natural regeneration of the Guyanese timber tree *Hymenaea courbaril* beneath its own canopy supports the assertion that primate dispersal is critical for recruitment, with 98% of undispersed seeds suffering mortality due to bruchid beetle attack (Hammond et al., 1992). Hammond et al. (1999) found that while dispersal of the timber tree *Chlorocardium rodiei* did not completely preclude natural enemy attack, it did delay predation long enough to promote germination success with increasing distance from conspecific adults, thus dispersal benefitted trees through a combination of spatial and temporal factors.

Documented recruitment failure in the absence of dispersal is a concern for timber production, given that animal dispersers – and their services – are strongly impacted by hunting. Most highly desirable game animals of tropical forests are prominent seed

**Table 1**

Ecological characteristics and plant-animal interactions of the 10 most commonly harvested timber tree species (based on volume exported in 2011 and 2012; ITTO, 2012) from the world's three main regions of tropical forest. Note the disproportionate representation of wind dispersed species by current harvests; these species are often favored because of their long, straight boles.

Scientific name	Family	Disperser(s)	Seed predator(s)	Herbivore(s)	Diaspore	Volume (1000 m <sup>3</sup> )
<b>Neotropics</b>						
<i>Tabebuia</i> spp.	Bignoniaceae	Wind	Saki monkeys <sup>a</sup>	Insects <sup>d</sup>	Winged	142
<i>Peltogyne venosa</i>	Leguminosae	Wind, monkeys	Beetles, ants, saki monkeys ( <i>P. paniculata</i> ) <sup>o</sup>	Insects	Pod	79
<i>Swartzia</i> spp.	Fabaceae	Bats, birds, rodents, monkeys	Rodents, ants	Insects, mammals	Fleshy	68
<i>Dicorynia guianensis</i>	Leguminosae	Wind, gravity	Insects, rodents, brocket deer <sup>i</sup>	Insects	Pod	37
<i>Mora excelsa</i>	Leguminosae	Water, fish, rodents (secondary)	Rodents	Insects	Pod	35
<i>Chlorocardium rodiei</i>	Lauraceae	Scatterhoarding rodents <sup>s</sup>	Insects, rodents	Insects	Woody nut	32
<i>Goupia glabra</i>	Goupiaceae	Birds	Insects, rodents	Insects	Fleshy	11
<i>Eperua falcata</i>	Leguminosae	Explosive dehiscence, scatterhoarding rodents (secondary) <sup>f</sup>	Insects, rodents, peccaries <sup>t</sup> , saki monkeys <sup>a,o</sup>	Insects, mammals <sup>s</sup>	Pod	10
<i>Manilkara bidentata</i>	Sapotaceae	Birds <sup>q</sup> , monkeys <sup>l</sup>	Peccaries <sup>t</sup> , beetles	Leaf miner insects	Fleshy	10
<i>Catostemma commune</i>	Bombacaceae	Monkeys, bats, other mammals	Brocket deer ( <i>C. fragrans</i> ) <sup>j</sup>	<i>Atta</i> spp. ants	Fleshy	9
<b>Afrotropics</b>						
<i>Aucoumea klaineana</i>	Burseraceae	Wind		Elephants; psyllids ( <i>Pseudophacopteron</i> spp.), caterpillars, chimpanzees (flowers)	Winged	1063
<i>Entandrophragma cylindricum</i>	Meliaceae	Wind	Rodents ( <i>Entandrophragma</i> spp.) <sup>p</sup>		Winged	509
<i>Triplochiton scleroxylon</i>	Sterculiaceae	Wind	Insects	Psyllids, <i>Anaphe venata</i> silkworm, other insects	Winged nut	364
<i>Chlorophora excelsa</i> / <i>Milicia excelsa</i>	Moraceae	Birds, bats, and squirrels		Iroko gall fly, gorillas	Fleshy	306
<i>Ceiba pentandra</i>	Malvaceae	Wind	<i>Dysdercus</i> cotton stainer, other insects	Insects	Cottony floss	202
<i>Cylicodiscus gabonensis</i>	Leguminosae	Wind	Primates	Insects	Pod/winged	181
<i>Erythrophleum ivorense</i>	Leguminosae	Gorillas <sup>c</sup> , other primates	Colobus monkeys <sup>R</sup>	Colobus monkeys <sup>R</sup> , insects	Pod	143
<i>Pterocarpus soyauxii</i>	Fabaceae	Wind, animals (secondary)		Numerous animals	Winged	75
<i>Tectona grandis</i>	Lamiaceae	Wind	Beetles	<i>Hyblaea</i> and <i>Eutectona</i> caterpillars, other arthropods	Woody nut	71
<i>Entandrophragma utile</i>	Meliaceae	Wind	Rodents <sup>E,D</sup> antelopes, shoot borers, lepidopterous insects		Winged	63
<b>Indo-Malayan Tropics</b>						
<i>Shorea</i> spp.	Dipterocarpaceae	Wind, scatterhoarding rodents	Insects, rodents, primates, bearded pigs	Insects <sup>p</sup> , rodents <sup>p</sup> , other mammals	Winged nut	4041
<i>Dipterocarpus</i> spp.	Dipterocarpaceae	Wind, scatterhoarding rodents	Insects, rodents, primates, bearded pigs	Insects, mammals	Winged nut	2700
<i>Tectona grandis</i>	Lamiaceae	Wind	Beetles	<i>Hyblaea</i> and <i>Eutectona</i> caterpillars, other arthropods	Woody nut	965
<i>Dryobalanops</i> spp.	Dipterocarpaceae	Wind, scatterhoarding rodents	Insects, rodents, primates, bearded pigs	Insects, porcupines, other mammals	Winged nut	810
<i>Xylia xylocarpa</i>	Leguminosae	Explosive dehiscence	Insects	Insects	Woody pod	718
<i>Hevea brasiliensis</i>	Euphorbiaceae	Explosive dehiscence			Capsule	172
<i>Koompassia</i> spp.	Leguminosae	Wind, orangutans <sup>f</sup>			Winged	163
<i>Acacia mangium</i>	Fabaceae	Birds, ants	Beetles, ants	Mammals, insects	Coiled pod	152
<i>Parashorea</i> spp.	Dipterocarpaceae	Wind, scatterhoarding rodents	Insects, rodents, primates, bearded pigs	Beetles and other insects, snails, mammals	Winged nut	85
<i>Anisoptera</i> spp.	Dipterocarpaceae	Wind, scatterhoarding rodents	Insects, rodents, primates, bearded pigs	Insects, mammals	Winged nut	81

dispersers, including large primates, duikers, deer, tapirs, and other ungulates (Redford and Robinson, 1987; Feer, 1995; Fa et al., 2005;

Corlett, 2007; Peres and Palacios, 2007; Beaune et al., 2013). In general, frugivorous vertebrates suffer greater declines with

hunting pressure than either granivorous or folivorous species, regardless of body size (Peres and Palacios, 2007).

Animal dispersers can be partitioned into several non-overlapping “syndromes” based on morphological traits of the fruits they consume (Gautier-Hion et al., 1985). While there may be many potential dispersers for any one timber species (Howe and Smallwood, 1982), they can vary in their effectiveness (Schupp, 1993), and actual redundancy may be lower than anticipated based on dietary overlap (Poulsen et al., 2002). Additionally, the removal of a given disperser may change regeneration patterns by altering the tree’s seed shadow and susceptibility to predation (Janzen and Vázquez-Yanes, 1991). Large-bodied vertebrates are capable of ingesting – and dispersing, via endozoochory – a greater quantity and size range of fruit than smaller animals (Corlett, 1998; Peres and Van Roosmalen, 2002; Knogge and Heymann, 2003). Dispersal of timber trees reliant on large animals is thus unlikely to be compensated for by smaller non-game taxa, except perhaps in cases where a given species is additionally dispersed via synzoochory (as by bats). In the Guianas, for example, the seeds of most timber trees are animal-dispersed and larger than one gram – too large to be effectively dispersed by smaller animals (Hammond et al., 1996).

Some trees may have one or very few critical dispersers (Howe, 1977; Hallwachs, 1986; Tutin et al., 1991; Asquith et al., 1999), and face dispersal failure when these particular species are absent. In Uganda, chimpanzees are the primary – perhaps sole – dispersers of the timber tree *Cordia millenii* (Plumptre et al., 1994; Bakuneeta et al., 1995; Reynolds, 2005), and in Gabon, the only known disperser for the timber tree *Cola lizae* is the lowland gorilla (Tutin et al., 1991). Even moderate hunting of important dispersers, as in “half-empty” forests (Redford and Feinsinger, 2001), may be sufficient to alter timber regeneration patterns. McConkey and Drake (2006) found that hunted flying foxes ceased to function as dispersers for three timber species (*Pouteria grayana*, *Syzygium clusifolium*, and *S. dealatum*) long before they became rare.

Shifts in abundance of vertebrate dispersers may have variable effects on plants. While large-bodied dispersers are reduced or extirpated with hunting, densities of small-bodied fauna can increase through compensatory mechanisms (Peres and Dolman, 2000; Rosin and Swamy, 2013). As a result, hunting reduces dispersal of large-seeded trees, while those dispersed by small animals and wind tend to increase in abundance (Wright et al., 2007; Stoner et al., 2007; Nuñez-Iturri et al., 2008; Terborgh et al., 2008; Vanthomme et al., 2010; Effiom et al., 2013; Harrison et al., 2013; Kurten, 2013). This shift in dispersal based on reproductive traits such as seed size has important consequences for timber trees specifically. When compared against the tree community as a whole, the seeds of fleshy-fruited timber species can be significantly larger than those of non-timber species (Hammond et al., 1996), and thus more negatively affected by changes to the disperser assemblage due to hunting.

For one particular guild of small-seeded plants, the wind-dispersed lianas, hunting can promote significantly increased abundance (Wright et al., 2007), though widespread evidence is limited. Lianas are detrimental to timber trees; they induce stem deformations and other mechanical damage, slow diametric growth, and increase the likelihood of the host tree falling (Putz, 1982, 1991; Clark and Clark, 1990). Infested trees may suffer reduced seed production (Stevens, 1987; Nabe-Nielsen et al., 2009) and possible recruitment failure in adjacent gaps, given that lianas can impede the successional process (Schnitzer et al., 2000). Combined, these factors lead to poor timber regeneration when lianas are abundant (Grauel and Putz, 2004). Lianas also hinder timber harvest and complicate management, as liana-laden trees cause greater felling damage to the surrounding forest (Fox, 1968; Appanah and Putz, 1984; Johns et al., 1996) and raise costs

associated with liana cutting and herbicide treatment (Putz, 1991). By benefitting lianas, hunting may thus indirectly reduce timber production and profitability.

There is ample evidence both that animal-mediated dispersal is important for many timber species, and that hunting alters this process. Trees reliant on large vertebrates face dispersal failure, heightened natural enemy attack, and increased abundance of competitors such as lianas, all of which may hinder timber regeneration in forests subject to hunting pressure.

### 3. Seed predation

Seed predation is an important ecological interaction which can regulate plant population dynamics (Janzen, 1971; Crawley, 1992; Hulme, 1998). As seed predators are abundant and diverse in tropical forests, and consume the seeds of many timber tree species (see Tables 1 and 2), it is reasonable to assume that they may impact regeneration processes, though direct evidence is limited. In particular, changes to community composition of seed predators, as can occur under hunting, may alter seed predation regimes and differentially impact tree recruitment.

Large mammalian granivores such as pigs (Suidae) and peccaries (Tayassuidae) exert predation pressures that influence tree recruitment (Ghiglieri et al., 1982; Bodmer, 1991; Curran and Webb, 2000; Ickes et al., 2001; Silman et al., 2003; Beck, 2005; Beaune et al., 2012). Small mammals, particularly rodents, can be voracious seed consumers as well (Fleming, 1975; Smythe, 1986; Hulme, 1993; Blate et al., 1998), with potentially stronger seed predation pressures than larger mammals (Terborgh et al., 1993; DeMattia et al., 2004; Paine and Beck, 2007). Rodents prey on seeds even when alternative resources such as pulpy fruits are available (Adler, 1995), and can kill seedlings up to several weeks after germination, to exploit sprouts and seed reserves (DeSteven and Putz, 1984; Forget, 1997). Insects and other arthropods are also important seed predators of timber species (see below; Toy, 1988; Hammond et al., 1992), and impact seeds differently than vertebrates (Janzen, 1971; Terborgh et al., 1993; Notman and Villegas, 2005).

Small rodents tend to favor seeds of small size (Blate et al., 1998; Vieira et al., 2003; Dirzo et al., 2007), exerting predation pressures unique from large mammals (DeMattia et al., 2004; Mendoza and Dirzo, 2007; Hautier et al., 2010). Agoutis and peccaries also differ in their seed preferences based on the presence of chemical and/or physical defenses (Kuprewicz, 2012), and specialized invertebrates such as bruchid beetles and other weevils can process seed compounds toxic to larger animals (Janzen, 1971). Given that different granivores have distinct seed preferences, changes that alter the relative abundance of these fauna may substantially alter seed predation pressures.

Hunting contributes to compositional change of seed predator communities, with potentially important consequences. Pigs and peccaries are frequently hunted, as are some large rodents like agoutis and porcupines, while smaller rodents such as squirrels, rats, and mice are much less favored (Redford and Robinson, 1987; Clayton et al., 1997; Fa et al., 2005; Rao et al., 2005; Corlett, 2007). This disparity of harvest rates can shift faunal community composition, while interspecific dynamics may further enhance these changes. As with primates (described above), compensatory responses can occur when two or more species share a common resource and are differently impacted by hunting, thus small rodents may increase in abundance with hunting pressure even while total animal biomass declines (Smythe, 1987; Hapold, 1995; Phillips, 1997; Wright, 2003). Observational and experimental evidence support this, with greater abundance of small and medium-sized rodents documented in sites where their predators and/or competitors are absent (Glanz, 1991; Adler and

**Table 2**

Ecological characteristics and plant-animal interactions of less commonly harvested timber tree species from the world's three main regions of tropical forest. Harvest rates are currently low but expected to increase as the market for lesser-known timber species increases (Jansen and Zuidema, 2001). Species selected based on frequent mention in the literature and/or future market potential.

Scientific name	Family	Disperser(s)	Seed predator(s)	Herbivore(s)	Diaspore
<b>Neotropics</b>					
<i>Amburana</i> spp.	Leguminosae	Wind	Insects	Insects	Winged
<i>Araucaria angustifolia</i>	Araucariaceae	Birds, rodents, and other mammals <sup>e</sup>	Peccaries, rodents	Insects <sup>f</sup>	Fleshy nut
<i>Brosimum utile</i>	Moraceae	Monkeys <sup>c,l</sup> , tapirs ( <i>B. parinaroides</i> ) <sup>m</sup> , birds, peccaries <sup>n</sup>	Brocket deer ( <i>Brosimum</i> spp.) <sup>j</sup> , saki monkeys <sup>o</sup> , peccaries <sup>p</sup>		Fleshy
<i>Carapa guianensis</i>	Meliaceae	Scatterhoarding rodents	Brocket deer <sup>i</sup> , saki monkeys <sup>p</sup> , rodents, peccaries	Insects, deer	Woody nut
<i>Cedrela</i> spp.	Meliaceae	Wind	Saki monkeys <sup>a</sup>	Shootborer ( <i>Hypsiplya grandella</i> ), other arthropods	Winged
<i>Cordia goeldiana</i>	Boraginaceae	Birds, monkeys <sup>l</sup>	Brocket deer <sup>i</sup>		Fleshy
<i>Dinizia excelsa</i>	Leguminosae	Wind/gravity, rodents and other mammals (secondary) <sup>g</sup>	Parrots, macaws, beetles <sup>h</sup>		Pod
<i>Hymenaea courbaril</i>	Leguminosae	Monkeys, scatterhoarding rodents	Saki monkeys <sup>a</sup> , peccaries, rodents, beetles <sup>c</sup>	Atta spp. ants	Fleshy nut
<i>Ocotea</i> spp.	Lauraceae	Numerous birds and mammals	Small rodents <sup>l</sup> , insects, brocket deer <sup>i</sup> , peccaries	Insects, mammals	Fleshy
<i>Pradosia ptychandra</i>	Sapotaceae	Monkeys <sup>l</sup>	Saki monkeys <sup>a</sup> , peccaries ( <i>P. surinamensis</i> ) <sup>s</sup> , beetles	Insects, mammals	Fleshy
<i>Swietenia</i> spp.	Meliaceae	Wind, rodents (secondary)	Beetles, rodents <sup>b</sup>	Shootborer ( <i>Hypsiplya grandella</i> )	Winged
<i>Trattinickia</i> spp.	Burseraceae	Birds <sup>q</sup> , monkeys <sup>l</sup>			Fleshy
<i>Virola</i> spp.	Myristicaceae	Birds, monkeys <sup>k</sup>	Beetles, rodents, peccaries, brocket deer <sup>i</sup> , saki monkeys <sup>c</sup>	Insects, deer, tapirs	Fleshy
<b>Afrotropics</b>					
<i>Austranella congolensis</i>	Sapotaceae	Elephants, gorillas <sup>c</sup>	Bush pigs, porcupines		Fleshy
<i>Baillonella toxisperma</i>	Sapotaceae	Elephants, giant pouched rats, monkeys	Bush pigs, porcupines	Bush pigs, antelopes, elephants	Fleshy
<i>Copaifera mildbraedii</i>	Leguminosae	Birds <sup>z</sup>			fleshy
<i>Dacryodes buettneri</i>	Burseraceae	Numerous birds, squirrels, monkeys, apes <sup>u,v,w</sup>	Red river hogs <sup>x</sup> , mandrills <sup>y</sup> , rodents	Elephants	Fleshy
<i>Diospyros crassiflora</i>	Ebenaceae	Birds, gorillas <sup>29</sup> , mandrills <sup>A,y</sup> , other animals		Jumping plant-lice	Fleshy
<i>Gambeya africana</i>	Sapotaceae	Gorillas <sup>c</sup> , chimpanzees, elephants, birds	Red river hogs ( <i>G. lacourtiana</i> ) <sup>x</sup> , mandrills <sup>A</sup>		Fleshy
<i>Gilbertiodendron dewevrei</i>	Leguminosae	Explosive dehiscence, gorillas <sup>c</sup>	Red river hogs <sup>x</sup> , antelopes, elephants, rodents, primates	Forest buffaloes, bongos; elephants	Pod
<i>Guarea cedrata</i>	Meliaceae	Hornbills, monkeys, duikers, porcupines	Menemachus beetles		Fleshy
<i>Khaya ivorensis</i>	Meliaceae	Wind	Beetles, rodents	Psyllids, other insects	Winged
<i>Lophira alata</i>	Ochnaceae	Wind, mandrills <sup>A</sup>	Rodents, mandrills <sup>A</sup> , colobus monkeys <sup>R</sup>	Gall-forming insects, gorillas <sup>v</sup> , colobus monkeys <sup>R</sup>	Winged
<i>Millettia laurentii</i>	Fabaceae	Explosive dehiscence		Caterpillars, apes <sup>w</sup> , colobus monkeys <sup>R</sup>	Pod
<i>Nauclea diderrichii</i>	Rubiaceae	Birds, elephants, duikers, monkeys, gorillas <sup>B</sup>		Shoot-boring moth larvae	Fleshy
<i>Staudtia</i> spp.	Myristicaceae	Numerous animals	Mandrills <sup>A</sup>		Fleshy
<i>Testulea gabonensis</i>	Luxembourgiaceae	Wind	Grey parrots	Gorillas <sup>v</sup>	Winged
<b>Indo-Malayan Tropics</b>					
<i>Buchanania</i> spp.	Anacardiaceae	Animals	Rodents		Fleshy
<i>Calophyllum</i> spp.	Guttiferaceae	Birds <sup>q</sup> , orangutans <sup>F</sup> , gibbons <sup>G</sup> , bats, squirrels, monkeys	Rodents <sup>H</sup>	Insects	Fleshy
<i>Canarium</i> spp.	Burseraceae	Birds <sup>q</sup> , gibbons <sup>l</sup> , sun bears <sup>l</sup> , monkeys, bats	Rodents <sup>H</sup>		Fleshy
<i>Celtis</i> spp.	Ulmaceae	Birds <sup>q</sup> , rodents			Fleshy
<i>Dillenia</i> spp.	Dilleniaceae	Orangutans <sup>G</sup> , monkeys, elephants, pigs, squirrels, birds			Fleshy
<i>Gonystylus bancanus</i>	Thymelaeaceae	Orangutans <sup>F</sup> , Malayan flying foxes <sup>K</sup> , fruit bats	Squirrels, other rodents		Woody capsule
<i>Heritiera simplicifolia</i>	Sterculiaceae	Wind	Beetles, moth larvae		Winged
<i>Intsia</i> spp.	Leguminosae	Birds <sup>q</sup>	Red leaf monkeys <sup>l</sup> , rodents	Deer, mouse deer, rats	Pod
<i>Palaquium</i> spp.	Sapotaceae	Birds, gibbons <sup>l,M</sup> , orangutans <sup>F</sup> , civets <sup>N</sup> , sun bears <sup>O</sup> , fruit bats	Squirrels, other rodents <sup>H</sup> , birds	Insects	Fleshy
<i>Pometia pinnata</i>	Sapindaceae	Bats, birds	Conopomorpha moths		Fleshy
<i>Pouteria</i> spp.	Sapotaceae	Monkeys, bats, birds, squirrels	Squirrels, beetles		Fleshy
<i>Syzygium</i> spp.	Myristicaceae	Gibbons <sup>l,M</sup> , hornbills <sup>Q</sup> and other birds, civets <sup>N</sup> , sun bears <sup>O</sup> , small fruit bats, squirrels	Rodents <sup>H</sup>	Insects	Fleshy
<i>Terminalia</i> spp.	Combretaceae	Birds <sup>q</sup> , monkeys <sup>H</sup>	Rodents, insects	<i>Roesalia</i> moth caterpillars	Fleshy



General sources: Pan-tropical: World Agroforestry Centre Database, PROTAbase, Jansen and Zuidema (2001); Neotropics: van Roosmalen (1985) and Hammond et al. (1996); Afrotropics: Doucet (2003); Indo-Malayan tropics: Soerianegara and Lemmens (1993), Lemmens et al. (1995) and Sosef et al. (1998).

<sup>a</sup>Norconk and Veres (2011); <sup>b</sup>Lambert et al. (2005); <sup>c</sup>Terborgh et al. (1993); <sup>d</sup>Ribeiro et al. (1994); <sup>e</sup>Carvalho (1994); <sup>f</sup>Arnold and Fonseca (2011); <sup>g</sup>Embrapa Amazonia Oriental (2004); <sup>h</sup>Dick (2001); <sup>i</sup>Gayot et al. (2004); <sup>j</sup>Wenny (2000); <sup>k</sup>Howe et al. (1985); <sup>l</sup>Simmen and Sabatier (1996); <sup>m</sup>Henry et al. (2000); <sup>n</sup>Bodmer (1991); <sup>o</sup>van Roosmalen et al. (1988); <sup>p</sup>Altricher et al. (2001); <sup>q</sup>Snow (1981); <sup>r</sup>Forget (1989); <sup>s</sup>Hammond et al. (1999); <sup>t</sup>Beck (2005); <sup>u</sup>Sabater-Pf (1979); <sup>v</sup>Williamson et al. (1990); <sup>w</sup>Tutin and Fernandez (1993); <sup>x</sup>Beaune et al. (2012); <sup>y</sup>Astaras and Waltert (2010); <sup>z</sup>Hawthorne (1995); <sup>A</sup>Lahm (1986); <sup>B</sup>Morgan and Sanz (2007); <sup>C</sup>Doran et al. (2002); <sup>D</sup>Hall (2008); <sup>E</sup>Synnott (1975); <sup>F</sup>Galdikas (1988); <sup>G</sup>Ungar (1995); <sup>H</sup>Blate et al. (1998); <sup>I</sup>Marshall et al. (2009); <sup>J</sup>McConkey and Galetti (1999); <sup>K</sup>Hamzah et al. (2010); <sup>L</sup>Davies (1991); <sup>M</sup>Mumford (2009); <sup>N</sup>Mudappa et al. (2010); <sup>O</sup>Fredriksson et al. (2006); <sup>P</sup>Turner (1990); <sup>Q</sup>Kanwatanakid-Savini et al. (2009); <sup>R</sup>McKey et al. (1981); <sup>S</sup>Fragoso (1999).

Levins, 1994; Keesing, 1998; Lambert et al., 2003; Laurance et al., 2006; Poulsen et al., 2011; Effiom et al., 2013).

Logging itself modifies forest habitat in ways that additionally benefit small mammalian seed predators, such as opening canopy gaps (Struhsaker, 1997), and expanding road margins (Malcolm and Ray, 2000), increasing the density of vegetation through post-harvest regeneration. Overall these factors lead to increased rodent richness, diversity, and density in selectively logged forests (Isabirye-Basuta and Kasenene, 1987), and potentially more so in those subject to hunting pressure.

Hunting may also indirectly benefit some invertebrate seed predators such as insects. Seeds that contain bruchid beetle larvae may be preferentially fed on by mammalian granivores (Silvius, 2002; Gálvez and Jansen, 2007). When hunting reduces populations of these mammals, larvae have a greater chance of surviving the seed stage to adulthood, increasing their abundance (Stoner et al., 2007). As a result, seed predation by insects dramatically increases with hunting pressure, at least on the several species of palm for which much data is available; two reviews have noted this increased predation, which ranges from 2- to 14-times higher (Kurten, 2013) and from 4- to 70-times higher (Stoner et al., 2007) in hunted vs. non-hunted sites.

This change could have important consequences for timber trees, given the extent to which insects attack their seeds both pre- and post-dispersal, regardless of the dispersal mode. In Guyana, invertebrates heavily infest seed crops of the timber trees *Peltogyne* spp. and *Aspidosperma* spp. (ter Steege et al., 1996), and bruchid beetles destroyed nearly all undispersed *H. courbaril* seeds in one study (Hammond et al., 1992, see above). Weevils are a major predator of *V. surinamensis* in Panama (Howe et al., 1985), and can kill up to 90% of the seed crop of dominant dipterocarps in Malaysia (Toy, 1988).

Due to differential hunting intensity and potential compensatory responses, the functional make-up of the seed predator guild may be expected to change dramatically under hunting pressure. Such shifts in faunal composition and abundance directly affect species-specific and community-wide seed predation and recruitment (DeSteven and Putz, 1984; Sork, 1987; Asquith et al., 1997; DeMattia et al., 2004; Hautier et al., 2010). Asquith et al. (1997) documented increased seed and seedling predation in forests under extreme mammal defaunation – those in which only small rodents remained of the original terrestrial mammalian granivore/herbivore community – compared to forests with a more complete fauna. Rodent density was negatively correlated with the overall density of tree seedlings in a logged Ugandan forest (Kasenene, 1980), and with the density of preferred small-seeded seedlings in a hunted Mexican forest (Dirzo et al., 2007).

Increased rodent abundance may play an important role in reducing the regeneration of many timber trees (Kasenene, 1984; Struhsaker, 1997). Rodents are significant seed predators of mahogany (*Aglaiia* sp.) in Malaysia (Becker and Wong, 1985), and true mahogany (*Swietenia macrophylla*) in Brazil (Grogan and Galvão, 2006; Norghauer et al., 2006). In Guyana, rodents attacked 43% of monitored seeds of the timber tree *C. rodiei*, as late as 566 days after implantation (Hammond et al., 1999). Abundant small rodents in hunted and logged Costa Rican forest sites removed significantly more seeds of three timber species (*Dipteryx*

*panamensis*, *Minquartia guianensis*, and *Virola koschnyi*) than in a comparable site protected from hunting (Guariguata et al., 2000, 2002). In experimental plantings of the timber species *Strombosia scheffleri* in Uganda, 74.8% ( $n = 119$ ) of seedlings died within 122 days, with 95.7% of mortality attributed to rodents (Lwanga, 1994). Synnott (1975) documented comparably extensive rodent predation of the timber tree *Entandrophragma utile*, and Hall (2008) encountered predation pressure so intense that rodents dug under or squeezed through holes in wire mesh enclosure cages to consume 100% of experimentally scattered *Entandrophragma angolense* seeds. It is clear that rodent predation on seeds can be a significant filter on timber tree recruitment, particularly given their increased abundance in hunted forests.

The spatial aspects of seed deposition and granivore habitat preferences may also influence predation pressure on timber species. As small seed predators such as insects and rodents are generally more specialized and occupy smaller home ranges than large vertebrates, they may exert stronger Janzen–Connell type pressures (discussed above) on timber recruitment, increasing the value of seed dispersal away from parent trees. Rodents also favor the microhabitat conditions generated by young disturbed growth (Lambert and Adler, 2000), thus their seed and seedling predation can be higher in gaps than under closed canopy (Schupp, 1988; Schupp and Frost, 1989; Hammond et al., 1992). Wind-dispersed seeds – a common trait among currently harvested timber species – arrive more frequently in gaps than in the understory (Augspurger and Franson, 1988; Loiselle et al., 1996), so predation on these tree species may be especially high with increasing rodent abundance. While wind-dispersal may continue to be effective even in forests where large animal dispersers are absent (see above), increased rodent predation in gaps may depress overall recruitment. Evidence of this is limited, and merits further attention (see Future Research Priorities, below).

Alteration of the granivore guild through hunting will variably release plant species from seed predation or impose greater mortality, depending on the seed species' attractiveness to the remaining small fauna. In sum, due to the changes in seed predation intensity and selectivity of an altered granivore community, hunting may have strong indirect impacts on tree recruitment and timber regeneration dynamics.

#### 4. Herbivory

While the term “herbivory” sometimes encompasses both frugivory and granivory (discussed above), this section will focus on the consumption of leaf tissue; here, the term is used synonymously with folivory. Herbivores reduce leaf tissue and photosynthetic capacity, killing seedlings and harming or potentially killing saplings by uprooting and breaking stems. Herbivory is increasingly being recognized as an interaction which shapes tropical forest tree communities (Dirzo and Miranda, 1991; Marquis, 2005; Terborgh et al., 2006; Clark et al., 2012), and disruptions to this process may alter plant competitive interactions and impact timber tree recruitment.

Tropical forest herbivores are abundant and highly diverse in character, from invertebrates to elephants. Given this diversity, the effects of hunting on the herbivore guild vary, mostly as a

result of differences in body size and hunter preference. The extreme size classes of herbivores generally escape hunting pressure (illegal poaching for secondary animal products, as with elephants, is an exception, eg. [Maisels et al., 2013](#)), while mid-sized herbivores are among the most heavily hunted vertebrates. Ungulate herbivores such as tapirs, deer, and bovids are highly desired game species ([Redford and Robinson, 1987](#); [Fa et al., 2005](#); [Poulsen et al., 2009](#)), and their populations can be severely reduced in hunted sites ([Redford, 1992](#); [Peres, 2000](#); [Laurance et al., 2006](#); [Corlett, 2007](#)).

The removal of terrestrial herbivores by hunting may have both direct and indirect consequences for timber tree recruitment. In general, diminished herbivory results in increased survival and densities of seedlings and saplings, but reduced diversity ([Dirzo and Miranda, 1991](#); [Terborgh and Wright, 1994](#); [Bulinski and McArthur, 1999](#); [Alves-Costa, 2004](#); [Dyer et al., 2010](#); [Harrison et al., 2013](#)). In their pioneering study of a defaunated Mexican forest, [Dirzo and Miranda \(1991\)](#) observed dense seedling carpets and a complete absence of vertebrate herbivore leaf damage; lacking herbivores, the understory became an impoverished mosaic of virtual monocultures, dramatically altered in structure. How well timber species might fare in such an altered system is mostly unknown.

In addition to consuming leaf tissues, terrestrial herbivores can physically damage plants through trampling, rooting, and digging. Seedling responses to this damage can differ among species ([Clark and Clark, 1989](#)), which may result in disproportionately increased survival of more vulnerable species when large animals are no longer abundant ([Roldán and Simonetti, 2001](#)). Both direct impacts of herbivores – consumption and physical damage – may thus differentially affect plant species, though again, their effects on timber tree performance are not well documented.

The hunting of vertebrate herbivores may indirectly affect timber trees both by increasing invertebrate herbivory and by altering plant competitive interactions. As with small mammals (discussed above), insect herbivores can compensate with increased abundance when large vertebrates are extirpated ([Dirzo, 2001](#)). Insects exert strong and specialized herbivore pressures ([Coley and Barone, 1996](#); [Massey et al., 2005](#)) and are widely regarded as significant timber pests ([Gray, 1972](#); [Nair, 2007](#)). Hunting may thus indirectly lead to added timber losses by prompting increased insect herbivory, though evidence is extremely limited.

Hunting may also indirectly modify plant competitive interactions. Herbivory is by definition a net loss for plants, regardless of the herbivore involved. However, these losses may be unevenly distributed across the plant community, particularly when hunting alters herbivore pressures. Plant species that are less often consumed by remaining herbivores as well as those that invest little in anti-herbivore defense may realize a new competitive advantage within the plant community. Designating resources toward the production of plant defense compounds can promote increased seedling survival ([Molofsky and Fisher, 1993](#)), but involves a trade-off with investment in growth ([Coley et al., 1985](#)). Fast growing, competitively dominant species thus typically suffer high rates of herbivory in intact forests because of the palatability of their tissues ([Coley and Barone, 1996](#)), though this regulatory pressure is lost in the absence of herbivores. In an enclosure experiment by [Kurten \(2010\)](#), herbivore removal indeed favored less defended, higher leaf nutrient species. Seedlings which more quickly exhaust their reserves through fast growth also have less of a chance to be damaged by rodents ([Forget, 1997](#)). In a community-level study, [Poulsen et al. \(2013\)](#) documented the proliferation of fast growing, low wood density species in forests subject to hunting pressure. By way of explaining this trend, the authors' *forest herbivore hypothesis* implicates the relaxation of browsing by hunted mammals as the key mechanism of change.

Overall, current evidence suggests that hunting will favor plant species with fast growth, disadvantaging well-defended, high wood density species at the community level. This poses a concern for the regeneration of many timber species in hunted forests. Through its direct and indirect impacts on herbivory, hunting may alter the “competitive balance” between plant species ([Wright, 2003](#)), to the detriment of timber regeneration.

## 5. Conclusions

Hunting can affect regeneration through a variety of pathways ([Fig. 1](#)). Vertebrate seed dispersers are strongly impacted by hunting pressure, reducing seed movement for many species and shifting community composition to favor those plants dispersed by small animals and abiotic means. Timber species with large seeds and fleshy fruit are at particular risk for dispersal and recruitment failure. Hunting also alters granivore communities, resulting in increased predation on species favored by insects and small rodents, and changing the spatial template of seed predation. There is abundant evidence to suggest that many timber species will be detrimentally affected by such altered seed predation regimes. Large vertebrate herbivores decline with hunting pressure, resulting in the modification of plant competitive interactions. This process disadvantages several traits that are common among timber trees, including relatively slow growth and high wood density.

Timber species, like the broader tropical tree community, interact with wildlife through all stages of their life cycles. One cannot assume that regeneration will be successful in the face of hunting, when plant-animal interactions are so widely modified. A lack of appreciation for – and management of – these interactions could threaten forest biodiversity, limit future timber production, and increase the likelihood of forest conversion for other land uses.

### 5.1. Management considerations

Hunting will no doubt continue to affect tropical forests worldwide, though there is great potential to curtail its effects in production forests, through improved management. Many natural management systems rely on unlogged concession lands both to preserve biodiversity and to promote recovery after harvesting from adjacent forest units. However, unlogged tracts may be too small to maintain viable animal populations and too isolated to allow re-colonization of logged areas ([Pannell, 1989](#)). Forest managers expecting sustained timber production must thus ensure that the processes that contribute to regeneration occur within logged areas themselves ([Guariguata and Pinard, 1998](#)). This is only possible if wildlife populations are maintained and the impacts of hunting are reduced across concessions.

The most effective management modifications to reduce hunting in concessions are those which reduce market demand for wild meat and curb the transportation of hunters and their game ([Auzel and Wilkie, 2000](#); [Clark et al., 2009](#)). One way to curtail access would be to ban the transport of hunters and game meat on logging trucks, enforced with road blocks and spot checks, and to close or destroy unused bridges and roads post-logging ([Auzel and Wilkie, 2000](#)). Removing the transportation infrastructure that hunters rely on can be a very successful intervention, as evidenced by the collapse of bushmeat markets and closure of local hunting camps that followed a brief halt in traffic of a large Congo concession ([Pearce and Ammann, 1995](#)).

Demand for wild meat can only be reduced if alternatives are available at equal or lesser prices, perhaps subsidized by the logging companies themselves. This could be achieved by importing domestic animal meat, or by establishing livestock-raising programs within concessions ([Auzel and Wilkie, 2000](#)). [Poulsen et al. \(2009\)](#) outline several additional recommendations to reduce

hunting within concessions, including: concession support for wildlife law enforcement, ensuring that any workers who hunt do so legally, formalizing resource management in land-use planning, especially for indigenous people, and avoiding urbanization in concessions.

Such management requirements may seem extensive, but are not beyond the capacity of most extractive enterprises. In the Congolaise Industrielle des Bois (CIB) concessions in the Republic of Congo, wildlife and biodiversity are specifically managed through a combination of land-use planning, hunting law enforcement, developing economic and protein alternatives to hunting and wild meat, and formalizing wildlife management (Poulsen and Clark, 2010; Clark and Poulsen, 2012). Gabon's Rabi concession, though focused on oil rather than timber, is another exemplary case. The concession prohibits nighttime driving, restricts access for non-employees, and forbids the possession of firearms, snares, and bushmeat (Laurance et al., 2006). Workers are well compensated financially and domestic animal meat is made available at competitive prices (Laurance et al., 2006). Similarly, logging companies in Sarawak are tasked with enforcing a wildlife trade ban in rural areas and providing meat for workers, and forestry laws in Bolivia mandate comparable practices (Robinson et al., 1999).

The options open to forest managers are typically influenced by short-term financial and political priorities, often resulting in the dismissal of plant-animal interactions and the long-term consequences of disruptions to them (Smith and Garnett, 2004). However, these financial constraints are precisely why managers must strive to make informed decisions that promote efficient and cost-effective practices (Green, 2007). For example, protecting native seed dispersers can be much less expensive than artificially recreating lost dispersal services (Hougnier et al., 2006).

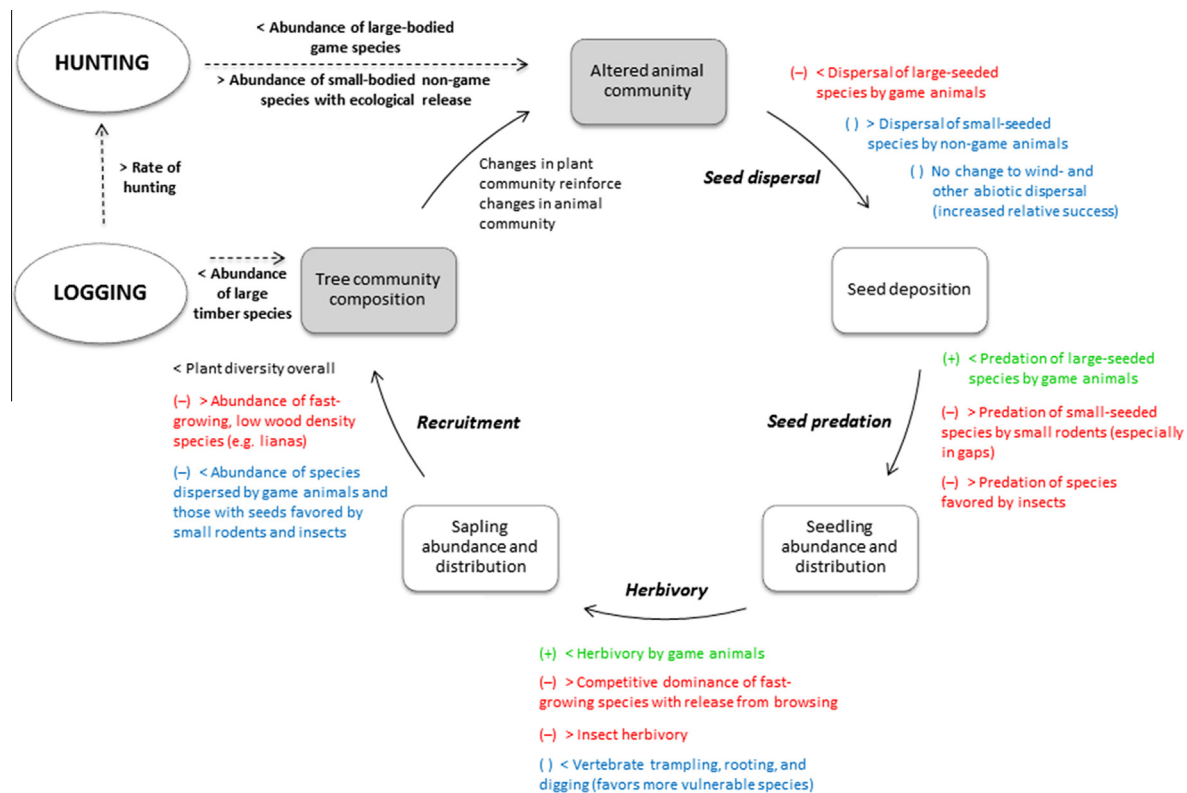
Management schemes and certification bodies such as the Forest Stewardship Council (FSC) should strive to be as specific

as possible regarding wildlife and ecological services; this process has benefitted in recent years from biologists becoming more involved in setting guidelines (Bennett, 2001). Revised FSC principles and criteria now include mention of hunting and ecosystem function (FSC, 2012), but the language remains non-specific and non-prescriptive. Additionally, there is currently little information on whether certification and improved practices actually reduce the pressures on wildlife associated with timber harvest (Kuijk et al., 2009), despite this being a stated goal of such management.

Ultimately, appropriate management decisions will come about only by recognizing the direct and indirect impacts the timber industry has on wildlife (Robinson et al., 1999; Poulsen et al., 2009). Few have acknowledged that wildlife management is a vital component of forest management (Smythe, 1987; Pannell, 1989; Terborgh, 1995; Corlett, 2011), though it is in many companies' best interests to do so, as such explicit consideration would benefit both biodiversity and timber regeneration.

## 5.2. Future research priorities

Knowledge of the ecological requirements and reproductive biology of most tropical timber species is sorely lacking (Bawa et al., 1990; Pinard et al., 1999). Though there is sufficient evidence to conclude that animals play many important roles (see Tables 1 and 2), few forestry studies directly address these relationships. The information presented here is far from exhaustive; these interactions are scattered few and far between in primary literature and natural history accounts, and very little is known on any generalizable scale. In particular, the impacts of potentially disruptive activities such as hunting must be documented and communicated well, so that governments, certifying bodies, and timber companies themselves can make informed management decisions.



**Fig. 1.** Conceptual model of pathways by which hunting may affect the regeneration of timber; adapted with permission from Poulsen et al. (2013). Hypothesized effects on timber regeneration are presented by subscripts: green (+) effects are beneficial, red (–) effects are detrimental, and blue ( ) effects are variable, depending on specific plant traits. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



One research priority is to obtain basic ecological data for timber trees and for hunted wildlife species, including their distribution, density, and rates of change under hunting (Milner-Gulland et al., 2003), particularly for animals that may play a role in timber regeneration. Such information is critically important for identifying important functional traits, as well as thresholds in plant-animal relationships beyond which wildlife are no longer ecologically effective in their roles (McConkey and Drake, 2006), or compensatory increases become deleterious to regeneration processes (see above). Specific studies addressing the dispersal, predation, or overall recruitment of timber trees with relation to wildlife are needed. Responses to hunting among wildlife and plant communities are not unidirectional; it is clear that disruptions to plant-animal interactions can vary in their downstream effects, promoting or inhibiting recruitment depending on several factors. Reconciling the sometimes contradictory outcomes of these processes will require manipulative field experiments.

Regardless of the focal theme, researchers must strive to promote access to ecological knowledge among the international forestry community, and to improve its translation into tangible management action (Sheil and Van Heist, 2000). The most effective research to promote change and mitigate deleterious impacts on wildlife will be that which addresses silviculturally and financially viable alternatives to exploitative practices (Putz et al., 2001). Without such efforts, timber operations and the bodies that oversee them will be unable to make the important decisions that will define the future of tropical forestry.

Forest wildlife and the ecological processes that influence regeneration can be of great importance for many timber species, and the effects of impacts such as hunting must be well understood in order to maintain them. The sustainability of logging from both an ecological and economic perspective will rely on careful management with a strong scientific foundation.

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