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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; Goméz-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 *Pycanthus 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

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