

## Predicting the Long-Term Effects of Hunting on Plant Species Composition and Diversity in Tropical Forests

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### ABSTRACT

Hunting can change abundances of vertebrate seed predators and seed dispersers, causing species-specific changes in seed dispersal and seed predation and altering seedling communities. What are the consequences of these changes for the adult plant community in the next generation and beyond? Here, I derive equations showing how reduced seed dispersal reduces plant reproduction by intensifying kin competition, increasing vulnerability to natural enemies, and reducing the proportion of seeds passing through disperser guts. I parameterize these equations with available empirical data to estimate the likely effects on next-generation abundances. I then consider the indirect effects and longer-term feedbacks of changed seed or adult abundances on reproductive rates due to density-dependent interactions with natural enemies and mutualists, as well as niche differentiation with competitors, and discuss their likely qualitative effects. The factors limiting seed disperser and seed predator populations in natural and hunted forests emerge as critical for determining the long-term effects of hunting on rates of seed dispersal and seed predation. For example, where seed dispersers are held to a constant abundance by hunters, decreases in the availability of their preferred food plants are expected to lead to increased per-seed dispersal probabilities, potentially to the point of compensating for the initial disperser decline. I close by discussing the likely reversibility of hunting-induced changes in tropical forests and key questions and directions for future research.

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*Key words:* defaunation; diversity maintenance; extinction risk; herbivory; hunting; population regulation; seed dispersal; seed predation; trophic cascades; tropical forest.

HUNTING ALTERS PLANT COMMUNITIES wherever it alters animal communities (Emmons 1989). Hunting, like global anthropogenic atmospheric and climate change, can influence even apparently pristine and otherwise undisturbed tropical forests (Redford 1992). Hunting changes the abundances of important vertebrate seed dispersers, seed predators, and browsers, whether through direct impacts on these species or via indirect impacts of the hunting of their competitors or predators (Emmons 1989, Peres & Palacios 2007). Thus, hunting has the potential to alter rates of seed predation, herbivory, and seed dispersal, and thereby plant survival and growth rates through different life stages. When such effects occur, they generally differ among plant species, altering reproductive rates of different species, and thus affecting the composition and potentially the diversity of the plant community (Wright 2003, Stoner *et al.* 2007b). Shifts in the composition of plant functional types could, in turn, affect forest structure, ecosystem function, and ecosystem services such as carbon storage (Bunker *et al.* 2005).

While ecologists can document the short-term responses of plant communities to hunting, the long-term implications remain a matter of speculation. In the short term, changes are often evident in rates of seed dispersal, seed predation and herbivory, in seed and seedling survival, and in the composition, diversity, and/or density of seedlings (see reviews by Wright 2003, Stoner *et al.* 2007b). The degree to which changes in the regeneration layer ultimately affect the adult plant community in the next generation depends on the degree to which changes in abundance at the seed and seedling stage are compensated, or potentially exaggerated, at subsequent stages.

Whether an initial first-generation decline is followed by further declines to extinction or stabilization at a new lower (but nonzero) abundance depends further on how initial changes in community composition affect interactions with the animal community. Short-term responses in the regeneration layer may be poor predictors of ultimate consequences for adult communities. For example, a strong immediate decline in seed survival could have no effect on adult abundance if the availability of safe sites is so limiting that density dependence at the seedling establishment stage is perfectly compensating. On the other hand, even a small decline in seed dispersal could presage ultimate local extinction if that decline is not compensated at another life stage and persists even as adult abundance declines.

Clearly, predicting the long-term influences of hunting on plant communities is a tremendous challenge, requiring integration of empirical evidence of short-term impacts with ecological theory and knowledge of tropical plant community structure and dynamics more generally. This paper is a first attempt at providing a quantitative framework for evaluating these effects. I focus on the effects of changes in abundances of seed dispersers and predators because these species have direct effects on plant recruitment and seedling communities and have been the subject of a number of studies (in contrast, there are very few studies of effects of hunting on folivory). I first use a simple model to show how the direct effects of reduced dispersal and changed seed predation are expected to affect plant reproductive rates, all other things equal. I identify the key quantities that determine these impacts, provide simple equations for calculating them, and parameterize these equations with empirical data to provide rough estimates of the range of likely impacts on affected plant species' abundances. I then examine the various feedbacks

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that might moderate or accelerate these impacts in the longer term, and discuss their likely qualitative effects. Finally, I close with a discussion of the limitations of these rough estimates, reasons for optimism and pessimism concerning the future of hunted tropical forests, and suggestions for future research.

## DECLINE OR LOSS OF SEED DISPERSERS

**IMPORTANCE.**—The decline and potential loss of seed dispersal services was the first and continues to be the most often invoked consequence of hunting for tropical plant communities (Emmons 1989). A recent review of the effects of hunting on the abundances of Neotropical animals lends support to this focus: 12 of the 15 taxa experiencing reductions in abundance averaging over 60 percent are frugivores (Peres & Palacios 2007). Many Paleotropical vertebrate frugivores also suffer from hunting (Corlett 2007). Large-bodied frugivores, like large-bodied vertebrates in general, are most strongly affected. Plant species dependent on large frugivores for seed dispersal (due to large seed size or other traits) are therefore expected to suffer strong and disproportionate decreases in seed dispersal. Undispersed seeds do not experience gut passage, potentially reducing their germination success and seed survival (Traveset & Verdú 2002). Further, undispersed seeds inevitably fall beneath parent trees, where survival is typically lower (Howe *et al.* 1985). As a result, it is hypothesized that some plant species are experiencing or will soon experience complete regeneration failure and imminent local extinction where their frugivorous seed dispersers have been extirpated (Chapman & Chapman 1995). More generally, decline and loss of seed dispersers is expected to result in changed spatial patterns of seed deposition and seedling recruitment, and less-diverse seedling communities (Dirzo & Miranda 1991, Dirzo 2001, Webb & Peart 2001, Wright 2003).

Hunting-induced declines in animal seed dispersers lead to lower removal of seeds from parent trees, shorter seed dispersal distances, reduced seedling abundance, and more clumped seedling distributions. Where human activities have reduced frugivore abundances, the proportion of fruit remaining on parent trees may increase (Guariguata *et al.* 2000, Beckman & Muller-Landau 2007, Wang *et al.* 2007), remain unaffected (Asquith *et al.* 1997, Guariguata *et al.* 2002), or even decrease (see table 1 in Beckman & Muller-Landau 2007). Seed dispersal distances also decline where hunters are active (Asquith *et al.* 1997, Guariguata *et al.* 2000, Wright *et al.* 2000, Wright & Duber 2001, Guariguata *et al.* 2002). Consistent with this, one study in central Panama found the total relative abundance of seedlings of species dispersed by hunted animal taxa is lower in hunted than protected forests (Wright *et al.* 2007). The spatial pattern of seedlings of affected species also differed, with more concentration around adults in hunted forests (Wright *et al.* 2000, Dirzo 2001).

**THEORETICAL EFFECTS ON REPRODUCTIVE RATE.**—To estimate the long-term effects of reduced seed dispersal, I first quantify the direct impact on reproductive rates, all other things equal. Decreased dispersal results in increased kin competition, increased suscepti-

bility to localized natural enemies, and decreased bet-hedging over environmental uncertainty, all of which reduce representation in the next generation (Muller-Landau & Hardesty 2005). These effects correspond to the selective advantages of dispersal (Levin & Muller-Landau 2000). In species experiencing directed dispersal to favorable recruitment sites, decreased dispersal has an additional impact of reduced arrival at such sites. And in species where gut passage enhances germination and/or survival, a decrease in the proportion of seeds experiencing gut passage directly reduces mean germination and/or survival. Here I consider each of these effects in turn.

The most fundamental effect of dispersal is reduction in kin competition, yet this role is often overlooked by tropical ecologists (Howe & Smallwood 1982). Even if per-seed survival or recruitment success is no different under parents than elsewhere, a species or genotype that disperses will always outcompete one that does not, because the disperser can occasionally win sites from the nondisperser, and the nondisperser can never win a site from the disperser (Hamilton & May 1977). Species whose dispersal is reduced due to hunting of their seed dispersal agents are at a disadvantage, as more of their seeds compete with each other under parents and fewer compete for other sites. I calculate the maximum disadvantage conferred just by reduced dispersal (increased proportion of seeds remaining under their parent) relative to global dispersal, in which seeds disperse equally across all sites in a lottery model with discrete generations. To isolate the effects of lowered dispersal from other factors, I assume species are equal in every other way, and that unaffected species continue to benefit from global dispersal of all their seeds. If the species or group of species affected by a loss of dispersal have total relative abundance  $P_t$  in generation  $t$ , and if the proportion of seeds dispersed declines by a proportion  $x$ , the ratio of the expected abundance in the next generation,  $P_{t+1}$ , to the previous abundance,  $P_t$ , declines as

$$\frac{P_{t+1}}{P_t} = \frac{x + P_t(1-x)}{x + 1 - P_t x} + \frac{(1-P_t)(1-x)}{1 - P_t x}. \quad (1)$$

The first term corresponds to the proportion of sites where the focal species is present that will be retained by the species, and the second term corresponds to the proportion of sites that the focal species will win from other species (Appendix S1). Thus, there is a more than proportionate decline in abundance with declines in dispersal (Fig. 1A). These declines are more severe if the affected group is less abundant initially; essentially, the declines are moderated if many other individuals or species experience the same reduction in dispersal (Fig. 1A). In the extreme case of no dispersal ( $x = 1$ ), the second term in the equation is equal to zero and the focal species wins no sites from other species. In this case, if the species or group of species affected by a loss of dispersal initially has relative abundance  $P$ , then their expected abundance decreases by almost 50 percent per generation to a fraction  $1/(2 - P)$  of the previous abundance.

Dispersal failure has additional disadvantages for the majority of tropical plant species that suffer higher seed and/or seedling mortality in areas where conspecifics are more common (Terborgh *et al.*

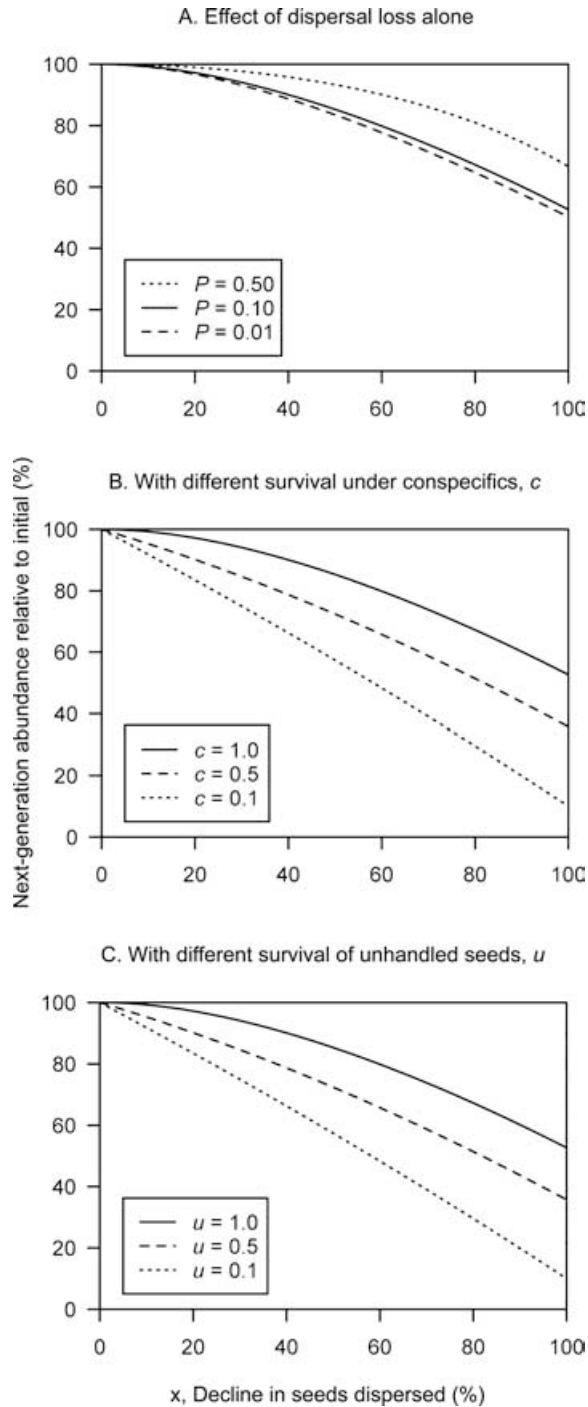


FIGURE 1. The effects of a decrease in the proportion of seeds dispersed away from parents on plant reproductive rates, expressed as expected per-generation changes in abundance. (A) The effect of dispersal loss alone due to increased kin competition, for different initial total relative abundances of affected species,  $P$ . (B) The effect of dispersal loss interacting with decreased survival under conspecifics, where  $c$  is the ratio of survival under conspecifics to survival elsewhere (with  $P = 0.1$  and initial relative abundance of individual species,  $N = 0.005$ ). (C) The effect of dispersal loss interacting with decreased survival of seeds that are not handled by a disperser, where  $u$  is the ratio of survival of unhandled seeds to handled seeds (with  $P = 0.1$ ).

1993, Hammond & Brown 1998, Webb & Peart 1999, Harms *et al.* 2000), as originally hypothesized by Janzen (1970) and Connell (1971). Decreases in dispersal expose more seeds and seedlings to environments of high conspecific density and thus high mortality. To account for this effect, I assume survival under conspecific adults is a proportion  $c$  of survival elsewhere. For dispersal declines  $x$ , individual species initial relative abundances of  $N_0$ , and initial total relative abundance of affected species  $P_0$ , abundance initially decreases as

$$P_1 = P_0 \frac{c(x + N_0(1-x)) + (P_0 - N_0)(1-x)}{c(x + N_0(1-x)) + (P_0 - N_0)(1-x) + (1 - P_0)} + (1 - P_0) \frac{P_0(1-x)}{P_0(1-x) + cN_0 + (1 - P_0 - N_0)} \quad (2)$$

(see Appendix S1 for the derivation of this and later rates of decline). As relative survival under conspecific adults,  $c$ , decreases towards zero, the relationship between the decline in dispersal and the per-generation decline in abundance becomes linear (Fig. 1B). Complete loss of dispersal ( $x = 1$ ) leads relative abundance to decrease to a fraction  $c/(c + 1 - P)$  of previous abundance every generation (Appendix S1). Thus the interaction with lower survival under adults leads to even more rapid declines than under loss of dispersal alone: for example, if survival under conspecifics is only one half of survival elsewhere, then the next-generation abundance is approximately 33 percent of the initial abundance or a decrease approaching 67 percent per generation rather than approaching 50 percent as before. In the extreme case in which dispersal decreases to zero and survival under conspecifics is zero, abundance of course goes to zero in one generation.

Frugivorous seed dispersers may benefit plants not only by removing seeds from the vicinity of parents but also by enhancing seed germination or survival via the direct effects of their handling (Krefting & Roe 1949, Traveset & Verdú 2002), or by disproportionately depositing seeds in favorable environments (Wenny & Levey 1998, Wenny 2001). For example, passage through the guts of frugivores may speed germination or reduce attractiveness to seed predators. In this case, a decline in the proportion of seeds removed by frugivores not only reduces seed dispersal but also reduces the proportion that benefits from these effects. These effects are easily incorporated into the simple model above. If  $u$  is the establishment probability of seeds that do not experience frugivore handling relative to the probability of those that do, then a decline in dispersal of  $x$  leads to abundance declines per generation of

$$P_{t+1} = P_t \frac{ux + P_t(1-x)}{ux + 1 - P_t x} + (1 - P_t) \frac{P_t(1-x)}{1 - P_t x} \quad (3)$$

(Appendix S1). This effect is quantitatively very similar to that of increased mortality under parents (Fig. 1C). Indeed, in the case of complete loss of dispersal, relative abundance decreases to a fraction  $u/(u + 1 - P)$  of previous abundance every generation, precisely the same effect as for decreased mortality under parents. If seeds that are not handled by the preferred disperser are dispersed by another animal species that does not enhance seed survival through gut passage, then the effect is formally identical to any other decrease

in seed survival such as could be caused by an increase in seed predation, as treated in the next section (see also Appendix S1).

Dispersal can also benefit species by providing a means for bet-hedging over spatiotemporal uncertainty in the environment (Cohen 1966; see Levin *et al.* 2003 for a review). If the probability of successful recruitment, and thus the expected payoff of a seed, varies sufficiently in space *and* time, then dispersal provides an additional advantage (Levin *et al.* 1984). Spatial variation in habitat alone in the absence of temporal variation generally selects against dispersal (Hastings 1983), and temporal variation alone has no effect on selection for dispersal (Ellner & Shmida 1981). Gap dynamics may offer the requisite type of variability, as every site (including the home site) has some probability of a gap opening up soon after seedfall. Unfortunately, this bet-hedging advantage to dispersal can be captured only in more complex models (Levin *et al.* 1984). Below, I argue that this advantage is likely to be relatively unimportant for the species suffering decreased dispersal in hunted forests.

COMBINING THEORY AND EMPIRICAL DATA TO ESTIMATE LONG-TERM EFFECTS.—In order to predict the impact of reduced seed dispersal on plant populations and communities, the first critical piece of information is how much hunting reduces seed removal from parent trees. Surprisingly few studies have quantified this effect; observed changes in seed removal rates vary among species, sites and studies, and range from an *increase* of 10 percent to a decrease of 96 percent (Stoner *et al.* 2007b). The largest decrease occurred in a large-seeded palm, *Attalea butyraceae* (Wright *et al.* 2000); in general, larger-seeded species suffered greater reductions in dispersal (Stoner *et al.* 2007b). Some degree of compensation by remaining vertebrates, often rodents, is likely to make complete (100%) dispersal failure an exceedingly rare event. In terms of the impact on reproductive rates from the loss of dispersal alone, however, there is little difference between a 96 percent and 100 percent reduction. Based on the equations above, a 96 percent reduction in dispersal would be expected to lead to as much as a 47 percent reduction in abundance in the next generation, if uncompensated by other factors. Decreases in removal rates could understate the decline in dispersal if there is a change in the identity of the species taking the seeds and a decline in the quality of seed dispersal. Overall, however, estimates of population consequences calculated under the assumption of a decrease from global to no dispersal are likely to overestimate the impacts of dispersal declines because they rest on the assumption that all removed seeds are perfectly ('globally') dispersed, when in fact dispersal is much more local (Clark *et al.* 1999, Dalling *et al.* 2002, Muller-Landau *et al.* 2002, Clark *et al.* 2005) and thus is less beneficial in escaping kin competition.

The second key piece of information is the recruitment success of undispersed seeds remaining under parents relative to that of dispersed seeds. This includes both effects of natural enemies concentrated around conspecific adults and effects of gut passage, and encompasses seed survival, seedling establishment, and early seedling survival (but not total probability of recruiting to adulthood). Of 52 tropical studies comparing seed or seedling survival near and far from conspecific adults with sample sizes of more than 100 in each location, 26 observed lower seed or seedling survival

near conspecific adults (including one with no survival near), 23 observed higher survival (including two with no survival far), and three observed no difference in survival (including one with no survival in either location; Hyatt *et al.* 2003). Among studies having nonzero survival in both locations, the ratio of survival near to survival far varied from  $c = 0.15$  to  $c = 3.67$ . Still stronger effects were observed in *Virola surinamensis*, where seed and seedling survival until 12 weeks of seedling age was  $1/24^{\text{th}}$  as high ( $c = 0.04$ ) under crowns as it was 45 m distant from any conspecific crown (Howe *et al.* 1985). The variation in effects among species may relate to variation in natural enemies. Hammond and Brown (1998) showed that Janzen–Connell effects of distance- or density-dependent survival were generally found in studies in which the principal enemies were invertebrates, and were generally not found when the main enemies were vertebrates. Survival under conspecifics at a rate only 4 percent as high as for dispersed seeds ( $c = 0.04$ ) produces severe consequences of dispersal reductions, with per-generation reductions in abundance almost equal to the reduction in the proportion of seeds dispersed (Fig. 1B).

Gut passage effects also vary strongly among plant species, with considerable variation explained by the disperser involved. In general, birds and bats have more strongly positive effects on final percentage germination than nonvolant mammals (Traveset & Verdú 2002). Based on the mean log odds ratio of germination found by Traveset and Verdú (2002), germination of seeds not experiencing gut passage is typically a proportion  $u = 0.67$  of germination following gut passage for species dispersed by birds and bats, and a proportion  $u = 0.95$  for species dispersed by nonvolant mammals. Traveset and Verdú (2002) included temperate and tropical tree, shrub and herb species from grasslands, shrublands, and woodlands, with significant differences among all groups; thus, average patterns may be somewhat different for tropical forest plants. Particularly large effects of gut passage on germination are found in some elephant-dispersed species (Hawthorne & Parren 2000). For example, 54.6 percent of *Balanites wilsonia* seeds collected from elephant dung piles germinated, compared with 20.6 percent of seeds remaining in rotting fruit under fruiting trees, suggesting  $u = 0.38$  in this species (Cochrane 2003). Germination also occurred twice as fast following elephant gut passage, reducing exposure to seed predators. Of course, passage through the gut of a frugivore can also destroy seeds, especially small seeds (*e.g.*, Kaplin & Lambert 2002), and appears to have no effect on germination for many plant species (*e.g.*, Knogge *et al.* 2003). Indeed, with the exception of a small minority of those species dispersed by elephants (Hawthorne & Parren 2000), most of the large-vertebrate-dispersed seeds that are most affected by dispersal reductions experience little or no direct benefit from gut passage (Traveset & Verdú 2002).

Essentially all tropical trees display considerable spatiotemporal variation in recruitment success beyond that due to natural enemies concentrated near parents. This variation is due to the effects of microsite environmental conditions and generalist enemy pressure, as well as moderately specialized enemy pressure under related taxa. Large-seeded species display relatively low spatiotemporal variation in recruitment success because their survival is much less affected by light availability, litter depth, and physical damage than is the

survival of small-seeded species (Rose & Poorter 2002). Like all species, however, large-seeded taxa may experience spatiotemporal variation in seed predation by generalists arising from temporal fluctuations in seed predator populations combined with spatial variation in the availability of alternate food sources (Forget 1993, Leigh *et al.* 1996). Nonetheless, I hypothesize that the benefits of dispersal for species affected by hunting are due mostly to escape from kin competition and from natural enemies concentrated around conspecifics, with little contribution from bet-hedging over environmental uncertainty or loss of gut passage (as discussed above). The pioneer species for whom bet-hedging via dispersal is likely to be more important generally have small seeds (Metcalfe & Grubb 1995) dispersed by abiotic means or small birds and bats, and often have some degree of seed dormancy or recalcitrance that allows for additional bet-hedging via dispersal in time (Pearson *et al.* 2002).

## CHANGED ABUNDANCES OF SEED PREDATORS

**IMPORTANCE.**—Hunting can lead to decreases or increases in seed predation by vertebrates, depending on the level of hunting and the animal and plant species involved. Large vertebrate seed predators, such as peccaries and agoutis, are often directly hunted and thus are likely to decline in abundance (Corlett 2007, Peres & Palacios 2007). In contrast, small vertebrate seed predators such as rats and mice are rarely hunted, and may increase due to hunting of their own predators and competitors (Peres & Dolman 2000, Wright 2003). This potentially leads to a double advantage for large-seeded species, which confront both reduced seed predation and reduced competition from small-seeded species, while small-seeded species suffer the double disadvantage of increased seed predation and increased competition from large-seeded species (Dirzo *et al.* 2007). In the extreme, it is feared that particular large-seeded plant species benefiting from decreased vertebrate seed predation might consequently increase greatly in abundance, thereby driving many other tree species locally extinct (Wyatt & Silman 2004).

Hunting-induced decreases in the abundances of vertebrate seed predators have been shown to reduce seed and seedling predation rates on the plant species these vertebrates consume (Wright *et al.* 2000, Roldan & Simonetti 2001). Decreases in the abundances of large vertebrate seed predators, due to whatever cause, lead to decreased vertebrate seed predation, higher seed survival (Wyatt & Silman 2004, Asquith & Mejia-Chang 2005), and higher seedling densities of the affected species (Wright *et al.* 2000, Silman *et al.* 2003), which are generally large-seeded. Where overall seed and seedling survival at the community level is substantially enhanced, the reduced vertebrate seed predation can also lead to higher overall seedling densities (Dirzo & Miranda 1991). The resulting more intense competitive environment is expected to further favor large-seeded species (Poorter & Rose 2005). No studies have compared seed predation of truly small-seeded species between hunted and protected sites. On small islands and forest fragments lacking large vertebrates, mice and rats have increased greatly in abundance (Fonseca & Robinson 1990, Adler 1996) and seed survival of their

small-seeded food plants decreased (Asquith *et al.* 1997). However, these fragments differ from intact forests in more ways than merely the absence of larger vertebrate residents, and thus additional studies are needed before we can conclude that similar effects would occur in hunted forests.

Many of the large vertebrate seed predators that are negatively affected by hunting are also seed dispersers. Monkeys are seed dispersers of many species and seed predators of others, and may be both for some species depending on whether seeds are spit out or pass through the gut (Stoner *et al.* 2007a). Scatterhoarding rodents, such as agoutis, are both seed dispersers and seed predators of large seeds. Thus, large-seeded species in particular may experience reductions in both dispersal and seed predation under hunting (Wright & Duber 2001). These effects act in opposite directions on reproductive rates, and thus are partially compensatory. For simplicity, I consider only the effects in isolation here. Additional research is needed to establish how often the species suffering decreased seed dispersal simultaneously benefit from decreased seed predation, to quantify these opposing effects, and, where appropriate, combine the effects on reproductive rates.

**THEORETICAL EFFECTS ON REPRODUCTIVE RATE.**—In a lottery model, the direct effects of a spatially and temporally constant increase or decrease in seed predation on reproductive rates vary proportionally with the change in seed survival. For example, if escape from vertebrate seed predation doubles, then abundance in the next generation is expected to approximately double, all else equal. Formally, if  $s$  is the ratio of the new probability that seeds escape vertebrate seed predation to the old probability, and  $p$  is initial abundance, next-generation abundance is expected to be simply  $sp$  absent any indirect effects on seed or seedling mortality from other causes (see Appendix S2 and the next section on feedbacks). As with the model used in calculating the direct impacts of a decrease in dispersal, this assumes that the community was previously at equilibrium such that all species had essentially equivalent reproductive rates and were not undergoing directional long-term changes in abundance.

Differential change in seed predation near to compared to far from conspecific adults, or in locales with high, relative to low, seed density, affects tree reproduction in more complex ways. These effects can be approximated by separately considering predation under conspecific adults and elsewhere, much in the same way as in the estimation of the effects of declines in seed dispersal. This requires information on the proportion of seeds remaining under parent trees as well as on the old and new vertebrate seed predation rates under parents and farther away.

**COMBINING THEORY AND EMPIRICAL DATA TO ESTIMATE TOTAL EFFECTS.**—A first estimate of the effects of changes in vertebrate seed predation on plant reproductive rates thus requires only basic data on the change in the proportion of seeds escaping such predation. Surprisingly few such data are available. Wright and Duber (2001) found that hunting reduces rodent seed predation of the large-seeded palm *Attalea butyraceae* from over 90 percent to approximately 40 percent of seeds. Thus escape increases approximately sixfold from 10 to 60 percent, and seedling and adult

abundances would be expected to increase accordingly under this influence alone (without considering decreases in seed dispersal). Similarly, Roldan and Simonetti (2001) observed a 1.6-fold increase in seed escape of vertebrate seed predation of *Astrocaryum murumuru* from occasionally hunted to intensively hunted forests, and Galetti *et al.* (2006) find as much as a twofold increase in escape of *Astrocaryum aculeatissimum* in heavily hunted sites relative to less hunted sites. In the smaller-seeded (but still relatively large-seeded) palm *Oenocarpus mapora*, escape of predispersal vertebrate seed predation is 25 percent higher in a moderately hunted than in an unhunted forest (Beckman & Muller-Landau 2007). In the next section, I consider how such increased escape of vertebrate seed predation may be compensated by increased attack by other natural enemies and other factors.

## INDIRECT EFFECTS AND FEEDBACKS

**VERTEBRATE-MEDIATED FEEDBACKS.**—How hunting-induced changes in adult tree abundances further affect rates of seed dispersal and seed predation, and thereby, plant reproductive rates, depend crucially on the degree of top-down versus bottom-up control of the remnant consumers (Silman *et al.* 2003). By remnant consumers I mean seed dispersers and seed predators in the hunted forest, encompassing both the remaining populations of game species and the nongame species. If these remnant consumers are strictly limited by availability of fruits and seeds, then subsequent changes in adult tree population density of affected plant species are expected to be associated with no changes in seed dispersal, seed predation, or other direct impacts on plant reproductive rates, because consumers will simply increase or decrease to match food availability. All other things equal, this will lead to continuing increases or decreases in abundance at near exponential rates (Figs. 2A and B). In contrast, if hunting, other top-down influences, or availability of alternative food sources perfectly regulate remnant consumers to relatively constant, nonzero abundances, then a decrease in abundance of their food plants will increase the ratio of consumers to their fruit and seed food, and thus is likely to cause an increase in seed dispersal and seed predation rates. This creates negative feedbacks via seed dispersal, and positive feedbacks via seed predation (see Appendices S1 and S2 for details). The net result, absent other influences, is that abundance declines due to decreases in seed dispersal are slowed or even arrested (Fig. 2C), while abundance changes due to altered vertebrate seed predation are accelerated (Fig. 2D). If remnant consumer abundances are affected by fruit and seed availability as well as other factors, then changes in seed dispersal or seed predation with adult plant abundance will be intermediate between these extreme trajectories.

The factors limiting vertebrate populations in undisturbed tropical forests continue to be debated (van Schaik *et al.* 1993, Leigh 1999, Terborgh *et al.* 2001). In hunted forests, game species would generally be limited by hunting pressure. However, remaining consumers could become limited by fruit and seed availability if some consumer species are eliminated by hunting and other un-

hunted species, released by the disappearance of larger competitors, multiply to the extent their food supply allows. In principle, fruit and seed availability might even limit abundances of game species experiencing ongoing hunting, if their ability to evade hunters was sufficiently strongly related to food availability. In general, frugivore and granivore abundances in tropical forests appear to be limited mainly by the availability of alternate food sources, such as insects or leaves, in seasons of scarcity (van Schaik *et al.* 1993, Leigh 1999). Insofar as this is true, frugivore abundances will not respond to small or intermediate changes in fruit or seed availability under which the alternate food sources remain limiting, and thus we expect strong feedbacks of changed adult tree abundances on seed dispersal and seed predation rates as the ratio of consumers to fruits and seeds changes. The clear exception would be changes in availability of keystone fruit and seed species that are themselves the limiting food source (Harrison 2005).

Vertebrate-mediated feedbacks may change abruptly if fruit or seed availability drops beneath critical thresholds for consumer population persistence. If hunted seed disperser species are dependent for their persistence on the presence of sufficient fruiting trees, then decreases in adult tree abundance, while initially leading to a rebound in dispersal services due to the increased ratio of dispersers to trees (a negative feedback), may beyond some threshold lead to local extinction of the disperser population, and complete loss of their dispersal services (a positive feedback). This could potentially lead to further and faster declines of the plant species involved. This risk should be quantified by integrating (and where necessary collecting) information on diet breadth and critical food plant abundances of frugivore species.

**DENSITY-DEPENDENT INFLUENCES.**—The degree to which the direct effects of changed seed dispersal and seed predation on a plant species' reproductive rates are manifested depends on the magnitude (and direction) of density dependence—both local and population-level—of all its life history transitions. Will a change in seed abundance due to changes in seed predation carry over into changed seedling and adult abundance (no density dependence), be dampened (negative density dependence), magnified (positive density dependence), or even reversed (overcompensating negative density dependence)? Density dependence further determines whether any resulting changes in a species' reproductive rate is maintained as the species increases or decreases in abundance as a consequence, or whether this change is accelerated, slowed or eventually halted as the species achieves a new equilibrium abundance. Attack by natural enemies, services provided by mutualists, and the strength of competitive effects may all depend on density of focal plant species (Howe & Estabrook 1977, Hammond & Brown 1998, Uriarte *et al.* 2004). Indeed, they may potentially also depend on the neighborhood community composition more generally—the abundances of alternative hosts for enemies, of alternative food sources for mutualists, and of plant species with similar life histories and habitat preferences (Howe & Manasse 1983, Uriarte *et al.* 2004, Webb *et al.* 2006).

In general, the balance of these factors tends to produce negative density dependence or negative feedbacks, increasing species'

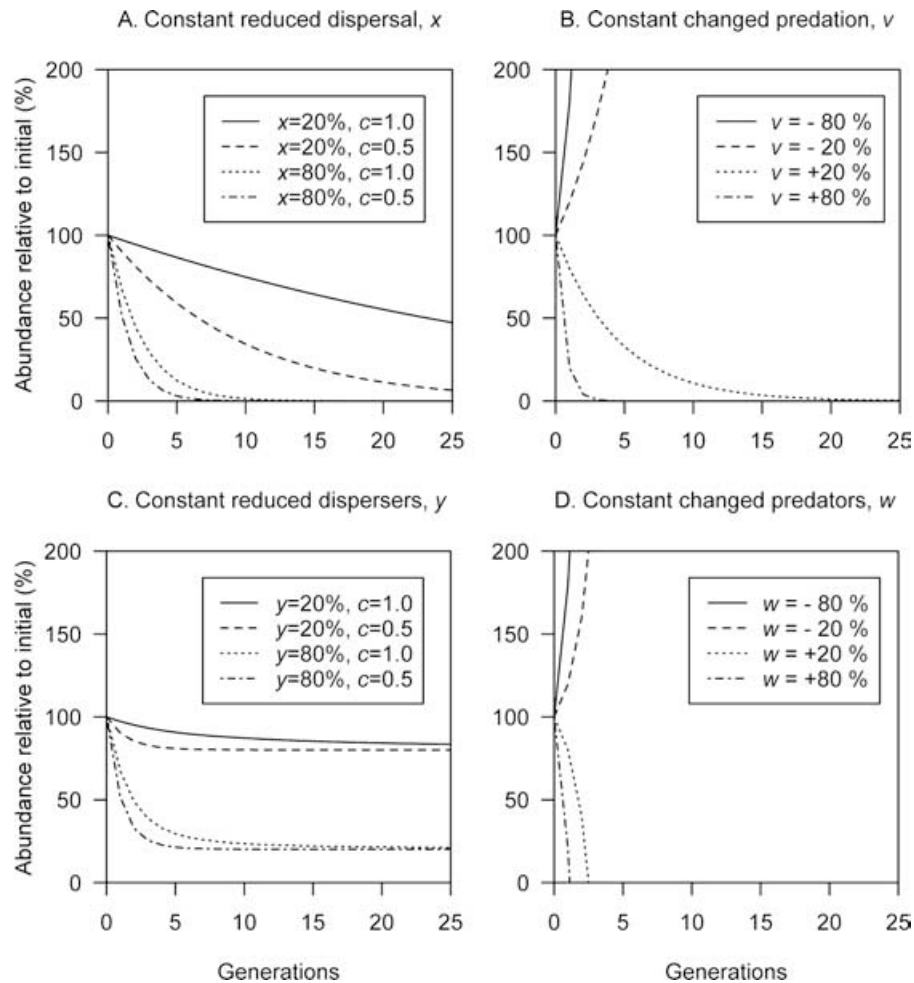


FIGURE 2. The different trajectories of plant abundances expected based on the direct effects of seed dispersal or seed predation changes alone depending on whether remaining consumers are limited by availability of fruits and seeds. If they are limited by fruit and seed availability, we expect (A) a constant proportion of seeds dispersed,  $x$  and (B) a constant proportion of seeds predated,  $v$  even as plant abundance changes because consumer populations change in parallel with food availability. If they are limited entirely by other factors, we expect (C) constant abundances of the seed dispersers,  $y$ , and thus increasing proportion of seeds dispersed as food plant abundance declines and (D) constant abundances of seed predators,  $w$ , and thus decreasing (increasing) proportions of seeds predated as food plant abundance increases (decreases). The assumption in panels C and D is that the affected plant species as a group are the sole food source for the consumers; see supplementary Appendices for details. For all cases, the initial total relative abundance of affected species is  $P = 0.1$ ; for panels B and D initial seed predation is  $q = 0.5$ ; for panels A and C, initial relative abundance of individual species is  $N = 0.005$  and relative survival beneath conspecifics is  $c = 1.0$  (no difference) or  $c = 0.5$  (survival is half as large).

reproductive rates as they become rarer and decreasing them as they become commoner (Webb & Peart 1999). Such negative density dependence, or 'stabilizing' forces *sensu* Chesson (2000), are necessary for the maintenance of diversity. The high diversity of tropical forests is a testament to the pervasiveness and dominance of negative density-dependent forces in these ecosystems. Harms *et al.* (2000) demonstrated that the seed-to-seedling transition is negatively density-dependent in all 53 woody species investigated on Barro Colorado Island, Panama, and showed in the aggregate this lead to higher diversity in the seedling layer. Wills *et al.* (2006) further demonstrated that diversity increases from one size class to the next in seven tropical forests, consistent with negatively

density-dependent survival of saplings and trees. These are merely two of the more comprehensive studies providing evidence of negative density dependence of life history transitions in tropical forests (see reviews by Hammond & Brown 1998, Wright 2002, Leigh *et al.* 2004). This sort of negative density dependence is most often attributed to attack by natural enemies, and is consistent with that mechanism. Less appreciated is the fact that all types of niche differentiation act in a negatively density-dependent manner on some spatial or temporal scale (Chesson 2000, Wills *et al.* 2006). As a result, the direct effects calculated in the previous section will generally be moderated by indirect effects related to changes in distance- and density-dependent forces.

Microbial and invertebrate natural enemies can cause negative density dependence, and are often invoked as the major cause of such patterns in tropical forests (Gilbert & DeSteven 1996, Hammond & Brown 1998, Harms *et al.* 2000, Wright 2002). As conspecific density increases, these relatively host-specific enemies are able to attack more efficiently and thus cause greater mortality. This leads to an increase in reproductive rate as host seed or adult abundance declines, potentially arresting the declines of newly disadvantaged species and stabilizing their abundances at a new, lower level. The strength of the negative density dependence of plant survival that results, however, itself is a function of the dispersal distance of the plant. When seed dispersal distances are shorter, seeds benefit less from the rarity of conspecific adults, because they still suffer high mortality associated with proximity to their own parent tree, and from related trees likely to be clumped nearby (Adler & Muller-Landau 2005). Thus, reductions in seed dispersal due to hunting not only increase the proportion of seeds subject to high rates of natural enemy attack under conspecific adults, but they also reduce the buffering against extinction that is provided by increased escape from natural enemies at low abundances (Fig. 3). As adult abundances decline, the proportion of seeds escaping does increase, resulting in negative feedbacks, but these negative feedbacks are weaker than they were in the intact community, and are thus less likely to be sufficient to prevent further declines.

All niche differences among plant species with respect to regeneration habitat, life history strategy, temporal variation in the environment, or other factors will also in general lead to negative feedbacks to changes in abundance. Given the high diversity of species in tropical forests and the correspondingly smaller niche differences between individual species, these negative feedbacks are likely to operate more at the level of groups of species sharing similar strategies, rather than providing strong benefits to individual species. The degree to which such niche differentiation is likely to protect species disadvantaged by hunting depends in large part on the degree to which these niche differences correspond with differences in the impacts of hunting. For example, consider a hypothetical community in which all canopy tree species were dispersed by large-bodied game species and thus suffered reduced dispersal, while all shrubs were dispersed by small birds and bats whose dispersal remained unchanged. Unless the canopy tree species completely failed to regenerate, one would not expect a major change in the total abundance of adult canopy trees and the total abundance of adult shrubs in the next generation, because species within each group compete most strongly with others in the same group. Given the small positive correlations of dispersal mode and susceptibility to vertebrate seed predation with life history strategy and regeneration habitat across tropical species (Gentry 1983, Rose & Poorter 2002, Poorter & Rose 2005), such niche-based rescue is likely to provide only a minor negative feedback on the direct effects of hunting. Indeed, the importance of these influences can be approximated by basing calculations on the total relative abundance of affected species within a particular niche whose total abundance is expected to be conserved (*e.g.*, drought-tolerant shrubs), rather than the relative abundance in the forest as a whole. In general, individual species that share life history or habitat niches mostly

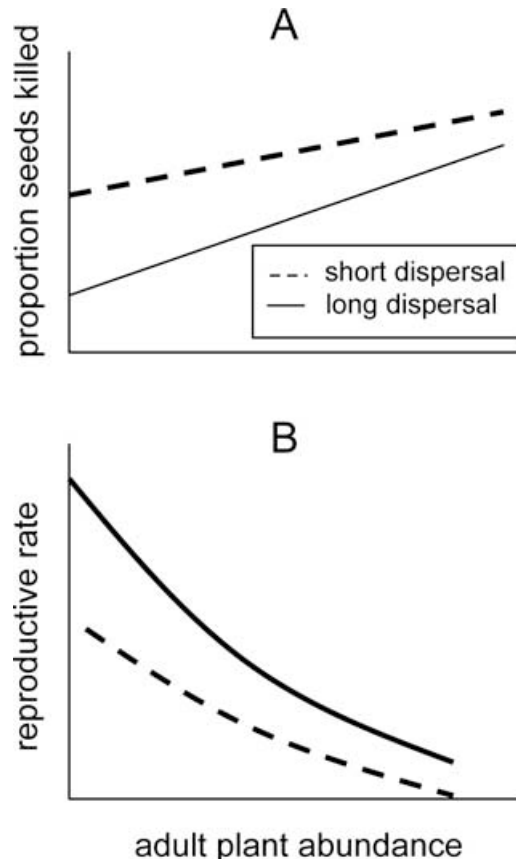


FIGURE 3. The effects of decreases in seed dispersal distances that are similar for all abundances of the focal plant species on interactions with specialized natural enemies concentrated around parent plants. (A) When seed dispersal distances are decreased, a higher proportion of seeds are killed by natural enemies, with especially strong effects at low densities and thus less of a change in seed mortality with adult density. (B) This effect not only decreases per capita reproductive rates but also reduces the density dependence of reproductive rates.

with others having the same dispersal system or same susceptibility to seed predators are likely to be relatively less affected while those sharing niches with species having other dispersal modes are more vulnerable to competitive exclusion (see effect of  $P$  in Fig. 1A, and in the equations above).

## DISCUSSION

**MERITS AND LIMITATIONS OF SIMPLE ESTIMATES.**—Though accurate and precise prediction of the effects of hunting on the relative abundances of adult plants in future generations is a long way away, if it is feasible at all, we can develop working hypotheses using simple models that encapsulate basic principles of population and community ecology. Even approximate estimates are useful for identifying those species and communities at greatest risk, and appropriately prioritizing conservation interventions. This paper



shows how first estimates of the direct impacts of changes in seed dispersal and seed predation can be made through the combination of simple theory and basic data. These estimates do not include indirect effects or feedbacks. I argue here that the total impact of indirect effects will in most cases be to moderate the direct effects, because of the dominance of negative density-dependent forces in diverse tropical forests. Thus, the simple estimates are likely to overestimate the effects of hunting. From a conservation perspective, this overestimation might be considered a virtue consistent with the application of the precautionary principle.

Accurate estimation of even the direct effects of changes in seed dispersal and seed predation would require a more complex and fully spatial model. Vertebrate seed deposition and seed predation vary spatially in complex ways that are not captured in the pseudospacial lottery model employed here. For example, the assumption here that all dispersed seeds are dispersed globally overstates the benefits of dispersal and thus the costs of dispersal loss. At the same time, the assumption that mortality under conspecifics is identical regardless of how many undispersed seeds are left there will understate the potential effects of dispersal loss if mortality continues to increase with conspecific seed density even at the high densities found under reproductive adults. The assumption that vertebrate seed predation changes equally everywhere will overstate the consequences of changes in seed predation if such a predation is in fact higher in areas of high seed density, and will understate them if it is higher in areas of low seed density. More complicated spatial models could capture more complexities such as these and in principle provide better estimates, but such models would require considerably more data to parameterize and would be more difficult to analyze. Ultimately, more may be gained using models of intermediate complexity and employing new methods for analyzing spatial models (Dieckmann *et al.* 2000) and/or capturing the benefits of spatially explicit dispersal in nonspatial equations (Levin & Muller-Landau 2000).

**THE FUTURE OF HUNTED TROPICAL FORESTS.**—The effects of hunting on plant communities are generally expected to be reversible provided all the affected plant and animal species are still present or are reintroduced. However, full recovery is likely to be slow, because many of the most affected large-bodied vertebrates have long generation times and low reproductive rates. These same traits make large vertebrates more likely to be lost from the community entirely under hunting pressure (Bodmer *et al.* 1997), in which case they would have to recolonize the site from more intact forests or be reintroduced, further slowing recovery and potentially making recovery dependent on human intervention. In addition, a dearth of seed dispersers is expected to lead to a decrease in their food plants, potentially slowing the subsequent recovery of frugivore populations. In the extreme, if the total abundance of plant species consumed by a frugivore species is no longer sufficient to support a viable population, then the return of the frugivores and plants to their prior abundance can only be accomplished by additional interventions such as provisioning of the frugivores and/or enhancement of the natural regeneration of their food sources. Fortunately, this bleak

scenario seems relatively unlikely in practice because of the lack of tight plant-disperser mutualisms in tropical forests (Howe 1993).

In contrast, a dearth of predators is expected to lead to an increase in prey, and thus the rebound of both carnivores and seed predators may actually be facilitated by past hunting-induced increases in the densities of their food sources. However, hunted seed predators and other herbivores are likely to rebound before their own carnivorous predators, resulting in a period of time in which herbivores are hyperabundant, a time period that may itself pose a danger to plant community integrity. For example, in temperate forests of the eastern United States where deer populations have rebounded and their predators have not (yet) returned, high herbivore pressure has caused complete regeneration failure of favored food plant species in some areas (Rooney *et al.* 2002, Coté *et al.* 2004).

The lack of historical evidence of plant extinctions following past human-induced extinctions or declines of seed dispersers and herbivores provides some reason for optimism that extant tropical plant species will survive the onslaught of today's human hunters, but this optimism must be tempered by consideration of the weaknesses of the historical record for tropical forests in particular and the differences between continental tropical forests and other ecosystems for which the historical record is better. The tropical paleorecord remains sparse and patchy, and although some species that appear to be adapted for dispersal by extinct gomphotheres have clearly survived (Janzen & Martin 1982, Donatti *et al.* 2007), evidence that others went extinct following Pleistocene overkill may yet emerge. The lack of extinctions following bison extermination from most of the Great Plains may be credited in part to the widespread introduction of grazing livestock with ecologically similar roles—local extinctions within fragments missing both may better presage the impacts of large-scale loss of all such herbivores (Leach & Givnish 1996). The persistence of plant species adapted for dispersal by dodos (Witmer 1991, Herhey 2004) may in part be credited to the lower plant species diversity on islands in general (Rosenzweig 1995), which may make individual species less vulnerable to extinction as niche differences between coexisting species are likely to be larger. The high plant diversity of tropical forests, in contrast, includes many species playing apparently very similar ecological roles (small niche differences), but not necessarily sharing similar seed dispersal and seed survival strategies, potentially making individual species more vulnerable to decline. Localized natural enemies may play a relatively more important role in stabilizing community composition in such species-rich systems, and their ability to provide negative density-dependent feedbacks is itself likely to be reduced for species whose seed dispersal declines.

In sum, there are reasons for both optimism and pessimism concerning the future of tropical forests currently affected by human hunting. On the one hand, there is no question that the long generation time of most tropical plant species provides a critical window of opportunity during which major impacts could be averted. If the problem of hunting is resolved within the next 50 yr, whether through conservation interventions or simply declining demand as the relevant human communities change, then there is a high probability that there will be no permanent changes to the plant

community due to hunting alone. On the other hand, removing hunting pressure is only the first step in restoring natural ecological processes that structure plant communities and are disrupted by hunting. Even in the best-case scenario, full recovery of the faunal community will take considerable time for the larger-bodied vertebrates and may require human assistance in the case of species that had been locally extirpated. More critically, tropical forests today face many anthropogenic influences simultaneously and these may act synergistically to alter and degrade tropical forests (Wright 2005). For example, recovery of large-bodied animals may not be possible at all where habitat destruction and fragmentation has left remaining forest areas too small or disconnected.

**DIRECTIONS FOR FURTHER RESEARCH.**—The first imperative for further research is to obtain the basic data necessary to begin to assess potential changes in plant reproductive rates due to hunting. This includes the change in proportion of seeds dispersed away from the parent tree, the change in vertebrate seed predation, and the *relative* recruitment success of undispersed seeds remaining under parent trees (note that densities of recruits alone are uninformative absent information on seed arrival, and that information on success under parents alone is uninformative absent information on success elsewhere). These data are currently available for only a handful of populations at a few sites. Because collection of even these basic data is a huge task when multiplied by the number of populations potentially at risk, research should focus on identifying more easily measured predictors of risk. Dispersal syndrome and seed size are already known to be associated with the impacts of hunting on seed dispersal and seed predation. Hopefully additional predictors of risk, whether based on traits or on phylogenetic affiliation, remain to be discovered.

Overall, the complexity of interactions in tropical forests and our limited understanding of the forces structuring tropical plant communities make accurate and precise long-term predictions of the effects of anthropogenic changes impossible at this time. Major, fundamental ecological questions about the functioning of intact tropical forests that need to be answered in order to predict the effects of hunting in particular include the following: (1) What determines spatial and temporal patterns of seed predation and seed dispersal by different species, and in particular, to what degree do rates of predation and dispersal parallel changes in seed and fruit availability and to what degree are they controlled by other factors, including top-down influences of carnivores? The answers to these questions are critical for understanding the impacts on seed dispersal and seed predation rates of both changes in plant abundance and loss of carnivores. They also link directly to a related question: (2) To what degree do seed predators and seed dispersers contribute to stabilizing niche differentiation among plant species? Such stabilization is possible only if seed dispersal and escape from seed predation are in part density-dependent, at least at the level of species sharing similar dispersal or escape strategies. Declines in particular groups of seed dispersers or predators will have bigger impacts if plant species variation in these strategies plays a major stabilizing role in plant communities. (3) To what degree are plant strategies for seed dispersal and escape from seed predators correlated

with (other) stabilizing axes of niche differentiation? The degree of such associations determines whether stabilizing processes acting on other niche axes will constrain changes in plant abundance resulting from altered seed dispersal and predation alone. And finally, (4) to what degree are individual species populations of tropical plants regulated by density-responsive natural enemies, and how do their activities interact with vertebrate seed dispersal and predation? In general, better, more mechanistic, and quantitative understanding of stabilizing coexistence mechanisms in tropical forests will help illuminate the degree to which such mechanisms could buffer tropical communities against change.

While these questions can and should be addressed through a variety of approaches, three general approaches are likely to be particularly useful. First, studies designed to take advantage of landscape-scale variation in the density of plant species and guilds, and in community composition, will be particularly well-placed to investigate the density dependence and composition dependence of ecological processes. Ideally, the landscape-scale variation in question would be historical, or even experimental, rather than environmentally determined. Examination of variation on these scales could help illuminate to what degree abundance affects seed predation and seed dispersal, mortality due to other natural enemies, life history transition rates, and ultimately reproductive rates. Second, the construction, testing, and application of appropriate models will be key to integrating effects across multiple life stages and understanding the implications of patterns and mechanisms involved in one process or life stage for the population and community as a whole. Especially for pressing conservation questions such as those concerning hunting impacts, we need answers concerning long-term consequences, and integration of results from multiple short-term empirical studies via modeling is the best hope for obtaining adequate answers. Third, studies of the effects of past losses of vertebrates from tropical forests, both in historical and prehistorical times, should be avidly pursued, as these past 'natural experiments' have the potential to offer unmatched insight concerning long-term responses of plant communities.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online at [www.blackwell-synergy.com/toc/btp](http://www.blackwell-synergy.com/toc/btp).  
Appendix S1 Derivation of the effects of dispersal declines  
Appendix S2 Derivation of the effects of changes in seed predation

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