

1. Synthesis article linking climate change and bushmeat hunting

Brodie J.F., and H. K. Gibbs (2009) Bushmeat Hunting As Climate Threat. November 4, 2009. Science Mag.

We suggest that degradations of carbon storage can also be driven by overhunting, as large-seeded trees with high wood density are deprived of their seed-dispersing animals:

Meanwhile, **overhunting is pushing many animals to extinction** (3, 4). Hunting rates in tropical Africa are more than six times greater than sustainable levels; large animals are already gone from most tropical Asian forests (4).

3. P. D. Walsh *et al.*, *Nature* 422, 611 (2003).

4. E. J. Milner-Gulland, E. L. Bennett, *Trends Ecol. Evol.* 18, 351 (2003).

Losses from overhunting are particularly severe among large-bodied animals because these species tend to be preferentially hunted and to have slower population growth rates (5).

5. A. Purvis, in *Conservation of Exploited Species*, J. D. Reynolds *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 2001), pp. 169–181.

Recent work in hunted forests of Peru reveals a **substantial shift in species composition as large-seeded trees are replaced by smaller-seeded species** (6).

6. J. Terborgh *et al.*, *Ecology* 89, 1757 (2008).

Furthermore, several studies highlight a positive relationship between **seed size and tree wood density** (7, 8). 7. S. A. Queenborough *et al.*, *J. Ecol.* 97, 555 (2009).

8. I. J. Wright *et al.*, *Ann. Bot.* 99, 1003 (2007).

Wood density is among the best predictors of aboveground carbon storage in tropical forests (9, 10). Simulations of species composition in Panama show that selective logging of trees with high wood density reduces forest carbon storage by a staggering 70% (10).

9. T. R. Baker *et al.*, *Glob. Change Biol.* 10, 545 (2004).

10. D. E. Bunker *et al.*, *Science* 310, 1029 (2005).

2. Articles on seed size and wood density

Wright I.J., Ackerly D.D., Bongers F., Harms K.E., Ibarra-Manriquez G., Martinez-Ramos M., Mazer S.J., Muller-Landau H.C., Paz H. , Pitman N.C.A., Poorter L., Silman M.R., Vriesendorp C.F., Webb C.M.O., Westoby M. and Wright S. J. (2007) *Relationships Among Ecologically Important Dimensions of Plant Trait Variation in Seven Neotropical Forests. Annals of Botany* 99: 1003–1015

In this study we compiled data for focal traits (SLA, seed and fruit size, leaf size, plant maximum height), as well as for wood density, for more than 2100 woody species from seven Neotropical forests. Seed and fruit size were expected, and confirmed, to be tightly related. As expected, plant height was correlated with each of seed and fruit size, **albeit weakly**. Weak support was found for an expected positive relationship between leaf and fruit size (Corner's Rules were weak rules at best). The prediction that specific leaf area (SLA) and wood density (WD) would be negatively correlated was not supported. Otherwise the traits were predicted to be largely unrelated, being representatives of putatively independent strategy dimensions. This was indeed the case, although WD was consistently, negatively related to leaf size.

Plant height showed little relationship to any other traits except seed and fruit size. Still, around 90% of height variation was not associated with seed or fruit size, suggesting that the plant height dimension could perhaps also be considered as largely orthogonal from the other strategy dimensions.

Wood density (WD) was largely unrelated to the other traits (except for leaf size, discussed below). Wood density and leaf size were negatively associated across all species, within individual sites, and when considered in terms of evolutionary divergences. Indeed, this was the strongest and most consistent relationship observed, after that between seed and fruit size.

Despite the general conclusion of orthogonality among the strategy dimensions, several quite consistent (though mostly weak) trait relationships did emerge (Fig. 5). That is, positive relationships were found between seed and fruit size, between leaf and fruit size, and between plant height and each of seed and fruit size, while a generally negative relationship was found between wood density and leaf size. Below we discuss possible underlying reasons for these relationships.

Queenborough S. A., Mazer S.J., Vamوسي S.M., Garwood N.C., Valencia R., Freckleton R.P. (2009) Seed mass, abundance and breeding system among tropical forest species: do dioecious species exhibit compensatory reproduction or abundances? Journal of Ecology. 1-12

Dioecious plant species divide reproductive function among individuals, with pollen production restricted to males, and seed and fruit production restricted to females. Reported sex ratios in tropical trees are generally male-biased; hence the proportion of seed-producing individuals in a population is usually < 50% (Queenborough *et al.*, 2007a). As a result, given equal population densities, populations of dioecious species will have fewer seed-producing individuals than their cosexual (i.e. hermaphroditic or monoecious) counterparts.

In this study, we tested for two compensatory fitness or demographic advantages in dioecious species compared to co-occurring hermaphroditic and monoecious species: (i) higher individual seed mass and (ii) higher densities of established individuals.

In addition to comparing dioecious species to those with cosexual flowers, we compared dioecious and monoecious species. Monoecious species serve as a control because, similar to dioecious species, they produce unisexual flowers (within individuals) but they do not suffer the disadvantage of having fewer seed-producing individuals (Heilbuth *et al.* 2001). We therefore predicted that dioecious species should produce larger seeds or persist at higher density than both monoecious and hermaphroditic species, but that monoecious and hermaphroditic species should not differ consistently with respect to these attributes.

Traits such as growth rate and maximum plant height may be strongly correlated with wood density due to the constraints wood density places on the movement of water and on structural support. Indeed, wood-specific gravity (WSG) is a good correlate of longevity and life-history strategy among Neotropical trees (Chave *et al.* 2006). Thus, we sought to isolate and measure the relationship between breeding system and seed size by including WSG as a covariate in our analyses as a proxy for longevity.

WOOD-SPECIFIC GRAVITY

There was a significant positive relationship between seed mass and WSG (linear regression, $F = 22.49$, d.f. = 497, $P < 0.001$, $R^2 = 0.04$, $y = -1.5 + 1.4x$); species with denser wood produce

larger seeds. Thus, we were justified in including WSG as a covariate in our analyses of seed mass. However, although the probable model included WSG, it did not include any interactions between WSG and breeding system or growth form (Table 2). The effect of WSG on seed mass did not differ among breeding systems or growth forms, even though lianas had significantly higher WSG than shrubs and trees (anova, $F = 4.33$, d.f. = 570, $P = 0.0049$).

First, we did not find that dioecious species produce heavier seeds than hermaphroditic species, in lianas, shrubs or trees. We did find that monoecious species produce heavier seeds than dioecious and hermaphroditic species in lianas, but lighter seeds in shrubs and trees. Secondly, although our analyses **corroborated the positive relationship between seed size and WSG** (which is, in turn, positively correlated with longevity (Chave *et al.* 2006)), we found no significant interaction between WSG and breeding system. We found no difference between the WSG of shrubs and trees, but within both of these growth forms life-history strategy varies enormously, so the absence of a significant difference between them is unsurprising.

3. Articles on the impact of hunting on seed dispersal and/or tropical forest composition

Terborgh J., Nunez-Iturri G., Pitman N.C.A., Cornejo Valverde F.H., Varun Swamy P.A., Pringle E.G., and Paine C.E.T. (2008) Tree Recruitment in an Empty Forest. *Ecology*. 89(6): 1757–1768

To assess how the decimation of large vertebrates by hunting alters recruitment processes in a tropical forest, we compared the sapling cohorts of two structurally and compositionally similar forests in the Rio Manu floodplain in southeastern Peru. Large vertebrates were severely depleted at one site, Boca Manu (BM), whereas the other, Cocha Cashu Biological Station (CC), supported an intact fauna.

We used the Janzen-Connell model to make five predictions about the sapling cohorts at BM with respect to CC: (1) reduced overall sapling recruitment, (2) **increased recruitment of species dispersed by abiotic means**, (3) altered relative abundances of species, (4) **prominence of large-seeded species among those showing depressed recruitment**, and (5) little or no tendency for saplings to cluster closer to adults at BM. **Our results affirmed each of these predictions.**

Interpreted at face value, the evidence suggests that few species are demographically stable at BM and that up to 28% are increasing and 72% decreasing. Loss of dispersal function allows species dispersed abiotically and by small birds and mammals to substitute for those dispersed by large birds and mammals. Although we regard these conclusions as preliminary, over the long run, the observed type of directional change in tree composition is likely to result in biodiversity loss and negative feedbacks on both the animal and plant communities. Our results suggest that the best, and perhaps only, way to prevent compositional change and probable loss of diversity in tropical tree communities is to prohibit hunting.

Recent research has demonstrated that tropical forests depleted of large vertebrates experience reduced dispersal, altered patterns of tree recruitment, shifts in the relative abundance of species, and various types of functional compensation (e.g., increased invertebrate seed predation in response to reduced vertebrate seed predation; Dirzo and Miranda 1991, Asquith *et al.* 1999, Wright *et al.* 2000, Cordeiro and Howe 2001, Wright 2003, Wyatt and Silman 2004, Wang *et al.* 2006, Andresen and Laurance 2007).

There is mounting evidence that hunting may have greater consequences for dispersal than for the escape process (Wright 2003, Wyatt and Silman 2004). Dispersal of large seeds is primarily carried out by large birds and mammals, among which primates predominate in continental forests (Andresen 1999, Peres and van Roosmalen 2002, Poulsen et al. 2002, Russo 2003). Canopy-dwelling birds and primates are easy targets for hunters because the upper strata of tropical forests are more open than vegetation near the ground. Thus, large primates are typically among the first animals to be depleted in hunted forests (Peres 2000). In contrast, seed predation and seedling herbivory are both carried out by a wide range of vertebrates and invertebrates, opening the potential for compensatory responses to missing larger guild members (Asquith et al. 1997, 2005, Peres and Dolman 2000, Wright 2003).

Nunez-Iturri G., Olsson O., Howe H.F. (2008) Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biological Conservation*. 141: 1536–1546

Hunting with firearms decimates primates of large and medium body size (>2 kg) that disperse the seeds of large-seeded trees. In continuous, un-fragmented forests of southeastern Peru regularly hunted with firearms for 30–40 years, large primates are extirpated and medium-sized (medium) primates are reduced 61% compared with protected forests. At hunted sites seedlings and small juveniles (<1m height) of trees dispersed by primates heavier than 2 kg are reduced 46%, a loss of one species *m_2*, and abiotically-dispersed plants are 284% more common, adding eight individuals *m_2*, compared with protected forests. Here we provide evidence consistent with the long-held prediction that commercial hunting changes plant communities. **We show that the composition of seedling and small juvenile tree communities that ultimately regenerate future forests differs markedly in forests hunted with firearms compared with protected forests.** This opens the possibility of shifts in tree species composition, even in hunted forests that are not logged or fragmented, towards forests dominated by trees dispersed by wind or non-game animals.

We hypothesize that **large-seeded plants** with a limited array of dispersal agents are most affected by hunting. We hypothesize that over-hunting large and medium fruit-eating primates deprives trees with larger seeds of dispersal agents, exposing seeds and seedlings accumulated under parent trees to **higher density-dependent mortality** from insects and pathogens than would occur among widely-scattered seeds (e.g. Janzen, 1970; see Harms et al., 2000; Hardesty et al., 2006). The goal is to test for distinctively different species compositions and plant densities of forest floor communities where primates have been extensively hunted with firearms, as compared with where they have not, in vast un-fragmented forests in which plant interactions are not confounded by commercial logging, habitat fragmentation, fire, or other anthropogenic disturbances.

Examples of tests in degraded land, forest fragments, and smaller areas of continuous forest indicate that the assumption is plausible. A classic comparison of the Los Tuxtlas understory with that of the Lacandon forest in Mexico suggests that terrestrial mammals maintain tree diversity through **suppression of aggressive species**, which become dominant if hunting eliminates the mammals (Dirzo and Miranda, 1991; Dirzo et al., 2007). In Madagascar, loss of the largest lemur species from forest fragments in dry deciduous forests is associated with reduced regeneration of trees that depend on it for **seed dispersal** (Ganzhorn et al., 1999). Similarly, combined effects of forest fragmentation and hunting in the Atlantic forest of Brazil depress seedling densities of the large-seeded endemic palm (*Astrocaryum aculeatissimum*) due to reduced densities of its main seed disperser (*Dasyprocta*) (Galetti et al., 2006). In Panama, a heavily-hunted mainland site has greater seed fall from wind-dispersed species, many of them vines, as compared with Barro Colorado Island and three nearby peninsulas, where hunting has been closely restricted for >25

years (Wright et al., 2007). **There is ample basis for predicting that hunting, by itself, will eventually change forest structure by affecting the differential survival and recruitment of tree seeds and seedlings, and thereby ultimately alter forest composition.**

Our results are consistent with the prediction that hunting has significant indirect effects on seedling and small juvenile plant communities in unbroken forests of the western Amazon. Differences in the composition of communities of tree seedlings and small juveniles in hunted and similar protected forests are fully consistent with the hypothesis that loss of key primate dispersal agents changes regeneration dynamics of hyper-diverse tropical lowland forests. This inference is especially compelling because primate-dispersed adult trees that started growing before firearms were widely used in the western Amazon are still common in the canopies of hunted sites, but their seedlings and juveniles are poorly represented in the understory. Local suppression to extermination of large fruit-eating primates appears to reduce the species richness of seedlings and small juveniles of trees dispersed by primates by half, and increases the density of abiotically-dispersed plants by nearly 3-fold. Our results suggest that hunting large fruit-eating monkeys reduces recruitment of large-seeded monkey-dispersed trees (Emmons, 1989; Peres and van Roosmalen, 2002), indirectly increases recruitment of abiotically dispersed species, and alters understory composition in tropical forests (Phillips, 1997). Elimination of large seed-dispersal agents by hunting appears to drastically change understory communities that ultimately will regenerate forest canopies.

Notably, we found much lower numbers of seedlings and juveniles of large-seeded primate-dispersed species in our hunted sites, despite abundance of adult trees of such species in the same forests. This is not consistent with the finding of some authors that large-seeded species in Panama are favored by hunting (Wright et al., 2007; taxa not indicated).

In our region in Peru, large rodents (e.g. *Dasyprocta*) that prey upon large-seeded species are an order of magnitude less common than in Panama (Terborgh and Wright, 1994), are not preferred commercial game, and indeed are about as common in pristine, protected sites in Peru as in heavily-hunted sites in Panama. Agoutis may remain sources of mortality for large seeds not dispersed by primates in hunted areas of the western Amazon, but they are probably one source among many.

An intriguing possibility is that some trees regularly fail to recruit genetic offspring close to parents, even if unrelated conspecifics do recruit near fruiting trees (Hardesty et al., 2006). Under severe dispersal limitation, offspring recruitment near parents of such species would be negligible, as we discovered earlier (Nunez-Iturri and Howe, 2007). In both central Panama and forests of the southwestern Amazon Basin, hunting alters dynamics of seedling regeneration by accentuating seed-recruitment limitation among large-seeded primate-dispersed trees.

Wright, S.J., Hernandez, A., Condit, R., 2007. The bushmeat harvest alters seed banks by **favoring large seeds**, and seeds dispersed by bats, birds, and wind. *Biotropica* 39, 363–371.

We evaluated predictions that hunters favor lianas, large seeds, and seeds dispersed by bats, small birds, and mechanical means for seedling banks in central Panama. We censused 3201 trees in 20 1-ha plots and 38,250 seedlings in the central 64 m² of each plot. We found significant differences in the species composition of the seedling bank between nine protected sites in the Barro Colorado Nature Monument and 11 hunted sites in the contiguous Parque Nacional Soberanía. Lianas, species with large seeds, and species with seeds dispersed by bats, small birds, and mechanical means were all overrepresented at hunted sites. The latter two findings could also be evaluated relative to the species composition of reproductively mature adults for canopy trees. The tree species present in the seedling bank had significantly heavier seeds than

the tree species present as adults at hunted sites but not at protected sites. The representation of seed dispersal modes among the species present in the seedling bank did not reflect pre-existing differences in the local species composition of adults. **We hypothesize that hunting large seed predators favors large seeds by reducing predation and increasing survival. We also hypothesize that the harvest of large birds and mammals that disperse many seeds favors other species whose seeds are dispersed by bats, small birds, and mechanical means.** This process also favors lianas because the seeds of disproportionate numbers of liana species are dispersed by wind

HUMANS ARE HUNTING FOREST VERTEBRATES AT UNSUSTAINABLE LEVELS throughout the tropics (Fa *et al.* 2002, Corlett 2007, Peres & Palacios 2007). Most of the preferred game species consume fruit, seeds, and/or leaves. Hunters alter these plant–animal interactions when they remove frugivores, granivores, and browsers (Emmons 1989, Redford 1992). This, in turn, raises the possibility that hunters might indirectly alter the species composition, diversity, and structure of forest plant communities (Dirzo & Miranda 1991, Dirzo 2001, Wright 2003, Muller-Landau 2007). **In particular, frugivores disperse and granivores kill seeds, and these interactions largely determine the spatial template for plant recruitment (Janzen 1970).**

Hunting is known to alter the spatial dynamics of seedling recruitment by removing seed dispersal agents and seed predators for selected plant species in tropical forests (Wright *et al.* 2000, Roldán & Simonetti 2001, Wright & Duber 2001, Galetti *et al.* 2006, Beckman & Muller-Landau 2007, Wang *et al.* 2007). Here, we ask whether hunters also alter the structure, species composition, and diversity of the entire community of the seedling and herbaceous layer along a strong gradient of hunting pressure in central Panama. We focus on three *a priori* predictions, each concerning a particular plant trait.

We hypothesize that hunters favor large seeds by removing large vertebrate seed predators and increasing survival rates for large seeds (Dirzo *et al.* 2007). This has been documented for two large-seeded palm species in central Panama (Wright *et al.* 2000, Wright & Duber 2001). We also hypothesize that hunters reduce seed dispersal and hence seed and seedling survival for species with seeds dispersed by game species and thereby indirectly favor species with seeds dispersed by bats, small birds, and mechanical means. Game species often disperse and consume the same large seeds. This raises the additional possibility that hunters might reduce both dispersal and predation for the same large-seeded plant species. This added complication was also documented for the same two large seeded palm species, and the decrease in seed predation outweighed effects mediated by seed dispersal such that the seedling densities of these two large-seeded palms were greatest at the most heavily hunted sites (Wright *et al.* 2000, Wright & Duber 2001).

There is probably not a single plant species whose seeds are *only* dispersed by game species in central Panama. Every species with fleshy fruit attracts multiple animal species and several potential seed dispersal agents. Although hunters only take large birds and mammals in central Panama, there are other large birds and relatively large mammals that are not hunted. Examples include toucans, parrots, red-tailed squirrels, and kinkajous (*Potos flavus*; Mendez 1970, Wright *et al.* 2000). Thus, even those plant species whose seed dispersal agents include game species are likely to have other nonhunted seed dispersal agents in this study. This complexity highlights the need for more detailed studies to identify the effects of hunting for seed dispersal versus seed predation.

The bushmeat harvest impacts several mechanisms that are widely believed to promote the coexistence of plant species in tropical forests (Wright 2003, Muller-Landau 2007). Poachers will

increase dispersal and recruitment limitation by reducing dispersal distances for seeds dispersed by game species, which has the potential to reduce local diversity in the short term and also to increase regional diversity in the longer term (Muller-Landau *et al.* 2002). Poachers alter the spatial dynamics of regeneration posited by Janzen (1970) by reducing dispersal distances and altering seed and seedling survival, which also has the potential to reduce local diversity (Wright & Duber 2001, Terborgh *et al.* 2002). Finally, poachers alter competitive interactions, by favoring larger seeds that already develop into larger, more competitive seedlings, and this too has the potential to reduce local diversity (Wright 2003, Dirzo *et al.* 2007, this study). **All mechanisms point toward the prediction first enunciated by Emmons (1989) and Dirzo and Miranda (1991) that hunting will eventually lead to declines in the local diversity of tropical forest plants (Muller-Landau 2007).**

Muller-Landau, H.C., 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* 39, 372–384.

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.

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).**

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).

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.

STUDY LOOKS AT LONG-TERM IMPACTS OF HUNTING. 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. 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.

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.

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.

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.

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)

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

STONER, K. E., P. RIBA-HERNÁNDEZ, K. VULINEC, AND J. E. LAMBERT. 2007a. The role of mammals in tropical forest regeneration and some possible consequences of their elimination: An overview. *Biotropica* 39: 316–327.

ABSTRACT

Mammal populations are increasingly hunted, yet the consequences of their disappearance from tropical forests have only recently been explored. Here, we summarize current research on the role of mammals in seed dispersal and postdispersal processes, such as seed predation and secondary dispersal, in different tropical regions. We evaluate how mammal features influence seed shadows and ultimately forest regeneration. Finally, we discuss the potential effect of changes in seed shadows caused by the elimination of many medium- and large-sized mammals. The complex role that mammals play in creating and modifying seed shadows in tropical forests cannot be easily quantified, and in this review we emphasize the variation that exists both within and among mammal taxa and across continents. To bridge this gap in information, we suggest that more studies should evaluate the relative importance of the disappearance of both seed dispersers and seed predators for particular plant species so that we may begin to understand the balance between these two influences. We also suggest that future studies identify ecological redundancy in nonhunted vertebrates within any particular community to evaluate compensatory

behavior that may help ameliorate some of the negative effects of hunting of large and medium mammals.

STONER, K. E., K. VULINEC, S. J. WRIGHT, AND C. A. PERES. 2007b. Hunting and plant community dynamics in tropical forests: A synthesis and future directions. *Biotropica* 39: 385–392.

ABSTRACT

This synthesis builds on the preceding articles of this Special Section and has three goals. We first review the nascent literature that addresses indirect effects of hunting for tropical forest plant communities. Next, we highlight the potential indirect effects of hunting for other groups of organisms. Our final goal is to consider what could be done to ameliorate the demographic threats to harvest-sensitive game species caused by unsustainable hunting. Three conclusions are possible at this time concerning the impact of hunting for tropical forest plant communities: (1) Hunting tends to reduce seed movement for animal-dispersed species with very large diaspores; (2) Hunting reduces seed predation by granivorous vertebrates for species with large seeds; and (3) Hunting alters the species composition of the seedling and sapling layers. The cascading effects of hunting are already known to affect bruchid beetles and dung beetles and are likely to affect other, nongame taxa. To ameliorate these problems, several lines of research should be further explored to facilitate the development of game management plans including: (1) alternative use of sources of animal protein; (2) income supplementation for local people from sources other than wild meat; (3) outreach and extension activities for communities; (4) recognition and facilitation of the shifting of attitudes towards hunting; (5) implementation of community-based wildlife management programs in regulated-use areas such as extractive reserves; and (6) landscape-scale conservation planning that maximizes the source-sink dynamics of harvested and unharvested game populations and enforces game regulations in strictly protected areas.

Moles A.T., Ackerly D.D., Tweddle J.C., Dickie J.B., Smith R., Leishman M.R., Mayfield M.M., Pitman A., Wood J.T., and Westoby M. (2007) Global patterns in seed size. *Global Ecology and Biogeography*. 16: 109–116

Seed mass is a key ecological trait that influences many aspects of a species' regeneration strategy, including seedling survival rates, seed dispersal syndrome, and the number of seeds that can be produced for a given amount of energy (Leishman *et al* 2000). Seed size exhibits a striking global pattern, declining by 2–3 orders of magnitude between the equator and 60° (Moles & Westoby, 2003).

Several theories have been proposed to explain this latitudinal gradient in seed size.

1 Tropical species might need large seeds in order to cope with the shaded understorey conditions associated with tropical rain forests (Salisbury, 1942). This theory is supported by strong experimental data showing that large-seeded species have higher survival under low-light conditions than do small-seeded species (Grime & Jeffrey, 1965; Leishman & Westoby, 1994; Osunkoya *et al.*, 1994; Walters & Reich, 2000), by strong relationships between seed size and the light environment under which species establish (Salisbury, 1942; Foster & Janson, 1985; Mazer, 1989), and by the high leaf area index of much tropical vegetation (Asner *et al.*, 2003).

2 The abundance of vertebrate seed dispersal agents in tropical ecosystems might have allowed tropical species to radiate into larger seed masses than was possible for species growing in the temperate zone, where the predominantly abiotic dispersal agents might favour small seeds (Lord *et al.*, 1997). Empirical data confirm that species with wind and unassisted dispersal have smaller seeds than species with animal dispersal (Leishman *et al.*, 1995) and that there is a

latitudinal gradient in the proportion of vertebrate-dispersed fruits (Willson *et al.*, 1989; Lord *et al.*, 1997).

3 The relationship between seed size and latitude could result secondarily from a latitudinal gradient in plant size and life form, with a shift towards smaller plants at high latitudes together with a **positive relationship between seed size and plant size** (Baker, 1972; Moles *et al.*, 2004).

4 A latitudinal gradient in the length of the growing season could place an upper limit on the size of seeds that can be produced at a given latitude (Stebbins, 1974). This idea is supported by data showing that larger seeds take longer to complete development than do smaller seeds (Eriksson & Ehrlén, 1991; Moles & Westoby, 2003).

5 The higher net primary productivity (NPP) of tropical ecosystems (Bondeau *et al.*, 1999; Schloss *et al.*, 1999) might translate to higher total seed production, thus increasing competition for space and favouring larger seeds (Moles & Westoby, 2003).

Here, we describe the shape and slope of the relationship between seed mass and latitude across an unprecedented number of species and ecosystems from around the world. The large size of the data set allows us to compare the proportion of variation in seed mass explained by plant growth form, seed dispersal syndrome, vegetation type and NPP, in a way that was not possible with smaller data sets.

Findings: **the latitudinal gradient in seed mass (including the step at the edge of the tropics) is almost entirely explained by changes in seed dispersal syndrome**, vegetation type, NPP and plant growth form.

4. Studies in grassland ecosystems

Jacob R. Goheen, Felicia Keesing, Brian F. Allan, Darcy Ogada, Richard S. Ostfeld (2004) Net Effects of Large Mammals on Acacia Seedling Survival in an African Savanna. *Ecology*. 85(6): pp. 1555–1561

Abstract. Trees of the genus *Acacia* are widespread and important components of savanna ecosystems. Factors or organisms that influence the survival of *Acacia* seedlings are likely to affect tree recruitment and therefore community and ecosystem dynamics. In African savannas, large mammals, especially elephants, have been considered the most important agents of mortality for adult trees, but their impacts on tree seedlings are not well known. We investigated the effects of large mammals on *Acacia* seedling survival by excluding large mammals from replicated 4-ha plots. Approximately twice as many seedlings were killed in plots with large mammals absent as on plots with large mammals present. Rodents and some invertebrates were more abundant on plots without large mammals and were responsible for these higher predation rates. Seedlings in areas with large mammals were more likely to die of desiccation; however, net seedling survival was approximately twice as high in the presence of large mammals. **Our results indicate that large mammals may indirectly increase *Acacia* seedling survival and thus accelerate, rather than inhibit, tree recruitment.**

5. Articles on digestive enzymes in large mammals and seed dispersal

Excerpt from Muller-Landau, H.C., 2007:

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 & Verdu 2002).**

Full reference of article cited by Muller-Landau (2007): TRAVESET, A., AND M. VERDU. 2002. A meta-analysis of the effect of gut treatment on seed germination. *In* D. J. Levey, W. R. Silva, and M. Galetti (Eds.). Seed dispersal and frugivory: Ecology, evolution and conservation, pp. 339–350. CABI International, Wallingford, UK.

6. Articles on carbon storage and tree species composition

Baker T.R., Phillips O.L., Malhi Y., Almeida S., Arroyo L., Di Fiore A., Erwin T., Killeen T.J., Laurance S.G., Laurance W.F., Lewis S.L., Lloyd J., Monteagudo A., Neill, S. Patino D.A., Pitman N.C.A., Silva J.N.M., and Martinez R.V. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*. 10: 545–562.

Abstract

Uncertainty in biomass estimates is one of the greatest limitations to models of carbon flux in tropical forests. Previous comparisons of field-based estimates of the aboveground biomass (AGB) of trees greater than 10 cm diameter within Amazonia have been limited by the paucity of data for western Amazon forests, and the use of site-specific methods to estimate biomass from inventory data. In addition, the role of regional variation in stand-level wood specific gravity has not previously been considered. Using data from 56 mature forest plots across Amazonia, we consider the relative roles of species composition (wood specific gravity) and forest structure (basal area) in determining variation in AGB.

Mean stand-level wood specific gravity, on a per stem basis, is 15.8% higher in forests in central and eastern, compared with northwestern Amazonia. This pattern is due to the higher diversity and abundance of taxa with high specific gravity values in central and eastern Amazonia, and the greater diversity and abundance of taxa with low specific gravity values in western Amazonia. For two estimates of AGB derived using different allometric equations, basal area explains 51.7% and 63.4%, and stand-level specific gravity 45.4% and 29.7%, of the total variation in AGB. The variation in specific gravity is important because it determines the regional scale, spatial pattern of AGB. When weighting by specific gravity is included, central and eastern Amazon forests have significantly higher AGB than stands in northwest or southwest Amazonia. The regional-scale pattern of species composition therefore defines a broad gradient of AGB across Amazonia.

Bunker, D. E., F. Declerck, J. C. Bradford, R. K. Colwell, I. Perfecto, O. L. Phillips, M. Sankaran, and S. Naeem. 2005. Species loss and aboveground carbon storage in a tropical forest. *Science* 310: 1029–1031.

Tropical forest biodiversity is declining, but the resulting effects on key ecosystem services, such as carbon storage and sequestration, remain unknown. We assessed the influence of the loss of tropical tree species on carbon storage by simulating 18 possible extinction scenarios within a well-studied 50-hectare tropical forest plot in Panama, which contains 227 tree species. Among extinction scenarios, aboveground carbon stocks varied by more than 600%, and biological insurance varied by more than 400%. **These results indicate that future carbon storage in tropical forests will be influenced strongly by future species composition.**

7. Articles on overhunting

Meanwhile, **overhunting is pushing many animals to extinction** (3, 4). Hunting rates in tropical Africa are more than six times greater than sustainable levels; large animals are already gone from most tropical Asian forests (4).

3. P. D. Walsh *et al.*, *Nature* 422, 611 (2003).

4. E. J. Milner-Gulland, E. L. Bennett, *Trends Ecol. Evol.* 18, 351 (2003).