SEED REMOVAL AND SEED DISPERSAL IN TWO SELECTIVELY-LOGGED FORESTS WITH CONTRASTING PROTECTION LEVELS IN COSTA RICA

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Abstract
We evaluated seed removal and the fate of removed seeds (as a measure of dispersal) in two nearby tropical rain forest sites in the Caribbean lowlands of Costa Rica that had been selectively logged but that differ in their degree of protection from human intrusion (primarily due to hunting) and habitat connectivity: We expected differences between sites in rates of seed removal and the fate of removed seeds, and predicted that secondary seed dispersal rates by mammals would be highest at the protected site. Patterns of seed removal under two protection treatments (semipermeable cages *vs.* uncaged) varied both within species across sites and within sites across species suggesting site differences in the abundance of vertebrate seed consumers. However, differences were largely species specific. For all species combined, twice as many seeds were dispersed after 50 d of observation at La Selva. We found evidence for differential seed survival in our study species between sites, probably related to altered mammal community composition probably as a result of hunting pressure and loss of habitat connectivity at Tirimbina with respect to La Selva.

Introduction
It has been suggested that in forested sites lacking a full complement of the mammalian community, tree recruitment rates may be altered due to local extinction caused by fragmentation or hunting of seed dispersing animals, or by overabundance of seed predators. In this paper, we evaluate seed removal and the fate of removed seeds of seven tree species (six of which are timber species) in two closely located forest sites in NE Costa Rica. Both sites underwent selective logging (La Selva Biological Station and Tirimbina Rain Forest Center) but they show contrasting levels of habitat connectivity and human intrusion. We predicted (1) differences between sites in rates of seed removal and the fate of those removed seeds, and (2) that seed dispersal rates by mammals were to be higher at the protected site.

Methodology
Species selection was dictated by their commercial value, their occurrence at both study sites, and by availability of seed. The species were *Pentaclethra macroloba, Welfia regia, Minquartia guianensis, Carapa nicaraguensis, Virola koschnyi, Otoba novogranatensis* and *Lecythis ampla.* Seeds of all species are known to be readily consumed and/or dispersed by a variety of mammals, including small to medium size scatterhoarding rodents, perhaps with the exception of *Pentaclethra macroloba* whose seeds contain compounds which are toxic to many animals. We performed all experiments described below simultaneously in both sites. The entire work lasted for about 6 mo during 1998.

We performed exclusion experiments in order to discern whether seed removal varied between sites according to mammal body size. At each site, fifteen random locations in the forest understory were selected, spaced by no less than 50 m. At each location, two groups of 10 seeds were placed on litter-free soil, each group randomly receiving a "caged" and "uncaged" treatment. The caged treatment consisted of an open-top cylinder made of galvanized chicken wire staked to the ground. The mesh size allowed the entrance of small rodents and probably squirrels through the top. For *Lecythis* and *Carapa*, the number of replicate locations had to be reduced to 10 in each species due to insufficient number of seeds. The number of seeds that remained at every location in each treatment were monitored over 50 d.

To assess whether the fate of seeds removed by terrestrial mammals varied between sites, a separate batch of seeds were threaded with fishing line. The thread was spray painted with fluorescent color to facilitate its detection after removal. We considered that a seed was "dispersed" if it was either removed or buried away from their original location but within a 10 m radius. All seeds that were not found and those for which only the thread was left were considered "predated". The location of all dispersed seeds was marked with a white plastic stake and followed over the same census intervals as above.
We quantified all mammal encounters during the whole study period while performing the seed censuses.

Results

Patterns of seed removal and dispersal varied both within species across sites and within sites across species suggesting site differences in the abundance of vertebrate seed consumers (Table 1). Compared to all species, *Pentaclethra* had the lowest removal in both caged and uncaged treatments. However, seeds at La Selva suffered higher removal rates than at Tirimbina. Seeds of *Lecythis* and *Carapa* also showed higher removal rates at La Selva, particularly in the uncaged treatment. The opposite result was found in *Virola*, where seed removal rates appeared higher at Tirimbina in both treatments. Two species, *Welfia* and *Otoba*, showed similar seed removal rates regardless of site and treatment. Any potential differences in mammal abundance among sites are masked by the fact that these latter species are consumed by a large array of mammals of different body sizes. Overall, twice as many seeds were dispersed after 50 d at La Selva (5.3 %) than at Tirimbina (2.2 %), being this difference statistically significant ($\chi^2 = 12.6$, 1 d.f., $p < 0.001$). Two of the study species, *Pentaclethra* and *Welfia* showed no detectable dispersal at any site, which suggests either that they are consumed (and not cached) at first encounter (likely for *Welfia*), or that they are simply avoided due to toxicity (likely for *Pentaclethra*). Seeds of *Carapa* and *Lecythis* showed no dispersal at Tirimbina.

Discussion

We found evidence for our initial prediction of differential seed and seedling survival in our study species between sites. This is probably related to altered mammal community composition (Table 1) as a result of hunting pressure and loss of habitat connectivity at Tirimbina with respect to La Selva. These differences, however, were not consistent across sites. Some species had higher removal rates at La Selva while other showed the opposite pattern. This suggests that potential alterations in tree recruitment patterns due to differences in animal community composition are likely to be species specific.

Seeds of *Carapa* are well known to be scatterhoarded by medium-sized rodents such as agouties (*Dasyprocta* spp), therefore maximizing the probability of seed germination and seedling establishment. Although in our case, *Carapa* suffered disproportionately higher seed removal at La Selva, than at Tirimbina, seeds were also dispersed (as opposed to zero dispersal at Tirimbina). A similar pattern was observed in *Lecythis* (whose seeds are also dispersed by agouties) where all undispersed seeds at Tirimbina were rapidly attacked by ants which consumed the endosperm. Two of the study species with the smallest seeds (*Minquartia* and *Virola*) seemed to experience more removal by small mammals at Tirimbina than La Selva. Our work seems to confirm earlier findings of other case studies that have dealt with the so called "defaunation" hypothesis that have also shown altered patterns of plant regeneration due to truncated trophic chains. We hypothesize that in NE Costa Rica, production forests adjacent to parks and conservation areas are more likely to maintain a wider spectrum of viable populations of plants and animals, given the assumption that human intrusion is also controlled. Even if forests are logged gently, sustained recruitment of at least mammal-dispersed timber species appear less likely if loss of habitat connectivity and excessive hunting pressure are combined.

Table 1. Number of sightings of mammalian fauna at the study sites in the Caribbean lowlands of Costa Rica over a 6 mo period.

	Tirimbina	La Selva
Species	No. (No./ha)	No. (No./ha)
Alouatta palliata (Howler monkey)	4 (0.06)	8 (0.13)
Ateles geoffroyi (Spider monkey)	2 (0.03)	15 (0.24)
Cebus capuchinus (White-faced monkey)	7 (0.10)	7 (0.11)
Dasyprocta punctata (Agouti)	--	2 (0.03)
Puma concolor (Puma)	--	2 (0.03)
Tamandua mexicana (Tamandua)	--	2 (0.03)
Tayassu tajacu (Collared peccary)	--	4 (0.07)
Sciurus variegatoides (Squirrel)	1 (0.01)	2 (0.03)
Total	14 (0.19)	32 (0.52)