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Dispersal vacuum in the seedling recruitment of a primate-dispersed Amazonian tree

Taal Levi [a,b], Carlos A. Peres [c,*]

[a] Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA
[b] University of Florida, Gainesville, Florida 32611, USA
[c] School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, Norfolk NR4 7TJ, United Kingdom

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ABSTRACT

Unregulated hunting of large-bodied frugivores is ubiquitous in tropical forests. Due to their low fecundity and complex social organization, large primates are often the first tropical forest vertebrates to be extirpated by hunting. Large primates are important seed dispersers and the only dispersal vectors of many large-seeded plants, leading to concerns that primate-dispersed trees will succumb to large-scale recruitment failure wherever they co-occur with overhunting. We used a field experiment in a remote, nonhunted region of the western Brazilian Amazon to test how the seedling recruitment success of a primate-dispersed Sapotaceae tree (*Manilkara bidentata*) is affected by distance from parent trees, protection from vertebrate seed predators, and gastro-intestinal seed cleaning associated with passage through frugivorous vertebrates. Only seed cleaning significantly increased the rate of seedling recruitment. Janzen–Connell effects have been widely purported as the central mechanism for recruitment failure, but our results suggest that for many tropical forest plant species Janzen–Connell effects are a second-order effect that acts once seeds have been successfully cleaned of fruit pulp by gut treatment. As an illustration of the relative importance of the sheer quantity of seeds ingested by woolly monkeys (*Lagothrix cana*), we further estimate the density and dispersal services provided by a complete primate assemblage to show that *L. cana* cleans and disperses nearly one million seeds per km^2 per 24-day *Manilkara* fruiting season, amounting to over 71% of the seed dispersal services provided by the entire primate assemblage. The disperser vacuum in the absence of *L. cana* greatly reduces the quantity of cleaned seeds deposited on the forest floor. For similar fleshy-fruited species where gut passage greatly increases survival, a simple lack of redundancy in seed consumption may be the primary driver of recruitment failure resulting from large-primate extirpation due to overhunting, with Janzen–Connell effects secondarily influencing recruitment success as a function of either dispersal distance or seed density.

1. Introduction

Many harvest-sensitive large-bodied vertebrates are extensively overhunted in tropical forests, resulting in marked population declines if not local extinctions (Milner-Gulland et al., 2003). Although some harvest-tolerant game species can compensate for elevated mortality via reproduction and immigration, large-bodied primates, such as spider monkeys (*Ateles* spp.) and woolly monkeys (*Lagothrix* spp.) in Amazonian forests, are easily overexploited due to very low fecundity and poor dispersal associated with complex social structures (Peres, 1990; Peres and Palacios, 2007). These species are typically the first to become locally extirpated near subsistence communities that depend heavily on wild meat. The local extinction radius away from a community depends on the hunting effort, weapon efficiency, and hunter selectivity (Jerozolimski and Peres, 2003; Levi et al., 2009, 2011), but can exceed 15 km, corresponding to a circular area >700 km^2. When many communities are distributed over a large area, entire landscapes can become depleted of large-bodied primate populations (Levi et al., 2011; Sirén et al., 2004).

The landscape-scale loss of large primates has led to concerns over widespread recruitment failure of the many primate-dispersed trees in tropical forests (Nuñez-Iturri and Howe, 2007; Terborgh et al., 2008). This argument has thus far rested primarily on the Janzen–Connell model (Connell, 1971; Janzen, 1970), which states that the per-capita recruitment success of a seed depends strongly on escape from pathogens and seed predators associated with conspecific neighborhoods. Without large primates many large-seeded plants are expected to go undispersed, or dispersed only a short distance by poor dispersers (Chapman, 1989), which is expected to lower per-capita seed and seedling survival. This

* Corresponding author. Tel.: +44 1603 592549.
E-mail address: C.Peres@uea.ac.uk (C.A. Peres).

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effect has been proposed to explain the widely observed paradox of dense aggregations of fruits and seeds underneath parent trees that fail to produce seedlings. Recent research supports the important role of Janzen–Connell effects in seedling recruitment (Swamy et al., 2011; Swamy and Terborgh, 2010), but a previous meta-analysis covering 40 studies failed to detect a general effect of distance on enhancing seed survival (Hyatt et al., 2003). Other research has found that the effect of seedling density is equally or more important than the effect of distance from a conspecific in driving seedling recruitment patterns (Clark and Clark, 1984), but recent work suggests that the seed-rain density of most tropical forest tree species is so low that density dependence is inconsequential to seedling recruitment dynamics except in the immediate vicinity of conspecific adults (Terborgh et al., 2011). However, many seeds may be deposited at high density under sleeping or congregating sites, which may lead to higher mortality if density dependent processes are important (Russo and Augspurger, 2004).

Importantly, Terborgh et al. (2011) sampled the rain of propagules over 6 years at a southwestern Amazonian forest site, but classified propagules as intact seeds, damaged seeds, seeds with adhered pulp, ripe fruit, and immature or damaged fruit. They suggested that 'net' fecundity, which considers only intact dispersed seeds, was more biologically relevant to recruitment dynamics than gross fecundity, which considers all propagules, because virtually no saplings arise from undispersed seeds. Dispersed seeds were well mixed and randomly distributed at low density throughout the forest. Nearly 90% of seed traps failed to capture intact seeds each year, suggesting extreme seed limitation. This was further reinforced by a strong positive correlation across species between the spatial distribution of dispersed seeds and the spatial distribution of saplings.

These results suggest that recruitment outside the immediate vicinity of a parent tree is most limited by the quantity of dispersed seeds, rather than post-dispersal forces acting on density or distance (Terborgh et al., 2011). Moreover, survival rates from the seed to seedling stage (i.e. seedling recruitment) is very low in tropical forests, representing a critical bottleneck in tree recruitment (Chambers and MacMahon, 1994). We thus hypothesized that the effect of distance from maternal trees on seedling recruitment would be swamped by the effect of seed treatment in the disperser's digestive tract. This effect is plausible because mildly abrasive gut passage removes the perishable exocarp from intact seeds and cleans the seed testa of the tightly adhered edible fleshy fruit pulp that can attract agents of mortality, including both pathogens (e.g. fungi and bacteria) and seed predators (e.g. bruchid beetles and rodents). There is a rich literature in diverse systems suggesting that germination success is reduced or prevented if seeds remain associated with pulp (Barnea et al., 1991; Izhaki and Safriel, 1990; Rick and Bowman, 1961; Temple, 1977; Traveset et al., 2001), but this has received little attention in tropical ecosystems (Dinerstein and Wemmer, 1988; but see Fragoso et al., 2003) and to our knowledge no attention in the recruitment failure literature associated with defaunation. This hypothesis asserts that fruiting plants rely on the quantitative effect of removal and benign gut passage of many thousands of seeds on a daily basis by co-occurring populations of relatively abundant endozoochores. The implication is that intact seeds trapped inside uneaten fruits falling below fruiting crowns fail to germinate primarily because they have not been removed from other fruit parts and cleaned by adequate gut passage rather than reduced per-capita survival due to proximity to parent plants. For fruits that require seed cleaning by gut passage for germination, the conservation implication is that plant recruitment success will decline more than suggested by Janzen–Connell experiments if seeds remain unprocessed regardless of dispersal distance.

To test whether large-primate extirpation could lead to seedling recruitment failure by creating a seed dispersal vacuum, we first estimated the seed dispersal services provided by a diverse primate guild in a remote and completely undisturbed *terra firme* forest of western Brazilian Amazonia, and the fraction of those seeds dispersed by a locally abundant large-primate, the gray woolly monkey (*Lagothrix cana*). In this low-productivity interfluvial forest region, black spider monkeys (*Ateles chamek*) are restricted to relatively productive seasonally-flooded riparian areas but are absent from the wider matrix of unflooded (*terra firme*) forest. We then used a large field experiment to test how seedling recruitment of *Manilkara bidentata*, a fleshy-fruited primate-dispersed canopy tree in the family Sapotaceae, is impacted by distance from the parent tree, seed cleaning associated with gut passage, and physical exclusion of vertebrate seed predators. Finally, we used the results of our experiment to project the seedling density in our study area with and without the seed dispersal services provided by *L. cana*, the dominant endozoochore in this system.

2. Methods

2.1. Study site

The study was conducted in an entirely undisturbed *terra firme* forest landscape in the headwaters of the Tefé River (hereafter, Alto Tefé), State of Amazonas, Brazil (5°20′28″S, 66°40′34″W, Fig. 1). This remote site was isolated by a fluvial distance of 682 km from the nearest town (Tefé), and had long been depopulated of native Amazonians and subsequently rarely visited by post-Conquest hunters and *Couma* latex tappers since at least the 1850s. The study area was bounded by a 16-km^2 trail grid containing five parallel 4-km transects spaced apart by 1 km. This grid consisted of mildly dissected *terra firme* forest (83–138 m asl) where soils are typically heavily leached and nutrient poor. The study area has a wet, tropical climate with a mean annual temperature of 27.1 °C and rainfall—based on daily records over three consecutive years (2008–2010) at the Bauana Ecological Station (65 km west of the trail grid)—averaging 3679 mm/yr, with only ~4.1% of annual rainfall available in the three driest months (July–September). Due to low productivity in this interfluvial region, the white-lipped peccary (*Tayassu pecari*), an important seed predator, was conspicuously absent from this site, but collared peccaries (*Pecari tajacu*) were present.

2.2. Line transect census

Forest vertebrate surveys of diurnal primates and other medium and large-bodied vertebrates were conducted over a 3-week period during the rainy season (January 2012) by a small team of six previously trained observers, followed by a second visit to the site during the subsequent dry season (July 2012). Following line-transect census guidelines of Peres and Cunha (2011), straight-line transects were cut along a compass bearing, measured with both a Hip-Chain© and a Garmin CSx60 GPS, and marked using brightly colored flagging at 50-m intervals to ensure adequate mapping resolution of all vertebrate sightings. Preparation of each transect was usually completed within 1 day, and surveys were not conducted within 2 weeks of line cutting. Each of the five 4-km transects was surveyed at least eight times, resulting in an aggregate census effort of 301.3 km walked. Analogous line-transect surveys in French Guiana showed that even 40–90 km of census walks can be sufficient to reliably assess the population abundance of a similar set of vertebrate species (Thoisy et al., 2008). Transects were walked in the morning (0630–1000 h) and in the afternoon (1330–1700 h), when animals are most active. Surveys were typically conducted by two observers who walked slowly (~1250 m/h) along the transect line, pausing at regular