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Falling palm fronds structure Amazonian rainforest sapling communities

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The senescence and loss of photosynthetic and support structures is a nearly universal aspect of tree life history, and can be a major source of disturbance in forest understoreys, but the ability of falling canopy debris in determining the stature and composition of understorey communities seems not to have been documented. In this study, we show that senescent fronds of the palm *Iriartea deltoidea* cause substantial disturbance in tropical forest sapling communities. This disturbance influences the species composition of the canopy and subcanopy by acting as an ecological filter, favouring sapling species with characteristics conducive to recovery after physical damage. The scale of this dominance suggests that falling *I. deltoidea* debris may be influencing sapling community structure and species composition in Amazonian rainforests over very large spatial scales.

Keywords: *Iriartea deltoidea*; physical disturbance; canopy litterfall; sapling suppression

1. INTRODUCTION

The journey from the forest understorey to the canopy is rarely linear, with most canopy tree juveniles encountering frequent periods of submaximal growth and major height losses from physical damage (Clark & Clark 2001). Even in the absence of large-scale disturbances (e.g. blowdowns) and treefalls, saplings in tropical forest understoreys experience frequent physical damage to their primary stems from branches and other coarse woody debris that falls from the canopy (Aide 1987; Clark & Clark 1989, 1991; Mack 1998; Paciorek *et al.* 2000; Scariot 2000; Drake & Pratt 2001; Gillman & Ogden 2001). Although small-scale physical disturbance resulting from canopy debris fall has long been recognized as a potential source of sapling mortality in tropical forest understoreys, the role of such localized, small-scale disturbances in structuring forest stature and community composition remains largely unexplored.

The neotropical stilt-rooted palm *Iriartea deltoidea* is the numerically dominant canopy tree species in nearly every western Amazonian forest sampled to date (Pitman *et al.* 2001). *Iriartea deltoidea* is remarkable for its exceedingly large leaves, which individually may be more than 6 m long (Rich *et al.* 1995) and weigh more than 15 kg, even when dry. Mature *I. deltoidea* trees typically abscise two or three of these fronds per year, dropping them from crowns that may surpass 35 m in height (Rich 1986). In this study we show that falling debris from the omnipresent neotropical palm *I. deltoidea* is a substantial source of physical disturbance in tropical rainforests, and that this disturbance influences forest structure and sapling species composition by creating sites with distinct requirements for sapling survival. The scale of this palm's dominance suggests that falling *I. deltoidea* debris may be an extremely prevalent influence on sapling community composition in Amazonian forests.

2. METHODS

This study was conducted in mature floodplain forest at the Cocha Cashu Biological Station in Peru's Manu National Park (11°52′ S, 71°21′ W). Annual precipitation at this site is *ca.* 2000 mm with the highest intensity of rainfall occurring during a pronounced November to May wet season. Detailed descriptions of the climate and flora of Cocha Cashu are available elsewhere (Terborgh 1983, 1990).

The distance over which *I. deltoidea* drops its fronds was measured for 27 randomly selected adult trees. Adults were defined as those greater than 10 cm diameter at breast height (DBH), where breast height is 1.3 m above ground, or above the tree buttress, whichever is higher. The density and spatial distribution of *I. deltoidea* at Cocha Cashu were assessed by mapping all adult *I. deltoidea* palms to the nearest 10 cm in a 2.25 ha (150 m × 150 m) research plot.

To determine whether physical damage is more common among saplings in the vicinity of *I. deltoidea* palms, we censused the incidence of physical damage on live saplings (0.5 m ⩽ sapling height ⩽ 2.5 m) in 4 m × 2 m plots. Plots were established in closed-canopy forests 1 m from randomly selected adult palms (one palm plots, $n = 25$) in the zone of *I. deltoidea* frond fall; and 10 m away from *I. deltoidea* and other palms (zero palm plots, $n = 25$) outside the area of probable frond fall (figure 1). These plots were randomly oriented from palms along the eight cardinal and intercardinal directions. Additional plots were established in areas in which two *I. deltoidea* palms were within 5 m of each other (two palm plots, $n = 5$). Physical damage was assessed according to previously established criteria (Clark & Clark 1991; Pauw *et al.* 2004). We counted the number of breakage scars along the main stem of each sapling. A break was recorded only if there was evidence that the apical meristem had been broken off. Evidence of a broken and healed stem included either (i) an abrupt change in the angle of the stem of greater than 10°; or (ii) a swelling and an abrupt stem diameter discontinuity of at least 10%.

To assess whether falling debris from *I. deltoidea* palms alters sapling community composition, censuses of the sapling communities were conducted in 2 m wide annular plots 1 m from adult *I. deltoidea* trees (one palm plots, $n = 11$), and 10 m from *I. deltoidea* trees (zero palm plots, $n = 11$), outside the zone in which *I. deltoidea* fronds were ever observed to fall. Additional plots were established 1 m from *I. deltoidea* palms, with a second *I. deltoidea* within 5 m (two palm plots, $n = 5$). In these plots all saplings that were 1 m tall or more and less than 1 cm DBH were mapped, tagged, measured and identified to species. We contrasted the sapling species composition of these plots using a multiple-response permutation procedure (MRPP); a non-parametric procedure for testing the hypothesis of no difference between two or more *a priori* groups of entities (Mielke & Berry 2001).

3. RESULTS AND DISCUSSION

Evidence of past physical damage is 40% to 125% more common in the vicinity of *I. deltoidea* than in other areas of the forest understorey ($p < 0.0001$; figure 2), resulting in the suppression of sapling stature (height/basal diameter) by 9% to 17% (ANOVA: $F_{2,311} = 4.223$, $p = 0.015$). This high observed incidence of physical damage near *I. deltoidea* may be a result of several factors, including the greater frequency and magnitude of debris fall, the disproportionate presence near *I. deltoidea* of species capable of persistence after repeated physical disturbance, or both. Many tropical

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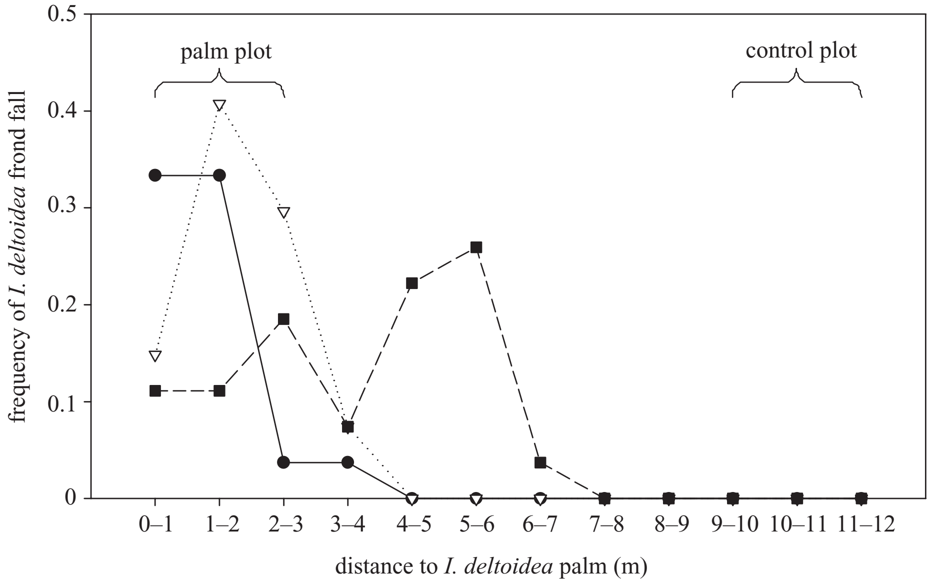

Figure 1. The distance over which *Iriartea deltoidea* drops its fronds was measured among adult trees greater than 10 cm DBH. Fronds tend to fall with the heavy sheath end near the base of the tree, and the lighter rachis, which supports the leaflets, farther away. Fallen fronds are rarely observed more than 7 m from the base of the palm. Circles and solid line, closest point; triangles and dotted line, sheath; squares and dashed line, rachis.

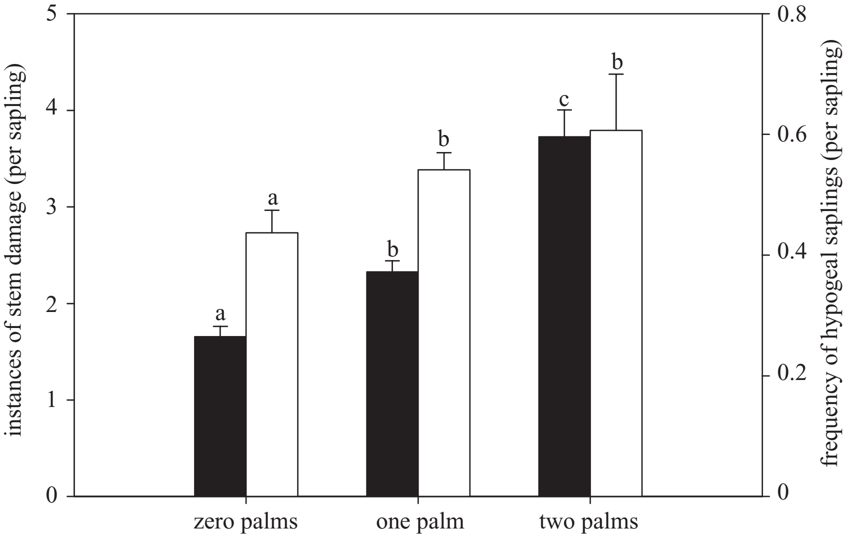

Figure 2. The *per capita* instances of sapling physical damage (ANOVA: $F_{2,311} = 28.524$, $p < 0.0001$; filled bars) and the proportion of saplings with storage cotyledons (ANOVA: $F_{2,24} = 28.524$, $p = 0.052$; open bars) increased with the number of *Iriartea deltoidea* palms in the vicinity. In each category, bars (mean ± 1 s.e.) with different letters are significantly different from each other.

forests' saplings are likely to spend years to decades in the understorey, where they are susceptible to damage from falling canopy debris (Clark & Clark 2001). For example, at Cocha Cashu, saplings that were 1 m or more tall but less than 1 cm DBH were mapped, tagged, measured and identified to species in 1997 in nine 30 m × 30 m plots in mature floodplain forest. A recensus of these plots in 2002 indicated that most surviving saplings grew less than 20 cm in the intervening 5 years, and that individuals of many canopy tree species experienced zero or negative growth (J. W. Terborgh, unpublished data).

Tree species vary in their ability to recover from physical damage (Guariguata 1998; Paciorek *et al.* 2000; Sipe & Bazzaz 2001; Gillman *et al.* 2003). Species capable of persistence after repeated disturbance often have below-ground storage organs such as coarse roots (Pate *et al.* 1990; Pauw *et al.* 2004) and hypogeal cotyledons (Silman 1996; Dalling *et al.* 1997; Harms & Dalling 1997; Harms *et al.* 1997; Dalling & Harms 1999), suggesting that the ability to replace lost above-ground tissues by accessing stored below-ground reserves may be critical to surviving damage. Debris fall may therefore act as an ecological filter if it influences the species composition of the canopy and subcanopy by favouring sapling species with characteristics conducive to recovery after physical damage.

We found that areas near *I. deltoidea* palms support sapling communities that are compositionally distinct from the sapling communities of the surrounding understorey. (MRPP: $p = 0.0333$). Irrespective of proximity to *I. deltoidea* the same four sapling species, *Malmea lucida*,

Table 1. The density (trees ha^{-1}) of *Iriartea deltoidea* in two western Amazonian tropical forests separated by *ca.* 1400 km. (*Iriartea deltoidea* was found to be the most dominant tree species in both forests. These unpublished data were provided by N. C. A. Pitman, and are extracted from previously summarized studies (Pitman *et al.* 2001; Condit *et al.* 2002). Data are presented as means ± 1 s.e.)

forest type	Manu, Peru	Yasuní, Ecuador
mature floodplain	68.6 ± 21.9	30.0 ± 12.6
terra firme	42.0 ± 7.8	49.1 ± 5.6
swamp	20.4 ± 19.1	43.5 ± 41.9

Piper laevigatum, *Quararibea wittii* and *Rinorea viridifolia*, are dominant, but these species are 20% more prevalent in the vicinity of *I. deltoidea*. Furthermore, species with storage cotyledons are 24–39% more common in areas susceptible to *I. deltoidea* debris fall ($p = 0.052$; figure 2). Tropical tree species with storage cotyledons typically have disproportionate allocation to roots, slower growth rates and greater shade tolerance (Kitajima 1992), mechanisms that facilitate persistence and recovery after the infliction of physical damage (Pauw *et al.* 2004). *Iriartea deltoidea* appears to physically structure the recruitment environment in its vicinity by creating zones hazardous to species without mechanisms for the avoidance of physical damage, survival after loss of above-ground biomass, or both. These differences in sapling species composition and stature are unlikely to reflect disparities in understorey light availability between sites near and far from *I. deltoidea* crowns. Data from Cocha Cashu indicate that understorey light penetration in the vicinity of adult *I. deltoidea* palms is no different than at other randomly chosen points in the forest understorey (J. W. Terborgh, unpublished data).

The results of this study suggest that *I. deltoidea*, through its leaf fall, can influence the structure and composition of the sapling community in its vicinity. Large tracts of western Amazonian forests are likely to be under the direct influence of this numerically abundant species. The density of adult *I. deltoidea* at Cocha Cashu in our floodplain demographic plot was 24.9 trees ha^{-1}. Given the spatial distribution of palms in our plot and the fact that the zone of *I. deltoidea* frond fall may extend over 7 m at Cocha Cashu (figure 1), at least 23% of the floodplain forest at this site is likely to be susceptible to physical disturbance by falling *I. deltoidea* fronds in a given year. Data from a network of tropical forest plots in Peru and Ecuador suggest that the density of *I. deltoidea* palms observed at Cocha Cashu is likely to be representative of vast tracts of western Amazonian forests, while also indicating that even higher densities are possible (table 1). *Iriartea deltoidea* is present from the southern Amazon to Costa Rica, and may be the most common canopy tree species in western Amazonian tropical forests (Pitman *et al.* 2001). The scale of its dominance suggests that falling *I. deltoidea* debris may be influencing sapling community structure and species composition in Amazonian rainforests over very large spatial scales.

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