

Herbivores limit the population size of big-leaf mahogany trees in an Amazonian forest

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The Janzen–Connell hypothesis proposes that specialized herbivores maintain high numbers of tree species in tropical forests by restricting adult recruitment so that host populations remain at low densities. We tested this prediction for the large timber tree species, *Swietenia macrophylla*, whose seeds and seedlings are preyed upon by small mammals and a host-specific moth caterpillar *Steniscadia poliophaea*, respectively. At a primary forest site, experimental seed additions to gaps – canopy-disturbed areas that enhance seedling growth into saplings – over three years revealed lower survival and seedling recruitment closer to conspecific trees and in higher basal area neighborhoods, as well as reduced subsequent seedling survival and height growth. When we included these Janzen–Connell effects in a spatially explicit individual-based population model, the caterpillar’s impact was critical to limiting *Swietenia*’s adult tree density, with a > 10-fold reduction estimated at 300 years. Our research demonstrates the crucial but oft-ignored linkage between Janzen–Connell effects on offspring and population-level consequences for a long-lived, potentially dominant tree species.

The Janzen–Connell (JC) hypothesis was proposed over 40 years ago to explain the high numbers of tree species found in many tropical forests (Janzen 1970, Connell 1971). The hypothesis makes two general predictions: 1) a mechanism of distance- or density-responsive attacks by host-specific predators, or ‘JC enemies’, impairs the vigor of tree offspring to space apart the recruitment events of conspecific adults; 2) these JC effects promotes species co-existence by stabilizing the sizes of co-occurring tree populations (Chesson 2000). Although many aspects of the JC mechanism have been studied and reported (reviewed by Carson et al. 2008, Terborgh 2012, Comita et al. 2014), including several showing it can increase local seedling diversity (but not that of adults; Harms et al. 2000, Mangan et al. 2010, Bagchi et al. 2014), far fewer have tackled the crucial link between the mechanism’s action and its population-level impacts (Silva-Matos et al. 1999, Blundell and Peart 2004, Steinitz et al. 2011).

Our ability to infer how post-dispersal, enemy-driven processes shape population dynamics of trees is limited in part because of the long lifespan of trees, but could be improved by better field-testing of the JC mechanism. Specifically, by considering not only enemy impacts upon survival but also upon growth, especially from insects, since seedling mortality risks are size-dependent (Connell 1971, Blundell and Peart 1998, Alvarez-Loayza and Terborgh 2011); by replicat-

ing across years and conspecific neighborhoods varying in adult tree density or basal area (Schupp 1992); by examining multiple life stages and enemies for their joint effects on tree recruitment (Schupp and Fuentes 1995, Terborgh 2012, Fricke et al. 2014); and finally, by considering dynamics not only in forest understory habitats where seedlings are suppressed (Clark and Clark 1984, Howe et al. 1985, Blundell and Peart 1998, Swamy and Terborgh 2010) but also those areas where the canopy has been disturbed, resulting in ‘gaps’ where local light levels are temporarily elevated (Hartshorn 1978, Denslow 1987, Connell 1989). Unless these aspects are given more attention, we suspect that a better understanding of the ‘population-bridge’ between the mechanism and the community consequences of the JC hypothesis will remain elusive.

Because most non-pioneer, overstory forest tree species have intermediate light requirements as seedlings and saplings, one or more gaps appear essential for their juveniles to recruit into the canopy, or at least for a new seedling to quickly grow into a sapling, even among more shade-tolerant species (Hartshorn 1980, Denslow 1987, Canham 1989, Wright et al. 2003, Rüger et al. 2009). Gaps, moreover, can form at variable distances from and amidst clusters of reproductive trees with size-dependent fecundity, and thus are likely critical for understanding the

population consequences of the JC mechanism, as well as general community dynamics (Janzen 1970, Augspurger 1983, Becker et al. 1985, Connell 1989). Interactions between dispersal distance, conspecific basal area, and gaps may therefore be expected to create synergistic effects for susceptibility to JC enemies, especially rodents and leaf-chewing or stem-boring insects (Augspurger 1984, Sullivan 2003, Norghauer et al. 2008, 2014). For example, gaps may attract these JC enemies because they are better protected from predation, or their preferred food is more abundant or easily found there (Schupp 1988, Beck et al. 2004, Norghauer et al. 2006, 2008, 2014). Yet to date, only a few studies have investigated how JC plant–enemy interactions operate in these transient habitats.

Implicit in the JC hypothesis is the inference that enemy impacts on tree regeneration ultimately affect adult population densities (see the ‘Population recruitment surface’ section in Janzen 1970; also Schupp and Fuentes 1995, Schupp and Jordano 2011, Steinitz et al. 2011). This should be manifest at the population level as negative density dependence (NDD): in the absence of predator satiation, the spacing mechanism must limit adult tree abundance (Janzen 1970, Schupp 1992). Canopy gaps also likely play an important role in determining the population consequences of NDD because rapid growth of a small proportion of saplings may contribute disproportionately to the population growth of a tree species (Zuidema et al. 2009). In fact, in Janzen’s original 1970 paper, in addition to stressing the need to confirm/identify predators responsible for JC effects, and explicit consideration of how clustered trees and overlapping seed shadows might further winnow recruitment opportunities in a population (Fig. 9 therein), one can also find references to forest habitats and succession modulating dispersal and predation of tree offspring. He writes, “Alternative population recruitment strategies, habitat heterogeneity, and differential competitive ability of the seedlings must also be considered when testing these hypotheses” (p. 518). However, no published study has yet shown that JC enemies and their effects can potentially limit the population size of any tree species. What has been shown instead, are observations consistent with the JC mechanism that would seem to limit tree population sizes, in that new saplings do not recruit from seedlings very close (< 10–15 m) to conspecific adult trees (e.g. *Trichilia tuberculata* in Condit et al. 1992; also see Swamy et al. 2011).

Indeed, these patterns or ‘signatures’ of NDD consistent with the JC mechanism seem to be widespread in species-rich forests (Carson et al. 2008, Zimmerman et al. 2008). Yet most of these NDD community-level studies come from permanent plots monitoring recruitment and mortality rates of stems > 1 cm diam., thus overlooking NDD processes in the earliest life stages when seeds and seedlings are most abundant and vulnerable to predators. Recently, Green et al. (2014) presented compelling empirical evidence that early life-cycle stages are paramount for nonrandom, diversifying processes in an Australian tropical forest. Where studies have focused on seedling recruitment and early growth, they often detect NDD and ascribe the putative JC mechanism to pathogen activity and feedbacks in the forest understory (Webb and Peart 1999, Harms et al. 2000, Metz et al. 2010, Terborgh 2012). However, without identifying and measuring

in some way the JC plant–enemy interactions responsible for these nonrandom dynamics (Augspurger 1984, Mangan et al. 2010, Bagchi et al. 2014, Fricke et al. 2014), these signatures cannot distinguish between genuine JC effects and classical NDD in plant populations caused by ‘self-thinning’ – though in the forest understory intraspecific competition for resources among seedlings is unlikely (Paine et al. 2008) – or by parent–seedling conflicts arising from asymmetric competition (Alvarez-Loayza and Terborgh 2011, Kobe and Vriesendorp 2011, Terborgh 2012, Comita et al. 2014).

We report here on a seed addition experiment repeated annually for three years in the southeastern Amazon that used a natural, unlogged population of the iconic Neotropical timber tree, big-leaf mahogany *Swietenia macrophylla* (Meliaceae), to quantify the attacks and demographic impact of JC enemies of seeds and seedlings. To test whether these predators can limit a tree species’ population size, we combined the field study’s results with long-term information from the same region on *Swietenia*’s vital and fecundity rates in a spatially-explicit population model. Using such a spatially-explicit model for testing JC effects is especially valuable because both the JC mechanism and seed dispersal are inherently spatial processes (Janzen 1970, Clark and Clark 1984, Terborgh 2012).

We asked four interconnected questions: 1) are more *Swietenia* seeds and seedlings attacked and killed closer to conspecific adult trees than further away? 2) Are predatory attacks and offspring mortality rates higher where adult trees are clustered? 3) Do synergistic effects on seed or seedling dynamics occur between dispersal and gap colonization? 4) Can mammal and insect predators jointly maintain low abundances of this fast-growing, long-lived, canopy tree species?

Methods

Study species

Big-leaf mahogany *Swietenia macrophylla* is a heavily exploited, large canopy-emergent timber tree with a historically extensive natural range throughout tropical America (Lamb 1966, Grogan et al. 2010). In the state of Pará, Brazil, prevailing dry season winds in July–August disperse most winged *Swietenia* seeds westward from fruiting adults (Grogan and Galvão 2006, Norghauer et al. 2010). On the ground, small mammals eat *Swietenia* seeds (Lambert et al. 2005), often removing the seed hull and leaving tooth-marks on the winged (endocarp) remnants, but they do not cache or move seeds as secondary dispersers (Supplementary material Appendix 1; Grogan and Galvão 2006). Tethered seeds placed in a single gap in areas of clustered *Swietenia* adult trees suffered 50% more predation than at lone trees when exposed to small mammals in 2001 (Norghauer et al. 2006). Germination occurs in October–November when wet season rains return; the rates are 70–95% and increase with seed size. In the forest understory, the newly establishing seedlings have 3–4 simple leaves that are highly susceptible to herbivory and defoliation by a distance-responsive specialist moth caterpillar, *Steniscadia poliophaea* Hampson (Noctuidae: Sarrothripinae; Supplementary material Appendix 1); while the understory impact of this caterpillar

peaks < 15 m of tree trunks, that is, very near fruiting adult *Swietenia* trees, ca 50% of new seedlings still do not escape attack 30 m away (see Fig. 3 in Norghauer et al. 2010). In between these annual pulses of seedling establishment, this predator attacks in density-responsive way growing *Swietenia* seedlings and saplings (up to ca 3–5 m tall), mainly in and around canopy gaps that provide the light levels necessary for height growth and the production of its only known food – young *Swietenia* leaves (Grogan et al. 2005, Norghauer et al. 2008). Mortality to *Swietenia* from pathogens in the understory was ca 15%, on average, in a 1997 field study and was not distant-dependent, or greater there than in gap areas (Grogan and Galvão 2006).

Forest sites

Seed addition experiments were undertaken in the Pinkaití forest reserve in the Kayapó Indigenous Area in southeast Pará, Brazil (7°46'14''S, 51°57'43''W; 200–450 m a.s.l.). The 8000-ha reserve protects an unlogged *Swietenia* population. Long-term *Swietenia* demographic data are from a second site, Marajoara, 180 km east of Pinkaití (Grogan et al. 2014). Marajoara is a forest industry-owned 4000-ha forest fragment where *Swietenia* was selectively logged during 1992–1994. Climate in this region is seasonally dry with 1600–2100 mm annual rainfall. For detailed site descriptions see Lambert et al. (2005) and Grogan et al. (2003, 2008), respectively.

The Janzen–Connell field experiment

Basic design

We used a blocked, split-plot design to evaluate the influence of conspecific neighborhoods and natural predators on the establishment of seedlings in canopy gaps. Seed dispersal downwind of interspersed fruiting *Swietenia* adults was emulated by adding seeds into naturally formed gaps at variable distances from the trees in three consecutive years (2001–2003; Table 1). Seeds were collected earlier in the same dry season from the same 3–4 large, adult trees (> 100 cm diam.). Only undamaged, viable winged seeds were used.

A unique aspect of the design was the inclusion of both relatively isolated focal *Swietenia* trees and those with one or more nearby conspecifics (Table 1). Following Janzen (1970), we reasoned that *Swietenia*'s enemies would be more active in areas with high adult basal areas where larger and/or overlapping seed shadows regularly concentrated their food.

Seed additions

In July of each year, we searched for fruiting *Swietenia* trees that had nearby canopy gaps formed by tree tip-ups or large crown- or branch-falls. Where *Swietenia* occurred in clumps, the most westerly fruiting tree was selected as the focal adult (except two cases in 2002 where the most fecund tree was used instead). In 2001 and 2002 we established two plots in each gap: one each in the trunk and crown zones of fallen tree(s). Distances of plots to focal adults were measured, for gap 'near' (< 35 m) and 'far' (40–95 m) far from them. In 2003, to better emulate long-distance dispersal to gaps, a third distance class of relatively 'very far' gap-plots was included (76–130 m, with 'far' at 33–88 m) (Table 1). Plots were first

searched for naturally fallen seeds, which were removed to ca 1 m away from each plot. Most of the gaps were formed by either single tree deaths, or large-branch falls. It was not possible to map the disturbed ground areas of > 100 gaps, but given their range in percent canopy openness (Table 1) it is reasonable to suppose that the minimum gap area was ≈ 25 m², and that it varied up to 20-fold across all gaps and years (since artificial gaps of the same size could not be made without felling trees in the Pinkaití reserve).

Each plot consisted of four adjacent 1-m² quadrats. In mid-to-late August of each year, into each quadrat five seeds were added: one in the center, with four 45-cm away to form an 'X'. Canopy openness above the 2001 and 2003 plots was measured with a hand-held spherical densiometer in October 2002 and May 2004, respectively, based on measurements in each of the N, E, S and W-facing directions. Plot-level means for percent canopy openness did not differ significantly across distance treatments in either 2001 or 2003 (2001: t-test, $t = 0.267$, DF = 38, $p = 0.79$; 2003: ANOVA, $F_{2,146} = 0.064$, $p = 0.53$; Table 1). These levels of canopy openness were probably underestimated as they were taken 9–15 months after seed additions.

Response variables

Seed predation

For the 2002 and 2003 cohorts we assessed seed fates at ca 9 and 11 weeks, respectively, after seed additions were made. We classified experimental seeds as follows: 1) entire diaspore missing; 2) diaspore present, but seed hull bitten off by small mammals (Supplementary material Appendix 1); 3) seed hull with insect attack(s); 4) seed hull intact but noticeably soft and rotted indicative of pathogen activity; and 5) intact diaspore with seed still viable. We reasonably equated seed removal with predation by small mammals, and calculated their proportions of seed predated (sum of classes 1 and 2; hereafter 'vertebrate predation').

Seedling herbivory

For the 2003 cohort, we surveyed attacks by the specialist caterpillar, *Steniscadia*, and leaf damage to new seedlings during establishment. Signs of *Steniscadia* attacks were confirmed by the presence of caterpillars and/or their webbing and frass, in addition to cutting of the leaf midrib vein and other known patterns of damage (Grogan and Galvão 2006, Norghauer et al. 2010). Leaf area losses were quantified to the nearest mm² on fully expanded leaves using a plastic transparent grid, averaged on a per seedling basis, and then averaged again at the plot level. Cases of 100% defoliated leaves and seedlings were included in this assessment.

Seedling recruitment

We revisited the 2001, 2002 and 2003 plots in May or June, 9–10 months after seeds were sown. We counted live seedlings per plot to calculate 'seedling recruitment' as the proportion of seeds sown in August that survived the 9–10-month period. Heights of seedlings (to growing tip) were measured for the 2001 and 2002 cohorts only. To assess subsequent seedling dynamics, we revisited the 2001 plots in May of 2003 and 2004, 21 and 33 months after seed addition, respectively. In addition, we revisited the 2002 plots in

Table 1. Details of *Swietenia macrophylla* trees and neighborhoods, and the downwind canopy gaps into which their seeds were added in three consecutive years (2001–2003) at a fixed density in the empirical test of the Janzen–Connell mechanism in an unlogged population at the Pinkaití forest (Pará, Brazil).

	2001 cohort	2002 cohort*	2003 cohort
Mahogany trees			
no. focal fruiting trees	20	12	25
trees isolated in 56.5-m radius (ha)	12	7	16
trees with 1 + conspecific adult in 56.5-m radius (ha)	8	5	9
stem diameters of focal fruiting trees (cm)	47–112	50–114	67–161
adult conspecific basal area (m ² ha ⁻¹):			
‘low’ (min – max)	0.17–0.29	0.20–0.33	0.35–0.77
‘medium’ (min – max)	0.30–0.85	0.82–1.02	0.84–1.60
‘high’ (min – max)	0.95–2.37	1.66–2.51	1.66–2.71
Forest area, min. polygon (ha)	490	330	670
Canopy gaps			
no. gaps downwind (west)	40	20	75
mean distance (m) to focal trees:			
‘near’ gap plots	28.6 (± 2.1 SE)	25.9 (± 2.1 SE)	25.6 (± 1.1 SE)
‘far’ gap plots	67.8 (± 2.8 SE)	71.3 (± 3.2 SE)	57.1 (± 1.9 SE)
‘very far’ gap plots	—	—	101.1 (± 2.2 SE)
mean canopy gap openness (%)	10.7 (± 0.28 SE)	n.a.	14.5 (± 0.74 SE)
Mahogany seeds			
no. seeds added	1600	480	3000
plot size used (m)	2 × 2	1 × 2	2 × 2
no. plots	80	48	150
density added (per m ²)	5	5	5
mean fresh weight (g)	0.53 ± 0.080 SD (n = 120)	0.57 ± 0.15 SD (n = 40)	0.50 ± 0.069 SD (n = 350)

*The sample size of fruiting trees was much reduced in 2002, and plots were necessarily smaller, because population-wide frequency of and tree-level seed production was unusually low that year. This may have been due to unusually low rainfall during the preceding rainy season coupled to a moderate El Niño event (Grogan et al. 2012).

May 2004, 21 months after seed addition. At each recensus, we counted the number of live *Swietenia* seedlings and, for the 2001 cohort only, measured seedling heights.

Analysis of the JC mechanism

We analyzed the main and interactive effects of ‘dispersal’ distance and basal area of *Swietenia* conspecific adults on plot-level proportions of seed predation and seedling recruitment using linear mixed models in Genstat ver. 14.0. In these models, focal trees were used as a random effect (i.e. ‘block’). Models were also fitted using a generalized mixed model approach (GLMM with binomial totals and logit link), but this did not improve model fits because plot replication was high and errors approached a Gaussian distribution. However, we used GLMMs to model ‘year-on-year’ survivorship of the 2001 cohort from 2002 to 2003 and 2003 to 2004. Neighborhood conspecific adult basal area (per ha) was calculated within a 56.5-m-radius, and inclusive, of focal trees, because ca 50 m is the mean distance which seeds are farthest dispersed west by winds (Supplementary material Appendix 2; Grogan and Galvão 2006, Norghauer et al. 2011a) and it yields basal area abundance on a 1-ha basis. Basal area served as the between-subject fixed factor, with three levels, formed at the block level that used focal parent trees as unit of replication. The three levels of basal area intervals for the ‘low’, ‘medium’ and ‘high’ levels differed slightly across years 1) to better equalize their sample sizes; 2) because total seed inputs per basal area unit varied across years, we could not assume that JC effects operated exactly the same for each cohort; and 3) because not all trees fruited every year, and in 2002 fewer

smaller-sized focal trees were used than in 2001 or 2003 (Table 1). Dispersal distance from the focal tree (‘near’ versus ‘far’; versus ‘very far’ in 2003) was the fixed, within-subject factor, with plots as the unit of replication.

The *Swietenia* population model

A spatially-explicit, individual-based model was used to test the hypothesis that JC enemies were capable of limiting *Swietenia*’s population size at Pinkaití. This model, developed in the NetLogo 4.13 software programming environment (Wilensky 1999), is an extension of a spatially-implicit population model for evaluating *Swietenia* forest management regulations in Brazil (see Grogan et al. 2014 for a full description). The model’s time step is 1 year and has empirical functions for *Swietenia* fecundity, survival and growth as a function of tree diameter as derived from long-term demographic studies at Marajoara. In addition, it is coupled with an annual canopy disturbance regime based on empirical data, whereby 2.6% of the canopy per ha is opened each year, drawn randomly from a [skewed] distribution of 87 gap sizes (median = 39.2 m²), with all gaps closing after 1 year. The model further assumes that seedlings can only become adults in gaps larger than 314 m²; this conservative approach accounts for poor seedling survivorship in the understory and in smaller-sized gaps because of this species low shade tolerance (Grogan et al. 2005). In the original model a uniform distribution of seeds within a 0.9-ha seed shadow was assumed. In the modified model presented here, adult trees are defined as trees ≥ 30 cm diam., because trees smaller than this threshold rarely fruit, and seed dispersal

was instead distributed west of fruiting trees as this is where ca 87% of seeds land (Grogan and Galvão 2006). Although some seeds do fall to the east, these go no farther than 10–12 m. Here, dispersal distances of seeds were determined using a Weibull function parameterized from a large empirical study that sampled dispersed seeds around 25 isolated trees at Marajoara (Norghauer et al. 2011a; Supplementary material Appendix 2).

In the original model, seedling recruitment into gaps within the seed shadow was assumed to be constant everywhere (0.085). Here, as described below, we modified that assumption and instead used six regeneration scenarios to evaluate JC-effects (Table 2). Multiple scenarios were used, instead of just one, to investigate the relative contribution of different effects at different key life stages. Possible population-level impacts of the mahogany shoot-borer *Hypsipyla grandella* on stems > 1 cm diam. was not investigated because the necessary data were unavailable.

Scenario M0 was the base model with no spatially explicit density- or distance-dependent dynamics. The base model used a first-year mean seedling recruitment rate of 0.241 (± 0.019 SE) obtained by bootstrapping ($n = 100$) seedling recruitment recorded in gap plots < 60 m from conspecific focal trees across the three experimental cohorts.

Scenario M1 applied a ‘minimum-spacing rule’ such that seedling recruitment events were only possible in gap areas > 20 m from live adult trees. However, subsequent scenarios 2, 3, 4 and 5 used explicit empirical functions to describe the effects of distance- and/or density-responsive predators on *Swietenia* seedling dynamics. Here, density is calculated as the basal area (m^2) of adults per circular ha, and distance is in meters to the stem trunk of the nearest conspecific adult.

In scenario M2, the fixed seedling recruitment rate of 0.241 was replaced with a JC function that spatially accounted for the joint impacts of small mammals and *Steniscadia* on the probability of 1st year recruitment ($p_{rec,1-yr}$), derived from the three cohorts in this study.

$$p_{rec,1-yr} = 0.2725 - 0.09175 \times (\text{basal area}) + 0.001342 \times (\text{distance})$$

This function was obtained from a single, composite linear mixed model with distance and basal area as continuous independent variables and with focal tree nested within cohort year, and seed addition plot nested within focal tree as the two random terms (Supplementary material Appendix 1–7).

In scenario M3, which focused on seedling recruitment and later survivorship, two empirically-derived functions describing distant-dependent post-establishment mortality risks in gaps were added to scenario 2. These used second- and third-year seedling survival rates of the 2001 cohort ($p_{sur,2-yr}$ and $p_{sur,3-yr}$) to quantify seedling mortality (i.e. 1 – proportion surviving):

$$p_{sur,2-yr} = 1 / \{1 + \exp(-0.9956 + 0.9523 \times (\text{basal area}) - 0.02476 \times (\text{distance}))\}$$

$$p_{sur,3-yr} = 1 / \{1 + \exp(0.4374 - 0.01892 \times (\text{distance}))\}$$

In scenario M4, which focused only on seedling recruitment and growth, JC effects on seedling height increment in

gaps after the first year were included to reflect the impact of herbivory in the early wet season from *Steniscadia* caterpillars (from Norghauer et al. 2008), whereas the explicit JC post-establishment mortality risks used in scenario 3 reverted to their formulation in the base model. Percent leaf damage to young leaves is a two-step asymptotic function of total conspecific diameters in a 125-m-radius of a gap (ca 5 ha; Supplementary material Appendix 3). The resulting function relates the percent leaf area removal from a seedling to its relative growth increment in height (later converted to diameter increment) until it becomes a sapling (i.e. = 1 cm diam. at 1.3 m, or has a total height of 1.66 m; Supplementary material Appendix 3):

$$\begin{aligned} \text{Height.incr.perc.} &= 0.3849 - 0.0026 \times (\% \text{ leaf damage}) \\ \text{Height}_{t,1} &= \text{Height}_{t,0} + \text{Height}_{t,0} \times (\text{Height.incr.perc.}) \end{aligned}$$

In scenario M5, which focused on seedling recruitment, survival and growth, all possible JC effects on the *Swietenia* population as described above in scenarios M2, M3 and M4 are operative. For each scenario, we simulated a population located in the 500-ha core area of Pinkaití, in which tree locations and sizes had already been determined (Supplementary material Appendix 4). We ran 100 simulations of 300 years for each scenario (Table 2).

Results

Seedling recruitment in the first year

For the 2001 cohort, the proportion of *Swietenia* seeds that survived to become seedlings 9–10 months later was higher ‘far’ than ‘near’ conspecific adults ($p = 0.012$), but lower where conspecific basal area was higher ($p = 0.025$) (see Supplementary material Appendix 5 for statistical reporting). The benefit of ‘far’ dispersal weakened where conspecific basal area was ‘high’ (Fig. 1a), although the interaction term was insignificant ($p = 0.243$). Seedling recruitment of the 2002 cohort was not significantly affected by distance or basal area (all three p -values > 0.145; Fig. 1b). However, when both factors were treated as continuous terms in a

Table 2. Summary of the six regeneration scenarios simulated for a population of *Swietenia macrophylla* trees in 500 ha of unlogged forest (Pinkaití in Pará, Brazil). For each model, 100 simulations lasting 300 years each were run. The ‘Exclusion’ scenario corresponds to a ‘dead-zone’ created by a minimum-spacing rule (20 m) for seedlings to recruit downwind of live source trees: this is the most basic formulation that the Janzen–Connell mechanism can take (Janzen 1970). Subsequent models increase in complexity in that they incorporate Janzen–Connell seed and seedling predation effects (NDD) on first-year recruitment (‘Establishment’), seedling mortality risk in second and third years, and leaf herbivory impacts on seedling height increment (‘Mortality’ and ‘Growth’, respectively), as driven by the proximity and abundance of conspecific adults (distance and basal area influences, respectively).

Model number	Model name	Exclusion (X)	Establishment (E)	Mortality (M)	Growth (G)
M0	O_{Model}	no	Null	Null	Null
M1	X_{Model}	yes	Null	Null	Null
M2	E_{Model}	no	E-NDD	Null	Null
M3	EM_{Model}	no	E-NDD	M-NDD	Null
M4	EG_{Model}	no	E-NDD	Null	G-NDD
M5	EGM_{Model}	no	E-NDD	M-NDD	G-NDD

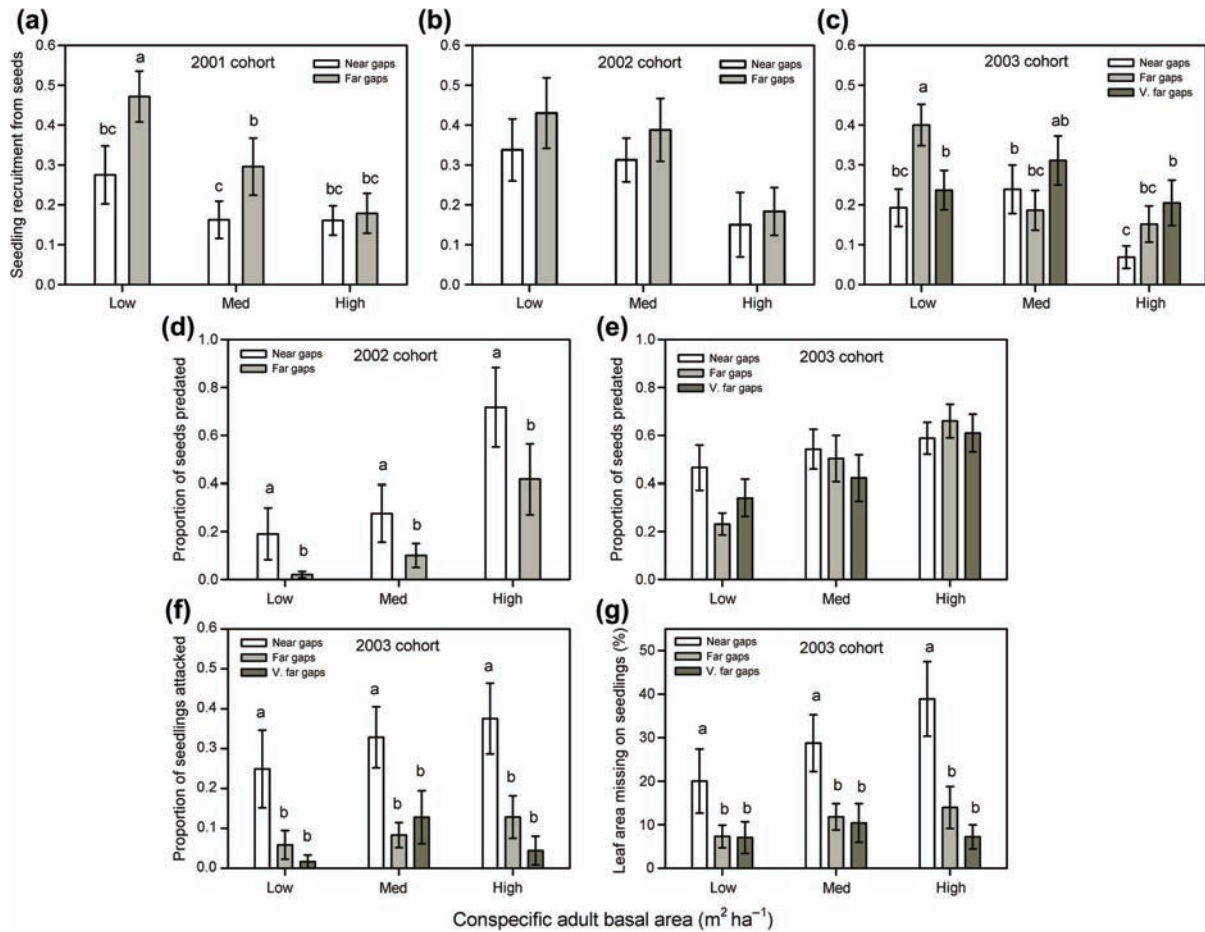


Figure 1. (a–c) The effects of local conspecific neighborhoods (basal area) and increasing distances downwind of fruiting conspecific trees at the Pinkaití forest (Pará, Brazil) upon first-year recruitment levels of *Swietenia macrophylla* seedlings in natural canopy gaps for three successive experimental seed cohorts. (d, e) Seeds lost to predation by small mammals, namely rodents, ca 9–11 weeks after seeds were sown. (f, g) Susceptibility of newly germinating seedlings to attacks by the specialist moth caterpillar, *Steniscadia poliophaea*, and the amounts of leaf damage incurred ca 9–11 weeks after seeds were sown. Bars are means \pm SE of plot-level data; different small letters indicate significant differences that were found among means ($a > b > c$) in each panel using preplanned comparisons for predicted outcomes based on the Janzen–Connell mechanism.

linear mixed model, the negative influence of ‘high’ basal area became significant ($F_{1,9,4} = 6.00$, $p = 0.036$) whereas the distance effect remained non-significant. In the cohort with the largest sample size (2003), recruitment near focal trees was lowest in areas of ‘high’ conspecific basal area. However, in areas of ‘low’ basal area, recruitment peaked at the intermediate ‘far’ distance (interaction term, $p = 0.002$; Fig. 1c, Supplementary material Appendix 5).

Seed predation and new seedling herbivory

In the 2002 cohort, seeds ‘near’ conspecific adults suffered significantly greater levels of predation than seeds ‘far’ from adults ($p = 0.002$; Fig. 1d). This pronounced distance effect went undetected in the 2003 cohort ($p = 0.330$; Fig. 1e). When averaged over the two distance categories, most of the 2002 seeds eaten by vertebrates were in areas of ‘high’ conspecific basal area ($p = 0.063$; Fig. 1d, Supplementary material Appendix 6). Outcomes were similar in 2003, when seed predation declined where conspecific basal area was ‘low’ ($p = 0.063$; Fig. 1e); when conspecific basal area was

analyzed as a continuous variable, its effect became marginally significant ($p = 0.045$).

Newly germinating *Swietenia* seedlings were highly susceptible to attacks by the specialist caterpillar *Steniscadia*, especially ‘near’ conspecific adults ($p < 0.001$; Supplementary material Appendix 6), but much less so at ‘far’ and ‘very far’ dispersal distances (Fig. 1f). Similarly, new seedlings in plots ‘near’ conspecific adults suffered the most damage (log-transformed response, $p = 0.001$; Fig. 1g, Supplementary material Appendix 6). An influence of conspecific basal area was not detected on either response variable ($p = 0.338$, 0.166).

Very few *Swietenia* seeds were killed by pathogens in both 2002 and 2003 cohorts (0.8% and 0.4% in 48 and 149 plots, respectively), while insects killed slightly more seeds (7.3% and 1.9%, respectively). For both of these enemies, the mortality they were associated with appeared random; it was not significantly greater than found for experimental seeds in understory plots in a parallel study on-site (Norghauer unpubl.); and it was so infrequent to preclude formal analyses of JC effects.

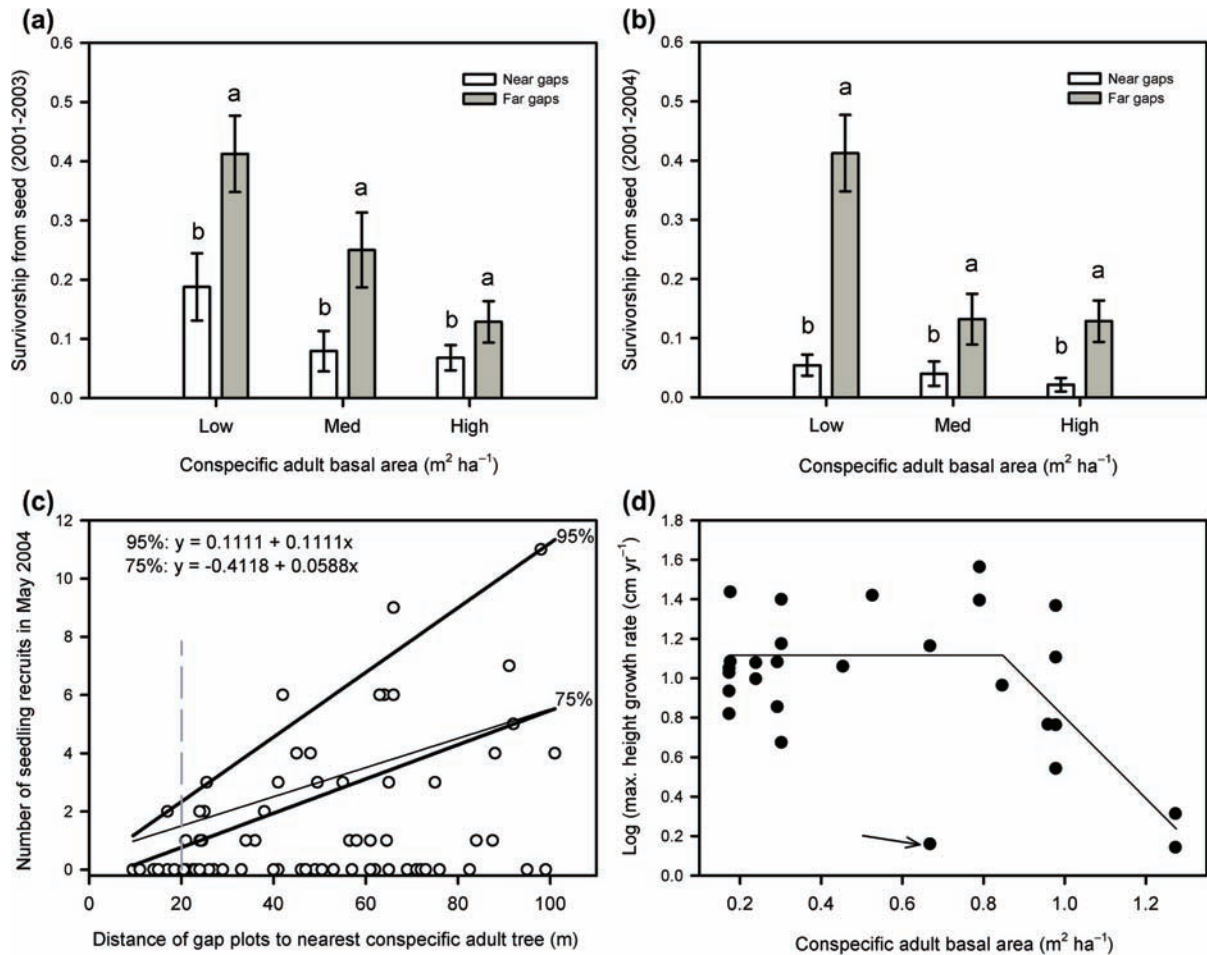


Figure 2. The dynamics of experimental *Swietenia macrophylla* seedlings at the Pinkaiti forest site. In panels (a, b) are shown the proportions of sown seeds that survived as seedlings in the 2nd and 3rd year of the 2001 experimental cohort; bars are means \pm SE. In (c), each symbol indicates the number of 2001 seedlings still alive in 2004 with the significant quantile regressions (thick lines) fitted to all plots; also shown, for comparison, is an OLS regression (thin line) fitted to the non-zero plot counts only ($F_{1,32} = 10.35$, $p = 0.003$, $R^2 = 0.22$). In (d), each symbol indicates the best height growth rate through 2004 per plot of a single seedling as a function of its local conspecific neighborhood. The arrow indicates a severe outlier omitted from the fitted split-line regression.

Seedling survival dynamics and final heights of the 2001 cohort

The effects of distance from conspecific adults and associated basal area on cumulative offspring survival, that is from the seed stage onward, intensified over time. Considered over a 2-year period, survival was twice as great ‘far’ versus ‘near’ to conspecific adults ($p < 0.001$), and lowest overall at ‘high’ conspecific basal area ($p = 0.003$; Fig. 2a, Supplementary material Appendix 7). Over a 3-year period, the effect of distance persisted ($p = 0.004$), but more so at ‘low’ than at ‘medium’ and ‘high’ conspecific basal areas ($p = 0.054$, Fig. 2b).

A greater proportion of seedlings survived the 1-year interval between June 2002 and June 2003 in plots situated ‘far’ from rather ‘near’ to conspecific adults (GLMM, $p < 0.001$; Supplementary material Appendix 7), and in areas of ‘low’ conspecific basal area when averaged over both distance categories ($p < 0.001$; interaction term, $p = 0.088$). In the subsequent year (2003–

2004), a significant effect of conspecific basal area on seedling survival was no longer detected ($p = 0.439$); instead, a weakened influence of distance persisted ($p = 0.079$; $p = 0.041$ in a reduced model lacking the interaction term; Supplementary material Appendix 7).

In May 2004, almost three years since seeds were sown, with a single exception only plots > 20 m from conspecific adult trees had any seedlings alive (Fig. 2c). In these latter plots seedling counts increased significantly with distance when fitted with ordinary least squares regression. But given the heterogeneous variance present – likely caused by density-independent mortality factors not measured at the plots – a better approach is quantile regression (Cade and Noon 2003); in this analysis, which accommodated plots with zero recruits, the 75th and 95th percentiles of seedling counts increased significantly with distance (respectively: $F_{1,71} = 6.97$, $p = 0.0102$ and $F_{1,71} = 21.8$, $p < 0.001$; Fig. 2c).

When the best-performing seedling in each plot was only considered – as only one seedling could ever occupy the plot space as an adult tree – log-transformed maximum height

growth rates showed little change with increasing conspecific basal area, but declined significantly at greatest conspecific basal areas (split-line regression used because a standard regression line could not be fit, $F_{3,23} = 146.8$, $p < 0.001$, $R^2 = 0.46$, one outlier omitted; Fig. 2d). Using instead the summed diameters of conspecific adults per 1-ha better met model assumptions (split-line regression, $F_{3,24} = 105.93$, $p < 0.001$, $R^2 = 0.38$; breakpoint = 100.3 cm). However, substituting distance for conspecific basal area in Fig. 2d yielded a non-significant relationship (regression assumption met, $F_{1,24} = 0.46$, $p = 0.503$; not shown).

Population models

After 300 years, without any JC effects at all and under a realistic disturbance regime, the number of adult *Swietenia* trees reached ≈ 4000 per 100 ha in scenario M0, or 40 times as many as seen under natural conditions (≈ 1 per ha), because of short-term exponential population growth that cannot continue over longer time runs (Fig. 3a). Invoking a simplistic JC spacing rule (scenario M1) reduced final abundance by about 10-fold (Fig. 3b) compared to no JC effects operating at all – yet the population was still increasing. Allowing JC effects to act only during the seed-to-seedling transition marginally reduced the tree density further (Fig. 3c). However, when these JC effects on seedling recruitment were coupled to JC effects on subsequent seedling survival in gaps (scenario M3), the final density was half (Fig. 3d) that predicted under the three prior model scenarios (Fig. 3a–c, M0–M2), yet the population was still increasing

after 300 years. In contrast to all these scenarios, the abundance of adult *Swietenia* was drastically reduced when the impact on seedling growth due to young-leaf herbivory from the specialist moth caterpillar, *Steniscadia*, was taken into account, leading rapidly to a population size that was more-or-less unchanging after 300 years (Fig. 3e). These small bounded trajectories in adult densities suggest their mortality was balanced by recruitment events, but this cannot be interpreted prima facie as evidence for a stationary population (i.e. one with exactly zero growth). This stabilization effect strengthened slightly when all JC effects operated concurrently on the *Swietenia* population, capping the adult densities at ca 20–30 trees per 100 ha, in line with natural densities in the region (Fig. 3f). In sum, when *Steniscadia*'s impact on growth was included (M4, M5; Table 2), the population size was three orders of magnitude lower than that predicted without any JC effects.

Predictions from the M5 model were checked against observed stem densities at Pinkaiti (Fig. 4). Except for the smallest size threshold, the values for most of the adult-sized trees in the population fell within the 95% confidence region of size-specific predicted densities after 300 years.

Discussion

The Janzen–Connell mechanism

These results demonstrate that pronounced and predictable JC effects operate in canopy gaps during the seed and

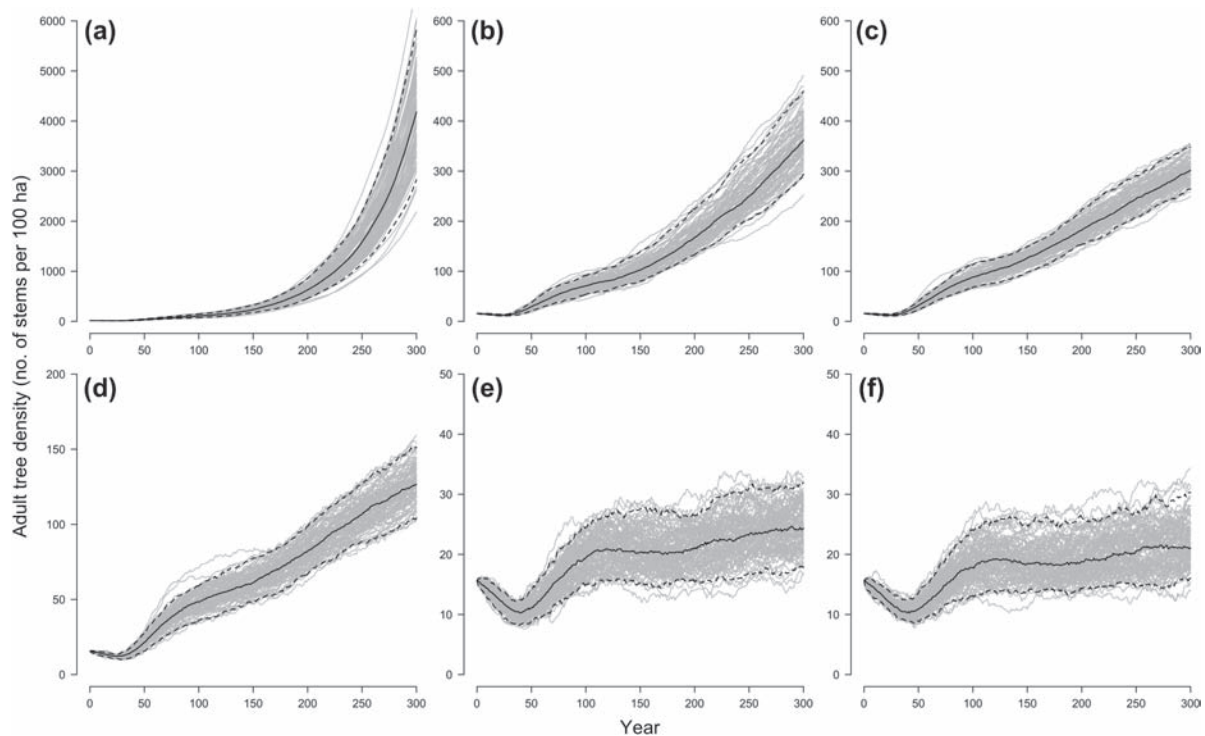


Figure 3. The density of adult-sized *Swietenia macrophylla* trees (≥ 30 cm diam.) during 300-year simulations under six Janzen–Connell (JC) model scenarios: (a) M0, the base model of population dynamics (0_{Model}); (b) M1, all new seedlings killed within 20 m of source trees (X_{Model}); (c) M2, with JC effects on first-year seedling recruitment (E_{Model} in Table 2); (d) M3, with JC effects on first-year recruitment and 2nd and 3rd year survival (EM_{Model}); (e) M4, with JC effects on first-year recruitment and later seedling growth rates (EG_{Model}); and (f) M5, with all JC effects operating together (EGM_{Model}). Gray lines indicate 100 replicate runs, the solid black line is the median, and dashed black lines are 95% confidence regions. Note the different ranges in y-axes across panels. (The procedures code for model simulations is given in Supplementary material Appendix 8.)

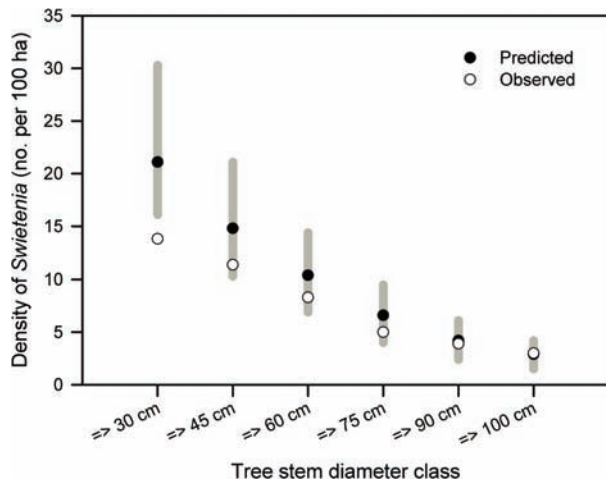


Figure 4. A comparison of adult-sized stem densities of *Swietenia macrophylla* after 300 years predicted by the model scenario M5 ('EGM'), which included full Janzen–Connell effects (Table 2), with observed densities of the unlogged population at the Pinkaití forest (Pará, Brazil). The shaded bars indicate 95% confidence regions obtained from model simulations ($n = 100$ runs). Note that it is assumed here that the current Pinkaití population is in a state of equilibrium with respect to its size-class frequency distribution.

seedling stages in an unlogged population of *Swietenia* in a southeastern Amazonian forest. For each of the three yearly seed cohorts, seedling recruitment was enhanced beyond 'near' dispersal distances, and was poorest where conspecific basal area was highest. This latter result is explained less by *Steniscadia* caterpillar herbivory than by more seeds being eaten by small mammals in these neighborhoods at the 1-ha scale studied (Lambert et al. 2005, Norghauer et al. 2006). Hence small mammals may function as 'facultative' specialist predators in dry season months (sensu Janzen 1970, Beck et al. 2004), perhaps by responding to more regular or higher densities of seed inputs to the forest floor when foraging. In so doing, they left fewer seeds available for this specialist moth caterpillar to consume as new seedlings, which they did so in a strongly distance-dependent way in 2003. The moth does this as well in the forest understory, as reported elsewhere already (Norghauer et al. 2010) – and probably did so in 2001, judging by the better foliar condition of recruited seedlings farther from conspecific adults in that year's cohort (Norghauer unpubl.). Incidentally, compared to gap areas, overall seed predation by small mammals was significantly lower in understory plots and apparently not distance-dependent (at fixed distances 5–100 m), whereas moth predation of new seedlings was general similar between habitats (results to be reported elsewhere).

The distant-dependent predation of seeds by small mammals seen in the 2002 cohort was not found in a caging experiment done onsite in 2001 (Norghauer et al. 2006) or at the Marajoara forest (Grogan and Galvão 2006), suggesting temporal variation in the JC mechanism when driven by seed-eating small mammals. A possible explanation for this result is that a scarcity of food resources in an El Niño year forced these animals to search more intensively for *Swietenia* seeds in the late dry season. This is, however, unlikely to have a lasting effect (Clark and Clark 1984) on *Swietenia* dynamics because post-establishment gap seedlings

will be later sought out by its defoliating caterpillar. As to the identity of the small mammals, the prime candidates are spiny rats, *Proechimys cuvierie* and *P. roberti*, a grass mouse (*Akodon* sp. nov.) and a mouse opossum *Marmosa murina* whose relative abundances were positively correlated with mahogany seed predation in separate field work onsite by Lambert et al. (2005). Less likely, but known to forage for seed at the nearby Marajoara site, are agoutis *Dasyprocta agouti*, pacas *Agouti paca* and rabbits *Sylvilagus brasiliensis* (Grogan and Galvão 2006).

We are unaware of any other field test of the JC mechanism that has investigated its effects on tree regeneration dynamics in gaps at variable distances from source trees, whether isolated or clustered in space, or that were repeated across multiple years. In Panama, Schupp (1988) protected tethered seeds of a common subcanopy tree to find that predation was lower > 5 m from its crowns, but also found that predators were being satiated at larger spatial scales across conspecific adult tree neighborhoods (Schupp 1992). Here, we did not find evidence for satiation of small mammals, or of *Steniscadia*. However, we did find evidence for context-dependent dispersal, in that all gaps were not equal for successful seedling recruitment. Though it was advantageous for a seed to land in a gap at 'far' and 'very far' distances from parents in neighborhoods with relatively 'low' to 'medium' basal areas, it was not so always in areas of 'high' adult basal area due to the combined impact of small mammals on seeds and *Steniscadia* caterpillars on seedlings. Enemy escape in these neighborhoods is only possible if a *Swietenia* seed travels 'very far' (> 75 m) during longer-distance dispersal events, likely as a result of intermittent stochastic wind turbulence (Grogan and Galvão 2006, Norghauer et al. 2011a).

Further monitoring of the 2001 cohort suggested that distance effects intensified over time, so that three years after seeds were sown, *Swietenia* seedling survival from seed was highest in gaps far downwind of lone conspecific trees. We interpret this result as evidence for a synergistic effect between dispersal distance and canopy closure, one driven by continued attacks and damage inflicted by *Steniscadia* caterpillars that increased *Swietenia*'s later risk of mortality due to suppressed seedling growth as gaps closed. Apart from the annual food pulse provided by the new *Swietenia* seedlings establishing in the understory (Grogan and Galvão 2006, Norghauer et al. 2010), female *Steniscadia* moths are evidently adept hunters of *Swietenia* foliage and foraged on a wider spatial scale (> 30 m from parent trees) in a density-responsive way for its only apparent food source, one best found in gaps that are themselves transient habitats (Grogan et al. 2005, Norghauer et al. 2008). This supports the view that JC effects should accrue over time (Clark and Clark 1984, Terborgh 2012), as well as Janzen's original argument that the most host-specific, mobile enemies of tree offspring should exert the strongest effects via density-responsive attacks. It further echoes his prediction, "...that conditions favoring the seed and seedling predators are likely to lower the density of reproducing adults of a given species and increase the distance of newly produced adults from their parents." (p. 516, Janzen 1970). Our results indicate that such 'conditions' could include habitat heterogeneity from gap disturbances that foster spatial variation in forest light levels important for seedling growth.

Increasing support for the JC mechanism also comes from a recent meta-analysis (Comita et al. 2014) and a synthetic review of research at a Peruvian forest (Terborgh 2012). In each case, however, the population or community consequences of the mechanism were never tested. While indeed inappropriate to include forest edge and pasture habitats in tests of the JC mechanism (Comita et al. 2014), our results suggest that gap areas should be considered, being a natural driver of forest dynamics that grade into understory habitat (Canham 1989, Connell 1989). Admittedly gaps are not where most tree seeds arrive and germinate – including those of *Swietenia* – but they are the ‘typical habitats’ for enhanced recruitment of saplings, which are, as reiterated by Terborgh (2012), the decisive outcome for appreciating population and community level consequences of the JC hypothesis (also see Wright et al. 2003, Rüger et al. 2009). However, interpreting sapling recruitment at a distance in of itself as evidence for the JC hypothesis (Terborgh 2012) might be problematic given that dispersed seeds will cover a greater area and hence be more likely to encounter a gap formation over time (Augsburger 1983, Becker et al. 1985). This thorny issue warrants further experimental field study. Finally, both Terborgh (2012) and Comita et al. (2014) point out that niche-based life history tradeoffs in juvenile stages of tree species are not incompatible with the JC hypothesis. We agree, and further suggest that their interaction is the key to a better understanding of tropical tree diversity, since species differences in shade-tolerance may govern the relative impact of JC effects (Norghauer et al. 2014): these being more important in the understory for the survival of more shade-tolerant species that ‘lie and wait’ for gap events, whereas they become increasingly important in gap areas for the growth of less shade-tolerant species, like *Swietenia*, for which colonizing gaps might be a better route to sapling recruitment.

Population-level consequences of the JC-mechanism

Although the JC hypothesis is aimed at explaining community-level richness, to do so mechanistically it must affect the population dynamics of co-occurring tree species, especially those that are competitively superior and potentially dominant users of limited abiotic resources (Chesson 2000, Carson et al. 2008). *Swietenia*, being a light-responsive, potentially fast-growing large tree that lives long and is wind-dispersed appears to fit the latter description well. However, in this part of its natural range, where no landscape-scale catastrophic disturbances are known to occur in upland forests, adult *Swietenia* densities are generally quite low (< 1 adult per ha; Grogan et al. 2008, 2010) – and thought to be lower than in Mesoamerica, where peak densities can range from 12–16 trees ha⁻¹ > 20 cm diam. over many hectares (in Petén, Guatemala) up to near pure stands of 60–75 stems ha⁻¹ in other countries, albeit over very limited areas (1–2 ha) (Lamb 1966). Our results provide evidence that these low Amazonian population densities are in part maintained by JC enemies, namely by *Steniscadia*, which interestingly appears to be restricted to South American forests. This inference is also supported by recent observations of ‘enemy release’ of *Swietenia* in invasive Caribbean populations from which *Steniscadia* is absent, and where

the density of trees > 25 cm diam. was ca 125 stems ha⁻¹ (Norghauer et al. 2011b). The widespread notion that the reliance on gaps to attain canopy size by non-pioneer, light-demanding tree species precludes their codominance at the stand level presupposes that their juvenile growth and recruitment rates are optimal in gaps, and that no JC effects suppress their performance across them.

The simulation of a 20-m radius ‘dead-zone’ around *Swietenia* adult trees, while slowing population growth, was insufficient to stabilize its population after 300 years (as were JC effects on 1st-year seedling recruitment). This counter-intuitive result can be explained by debunking a common, but mistaken view that JC effects must always lead to species’ distributions characterized by isolated, regularly-spaced adult trees in a population – it need not, because the mechanism does not preclude the recruitment of clustered adults at far distances, where a few dispersed individuals can jointly escape attacks and are eventually released together via gap formations (Augsburger 1983, Becker et al. 1985, Hamill and Wright 1986, Terborgh 2012). To better understand and appreciate how the JC mechanism functions in forests, its changing effects at multiple spatial scales through ontogeny must be critically evaluated.

Most importantly, however, the model simulations revealed that including JC effects on post-establishment seedling survival slowed *Swietenia*’s population growth, but that it was the additional impact of *Steniscadia* leaf herbivory on seedling height growth that was essential for regulating adult densities (to ca 20–30 stems / 100 ha). This impact depressed recruitment rates into the sapling stage (i.e. 1 cm diam. class), thereby keeping individuals smaller, which in turn increased their mortality rates (since these functions are themselves size-dependent in the base model). This lends further weight to collective evidence that JC effects are stronger in the tree seedling than seed stage (Terborgh 2012, Comita et al. 2014), and highlights the need to investigate JC enemies and their effects on seedling growth dynamics. We predict that in the absence of *Steniscadia*, the *Swietenia* population could attain a much larger density than it now has at Pinkaití, since more offspring should survive and the time to maturity would be much reduced.

A caveat to this modeling exercise of course is that the forest was ‘empty’ – i.e. interspecific interactions, other than those mediated by gap formation, are not explicitly considered. However, the empirical vital rates used for saplings through adult size-classes did come from *Swietenia* trees competing with other species in forest, and thus included any density-independent drivers of mortality. In addition, the onward dynamics of saplings partly accounted for any ‘self-thinning’ effects (because growth and mortality functions were derived from seedlings outplanted into large gaps at relatively high densities; see Grogan et al. 2014). In Fig. 3a, the ca 40 adult trees ha⁻¹ (1 per 250 m²) approached its carrying capacity, considering a mean of non-overlapping 15-m crown diameters for all sized-trees ≥ 30, which is not unrealistic. Outside its native range, in Asian plantations, the density of adult-sized *Swietenia* trees with a mean stem diameter of 45 cm can range from 100 to 200 trees per ha depending on site-class quality and thinning regime used (pp. 92, 110 in Mayhew and Newton 1998). Other factors, such as the soil substrate (Grogan et al. 2003) and

rates of canopy disturbance, are expected to further influence *Swietenia*'s local adult distribution.

Conclusions

To our knowledge, this is the first study to demonstrate that predation by a highly specialized insect herbivore is capable of stabilizing the population size of a tropical tree species as predicted by the JC hypothesis. We hypothesize that *Steniscadia*, and to lesser extent small mammals, are playing a crucial role in facilitating coexistence in this forest by maintaining the *Swietenia* population below its carrying capacity – a key criterion for herbivores to function as a density-dependent factor regulating plant population sizes (Halpern and Southwood 2006). The implications of our study may not be restricted to non-pioneer light-demanding 'gap specialists', but may extend to other species whose seedlings need some light from gaps to grow up (beyond merely persisting in the understory). And if juveniles of other tree species are similarly affected by moth caterpillars, as *Swietenia* is by *Steniscadia*, then this little-studied herbivore guild may be exercising a critical yet underappreciated role in promoting their host species coexistence in other forests.

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Supplementary material (available online as Appendix oik-02324 at <www.oikosjournal.org/appendix/oik-02324>). Appendix 1–8. Appendix 1. Seed and seedling predators of *Swietenia macrophylla*. Appendix 2. Dispersal of *Swietenia macrophylla* seeds. Appendix 3. Modeling the impact of leaf herbivory on *Swietenia* seedling growth. Appendix 4. Distribution of the *Swietenia* population at Pinkaití. Appendix 5. Statistical tables for 1st year seedling recruitment in the field experiment. Appendix 6. Statistical tables for predation and herbivory in field experiment. Appendix 7. Statistical tables for 2nd and 3rd year survival dynamics of the 2001 cohort. Appendix 8. Procedures code for model simulations.