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POLIOPHAEA (NOCTUIDAE):  
POTENT MOTH ENEMY OF YOUNG MAHOGANY  
TREES IN AMAZONIAN FORESTS

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*Chapter 2*

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POTENT MOTH ENEMY OF YOUNG MAHOGANY  
TREES IN AMAZONIAN FORESTS**

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**ABSTRACT**

The super-family Noctuoidea is the most species-rich of Lepidoptera, and many appear to be specialized herbivores. Yet little is known about their abundance and ecological significance in diverse forests of the tropics. In this chapter we briefly review these two aspects in the context of diversity maintenance (Janzen-Connell hypothesis), and present the case of the South American moth *Steniscadia poliophaea*. This species feeds only on expanding leaf and stem tissues of seedlings and saplings of the prized timber tree, big-leaf mahogany (*Swietenia macrophylla*). We synthesize published research, observational reports, and anecdotal evidence about *S. poliophaea*'s life history, ecology, and impact on host mahogany populations across southern Brazilian Amazonia. This moth plays an important role in suppressing the early recruitment and growth, and hence potential local dominance, of the fast-growing *S. macrophylla*. We doubt this moth plays a contributing role in structuring local adult densities of *S. macrophylla* in Central America and Mexico where it has not been reported to occur. We compare the ecological significance of *S. poliophaea* to the better known shoot-boring moth, *Hypsipyla grandella* (Pyrallidae) that is a major pest in mahogany plantations throughout the Neotropics. Finally, we consider implications of these findings for host-competition and control in the recovery and sustainable management of threatened *S. macrophylla* populations in logged and unlogged South American forests. Moth herbivores in general,

and the Noctuidae in particular, warrant further investigation as potential drivers of Janzen-Connell effects on trees in species-rich tropical forests.

## 1. DIVERSITY OF MOTHS AND TREES IN TROPICAL FORESTS: THE HERBIVORY NEXUS

Flowering plants and their insect herbivores dominate Earth's organismal diversity on land (Strong et al. 1984, Price 2002). This antagonistic interaction offers insight into the origins of biodiversity and ecosystem function — herbivory is a major channel for energy flow to higher trophic levels — and is a key feature of natural and managed ecosystems (Fraenkel 1959, Howe and Westley 1988, Huntly 1991, Cyr and Pace 1993, Schoonhoven et al. 2005). The breadth and complexity of plant-herbivore interactions reaches its pinnacle in tropical forests (Nair 2007, Speight et al. 2008, Kricher 2010), which harbor > 50% of the world's terrestrial species on 7% of its land surface (Laurance 1999). There is an urgent need to examine both evolutionary and ecological processes that contributed to such high plant and herbivore diversity (Dethier 1954, Ehrlich and Raven 1964, Thompson 1999), and how these interactions help explain present and predict future community composition, maintenance, and dynamics (Strong et al. 1984, Futuyma and Agrawal 2009).

Among the insects, the order Lepidoptera — the moths and butterflies of the world — is extremely diverse (Scoble 1992). While not as species-rich as the Coleoptera, there are ~160 000 described Lepidoptera species, with up to ~500 000 believed to exist. The primary era of speciation by this group tracked that of the angiosperms in the Cretaceous period (Kristensen et al. 2007). In recent years, more than 800 new Lepidoptera species have been described annually, aided in part by the use of increasingly sophisticated molecular tools (e.g., DNA bar-coding, Hebert et al. 2004) and the revision of phylogenies using computer-intensive methods (Zahiri et al. 2010). Among currently described species, the super-family Noctuidae dominates with at least ~45 000 species, more than twice that of the next largest clade, the Geometroidae (~21 500 species). This super-family Noctuidae presently comprises six families: Eribidae, Euteliidae, Oenosandridae, Notodontidae, Nolidae and Noctuidae (Zahiri et al. 2010). A large number of Noctuidae herbivore species, many probably locally rare, have yet to be described from tropical zones (Scoble 1992, Price et al. 1995, Nair 2007), especially from forests sustaining high levels of host diversity, with up to several hundred woody plant species per hectare (Richards 1996, Turner 2001, Kricher 2010). For example, moth diversity (excluding Pyralidae) sampled in a Bornean forest over a 12-month period totaled 1053 species, of which 39% were in the Noctuidae family (Barlow and Woiwod 1989). In a temperate deciduous forest, 27% of moth species (141 of 512) also were Noctuidae (Summerville and Crist 2002). The vast majority of Lepidoptera are herbivores during larval stages (Strong et al. 1984, Scoble 1992, Schoonhoven et al. 2005, Speight et al. 2008).

Owing almost entirely to the negative impact of their larvae on host plants' survival, growth and fruit production, a disproportionate number of Lepidoptera species are of great economic importance (Nair 2007). The family Noctuidae alone accounts for 1034 of 5781 Lepidoptera species considered economically important by Zhang (1994) — followed by the Pyralidae (748 spp.), Tortricidae (687) and Geometroidae (351). According to Barbosa (1993), close to half of all Lepidopteran pest species are Noctuidae, Pyralidae and Tortricidae (51% and 46% for tropical and temperate zones, respectively). In timber tree plantations in

the tropics, which have expanded rapidly since the end of WWII (Gray 1972), Noctuidae caterpillars can be formidable defoliators of tree seedlings and saplings (e.g., widespread *Hyblaea peura* on *Tectona grandis*, Gray 1972; *Eligma narcissus* on *Ailanthus* spp. in Asia, Nair 2007). In natural forests, where pest outbreaks are thought to be rare, two documented cases were both by Noctuid larvae feeding on newly flushing leaves, *Eulepidotis superior* and *E. phrygionia* each on a single host tree species (*Quararibea asterolepis*: Bombacaceae and *Peltogyne gracilipes*: Caesalpiniaceae in Panama and Brazil, respectively; Wong et al. 1990, Nascimento and Procter 1994). Another Noctuid, *Antiblemma leucocyma*, heavily damages young leaves of the small tree *Miconia calvecsens* (Melastomataceae) in Brazil. This plant was the only species *A. leucocyma* was found to eat, suggesting a narrow diet breadth (Badenes-Perez and Johnson 2008).

What traits enable a given insect herbivore capable of feeding on the host plant to become a 'pest'? When agricultural crops or trees are planted as monocultures at high density, they are likely to become evermore susceptible to herbivore enemies whose populations grow at faster rates than under natural conditions (Root 1973, Nair 2007, Speight et al. 2008), at least in part due to lowered mortality factors under artificial conditions (e.g., pathogens, animal predators, parasitoids, etc.; Letourneau et al. 2011). This predictable response suggests indirectly that insect herbivores are density-responsive, able to increase numerically in response to increasing host abundance, and thus probably also highly efficient at locating host plants. This ability may be enhanced if herbivores also have a narrow diet breadth (Bernays 2001) and thus we expect many Lepidoptera pests to be specialists (Barbosa 1993). Yet while there is little doubt that insect herbivores can reduce the fitness of individual plants, whether they also regulate plant populations and communities (Louda and Potvin 1995, Carson and Root 2000) under more natural conditions remains unclear (Crawley 1989, Huntly 1991, Maron and Crone 2006).

Herbivory by insects is especially problematic in forests because young and small tree progeny (seedlings and saplings) are relatively abundant, highly vulnerable to mortality, and exposed to enemies for extended periods because of the many years (20–50) typically needed to reach maturity (Harper 1977, Richards 1996, Swaine 1996, Hanley 1998, Turner 2001). This brings us to a classic hypothesis at the herbivory nexus that is potentially very important for promoting tree species diversity and coexistence in the tropics: the Janzen-Connell (J-C) hypothesis, which states that specialized natural enemies help keep host species rare by weakening or killing juveniles where they are concentrated, typically close to the parent plant, thereby freeing up space and resources for other tree species in the community (Figure 1; Janzen 1970, Connell 1971). The result of this overcompensating form of density-dependence is that parent tree will not be replaced in the same place by one of its progeny when it dies. Instead, as a corollary, the J-C hypothesis predicts enhanced host species fitness and recruitment through 'escape in space' via dispersal away from conspecific individuals (Howe and Smallwood 1982). This in turn can be viewed as a qualitative defense against specialist herbivores, though not likely against generalist herbivores, which are probably deterred more by a suite of chemical and physical defenses (Marquis 2005). In this way, the J-C hypothesis can function as a 'stabilizing force' in the community to prevent competitive exclusion, especially by key potentially or already dominant species, and may explain in part why so many rare tree species persist in these forests (Janzen 1970, Clark and Clark 1984, Carson et al. 2008, Kricher 2010).

Although Janzen-Connell effects (density- and or distant-dependent plant recruitment and mortality) have increasingly been found in tropical forests (Harms et al. 2000, Queenborough et al. 2007, Comita et al. 2010, Metz et al. 2010; reviewed by Carson et al. 2008 and Zimmermann et al. 2008), their biotic mechanisms remain uncertain. This is because, apart from seeds (Wilson and Janzen 1972, reviewed in Turner 2001), the actual impact of insect enemies on seedlings and saplings in terms of growth and mortality has rarely been identified and quantified in the context of natural or semi-natural forest conditions (Leigh 2004, Carson et al. 2008). And while pathogens are increasingly understood to drive J-C effects under more *shaded* forest conditions (Bell and Freckleton 2006, Bagchi et al. 2010, Mangan et al. 2010), insect herbivores remain woefully understudied by comparison (Janzen 1971, Blundell and Peart 1998, Marquis 2005, Massey et al. 2005).

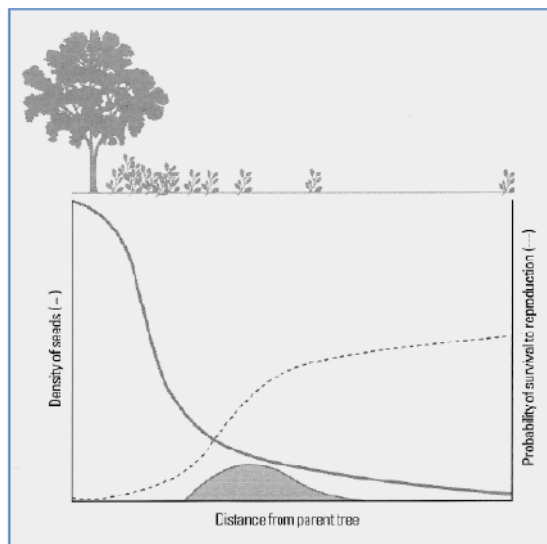


Figure 1. The mechanism underpinning the classic Janzen-Connell hypothesis predicts that the probability of a seed becoming an adult is related to distance from the parent tree. Beneath and near crowns adult recruitment is effectively zero because of overcompensating density-dependent predation and herbivory by biotic enemies upon seeds, seedlings and/or saplings. Although proportionally fewer seeds move farther away from their parent, these locally rare progeny are more likely to escape enemy attacks and avoid being eaten. Also shown is how, for a given species, the interplay between limited seed dispersal and individual susceptibility to host-specific enemy(s) results in a distance from the parent tree where an adult recruitment event is most likely to happen. It is important to bear in mind that in two dimensions, in contrast to seed density (solid line), the relative frequency of seeds usually peaks some intermediate distance from the parent. The mechanism is driven by host-specific enemies, and not intraspecific competition among conspecific seedlings, or asymmetric competition with parents. The graphic is a modified version of the original in Janzen (1970) and reproduced with permission from p. 103 in the book chapter entitled “Plant-insect interactions in terrestrial ecosystems” by SS Strauss and AR Zangerl in *Plant-Animal Interactions: An Evolutionary Approach* (2002), edited by CM Herrera and O Pellmyr and published by Wiley-Blackwell.

Furthermore, insect herbivores generally prefer younger over older plant stages, and vigorous individuals over weakened ones (Feeny 1970, Strong et al. 1984, Price 1991, Hanley 1998). For these reasons, tree seedlings or saplings are expected to be under stronger selective pressure to deploy anti-herbivore defenses to minimize loss of valuable photosynthetic tissues

compared to reproductive adults (Hanley 1998, Boege and Marquis 2005). This strategy is thought to be under strong selection in nutrient-poor habitats where it is very difficult to replace plant parts lost to herbivory (Janzen 1974, Coley et al. 1985, Fine et al. 2004). Within plants, expanding young leaves in particular (Harper 1989) — tender and more nutritious than mature leaves (Feeny 1970, Coley 1983, Choong 1996, Coley and Kursar 1996) — are especially vulnerable to leaf-chewing insect herbivores, especially Lepidoptera, many of which are presumably specialized to survive consumption of defensive secondary compounds (Ehrlich and Raven 1964, Coley and Barone 1996, Kursar and Coley 2003, Coley et al. 2006, Kursar et al. 2006, Novotny et al. 2006, Bluthgen and Metzner 2007, Dyer et al. 2007, Richards and Coley 2007, Kursar et al. 2009, Novotny et al. 2010).

## 2. *STENISCADIA POLIOPHAEA*: A NOCTUIDAE SPECIALIST HERBIVORE

In this broader context of tree species coexistence, one recently studied moth-plant interaction of ecological significance is found in tropical lowland Amazonian forest, between the microlepidopteran *Steniscadia poliophaea* (Noctuidae: Sarrorthripinae) and its only known host plant *Swietenia macrophylla* (Meliaceae). The host is better known as big-leaf mahogany, a canopy emergent tree long renowned for its prized timber (Lamb 1966) and currently threatened throughout its natural range (Snook 1996, Kometter et al. 2004, Grogan et al. 2010). Hence our investigation of the moth was admittedly pursued from the viewpoint of its host: we were interested in the patterns of attack and impacts of this moth's larval instars on mahogany populations from both basic ecological and forest management perspectives. What follows is a synthesis of field research pursued to date, mainly in two forests c. 200 km apart in the southeast corner of the state of Pará, Brazil, one unlogged and one logged.

While our scientific understanding of this specific moth-plant interaction is relatively new, *S. poliophaea* was first identified in the early 20<sup>th</sup> century by Sir George F. Hampson (Hampson 1912, V. Becker *pers. comm.*). Nursery managers in this region became aware of the moth's predations as soon as plantation efforts, requiring large numbers of nursery-grown mahogany seedlings, began in the late 1980s. However, so far as we are aware there has been no further mention of *S. poliophaea* in the scientific literature until recently.

Like all Lepidoptera, the life cycle of *S. poliophaea* has four distinct life stages: (1) egg, (2) larva, (3) pupa, and (4) adult (Scoble 1992). These life stages are intimately linked to mahogany's size, phenology, local abundance and distribution, and capacity for vigorous growth.

*S. poliophaea* adult females are active at night, laying eggs on young expanding mahogany leaves. These can be either the first new simple leaves of germinating seedlings at ground level (Figure 2.H), or flushing leaves — simple or compound — of established seedlings and saplings shorter than c. 5 m tall (Figure 2.B). Though *S. poliophaea* females may accidentally oviposit on other plant species' leaves, as noted in other Lepidoptera (Thompson and Pellmyr 1991), this herbivore appears to be truly monophagous at the genus (*Swietenia*) level. Feeding trials and *in situ* transferal of early instars to young leaves of neighboring plants in the unlogged forest, called Pinkaití, resulted in no signs of herbivory and the

caterpillars' rapid disappearance. In this respect, targeted oviposition by *S. poliophaea* is truly remarkable, insofar as females must search for an ephemeral resource on host plants within a species-rich and structurally complex forest understory. *S. poliophaea* caterpillars do not leave their host mahogany plants, and thus are not 'free-moving' among individual plants as has been documented for some tropical moth species elsewhere (Janzen 2003). The latter are likely more generalist herbivores, capable of feeding on many distant genera within and/or among families. This highlights the well recognized importance of female choice in host plant oviposition for offspring success (Thompson and Pellmyr 1991, Renwick and Chew 1994, Bernays 2001).

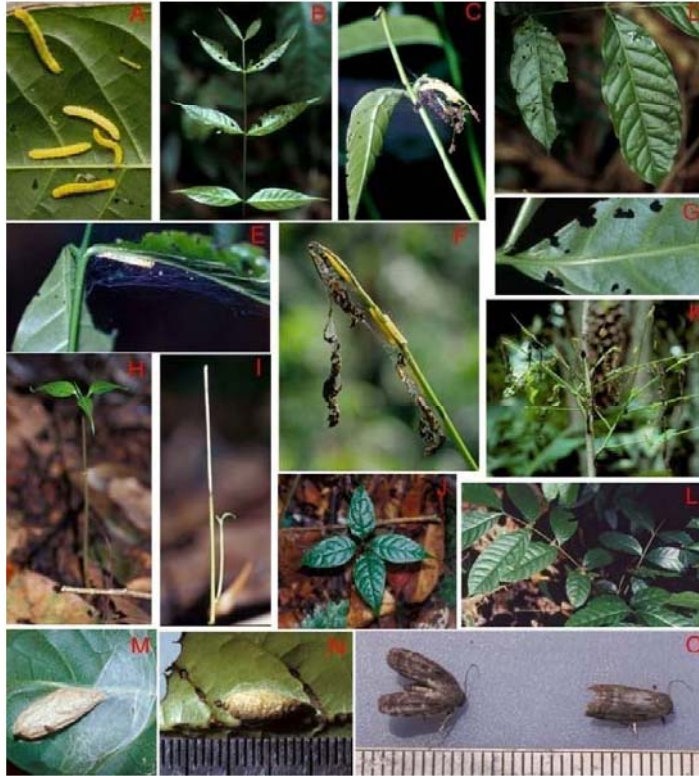


Figure 2. Photos showing the life history, feeding behavior, and impact of the small Noctuid moth *Steniscadia poliophaea* on its only known host, the neotropical forest timber tree, big-leaf mahogany (*Swietenia macrophylla*, Meliaceae). Shown in (A) the variation in caterpillar sizes associated with early, mid and late instars; (B) distinctive early feeding patterns on an expanding mahogany leaf; (C, E) late instars feeding from underside of leaves; note the collapsed leaflets from chewed midrib vein and characteristic webbing and frass; (D) an attacked mature leaf that escaped severe damage; (F, K) multiple late instars (~2 cm length) atop defoliated leaf flush of a mahogany sapling; (G) early instars trying to feed on a recently expanded leaf resulting in negligible damage; (H) first leaves of newly germinating seedling; (I) new seedling stem 100% defoliated by a caterpillar – note the new shoot at base; (J) newly established seedling that escaped timely female oviposition, resulting in negligible damage to its leaves (< 5% leaf area eaten); (L) recently expanded leaf flush and older, dark green leaves lower on the stem of a mahogany sapling; (M, N) boat-shaped cocoons of the microlepidopteran moth (~1 cm length); (O) gray-colored adults, ~1 cm length, that emerge after ~8–11 days in the pupae life-stage. Photos A, F, and K were taken at Marajoara and the rest at the Pinkaití forest reserve in the state of Pará, Brazil.



We have only observed *S. poliophaea* eggs, translucent and circular in shape, laid near the petiole on the underside of new leaves and not on their surface. The majority (73%) of microlepidopteran leaf miners in Britain laid eggs in a similar way (Reavey and Gaston 1991). The number of eggs laid on a single leaf is variable, but seems to increase with stem size of the plant and potential surface area available. Since larger leaves can sustain more caterpillars, this suggests that female moths are able to judge the potential size and food resource available to hatching instars, perhaps via a combination of leaf shape and reflectance, and/or chemical and physical sensory information further available upon plant contact (Visser 1986, Renwick and Chew 1994, Schoonhoven et al. 2005). Unfortunately we lack photos of the eggs to complete the life stages illustrated in Figure 2.

The eggs hatch quickly, in 1–3 days. The first pale green-yellow instar is barely visible to the eye (see arrow in Figure 2A). Like most moth larvae, *S. poliophaea* instars eat specific plant parts, feeding almost exclusively on newly flushing leaf tissues (Figure 2A). Tender young mahogany leaves are crucial during the early instar stages because caterpillar jaws are poorly formed. Early instars cannot chew through mature leaf tissues, though we have observed later instars occasionally 'back-feeding' onto mature leaves to complete their life cycle. Thus the timing of oviposition is crucial for larval fitness because as mahogany leaves mature, growing tougher and darker green in color, they become less palatable to *S. poliophaea* larvae.

This restricted chewing ability of *S. poliophaea* is not unlike that reported for caterpillars of the larger Sphingidae moths, whose early instars feed only on new leaves but can consume mature leaves during later, larger instar stages. These species' mandibles are adapted to eating softer 'flimsy' leaves, whereas co-occurring Saturniidae caterpillars are better at chewing through tough mature leaves high in phenolics, especially tannins (Bernays and Janzen 1988). It is notable, and we later argue perhaps no coincidence, that the Costa Rican sphingid moth species are also more specialized in their host diet breadth, being restricted to one or a few closely related species (Janzen 1984 in Bernays and Janzen 1988).

*S. poliophaea* caterpillars grow rapidly — they must in order to complete larval development before mahogany seedling and sapling leaves mature and become unpalatable. The signs of first and second instar activity are quite distinct: very small holes (< 1–2 mm diameter) appear on expanding leaf blades, accompanied by irregular nibbling along the leaf margins (Figure 2B). As the caterpillars grow larger during mid to late instar stages, and leaves approach full expansion, characteristic frass and webbing appears, and caterpillars often attempt to cut the growing leaf's midrib in one or more places (Figure 2C, E). This crippling of the leaf, which, if successful, causes the leaf to fold over, though not necessarily to fall off because of caterpillar-generated webbing, could serve two functions. First, it may prevent the host plant either from deploying more potent toxins or from transferring signals to hasten leaf maturation against feeding caterpillars. Second, cutting the midrib with subsequent collapse of the leaf onto itself may also provide temporary shelter from potential predators. This behavior has been documented in other Lepidoptera caterpillars in many systems (Dussourd 1993). As in other tree leaf Lepidoptera herbivores (Feeny 1970, Aide and Londono 1989), when *S. poliophaea* oviposition occurs later in the leaf maturation cycle, the small instars are ineffective feeders on nearly mature leaves (Figure 2G), resulting in negligible leaf damage (Figure 2D, J, L).

Unpublished field trials at Pinkaiti suggest there are 5–6 instar stages, ending with late instars that are bright yellow with a discernable halo of fine protruding hairs (Figure 2A, F).

By the time *S. poliophaea* caterpillars reach the final instar, they typically have consumed more than 50% and up to 100% of host leaves (Figure 2F, K, I). As mahogany seedlings germinate from seeds in late October and early November, hungry caterpillars may consume all leaf tissue and then move on to seedling stems, stripping them down to the 'bone', leading to certain death even if seedlings have enough reserves to resprout new leaf shoots (Figure 2I). Severe damage occurs especially in the early wet season, and, consistent with the basic premise and predictions of the Janzen-Connell hypothesis, in close proximity to mahogany adult trees or where these are aggregated (Norghauer et al. 2006a,b, 2008a, 2010).

After 10–14 days of intense feeding, final caterpillar instars, c. 1.5–2.0 cm long, spin themselves into boat-shaped cocoons, c. 1 cm long (Figure 2N), either affixed to the leaf undersurface if any leaves remain (Figure 2M) or in the leaf litter near the seedling stem. This pupae stage lasts 9–11 days after which a pale grey moth emerges. We estimate a single generation to require c. 18–22 days in total.

We know little about the population dynamics of this moth herbivore. Sources of mortality at the larval stage likely include viral or fungal pathogen infection of caterpillars, as we have noticed cases of stalled instar development (though not motion paralysis) — not for lack of tender leaf food — and disease symptoms as suggested by discoloration combined with compromised health. We have not yet witnessed parasitism of caterpillars in the field. This third trophic level, in addition to bottom-up forces in the form of leaf toxins sequestered by caterpillars as anti-predator defenses, might play an underappreciated role in the evolution of narrow host-specificity in tropical forest moths (Bernays and Graham 1988, Janzen 1988, Dyer 1995, Dicke 2000). The disappearance of one or more *S. poliophaea* caterpillars from both new mahogany seedlings and large leaf flushes may indicate predation by understory birds or other arthropods (reviewed by Heinrich 1993, Montllor and Bernays 1993), especially ants less deterred by toxic specialists (Dyer et al. 2004); or cannibalism among competing larvae for rapidly diminishing food resources — more common in Lepidoptera than other insect orders (reviewed by Richardson et al. 2010). In addition, herbivore competition for hosts may be limited by territorial behavior via 'host-marking pheromones' that deter oviposition by females arriving later (Damman 1993, Schoonhoven et al. 2005).

Because *S. poliophaea* caterpillars need young mahogany leaves for food, we anticipate that moth populations closely track mahogany phenology. Mahogany seedlings and saplings can flush new leaves 3–4 times during the course of a year in well-lit gaps, whereas in the understory leaf flushing is typically limited to once per year, in the early wet season. The onset of rains marking the transition to the wet season results in a synchronous population-wide leaf flush by host seedlings and saplings. As this first pulse of food becomes available, both in bright canopy gaps and in the shaded forest understory within seed dispersal distance of fruiting mahogany trees, moths demonstrate incredibly effective locational skill, and the caterpillar population growth rate spikes.

*S. poliophaea* population growth presumably continues with the next leaf flush during November-December, with first generation females searching for mahogany host leaf flushes on a broader spatial scale (Norghauer et al. 2008a), but then begins to decline in the latter half of the wet season (January onward). Leaf flushes increasingly occur out of synchrony as the wet season progresses, possibly because of detrimental effects on host plants caused by prior attacks.

We propose that this forces foraging of second or third generation adults on a wider spatial scale for leaf flushing, possibly by seeking out high-light patches, namely canopy gaps

formed by tree or branch-falls, where newly flushing mahogany leaves are more likely to be found (that is, where seedling and sapling growth rates are higher than in the forest understory).

At Pinkaiti, for example, mahogany seedlings planted in gaps more than 200 m away from the nearest adult stem — albeit at unnaturally high density (c. 2 m<sup>-2</sup>) — were eventually located and attacked by *S. poliophaea* in the late wet season (February–April). By the end of the wet season (May), *S. poliophaea* activity is infrequent, presumably curtailed by population reductions driven by bat predation of adults, and/or built-up parasitism or infection loads on caterpillars. With the wet season's last heavy rainfall, a final leaf flush by mahogany can occur, but few of these leaves suffer attacks (Norghauer, unpublished data).

In the dry season (June–August) caterpillars are noticeably absent in the forest. Though population-wide leaf production is diminished by water stress, limited occasionally to only well-rooted seedlings and saplings in gaps, attacks seldom occur. What happens to moth adults during the dry season? Do they die or become inactive? Or do *S. poliophaea* pupae undergo a form of obligatory diapause until the rains return? Might the adults move elsewhere to where moister conditions prevail, or possibly even seek out a second food source, possibly higher in the forest canopy?

Where do all the females come from in the early wet season to pounce, in unison, upon that first pulse of fresh mahogany leaves in the forest understory? It may be that *S. poliophaea* adults are active year-round, not unlike the highly host-specific *Eulepidotis* moth species — also in the family Noctuidae — which will attack flushing new leaves of host trees whenever available in Costa Rican dry forest in the latter half of dry season and first half of the rainy season (Janzen 1993). These are all open questions for future research.

For insect herbivores, lifetime fitness crucially depends on distinguishing among plants to find suitable hosts and evaluating their individual quality for oviposition (Visser 1986, Thompson and Pellmyr 1991, Bernays 2001, Schoonhoven et al. 2005). Clearly, *S. poliophaea* adult females are equipped with highly accurate identification capacity to be such exceptionally effective foragers for oviposition sites on mahogany seedlings and saplings. As mentioned above, attraction to unique host odors — which should increase in strength with host patch density — may be one strategy to enhance oviposition success and thus attack rates (Visser 1986, Thompson and Pellmyr 1991). While some Lepidoptera can make use of leaf optical properties (shape, color or reflectance) in choosing habitat or which plant to alight upon (Schoonhoven et al. 2005), highly specialized nocturnal foragers likely rely primarily upon strong, wind-borne chemical olfactory cues emanating from host plants to locate them across long distances (Visser 1986, Scoble 1992, Cardé and Willis 2008). These olfactory cues might even include host-specific volatile compounds associated with leaf chemical defenses against the more general herbivore community, and chemical deterrents from non-host plants (Renwick and Chew 1994, Bernays 2001).

In sum, because young leaves are a rare and ephemeral food resource, *S. poliophaea* must have a way to efficiently process sensory information. Following Bernays (2001), we expect this species to have evolved an efficient neural processing system that makes best use of high-contrast signals in the forest vegetation matrix, which further minimizes predation risk. This refined detection system may extend to adult mahogany trees too: we hypothesize that *S. poliophaea* might also use adult trees as resource markers in the forest. After all, seeds, and hence future seedlings, are concentrated near parent trees. In addition to mahogany's distinctive bark pattern, it is possible that *S. poliophaea* detects secondary compounds

specific to mahogany, of which many have been described and to which this tree's timber at least in part owes its great durability. Moreover, such towering 'odor-plumes' would steer the moths' search for host plants primarily downwind, where the wind-dispersed mahogany seeds land and are more likely to be found (Grogan and Galvão 2006, Norghauer et al. 2011a).

### 3. IMPACT ON MAHOGANY JUVENILES AND POPULATIONS IN SOUTH AMERICA

That herbivory by invertebrates can negatively impact plant fitness, including that of trees, has been generally accepted for some time (Kulman 1971, Hawkes and Sullivan 2001). However, the impacts of insect herbivores on long-lived trees in tropical forests — in contrast to plantations (Gray 1972) — remains poorly understood (Swaine 1996, Turner 2001, Marquis 2005). Two early studies in Costa Rica demonstrated that heavy defoliation of mature plants can reduce seed production in six small-statured (5–20 m tall) tropical tree species (Rockwood 1973, see also Wong et al. 1990), and both individual growth and seed set in an understory *Piper* shrub (Marquis 1984). More recently, there is evidence that higher leaf damage can occur in gaps among conspecific tree seedlings of *Shorea leprosula* (Massey et al. 2006), and that rates of damage on mature (as opposed to newly flushed) leaves are associated with higher seedling mortality risk in the following year (Eichhorn et al. 2010).

Yet little empirical study has actually examined patterns of herbivory and their impact on tree juveniles in the context of the Janzen-Connell hypothesis (Clark and Clark 1984, 1985, Barone 1996, Blundell and Peart 1998, Sullivan 2003, Massey et al. 2005, 2006). The enemy-driven mechanism underpinning the J-C hypothesis presupposes a negative impact of herbivores on individual seedlings and saplings (seeds can also be affected in terms of mortality alone; Wilson and Janzen 1972). In the context of the *Steniscadia poliophaea*–*Swietenia macrophylla* interaction, a seed addition experiment at the logged site in southeast Amazonia, called Marajoara, found significantly higher seedling survival 50 m downwind from heavily fruiting mahogany trees than at 25 m and 10 m (Grogan and Galvão 2006). A similar positive distance effect in the forest understory for seedling establishment was reported in a field experiment at the unlogged Pinkaiti forest (Norghauer et al. 2006a). In both studies, *S. poliophaea* was thought responsible for accelerated seedling mortality near mahogany adults. At Marajoara, up to 80% of new seedling regeneration was attacked by *S. poliophaea*.

In a separate seed addition experiment at Pinkaiti, we reported clear evidence linking *S. poliophaea* attacks to higher seedling death near parent trees, in support of the J-C hypothesis (Norghauer et al. 2010). Percent damage and cases of 100% defoliation were disproportionately higher near parent trees, declining with distance downwind (Figure 3a). In turn, seedling survival after 10 months was significantly higher beyond 30 m and especially beyond 50 m from adult trees (Figure 3b). Based on more than 15 years of fieldwork, we are confident that attacks by the specialist *S. poliophaea* on newly germinating seedlings are an annual source of mortality for mahogany in this region.

In the early wet season following mahogany seed dispersal, population-wide seedling emergence is largely synchronized following moisture imbibition by seeds (Morris et al. 2000). These emerging seedlings represent a large resource-pulse of food for *S. poliophaea*

which dissipates with distance from tree crowns. We suggest that adult trees are used by *S. poliophaea* as a cue for locating these new seedling cohorts. At a single heavily fruiting tree where all seeds were removed by hand except for those in three 1-m-wide downwind transects, *S. poliophaea* caterpillar defoliations peaked near the parent tree (Norghauer, unpublished data). Rarer seeds further away with fewer nearby siblings were in a better position to escape severe attack.

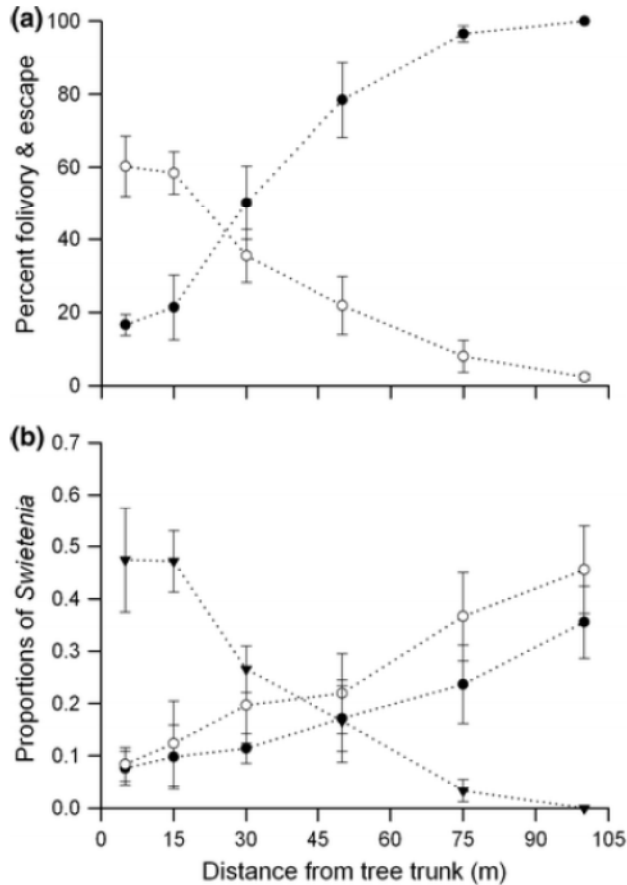


Figure 3. Impact of *Steniscadia poliophaea* caterpillars on new big-leaf mahogany seedlings at Pinkaiti. Shown in (a) are percentages of leaf area damaged by the specialist (open circles) and new seedlings escaping attacks altogether (closed circles); in (b) proportions of 100% defoliation (triangles) and seedlings surviving 8 months after rainy season onset (closed circles = of germinating seedlings, open circles = all sown seeds). The experiment was conducted at seven reproductive trees in 2003 with a total sample size of 42 quadrats, each sown with 20 seeds. All symbols are means ( $\pm$  SE) and all linear regressions were highly significant ( $P < 0.0001$ ). Reproduced with permission from Norghauer et al. 2010 in the journal *Oecologia* published by Springer-Verlag.

Newly germinating seedlings in higher light conditions of canopy gaps may not be as susceptible to *S. poliophaea* regardless of distance to the parent tree, possibly because of delayed germination and rodents that predate more seeds in gaps than in the forest understory, reducing seedling density (Grogan and Galvão 2006, Norghauer et al. 2006a), and/or because

more dense vegetation or natural enemies present in gaps interferes with host location (Brokaw 1985, Denslow 1987, Uhl et al. 1988, Grogan et al. 2005, Schoonhoven et al. 2005).

Canopy gaps merit special attention because mahogany is a ‘non-pioneer light-demanding’ tree. Like many plant species it germinates well in shaded conditions, but early in its development mahogany needs above-average light levels found in or near gaps for vigorous growth, otherwise most seedlings will die within a few years (Lamb 1966). At Marajoara, a long-term experiment (80 months) found that *S. poliophaea* — along with other mortality factors, namely pathogens and drought stress — reduced overall seedling survivorship in the understory around 8 adult trees to just 1–2% (Grogan et al. 2005). Here mahogany seedlings lack the energy needed for leaf production. By contrast, canopy gaps can promote vigorous plant growth in terms of height and leaf production (Augsburger 1984b, Brokaw 1985, Uhl et al. 1988, Blundell and Peart 2001). For this reason, many tropical forest tree species are thought to require repeated local disturbances to reach the canopy and attain maturity (Hartshorn 1978, Denslow 1987, Richards 1996, Turner 2001) — probably in pulses, separated by years of suppression under low light following gap closure (Baker and Bunyavejchewin 2006). In contrast to the more shaded forest matrix, which, per unit area, is more food-limited in terms of leaf production (Richards and Coley 2007, 2008), it follows that herbivory of new plant material should be greater in gap microhabitats (Harrison 1987, Price 1991, Richards and Coley 2007, 2008).

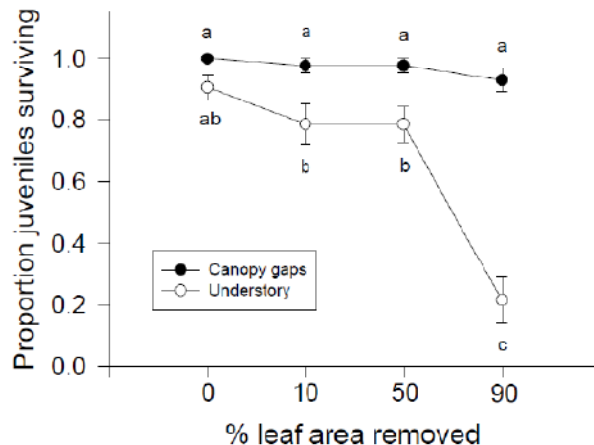


Figure 4. Survival over an 8-month period (April–December 2003) of big-leaf mahogany seedlings transplanted into canopy gaps and paired understory locations at Pinkaiti under different levels of simulated herbivory. Nursery-grown seedlings had their leaves artificially clipped to simulate early specialist leaf damage to new germinants, but were left exposed to *Steniscadia poliophaea* herbivory during the experiment. Lower-case letters indicate significantly different means ( $\pm$  SE) from nested ANOVAs. Reproduced with permission from Norghauer et al. 2008a in the *Journal of Ecology*, published by Wiley-Blackwell on behalf of the British Ecological Society.

The impact of *S. poliophaea* on mahogany fitness in gaps is, we believe, primarily one of suppression, not outright death, weakening seedling competitive ability for diminishing light with heterospecific neighbors. At Pinkaiti, nursery-grown mahogany seedlings were planted into 14 naturally formed canopy gaps paired with shaded sites in the forest understory, and their response to artificial defoliation and caterpillar damage to new leaves monitored. We

found that light-rich gaps promoted both mahogany growth and tolerance to defoliation. Remarkably few individuals died in gaps despite removal of almost all leaf area, whereas mortality was significantly higher in the forest understory (Figure 4). On average, 50% or more leaf removal in gaps was required before seedlings exhibited significantly lowered height and basal stem growth rates (Figure 5a,c), similar to findings by Gerhardt (1998) for mahogany, and those reported by Blundell and Peart (2001) for another tropical tree species. In the forest understory seedling growth was negligible (Figure 5), but in gaps, although leaf production was not impaired during the 8-month study period (Figure 5b), the potential size of new leaves produced was reduced by heavy prior damage (Figure 5d). Sub-optimal growth will leave a mahogany seedling smaller and at greater risk for mortality following gap closure, requiring more gap events and thus longer time to reach maturity.

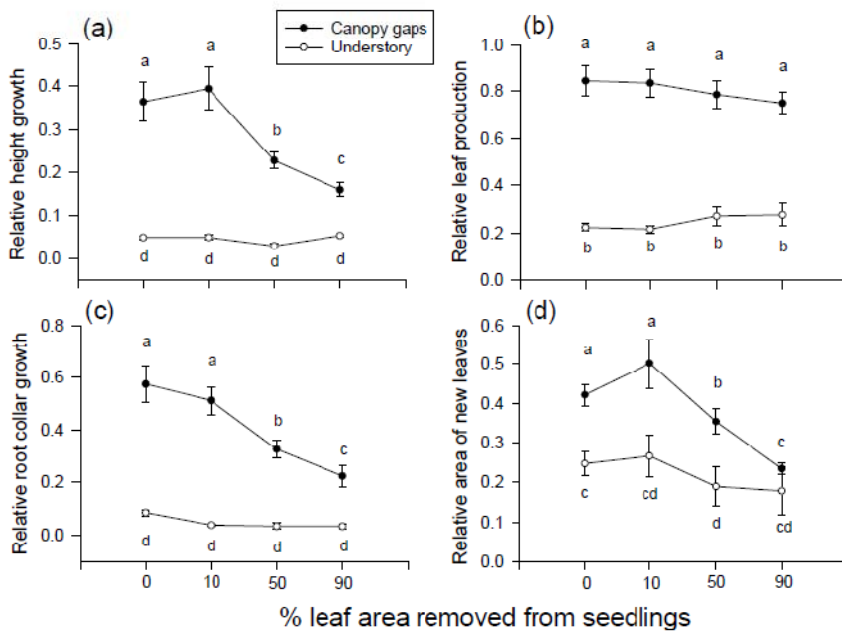


Figure 5. Proportional growth of big-leaf mahogany seedlings transplanted into canopy gaps and understory locations across different levels of simulated herbivory at Pinkaiti. Lower-case letters indicate different means ( $\pm$  SE) from four separate nested ANOVAs that were all highly significant for the clipping treatment except for leaf production. Reproduced with permission from Norghauer et al. 2008a in the *Journal of Ecology*, published by Wiley-Blackwell on behalf of the British Ecological Society.

The impact of a specialist herbivore able to circumvent the constitutive defenses of its main host plant should further depend on the proximity to conspecific parent trees and local abundance of adults (or conspecific hosts) at larger spatial scales (Janzen 1970, Blundell and Peart 2004). At Pinkaiti, first attacks in the shaded understory on seedlings established during the previous year occurred only very near adult mahogany trees (typically within 20–30 m), but the benefit of escape during synchronous germination and leaf flushing by emerging and established mahogany seedlings diminished where adults were aggregated (Norghauer, *unpublished manuscript*, Norghauer 2006b). At Pinkaiti for example, specialist attack and damage on mahogany seedlings already established in the forest understory increased with

local adult basal area, suggestion no satiation at the population level (Figure 6). By contrast, seedlings in gaps are easily discovered by *S. poliophaea*, consistent with the Plant Vigor Hypothesis (*sensu* Price 1991) and earlier studies. For example, Williams (1983) found that *Euphydras chalcedona*, a nearctic butterfly, also sought out sunlit habitats for oviposition on two preferred host plants. Likewise, in a Panamanian forest, the better quality of foliage in gaps vs. forest understory explained the higher levels of herbivory in the former by a specialist moth caterpillar, *Zunacetha annulata*, on its host shrub *Hybanthus prunifolius* (Harrison 1987).

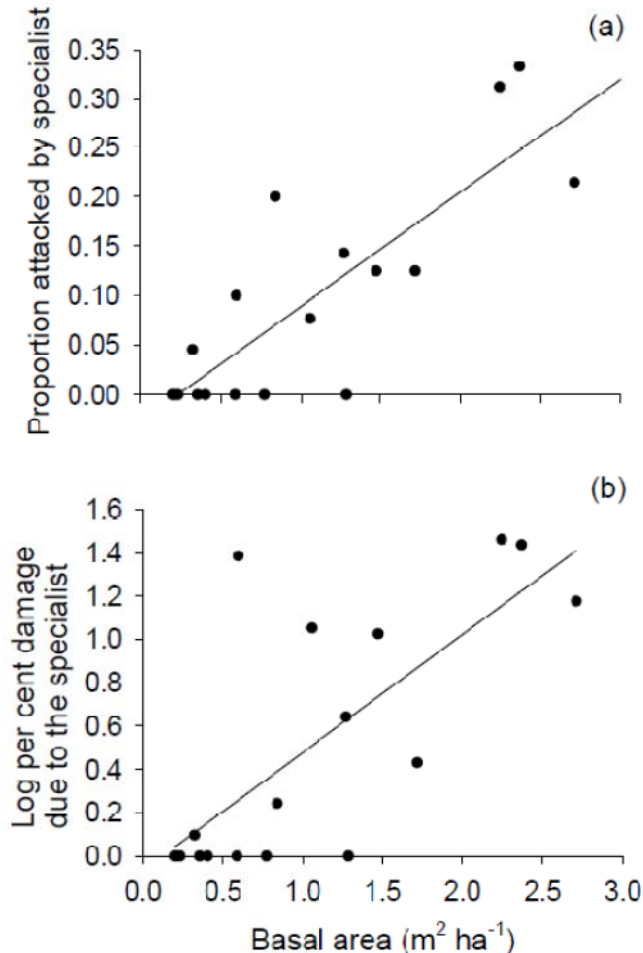


Figure 6. Incidence of attack by *Steniscadia poliophaea* caterpillars (a) and their associated leaf damage on naturally established big-leaf mahogany seedlings (b) within a 56.5-m radius of 18 adult mahogany trees at Pinkaiti. The increases in specialist activity with increased adult tree basal area were significant in both regressions ( $P < 0.0001$ ,  $r^2 = 0.75$  and  $0.68$ , respectively). Symbols are means of the averaged leaf damage for individual seedlings at each parent tree. Reproduced with permission from Norghauer et al. 2006a in the *Journal of Tropical Ecology* published by Cambridge University Press.



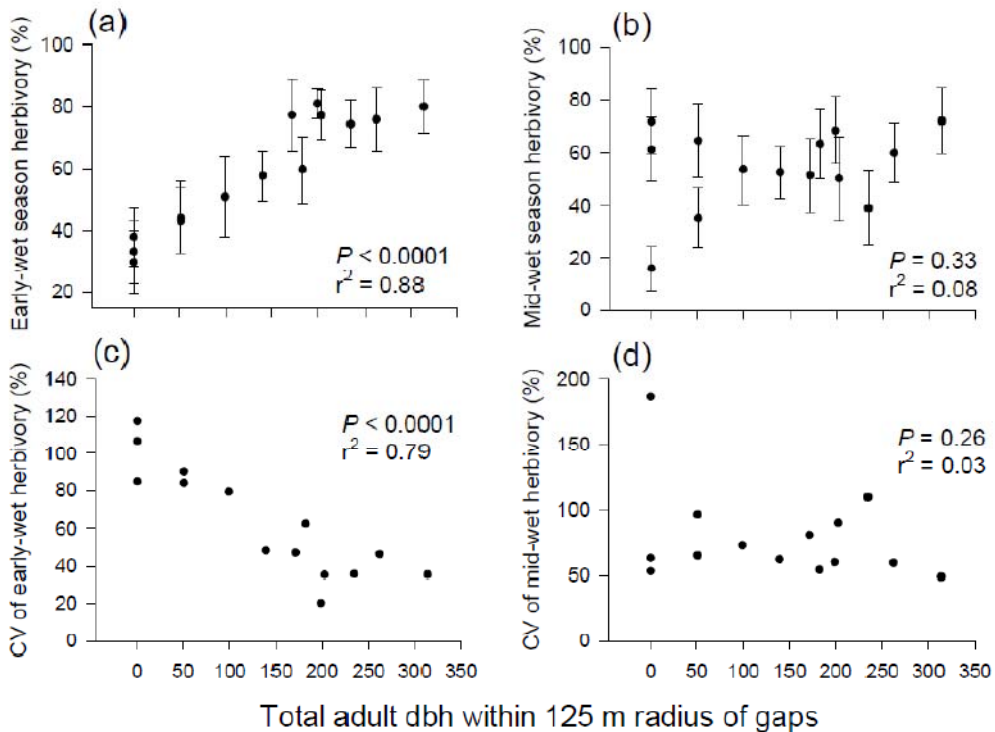


Figure 7. *Steniscadia poliophaea* damage to young leaves of mahogany seedlings in the early wet season (September–October) and mid wet season (November–December) in canopy gaps at Pinkaiti in 2003. Damage is expressed as the mean ( $\pm$  SE) of 12 seedlings per gap, and as a function of mahogany adult tree size and density (i.e., total summed diameters) surrounding each canopy gap location. In generating these means, all new leaves were measured to the nearest  $0.01 \text{ cm}^2$  and  $0.25 \text{ cm}^2$  for damage and potential leaf area respectively, then averaged first at the individual seedling unit. The two lower panels show changes across these gaps in the coefficient of variation (CV) in specialist herbivory. The  $r^2$  values for the linear regressions have been adjusted for the low sample size ( $n = 14$  gaps). Reproduced with permission from Norghauer et al. 2008a in the *Journal of Ecology*, published by Wiley-Blackwell on behalf of the British Ecological Society.

In the early wet season (September–October) at our field sites, prior to germination, *S. poliophaea* caterpillar damage was also density-dependent on a larger spatial scale, that is, at the population level of mahogany: gaps with flushing mahogany seedlings that were further from one or more adult trees had the best chance to escape attacks at this time (Figure 7a; Norghauer et al. 2008a). During the next major leaf flush in November–December, the density-dependent pattern of attack was dampened as moths found these more remote seedlings in gaps (Figure 7b). The female moth, being active only at night, may be highly sensitive to specific odors emitted by mahogany seedlings flushing new leaves in gaps. In short, the moth engages in non-random host searches, orienting itself to odor plumes, as would be expected in more specialized insect herbivores (Visser 1986, Scoble 1992, Cardé and Willis 2008), and probably within a given ‘discovered’ gap it then searches specifically for mahogany hosts and compares their quality for oviposition via contact evaluation (Figure 7c; Renwick and Chew 1994, Bernays 2001, Schoonhoven et al. 2005). This ability to locate

mahogany individuals in gaps moving downwind from parent trees should diminish as the density of host seedlings falls with distance.

Further evidence for a negative impact of *S. poliophaea* at the population level comes from a recent study of big-leaf mahogany introduced to the island of Dominica, in the Lesser Antilles, where the moth is absent. Here, first and second generation saplings and pole-sized trees are growing at high density beneath conspecific crowns — something never observed in forests within mahogany's natural range — and have little to no leaf area damaged (Norghauer et al. 2011b). Apart from expected self-thinning through larger size classes, the only limitation to growth and abundance of mahogany at this site seems to be light required by new seedlings. The 'Enemy-Release Hypothesis' (reviewed by Keane and Crawley 2002) — that plant species introduced to habitats outside their natural range are freed from top-down regulation, and thereby gain a competitive advantage versus native flora in the new community — can be seen as a biogeographical extension of Janzen-Connell 'escape' from native enemies via anthropogenic dispersal at an extreme spatial scale (DeWalt et al. 2004).

While herbivory may have consequences for host individuals, it does not necessarily follow that host plant populations must also be affected (Harper 1977, Crawley 1989). In other words, the population dynamics of mahogany could be unaffected if *S. poliophaea* were somehow magically excluded from local communities. But the J-C hypothesis suggests that insect herbivores can regulate population dynamics by slowing and spacing adult trees to some minimal distance within a community (Clark and Clark 1984, Schupp 1992). Our observations, like those of many other mahogany field researchers, indicate that saplings rarely occur beneath or near parent trees. This outcome cannot be solely the product of fewer gap formations per year near parent trees than further away on a per unit area basis (Augspurger 1983, Becker et al. 1985, Norghauer et al. 2011b). Instead, this suggests an herbivore-driven decoupling of the seed shadow from the larger juvenile shadow for a given tree species cohort through time (Augspurger 1983, Clark and Clark 1984), and runs counter to the expected null scenario of dispersal limitation (Makana and Thomas 2004): that is, near fruiting adult trees, more seeds should yield more recruits.

Nevertheless, the occurrence of mahogany adult trees in local aggregations is common in South American forests. Some researchers mistakenly cite clumping of adult trees as evidence against the J-C hypothesis. But local-scale aggregations may still arise via the J-C mechanism (Clark and Clark 1984, Becker et al. 1985): over many years of dispersal it is plausible that patches of mahogany juveniles could accumulate downwind through one or more gap events. In this way, patches of adult trees should cycle in space to create a moving mosaic over successive generations. This could occur as well in other tree species whose seed propagules are dispersed over long distances, often in clusters, by birds or mammals (Howe and Westley 1988, Wenny 2000, Fragoso et al. 2003, Russo and Augspurger 2004). Another interesting possibility not yet explored is that this density-dependent decoupling between key early stages in tree development fails to work soon after reproductive onset in mahogany trees (20-30 cm stem dbh). This is because the moth has not yet learned of that adult's presence, thus missing the first few years of seedling cohorts, especially if seed production rates are low, as expected from small-statured reproductive trees (Snook et al. 2005, Grogan and Galvão 2006, Norghauer et al. 2011a).

Taken together, the evidence presented here points to a strong Janzen-Connell effect in the Brazilian Amazonian forests of southeast Pará, driven by the Noctuid moth *S. poliophaea*, limiting recruitment of a fast-growing, potentially dominant tree species, big-leaf mahogany.

Herbivores have been increasingly shown to stabilize population dynamics of short-lived herbs and shrubs from temperate zones (Maron and Crone 2006). But to conclusively show that *S. poliophaea* is limiting the local abundance of mahogany adults would require long-term monitoring of very many individual juveniles. The long lifespan of the mahogany host species — and trees in general — makes this a daunting task. Other approaches are possible however. These include building population matrix projection and/or spatially explicit neighborhood models (Halpern and Underwood 2006) based on experimental field data from both Pinkaiti and Marajoara, and observational data on gap disturbance regimes at these sites.

#### 4. ECOLOGICAL SIGNIFICANCE OF *STENISCADIA POLIOPHAEA* VS. *HYPSIPYLA GRANDELLA*

If big-leaf mahogany is indeed the only, or rather the locally most preferred, host plant of *S. poliophaea*, then the distance- and density-dependent impacts described above might be expected to extend throughout the host plant's range. Mahogany's natural range coincides with seasonally dry semi-evergreen forests from Mexico through Central America and into South America's Amazon Basin as far south as Bolivia (Figure 8; Lamb 1966, Grogan et al. 2002, 2010).

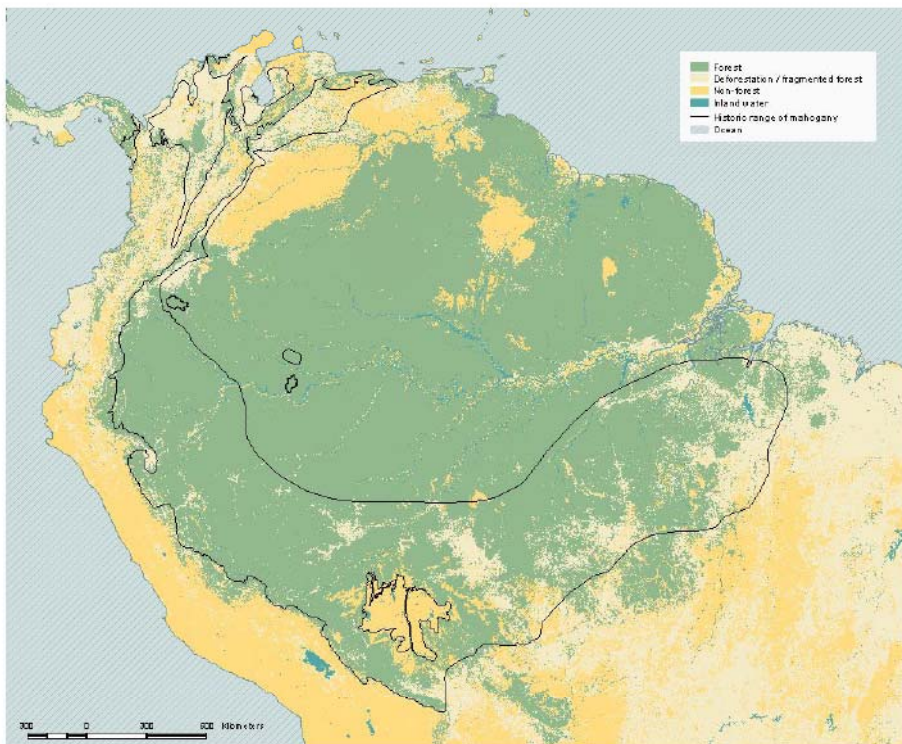


Figure 8. Historic range of big-leaf mahogany (*Swietenia macrophylla*) in South America overlaid on forest cover based on 2001 satellite data. Reproduced with permission from Grogan et al. 2010 in the journal *Conservation Letters* published by Wiley-Blackwell.

However, as far as we currently know, *S. poliophaea* is restricted to southern Amazonia, with confirmed sitings from our study region in southeast Pará to Acre in Brazil's far west. Outside Brazil, researchers in southeast Peru have documented caterpillar infestations on new mahogany seedlings in November in an area of undisturbed forest (G. Barrios, *pers. comm.*). For this reason, we suspect that *S. poliophaea*'s range extends to the forests of Peru and Bolivia, and possibly Ecuador. No sitings have been confirmed from Central America or Mexico.

A second and far more widely distributed mahogany 'pest' is the shoot-borer *Hypsipyla grandella* Zeller (Pyralidae), which occurs throughout big-leaf mahogany's neotropical range. *Hypsipyla grandella* is a nocturnal moth whose larval caterpillars bore into and consume expanding apical meristems on vigorously growing mahogany saplings (Lamb 1966). The flushing leader is hollowed out and frequently collapses, slowing vertical growth; many lateral shoots typically form from the damaged top, ruining stem form (Newton et al. 1993). In order for larval caterpillars to find sufficient food resources to mature through 5 to 6 instars, mahogany saplings generally must be at least 1 m tall and growing vigorously to serve as host plants. *H. grandella* attacks saplings and larger juveniles up to pole size and can also infest adult trees, especially injured or otherwise weakened individuals (Grogan 2001). They commonly infest woody fruit capsules in adult mahogany crowns (*S. poliophaea* has not been seen in adult mahogany crowns). A great deal of research has been conducted on the shoot-borer's biology and control due to its economic impact in plantations. Like *S. poliophaea*, *H. grandella* is most active when potential hosts are flushing new leaves, mainly in the wet season (Yamazaki et al. 1992, Newton et al. 1998, Taveras et al. 2004); females are attracted to flushing meristematic tissues via chemoreception, likely of essential oils (Soares et al. 2003); and they target vigorously growing juveniles, with the number of larvae increasing with shoot size. Might the shoot-borer, like *S. poliophaea*, generate a Janzen-Connell effect in natural and secondary forests? And if so, what interaction between these two insect herbivores might we expect where their natural ranges overlap?

Surprisingly, the ecological significance of *H. grandella* in the context of the J-C hypothesis is relatively unknown. No published study explicitly tests distance- or density-dependent shoot-borer attack on mahogany in natural forests (but see Yamazaki et al. 1992 for line plantings in Peruvian Amazon forest). At the unlogged Pinkaití forest, the shoot-borer's effects on mahogany saplings were not observed in naturally formed canopy gaps where nursery-grown seedlings were outplanted. But we did see signs of the shoot-borer in saplings > 2 m tall growing in very open conditions at the Pinkaití campsite. In thinned forest stands in Costa Rica, < 1% of 3-yr-old mahogany seedlings were attacked by *H. grandella*, and none in plantings made in natural forest in Peru (Yamazaki et al. 1990). At the selectively logged Marajoara forest, signs of the shoot-borer were more common, and incidence increased with canopy opening, host density and exposure of juvenile crowns (Grogan 2001 Appendix B.2, Grogan et al. 2005). In one outplanting experiment, the shoot-borer was not associated with any mahogany seedling deaths in 16 artificial gaps 200–400 m<sup>2</sup> in size (Grogan et al. 2003a Table 3). Because the minimum host size is larger than required for *S. poliophaea*, *H. grandella* will rarely kill mahogany saplings directly in well-lit conditions (Lamb 1966, Grogan et al. 2003a), since sufficient light allows saplings to continue growth after resprouting (i.e., tolerate attacks). Only repeated severe attacks over several years can cause juvenile mortality, all else being equal (Newton et al. 1993, Mayhew and Newton 1998, Nair 2007).

The ecological significance of *S. poliophaea* herbivory may extend to interactions with *H. grandella*, and possibly other insect herbivores as well. In one sense both predators are competing for the same host, but interspecific competition between the moths would best be described as asymmetric. Indeed, competition among multiple phytophagous insects sharing a host species is usually asymmetric, rarely satisfying the critical assumption of symmetry which can lead to competitive exclusion (Denno 1995, Kaplan and Denno 2007). Instead, herbivores might partition resources in time and space, so that specialized feeding on different plant parts can promote co-existence on the same host. In the present case there is partial temporal segregation in host use driven by plant ontogeny. Seedlings smaller than ~1 m height are only prone to attacks by *S. poliophaea*. But once they exceed this minimum size threshold and occur in gaps large enough to sustain vigorous shoot growth, *H. grandella* and *S. poliophaea* may overlap in host use, which may lead to direct interactions between them in the form of exploitative competition (Damman 1993). At Marajoara, attacks from both enemies have been observed on the same sapling(s), though whether this occurs on the same flushing event has not been confirmed. This seems unlikely, because *H. grandella*'s impact on the flushing apical leader is generally such that new leaves cannot survive long enough for *S. poliophaea* to grow to final instar size.

We propose that, by thinning and slowing growth of mahogany at early seedling and sapling stages, *S. poliophaea* functions in the herbivore community as a limiting factor on host numbers available later for the shoot-borer. This physically mediated resource limitation apparently imposed by *S. poliophaea* on *H. grandella* — coupled to very low density of individuals growing far downwind under natural dispersal — may in part explain the latter's near absence at Pinkaiti. And because *S. poliophaea* is a highly effective distance- and density-dependent herbivore, we might expect a negative association between the two herbivores in their activity: *S. poliophaea*-attacked seedlings and saplings should appear less suitable to foraging *H. grandella* for being smaller and less vigorous than seedlings and saplings that escaped *S. poliophaea* attacks. We do not know, however, if *S. poliophaea* further negatively affects mahogany host availability and quality for foraging adult *H. grandella* via damage-induced chemical responses in attacked saplings, which might lead to complex resource-mediated interactions between these two Lepidoptera specialist herbivores (Damman 1993). These preliminary insights suggest that one potent specialized J-C enemy (*S. poliophaea*) might be able to disrupt the predicted J-C pattern (increased herbivory of hosts closer to parent trees) expected from another enemy (*H. grandella*) that also feeds on new mahogany plant tissue. We might also expect that in mahogany's northern range where *S. poliophaea* has not been reported, enemy compensation may occur such that *H. grandella* attacks in gaps are negatively correlated with proximity to adult mahogany trees, as predicted by the J-C hypothesis.

Resource limitation imposed by *S. poliophaea* does not necessarily translate into limited *H. grandella* abundance or densities because, unlike *S. poliophaea*, the shoot-borer can shift hosts to other Meliaceae genera such as *Carapa*, *Cedrela*, and *Guarea*. If among the three *Swietenia* species, which closely resemble *Khaya* spp. in Central Africa, *S. macrophylla* in South America is the oldest (i.e., evolved first) and spread north into Central America (Lamb 1966 p. 130), it is plausible that *S. poliophaea* herbivory may have exerted selection pressure on *H. grandella* leading to the latter's broader diet.

## 5. FOREST MANAGEMENT IMPLICATIONS OF *STENISCADIA POLIOPHAEA*

*Steniscadia poliophaea*'s apparent obligate enemy relationship to *Swietenia macrophylla* is important for reasons extending beyond theoretical considerations of the Janzen-Connell hypothesis. Big-leaf mahogany is the world's most valuable widely traded tropical timber species, with a cubic meter of sawn timber fetching upwards of US\$ 1700 (ITTO 2011). After centuries of overexploitation in neotropical forests, mahogany's conservation status had deteriorated by the late 1990s to the point where it was listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in late 2002. The CITES Appendix II listing requires cooperation between producer and consumer nations to verify that internationally traded volumes of sawn timber are harvested legally, and that harvests are non-detrimental to mahogany's role in ecosystems where it naturally occurs (Grogan and Barreto 2005). Mahogany's Appendix II listing has slowed the rate of predatory logging since 2003, especially in the three principal South American range nations of Brazil, Bolivia, and Peru, and contributed to improved forest management regulatory frameworks and practices (Mejía et al. 2008).

However, sustained yield management of mahogany from natural forests remains an elusive and unachieved goal for several reasons. Legal logging intensities remain too high, and minimum diameter cutting limits too low, for adequate population recovery between harvests on 25–30 year cutting cycles. Pre-logging densities of advance seedling regeneration and juvenile stems are typically too low for eventual replacement of logged trees. Growth rates by pole-sized and sub-adult trees, while relatively high for tropical forest species, are generally too low for production purposes on fixed-length cutting cycles. Silvicultural treatments reducing mortality and accelerating growth rates by individual trees are rarely implemented at industrial scales. And the mahogany shoot-borer, *Hypsipyla grandella*, plagues vigorously growing saplings and poles in logging gaps and plantations, slowing vertical growth rates and ruining bole form (Grogan et al. 2011). Now add *S. poliophaea* to these obstacles to sustainable management in South America: a specialist herbivore that targets seedlings and saplings, the most vulnerable phases of mahogany's life cycle.

Sustained yield management of mahogany requires balancing timber production — the extraction of commercial-sized adult mahogany trees — with reproduction, regeneration, recruitment and eventual replacement of logged stems with new adult trees. Management responses to *S. poliophaea* must therefore mitigate the moth's impacts on critical early life phases to reduce seedling mortality rates and accelerate growth. These efforts will be most successful if management practices are designed to coincide — or not — with *S. poliophaea*'s spatial and temporal appearance within the forest matrix.

The moth's distant- and density-dependent relationship with fruiting mahogany trees means that, all things being equal, seedlings experience declining early mortality rates moving away from parent trees. Though we have found that *S. poliophaea* is capable of locating flushing seedlings beyond the immediate perimeter of parent tree crowns, this ability necessarily declines with distance. Forest managers attempting to 'release' advance regeneration through targeted overhead canopy openings (Grogan et al. 2005) should therefore focus their efforts on seedlings or seedling patches occurring far (> 40–50 m) from rather than near retained seed trees or logged stems. However, as common-sensical as this

recommendation may be, the fact remains that dispersal limitation of mahogany's wind-borne seeds means that few natural seedling clusters will be found in natural forests beyond 100 m of fruiting adults (Grogan and Galvão 2006, Norghauer et al. 2011a).

For seedlings and saplings growing in canopy gaps, the best defense against *S. poliophaea* will be excellent offense, that is, vigorous height growth so that juvenile crowns rapidly attain and exceed 5 m. For unknown reasons, the moth does not target mahogany saplings taller than this height. Robust mahogany seedlings are capable of growing up to 3 m height per year, though 1–1.5 m is more typical under optimal growing conditions (full sun exposure, in nutrient-rich and well-drained soil; Lopes et al. 2008). For forest managers, tending operations at the seedling and sapling stages must focus on encouraging height growth through removal of vines and directly overtopping competing vegetation (Snook and Negreros-Castillo 2004). Dense surrounding secondary vegetation probably shields seedlings and saplings from *S. poliophaea* attack to some degree, similar to the mahogany shoot-borer (Newton et al. 1993, Mayhew and Newton 1998), so surrounding vegetation should be retained for protection and 'training' vertical seedling growth.

Widely reported mahogany regeneration failure after logging combined with low background levels of advance regeneration mean that enrichment planting of nursery-grown seedlings into treefall gaps will be necessary for sustained yield production (Snook 1996; Gullison et al. 1996; Grogan et al. 2003b, 2005, 2008). *S. poliophaea* has proven a scourge in nurseries supplying mahogany seedlings for plantations in southeast Pará and Acre in western Brazil, especially where nurseries are located inside managed forests. Protection against *S. poliophaea* must be provided in these settings, either by mesh enclosure to prevent access to flushing seedlings by female moths or through periodic application of insecticides targeting larval instars.

*S. poliophaea*'s density-dependent behavior indicates that mahogany seedlings should be outplanted into logging gaps at low densities, spaced 5 or more meters apart. Similar to released natural regeneration discussed above, tending operations should be restricted to vines and directly competing vegetation (overhead shading), leaving seedlings to grow in a dense matrix of secondary vegetation. As in nursery settings, periodic insecticide application may be warranted, but our experience has been that wet season rains may shorten the effective treatment period to a matter of days, requiring repeated application. As well, as seedlings gain height, insecticide application may become hazardous to management crews. The various costs of such treatment must be weighed against potential benefits.

Selection of enrichment planting gaps should consider the locations of both logged and retained mahogany seed trees as well as sub-commercial stems. All things being equal, *S. poliophaea*'s impacts are likely to be mitigated by selecting enrichment sites up- rather than downwind of adult trees, and far rather than close. However, locating enrichment gaps on portions of the landscape where adult mahoganies do not naturally occur, or where it occurs at extremely low densities, is unlikely to yield optimal seedling growth rates due to soil nutrient deficiencies or poor drainage (Grogan et al. 2003a, Norghauer et al. 2008b).

From a biodiversity monitoring and conservation perspective, the impacts on *S. poliophaea* and other insects of selective logging and forest management must also be considered. If *S. poliophaea* is truly monophagous, then local mahogany extirpations will mean the same for its specialized herbivore. However, short of forest conversion to other land uses such as pasture or agriculture, complete elimination of mahogany from forests once containing it will be a rare occurrence due to persistence of unlogged juveniles and natural

regeneration. We have seen no evidence that extremely low density of mahogany at landscape scales reduces *S. poliophaea* occurrence correspondingly. For example, attack rates on seedlings in Acre, where 12 mahogany trees > 20 cm diameter occur per 100 ha, appear equivalent to attack rates on seedlings at Marajoara in southeast Pará, where 65 trees > 20 cm diameter occur per 100 ha (Grogan et al. 2008). For this reason we expect that *S. poliophaea* populations will adjust their size to match new post-logging mahogany population densities (as expected for a resource-limited insect herbivore, Dempster and Pollard 1981).

However, other aspects of logged environments could have unforeseen consequences for *S. poliophaea*. For example, the drier, more open environment that characterizes selectively logged forests may influence the moth's population dynamics by increasing food availability (Basset et al. 2001) and female moth detection of mahogany host plant odors against the contrasting backdrop of non-host odors, though this might be offset by greater interference from vegetation re-growth of early-successional species. By contrast, drier forest conditions could also lead to reduced larval feeding rates and faster maturation rates by mahogany leaves, and to higher risks of larval desiccation. As well, changes in forest structure could lead to changes in natural enemy pressure on *S. poliophaea* larvae and adults. The possibility also exists that changes in microclimate associated with logging may exacerbate asynchrony in mahogany leaf phenology and/or reduce host plant quality, either of which might impact *S. poliophaea* population dynamics because of its restricted diet and limited larval mobility. Skid trails may create directional 'highways' allowing *S. poliophaea* to more easily find hosts, not unlike that suggested to have resulted from line plantings in Peruvian forests (Ikeda et al. cited in Mayhew and Newton 1998).

For these many reasons, research into the moth's seasonal dynamics and spatial patterns of herbivory in both logged and unlogged forests across years is vital. Depending on what this research reveals, the close association between *S. poliophaea* and mahogany invites the interesting possibility of using the former as a barometer of forest change and recovery after logging in Amazonia landscapes.

## 6. ARE ALL HERBIVORES EQUAL?

### MOTH HERBIVORES AND THE JANZEN-CONNELL HYPOTHESIS

At the heart of the J-C hypothesis are host plant–natural enemy interactions. In this context, these interactions are presumably widespread and involve co-evolution because of the negative impact on host fitness by herbivores (Ehrlich and Raven 1964, Howe and Westley 1988, Thompson 1999, Weiblen et al. 2006, Futuyma and Agrawal 2009). In this chapter we have reviewed and synthesized compelling evidence for one example of this antagonistic interaction, that between a Noctuid moth caterpillar and an emergent canopy tree, which generates a powerful J-C effect limiting the potential dominance of a widely distributed tree species in Amazonian lowland tropical forest. Top-down regulation is not a new idea in ecology, but it is necessarily spatially explicit for plants because of their mostly sessile life habit (Harper 1977). The J-C hypothesis proposes that the negative effect of parent trees on the probability of a given seed–seedling becoming a sapling, and later potentially an adult, decreases with dispersal distance (Figure 1) — as offspring escape high densities of conspecific siblings and predator attacks — and is species-specific. While distance from close



relatives clearly matters (Howe and Smallwood 1982, Clark and Clark 1984, Swamy et al. 2011), the latter consideration is also crucial because it enhances intraspecific effects relative to interspecific effects of tree species, thereby promoting diversity by stabilizing species' populations (Chesson 2000).

The simplest explanation for strong species-specific J-C effects on tree seedling and sapling mortality and recruitment processes is not intraspecific competition for scarce nutrients (Wright 2002, Paine et al. 2008, Svenning et al. 2008), but rather insects and pathogens specialized to one or a few closely related host plants, particularly at the genus level (Novotny et al. 2002a, Leigh 2004, Kricher 2010, Swamy and Terborgh 2010). Whether insect herbivores can attack or nibble on leaves of other plants in laboratory choice tests is largely irrelevant; rather, it is their preference for and/or restricted diet in terms of what is locally available that matters in the J-C context. For example, many genus-specialized insect herbivores might effectively (*de facto*) be monophagous in part because of the lack of congener hosts in the local forest community. At the other extreme, a rodent species may function as a *facultative specialist* enemy (Janzen 1970) if it predares a single tree species' seeds during the dry season when these represent the best or only food available in the community. Nevertheless, it is well-established, both theoretically and empirically, that insect herbivores are more diverse, abundant, and better able than mammals to increase population growth rates in response to increasing food resource densities and thus avoid satiation (Janzen 1970, 1974, Dempster and Pollard 1981, Howe and Westley 1988, Hammond and Brown 1998, Muller-Landau et al. 2003, Nathan and Casagrandi 2004, Schoonhoven et al. 2005, Nair 2007, Speight et al. 2008).

Moth Lepidoptera, especially the species-rich Noctuidae and Pyralidae super-families, may harbor many such specialized enemies, and thus we argue they are the best candidates to generate J-C effects on established woody seedlings and saplings in tropical forests. From rigorous, large-scale insect collecting field studies, a recurring theme is the narrow host-specificity of larval Lepidoptera (Janzen 1988, Novotny et al. 2002a, 2006, Dyer et al. 2007). For example, a randomly selected caterpillar from New Guinean forest vegetation will likely ( $\geq 50\%$  probability) have nearly all of its population ( $\geq 90\%$ ) concentrated on a single host species (Novotny et al. 2004). In the same forest, Lepidoptera dominated the genus-level specialists, especially in terms of total biomass — which should correlate with impact on host plants — whereas the species-rich Coleoptera were mostly generalists and much lower in biomass (Novotny et al. 2002b). A recent phylogenetic study revealed that many more rain forest insect herbivores fed on closely related plants rather than on divergent hosts than expected by chance alone, and that Lepidoptera was the most specialized herbivore group (Weiblen et al. 2006).

Further favoring a key J-C role for moth Lepidoptera is plant leaf age. Along with tree ontogeny, plant leaf age represents a crucial yet neglected factor influencing the host-specificity of leaf-chewing insects (Novotny and Basset 2005). From the plant's perspective, young leaves are more valuable than mature leaves (Harper 1989). From an insect herbivore's perspective, mature and young leaves are very different kinds of food (Feeny 1970, Strong et al. 1984). Mature leaves are abundant and ever-present, but well-defended and tough to chew; young leaves are easier to chew, richer in nutrients, but ephemeral and often poisonous. In many forests most ( $> 70\text{--}80\%$ ) of a given leaf's lifetime damage occurs during the brief period of expansion, and this damage occurs irrespective of how fast young leaves expand or how toxic they are (Coley 1983, Coley and Aide 1991, Coley and Barone 1996, Kursar and

Coley 2003, Kursar et al. 2006, Kursar et al. 2009). It stands to reason then that whatever is eating new leaves is highly specialized to locate and use them as nourishment, whereas whatever is eating mature leaves is more likely to have a broader diet. Such a trend was recently seen in stick insect herbivores as well (Phasmida; Bluthgen and Metzner 2007). The narrow host-specificity of Lepidoptera suggests that many species target new leaves that are otherwise less edible to the general herbivore community (Coley et al. 2006). For example, of insects causing damage to young expanding sapling leaves in a Panamanian forest, 38 of 46 herbivore species were Lepidoptera, of which almost half were specialized to genus or species levels (Barone 1998). Similarly, 97% of caterpillars on 11 species of *Inga* tree saplings occurred on young leaves (Kursar et al. 2006). In their recent report of an exhaustive field study, Novotny et al. (2010) concluded that the herbivore guilds most likely to cause density-dependent effects on plant fitness — i.e., J-C type enemies — were those found to be most highly specialized in diet: larval leaf chewers (Lepidoptera), leaf-miners (Lepidoptera, Coleoptera, Diptera), and leaf-suckers (Hemiptera).

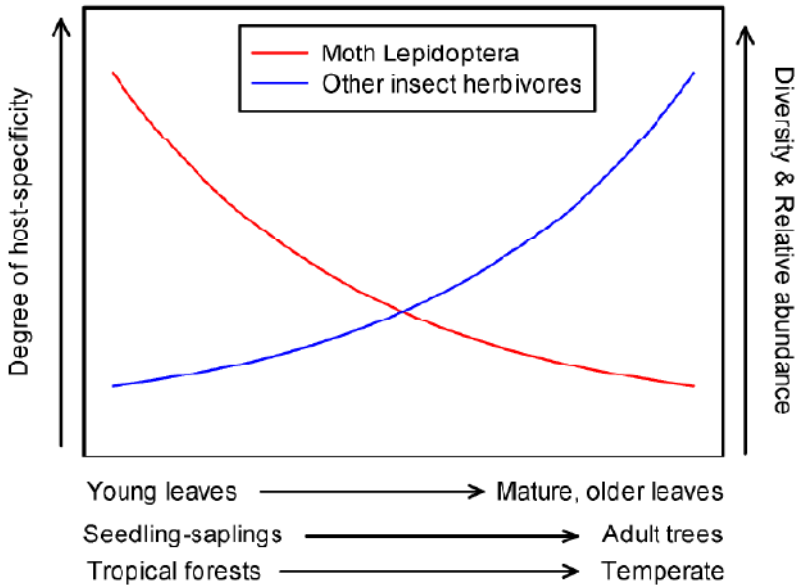


Figure 9. Conceptual diagram showing the hypothesized relevance of Lepidoptera larvae as key herbivores in the Janzen-Connell context in contrast to other insect herbivores. In this generalized scheme, the caterpillars' degree of local host-specificity is higher on younger plant parts and on younger or smaller-sized host plants or trees. Conversely, both species richness and relative abundance are higher moving further along the axes of host plant ontogeny. Finally, both trends should be less pronounced in temperate than in tropical broad-leaved forests when host ontogeny is taken into consideration.

We may refine this argument further: it is Lepidoptera feeding on *tree seedlings and saplings* that matter most in the context of the J-C hypothesis. Thus, sampling insects on large juvenile (> 5–10 cm diameter) and adult trees to gauge herbivore host-specificity yields little insight into the J-C hypothesis because its mechanistic effect has already transpired — these trees are now in an excellent position to recruit into the canopy. Further, as with *S. poliophaea*, the J-C hypothesis in its original formulation was never predicated on insect

herbivores being present in parent tree crowns and from there descending upon conspecific seedlings and saplings, though this may happen (Janzen 1970). Most post-dispersal seed-eating small mammals and insects likely do not dwell in parent crowns, and can still generate J-C type effects (reviewed by Turner 2001, Carson et al. 2008). If anything, differences in the vertical stratification — and relative host impact — of herbivore assemblages in tropical forests are expected, perhaps more so than in temperate forests, which could reflect differences in food palatability or abundance of both trees and lianas; microclimatic changes and constraints (temperature, wind) on insect development and behavior; or changes in susceptibility to faunal predators, ants and birds in particular (Heinrich 1993, Basset et al. 2003). So, in addition to leaf age, we anticipate that insect herbivore host-specificity is likely very different between host plant species' ontogenetic stages (summarized in Figure 9) in part of because differences in host abundance and changes in plant resource allocation to defense and increased tolerance with tree age/size (Boege and Marquis 2005). That is, insect herbivores feeding on adult trees do not likely also feed on conspecific seedlings and saplings (Basset 2001, Barrios 2003).

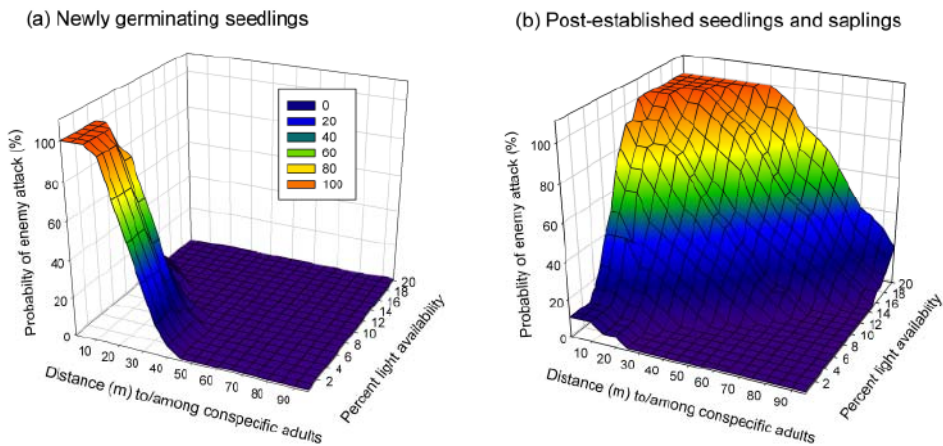


Figure 10. Three-dimensional graphics showing the proposed augmentation in the spatial scale of foraging and attacks by the specialist moth *Steniscadia poliophaea* on its host tree, big-leaf mahogany in the latter's South American range. Two factors, increased local light availability, mainly in canopy gaps, and proximity to conspecific adults interact to shape mahogany susceptibility to the specialist moth in forests. Once a year, newly germinating seedlings emerge in the vicinity of fruiting mahogany trees, mostly in shaded forest understory conditions, and the probability of attacks to the modal seedling declines with distance from the parent tree (a). At other times in the wet season, food for *S. poliophaea* is very limited in the understory because mahogany leaf production requires above-average light availability, and the probability of attacks to the modal established seedling or sapling increases both with flushing vigor in canopy gaps and proximity to nearby conspecific adults (b). The net result for this antagonistic interaction is that the Janzen-Connell effect generated by this moth on its host population is likely strengthened, operating over a larger area, thereby increasing the spacing apart of adult recruitment events (i.e., shifting the PRC further to the right in Figure 1.).

As demonstrated by the *S. poliophaea* case study, an herbivore diet restricted to new leaves might increase the spatial scale of host searches. This could extend the J-C effect well beyond the parent tree crown to new forest canopy gaps where seedling growth is promoted

by increased light levels (Figure 10b). In these microhabitats, depending on host plant density, flushing vigor, and proximity to conspecific adults, insect predators might exert a 'brake' on host recruitment rates. Because herbivores restricted to young foliage are likely very resource limited (Dempster and Pollard 1981), attacks in distant canopy gaps are thus predictable, as these herbivores are effectively food-limited in the shaded forest understory (Richards and Coley 2007, 2008). Lepidoptera specialists thus may search for hosts at further distances than other insect herbivores, and colonize them faster than polyphagous Lepidoptera, as reported for the monophagous butterfly *Heliconius hewitsoni* which preys on the neotropical vine *Passiflora pittieri* (Thomas 1990 Figure 1). Consequently the J-C effect on a host population is strengthened because the spatial repulsion between parent and offspring is enhanced. Considering that light availability is generally the most limiting resource for new seedlings and saplings (Chazdon and Fetcher 1984, Richards 1996, Turner 2001), the effects of light levels on their susceptibility to different enemy guilds (insects vs. pathogens vs. mammals) may prove useful to detect J-C effects, and provide a deeper understanding of them — and this should further benefit from consideration of different spatial scales for conspecific density-dependent effects (Angulo-Sandoval and Aide 2000, Sullivan 2003).

Little doubt remains that negative density dependence in tree dynamics is a widespread phenomenon, capable of promoting species coexistence in hyperdiverse tropical forest communities (Wright 2002, Carson et al. 2008, Zimmerman et al. 2008, Kricher 2010). Pests are the most plausible explanation for these patterns (Leigh 2004), as envisaged in the J-C hypothesis 40 years ago. Much attention has recently been paid to fungal pathogens, which can cause severe density-dependent mortality to cohorts of new seedlings (Bell et al. 2006, Bagchi et al. 2010, Mangan et al. 2010) and enhance species differences in shade tolerance (McCarthy-Neumann and Kobe 2008). But pathogen host-specificity is likely weak (McCarthy-Neumann and Kobe 2010) and their population-level impacts are probably limited to beneath tree crowns only (Figure 9a; Burdon and Chilvers 1982, Augspurger 1984b). However, as causal agents underpinning the J-C hypothesis, pathogens and moth Lepidoptera need not be mutually exclusive. As proposed here, their respective roles and impact may wax and wane depending on changing light availability to seedlings and saplings in forests and on the host density of conspecifics and possibly congeneric species (Figure 10). In this way, the presence and action of both enemy guilds can occur on a single or many canopy tree species, and in combination exert as a powerful force to help maintain community diversity.

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