Leaf damage and density-dependent effects on six *Inga* species in a neotropical forest

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Abstract: Many models have been proposed to explain the possible role of pests in the coexistence of a high diversity of plant species in tropical forests. Prominent among them is the Janzen-Connell model. This model suggests that specialized herbivores and pathogens limit tree recruitment as a function of their density or proximity to conspecifics. A large number of studies have tested the predictions of this model with respect to patterns of recruitment and mortality at different life stages, yet only a few have directly linked those density- or distance-dependent effects to pest attack. If pest-attack is an important factor in density- or distance-dependent mortality, there should be spatial heterogeneity in pest pressure. I studied the spatial distribution of leaf damage in saplings of six common *Inga* species (Fabaceae: Mimosoideae) in the 50ha forest dynamic plot of Barro Colorado Island, Panama. The percent leaf damage of *Inga* saplings was not heterogeneous in space, and the density of conspecific, congener or confamilial neighbors was uncorrelated with the observed damage levels in focal plants. One of the focal species did suffer density-dependent mortality, suggesting that spatial variation in plant performance in these species is not directly driven by leaf damaging agents. While multiple studies suggest that density-dependent effects on performance are common in tropical plant communities, our understanding of the mechanisms that drive those effects is still incomplete and the underlying assumption that these patterns result from differential herbivore attack deserves more scrutiny. Rev. Biol. Trop. 60 (4): 1503-1512. Epub 2012 December 01.

Key words: density-dependence, herbivory, *Inga*, Janzen-Connell hypothesis, Panama.

One of the central problems in tropical biology has been to understand the mechanisms that permit the coexistence of so many potentially competing tree species. Many diverse mechanisms such as habitat associations and stochastic processes are probably involved in maintaining tree species coexistence (*e.g.*, Denslow 1987, Hubbell 2001, Wright 2002). Among these, frequency- and density-dependent processes have received considerable attention (Webb & Peart 1999, Harms *et al.* 2000, Hubbell *et al.* 2001, Chave *et al.* 2002, Peters 2003, Uriarte *et al.* 2004, Wills *et al.* 2006). In particular, a large number of empirical tests and theories (Wright 2002, Leigh *et al.* 2004, Adler & Muller-Landau 2005) have focused on the Janzen-Connell model

of species coexistence (Janzen 1970, Connell 1971). The Janzen-Connell model predicts that juvenile survival will be disfavored close to the parent tree due to the locally high herbivore abundance associated with the large crown of the adult tree or with the higher density of recruiting conspecifics.

These density- and distance-dependent predictions of the Janzen-Connell model provided clear, testable hypotheses regarding plant distribution and mortality. For that reason, there is a considerable body of literature evaluating these predictions (see reviews in: Clark & Clark 1984, Hammond & Brown 1998, Hyatt *et al.* 2003). Most studies have focused on seeds or seedlings since they are more likely to die from herbivore attack than larger plants (*e.g.*,

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Augspurger 1984, De Steven 1994, Webb & Peart 1999). However, folivores and pathogens can also influence the growth of larger saplings (Sullivan 2003) and a number of studies have also tested larger size classes at the community scale (Hubbell *et al.* 1990, Condit *et al.* 1992, Wills *et al.* 1997, Hubbell *et al.* 2001, Peters 2003, Uriarte *et al.* 2004, Comita *et al.* 2010). The results of the studies are quite variable among species (Hyatt *et al.* 2003) and also among types of predators (Hammond & Brown 1998). However, community-level studies have shown that there is a general trend for negative density-dependence in the seed-seedling transition (Harms *et al.* 2000), and in the survival of seedlings, saplings and larger size classes (Peters 2003, Comita *et al.* 2010).

One component of the Janzen-Connell model that has not been thoroughly evaluated, is the assumption that specialized pests are the mechanism driving density-dependent effects in tree performance. Studies testing the Janzen-Connell model have typically focused on the model prediction of variation in plant performance (recruitment, growth or mortality), and the specific mechanisms affecting plant performance are seldom identified. For studies that focused on seeds, disappearance can only be attributed to predation, but seedling and sapling performance is subject to a plethora of other challenges including competition for water, nutrients or light. Thus unlike seeds, the evidence for spatial heterogeneity in seedling or sapling performance does not necessarily amount to evidence for spatial heterogeneity in pest pressure (Clark & Clark 1984). Only a few studies have explicitly tied distance-dependent mortality to the effect of pests (*e.g.*, Clark & Clark 1985, Gilbert *et al.* 1994, Packer & Clay 2000); and among those, the evidence indicates that soil pathogens may be more important drivers of distance-dependent seedling mortality than insect herbivores (Mangan *et al.* 2010, Swamy &Terborgh 2010).

Overall, for specialized pests to drive Janzen-Connell effects they also have to meet a number of underlying assumptions: 1) Pest pressure should be driven by bottom-up effects, such that local abundance of food resources drives local herbivore populations; 2) pests should be very specialized, such that they respond to spatial distribution of only one host; and 3) pests should have low dispersal ability. If they meet these assumptions, there should be spatial heterogeneity in pest pressure, such that it matches the spatial distribution of the conspecific density. With the main exception of insect specialization, these assumptions have not been thoroughly evaluated.

With the intention of specifically test the Janzen-Connell assumption of spatial heterogeneity in pest pressure, I investigated the spatial distribution of leaf damage and mortality in saplings of six species of the genus *Inga* (Fabaceae: Mimosoidae). I specifically asked the following two questions: (1) is there spatial heterogeneity in the leaf damage of the focal *Ingas*?; and (2) are individual leaf-damage levels explained by the local density of hosts? For this, I analyzed a data set of herbivory measurements collected in the 50Ha Forest Dynamic Plot in Barro Colorado Island, Panama.

MATERIALS AND METHODS

Study site: The study was done in the 50ha Forest Dynamic Plot on Barro Colorado Island (BCI), Panama. In this plot all the trees larger than 1cm diameter at breast height (dbh) have been mapped and identified to species every five years since 1984 (Condit *et al.* 2005). BCI is a 1500ha artificial island in Gatun Lake, created when the Panama Canal was flooded in 1914. The plot is located on the plateau of the island at 9º09' N - 79º51' W, with an elevation of 162m. The climate is typical of a lowland tropical moist forest. The average daily temperature is 27ºC and the average total yearly rainfall 2 600mm, 90% of which falls during the rainy season, from May through December. The field station is managed by the Smithsonian Tropical Research Institute and the plot by the Center for Tropical Forest Science (CTFS).

Study species: The genus *Inga* (Fabaceae: Mimosoideae) comprises about 300 species

that may have radiated as recently as 2Mya (Pennington 1997, Richardson *et al.* 2001). It is widespread and abundant throughout the Neotropics, and in most communities where *Inga* is present, there are multiple species of the genus growing sympatrically. In the BCI 50ha plot there are 15 *Inga* species, which comprise 7% of the tree species and 2.2% of the total number of stems (Condit *et al.* 2005). I worked with the six most abundant *Inga* species in the plot, namely: *Inga acuminata* (16), *I. goldmanii* (25), *I. marginata* (58), *I. nobilis* (38), *I. sapindoides* (19) and *I. umbellifera* (51) where the numbers in parentheses represent the mean abundance per hectare for stems >1cm dbh.

Herbivory measurements: I measured percent leaf area damaged using a grid on at least three mature leaves per plant in a total of 209 saplings (roughly 35 plants per species) throughout the BCI 50ha plot (Fig. 1). All plants were juveniles smaller than 5cm dbh, with foliage that could be reached by hand. I did not measure seedlings. While I did not specifically avoid gaps, most of my measurements were in the understory. These herbivory data have already been published elsewhere as species means, and other method details can be found in Brenes-Arguedas *et al.* (2008). While these data were not specifically collected for this analysis, their location in the mapped 50ha plot provides a useful framework to run a spatial analysis. Most measured plants were already mapped in the plot database, and for some smaller saplings (<1cm dbh) that had not yet entered the censuses, I estimated the coordinates in the 50-ha plot using the 5m quadrants.

Spatial heterogeneity in leaf damage: All data were analyzed with the R software (R Development Core Team 2009). If there was spatial heterogeneity in pest pressure I expected to find 'hot-spots' and 'cold-spots' of herbivore pressure in the 50ha plot. Such a pattern can be detected using spatial autocorrelation analysis. This analysis tests the hypothesis that neighboring plants suffer more similar damage levels than more distant plants because they are exposed to the same local conditions of herbivore pressure. To test for spatial autocorrelation
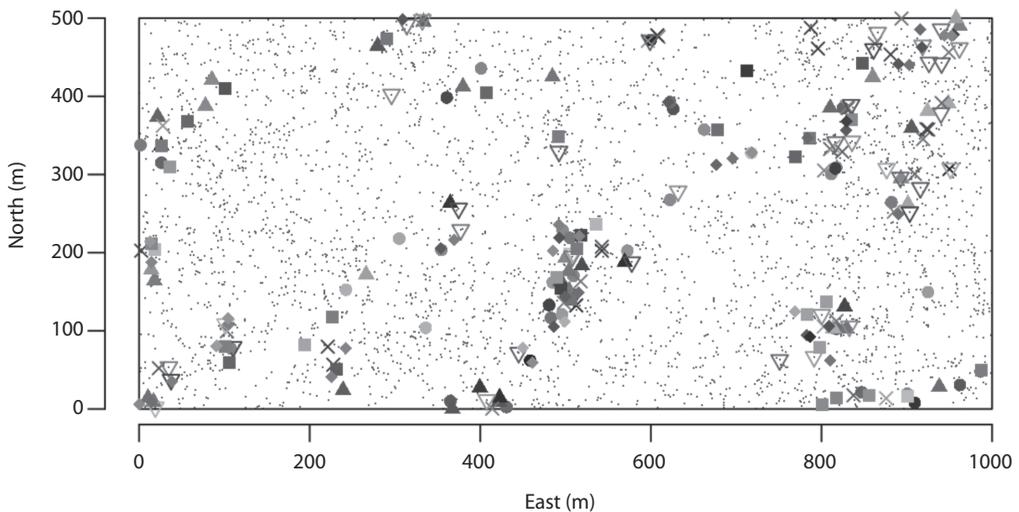

Fig. 1. Map of the 50-ha Forest Dynamics Plot in BCI showing the distribution of all *Inga* stems alive in the census of the year 2000 (dots). The *Inga* individuals for which I measured leaf damage are indicated by symbols (*I. acuminata*, ●; *goldmanii*, p; *marginata*, Î; *nobilis*, s; *sapindoides*, ¾; and *umbellifera*, ®). For each individual leaf damage levels are indicated by a shade of gray, with darker colors indicating higher damage.

I used the plot coordinates of the individuals for which I had damage measurements to calculate the Moran's I statistic defined as:

$$I = n \sum \sum w_{ij}\,(d_i - d)(d_j - d) \sum w_{ij} \sum (d_i - d)$$

where w_{ij} is the inverse of the linear distance between plants i and j; d_i and d_j their respective leaf damage levels, and $\bar{d}$ is the mean damage for all plants. $I=0$ indicates no autocorrelation and $I>0$ indicates positive autocorrelation. Because I was interested in the presence of clusters of high or low herbivory, negative autocorrelation does not have an ecological interpretation in this context. I calculated the Moran I for each species individually (to test only conspecific effects), and for all *Inga* together (to test congener effects). I generated correlograms by grouping w_{ij} into 20m distance classes. I tested for significant departures from zero using Monte Carlo randomizations where the herbivory data of each sapling was randomly assigned to the position of a different sapling. The 95% confidence intervals were calculated as the percentiles from 200 randomizations.

Neighbor density estimates: To determine the local densities of neighbors, I used the plot data from the census of the year 2000 (Condit *et al.* 2005). I calculated density for all individuals larger than 1cm dbh inside circles centered on each of the focal plants. To account for the possible use of alternative hosts in the population, I separately estimated density of conspecific, congeners, and confamilial neighbors. I estimated density as a simple count of all stems and as the sum of the basal area of the neighbors. In the count of stems all neighbors are considered equally important regardless of their size. In the sum of basal areas, larger trees, which have larger crowns and may be stronger infection sources, have more weight than smaller saplings. All densities were corrected for edge effects dividing by a parameter equal to the fraction of the circle area that falls inside the plot. This correction assumes that the distribution of trees outside the plot is the same as inside the plot.

The effect of neighbor density on leaf damage: To test for density-dependent effects on pest attack, I correlated leaf damage to the neighbor density around each of the measured focal plants using a multiple linear model (R 'lm' procedure) of the form:

$$\text{Damage} = \beta_0 + \beta_{sp} \cdot sp. + \beta_{gn} \cdot gn + \beta_{fm} \cdot fm$$

where b_i are the parameters and *sp*, *gn* and *fm* are the corrected densities of conspecifics, congeners (not including conspecifics), or confamilials (not including congeners), respectively. Hence, the effects of congeners and confamilials are tested as additions over the effect of conspecifics. Based on the analysis by Hubble *et al.* (2001) I evaluated the multiple regression at 10, 15 and 20m radius from the focal plant, but for simplicity I showed only the results from the analysis at 15m radius. Model residuals were tested for spatial autocorrelation using the 'moran.test' procedure of the 'spdep' package (version 0.4-34 by Roger Bivand & contributors).

Density dependent mortality: To test whether the focal species suffered density dependent mortality, I tested all individuals of the focal species smaller than 5cm dbh, that were alive in the 1985 census (second census; Condit *et al.* 2005). I included all mortality events that happened in the following 20 years until the census of 2005. I evaluated a multiple regression with the same parameters as the leaf damage regression but using the logit transformed data and binomial errors appropriate to mortality data (R 'glm' procedure). Spatial autocorrelation was tested as above and when necessary I corrected for autocorrelation by adding an autocovariance distribution parameter to the model (estimated with the 'autocov_dist' function of 'spdep' package).

Spatial heterogeneity in leaf damage: There was little evidence for spatial heterogeneity in herbivore pressure based on the spatial autocorrelation analysis. When analyzing each species separately, only *Inga goldmanii* and *I. umbellifera* had a positive Moran's *I* statistic, consistent with positive spatial autocorrelation in leaf damage (Moran's *I*: *I. acuminata*: -0.41, *I. goldmanii*: 0.36, *I. marginata*: -0.11, *I nobilis*: -0.2, *I. sapindoides*: -0.1, and *I. umbellifera*: 0.23). However, the correlograms showed that none of the correlation patterns significantly differed from a random distribution (Fig. 2). Similarly, when analyzing all focal *Inga* together as a genus, Moran's *I* was not different from zero (I=0.0073, N=235, p=0.34).

Effect of neighbor density on leaf damage: I found only weak evidence suggesting that neighbor density significantly explained the variation in standing leaf damage observed

on the focal *Inga* species. For *I. goldmanii*, conspecific basal area at 15m radius, showed a weak positive effect on leaf damage with p=0.03 (Table 1). However, applying a Bonferroni correction that accounts for the 18 independent species x radius tests, significance would require p<0.003 (even a very lax Bonferroni correction that accounts only for the three separate radius analyzed, requires p<0.017). Hence, this value cannot be considered significant. Consistent with this, when the analysis was repeated for radius 10 or 20m this species does not show any more effects with p<0.05. Indeed, for all species the variation in damage at any given density was extremely large, and it is clear that some trends are driven by one individual (Fig. 3).

Density dependent mortality: For this analysis, two of the species had to be corrected for significant autocorrelation in the residuals. After correction for autocorrelation, only one of the six focal species, *I. marginata*,
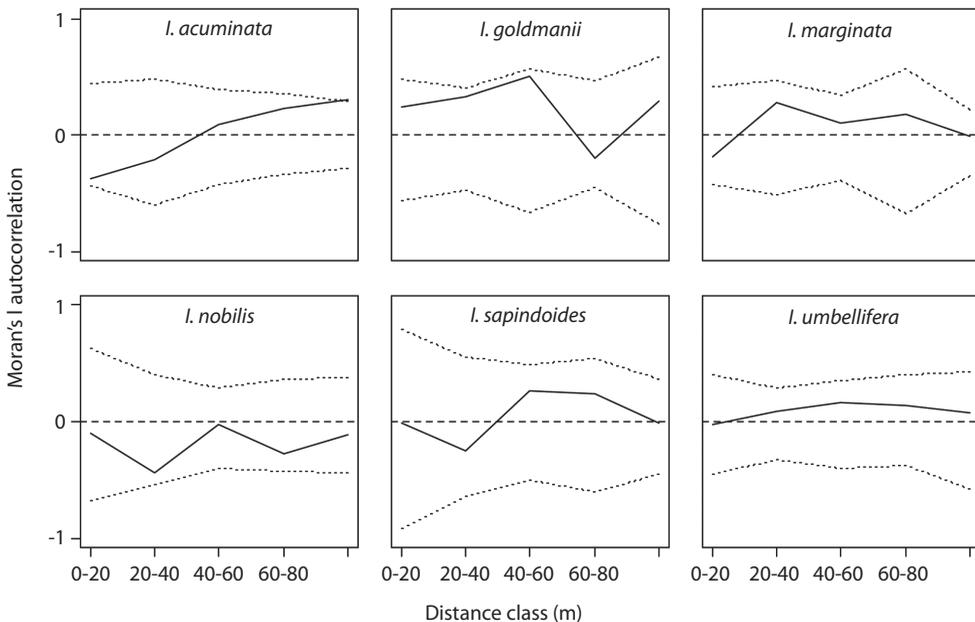

Fig. 2. Correlograms showing the Moran's *I* statistic (solid line) as a function of distance class for the six focal *Inga* species. The dashed line represents zero autocorrelation and dotted lines represent Monte Carlo 95% CI. No species differs significantly from zero.

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TABLE 1
Parameter estimates for the multiple regressions that explain leaf damage and mortality as a function of
the density of conspecific (sp), congeners (gn) and confamilial (fm) neighbors within a 15m radius

	Species	Herbivory			Mortality		
		β_{sp}	β_{gn}	β_{fm}	β_{sp}	β_{gn}	β_{fm}
Stem counts	*I. goldmanii*	0.019	-0.001	0.002	0.094	-0.002	-0.014
	I. marginata	0.029	0.006	0.004	0.076**	0.007	-0.005
	I. nobilis	-0.032	-0.008	0.001	-0.030	-0.028	-0.011
	I. acuminata	-0.002	0.009	-0.004	0.063	0.001	0.023
	I. sapindoides	0.001	-0.002	-0.002	-0.134	0.010	-0.016
	I. umbellifera	0.007	-0.002	-0.007*	0.020	-0.007	-0.005
Basal area	*I. goldmanii*	0.125*	0.008	0.000	8.598	-4.259	-0.085
	I. marginata	-0.007	-0.007	0.001	1.392	-1.066	0.166
	I. nobilis	-0.024	-0.002	-0.001	-3.246	-1.789	-0.231
	I. acuminata	-0.015	0.016	0.001*	7.953	4.278	-0.223
	I. sapindoides	0.010	0.003	0.000	31.835	2.790	-0.396
	I. umbellifera	0.136	0.004	0.000	51.481	-2.529	-0.246

Densities were evaluated both as count of stems and sum of basal areas of stems. Parameters that improve the model are
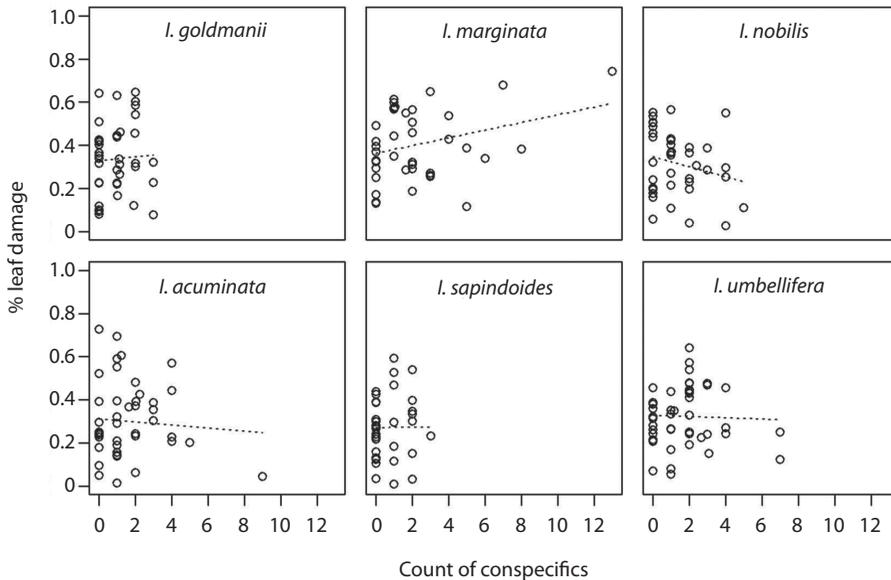indicated with * ($p<0.05$) and ** ($p<0.003$, significant based on a Bonferroni correction).

Fig. 3. Scatterplots showing the percent damage for all individuals as a function of the count of conspecific neighbors within
a 15m radius. Dotted lines represent the best fit for the univariate linear model. None of the regressions is significant at
a=0.05.

showed significant evidence of density dependent mortality (p=0.0001, Table 1). This result is strongly significant even after a conservative Bonferroni correction and, more over, remained significant when the model was evaluated at different radii.

Including the presence of congeners or confamilials did not improve any of the herbivory or mortality models evaluated (Table 1). For *I. umbellifera* and *I. acuminata* the parameter for the effect of confamilial density on damage had p<0.05. This value is not significant using the Bonferroni corrections described above, but also, conspecific and congener density did not correlate with damage, and in this analysis the role of confamilial density alone has little ecological significance. Consistent with this, the p value was also >0.05 when evaluated at a different radii.

DISCUSSION

In this study I evaluated one of the assumptions of the Janzen-Connell model using a novel approach and the statistical methodology normally used in spatially explicit population level studies of density-dependent mortality. My results suggest that the Janzen-Connell assumption of spatial heterogeneity in herbivore pressure does not apply to the *Inga* study species with respect to leaf damaging agents.

While I found a few trends in the spatial structure of *Inga* leaf damage, in general these were not very strong. Hence, the spatial analyses of leaf damage were, at best, inconclusive. I found no evidence that spatial autocorrelation in leaf damage was significantly different from random. Also, while there were a few correlations with p<0.05 between neighbor density and leaf damage, these did not hold when the analysis conditions were changed (different radii or different subsets of stems). Furthermore, this p value is not significant if corrections for multiple testing (Type II error) are taken into account. Hence, these data provide little evidence that there is spatial aggregation in leaf damaging agents. It is possible that the herbivory data I used here were not collected broadly enough in the 50ha plot to maximize the power to evaluate this hypothesis. However, for the analysis of density-dependent mortality I used the complete plot data set and 20 years of mortality data. Yet, only one of the six study species, *I. marginata*, showed clear evidence of density-dependent mortality. This second analysis supports the absence of spatial heterogeneity in leaf damage for my study species.

A few other studies have found distance-dependent effects of herbivory using methodologies that focus on only a few adult trees (Clark & Clark 1985, Blundell & Peart 1998, Barone 2000). Unlike those studies, here I focused on density-dependence and used a methodology based on analysis of spatial dynamics at the population scale. Hence, the different results might be due to the different methodology or to the different set of species used. However, a number of recent studies that have experimentally evaluated herbivore pressure, found little evidence that insect herbivores drove distance-dependent effects (Mangan *et al.* 2010, Swamy &Terborgh 2010). As my measurements were limited to leaf damage, my results might indeed be consistent with those studies. Indeed, pathogens often attack other parts of the plant and cause density-dependent mortality (Gilbert *et al.* 1994). This distinction might explain why *I. marginata,* the only species that suffered density-dependent mortality, did not show clear evidence of density-dependent leaf damage.

Why would the other *Inga* species not suffer density-dependent mortality or damage? There are two factors that might explain the absence of these effects. The first is that for pest pressure to increase in a density-dependent manner, as is assumed in the Janzen-Connell model, local herbivore pressure should be driven by bottom-up controls, in other words, by resource availability in the form of host density. However, top-down effects from predators can also impose controls on herbivore populations (Hunter *et al.* 1997). These may be especially important in my *Inga* study system, as species

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in the genus *Inga* have nectaries on the leaves that attract ant defenders (Koptur 1984), thus actively involving top-down interactions in their defense. If ants do respond to the density of plants with nectaries, it is possible that the same density-dependent effects that might locally increase herbivore abundance could also increase the abundance of defensive ants. This could neutralize positive density-dependence resulting from herbivore attack.

It is also possible that pest attack becomes spatially random if herbivores in the population have a complex combination of hosts. The Janzen-Connell model assumes that density-dependent effects occur at the species level due to high specialization of tropical herbivores. A sizable body of literature has discussed the specialization levels of tropical herbivores (Janzen 2003, Novotny & Basset 2005, Dyer *et al.* 2007, Novotny *et al.* 2007), and such high specialization is not necessarily the norm in complex herbivore assemblages typical of tropical species (Basset *et al.* 1996). Indeed, high specialization is not the norm in my study system in particular (Kursar *et al.* 2006). I tried to account for this by testing for the effects of congeners or confamilials on leaf damage and mortality, but found that these did not significantly influence density-dependence. It is possible that the combination of potential hosts that could influence pest pressure is more complex than what I used here. If so, this would further support the absence of spatial heterogeneity in leaf damage.

Community-wide analyses have shown that density-dependent effects on mortality are pervasive but they are not present for all the species. For example, in two 50ha plots in Pasoah, Malaysia and BCI, Panama, only 46 and 47% of the species analyzed suffered positive density-dependent mortality (Peters 2003). Here I took a closer look at the spatial dynamics of six common *Inga* species to argue that our understanding of the mechanisms that might mediate these effects is still too incomplete. Looking at the characteristics of the species that do not suffer density-dependent mortality may provide valuable insight into the mechanisms that mediate this effect. For example, the absence of density-dependent mortality for some species might be due to lack of analytical power or due to the absence of heterogeneity in pest attack. Studies might have to integrate the spatial dynamics of different kinds of pests, such as pathogens, insects or mammals; the dynamics of complex herbivore assemblages; the effect of predators; and the types of plant defensive strategies. While this is not an easy task, this insight will provide a valuable understanding of the role of plant-pest interactions in the dynamics of tropical forests.

RESUMEN

Se han propuesto muchos modelos para explicar la coexistencia de una alta diversidad de especies de árboles en bosques tropicales. Prominente, entre estos modelos es el de Janzen-Connell, que sugiere que los herbívoros especialistas limitan la colonización de árboles en función de la densidad o proximidad de con-específicos. Si este efecto es en realidad el resultado de ataque por herbívoros, debiera haber heterogeneidad espacial en la herbivoría. Aquí se evalúa esta hipótesis estudiando la distribución espacial de la herbivoría en juveniles de seis especies comunes de *Inga* (Fabaceae: Mimosoideae) en la parcela de 50ha de la Isla de Barro Colorado, en Panamá. Análisis de auto-correlación espacial no mostraron heterogeneidad en la herbivoría de estas especies, y la densidad local de con-específicos, congéneres o confamiliares no se correlacionó con la herbivoría de las plantas estudiadas. Solo una de las especies de estudio sufrió mortalidad densidad-dependiente en 20 años de censos. Aunque muchos estudios han demostrado que los efectos densidad-dependientes en la mortalidad

de las plantas son comunes en bosques tropicales, nuestro entendimiento de los mecanismos que causan esos efectos es aún limitado, y la suposición de que estos resultan de heterogeneidad espacial en el ataque de herbívoros merece más escrutinio.

Palabras clave: densidad-dependencia, herbivoría, *Inga*, hipótesis Janzen-Connell, Panamá.

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