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THE ADVANTAGE OF THE EXTREMES: TREE SEEDLINGS AT INTERMEDIATE ABUNDANCE IN A TROPICAL FOREST HAVE THE HIGHEST RICHNESS OF ABOVE-GROUND ENEMIES AND SUFFER THE MOST DAMAGE

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Running headline: Tropical tree abundance and enemy richness

SUMMARY

1. Tropical forest tree diversity has been hypothesized to be maintained via the attraction of density responsive and species-specific enemies. Tests of this hypothesis usually assume a linear relationship between enemy pressure (amount of damage and enemy richness) and seedling or tree density. However, enemy pressure is likely to change non-linearly with local seedling abundance and community scale tree abundance if enemies are characterized by non-linear functional responses.
2. We examine the abiotic and biotic factors associated with richness of above-ground enemies and foliar damage found in tree seedlings in a tropical forest in Puerto Rico. Rather than identify specific enemies targeting these seedlings, we used damage morphotypes, a paleo-ecological method, to derive a proxy for enemy species richness.
3. We found that the relationships between local and (conspecific seedling density) and community scale (conspecific basal area of adult trees) abundance and both richness of above-ground enemies and foliar damage were hump-shaped. Seedlings of tree species existing at intermediate levels of abundance, at both local and community scales, suffered more damage and experienced pressure from a greater diversity of enemies than those existing at high or low densities.
4. We hypothesized that greater damage at intermediate abundance level could arise from a rich mixture of generalist and specialist enemies targeting seedlings of intermediate abundance tree species. Consistent with this hypothesis, we found that generalist enemies were more diverse on species at rare or intermediate abundance relative to common tree species. However, specialist enemies showed no significant trend across tree species abundance at either the local or community scales.
5. *Synthesis*: Our results suggest that interspecific variation in tree species abundance leads to differences in the magnitude and type of damage tropical tree seedlings suffer. This variation

leads to a non-linear, hump-shaped relationship between species abundance and enemy damage, highlighting fruitful directions for further development of species coexistence theory.

Key-words: Community compensatory trend, enemy richness, foliar damage, hump-shaped relationship, Janzen-Connell effects, plant–herbivore interactions, specialization, species coexistence.

INTRODUCTION

Negative density feedbacks are key components of most species coexistence theories: as a species becomes more abundant, its performance declines, which in turn reduces its abundance (Lotka 1925; Volterra 1926; MacArthur and Levins 1964; Chesson 2000). In highly diverse tropical forests, negative density and distance-dependent factors (also known as Janzen-Connell (JC) effects; Janzen 1970; Connell 1971) are the most frequently studied mechanisms that could explain the persistence of rare tree species (reviewed in Wright 2002; Comita *et al*. 2014). JC effects operate through the attraction of species-specific enemies such as seed predators, herbivores, or pathogens to areas with high density of conspecific seedlings and near conspecific adult trees (Schweizer *et al*. 2013). This reduces conspecific survivorship near the adult tree, leaving ecological space for heterospecifics to recruit. At the community level, this mechanism can promote diversity if common tree species suffer from higher mortality than rare tree species, a pattern known as the community compensatory trend (Connell *et al*. 1984).

Empirical evaluations of JC effects in forests have generally focused on the predictions that seedling survival should linearly increase with lower local abundance of parent trees and conspecific seedlings (e.g., Augspurger 1983; Clark and Clark 1984; Carson *et al*. 2008; Comita *et al*. 2014). Experimental manipulative studies have combined insecticide, fungicide, and exclosure treatments to directly evaluate the role of enemies as agents of negative-density dependent mortality (e.g. Bell *et al*. 2006; Bagchi *et al*. 2010a; 2010b; Gallery *et al*. 2010; Lewis 2010; Konno *et al*. 2011; Mordecai 2011; Liu *et al*. 2012a; 2012b; Gripenberg *et al*. 2014; Fricke *et al*. 2014). Despite the recognized importance of enemies in maintaining high tree diversity (Terborgh 20012), it remains unclear how conspecific and heterospecific seedling densities alter enemy pressure, a combination of both enemy richness and amount of damage. Enemy richness is an important measure of enemy pressure because high enemy richness translates into more diverse types of damage. The costs involved in resisting different types of damage might be greater that for one type of damage, thereby increasing the carbon costs and mortality risk associated with hosting a high richness of enemies. Enemy richness and foliar damage might be greater near conspecific adult trees that have had time to accumulate enemies, and at high seedling conspecific density if more enemies are attracted by the presence and abundance of target tree species (Janzen 1970; Connell 1971; Huntly 2001; Ricciardi and Ward 2006; Strauss *et al*. 2006; Dawson *et al*. 2009; Gossner *et al*. 2009; Hill and Kotamen 2009; 2010). At the local and community scales, enemy richness is expected to increase linearly with conspecific tree density (Moran *et al*. 1994; Bachelot and Kobe 2013) and foliar damage (Ness *et al*. 2011; Schuldt *et al*. 2012; Cárdenas *et al*. 2014). Yet, invertebrates and possibly other types of enemies are likely to respond non-linearly to conspecific density. In other words, enemies are unlikely to have a type I functional response (Holling 1965). Rather, it is thought that many enemies have type III or IV functional responses, which respectively predict saturation and decrease of enemy response at high seedling densities (Holling 1965, Tener 1965). In natural conditions, quantifying intra and interspecific variation in the pressure from enemies (Garibaldi *et al*. 2011a; 2011b; Hill and Kotanen 2011; Ness *et al*. 2011; Bachelot and Kobe 2013; Cárdenas *et al*. 2014) can help us understand non-linear relationships between enemy richness, amount of foliar damage, and tree species abundance.

Some ecological and evolutionary processes may result in a non-linear relationship between conspecific density and enemy richness and amount of foliar damage (Ness *et al*. 2011). For example, from an ecological perspective, rare tree species might escape enemies due to low detectability and also might experience interspecific herd protection (Wills and Green 1995; Peter 2003; Lan *et al*. 2012), resulting in a low richness of enemies (Chew and Courtney 1991; Castagneyrol *et al*. 2014). In contrast, high apparency of common tree species means that enemies can easily find these tree species (Root 1973; Feeny 1976; Castagneyrol *et al*. 2013), and this could lead to high richness of enemies and greater foliar damage, but on the other hand, enemy satiation could result in a non-linear relationship between abundance and enemy richness and foliar damage (Silvertown 1980; Otway *et al*. 2005). Intraspecific herd protection resulting from intraspecific variation in resistance or attractiveness to enemies, whereby conspecific neighbors at high density act as a shield against enemies for other conspecific individuals, can also decrease the richness of enemies targeting common tree species and foliar damage (Barbosa *et al*. 2009). Finally, the predators of tree enemies may experience a positive-density dependent response due to the high density of enemies at high conspecific seedling density (this process is referred to as "predator attraction", Bernays and Graham 1988; Denno *et al*. 2002; Visser *et al*. 2011), ultimately leading to a low richness of enemies. Ecological escape, satiation, intra- and interspecific herd protection, and predator attraction might result in a hump-shaped relationship between tree species abundance and enemy richness and foliar damage (Fig. 1A).

From an evolutionary perspective, intraspecific variation in enemy specialization and host defenses might also lead to a hump-shaped relationship between tree species abundance and enemy richness and foliar damage at the local and community scales (Fig. 1B). Patterns and causes of specialization remain an active field of research (Rueffler *et al*. 2006; Singer 2008; Barrett and Heil 2012; Forister *et al*. 2012), and hypotheses for specialization are currently grouped into four classes: 1) the physiological efficiency hypothesis predicts that specialization arises as an adaptation of the enemies to the nutritional and secondary compounds of the tree host (Dethier 1954); 2) the optimal foraging hypothesis claims that specialization takes place to maximize enemy adult fitness (Scheirs and de Bruyn 2002); 3) the neural-constraints hypothesis expects specialization to occur because enemies recognition of target species and host-tree acceptance abilities are limited (Bernays and Wcislo 1994),; 4) the enemy-free space hypothesis advocates that enemies specialize on a tree host to escape from or defend themselves against their own predators (Jeffries and Lawton 1984). Together, these theories predict that specialist enemies are more likely to target common tree species, rather than rare tree species (Jaenike 1990) because high host abundance reduces the costs and risks associated with specialization (Feeny 1976; Fox and Morrow 1981; Coley and Barone 1996; Silvertown and Dodd 1996; Bustamante *et al*. 2006; Agrawal 2007; Schuldt *et al*. 2012). Research on interaction networks has demonstrated that rare tree or plant species are typically involved in fewer interactions with enemies than common hosts and that these interactions tend to be generalists (Vázquez *et al*. 2005; Montoya *et al*. 2006; Bascompte and Jordano 2007). For these evolutionary reasons we might expect that common tree species should host a higher richness of specialist enemies while rare tree species should be targeted by generalists enemies (Fig. 1B). As a result species at intermediate abundance at local and community scales might have a high richness and a mixture of both generalist and specialist enemies (Kunin 1999; Ives *et al*. 2004), resulting in a hump-shaped relationship between enemy richness and foliar damage and tree species abundance (Fig. 1B).

Besides host abundance at the local and community scales, a number of abiotic and biotic factors might determine whether or not an enemy targets a plant host (Agrios 2005). Abiotic factors such as soil moisture, and light conditions are likely to affect the enemy communities directly (Hairston *et al*. 1960; Augspurger and Kelly 1984; Price *et al*. 2011) and indirectly via effects on seedling performance (Aerts and Chapin 2000; Nystrand and Granstrom 2000; Whitfeld *et al*. 2012). For example, the amount of damage by fungal pathogens responsible for damping-off disease decreases in gaps where the irradiance is high (Augspurger and Kelly 1984). Furthermore, light availability is likely to affect the potential of individual trees to invest in defenses due to tradeoffs with light requirements (Coley 1993; Shure and Wilson 1993; Kitajima and Poorter 2010). Host-tree characteristics such as tree size and functional traits might also affect the enemy communities. Species exhibit ontogenetic variation in leaf characteristics with potential effects on herbivory rates (Boege and Marquis 2005; Kitajima and Poorter 2010; Boege *et al*. 2011). Seedling size might therefore be an important predictor of the enemy communities by capturing the impact of an ontogenetic shift in defense traits (Herms and Mattson 1992; Barton and Koricheva 2010; Castagneyrol *et al*. 2013). Finally, seedling shade tolerance may be correlated with a high level of plant defenses (Coley and Barone 1996). Therefore, one might expect shade tolerant species to host lower richness of enemies and lower amount of damage than shade intolerant species (but see Bachelot and Kobe 2013).

In this study, we investigated the relationship between the richness of above-ground enemies hosted by individual tree seedling and foliar damage, and species abundance at the local and community scales in a tropical forest of Puerto Rico. Specifically we asked three questions:

(1) At the level of individual tree seedlings, which abiotic and biotic factors explain variation in the richness of above-ground enemies hosted by the seedling and variation in foliar damage? We hypothesized that the richness of above-ground enemies hosted by individual seedlings would peak at

intermediate conspecific seedling density (Fig. 1A) to create a hump-shaped relationship. Similarly, we expected foliar damage to peak at intermediate conspecific seedling density if enemies exhibit a type IV functional response. We also expected that both richness of above-ground enemies and foliar damage should increase with seedling size, conspecific adult crowding, soil moisture, and irradiance, but decrease with shade tolerance (Table 1).

(2) At the community level, what is the relationships between tree species abundance and richness of above-ground enemies hosted by tree species and, and between foliar damage and tree species abundance? We hypothesized that tree species existing at intermediate abundance in the community would host, on average, a higher richness of above-ground enemies and suffer greater damage than rare or common tree species (Table 1) because the aforementioned ecological and evolutionary processes (Fig. 1).

(3) Which type of enemies target seedlings at different local and community abundance? We hypothesized that the richness of generalist enemies such as grazing and skeletonizing insects and epiphyllous fungi will be greater on seedlings of rare tree species and at low conspecific seedling density, when compared to seedlings of common tree species and at high conspecific seedling density (Fig. 1B). In contrast, we expected the richness of specialist enemies such as pathogens, gall makers, and leaf miners to be greater on seedlings of common tree species and at high conspecific seedling density, when compared to seedlings of rare tree species and at low conspecific seedling density (Fig. 1B). The rationale behind this hypothesis is that endophages (enemies that penetrate in the host) tend to be more specialized than ectophages (enemies that remain outside the host) (Gaston *et al*. 1992) and high host abundance has often been shown to promote enemy specialization (Jaenike 1990; Barrett and Heil 2012; Forister *et al*. 2012; Wardhaugh 2014).

MATERIALS AND METHODS

Study Site

The study took place in the 16-ha Luquillo Forest Dynamics Plot (LFDP; 1820'N, 6549'W) in northeast Puerto Rico with elevation ranging from 333 to 428 m above sea level (Thompson *et al*. 2002; Zimmerman *et al*. 2010). Since the establishment of the plot in 1990, all free-standing woody stems > 1 cm dbh (diameter at 1.3 m) have been mapped, identified to species, and measured approximately every 5 years (Thompson *et al*. 2002; Uriarte *et al*. 2009). Mean annual rainfall is 3,500 mm (Thompson *et al*. 2004), which classifies the forest as tropical montane (Walsh 1996).

In 1998, 213 x 2 m^2 seedling plots were established throughout the plot (Uriarte *et al*. 2005; Comita *et al*. 2009). These plots were positioned every 20 m along six north-south running transects spaced 60m apart to systematically cover the 16-ha plot with an additional 21 seedling plots between each pair of transects 2 and 3, 3 and 4, and 5 and 6. Seedlings in these plots were mapped, identified to species, and measured in 2000, 2002, and 2004, and the annually after 2007. An additional 360 x 1 m^2 seedling plots were established in 2007 and have also been censused annually since 2007. The 1 m^2 seedling plots were clustered in sets of three around each of 120 seed collection baskets (i.e., 120 sets of 3 seedling plots). The criteria to include seedlings in the censuses differ between the two sets of seedling plots (1 m^2 and 2 m^2 plots), so we restricted our analyses here for both sets of plots to seedlings that were at least 10cm tall in the 2012 census.

Seedling Leaf Above-ground Enemy Community

Between May and July 2012 (following the 2012 seedling census), we collected data on above-ground enemies on seedlings in one plot of the three 1 m^2 seedling plots around each of the 120 seed collection baskets, and in 117 of the 213 x 2 m^2 seedling plots. To make data comparable across plots, the 2 m^2 seedling plots were divided in half, and we collected data from only 1 m^2. We excluded liana seedlings, and we only sampled 10 individuals per plot of the most abundant species, the palm *Prestoea acuminate var montana*, due to its extremely high abundance. In total, we obtained data for 237 seedling plots and

1,986 individual seedlings representing 48 tree species. To quantify the richness of enemies, we used a digital camera (Nikon D3100) with a microlense (18-55 mm VR lens) to photograph the total number of leaves of every seedling, up to a maximum of five leaves. From these photos, we visually identified leaf damage morphotypes, using the following criteria: (i) position of the damage (e.g. edge or middle of leaf, proximity to principal vein), (ii) shape of the damage (rounded, linear cut, irregular), (iii) size of the damage (< 1 mm, < 1 cm, > 1 cm), (iv) color (especially relevant to disease and pathogens), and (v) other defining characteristics (cut through veins, penetration through leaf or superficial grazing) (Bachelot and Kobe 2013). We used richness of damage morphotypes as a proxy for above-ground enemy richness because studies have shown that these two metrics are strongly correlated (Carvalho *et al*. 2014). We also organized damage morphotypes into six feeding categories, which represent increasing levels of host specialization: epiphyllous fungi, grazing insects, skeletonizing insects, pathogens, leaf miners, and gall makers. For each seedling, we were able to quantify the richness of enemies in each category. Finally, we estimated the amount of foliar damage for each seedling in order to assess its relationship to the richness of above-ground enemies, using percentage of damaged leaf (from 0 to 100 binned by 5). Damage on each seedling was evaluated and reported as a categorical variable representing the percentage of damaged leaf.

Biotic Factors

Using the 2012 annual seedling census data (January-May) and the 2011 adult tree census (June 2011-March 2012), we extracted data on seedling height and calculated the density of conspecific seedlings present in each seedling plot (214 x 1 m^2). Conspecific seedling density represents the local tree species abundance. From the tree census data, for each seedling i, we calculated the distance-weighted sum of conspecific adult tree basal areas within a 20m radius (NCI_i) around the seedling plots as follows:

$$NCI_i = \sum_{j=1}^{n} \left(\frac{dbh_j}{Distance_{ij}}\right)^2 \qquad \text{[Eqn. 1]}$$

where dbh_j is the diameter of a conspecific tree j and $Distance_{ij}$ corresponds to the distance of that conspecific tree j to seedling i. For each of the 48 seedling species, we also extracted the sum of total basal tree area at the community level as a measure of tree species abundance in the entire 16ha plot (*BA*).

Shade tolerance

We evaluated species-specific shade tolerance using average sapling (≤ 10 cm DBH) survival (Augspurger 1984). Specifically, we used sapling survival from the LFDP 1995-2000 tree census (Table S1). Sapling mortality over this period was high following pulses of recruitment after hurricane Hugo and subsequent canopy closure (Uriarte *et al*. 2009).

Abiotic Factors

Canopy closure, a proxy for shade, was assessed for each of the seedling plots using the mean of three densiometer readings taken above each seeding plot. To estimate potential soil drainage at each plot (inversely correlated with soil moisture), we assessed water flow potential using an elevation map of the LFDP (5 x 5 m) and the hydrology toolset of ArcGIS (ESRI 2011).

Statistical Analysis

To investigate the effect of abiotic and biotic factors on above-ground enemy richness, we used a generalized linear model in a hierarchical Bayesian framework. Since leaf area is likely to influence the amount of damage and the richness of above-ground damage morphotypes (Garibaldi *et al*. 2011a; 2011b), we standardized the observed richness of leaf damage morphotypes ($Richness_{observed}$) by dividing this metric by the number of leaves sampled (N_{leaves}) for each individual seedling i multiplied by the seedling species-specific leaf area (*LA*) as follows:

$$Richness_{standardized} = \frac{Richness_{observed}}{N_{leaves} * LA} \qquad \text{[Eqn. 2]}$$

This allows us to compare the richness of damage morphotypes per cm^2 of leaf area across individual seedlings and species. The richness of above-ground enemies and the total amount of foliar damage are highly correlated (Fig. 2). Therefore, we used only the richness of above-ground enemies in our study. Finally, we also calculated the richness of damage morphotypes per cm^2 of damaged leaf and ran the analyses described below using this response variable and obtained similar results as those found when using the richness of damage morphotypes per cm^2 of leaf.

Our response variables, standardized richness of above-ground damage morphotypes and standardized amount of foliar damage were similarly modeled as a function of abiotic characteristics of the plot, namely shade ($Shade_p$) and water flow ($Flow_p$), and conspecific density ($Consp_i$), adult neighborhood crowding (NCI_i), heterospecific density (Het_i), and focal seedling height ($Size_i$). We also included the quadratic term of the conspecific seedling density to allow for non-linear effects. The richness model takes the form:

$$Richness_{ijp} \sim dnorm(\Psi_{ijp}, \pi^2_{richness})$$

$$\Psi_{ijp} = \beta_1 * Size_i + \beta_2 * Flow_p + \beta_3 * Shade_p + \beta_4 * Consp_i + \beta_5 * Consp_i^2 + \beta_6 * NCI_i + \beta_7 * NCI^2_i + \beta_8 * Het_i + \beta_9 * Het^2_i + \mu_j + \gamma_p \qquad \text{[Eqn. 3]}$$

where $Richness_{ijp}$ and Ψ_{ijp} represent the observed and predicted standardized richness of above-ground enemies hosted by seedling i from species j in plot p. $\pi_{richness}$ is the standard deviation of richness of above-ground enemy species and μ_j and γ_p represent species and plot effects respectively. The species effect μ_j represents the average richness of above-ground enemy species hosted by a tree seedling species. It was modeled in a second level regression as a function of abundance of the tree species at the community scale (calculated as the total sum of basal tree area at the community level, BA_j), its quadratic form (BA^2_j) to account for potential non-linear effects, and shade tolerance ($Tolerance_j$) to account for variation in life history strategies across tree species which could influence seedling survival. For species j, the intercept is modeled as:

$$\mu_j \sim dnorm(a_0 + a_1 BA_j + a_2 BA_j^2 + a_3 Tolerance_j, \epsilon) \qquad \text{[Eqn. 4]}$$

where a_0 represents the mean richness of above-ground enemies hosted across tree species, a_1 and a_2 are the linear and quadratic effects of tree species abundance calculated at the community scale (*BA*), a_3 *is the* effect of shade tolerance, and ε is the standard deviation associated with the second level of the model. More specifically, parameters a_1 and a_2 represent variation in enemy richness or amount of foliar damage due to community abundance-dependent enemies, whereas a_0 represents enemy richness or amount of foliar damage due abundance-independent enemies. This second hierarchical level allows us to incorporate the idea of a community compensatory trend and assess whether or not intermediate abundance tree species host a greater richness of enemies than both rare and common tree species. The damage model has the same structure as the richness model.

To answer the first question about the hump-shaped relationship between tree species commonness at the local scale and enemy richness, and about the effects of abiotic and biotic factors on the richness of enemies, we examined the posterior distribution of all the $\beta_{1\text{-}6}$. To address the second question about the effect of species commonness at the community scale on the richness of enemies, we focused our attention on the posterior distribution of a_1 and a_2. Specifically, we asked whether the credible intervals of these parameters ($a_{1\text{-}3}$ and $\beta_{1\text{-}9}$) did not overlap zero, indicating significant effects. The model was fitted using JAGS (Plummer 2005) statistical software. Convergence was assessed using R-hat (Brooks and Gelman 1997). The significance of the parameters was evaluated using the 95% credible intervals. Model goodness of fit was evaluated with predictive checks (Gelman *et al.* 2013). The spatial structure of the residuals was assessed visually by fitting a semi-variogram and statistically by using a Mantel test between the residuals and the locations with 9999 permutations.

To answer the third question, we compared the richness of enemies belonging to each of the six enemy types (epiphyllous fungi, grazing insects, skeletonizing insects, pathogens, leaf miners, and gall makers) at low, intermediate, and high conspecific seedling density, using t-tests. We also compared the richness of enemies in each category at low, intermediate, and high conspecific tree abundance (as the total sum of basal tree area) using t-tests. Low, intermediate, and high abundances (at the local and community scales) were defined as abundances below the 15%, between 42.5% and 67.5%, and above the 85% quantiles. In order to correct for varying sampling size across the abundance categories, we bootstrapped the richness of enemies 500 times using the lowest sample size across the three categories. We then corrected for multiple comparisons using the false discovery rate (Benjamini and Hochberg 1995).

All covariates except shade from densiometer measurements of canopy cover were first log-transformed to correct for skewness and then z-transformed prior to analyses. We checked for collinearity among covariates using Pearson correlation tests and we found that slight correlations between seedling conspecific density and total sum of basal tree area ($r = 0.36$), and seedling height and sum total of tree basal area ($r=0.32$). To assess whether these correlations might be problematic, we measured collinearity between posterior chains of the parameters associated with seedling height, sum total of tree basal area, and conspecific seedling density, using Pearson correlation tests. All analyses were performed in R 3.1.1. (R Core Team 2013) using JAGS (Plummer 2005).

RESULTS

Overall, we quantified enemy richness for 1886 seedlings representing 48 species. Individual seedlings exhibited great variation in the richness of above-ground enemies and in the amount of leaf damage per cm^2 of leaf area among and within species (Fig. S1, Table S1 in Supporting Information). On average, seedlings hosted 0.09±0.09SD enemies.cm^{-2} (range 0-1.22 enemies.cm^{-2}) of leaf area, and the amount of damage ranged from 0-9.2% damaged.cm^{-2}. Various types of enemies were identified: Pathogens and grazing insects were the most common enemies across tree species (Fig. S1). Leaf miners and gall makers were rare and appeared on a few host species (Fig. S1). The distribution of the richness of above-ground enemies per cm^2 exhibited a right-skewed shape typical of parasite/host interactions (Vázquez and Poulin 2005), suggesting that most seedlings host a small number of enemy species (Fig. S1).

1) At the level of individual tree seedlings, which abiotic and biotic factors explain variation in the richness of above-ground enemies hosted by the seedling and foliar damage?

The model captured 45% of the observed variation in above-ground enemy richness at the individual seedling level (Table S2, Fig. 3, and Fig. S2, Bayesian *P* value of the mean = 0.50). No spurious correlations were found between posterior chains suggesting that the slight correlations between covariates were not a problem. Spatial analyses of the residuals revealed no spatial structure, suggesting our model captured most of the spatial structure in the above-ground enemy community (Mantel test, *P* = 0.74).

Consistent with our prediction, the relationship between conspecific seedling density and enemy richness of above-ground enemies was hump-shaped (Table S2, parameters β_4 and β_5 in eqn. 3, Fig. 3, Fig. 4). The richness of above-ground enemies peaked at intermediate seedling conspecific abundance at the local scale. Furthermore, the richness of enemies also increased with greater heterospecific density (Table S2, parameters β_8 and β_9 in eqn. 3, Fig. 3, Fig. 4).

Consistent with our hypotheses, the richness of above-ground enemies significantly increased with seedling size (β_1 in eqn. 3), and decreased with soil drainage (β_2 in eqn. 3) although the latter effect was only marginally significant (Table S2, Fig. 3). Surprisingly, adult tree neighborhood crowding (β_6 and β_7 in eqn. 3) and shade (β_3 in eqn. 3) had no effect on the richness of above-ground enemies hosted by individual seedlings (i.e., credible interval overlapped 0, Table S2).

The relation between foliar damage and local host abundance exhibited similar patterns as the richness of above-ground enemies (Table S2). Locally, seedlings at intermediate seedling conspecific abundance experienced the highest amount of foliar damage. Unlike the richness of above-ground enemies, foliar damage significantly increased in the shade (parameter β_3 in eqn. 3, Table S2, Fig. 3) but was not correlated with soil drainage (parameter β_2 in eqn. 3, Table S2, Fig. 3) or heterospecific seedling density (parameters β_8 and β_9 in eqn. 3, Table S2, Fig. 3).

2) At the community level, what are the relationships between the richness of above-ground enemies hosted by tree species and tree species abundance, and between foliar damage and tree species abundance?

The average richness of above-ground enemies did not change linearly with the commonness of tree species (i.e., parameter a_1 in eqn. 4 overlapped 0), calculated as the sum of conspecific adult tree basal area throughout the whole LFDP (Table S2). Yet, there was a significant negative quadratic effect of tree commonness on the richness of above-ground enemies hosted by seedlings (parameter a_2 in eqn. 4, Fig. 3 and Fig. 4, Table S2). Thus, richness of above-ground enemies peaked at intermediate tree abundance at the community scale, which is consistent with our findings at the local scale. Contrary to our expectation, the average richness of above-ground enemies was not significantly altered by the shade tolerance of tree species (parameter a_3 in eqn. 4, Fig. 3, Table S2).

Average foliar damage followed similar patterns as average above-ground enemies richness at the community scale. Specifically, foliar damage did not linearly change with tree species commonness. Instead, it peaked at intermediate tree species abundance (parameter a_2 in eqn. 4, Fig. 3 and Fig. 4, Table S2). Contrary to our expectation, shade tolerance did not alter the average amount of damage experienced by seedlings (parameter a_3 in eqn. 4, Fig. 3, Table S2).

3) Which type of enemies target seedlings at different local and community abundance?

Among the six categories of enemies, grazing and skeletonizing insects and epiphyllous fungi, which are expected to exhibit low levels of host specialization, show significant variation across abundance classes. Specifically, the richness of grazing and skeletonizing insects and epiphyllous fungi was greater at low and intermediate tree abundance and conspecific seedling density (Fig. 5, Table S3). This is consistent with the ecological expectation of enemy satiation, intraspecific herd protection, and enemy predator attraction occurring at high seedling abundance (Fig. 1A), and with the evolutionary expectation that rare and intermediate abundance tree species should host a higher richness of generalist enemies relative to common tree species (Fig. 1B).

At the local scale, the richness of generalist enemies peaks at intermediate conspecific density consistent with escape from enemies at low density. Contrary to our expectation (Fig. 1B), there was no significant change in the richness of specialist enemies hosted by seedling across local conspecific seedling densities (Fig. 5, Table S3). At the community scale, consistent with our expectation, generalist enemy richness dropped at high tree species abundance, sometimes showing a peak at intermediate abundance (for the skeletonizing insects, Fig. 5, Table S3). Among specialist enemies, only pathogens exhibited a significant change in richness with abundance of tree species (Fig. 5, Table S3). Specifically, pathogen richness dropped at high tree species abundance similarly to the pattern observed in generalist enemies.

DISCUSSION

In this study, we investigated the ecological factors associated with the richness of above-ground enemies and foliar damage, which exhibit great variations in the LFDP within and across tree species (Fig. S1). Specifically, we tested the hypothesis that seedlings at intermediate conspecific seedling density and from tree species that exist at intermediate level of abundance at the community host a high richness of above-ground enemies and experience high foliar damage. Our results contribute to ecological understanding of the factors that control rarity and abundance of tree species, and the interactions between enemies and tree species in tropical forest. We also highlight fruitful directions for further development of species coexistence theory.

At the level of individual tree seedlings, which abiotic and biotic factors explain variation in the richness of above-ground enemies hosted by the seedling and foliar damage?

Previous studies (Strong *et al*. 1984; Moran *et al*. 1994; Bachelot and Kobe 2013) suggested that the richness of enemies should increase with conspecific seedling density. Our results are partially consistent with these theories as we found that the relationship between species abundance and richness of above-ground enemies hosted by an individual seedling exhibited a hump-shaped pattern with richness, peaking at intermediate densities of conspecific seedlings. For example, *Schefflera morototoni* had low local abundance (0. 19 seedlings.m^{-2}) and hosts on average 0.07 above-ground enemy species per cm^2 of leaf. *Inga laurina,* which has high local abundance (4.62 seedlings.m^{-2}), hosts only 0.01 above-ground enemy species per cm^2 of leaf. In contrast to these species that represent low and high local seedling abundances respectively, *Casearia arborea* has an intermediate local abundance of 1.18 seedlings.m^{-2} and hosts richness of 0.34 above-ground enemies per cm^2 of leaf. This hump-shaped relationship between enemy richness and seedling conspecific density is also consistent with a previous study that aimed at uncovering the shape of negative density dependent mortality (Bagchi *et al*. 2010b). Bagchi et al. (2010b) found lowest survival at intermediate initial seedling density, which is in line with our ecological prediction, which suggests that seedlings at high conspecific density might experience intraspecific herd protection (Peters 2005; Barbosa *et al*. 2009), satiate enemies (Silvertown 1980; Otway *et al*. 2005), and attract predators of enemies (Denno *et al*. 2002; Visser *et al*. 2011), whereas seedlings at low conspecific density manage to escape these enemies (Chew and Courtney 1991; Castagneyrol *et al*. 2014) and experience interspecific herd protection (Wills and Green 1995). Studies on damage to seedlings of the most common tree in a New Guinea forest (*Parashorea malaanonan*) have also demonstrated that damage significantly decreased at high conspecific density (e.g. Bagchi *et al*. 2010a), consistent with our finding that seedlings at intermediate conspecific density experience more damage than seedlings at high conspecific density. For example, *Schefflera morototoni* had a low local abundance of 0. 19 seedlings.m^{-2} and suffers on average 0.14 % of damage per cm^2 of leaf. *Inga laurina* has a high local abundance of 4.62 seedlings.m^{-2} and suffers only 0.24 % of damage per cm^2 of leaf. In contrast to these species that represent low and high local seedling abundances respectively, *Casearia arborea* has an intermediate local abundance of 1.18 seedlings.m^{-2} and suffers on average 0.58 % of damage per cm^2 of leaf. Additionally, species occurring at high seedling densities may be better defended because past or concurrent favorable environmental conditions lead to greater availability of plant resources for allocation to defense. One can therefore argue that in high-density conspecific patches, seedlings have enough resources to defend themselves against pathogens, which results in a low richness of enemies successfully attacking them and therefore low damage (Coley *et al*. 1985; Coley1983a; Coley 1983b; Coley and Barone 1996).

Finally, we found a correlation between heterospecific seedling density and richness of above-ground enemies, but not for foliar damage. As density of heterospecific seedlings increases, more enemies might be attracted by different hosts, which would in turn increase the richness of enemies hosted by individual seedlings. This result is contrary to the herd protection hypothesis, which predicts a decrease in enemies when surrounded by many heterospecific seedlings (Barbosa *et al*. 2009). However, it is consistent with the attraction of shared specialist enemies and of generalist enemies. Interestingly, heterospecific seedling density was not significantly correlated with the amount of damage. This pattern could arise if the enemies, which are attracted by heterospecific seedlings, only target the focal seedling by accident.

Abiotic factors also influenced the richness of above-ground enemies and the amount of foliar damage. Although we detected a positive association between light availability and above-ground enemy richness, the effect was not significant. The lack of a significant relationship between light and enemy richness is not totally surprising since these effects are known to be complex and specific to individual enemy-tree interactions. For example, Augspurger *et al*. (1984) found a negative effect of light on the success of pathogenic fungi responsible for damping off in Panama, whereas Alvarez-Loayza *et al*. (2008) found that light activates the pathogeny of an endosymbiotic fungus in Peru. Therefore, the lack of a clear significant effect of light on the richness of above-ground enemies hosted by seedlings might arise from enemy species-specific response to light. However, we found that foliar damage significantly increased in shaded plots, consistent with previous studies (Eichhorn *et al*. 2010; Münzbergová and Skuhrovec 2013). Our index of potential soil moisture (soil drainage) was positively correlated with the richness of above-ground enemies although the effect was only marginally significant (90% credible intervals did not overlap with 0). Specifically, seedlings in plots with high soil drainage (low soil moisture) had lower richness of above-ground enemies. This trend was consistent with our expectation and results from other studies (e.g. Münzbergová and Skuhrovec 2013; Spear *et al*. 2014), but inconsistent with other work that found decreasing attack by enemies with increasing soil moisture (e.g. Stona and Bacon 1994; Nystrand and Ganström 2000). It is important to note that 2012 was a wet year, which might have resulted in lack of variation in moisture across seedling plots, masking a potential relationship between soil moisture and enemy richness. However, we detected no significant correlation between the amount of foliar damage and soil moisture. Overall, the effects of light and soil moisture on above-ground enemy community richness and on foliar damage remain unclear and are likely to be context-dependent.

Seedling characteristics were also important predictors of the richness of above-ground enemies and foliar damage. In particular, we found that the richness of above-ground enemies and the amount of foliar damage increased with seedling size. The most parsimonious explanation for this pattern is that larger seedlings were likely older and exposed to pathogens and herbivores for a greater length of time. Seedling size can also be correlated with above-ground enemy community richness and foliar damage because changes in nutritional status and defense traits occur along ontogeny (Boege and Marquis 2005). The nutritional quality of tree leaves has been shown to initially increase with seedling size, before decreasing once seedlings start allocating more resources to defense rather than growth (Herms and Mattson 1992; Coley *et al*. 1985; Coley 1987; Boege and Marquis 2005).

Finally, contrary to our hypothesis that the richness of the above-ground enemies and foliar damage would increase with conspecific adult crowding, we did not find a significant effect at the local scale. The absence of an adult neighborhood effect might indicate that adult trees and seedlings have different communities of above-ground enemies, which may be due to differences in tree functional traits through ontogeny (Boege and Marquis 2005; Kitajima *et al*. 2013). The lack of an adult neighborhood effect was consistent with other recent studies that found no effect of distance from conspecific adult trees or adult neighborhood density on the amount of herbivory in other tropical forests (Bachelot and Kobe 2013; Cárdenas *et al*. 2014; but see Schweizer *et al*. 2013).

At the community level, what are the relationships between the richness of above-ground enemies hosted by tree species and tree species abundance, and between foliar damage and tree species abundance?

A recent study from a primary forest in Costa Rica showed that seedlings from common tree species hosted a high richness of enemy species (Bachelot and Kobe 2013). Our results in Luquillo do not support the Costa Rican study as we found that the abundance of tree species at the plot scale was not linearly related to the richness of above-ground enemies hosted by tree species or to foliar damage, but followed hump-shaped patterns. In particular, we found that tree species of intermediate abundance hosted a greater richness of above-ground enemy richness and suffered high levels of foliar damage, consistent with our hypothesized ecological and evolutionary processes. The parallel hump-shaped patterns at both the local and plot scale suggest that similar processes may be at play at these two scales. For example, *Matayba dominguensis* is a tree species of intermediate abundance within the LFDP, yet it hosts the highest richness of above-ground enemies per cm^2 of leaf (0.61) and experiences a high amount of damage (1.26). In contrast, *Casearia decandra*, a rare tree species, and *Prestoea acuminata,* the dominant palm species, host a low load of above-ground enemy species per cm^2 of leaf (both species 0.05) and they both suffer low amount of foliar damage (0.20 and 0.14 respectively).

The community compensatory trend predicts that common tree species should experience greater mortality due to enemies than rare tree species because common tree species are more clumped and at higher conspecific density (Connell *et al*. 1984). Many studies have attempted to test this idea by comparing mortality of seedlings belonging to rare and common tree species (Welden *et al*. 1991; He *et al*. 1997; Webb and Peart 1999; Queenborough *et al*. 2007; Chen *et al*. 2010; Metz *et al*. 2010). In Borneo, pathogens were hypothesized to be at the origin of the community compensatory trend detected (Webb and Peart 1999). In Malaysia, mortality was shown to increase with tree species abundance, consistent with a community compensatory trend (He *et al*. 1997). In Ecuador, however, both a community compensatory trend (Queenborough *et al*. 2007) and no community compensatory trend were detected (Metz *et al*. 2010). Similarly, in Panama, no community compensatory trend was detected

(Welden *et al*. 1991). Together these studies demonstrate a high degree of variability across different tropical forests, which might be partly explained by methodology (Zhu *et al*. 2015), or by variation in climate (Swinfield *et al*. 2012; Comita *et al*. 2014; Spear *et al*. 2014; Bachelot and Kobe *in press*). Another possibility for inconsistencies across studies is that the community trend is not linear and with further analysis of these other studies a hump-shaped relationship might become apparent. Although in this paper we have not considered seedling mortality, our results suggest that species at intermediate abundance host a high richness of enemies and experience high levels of foliar damage, which could result in higher mortality at intermediate abundance relative to low or high tree species abundance.

Surprisingly, shade tolerance had no significant effect on the average amount of foliar damage experienced by seedlings or on the average richness of above-ground enemies hosted by seedlings. Shade tolerance has been associated with higher levels of defense and resistance to enemies (Coley and Barone 1996). Therefore, we expected shade tolerant species to host more enemy species and to suffer greater amount of damage than shade intolerant species. However, shade tolerance has also been associated with longer leaf lifespan suggesting that leaves might be exposed to enemies for longer periods of time than leaves of shade intolerant species (Coley 1988), resulting in higher amount of damage and richness of enemies. Together these potentially opposite effects of shade tolerance might explain the lack of significant effects detected in our study.

Which type of enemies target seedlings at different local and community abundance?

The result that seedlings at intermediate conspecific seedling density and from tree species that exist at intermediate abundance levels in the community host a high richness of enemies and suffer greater foliar damage might be in part explained by differential attraction of generalist and specialist enemies. We predicted that rare species attract a few generalist enemies, common species attract a few specialist enemies, and intermediate abundance species might host a rich mixture of generalist and specialist enemies, resulting in high foliar damage. To assess this hypothesis, we distinguished six enemy categories, which are thought to exhibit various level of host specialization. Generally, endophages (leaf miners, gall makers, and pathogens) show the tightest host specificity, whereas ectophages (grazing and skeletonizing insects and epiphyllous fungi) are more likely generalists (Jaenike 1990; Gaston *et al*. 1992; Ward and Spalding 1993; Novotny and Basset 2005; Novotny *et al*. 2010; Forister *et al*. 2015). We expected that the richness of generalist enemies would be lower at high tree species and seedling abundances due to satiation (Otway *et al*. 2005), high levels of physiological and chemical defenses (Feeny 1996), intraspecific herd protection (Barbosa *et al*. 2009), and predator attraction (Denno *et al*. 2002; Visser *et al*. 2011). Consistent with our expectation, rare and intermediate tree species hosted a greater number of grazing and skeletonizing insects and epiphyllous fungi, which were all expected to exhibit low levels of host specificity (Novotny and Basset 2005; Novotny *et al*. 2010). This result is also consistent with network theory, which predicts that rare tree species should interact with generalist enemies rather than specialist enemies because host relative abundance predicts the number and type of interspecific interactions (Vazquez *et al*. 2005).

Contrary to our expectation that the richness of specialist enemies such as pathogens should increase with tree species and seedling abundances, we found that overall all seedlings hosted the same richness of specialist enemies. This suggests that generalist enemies might be at the origin of the hump-shape patterns observed between the richness of enemies and species abundance, and between the amount of foliar damage and species abundance. The overall similar richness of specialist enemies in rare and common tree species was however surprising given the anticipated higher resource and evolutionary costs required to specialize on rare hosts (Jaenike 1990; Barrett and Heil 2012; Forister *et al*. 2012; Wardhaugh 2014). Enemies might have evolved specialized attributes to enable them to detect and overcome the defenses developed by rare hosts, as it is the case in some Lepidoptera species (Courtney and Courtney 1982), particularly in highly diverse ecosystems that exhibit high levels of enemy specialization (Novotny *et al*. 2004; Forister *et al*. 2015 but see Morris *et al*. 2014). One potential hypothesis of enemy specialization on rare plants is that such strategy would allow enemies to escape their predators (Enemy-free space hypothesis, Jeffries and Lawton 1984). The ecological and evolutionary causes of host specialization are a very active field of theoretical and empirical research and this remains an open question (Bolnick *et al*. 2003; Ruefller *et al*. 2006; Gilbert and Webb 2007; Singer 2008; Barrett and Heil 2012; Forister *et al*. 2012; Morris *et al*. 2014; Forister *et al*. 2015).

Both ecological and evolutionary processes could lead to a hump-shaped relationship between enemy richness or foliar damage and tree abundance at the local and community scales. Future studies could tackle the task of understanding the ecological processes that underlie the hump-shaped relationships between tree abundance and enemy richness or foliar damage while accounting for evolutionary processes. Such studies could for example involve field experiments to characterize the above- and below-ground enemy communities targeting seedlings grown at various conspecific and heterospecific densities. Combining these experiments with knowledge about the phylogeny of the host plants and enemies could provide a way to disentangle herd protection from evolutionary processes. Similarly, combining tri-trophic studies with a good understanding of enemy/host phylogenies could shed light on the effects of predator attraction and evolutionary processes on the richness of enemy communities.

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DATA ACCESSIBILITY

Long-term data are available on the Luquillo LTER data website (http://luq.lternet.edu/data/datacatalog).

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Table 1. Hypothesized effects of abiotic and biotic variables on the richness of enemies hosted by individual seedlings.

Question	Covariate	Effect	Hypothesized Mechanism	Reference
At the individual level, which abiotic and biotic factors explain variation in the richness of enemies hosted by a tree seedling and in the amount of damage?	Size	+	Increase feeding efficiency of enemies	Garibaldi *et al*. 2011a; 2011b
	Conspecific adult crowding	+	Adult trees are source of enemies	Janzen 1970; Connell 1971
	Conspecific density	+/-	High density attracts enemies, but ecological and evolutionary processes might result in a hum-shape relationship (Fig. 1)	Janzen 1970; Connell 1971; Lewis *et al*. 2010; Ness *et al*. 2011
	Heterospecific density	+/-	High density attracts generalist enemies but might deter specialists (herd protection, Fig. 1)	Janzen 1970; Connell 1971; Barbosa *et al*. 2009
	Water flow	+	Via tree quality and enemy physiology	Price *et al*. 2011
	Light	-	Via tree quality and enemy physiology	Kitajima and Poorter 2010
At the community level, what are the relationships between the richness of above-ground enemies hosted by tree species and tree species abundance, and between foliar damage and tree species abundance?	Sum of basal tree area (conspecific)	+/-	Enemies tend to target common tree species, but ecological and evolutionary processes might result in a hum-shape relationship (Fig. 1)	Connell *et al*. 1984 Bachelot and Kobe 2013
	Shade tolerance	-	Shade tolerant species are hypothesized to have higher levels of defense than shade intolerant species	Coley ad Barone 1996

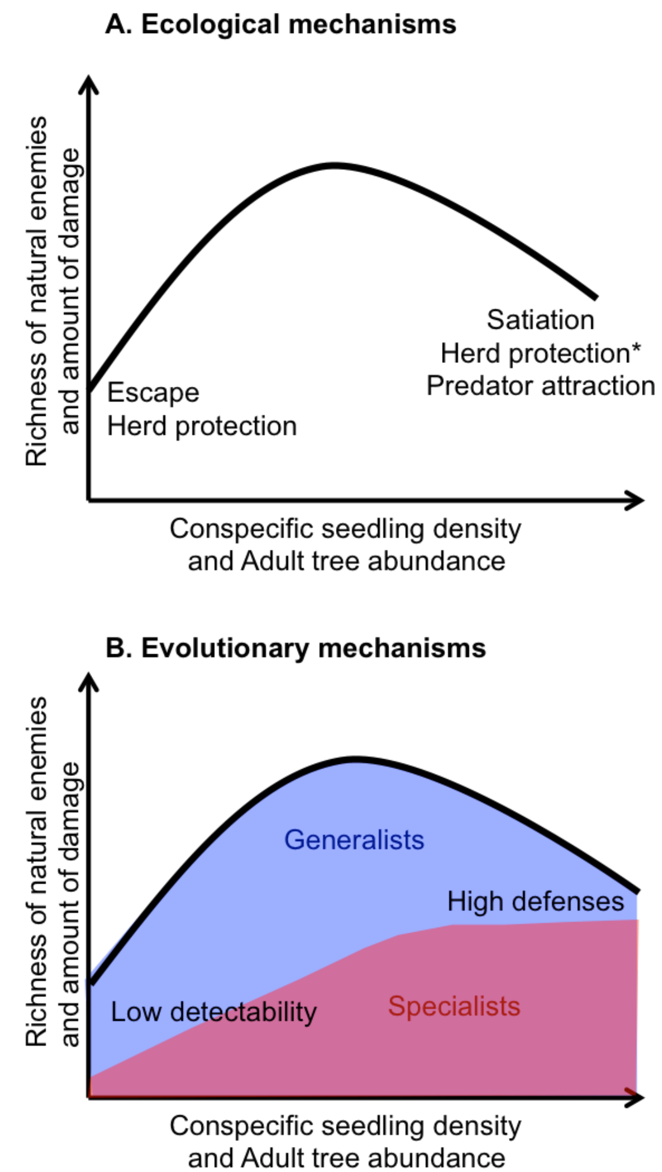

Figure 1: Diagram representing the proposed hump-shaped relationship between enemy richness a species abundance due to (A) ecological processes and (B) evolutionary processes. From an ecolog perspective, seedlings at low conspecific abundance might escape enemies and experience interspe herd protection. In contrast, at high abundance, enemies might satiate or be deterred by their densi responsive predators and seedlings might experience intraspecific herd protection (denoted with an against enemies, leading to lower enemy richness. These ecological processes would lead to a high richness of enemies at intermediate abundance. From an evolutionary prospective, rare tree species only be targeted by generalist enemies (blue) whereas common tree species might be targeted by specialist enemies (red). These patterns might result from trade-offs between the costs of searching common or rare tree species versus the fitness benefits gained via specialization. These evolutiona processes would also result in a hump-shaped pattern between host abundance and enemy richness because host species at intermediate abundance species host both generalist and specialist enemies

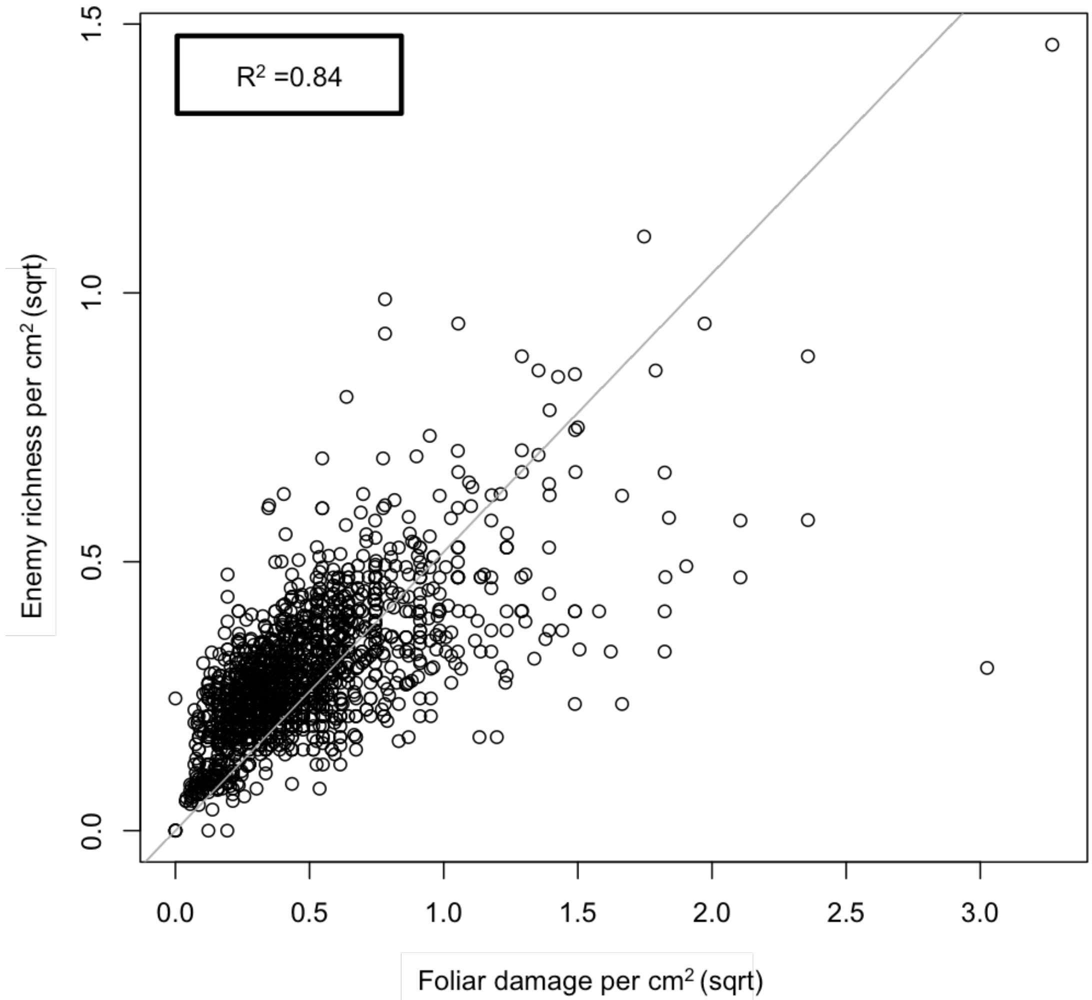

Figure 2: Relationship between foliar damage and richness of above-ground enemies. Regression was significant at $p < 0.001$.

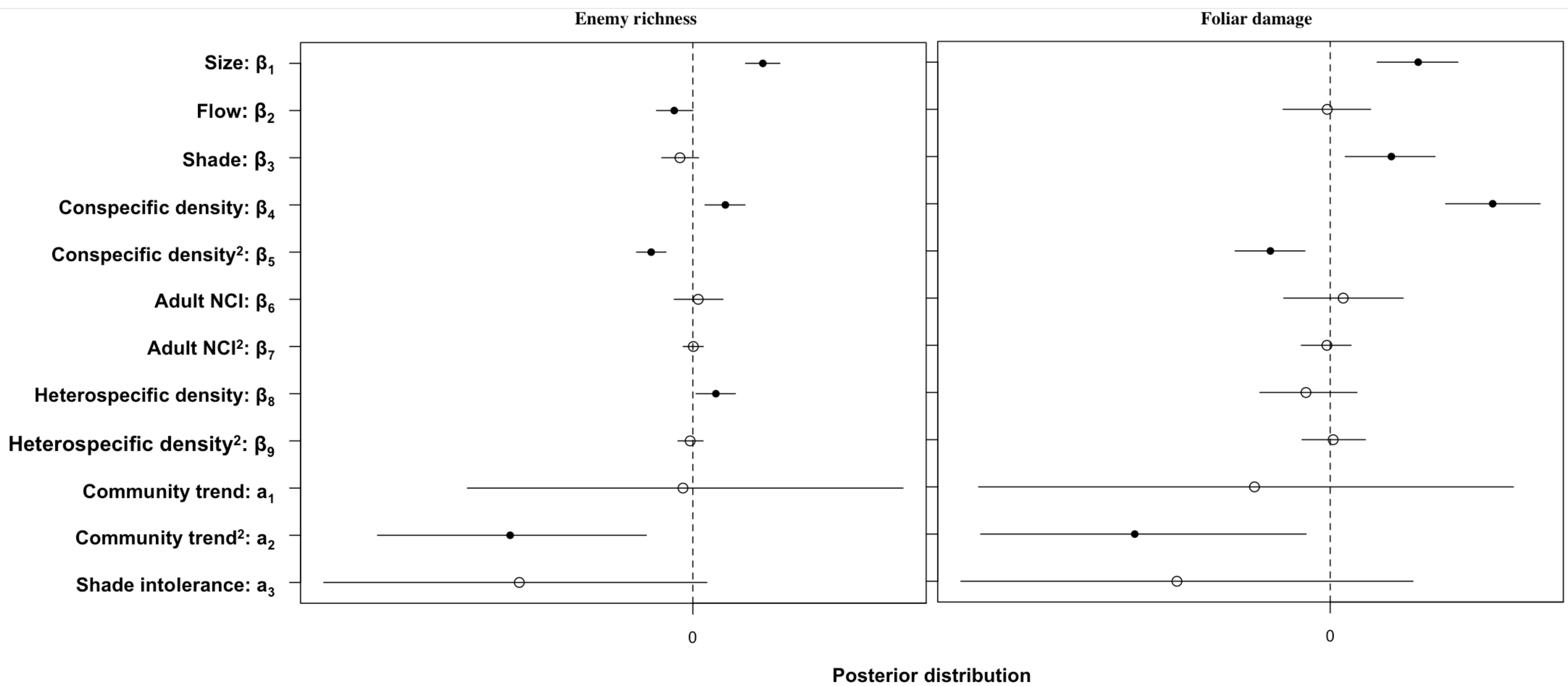

Figure 3: Posterior distributions (median and credible intervals) of each parameter of the enemy richness and foliar damage models. Filled symbols mean that the posterior distribution was significantly different from zero.

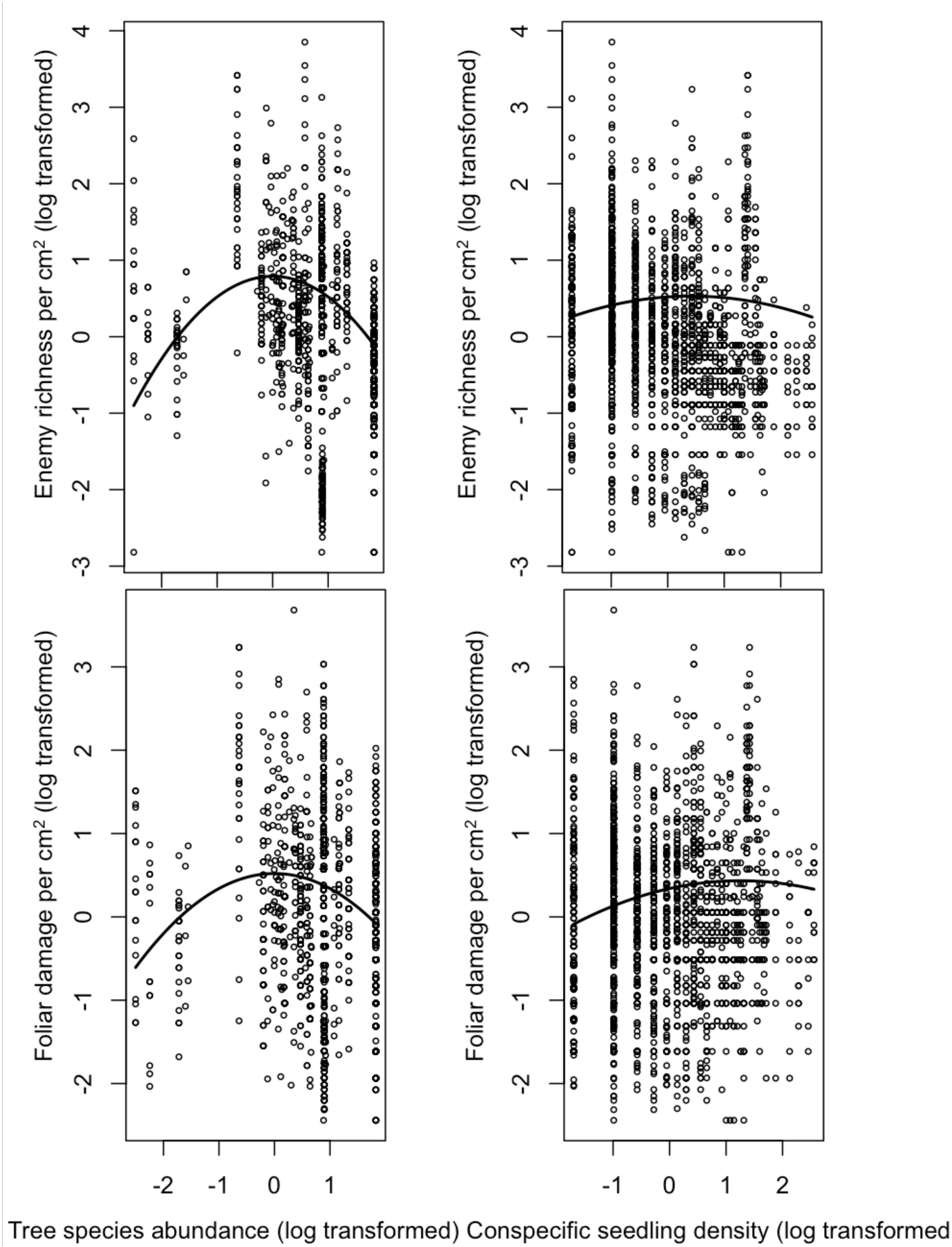

Figure 4: Richness of enemies (per cm^2) as a function of seedling conspecific density and tree abundance (sum of conspecific basal tree area in the whole plot).

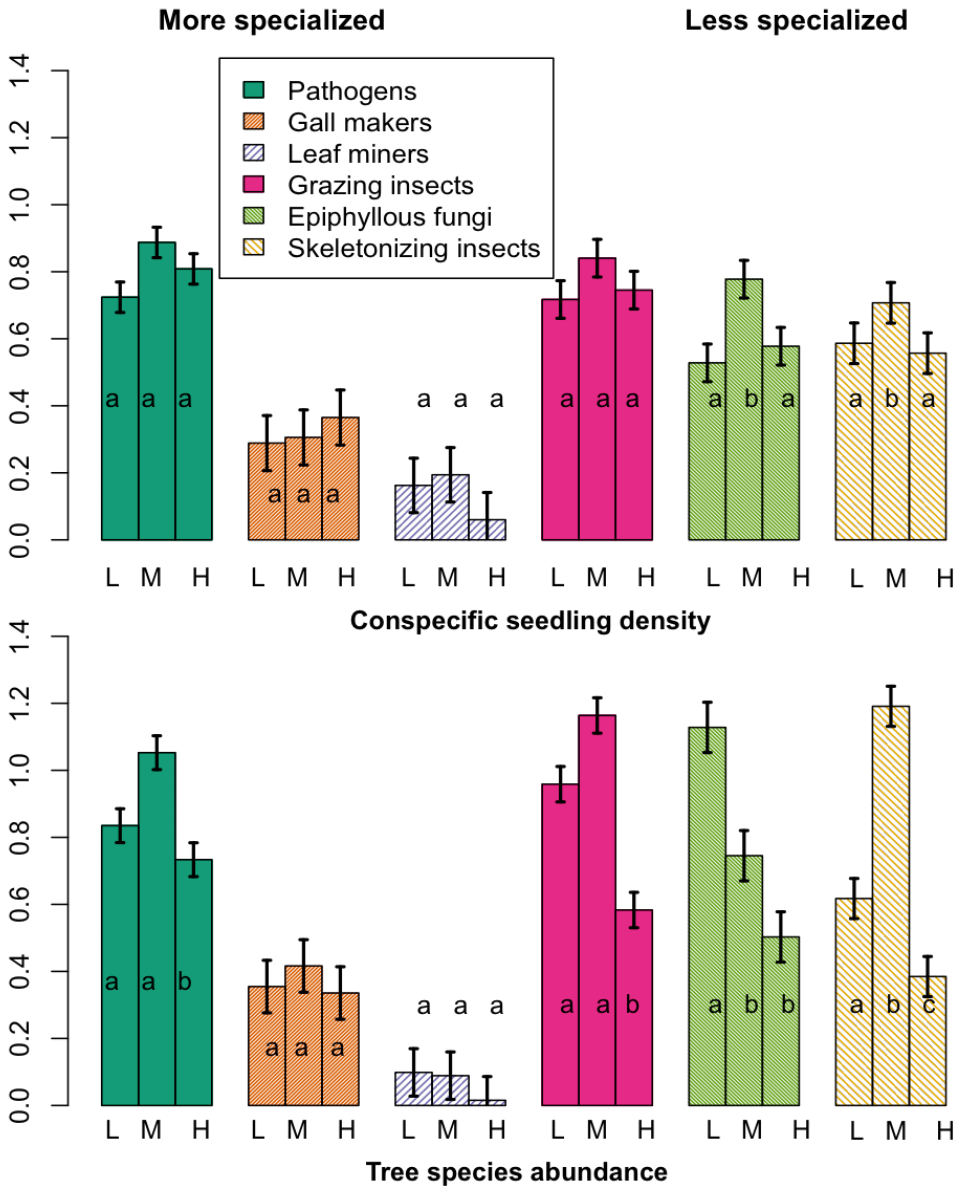

Figure 5: Enemy richness across low (L), medium (M) and high (H) abundance of conspecific seedling density and tree abundance (sum of conspecific basal tree area in the whole plot). These abundance classes were determined using the 15th, 42.5th, 57.5th, and the 85th quantiles of the abundance distributions. Low correspond to species with abundances below the 15th quantile, medium comprises species falling between the 42.5rd and the 57.5th quantiles, and high species above the 85th quantile. Letters indicate statistically significant differences between abundance groups within each enemy type category.

Supporting Information

Table S1. List of the species used in the study with the sample size (N), the mean and standard deviation of the above-ground enemy richness (number of enemies per cm^2), and foliar damage (% of damage per cm^2), the sum of basal tree area (cm), and shade tolerance of the species.

Species	N	Enemy richness mean	Enemy richness sd	Foliar damage mean	Foliar damage sd	BA	Shade tolerance
Alchornea latifolia	2	0.105	0.016	0.117	0.071	29.202	0.941
Andira inermis	1	0.049	0	0.106	0	7.743	0.952
Calophyllum calaba	3	0.054	0.011	0.144	0.13	0.002	0.91
Casearia arborea	11	0.343	0.117	0.583	0.348	2269.489	0.926
Casearia decandra	1	0.05	0	0.201	0	0	1
Casearia sylvestris	4	0.081	0.028	0.195	0.154	220.227	0.954
Cassipourea guianensis	1	0.107	0	0.699	0.791	1.196	0.955
Chionanthus domingensis	7	0.264	0.158	0.818	0	1.831	0.976
Cordia borinquensis	1	0.082	0	0.006	0	28.799	0.882
Cordia sulcata	1	0.018	0	0.248	0	6.733	0.938
Croton poecilanthus	1	0.159	0	0.23	0	2.07	0.98
Dacryodes excelsa	43	0.128	0.058	0.254	0.236	1433.597	0.997
Dendropanax arboreus	1	0.076	0	0.163	0	4.147	0.971
Dolichandra unguis	16	0.162	0.115	1.401	3.141	0	0.948
Drypetes glauca	8	0.157	0.076	1.434	1.388	13.938	0.857
Eugenia domingensis	32	0.35	0.223	0.708	0.464	0.161	0.955
Eugenia stahlii	3	0.253	0.098	0.347	0	20.095	0.993
Faramea occidentalis	1	0.194	0	0.018	0.014	11.744	0.98
Guarea glabra	2	0.012	0.004	0.564	0.605	3.645	0.798
Guarea guidonia	362	0.146	0.073	0.23	0.226	129.648	0.972
Homalium racemosum	4	0.139	0.063	0.024	0.033	33.088	0.96
Inga laurina	89	0.008	0.003	0.242	0.193	291.582	0.918
Inga vera	10	0.108	0.052	0.168	0.101	2.218	0.964
Ixora ferrea	16	0.079	0.029	0.327	0.282	8.962	0
Manilkara bidentata	33	0.113	0.051	0.243	0.177	1093.293	0.986
Matayba domingensis	10	0.609	0.323	1.246	0.959	22.904	0.866
Miconia racemosa	3	0.12	0.019	0.2	0.167	0.004	0.453
Myrcia deflexa	2	0.094	0.044	0.218	0.132	8.918	0.92
Myrcia leptoclada	12	0.251	0.123	0.604	0.43	4.309	0.989
Myrcia splendens	1	0.651	0	0.407	0	3.839	0.94
Ocotea leucoxylon	96	0.076	0.026	0.182	0.165	57.564	0.949
Ocotea sintensis	39	0.103	0.035	0.209	0.298	0.763	0.899
Ormosia krugii	5	0.205	0.091	1.926	1.457	2.798	0.89
Piper glabrescens	24	0.06	0.018	0.113	0.073	0.001	0.916
Piper hispidum	1	0	0	0.037	0	0	0.804

Prestoea montana	836	0.047	0.021	0.142	0.157	37591.37	0.992
Pseudolmedia spuria	2	0.11	0.019	0.172	0.146	4.475	0.992
Psychotria berteroana	18	0.058	0.017	0.111	0.079	17.367	0.852
Psychotria brachiata	7	0.066	0.019	0.137	0.043	13.888	0.959
Psychotria deflexa	13	0.069	0.025	0.139	0.131	0	0.958
Roystonea borinquena	39	0.149	0.062	0.479	0.554	1.662	0.91
Sapium laurocerasus	1	0.047	0	0.047	0	2.565	0.923
Schefflera morototoni	16	0.068	0.033	0.136	0.147	300.091	0.902
Sloanea berteroana	8	0.065	0.029	0.141	0.133	1468.845	0.983
Syzygium jambos	4	0.169	0.068	0.584	0.726	2.964	0.986
Tabebuia heterophylla	42	0.051	0.048	0.095	0.1	59.406	0.94
Tetragastris balsamifera	31	0.093	0.034	0.17	0.18	72.236	0.988
Trichilia pallida	21	0.14	0.068	0.277	0.154	35.728	0.966

Table S2. Results of the Bayesian models described in equation 3 and 4 (median follows by the credible intervals in parentheses). Bold font indicates the effect was significant.

Variable	**Symbol**	**Posterior of the enemy richness model**	**Posterior of the foliar damage model**
Size	β_1	**0.11** (0.08:0.13)	**0.08** (0.04:0.12)
Flow	β_2	**-0.03** (-0.05:0)	0 (-0.04:0.04)
Shade	β_3	-0.02 (-0.05:0.01)	**0.06** (0.01:0.1)
Conspecific	β_4	**0.05** (0.02:0.08)	**0.15** (0.11:0.19)
Conspecific^2	β_5	**-0.06** (-0.08:-0.04)	**-0.06** (-0.09:-0.02)
NCI	β_6	0.01 (-0.03:0.05)	0.01 (-0.04:0.07)
NCI^2	β_7	0 (-0.01:0.02)	0 (-0.03:0.02)
Heterospecific	β_8	**0.03** (0:0.06)	-0.02 (-0.06:0.02)
Heterospecific^2	β_9	0 (-0.02:0.02)	0 (-0.03:0.03)
Richness average	a_0	**0.79** (0.46:1.11)	**0.52** (0.27:0.78)
BA	a_1	-0.01 (-0.34:0.32)	-0.07 (-0.32:0.17)
BA^2	a_2	**-0.27** (-0.47:-0.07)	**-0.18** (-0.32:-0.02)
Shade intolerance	a_3	-0.26 (-0.55:0.02)	-0.14 (-0.34:0.08)
Species deviation	ε	**0.98** (0.81:1.2)	**0.73** (0.71:0.75)
Plot deviation	γ_p	**0.14** (0.11:0.17)	**0.67** (0.54:0.83)
Richness deviation	$\pi_{richness}$	**0.53** (0.51:0.54)	**0.24** (0.2:0.29)

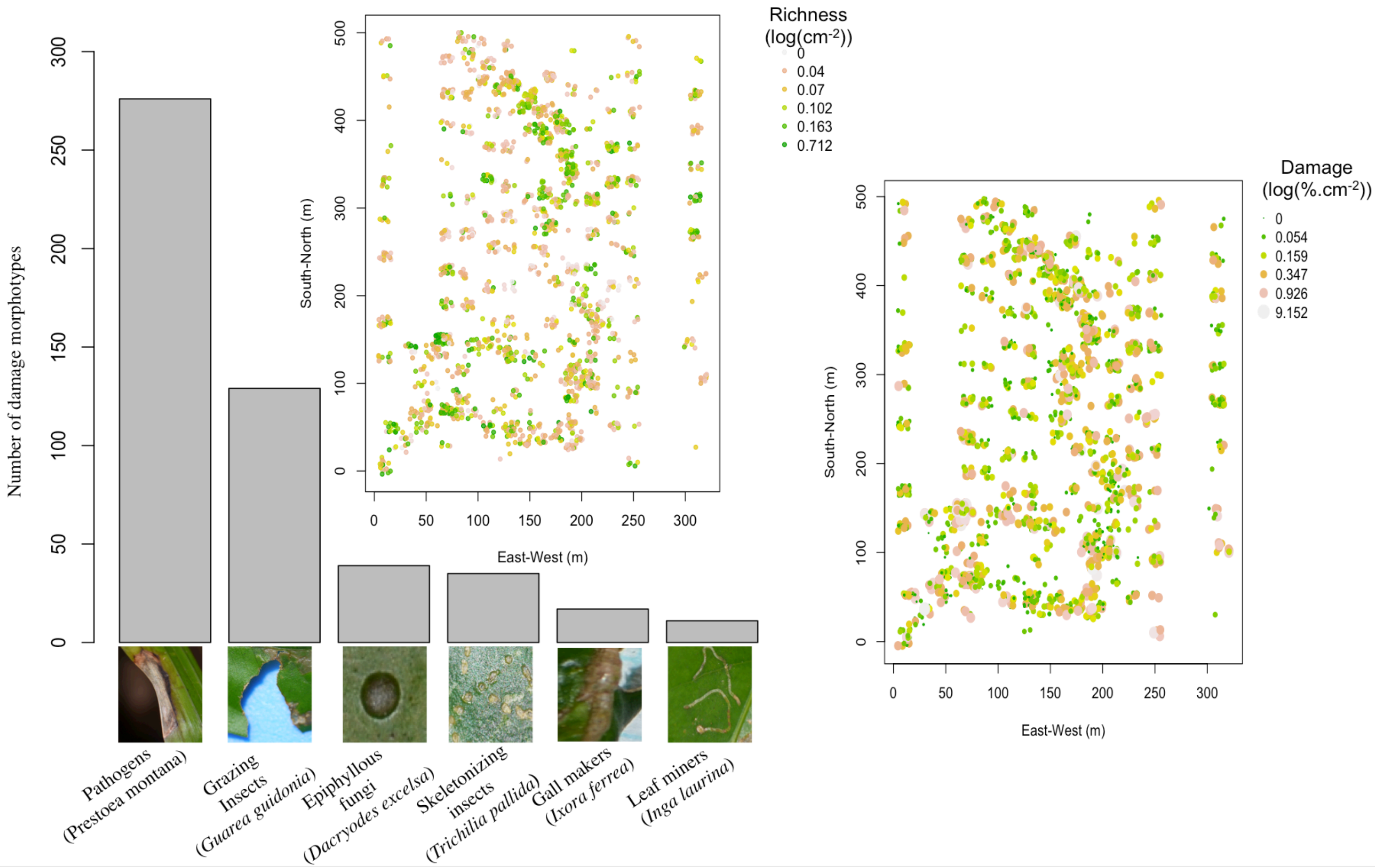

Figure S1, Spatial map of the richness (per cm^2) of enemy found on individual seedlings and of the amount of leaf damage (% per cm^2) found on each seedling. The histogram depicts the richness of above-ground enemies organized into 5 categories, pathogens, grazing insects, epiphyllous fungi, skeletonizing insects, leaf miners, and gall makers. Names of the tree species used as examples of damage are indicated in parentheses.

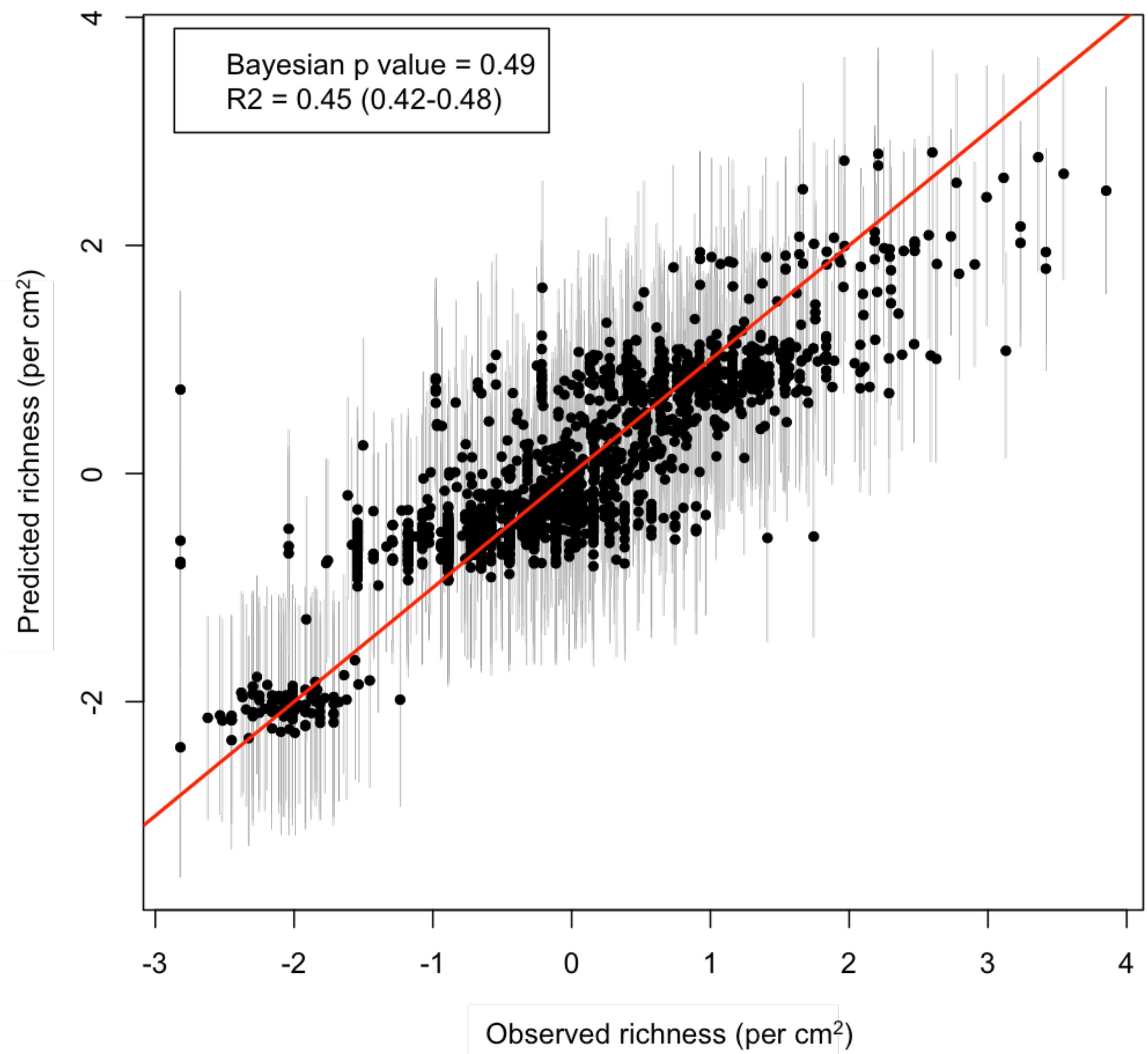

Figure S2, Predicted richness (per cm^2) versus the observed richness of enemies. The red line represent the 1,1 line, and the grey lines extend to the credible intervals of each prediction.