ECOLOGY LETTERS

Ecology Letters, (2015) doi: 10.1111/ele.12452

LETTER

Indirect interactions among tropical tree species through shared rodent seed predators: a novel mechanism of tree species coexistence

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Abstract

The coexistence of numerous tree species in tropical forests is commonly explained by negative dependence of recruitment on the conspecific seed and tree density due to specialist natural enemies that attack seeds and seedlings ('Janzen–Connell' effects). Less known is whether guilds of shared seed predators can induce a negative dependence of recruitment on the density of different species of the same plant functional group. We studied 54 plots in tropical forest on Barro Colorado Island, Panama, with contrasting mature tree densities of three coexisting large seeded tree species with shared seed predators. Levels of seed predation were far better explained by incorporating seed densities of all three focal species than by conspecific seed density alone. Both positive and negative density dependencies were observed for different species combinations. Thus, indirect interactions via shared seed predators can either promote or reduce the coexistence of different plant functional groups in tropical forest.

Keywords

Apparent competition, apparent mutualism, *Astrocaryum standleyanum*, *Attalea butyracea*, *Dipteryx oleifera*, indirect effects, Janzen–Connell hypothesis, seed predation, shared enemies, tropical forest.

Ecology Letters (2015)

INTRODUCTION

Understanding the mechanisms that allow species to coexist is a key goal in ecology (Chesson 2000). A much-favoured explanation of plant species coexistence in diverse tropical forests is the Janzen–Connell hypothesis (Janzen 1970; Connell 1978; hereafter J–C; Wright 2003). It proposes that seed or seedling mortality is negatively dependent on conspecific population density due to the attraction of specialist (species-specific) enemies to high densities of seeds, seedlings or adults of their favoured food or host plant species. Such disproportionate seed or seedling mortality around adults translates into negative density dependence of recruitment at the population level, preventing local dominance of any plant species. As a result, a high diversity of specialist enemies promotes plant species diversity at the community level (Janzen 1970; Chesson 2000).

Offspring mortality under the J–C hypothesis, thus, varies primarily with the density of conspecifics attracting specialist enemies, usually either specialised herbivorous insects (such as most bruchid beetles) or host-specific soil-borne fungal pathogens. Escape from such specialist enemies is more likely in offspring located further from conspecifics (Jansen *et al.* 2008). However, the distribution of feeding strategies by different species of herbivores or seed predators ranges from specialist species, to shared enemies of functional groups (as species with large seeds or with fleshy fruits) to true generalist species (rare due to the variety in plant adaptations, Janzen 1970) in a true graded continuum (Ali & Agrawal 2012). In tropical forests, an important part of seed and seedling mortality appears to be caused by such shared enemies which eat seeds or fruits of a whole group of tree species with similar size, texture and internal structure (Holt 1997). For example, vertebrates such as agoutis, peccaries and parrots each consume seeds of many different species within the group of large-seeded tree species. By sharing such guilds of shared enemies, different plant species may enhance or reduce each other's mortality, depending on their relative local abundance and smaller differences in palatability (Brown & Mitchell 1989). These two situations can be viewed as 'apparent competition' and 'apparent mutualism' respectively (Holt & Kotler 1987; Chaneton & Bonsall 2000). Apparent competition occurs when one species, by attracting similar shared enemies, increases predation of another species at the same location,

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even if the density of the latter is low (Holt 1997). Apparent mutualism arises when one species promotes the abundance of another species by distracting or satiating shared enemies (Janzen 1974; Abrams *et al*. 1998). Such indirect interactions between trees via shared predators can induce dependence of the probability of offspring mortality on the density of functionally similar heterospecific trees, in addition to the density of conspecific trees. Both apparent competition and apparent mutualism through shared enemies are potential balancing mechanisms, which prevent the local dominance of a single species by providing minority advantages. Hence, they can operate in complement at the level of functional groups, to J–C mechanisms at the individual species level, in contributing to species coexistence in tropical forests.

Despite the theoretical importance of indirect interactions between different species through shared enemies for density dependence and the maintenance of diversity, empirical tests are still lacking. Density-dependent mortality of seeds and seedlings is thought to be more intense in tropical forests than in other ecosystems (Hille Ris Lambers *et al*. 2002). The consequences of focal species density and identity, seed neighbourhood characteristics and the importance of predator specialisation for seed predation rates are frequently studied in these ecosystems. Given the theoretical consequences for community organisation of indirect interactions between tree species with shared enemies, there is a need for field studies that quantify the extent to which either specialist predators, shared predators or both could contribute to the mortality of plant species in different spatial contexts of both the focal species and of heterospecific species with shared enemies.

In this study, we measured indirect interactions among three large-seeded tree species mediated by shared predators (rodents) in a tropical forest. To assess its importance relative to classic J–C mechanisms, we measured the probability of seed predation by specialist vs. shared seed predators and the dependence of predation patterns on densities of seeds for each tree species. We tested the hypothesis that these species' seed predation rates are better explained by the abundances of seeds of different combinations of functionally similar species than by the abundance of conspecifics alone. Our results confirm that indirect interactions with heterospecifics via shared enemies can indeed operate complementary to J–C mechanisms explaining the coexistence of different plant functional groups in tropical forest.

METHODS

Study site and species

Data were collected on Barro Colorado Island (hereafter BCI; 9°9' N, 79°51' W), a 1560-ha island located in the Gatun Lake section of the Panama Canal, Panama. BCI is covered with old growth and late-secondary (100–200 years old) lowland tropical moist forest (Leigh 1999). Average rainfall is 2612 mm per year with a dry period between December and early May. Average daily temperature (24 h) is 27 °C (Leigh 1999).

We focused on three of the most abundant large-seeded tree species of BCI: *Astrocaryum standleyanum* Bailey (Aracaceae), *Attalea butyracea* (Mutis ex L.f.) Wess. Boer (Aracaceae) and *Dipteryx oleifera* (Pittier) Record & Mell (Fabaceae; formerly *Dipteryx panamensis*), henceforth referred to by their genus names. *Attalea* is attacked by two specialised bruchid beetle species, *Pachymerus cardo* and *Speciomerus giganteus*, that develop and pupate inside the seed (Wright 1983). Two specialist beetles attack *Astrocaryum*: the bruchid *Pachymerus bactris* and an unidentified scolytid (Jansen *et al*. 2010). *Dipteryx* has no known specialist seed predators. Emerging adult bruchids leave a large (6–7 mm) exit hole in endocarps (Wright 1983), whereas scolytids leave small (1 mm) entrance holes (Jansen *et al*. 2010). Both holes can be counted to assess predation. In addition, the seeds of all evaluated tree species are jointly predated by three rodent species (Jansen *et al*. 2012, 2014; Table 1): the Central-American agouti (*Dasyprocta punctata*), the Red-tailed squirrel (*Sciurus granatensis*) and the Central American spiny rat (*Proechimys semispinosus*) which also leaves distinct feeding scars on endocarps (Visser *et al*. 2011). These rodents represent a group of shared predators for these large-seeded tree species. These rodents, especially the agouti, also scatter-hoard the palm seeds as food supplies that they feed upon after the fruiting season ends (Smythe 1978; Jansen *et al*. 2012, 2014).

Fruiting periods of the three study trees species have little overlap. However, the seeds of both palms have multi-year dormancy making them potentially available to consumers all year round. *Dipteryx* fruits in the dry season when few other species do. Thus, the density of each tree species' seeds could influence predation of each other's seeds, for example, by attracting shared rodent seed predators and/or by sustaining these predator populations year round. Additionally, rodents are known to interfere with seed predating insects by caching seeds out of reach of beetles (Jansen *et al*. 2010), and by eating larvae-infested seeds (Forget 1993).

Data collection

To capture large-scale variation in adult tree densities, we compared seed fate across 54 plots of 100 × 100 m (1 ha), placed across BCI in a stratified manner. Plot locations were based on the density of canopy-sized individuals of the three focal tree species, determined from high-resolution aerial photographs of BCI (Garzon-Lopez *et al*. 2012). Using the Kernel density function in ArcGIS 9.3 with 100 × 100 m grid size (ESRI 2008), we identified the grid squares with relatively low (lowest 25%) and high (highest 25%) density of each of the focal tree species. We selected plots within 200 metres from the trails to facilitate fieldwork. The selection process resulted in 54 plots, which included 6 plots in every combination of relatively high or low density of each focal species (eight possible combinations). The assessment of the correlation between observed seed abundance (seeds found on the ground) and aerial photo-based estimates of tree density allowed us to verify that tree density was an accurate proxy of seed density for the three focal species (Poisson regression; *Attalea*: $z = 10.73$, $P < 0.000$; *Astrocaryum:* $z = 5.94$, $P < 0.000$; *Dipteryx:* $z = 3.77$, $P < 0.01$).

Within each 1-ha plot, 10 random points were generated in ArcGIS and loaded to a handheld GPS receiver (Garmin GPSmap 60CSx, Olathe, KS) so that they could be located in

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the field. At each random point, we established one 1-m² quadrat in which we collected the endocarps of all three species that were on the soil surface or buried up to 5 cm deep in the soil, following the protocol described in Wright & Duber (2001) and Visser *et al.* (2011). The collections were carried out from March to June 2008. In the laboratory, we counted the endocarps to obtain a measure of the local seed abundance, and determined the predation state (presence/absence) and predator type (rodent/insect) from the typical scars that each predator group leaves on the endocarps. Non-predated seeds were placed in the 'intact' category.

Statistical analyses

For each species separately, we used logistic regression in combination with model averaging (Burnham & Anderson 2002) to determine whether the proportion of seeds predated per 1-ha plot (i.e. sum of the 10 quadrats) was best explained by the seed density of conspecific tree species alone (Cons), the seed density of the two other tree species (Het1 and Het2) and the interactions between them (symbolised as Cons:Het1 and Cons:Het2). Seed density was $\log_{10}(x + 1)$ transformed to test differences between geometric means rather than arithmetic means between plots, and homogenise variances. We found a significant spatial autocorrelation between the 1-ha plots based on Moran's I-test (Cliff & Ord 1981), indicating that statistical models that account for the spatial association or spatial autocorrelation between samples were required for the analysis. Thus, we fitted a residuals autocovariate model (Crase *et al.* 2012), which includes an autocovariate representing the spatial autocorrelation in the residuals. This autocovariate term (Acla) was implemented as a spatial weights matrix, a representation of the spatial relationship between observations, which quantified patterns in the response variable that are related to the values in the neighbouring locations (cf. Dormann *et al.* 2007; Crase *et al.* 2012). The spatial-weights matrix was calculated with a row-standardised coding scheme that scaled the covariates based on the number of neighbours in each region (Bivand 2014).

In each analysis, we fitted a global model (i.e. Cons + Het1 + Het2 + Cons:Het1 + Cons:Het2 + Acla) as well as all possible combinations of covariates, and calculated the Akaike weight (AICw_v) across all fitted models for each variable v (Burnham & Anderson 2002). An AICw_v value can be interpreted as a normalised relative likelihood representing the fit of the model, facilitating model comparison and model averaging. In other words, it represents the conditional probability of a model based on all other related models. Thus, to estimate the relative importance of each explanatory variable, we summed the AICw across all models in which the variable v occurred, thus, the higher the value, the higher the importance of that variable relative to the other variables. Such 'model averaging' allows assessments to be based on multiple models, avoiding bias in parameter estimation that may occur in the selection of a single best model and problems with colinearity among predictors (Burnham & Anderson 2002). The set of models with a gamma value higher than four was selected for each analysis to best approximate to the true model (Burnham & Anderson 2002).

All the analyses were performed in R version 2.15.3 (R Core Team 2013) using the packages: MuMIn (Barton 2013), arm (Gelman *et al.* 2013) and spdep (Bivand 2014) for the statistical analyses, and igraph (Csardi & Nepusz 2006) and ggplot2 (Wickham 2009) for the plots and figures.

RESULTS

General trends

A total of 4585 seeds were collected. The overall predation level per species was high, ranging between 95.2 and 98.3% of all surveyed seeds (Fig. 1). Per plot, the proportion of seeds predated by specialists was lower than the proportion by shared predators. The proportion of seeds showing predation by both specialist and shared predators was 34% for *Astrocaryum* and 48% for *Attalea* (Fig. 1). Seed predation rates were very high for all species (Mean number of seeds predated per 1 m^2 plot: by specialists ± SD*: Astrocaryum*: 11.8 ± 2.05 and *Attalea*: 10.9 ± 2.54, by shared predators ± SD*: Astrocaryum*: 26.0 ± 3.44 and *Attal*ea: 18.8 ± 4.36 and by both ± SD *Astrocaryum:* 9.9 ± 1.71 and *Attalea:* 9.9 ± 2.37). Nevertheless, there was an enormous variation between plots, where few plots had as little as 1% predation rate while in many other plots almost 100% seeds were predated. Hence, specialist predators alone accounted for a smaller portion of the overall seed mortality than shared predators.

In all three species, models that included seed density of both conspecifics and heterospecifics better explained the total

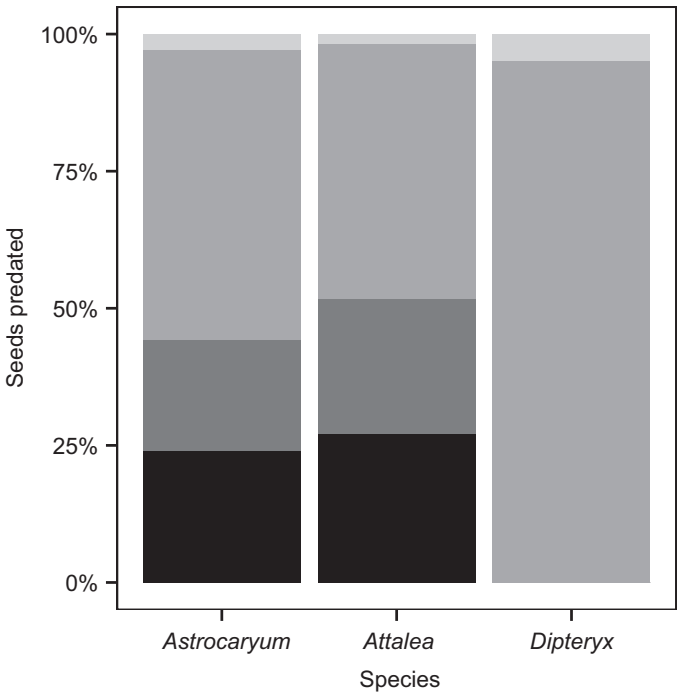

Figure 1 Fate of seeds of three large-seeded tree species on Barro Colorado Island, Panama, averaged over 540 1-m² sampling quadrats distributed over 54.1-ha plots. Colour gradient from black to light grey represent seed predation by specialists, specialists + generalists, generalists and intact seeds. *Dipteryx* has no seed predation by specialists.

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proportion of seeds predated than models based on conspecifics seed density alone (Table S1 in supporting online material). In fact, seed densities of the other two study species strongly influenced total seed predation of each species, whereas conspecific seed density did so only in *Astrocaryum* (Fig. 2a; Fig. S2) and *Dipteryx* (Fig. 2c; Fig. S3), but not in *Attalea* (Fig. 2b; Fig. S1). In *Astrocaryum* (where specialists played an important role, Fig. 1), predation increased with conspecific density as expected under the J–C hypothesis (Fig. 2a). In contrast, *Dipteryx,* which is used only by shared predators (Fig. 1), the relationship was the opposite, with seed predation decreasing with increasing conspecific seed density (Fig. 2c) suggesting predator satiation and apparent mutualism (see Discussion).

Predation by specialists

The proportion of seeds predated by specialists in the two palm species was also best explained by models that included the sand and the seed densities of all three focal species (Table S1). In *Astrocaryum*, seed predation by specialists increased with both conspecific and *Attalea* seed densities, with a negative interaction between the two, and decreased with *Dipteryx* seed density (Fig. 2d; Fig. S2). In *Attalea*, seed predation by specialists increased with conspecific seed density and *Astrocaryum* seed density, with a negative interaction between the two (Fig. 2e; Fig. S1).

Predation by shared predators

In two of the tree species, levels of seed predation by shared predators were also best explained by models that included the seed densities of all three focal species as separate variables. (Table S1). In *Attalea*, seed predation by rodents increased with the density of conspecific and *Dipteryx* seeds, but decreased with the density of *Astrocaryum* seeds (Fig. 2h, Fig. S1). In *Astrocaryum*, seed predation by rodents decreased with the density of conspecific seeds, and showed no influence of heterospecific seed densities (Fig. 2g, Fig. S2). In *Dipteryx,* seed predation by rodents decreased with the density of conspecific seeds, but increased with seed densities of the other two focal species, with negative interactions between all three species (Fig. 2i, Fig. S3). For all the tree species, the spatial component (Acla) had a high relative importance in seed predation by generalists (Fig. 2g–i).

Overall, seed densities of *Dipteryx* and *Astrocaryum* explained well the variation in seed predation by shared predators in most of the interactions evaluated, whereas

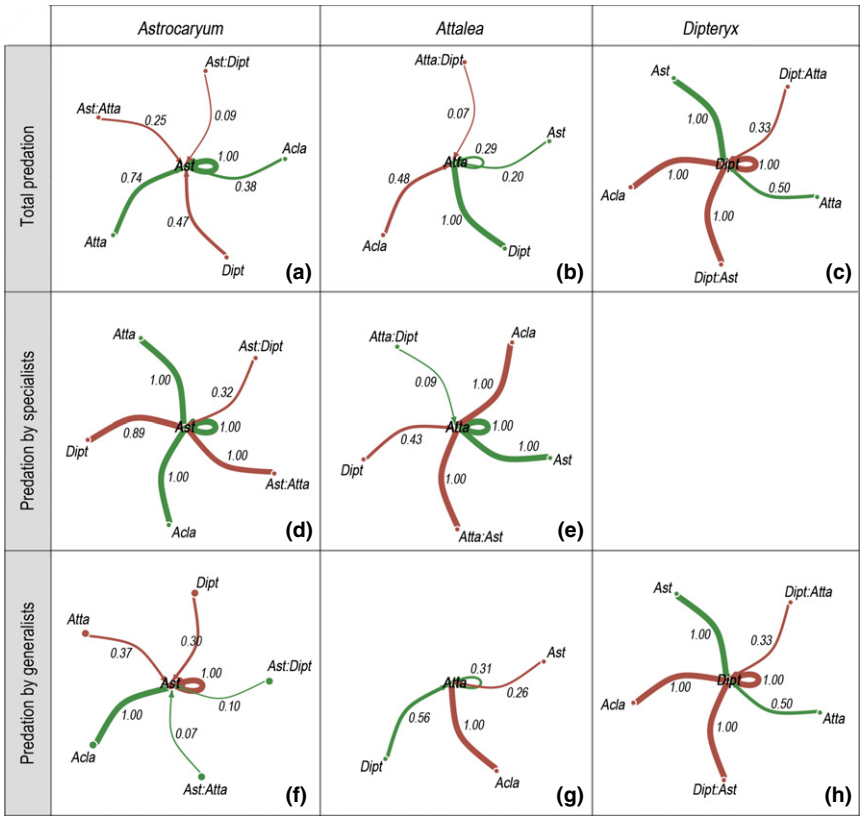

Figure 2 Relationship of seed predation with the density of conspecific and heterospecific seeds for three large-seeded tree species on Barro Colorado Island, Panama. The arrows represent the effect of one species, the interaction between species (indicated by species1:species2), or the effect of the spatial autocovariate (Acla) on the predation rates of the focal species (at the centre of each panel). Line thickness scales with relative importance of the interaction averaged over the models, as indicated by the numbers along the arrows (relative variable importance w_{+v}). Arrow colour indicate whether seed predation of the focal species increased (green) or decreased (red) with increasing density of the interacting variable. The variables missing in two of the figures were not included due to their low correlation with the response variable. See Table S1 for models.

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Attalea densities explained less variation in seed predation by shared predators. This suggests that the tree species, especially *Dipteryx* and *Astrocaryum*, influenced each other's seed predation by shared enemies, likely by attracting (apparent competition) or distracting (apparent mutualism) rodents that consume seeds of both species. Only in *Astrocaryum* was conspecific seed density the single best predictor of seed predation by shared predators. In addition, in two of the species (*Astrocaryum* and *Dipteryx*), seed predation by shared predators declined with increasing seed density (contrary to J–C predictions), suggesting that predator satiation was important in these species.

DISCUSSION

Our analysis of seed mortality in three coexisting big-seeded tropical tree species yielded several striking patterns that hint at complementary mechanisms to the classic J–C explanation on how natural enemies can promote tree species coexistence. First, we found that models based on heterospecific and conspecifics seed densities explained seed predation rates better than models based on conspecific seed density alone. This implies that, in our focal species, seed mortality is affected by indirect interactions with seeds of both the two other tree species through shared seed predators (rodents). Second, we found that levels of seed predation depended on the identity and density of both the other tree species, indicating that feeding preferences of these shared predators determined whether indirect interactions with heterospecifics take the form of apparent competition or apparent mutualism. Finally, we found that seed densities of the other two species influenced seed predation by specialist insects, suggesting that shared seed predators could pre-empt seed predation by specialist enemies.

Our findings, thus, imply that seed mortality in tropical forests is not always a simple function of conspecific density mediated by host-specific specialist enemies, as assumed under the J–C hypothesis (Janzen 1970; Connell 1978), but also can be a more complex function of the densities of species with shared enemies. Our findings have important implications for the role of intraspecific density-dependent population regulation of tropical trees, which is one of the major mechanisms thought to facilitate the coexistence of tree species in tropical forests (Chesson 2000; Comita *et al*. 2010).

Interplay between specialist and shared seed predators

We found that specialist seed predators (insects) caused substantial seed mortality in the two palm species. Fully intact surviving seeds in the soil were a small minority, where our study could not distinguish if such seeds are permanently safe and will recruit as a seedling, or are still in storage awaiting the future return of a scatter-hoarding rodent. Levels of seed predation by insects increased with conspecific seed density, as predicted by Janzen–Connell and consistent with previous studies (for a review see Comita *et al*. 2014). Yet, shared seed predators (rodents) were the major cause of seed mortality as, conspecific density was not the best predictor. This confirms results of Hammond & Brown (1998) who observed that invertebrate seed predators (insects) follow the patterns expected under Janzen–Connell while vertebrates (rodents) generally do not, as further quantified in this study. The level of seed predation by rodents in our study increased with conspecific seed density in *Attalea*, as also reported by Visser *et al*. (2011), but decreased with conspecific seed density in *Astrocaryum* and *Dipteryx*. The latter decreases suggest shared predator satiation, meaning seed survival increases when seeds are too abundant to be all eaten by this type of seed predator (Janzen 1971). As rodents were responsible for a greater proportion of predation, than were insects in all three of the study species (Fig. 1), the relationship of total seed predation with conspecific seed density is clearly not driven solely by specialised natural enemies, as assumed under the J–C hypothesis.

Indirect interactions via shared predators

We found clear evidence for indirect interactions among species via shared seed predators, even though the three study species show little overlap in fruiting period. This might be explained by the fact that seeds of the two palm species have long dormancy, thus, are present at varying densities and available to predators all year round. *Dipteryx*, despite having a short dormancy, remains viable in the soil for at least 3 months after fruiting.

For all of the three species in our study, seed densities of the other two species seemed to have a pervasive influence on the level of seed mortality caused by specialists, shared predators and both combined. This result agrees with earlier studies showing both significant shared seed predation rates compared to predation by specialists, and interactions between seed predator types on the overall seed mortality patterns (Ferreira *et al*. 2011). However, our study is the first to examine the implications of the strength and direction (positive or negative) of these indirect interactions for density dependence of species recruitment and the role of the spatial heterogeneity on the prevalence of these patterns at the landscape scale (Comita *et al*. 2014).

As generalist seed predators feed on more than one seed species, their behaviour and distribution are, thus, determined by the distribution and availability of several food resources. In addition, rodent densities are constrained by habitat quality and by territoriality, and consequently, their abundance may not be proportional to food availability. Guilds of shared seed predators respond to the distribution and densities of more than one prey species in accordance with their habitat and resource preferences as shown in a recent literature review (Côrtes & Uriarte 2013). In addition, seed abundance not only varies in space, but also fluctuates over time, according to the phenology of the tree species that produce them (Table 1, Wright & van Schaik 1994). These fluctuations influence the degree of overlap in resource use by different seed predators, generating a complex set of trophic interactions through time among such seed predators with different degrees of specialisation.

We speculate that the pathway of interaction among the three tree species is as follows: when *Astrocaryum* starts fruiting, the high densities of *Dipteryx* that have attracted and

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Table 1 Characteristics of the study species

	Astrocaryum standleyanum	*Attalea butyracea*	*Dipteryx oleifera*
Family	Aracaceae	Aracaceae	Fabaceae
Growth form	Tree palm	Tree palm	Tree
Fruiting period	April–July†	May–October†	January–March‡
Seed dormancy	≥ 1 year*	≥ 1 year†	None
Host-specific seed predators	*Pachymerus bactris* (bruchidae)§ *Cocotrypes sp.* (Scolyotidae)§	*Speciomarus giganteus* (bruchidae)* *Pachymerus cardo* (bruchidae)*	
Generalist seed predators	*Dasyprocta punctata* (agouti)‡‡ *Sciurus granatensis* (Red-tailed squirrel)‡‡ *Proechimys semispicous* (Spiny rats)‡‡	*Dasyprocta punctata* (agouti)* *Sciurus granatensis* (Red-tailed squirrel)* *Proechimys semispicous* (Spiny rats)*	*Dasyprocta punctata* (agouti)¶ *Sciurus granatensis* (Red-tailed squirrel)¶ *Proechimys semispicous* (Spiny rats)¶ *Tayasu tajacu* (Pecaries)††
Dispersers	*Dasyprocta punctata* (agouti)‡‡ *Proechimys semispicous* (Spiny rats)‡‡ *Sciurus granatensis* (Red-tailed squirrel)‡‡	*Dasyprocta punctata* (agouti)* *Proechimys semispicous* (Spiny rats)* *Sciurus granatensis* (Red-tailed squirrel)*	*Dasyprocta punctata* (agouti)¶ *Proechimys semispicous* (Spiny rats)** *Sciurus granatensis* (Red-tailed squirrel)** Bats††

*Jansen *et al.* (2014).
†Forget *et al.* (1994).
‡Terborgh & Wright (1994).
§Jansen *et al.* (2010).
¶Hoch & Adler (1997).
**Clark & Clark (1984).
††Bonaccorso *et al.* (1980).
‡‡Jansen *et al.* (2012).

satiated rodents promote scatter-hoarding of those *Astrocaryum* seeds that escape from specialist predation. By the time *Attalea* starts fruiting, both *Astrocaryum* and *Dipteryx* seeds are already on the ground, thus, the influence of *Astrocaryum* and *Dipteryx* seeds on the fate of *Attalea* seeds is greater than vice versa. Yet, the combined seed densities that occur during the overlapping fruiting periods of *Attalea* and *Astrocaryum* (May–July) reduce the predation pressure by rodents on the specialist larvae, which could result in higher specialist predation at high *Attalea* and *Astrocaryum* densities. However, the outcome of such interactions is likely affected by the order in which the predators arrive to the seed. Specialists more often lay eggs on intact fruits in early developmental stages, while generalists attack all the seeds also in later stages of development, often on the ground (Visser *et al.* 2011). In the case of *Attalea* these preferences can be modified by the presence of the specialist larvae inside the seed (Visser *et al.* 2011).

The probability of a seed being consumed by a shared predator (that a tree species shares with other tree species), is a complex function of the combined effect of the density, phenology and spatial distribution of conspecific as well as that of heterospecific seeds (Smythe 1978). For example, predator attack in *Attalea* covaries with heterospecific density (Fig. 3c). Specifically, at low heterospecific densities, predation appears to be driven by specialists, while as the heterospecific seed density increases, predation by shared species gradually becomes more important up to the point that they become the major determinant of seed predation. In *Astrocaryum* (Fig. 3f), the probability of predation is largely determined by the effect of heterospecific densities on attracting shared predators. Only at high heterospecific densities do specialist seed predators of *Astrocaryum* affect the probability of predation, especially at high conspecific densities. Moreover, seeds already predated by specialists can then be attacked by shared predators, which kill the larvae of the specialist, a type of interaction between predator types known as intraguild predation (Holt 1997).

Our results, on the importance of indirect competition and indirect mutualism, are linked to the concept of associational resistance and associational susceptibility in the plant–herbivore literature (Olff *et al.* 1999; Barbosa *et al.* 2009; Underwood *et al.* 2014), a framework that so far has not been applied to tropical forests and seed predation. Associational resistance implies that a species that is in itself highly palatable to herbivores (in this case, attractive to seed generalist predators) will not be grazed (in this case, suffer little seed predation) if it is in-between species that are not attractive to an enemy of the focal species (in this case, have very different seeds). Associational palatability implies that a species that in itself is not very interesting for herbivores (in this case, seed predators) can be grazed more (in this case, will suffer more seed predation) if it is among plants of other species with which the focal species shares enemies. We conclude that in this context of tropical forests, associational resistance promotes small-scale diversity as it provides spatial refuges against enemies by 'having the right (unattractive) neighbour species', while associational susceptibility can either reduce small-scale diversity by 'having the wrong (attractive) neighbour species' in case of shared non-saturated enemies, while it can promote small-scale coexistence when neighbour species saturate shared enemies of species. As a result, our concept is likely much wider applicable than just in the case of

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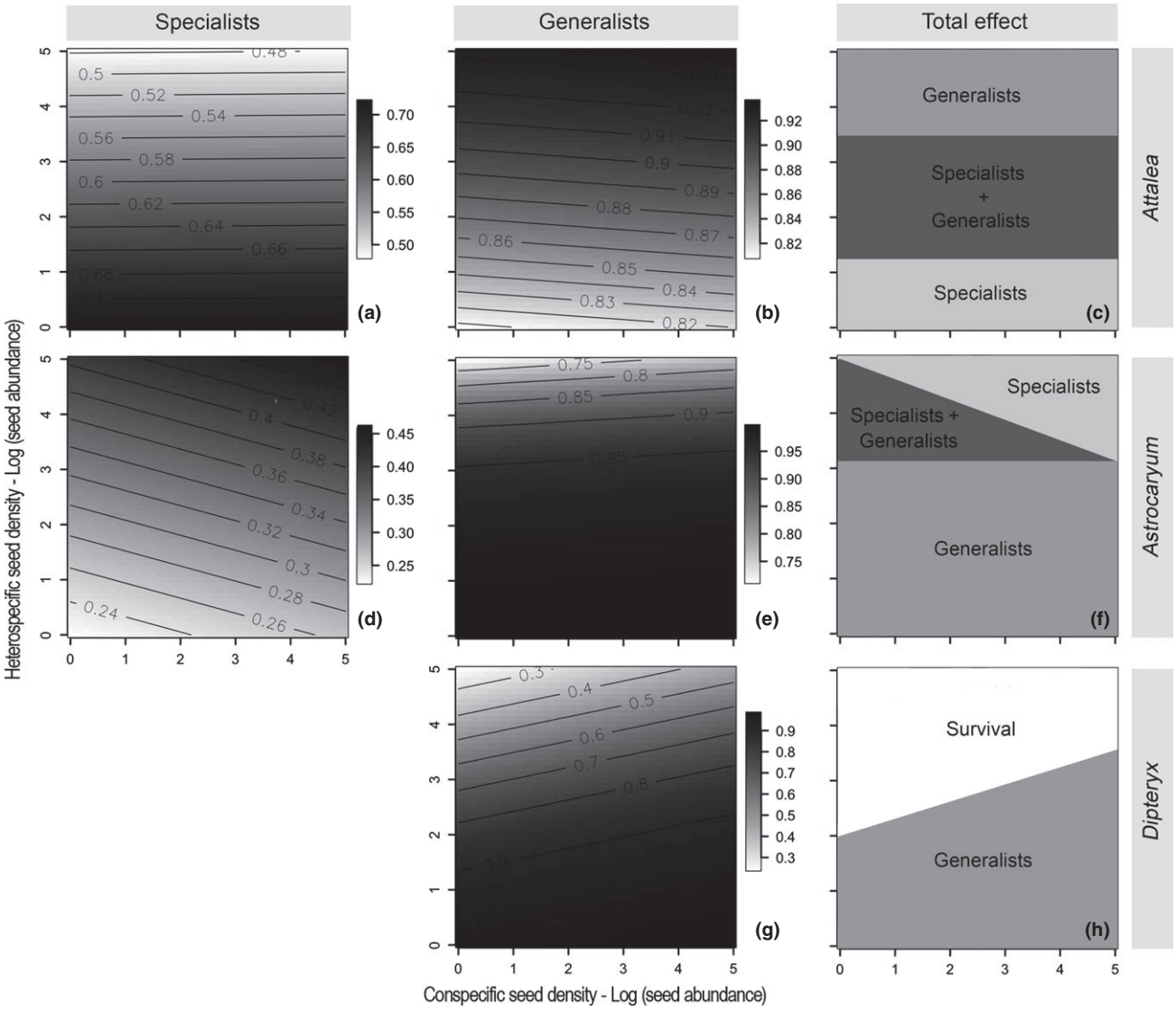

Figure 3 Predicted levels of seed predation by specialists and generalists for three large-seeded tree species on Barro Colorado Island, Panama, across conspecific and heterospecific seed densities. The greyscale ramp corresponds to the probability of predation, ranging from high (black) to low (white). Panels C and F show overall seed predation per species as a function of seed density.

large-seeded tropical trees. We suggest that similar mechanism can hold for any group of tree species with shared enemies, such as trees with a similar type of leaf chemical defence, and thus, shared folivores, species with similar fruits, and thus, shared frugivores, etc.

The strength and direction of indirect interactions in our study strongly depended on the identity of the tree species in our study. *Dipteryx* appeared to be the most preferred resource by the guild of shared seed predators and *Attalea* the least preferred (Fig. 1). This might be related to the lack of dormancy of *Dipteryx* seeds and the fact that it is the first resource available after a period of relative fruit scarcity. The differences in the preference of rodents between *Astrocaryum* and *Attalea* might be related to the chemical composition of the seeds: both have high oil content in the seed, but the high concentration of sugars in the pulp of *Astrocaryum* might attract more predators (Jansen *et al*. 2010).

In our study system, the interaction of multiple predators with multiple tree species yielded interesting context-dependent predation rates, pointing at the need for studies on other aspects of multispecies trophic interactions that we did not yet address. For example, emergent multiple predator effects (MPEs) can arise in such systems, including risk enhancement, where more prey can be killed or removed than predicted due to pre-emptive competition, or less prey can be killed due to interference competition between the predators (McCoy *et al*. 2012). In addition, the modification of the spatial distribution by scatter hoarding generalist predators, that can cause seeds to end up in safe sites, will affect the interaction between multiple predators (Jansen *et al*. 2008, 2014). In addition, different shared seed predators, such as squirrels, spiny rats and agoutis, will all have specific preferences within the group of tree species, leading to resource partitioning within this guild. Furthermore, the interaction between multiple trees and

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multiple seed predators can be modified by differences between seed species in longevity of seeds as part of the seed bank. Finally, interactions between multiple predators can produce non-linearities in how predation risk changes with overall density (Holt & Kotler 1987; Holt 1997). The relatively strong interactions observed in Fig. 2 hints at the operation of such MPEs. However, we expect that our general results are relatively robust but further work is needed to assess the importance of MPEs in neighbourhood interactions in tropical forest.

Our study suggests that more generalist, shared enemies can play a major role in maintaining the functional diversity of tree species diversity in tropical forests in addition to specialists. However, rodents, parrots, peccaries and similar shared seed predators of large seeded trees are now rapidly lost through human overexploitation (hunting) and habitat fragmentation (Wright 2003; Laurance *et al.* 2012). Increased conservation efforts that protect vertebrate seed predators may therefore not only protect these species alone, but may also be critical for the long-term maintenance of the functional diversity of trees in tropical forest and their associated bird and invertebrate biodiversity.

CONCLUSION

In summary, our study provides evidence that seed mortality in large-seeded tropical trees is influenced not only by conspecific densities but also by those of other species that share the same seed predators, in agreement with predictions from simulations (Sedio & Ostling 2013). The co-occurrence of species with shared enemies determines how consumers respond to seed density of a given species, yielding mortality–abundance relationships that may deviate from patterns based on host-specific J–C mechanisms alone. Seed mortality in tropical trees therefore is affected by the spatial arrangement of both heterospecific and conspecific adult tree and seed densities and the response of shared enemies to them.

ACKNOWLEDGEMENTS

We thank Erik Vásquez, Helen Esser and Eduardo Medina for their help in the field and laboratory; and Egbert Leigh, Robert Holt and two anonymous reviewers for their very helpful comments. This work was supported by the Smithsonian Tropical Research Institute, the Ubbo Emmius Scholarship programme (CXG) and the Marco Polo funds (LBM) of the University of Groningen. CXG was partially funded by the EU BON (Building the European Biodiversity Observation Network) project, funded by the European Union under the 7th Framework programme, Contract No. 308454. AO was supported by the European Research Council grant ERC-2012-StG-310886-HISTFUNC.

AUTHORSHIP

CGL and LBM designed the study, LBM collected the field data, CGL, LBM and AO did the analyses, CGL wrote the first draft of the manuscript, and all authors contributed intellectually to the manuscript.

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Editor, Prof. Marcel Rejmanek
Manuscript received 5 January 2015
First decision made 1 February 2015
Second decision made 2 April 2015
Manuscript accepted 14 April 2015

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