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Assessing the potential for indirect interactions between tropical tree species via shared insect seed predators

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Abstract

Natural enemies of plants have the potential to influence the dynamics of plant populations and the structure of plant communities. In diverse tropical forests, research on the effects of plant enemies has largely focused on the diversity-enhancing effects of highly specialized enemies, while the community-level effects of enemies with broader diets have rarely been considered. We investigated the community of insect seed predators interacting with seven tree species in the family Lauraceae on Barro Colorado Island (Panama). We present one of the first quantitative food webs for pre-dispersal insect seed predators and their host plants, and use the information in the web to assess the potential for indirect interactions between the tree species. Our data suggest that there is high potential for indirect interactions between Lauraceae species via their shared seed predators. The strength and direction of these interactions are largely unrelated to the phylogenetic distance and trait similarity between species but are likely governed by the volume of fruit produced by each tree species. Abstract in Spanish is available with online material.

KEYWORDS

apparent competition, indirect interactions, Janzen–Connell hypothesis, *Pagiocerus frontalis*, pre-dispersal seed predator, quantitative food web, tropical forest

1 | INTRODUCTION

The interactions between plants and their natural enemies are among the commonest ecological interactions observed in nature (Bernays, 1992; Strong, 1988). Plant enemies such as herbivores and pathogens have the potential to affect the fitness of individual plants, the dynamics of plant populations, and the structure of plant communities (Crawley 1989; Maron & Crone, 2006).

The community-level effects of plant enemies have received particular attention in highly diverse communities of woody plants in tropical forests, where natural enemies are thought to contribute to the coexistence of a large number of plant species (Bagchi et al., 2014; Wright, 2002). Many studies have investigated whether host-specific enemies contribute to structuring and maintaining plant diversity through processes outlined in the Janzen–Connell hypothesis (e.g., Comita et al., 2014; Fricke, Tewksbury, & Rogers, 2014). In contrast, the potential for less-specialized enemies to structure plant communities via enemy-mediated indirect interactions such as "apparent competition" (Holt, 1977) has received less attention. While it seems plausible that indirect interactions mediated by non-specialist enemies could be important (e.g., Novotny et al., 2002), few studies have explicitly assessed the role of enemy-mediated indirect interactions in tropical plant communities (but see Downey, Lewis, Bonsall, Fernandez, & Gripenberg, 2018; Garzon-Lopez et al., 2015).

One guild of plant enemies that could have a considerable effect on plant fitness is pre-dispersal insect seed predators (Fedriani & Manzaneda, 2005; Hulme & Benkman, 2002; Mezquida & Olano, 2013). By killing mature and developing seeds, pre-dispersal insect seed predators have the potential to drastically reduce plant fecundity. Individual plants have been shown to lose up to 90% of their seed crop to pre-dispersal seed predators (Crawley, 2000). Despite this, the impact of reduced seed crops on plant population dynamics is often unknown. Some studies suggest that the effect of seed predators is minimal (e.g., Andersen, 1989). However, it has now been established that pre-dispersal seed predators can reduce plant population growth as much as any other insect guild (Hulme & Benkman, 2002; Maron & Crone, 2006). Despite this, pre-dispersal insect seed predators have been largely neglected in tropical forest ecology (Gripenberg 2018, but see e.g., Basset et al., 2018; Beckman & Muller-Landau, 2011; Jones & Comita, 2010).

Existing studies of internally feeding insect seed predators (including post-dispersal seed predators) suggest that these plant enemies tend to be relatively host-specific (Gripenberg et al., 2019), but there are also cases where individual seed predator species are associated with multiple plant species, typically within the same genus or family (Ctvrtecka, Sam, Miller, Weiblen, & Novotny, 2016; Janzen, 1980; Sam et al., 2017). Such seed predator species could potentially link the regeneration dynamics of their host plant species via enemy-mediated indirect interactions such as apparent competition (Holt, 1977; Lewis & Gripenberg, 2008). When plant species sharing seed predator species co-occur in space or time, this might allow for larger populations of seed predators to build up than would be the case in any single-host scenario. This could in turn suppress the reproductive output of one or more of the plant species, reduce their abundances, and provide a mechanism structuring plant communities. The alternative scenario, where co-occurring host species jointly satiate natural enemies with more resources than they can consume, is known as “apparent mutualism” (Abrams & Matsuda, 1996) and is a possible explanation for the mast fruiting events seen, for example, in some tropical forests in Asia (Kelly & Sork, 2002). Although it seems plausible that indirect interactions mediated by non-specialist pre-dispersal insect seed predators could be important in some systems, the role of this enemy guild in linking the recruitment dynamics of different plant species has been little investigated (but see Lyal & Curran, 2000).

Since the potential for enemy-mediated indirect interactions between plant species depends on the degree of overlap in host use by natural enemies, predicting which species are most likely to interact via shared enemies requires information on patterns of host use by enemies. For many enemy groups, obtaining such information is challenging. This is particularly true in tropical forests, where the high diversity of both plants and enemies makes it difficult to establish patterns of enemy attack. In the absence of detailed information on host–enemy associations, it has been suggested that using phylogenetic information (Gilbert & Webb, 2007) or morphological traits (Beckman & Muller-Landau, 2011) as proxies for degree of overlap in enemy attack might be helpful. In the context of insect seed predators, pairs of closely related species or species with similar seed or fruit traits might be most likely to share enemies, and thus to interact via seed predator-mediated indirect interactions. Likewise, species with similar reproductive phenologies and habitat requirements might be most likely to interact via their shared enemies due to their temporal and spatial overlap. Nevertheless, even in cases where information on host–enemy associations (e.g., diet breadths of enemies) is available, predicting the strength of enemy-mediated indirect interactions is difficult without quantitative information on rates of enemy attack. In this context, quantitative food webs are a useful tool (e.g., Lewis et al., 2002; Morris, Lewis, & Godfray, 2004). In addition to depicting the presence or absence of specific feeding links (as is the case in conventional binary food webs), quantitative food webs also show the *frequencies* of interactions. This makes it possible to accurately predict which species are most likely to interact via their shared enemies through density-mediated indirect effects (van Veen, Morris, & Godfray, 2006). Quantitative food webs have been used for this purpose in studies assessing the role of parasitoids in structuring communities of herbivorous insects (Morris et al., 2004; Tack, Gripenberg, & Roslin, 2011). Although existing methods (e.g., Lewis et al., 2002; Müller, Adriaanse, Belshaw, & Godfray, 1999) are directly applicable to studies of plants and their internally feeding seed predators (Lewis & Gripenberg, 2008), quantitative food web methods have only recently been applied in this novel context (Gripenberg et al., 2019; Jeffs et al. 2018).

In this study, we constructed quantitative food webs describing the interactions between seeds within the Lauraceae family and internally feeding pre-dispersal insect seed predators on Barro Colorado Island (BCI) in Panama. We used the food webs to address the following questions: (a) Is there potential for indirect interactions between tree species within Lauraceae, mediated by shared pre-dispersal insect seed predators? (b) What is the relative importance of conspecific and heterospecific seeds as sources of seed predators affecting each host species? and (c) Are Lauraceae species that are closely related and those with similar traits more likely to share enemies than pairs of species that are more distantly related or have greater trait dissimilarity? To assess the temporal consistency of patterns observed, we also quantified inter-annual variation in the interactions between Lauraceae species and their seed predators.

2 | MATERIAL AND METHODS

2.1 | Study site

Barro Colorado Island (BCI) is a 1,500 ha island in Gatun Lake, Panama (Lat: 9.1543, Long: −79.846), that was isolated from the surrounding mainland in 1914 when Rio Chagres was dammed to form part of the Panama Canal. The island is covered with tropical semi-deciduous forest. The climate of BCI is seasonal, with a dry season from December to April/May. The mean yearly rainfall is 2,612 mm (Leigh 1999). Data collection for our study was carried out in four mapped forest plots (one ten ha, one 25 ha and two 6 ha plots; Figure S1), which were established in the mid-1990s. The 10-ha plot runs along the northern edge of the 50-ha BCI ForestGEO plot. In these plots, which jointly cover an area of 47 ha, every freestanding woody stem ≥20 cm diameter at breast height (dbh) has been tagged, measured (dbh), and identified to species level. These plots were last censused in 2013–2014.

2.2 | Study system

The Lauraceae is one of the commonest and ecologically most significant woody plant families in tropical and subtropical forests (Gentry, 1988). Lauraceae fruits are an important food source for many bird (Wheelwright, 1983) and mammal species (Tabarelli & Peres, 2002). The Lauraceae family includes many species of economic value, such as avocado, bay, and cinnamon. Nine species of Lauraceae representing four genera occur on BCI (Table 1) (Croat, 1978). All have single-seeded fleshy fruits that are animal-dispersed, but there is substantial variation among species in fruit size and shape. In addition to the species in Table 1, the avocado (*Persea americana*) also occurs on BCI, but was likely introduced there by humans and is too rare to be included in this study.

Preliminary investigations in 2011–2013 showed that insects damage a substantial proportion of Lauraceae fruits. Rearing of internally feeding seed predators revealed some overlap in the pre-dispersal insect seed predator fauna associated with individual Lauraceae species (Gripenberg et al., 2019). While little is known about the biology of individual seed predator species, typically adult females lay one or several eggs on or in developing or mature fruits. The resulting larvae feed on the endosperm before boring their way out of the fruit. Occasionally, multiple seed predator individuals may successfully develop within a single seed (Basset et al., 2018).

2.3 | Data collection

2.3.1 | Is there potential for indirect interactions between Lauraceae species mediated by shared pre-dispersal seed predators?

To assess the potential for seed predator-mediated indirect interactions between Lauraceae species on BCI, we constructed a set of quantitative food webs. This required data on (a) densities (m^{-2}) of fruits of each species in the study area (in our case the abovementioned mapped forest plots on BCI); and (b) the frequencies of interactions between each seed predator and host species (interactions/m^2).

Estimating host densities

To estimate species-specific fruit densities, we visited all adult Lauraceae trees in our study plots in February 2015 (Figure S1). From these, we selected up to six individuals of each species to quantify fruit abundances using seed traps. The criteria for selection were that the tree was reproductive (presence of flowers or fruits), the canopy was reasonably clear of lianas, and the terrain was open enough to allow us to place seed traps (described below) underneath its canopy. Based on these criteria, it was not possible to find six reproducing individuals for all of the nine species. In total, we selected 41 trees. In 2016, we added eight trees, bringing the total number of trees with traps to 49 (Table 2). We placed four 0.5 m^2 seed traps in scattered locations underneath the canopy of each selected tree and visited these monthly to assess when a fruiting period began. We visited traps weekly throughout the fruiting period of each individual. Fruit collections took place between 26 February 2015 and 26 January 2017. Upon each visit, we collected all fruits (immature and mature) and emptied debris from each trap. We brought fruits back to the laboratory and recorded the abundance, total mass, and maturity status of fruit samples for each trap. We used the fruit data obtained from the traps to estimate tree-specific fruit crop sizes following the approach described in Supplementary Information.

For each Lauraceae species, we combined the predicted fruit crop sizes of trap and non-trap trees to obtain an overall estimate of fruit numbers in the studied forest area. To express fruit abundances as densities per m^2, we divided these estimates by the area of mapped forest (470,000 m^2).

Quantifying interaction frequencies

We used the fruits collected from the seed traps to estimate interaction frequencies between Lauraceae and their internally feeding insect seed predators. We placed collected fruits in transparent plastic pots covered with a mesh lid, keeping fruits from different species, collection dates, and traps separately; we also separated mature and immature fruits. We checked pots twice weekly for emerging adult insects for up to three months after collection. At the end of the rearing period, we opened each fruit and removed any remaining adult insects or larvae. We stored Coleoptera, Hymenoptera, and Diptera and all larvae in 95% ethanol in a freezer, and spread Lepidoptera to facilitate morphological identification. All specimens were morphotyped and compared against specimens in S. Gripenberg's seed predator reference collection in the insect collection of the Smithsonian Tropical Research Institute in Panama City. We estimated the mean density of each seed predator species (individuals/m^2) on each Lauraceae species by calculating the average number of seed predator individuals per fruit (number seed predator individuals/number of fruits attacked) for each predator × prey combination. For each seed predator × Lauraceae species combination, we multiplied the average numbers of seed predators per fruit by the number of fruits/m^2 of each Lauraceae species to obtain information on the density of seed predators (m^{-2}). Since the seed traps were emptied regularly, infested fruits were both immature and mature, and since the most abundant seed predator species (*Pagiocerus frontalis*) has been observed on fruit samples obtained directly from the canopy (H. Downey &

TABLE 1 Summary of the Lauraceae species investigated in this study. Descriptions of tree and fruit attributes are based on information in Croat (1978) (tree size, reproductive phenology), our own measurements taken in the first year of data collection (mean fruit weights, lengths, and widths), and trait data collected within the ForestGEO 50 ha forest dynamics plot (Wright et al., 2013)

Species	Adult tree size	No. individuals in study plots	Reproductive phenology
Beilschmedia tovarensis (Meisn.) Sa. Nishida	13–40 m tall, max 75 cm dbh	56	Flowers December to January, fruits attain full size by March and ripen during May and June.
Ocotea oblonga (Meisn.) Mez 1889	Max 30 m tall, max 45 cm dbh	35	Flowers July to Sept, immature fruits February to April, maturing in May and June.
Ocotea puberula (Rich.) Nees 1920	Max 27 m tall, max 50 cm dbh.	13	Flowers at the beginning of the dry season, fruiting January to April with fruits maturing in July.
Ocotea cernua (Nees) Mez 1889	Max 12 m tall	11	Flowers February to March (sometimes longer). The fruits mature August and September.
Ocotea whitei Woodson 1945	15–30 m tall	21	Flowers April. Fruits February to April, fruits mature in May to July.
Nectandra cissiflora Nees 1836	To 27 m tall, to 30 cm dbh	40	Flowers Feb, fruits March and April, fruits mature in May and June.
Nectandra lineata (Kunth) Rohwer		10	Fruits February and March, fruits mature in May and June.

S. Gripenberg, pers. obs.), we are confident that the vast majority of insect individuals were indeed pre-dispersal seed predators.

Constructing and analyzing the quantitative food webs

The quantitative food webs provide a graphical representation of interactions between Lauraceae and their internally feeding seed predators. The upper trophic level is represented by the numbers of seed predators/m^2 and the lower trophic level by the abundance of fruits/m^2 (including both attacked and unattacked fruits). We present a summary web (data from 2015 and 2016 combined), as well as webs displaying data collected in 2015 and 2016 separately. As the dry season begins in late December, the wet and dry seasons are combined in the webs.

Using the information in the quantitative food webs, we assessed the potential for Lauraceae species to interact with each other via their shared insect seed predators following Müller et al. (1999). For each Lauraceae species, we calculate the probability (d_{ij}) that a seed predator attacking host species *i* developed on species *j*:

$$d_{ij} = \sum_k \left[\frac{a_{ik}}{\Sigma_l \alpha_{il}} \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \right]$$

Here, α_{ik} represents the strength of the link between host *i* and seed predator *k*. d_{ij} sums interactions between two hosts via all of their shared seed predators. The sum of both *k* and *l* includes all seed predators, and the sum of *m* includes all hosts. The first term in the brackets represents the fraction of seed predators of host *i* that belong to species *k*. The second term represents the fraction of seed predators of species *k* that develops on host species *j*. d_{ij} equals zero when no seed predators are shared between a pair of host species (*i* and *j*) and equals 1 when all seed predator species on host species *i* develop on host species *j*. The fraction of seed predators attacking plant species *i* that are likely to have developed on the same host plant species (i.e., d_{ii}) can also be defined by this equation. Since the d_{ij} values depend on host densities, we calculated d_{ij} for the two years combined as well as for 2015 and 2016 separately. We calculated the d_{ij} values using the PAC function in the R package bipartite (Dormann, Gruber, & Fründ, 2008).

2.3.2 | What is the relative importance of conspecific and heterospecific seeds as sources of seed predators affecting each host species?

To investigate whether seed predation on individual Lauraceae species is likely to be caused primarily by seed predators that have developed on other Lauraceae species or by seed predators that have developed on the focal Lauraceae species, we compared d_{ii} and d_{ij} values. Using a paired *t* test, we assessed whether the d_{ii} value for each plant species was significantly different from the sum of its d_{ij} values. This was done using data from each of the three food webs, that is, both years combined and 2015 and 2016 separately.

2.4 | Are closely related Lauraceae species and Lauraceae species with similar traits more likely to share enemies than more distantly related species/species with greater trait dissimilarity?

For each of the quantitative food webs, we assessed how the degree of phylogenetic relatedness and the similarity in trait values between species *i* and *j* affected the d_{ij} values. We obtained data on phylogenetic distances between pairs of Lauraceae species from a phylogeny of woody plant species on BCI provided by David Erickson (Smithsonian Institution) constructed using methods described in Kress et al. (2009). We obtained pairwise phylogenetic distances using the ape package in R (Paradis, Claude, & Strimmer, 2004). Fruit morphology measurements were taken on a subset of the fruits collected from the seed traps. From

Mean immature fruit weight (g)	Mean mature fruit weight (g)	Mean immature fruit length (mm)	Mean mature fruit length (mm)	Mean immature fruit width (mm)	Mean mature fruit width (mm)
2.19	6.80	23.5	37.0	9.88	17.89
0.72	0.94	16.25	18.60	8.53	10.07
0.12	0.78	5.72	12.23	4.87	7.69
0.26	0.56	10.15	13.28	6.46	7.46
0.33	0.70	14.17	14.5	6.23	9.33
0.42	0.90	10.66	11.53	10.70	11.68
0.35	0.42	8.89	9.33	0.29	0.35

each trap and collection date, we randomly selected three fruits and measured their mass (g), width (mm) and length (mm). Because the measured fruit traits were highly correlated (Table S4), we selected one trait, fruit mass (g), for our analyses. For each pair of Lauraceae species, we calculated pairwise fruit size differences by calculating fruit mass ratios (mass of species *i*/mass of species *j*). Following Fleming and Partridge (1984), we calculated pairwise overlap (O_{jk}) in fruiting phenology using Pianka's (1974) niche overlap equation:

$$O_{jk} = \frac{\Sigma_{i=1}^{n} P_{ij}P_{ik}}{\sqrt{\Sigma P_{ij}^{2}\, \Sigma P_{ik}^{2}}}$$

Here, P_{ij} and P_{ik} are the proportion of species *j* and *k* fruiting at time interval *i*, which refers to the time between phenological surveys (one month). O_{jk} equals 0 when there is no phenological overlap and 1 when there is a complete overlap between any given pair of species. Phenological overlap was calculated separately for 2015 and 2016.

To assess whether the phylogenetic relatedness and similarity of trait values between pairs of Lauraceae species were correlated with d_{ij} values, we performed Mantel tests using the R package vegan (Oksanen et al.,2017) to assess the correlation between d_{ij} values and phylogenetic distance, fruit size difference, and phenological overlap, respectively. We analyzed data for both years combined and separately for 2015 and 2016. In addition, we tested whether the abundance of species *j* (m^{-2}) affected the magnitude of d_{ij} values using logistic generalized linear models (GLM). All analyses were carried out in Rstudio version 3.3.1 (2016-06-21) “Bug in Your Hair.”

3 | RESULTS

We collected 15,938 fruits of eight species of Lauraceae and reared 14,540 seed predator individuals from these fruits. The seed predators represented six species: two weevils (Curculionoidea: Curculionidae) and four moths (Lepidoptera). A further 151 Lepidoptera individuals (129 adults and 22 larvae) could not be assigned to morphospecies due to their poor condition and were excluded from further analyses. All seed predator species were represented by more than one individual. Seed predators attacked both immature and mature fruits of all Lauraceae species. Table 3 summarizes the materials from fruit collections and seed predator rearing.

The quantitative food webs are depicted in Figure 1. The summary web (Figure 1a) comprises six seed predator species, seven Lauraceae species, and 29 feeding links. Fruits of an eighth species (*Nectandra purpurea*) were collected, but in such small quantities (eight fruits from which no seed predators were reared) that we excluded this species from further analyses. The 2015 web (Figure 1b) has six seed predator species, seven Lauraceae species, and 19 links. No seed predators were reared from *Ocotea whitei*. The 2016 (Figure 1c) web contains six species of seed predator, seven species of host plants, and 22 links. In this year, no seed predators were reared from *Ocotea cernua*. *Pagiocerus frontalis* (Scolytidae) was the most abundant seed predator in all three webs, comprising over 90% of the seed predator individuals and killing around 93% of all predated seeds.

3.1 | Is there the potential for indirect interactions between Lauraceae tree species, mediated by shared pre-dispersal seed predators?

The quantitative food webs (Figure 1) show that the majority of seed predator species were associated with multiple Lauraceae species. The potential for apparent competition (PAC) plot for 2015 (Figure 2b) and the corresponding d_{ij} values show potential for indirect interactions (i.e., $d_{ij} > 0$) between six species pairs, with

TABLE 2 Numbers of individuals of each species of Lauraceae monitored using seed traps and summary of data on fruit fall, seed predator attack, and premature fruit abscission

Species	Total no. trap trees	Total no. fruits	No. fruits attacked	Prop. fruits attacked	No. fruits abscised	Prop. fruits abscised	No. abscised fruits attacked by insects	Prop. abscised fruits attacked by insects	No. mature fruits	No. mature fruits attacked by insects	Prop. mature fruits attacked by insects
B. tovarensis	14	4,281	2,859	0.67	2,805	0.66	1,435	0.51	2,016	470	0.23
O. oblonga	6	2033	1,054	0.52	1,009	0.50	473	0.47	1,024	559	0.55
O. puberula	6	9,569	2,528	0.26	8,540	0.89	2,151	0.25	1,029	440	0.43
O. cernua	4	274	22	0.08	17	0.06	3	0.18	257	19	0.07
O. whitei	5	616	121	0.20	565	0.92	93	0.16	51	27	0.53
N. cissiflora	5	391	335	0.86	355	0.91	304	0.86	36	34	0.94
N. lineata	5	1,215	305	0.25	1,165	0.96	298	0.23	50	7	0.14

four of these being high potential ($d_{ij} > 0.5$). The PAC plot for 2016 (Figure 2c) and corresponding d_{ij} values show potential for indirect interactions between six species pairs, with one of these being high potential ($d_{ij} > 0.5$) (Table S1).

3.2 | What is the relative importance of conspecific and heterospecific seeds as sources of seed predators affecting each host species?

In all data sets (both years, 2015, 2016), there was a significant difference between d_{ii} and d_{ij} values. In all instances, the mean of d_{ij} was significantly higher than the mean of d_{ii} (*t* tests; both years $t = -7.61$, $p < .001$, $df = 12$, mean $d_{ii} = 0.16$, mean $d_{ij} = 0.83$; 2015 $t = -4.61$, $p < .001$, $df = 10$, mean $d_{ii} = 0.19$, mean $d_{ij} = 0.81$; 2016 $t = -5.91$, $p < .001$, $df = 10$, mean $d_{ii} = 0.19$, mean $d_{ij} = 0.81$), suggesting that seed predator attack is likely to depend more strongly on heterospecific than conspecific fruit densities.

3.3 | Are closely related Lauraceae species and Lauraceae species with similar traits more likely to share enemies than more distantly related species and those with greater trait dissimilarity?

There were no significant correlations between the magnitude of d_{ij} values and genetic distances in any of the three data sets (Mantel test; all $p > .05$). In two data sets (both years combined and 2015), there was no significant correlation between the magnitude of d_{ij} and phenological overlap (O_{ij}) (Mantel tests; $p > .05$). In 2016, there was a significant positive correlation between O_{ij} and the magnitude of d_{ij} values ($r = .65$, $p = .04$) suggesting that species that overlap in their fruiting phenology were also more likely to interact via their shared seed predators. There was no significant correlation between the magnitude of d_{ij} and difference in fruit size in the combined data set and in 2016 (Mantel tests; $p > .05$). In the 2015 data set, there was a non-significant trend for d_{ij} to increase with increasing fruit size difference ($r = .44$, $p = .056$).

In two data sets (2015 and 2016), there was a significant effect of the abundance of species *j* upon the magnitude of d_{ij}: As the abundance of species *j* increased, d_{ij} increased (2015: $\beta = 25.13$, $SE = 12.13$, $z = 2.04$, $p = .04$; 2016: $\beta = 1.82$, $SE = 0.86$, $z = 2.12$, $p = .03$). In the data set combining the two years, there was a non-significant trend for d_{ij} to increase with increasing abundance of species *j* ($\beta = 1.51$, $SE = 0.80$, $z = 1.88$, $p = .06$).

4 | DISCUSSION

To our knowledge, our study is one of the first to construct a quantitative seed predator–host food web using techniques that have long been used in the study of insect host–parasitoid communities (e.g., Lewis et al., 2002; Morris et al., 2004). Quantitative food webs have

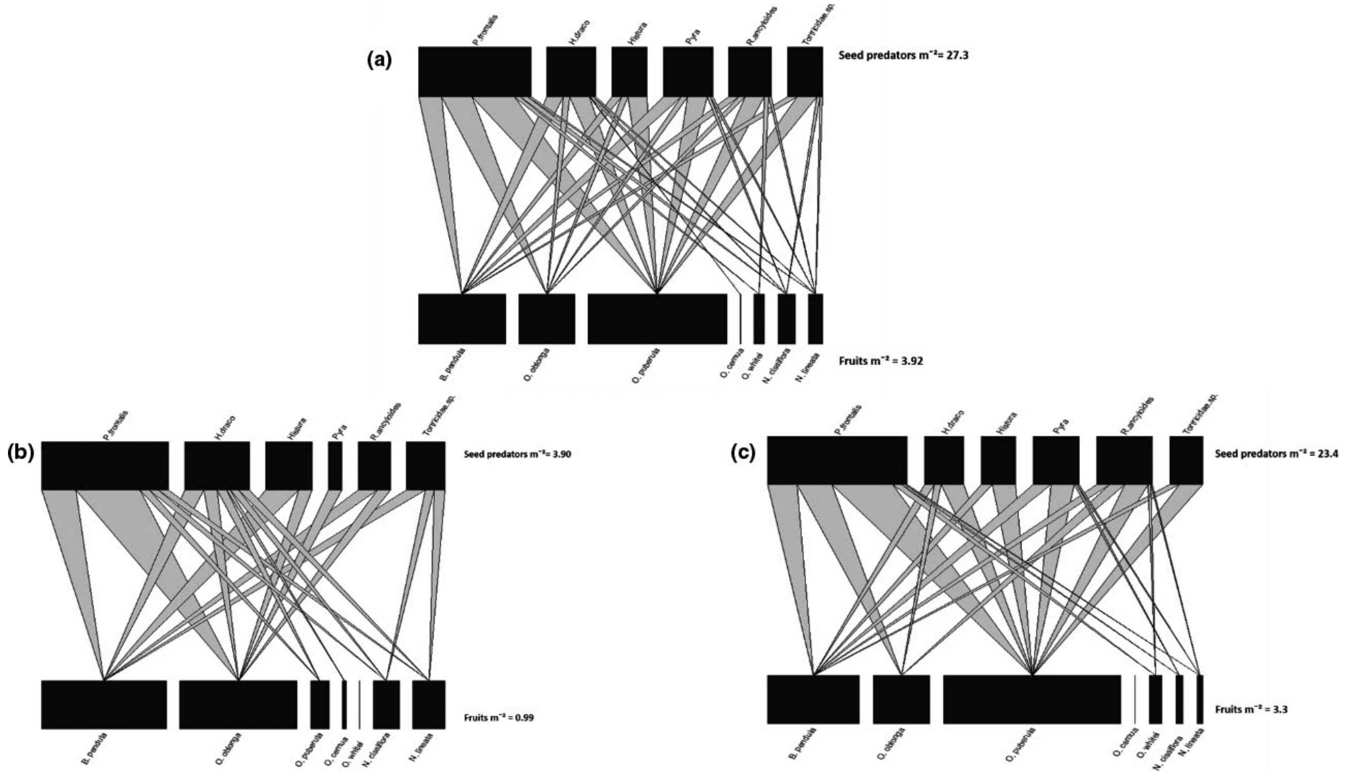

FIGURE 1 Quantitative plant–seed predator food webs for (a) 2015 and 2016 combined, (b) 2015 and (c) 2016. The lower bars represent the density of fruits (m^{-2}) of each plant species in the study area (47 ha of mapped forest on BCI), and the upper bars represent seed predator densities (m^{-2}). The widths of the links represent the frequency of interactions

proven to be the useful tools for exploring the mechanisms driving community structure and for predicting which sets of species are most likely to interact via their shared enemies (Lewis & Gripenberg, 2008; Morris et al., 2004; Tack et al., 2011; van Veen et al., 2006).

Numerically, our webs were dominated by three host plant species (*Beilschmiedia tovarensis*, *Ocotea puberula*, and *Ocotea oblonga*) and one seed predator species (*Pagiocerus frontalis*). All seed predator species in the webs attacked more than one host plant species. Host-use patterns by seed predators appeared not to be influenced by host phylogeny, and there was some flexibility in resource use between years, suggesting that the seed predator species in our study system are not restricted to individual species or genera, but are specialized at the family level. This contrasts with previous studies (e.g., Janzen, 1980) that have shown that insect seed predators tend to be specialized at lower taxonomic levels (species or genus level). What makes the seed predators of Lauraceae less specialized remains unknown.

Our quantitative food webs suggest that there is potential for indirect interactions between tree species mediated by shared pre-dispersal seed predators. Overall, the d_{ij} values were greater than d_{ii} values, suggesting that interspecific effects mediated by seed predators are more important than intraspecific effects. The potential enemy-mediated indirect interactions appear to be driven by the abundance of the host species: Abundant tree species tend to have a negative impact on less common ones by acting as a source of seed predators. In contrast, phylogenetic relatedness and trait similarity between pairs of plant species had little effect on the corresponding d_{ij} values, except for in one year (2016), when there was a significant positive association between the temporal overlap in fruit production and d_{ij}. These host-use patterns contrast strongly with those described by Gripenberg et al. (2019), who found that the majority of woody plant species on Barro Colorado Island are attacked by highly host-specific seed predators and that there is low potential for apparent competition in the wider plant community. What makes species in the Lauraceae family different from other taxa remains unclear, but the fact that many of the Lauraceae species on Barro Colorado Island have similar fruit morphologies and overlap in their fruiting phenology (supplying seed predators with a permanent food resource for much of the year) may have contributed to the high degree of overlap in seed predator–host use.

While the results from our quantitative food web study indicate that enemy-mediated indirect interactions could be an important mechanism in the dynamics of Lauraceae on BCI, the approach comes with several caveats. First, our study only captures a short time period in the long life cycle of trees. Hence, even if seed predator-mediated indirect interactions between Lauraceae species might be important in determining community-level patterns of seed production, we cannot tell whether such patterns will leave an imprint on community structure at larger size classes. Nevertheless, the high seed predation rates (see Table 2) suggest that these enemies might indeed be important, and previous studies have shown that mechanisms operating at the early life stages can be important

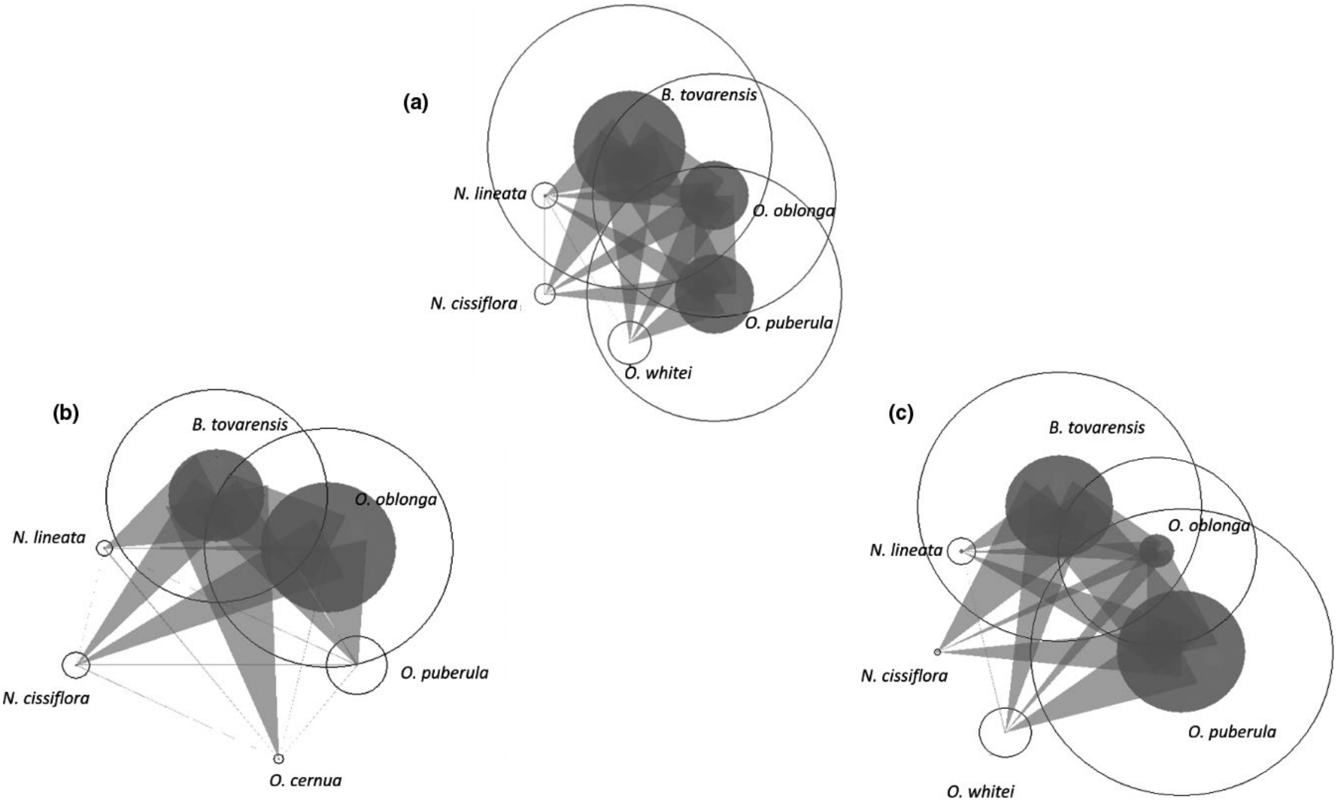

FIGURE 2 Potential for Apparent Competition (PAC) plots for (a) 2015 and 2016 combined (b) 2015 and (c) 2016. The areas of the circles reflect the total fruit abundances of each Lauraceae species. The shaded fraction of each circle represents self-loops (i.e., the fraction of seed predator individuals whose parents are expected to have developed on the same host species). The widths of the connecting wedges are proportional to the flow or export of seed predators between species

determinants of community structure at later stages (Green, Harms, & Connell, 2014). Theoretical and empirical studies investigating the longer-term consequences of the patterns observed in this study would be helpful. Second, the quantitative food web methods rely on a number of assumptions. One assumption is that there is no spatial or temporal separation of host species from the perspective of their enemies leading to host-dependent structuring of the seed predator population. We believe that this is unlikely to be an issue in our study: The study plots were likely small enough for insects to move between trees, and there was considerable overlap in the timing of fruit production between different Lauraceae species. A further assumption is that adult seed predators show no preference for the host species on which they developed as larvae. The phenomenon of insects preferring their natal host species (Hopkin's host-selection principle; Barron, 2001) has been documented in other plant–insect systems (e.g., Saadat, Seraj, Goldansaz, & Karimzadeh, 2014; Takasu & Lewis, 1995) but we are not aware of studies having investigated it in insect seed predators. If ovipositing seed predator females actively prefer the species on which they developed, this could over time lead to the formation of cryptic seed predator races (e.g., Blair, Abrahamson, Jackman, & Tyrrell, 2005) associated with individual plant species. Under such a scenario, individual seed predator races would act like host-specific enemies and would not have the potential to mediate interactions across tree species. To ensure that the predictions based on the food webs are not undermined by the abovementioned complications, they should ideally be verified by experimental manipulations of the system. This could involve removing individual enemy or host species or introducing a host species to an area where it normally does not occur (e.g., Morris et al., 2004). While such experiments would be logistically challenging in our study system, they might be feasible in systems involving dispersed seeds, seedlings or saplings attacked by enemies such as folivores, gallers, or post-dispersal seed predators.

Our study provides some insights into the temporal variation in seed production and patterns of seed predator attack. The changes in the relative abundances of seeds of different species between the two study years were reflected in the patterns of seed predator attack. For example, seed predators were more generalized in their diets and there was a higher number of feeding links in 2016 than in 2015. Substantial variation in fruit crop sizes appears to be a normal feature of the Lauraceae (see Supplementary Information). Such high temporal variability in host abundances might lead to temporal variation in both the strength and direction of any indirect interactions between host species (Abrams, Holt, & Roth, 1998). Overall attack rates of fruits sampled from traps were slightly lower in 2016 (36%) than in 2015 (49%). One possible explanation for this could be seed predator satiation (Janzen, 1971): During periods of high fruit production, predators may be satiated with more resources than they can consume, leading to individual seeds being less likely to be attacked than in periods of lower resource abundance. Several studies

TABLE 3 Summary of fruits collected from traps and seed predators reared from these fruits over 2 years

Tree species	Total no. fruits collected	Total no. seed predators	Total *Pagiocerus frontalis* (Coleoptera)	Total *Heilipus draco* (Coleoptera)	Total *Histura* (Lepidoptera)	Total Pyra (Lepidoptera)	Total *Riculorampha ancyloides* (Lepidoptera)	Total Tortricidae sp. (Lepidoptera)
B. tovarensis	3,404	6,082	5,850	116	14	84	16	2
O. oblonga	1,125	2,212	2,191	2	0	5	14	0
O. puberula	8,778	5,481	5,442	5	7	17	9	1
O. cernua	273	5	0	5	0	0	0	0
O. whitei	622	159	156	0	0	0	3	0
N. cissiflora	389	27	22	3	0	1	0	1
N. lineata	1,181	61	29	11	0	1	19	1

suggest that seed predator satiation might be a relatively common phenomenon in tropical forests and elsewhere (e.g., Cannon, Curran, Marshall, & Leighton, 2007; Norden et al., 2007; Sork, Bramble, & Sexton, 1993).

Although theoretical work suggests that enemy-mediated indirect interactions could be an important mechanism structuring ecological communities (Holt, 1977; Holt & Kotler, 1987), empirical studies testing for herbivore-mediated interactions between plant species remain scarce (but see Chaneton & Bonsall, 2000; Downey et al., 2018). Some studies have shown that plants experience increased herbivory rates when surrounded by heterospecifics that share a common enemy (Barbosa et al., 2009; Root, 1973; White & Whitham, 2000) but few explicitly test for indirect interactions and subsequent impacts upon community structure (but see Rand, 2003).

We are aware of only two previous studies of enemy-mediated indirect interactions between plant species in the tropics (Downey et al., 2018; Garzon-Lopez et al., 2015), and only one of them (Downey et al., 2018) focused on insect enemies as the primary mechanism. One possible reason for the scarcity of studies on this topic might be the difficulty of identifying and quantifying host–enemy associations in highly diverse tropical plant communities. In cases where host use by tropical insect herbivores has been assessed, the diet breadths have often been found to span multiple species (e.g., Novotny et al., 2002, 2010). This opens up the possibility that indirect interactions between plant species may be widespread and challenges current views on the roles of insect herbivores in shaping tropical plant communities, which tend to focus almost exclusively on the role of specialist insect herbivores in driving conspecific negative density dependence in plant survival (e.g., Connell 1971; Janzen, 1970). Although competition for resources between tree seeds and seedlings appears to be weak in tropical forests (Paine, Harms, Schnitzer, & Carson, 2008; Svenning, Fabbro, & Wright, 2008), it is still possible that seeds and seedlings will be negatively influenced by the presence of heterospecifics with which they share enemies.

In conclusion, our study suggests that, in some groups, enemy-mediated indirect interactions such as apparent competition could be an important mechanism structuring tropical plant communities. Understanding in what contexts and under what circumstances these interactions take place could fundamentally increase our understanding of the dynamics of diverse tropical plant communities. Research into enemy-mediated indirect interactions may also provide insights into the potential responses of plant species to disturbances such as selective logging or other disturbances that increase or decrease the abundance of potential apparent competitors.

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AUTHOR CONTRIBUTION

HD, SG, OL, and MB conceived and designed the study. HD led the data collection, analyzed the data, interpreted the results, and drafted the manuscript with input from SG, OL, and MB. AW assisted with data collection.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8w9ghx3h6 (Downey, Lewis, Bonsall, Ward, & Gripenberg, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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