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Insect Seed Predation on Barro Colorado Island

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ABSTRACT. The seeds of many woody plant species on Barro Colorado Island (BCI) are fed upon by insect seed predators—insects that develop inside the seed, killing it in the process. Studies conducted on BCI reveal that insect seed predation varies substantially in space and time as well as among plant species. A major rearing study (more than 200,000 seeds and fruits of 478 plant species and 369 species of insect seed predators) found that most insect species feed on a single local host plant species or a few closely related species. This suggests insect seed predators have the potential to contribute strongly to plant diversity maintenance, although they have received less attention than other plant enemy guilds. Given the strong foundation of prior work, the insect seed predators of BCI are an interesting and relevant target for future studies of plant diversity maintenance and the ecology and evolution of plant–enemy interactions.

Keywords: granivory; Janzen–Connell hypothesis; plant chemistry; plant–insect interaction; plant reproduction; seed parasitism; species coexistence; tropical forest

INTRODUCTION

Seed predation (granivory) is the consumption and killing of seeds by animals (Janzen, 1971; Crawley, 1983). It is a form of herbivory, but compared with other types of herbivory, such as leaf herbivory, its negative effect on plant fitness is often more direct, obvious, and extreme: the immediate death of the seed. Seed predation is of interest to plant ecologists because it can keep plant populations at low density (e.g., Crawley, 2000; Maron and Crone, 2006) and can have an effect on the structure and diversity of plant communities (e.g., Gillett, 1962; Janzen, 1970; Connell, 1971; Lewis and Gripenberg, 2008). Seed predation can happen at different stages of the development of the seed. Predispersal seed predation refers to situations in which seed predators attack seeds that are still attached to the mother plant, when seeds may not be fully mature. Postdispersal seed predation happens in the period between seed dispersal and germination. Seed predation can be inflicted by vertebrates (mainly mammals and birds) and invertebrates (mainly insects). Both groups of seed predators have been studied on Barro Colorado Island (BCI).

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In this contribution, I provide an overview of studies conducted on BCI that have targeted insect seed predation and insect seed predators, a guild that my colleagues and I have studied on the island since 2010.

INVESTIGATING SPATIAL AND TEMPORAL PATTERNS OF INSECT SEED PREDATOR ATTACK

Plant ecologists working on BCI have long noticed the feeding marks left by insects on seeds of particular tree species. Conspicuous examples include the circular exit holes on *Prioria copaifera* seeds caused by the weevil *Eubulus fulvosquamis*, and the perforations in seeds of *Beilschmedia tovarensis* made by tiny bark beetles.

Since the 1970s, a small number of studies—inspired by Janzen's (1970) and Connell's (1971) ideas about the role of enemies for plant diversity maintenance in tropical forests—have investigated patterns of insect seed predator attack on selected plant species in relation to spatial and temporal patterns of seed and fruit availability.

In a study investigating the potential benefits of reproductive synchrony in plant populations, Augspurger (1981) manipulated the reproductive phenology of *Hybanthus prunifolius* individuals in local populations and assessed the subsequent patterns of attack by microlepidopteran and dipteran seed predators in the manipulated (asynchronous) populations and in unmanipulated control populations in which individuals were reproducing in synchrony. In line with her predictions, Augspurger reported reduced levels of insect seed predator attack when individuals within plant populations were reproducing in synchrony, as would be expected by the predator satiation hypothesis (Janzen, 1971). The levels of seed predation, however, were generally low and Augspurger concluded that the main benefits of reproductive synchrony likely derived from interactions with pollinators rather than seed predators.

Around the same time, De Steven (1981) investigated patterns of attack by host-specific moths on fruits of *Mabea occidentalis* in two stands on BCI. The moths were initially identified as members of the *Laspeyresia* genus, but later were reidentified as *Grapholita yurubina* (Brown et al., 2020). De Steven found high levels of seed predation (~80%), but no effects of spatial isolation (mean distances to the three nearest fruit-bearing conspecifics) on levels of seed predation on individual treelets within stands, contrary to predictions by Janzen (1970). She therefore concluded that if spatial effects of isolation on seed predator attack exist in the *Mabea-Grapholita* system, they must operate at larger scales than those considered in her study. There was, however, a temporal effect: Fruits produced early in the season were most likely to escape seed predator attack—a pattern that contrasts with the results from Wright's studies in the *Attalea-Speciomerus* system discussed next (Wright, 1990).

The most frequently studied interaction between plants and insect seed predators on BCI is the one between the palm *Attalea rostrata* (formerly *A. butyracea* and *Scheelea zonensis*) and its postdispersal bruchid seed predator *Speciomerus giganteus* (formerly *Caryobruchus giganteus*). In the first of a series of papers published on this system, Wright (1983) reported distance-dependent patterns of bruchid oviposition in line with predictions from the Janzen–Connell hypothesis: Seeds placed 100 m or farther away from a fruiting *Attalea* palm were less likely to be colonized by egg-laying bruchid females within 24 hours than seeds closer to (within 16 m of) fruiting palms. The abundance of *Attalea* seedlings was still highest in the vicinity of fruiting palm individuals, illustrating that seedling distributions reflect patterns of seed dispersal as well as seed survival and establishment success. Other studies on BCI and in nearby forests have targeted the *Attalea-Speciomerus* system, revealing, for example, that late-fruiting *Attalea* individuals escape bruchid seed predation with potential demographic and evolutionary consequences for the palm (Wright, 1990) and that density-dependent patterns of bruchid attack can be counteracted by predators of bruchid larvae (Visser et al., 2011).

Research in the *Attalea-Speciomerus* system has also yielded valuable insights into the ecology of the seed predator, including its movement and oviposition behaviors (e.g., Wright, 1983). Focusing on *Speciomerus giganteus* and another bruchid seed predator of *Attalea rostrata* (the predispersal seed predator *Pachymerus cardo*), Peguero et al. (2017) investigated mechanisms of competition and coexistence between insect species sharing the same food resource (*Attalea* seeds). The study reveals a likely role of vertebrates in mediating interactions between the two seed predator species: On BCI, which has an intact vertebrate fauna, *Speciomerus giganteus* (which tends to be the better competitor of the two inside coinfested seeds) is the most abundant insect seed predator of *Attalea*. At sites where vertebrate frugivores and granivores are rare or absent, however, *Speciomerus giganteus* is at a disadvantage because it only oviposits on *Attalea* fruits that have been fully or partially stripped of their pulp by frugivores, whereas predispersal oviposition by *Pachymerus cardo* remains unaffected.

The establishment of mapped forest plots on BCI, notably the 50-ha Forest Dynamics Plot, has provided opportunities for studies assessing the effects of conspecific densities on levels of enemy attack. These opportunities remain relatively little exploited for studies of insect seed predation, with the exception of one study on the tree *Jacranda copaia* and a galling hymenopteran seed predator. Among-tree variation in insect seed predation rates in the 50-ha plot was positively related to the density of fruiting conspecifics in the neighborhood (Jones and Comita 2010). Nonetheless, the net effect of conspecific density on the production of intact mature fruits was still positive—likely because of higher pollination success and fruit set in areas with a high conspecific density. This illustrates that results from studies targeting one specific type of interaction (such as seed predation) will ultimately need to be interpreted in their broader context (for other examples, see Augspruger, 1981, and Visser et al., 2011).

EXPANDING OUR KNOWLEDGE ON THE ECOLOGY AND EVOLUTION OF POORLY KNOWN TROPICAL INSECT TAXA

Most studies reviewed thus far were conducted by researchers with a primary interest in plant ecology. Over the years, a small number of studies have more explicitly targeted the insect seed predators themselves, generating new knowledge on the ecology and natural history of some species-rich, yet poorly known, tropical insect taxa. Pinzón-Navarro and colleagues conducted molecular-based studies of seed eating weevils reared from seed samples collected on BCI, revealing novel host associations and evolutionary relationships in this highly speciose insect group (Pinzón-Navarro et al., 2010a, Pinzón-Navarro et al., 2010b). Based on observations from BCI, Harms and Aiello (1995) reported the first published record of seed feeding in tropical Sesiidae (clearwing moths): feeding on *Gustavia superba* seeds by *Carmenta foraseminis* (Sesiidae). This was considered to be an unexpected feeding mode at the time. However, our subsequent work not only corroborated this observation but also found members of the Sesiidae family to be associated with seeds of another nine plant species on BCI (Gripenberg et al., 2019). This finding suggests that the seed-feeding habit of sesiid moth larvae may be a more widespread phenomenon than originally appreciated, although infested seeds may in some cases still be able to germinate (Harms and Dalling, 2024).

With BCI having developed into a hot spot for studies on plant diversity maintenance (e.g., Harms et al., 2000; Hubbell, 2001; Comita et al., 2010) and an increasing number of studies providing direct or circumstantial evidence for natural enemies driving negative density dependence in tropical forest plant populations (e.g., Bell et al., 2006; Mangan et al., 2010), my colleagues and I decided to initiate a study to collect novel information on insect seed predators that could help predict the likely effects of this plant enemy guild in shaping the forest plant community of BCI. More specifically, we wanted to document patterns of host use by insect seed predators across the woody plant community to assess whether the degree of host specificity within this enemy guild is high enough for them to have a potential diversity-maintaining effect on the plant community, as envisaged by Gillett (1962), Janzen (1970), and Connell (1971). We also wanted to assess which plant species are routinely attacked by the same insect seed predator species and could therefore—in theory—interact through seed predator-mediated "apparent competition" (Holt, 1977).

Inspired by Dan Janzen's work in Costa Rica (Janzen, 1980) and using rearing methods similar to those developed by Pinzón-Navarro et al. (2010a, 2010b) on BCI, we set out to catalog insect seed predator-host associations across the entire BCI woody plant community (trees, shrubs, and lianas). Over a period of approximately three years (2010–2013), we collected more than 200,000 seeds and fruits from 478 plant species, including 87% of species known to reproduce in the 50-ha plot during that period. A total of 369 insect seed predator species were reared form these samples (Gripenberg et al., 2019) alongside a bycatch of pulp-feeding insects, which are interesting in their own right but not considered here. In addition to confirming previously documented species interactions (e.g., Augspurger, 1981; De Steven, 1981; Wright, 1983; Harms and Aiello, 1995; Jansen et al., 2010; Pinzón-Navarro et al., 2010a, Pinzón-Navarro et al., 2010b), we detected a large number of interactions between plants and their insect seed predators that previously had not been formally documented on BCI.

Our study (Gripenberg et al., 2019) revealed that approximately two-thirds of the most well-sampled plant species are routinely attacked by at least one species of insect seed predator. The most common groups of insect seed predators are beetles (weevils and bruchids; Fig. 1a–d) and moths (various families; Fig. 1e,f), with some plant species also attacked by seed-predating wasps and flies. A key finding from our work is that most seed predators on BCI appear to be highly host-specific: 80% of the insect species encountered were reared from one single plant species, although note that this number could decrease if we were to sample more extensively. Our BCI-focused study was followed up by similar work at two other tropical forest sites: Wanang in Papua New Guinea and Khao Chong in Thailand (Basset et al., 2018; Basset et al., 2021). Interestingly, levels of seed predator host specificity tend to be higher on BCI than at the other sites. The reasons for these differences remain unknown but could be linked to the higher levels of plant diversity at the other sites, and perhaps especially a higher number of cooccurring congeneric plant species. Collectively, these studies illustrate that patterns observed in one system should not be uncritically extrapolated to other systems.

Although high host specificity seems to be the norm among seed predators on BCI, in some cases, insect seed predator species are associated with several, typically closely related, plant species. One such case is the Lauraceae family, within which most tree species tend to be attacked by the same insect seed predator species (the bark beetle *Pagiocerus frontalis* being the by far most common one). This opens up the possibility for apparent competition (Holt, 1977) between tree species in the Lauraceae family – a possibility investigated and discussed in more detail by Downey et al. (2020).

FUTURE OUTLOOK

The studies reviewed in this chapter illustrate that insect seed predators are an interesting target for further studies on BCI and in other tropical forests. The high levels of seed mortality inflicted by insect seed predators, at least for some plant species and under some circumstances (e.g., De Steven, 1981; Downey et al., 2020), suggest that they are likely to be important determinants of the reproductive success for at least some plant species. Their host specificity (Gripenberg et al., 2019; Basset et al., 2021), which is likely to be higher than that of many other herbivore groups (Novotny et al., 2010), suggests that they

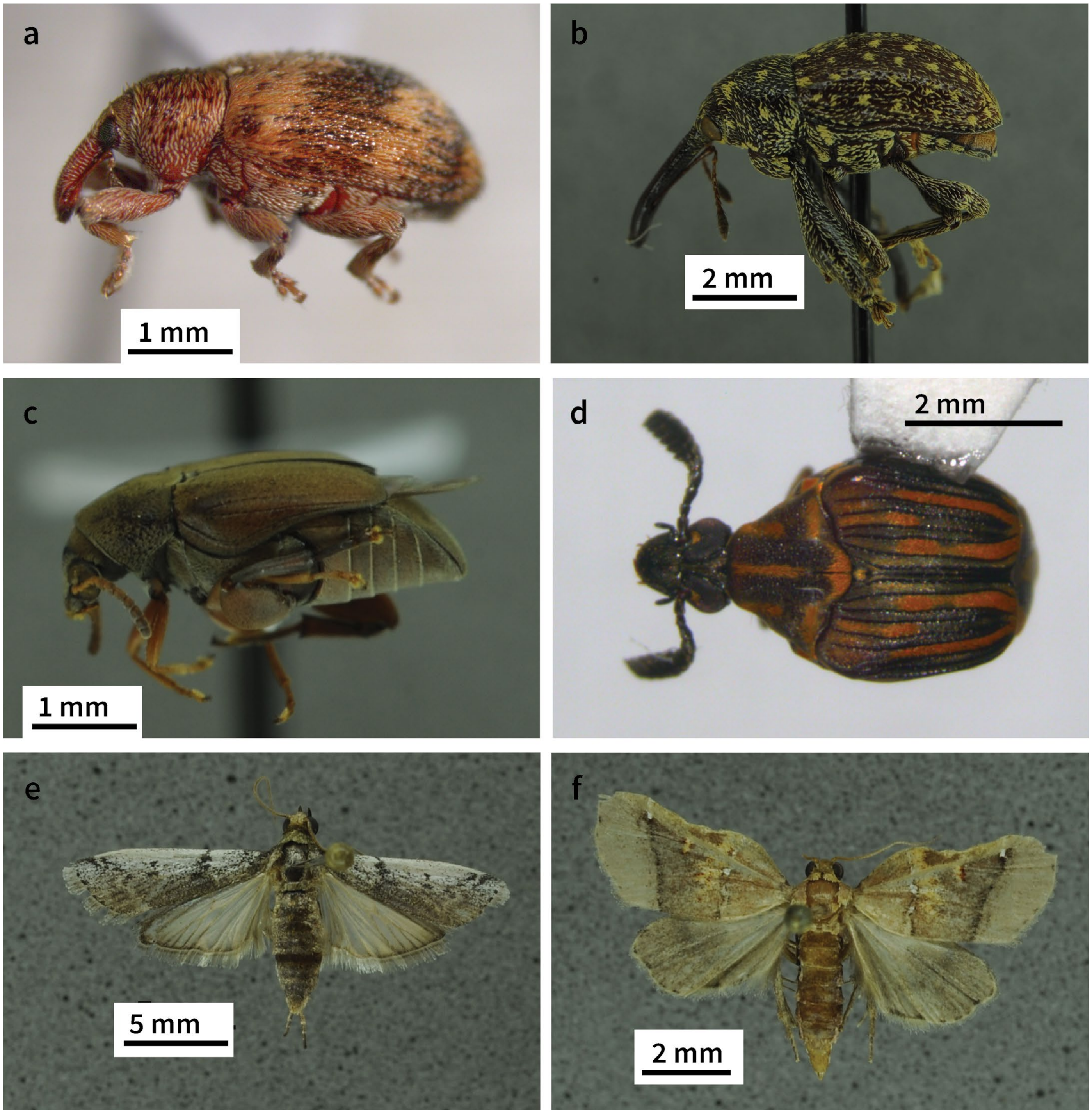

FIGURE 1. A representative subset of insect seed predator species reared from tree and liana seeds collected on Barro Colorado Island: (**a**) *Plocetes beluosus* (Curculionidae) from *Coutarea hexandra*, (**b**) *Chelotonyx* sp. (Curculionidae) from *Quararibea asterolepis*, (**c**) *Mimosestes enterolobii* (Bruchinae) from *Enterolobium cyclocarpum*, (**d**) *Megacerus lunulatus* (Bruchinae) from *Maripa panamensis*, (**e**) *Ectomyelois muriscis* (Pyralidae) from *Hymenaea courbaril*, and (**f**) *Clydonopteron pomponius* (Pyralidae) from *Callichlamys latifolia*.

could play a pivotal role in plant diversity maintenance if they attack their hosts in a density-dependent fashion (Gillett, 1962; Janzen 1971). Further tentative support for the idea that insect seed predators have the potential to contribute to tree species coexistence on BCI was presented in a recent study (Jackson et al., 2022), which showed that seed mortality through premature fruit drop—possibly triggered by insect seed predators—was highest in locally abundant species in the BCI plant community. Taken together, these points suggest that the insect seed predators of BCI should be further investigated as potential contributors to the maintenance of plant diversity alongside other enemy guilds, such as seedling pathogens, that have recently received more attention (e.g., Mangan et al., 2010; Eck et al., 2019).

As demonstrated by Visser et al. (2011), the potential diversity-enhancing effects of insect seed predators could still be counteracted by strong top-down control, that is, predation on the seed predators themselves. Although such top-down control may be important in some species (Visser et al., 2011), it appears unlikely to be a major determinant of the abundances of predispersal insect seed predators associated with immature fruits in the canopy (Sallabanks and Courtney, 1992): Vertebrate seed predators and seed dispersers do not typically consume the unripe fruits in which most predispersal insect seed predators reside, and in our large-scale insect-rearing exercise (Gripenberg et al., 2019; Basset et al., 2021), the number of insect parasitoid individuals was low.

Although much of the insect seed predator–related work conducted on BCI to date has focused on their potential role in facilitating plant species coexistence, the insect seed predators of BCI could also form a relevant study system for research on other topics, including the coevolutionary dynamics between plants and their insect enemies. Although substantial attention has been given to Ehrlich and Raven's escape and radiate hypothesis (Ehrlich and Raven, 1964), which states that the diversification of plant and insect lineages are linked to novel chemical plant defenses and counteradaptations in the insects, finding suitable study systems for testing the key predictions of this hypothesis is not straightforward. Given the wealth of background information already available, the insect seed predators of BCI and their host plants could be a useful system to explore in this context. Information on some aspects of the defensive chemistry of seeds (concentrations of key groups of polyphenols) is already available for many species (Gripenberg et al., 2018), and recent methodological developments in the field of metabolomics makes screening plant species for a much broader range of chemical compounds of potential relevance to insect seed predators a real possibility (Sedio, 2017, 2024).

To conclude, the insect seed predators of BCI form a convenient and relevant study system for researchers studying the ecology and evolution of plant–enemy interactions. The wealth of information already available on the plant species of BCI (including phylogenetic relationships and information on plant and seed traits) provides the perfect backdrop for studies of plant–enemy interactions. The documented interactions between plant species and insect seed predator species (published as part of Gripenberg et al., 2019), in combination with the seed predator reference collection deposited at the Smithsonian Tropical Research Institute and photographs and DNA barcodes made available through the Barcode of Life project website (https://www.boldsystems.org; project BCISP), provide a resource for plant ecologists, insect ecologists, systematicists, and evolutionary biologists who want to investigate insect seed predators and their wider impacts in tropical forest systems.

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