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LRH: Gripenberg

RRH: Pre-dispersal Seed Predation by Insects

Do pre-dispersal insect seed predators contribute to maintaining tropical forest plant diversity?

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25 **Abstract**

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27

28

29 **Key words:** density-dependence; fruit abscission; host specificity; Janzen-Connell hypothesis;

30 plant reproduction; seed predation

31 UNDERSTANDING THE MECHANISMS BEHIND THE EXTRAORDINARY LEVELS OF PLANT DIVERSITY
32 observed in many tropical forests is a key aim in tropical ecology (*e.g.*, Wright 2002, Leigh *et al.*
33 2004). What allows hundreds of tree species (Valencia *et al.* 1994) and a substantial number of
34 liana species (Schnitzer *et al.* 2012) to co-occur locally in these forests? Among the many and
35 mutually non-exclusive mechanisms proposed (Wright 2002), the role of natural enemies has
36 received particular attention.

37 According to the Janzen-Connell hypothesis (Janzen 1970, Connell 1971), the
38 coexistence – and the consequent high alpha diversity – of plant species in tropical forests is
39 promoted by specialised natural enemies such as pathogens and insect herbivores that cause
40 density- and/or distance-dependent patterns of plant survival. By making individuals more prone
41 to enemy-attack when surrounded by conspecifics, plants will tend to fare better when
42 conspecific density in the neighbourhood is low, thereby enhancing diversity at the community
43 level. Many studies have documented distance- and density-dependence in the survival of seeds
44 and seedlings in line with these predictions (for a recent meta-analysis, see Comita *et al.* 2014).
45 Although it is often not clear what types of enemies contribute to observed patterns of plant
46 mortality, data have slowly started to accumulate (*e.g.*, Bell *et al.* 2006, Mangan *et al.* 2010,
47 Bagchi *et al.* 2014, Fricke *et al.* 2014).

48 The current literature on the role of enemies in plant diversity maintenance is dominated
49 by studies assessing conspecific density and distance effects at relatively small spatial scales and
50 focusing on seedlings or seeds that have already dispersed from the mother plant (*e.g.*, Harms *et al.*
51 2000, Bagchi *et al.* 2014). However, as noted by Gillett (1962), enemy-inflicted plant
52 mortality with implications for diversity can also involve pests attacking seeds that are still
53 attached to the mother plant. This idea was reiterated by Janzen (1970), who suggested that host-

54 specific pre-dispersal enemies can enhance diversity if they destroy a particularly large
55 proportion of the seed crop where multiple reproductive conspecifics grow close to each other.
56 However, in an alternative line of reasoning (see Fig. 2 and 3 in Janzen’s publication), Janzen
57 also illustrates how pre-dispersal enemies – regardless of their specificity – may in fact have the
58 potential to *erode* plant diversity. According to this argument, the reduction in seed crop sizes
59 caused by pre-dispersal enemies will truncate seed dispersal kernels, since with fewer seeds the
60 probability of long-distance dispersal will decrease. This will inevitably decrease the distance
61 between conspecific adults unless offset by foraging patterns of post-dispersal enemies and/or
62 negative density-dependence acting across larger spatial scales. Almost 50 years on, while some
63 aspects of Janzen’s predictions have been hugely influential on empirical research, the pre-
64 dispersal element has been largely neglected. As I argue below, pre-dispersal insect seed
65 predators fulfil several criteria for being important diversity-enhancing plant enemies; yet they
66 have been summarily ignored by ecologists interested in Janzen-Connell effects. Here I propose
67 a research agenda for rectifying this.

68

69 CURRENT EVIDENCE. – Pre-dispersal insect seed predators have the potential to influence the
70 ecological and evolutionary dynamics of their hosts (Kolb *et al.* 2007). Several lines of evidence
71 suggest that they may also be important for plant diversity maintenance in tropical forests:

72 ***A large proportion of plant species are attacked by pre-dispersal seed predators and the***
73 ***number of seeds killed can be substantial.*** – Since Janzen’s pioneering work on bruchid beetles
74 in Costa Rica (1980), several studies have assessed patterns of insect seed predation in tropical
75 forest plant communities in different parts of the world (Table 1). The results from these studies
76 suggest that insect seed predation is common: a substantial proportion of surveyed plant species

77 were observed to be attacked by at least one species of insect seed predator, many of which are
78 likely to have attacked the seeds while they were still attached to the mother plant. Only some of
79 the studies in Table 1 attempted to quantify the proportion of seeds falling victim to predators
80 through seed dissection or experimental manipulations. Where assessed, seed predation rates
81 varied widely among species. While some authors (*e.g.*, Ctvrtecka *et al.* 2014) have concluded
82 that their focal seed predator taxa are too rare to contribute to plant diversity maintenance, care
83 should be taken in extrapolating such conclusions to other contexts and systems. It is worth
84 noting that seed predation rates obtained through rearing or visual examination of seeds could
85 severely underestimate the true impact of insect seed predators (Andersen 1988), for example
86 where seed predators do not leave any clear feeding marks on their hosts. True seed predation
87 rates are therefore likely to be higher than those reported in the literature.

88 ***Seed predators show remarkable levels of host-specificity.*** – For the Janzen-Connell
89 mechanism to contribute to diversity maintenance, enemies need to be relatively specialised
90 (Sedio & Ostling 2013, Stump & Chesson 2015). Several studies have assessed host specificity
91 of internally feeding insect seed predators (*e.g.*, Janzen 1980, Ctvrtecka *et al.* 2014). An overall
92 pattern to emerge is that these insects typically feed on one or a few closely related species and
93 tend to be more specialised than other feeding guilds (Novotny *et al.* 2010; but see Sam *et al.*
94 2017). Less is known about the specificity of other guilds of seed-eating insects (*e.g.* sap-suckers
95 and external feeders), but there is no doubt that at least the internally feeding seed predators are
96 good candidate enemies in the context of plant diversity maintenance.

97 ***There is high potential for landscape-level density-dependence in pre-dispersal seed***
98 ***predation rates.*** – Studies testing for density-dependence of insect seed predation and/or seed
99 survival over large spatial scales remain scarce (but see *e.g.* Visser *et al.* 2011). In one of the few

100 studies involving pre-dispersal seed predators, Jones and Comita (2011) assessed premature fruit
101 abscission caused by a hymenopteran seed predator on *Jacaranda copaia* in the 50-ha forest
102 dynamics plot on Barro Colorado Island (Panama). In line with Janzen's predictions, seed
103 predation rates increased with increasing fruit densities. Nevertheless, this increase was not large
104 enough to cancel out the positively density-dependent fruit set (a likely result of pollination
105 success being highest in parts of the forest where there are many fruiting conspecifics). It is
106 plausible that landscape-level density dependence in seed predation rates might occur in other
107 species as well: The patchy distribution of host plants across the forest landscape (Condit *et al.*
108 2000) may impose spatial structure in insect abundances through behavioural responses of
109 insects to local resource abundances. Studies of host-specific folivorous insect herbivores
110 associated with trees in temperate regions have shown that the degree of host tree isolation can
111 be an important determinant of landscape-level patterns of insect distribution (*e.g.*, Gripenberg *et*
112 *al.* 2008, Tack *et al.* 2010). Spatially-structured populations driven by – and in turn potentially
113 influencing – tree distributions may be particularly prevalent in species-rich tropical forests,
114 since the low abundance of individual tree species will make their distributions patchy. Since the
115 area as well as the isolation of habitat patches is key to influencing incidence and abundance in
116 spatially-structured populations (*e.g.* Hanski 1994), it seems possible that any positive effects of
117 landscape-level tree densities on seed predator incidence, abundance, and attack rates may be
118 particularly pronounced in relatively small-sized tree species, where the small size of host
119 individuals could lead to higher patch-level extinction rates.

120

121 WHAT NEXT? – Pre-dispersal seed predators cannot be dismissed as potentially important agents
122 of diversity maintenance, but we are still a long way from answering the question of whether

123 they do indeed facilitate coexistence of plant species in tropical forests. The logistical challenges
124 of studying seed predation in the canopy are substantial and community-level manipulations of
125 pre-dispersal enemies analogous to those that have been done for post-dispersal enemies (Bagchi
126 *et al.* 2014) will be unfeasible. To answer the question of whether pre-dispersal insect seed
127 predators promote the coexistence of plant species in tropical forests a combination of multiple
128 approaches (experiments, field observations, modelling) will therefore be needed. Below I
129 identify a few starting points for moving the research field forward:

130 First, manipulative experiments excluding seed predators from selected plant individuals
131 could yield important insights into the ecological role of pre-dispersal insect seed predators in
132 tropical forests. These experiments could focus on single plant species, although it would be
133 helpful to conduct experiments across a range of species to assess the generality of patterns
134 observed. In addition to allowing us to quantify levels of seed predation, manipulative
135 experiments could verify that pre-dispersal insect seed predators are indeed causing additional
136 seed mortality: If, as has been suggested (Ghazoul & Satake 2009), trees sometimes initiate more
137 seeds than could possibly be brought to maturity and then selectively abort insect-infested seeds,
138 seemingly high levels of seed infestation rates recorded in observational studies may have little
139 effect on plant fitness. In the context of plant diversity maintenance, it would be particularly
140 interesting to assess the effects of seed predator exclusion on seed dispersal kernels and seedling
141 recruitment curves (see Fig. 2 and 3 in Janzen, 1970), and to use sensitivity analyses to
142 determine what levels of pre-dispersal seed predation would influence diversity through
143 alternations in dispersal kernels. While experiments on single species do not answer the question
144 of what happens in the wider community following seed predator exclusion, the community-
145 level implications could be assessed by inputting results of individual species experiments to

146 models that predict community patterns (e.g. changes in species abundance distributions through
147 early ontogeny) and exploring how community-wide patterns deviate from the predictions based
148 on these models. Conducting manipulative experiments at the whole-tree scale does not come
149 without challenges, but excluding pre-dispersal seed predators from selected tree individuals
150 using insecticides (Louda 1982) or bagging (Nakagawa *et al.* 2005) – combined with appropriate
151 control procedures – might be feasible for selected understorey tree species, for species
152 producing seeds in discrete clusters (e.g. palms), or for species that can be accessed through one
153 of the canopy cranes available for canopy research (e.g. Parker *et al.* 1992).

154 Second, further observational studies assessing spatial and temporal patterns of pre-dispersal
155 seed predation are needed before generalisations about ‘typical’ responses of seed predators to
156 variations in resource abundances can be made. A primary aim of these studies would be to test
157 if the positive landscape-level density-dependence in seed predation hypothesised by Janzen
158 (which could serve as a stabilising factor promoting species coexistence) occurs, or if seed
159 predators are more typically satiated under high seed abundances. Given the potential scale-
160 dependence of density-effects (Schupp 1992, Xiao *et al.* 2017), sampling protocols should be
161 designed to allow testing for density-responses across multiple spatial scales. Since temporal
162 variation in seed predation rates may also have implications for coexistence (Chesson 1985),
163 studies should ideally be conducted over several fruiting seasons. The seed and fruit monitoring
164 schemes established at some permanent forest dynamics plots (e.g. Anderson-Teixeira *et al.*
165 2015) could provide opportunities for assessing long-term temporal variation in seed predation
166 rates if combined with protocols for scoring insect damage. Ideally, observational studies on
167 density-responses of seed predators would be followed by modelling studies to assess whether
168 observed density responses (which may be positive at some spatial scales, negative at other) are

169 sufficient to act as a mechanism regulating plant population growth. One challenge is that studies
170 need to be conducted over large spatial scales given the potentially high dispersal ability of
171 insect seed predators. For many species, existing forest dynamics plots may be too small for this
172 purpose. Newly developed remote sensing techniques might prove useful when identifying
173 landscape-level variation in conspecific densities of canopy trees over larger areas (see Jansen *et*
174 *al.* 2008). Another challenge in quantifying pre-dispersal seed predation rates through
175 observations is removal of seeds from the canopy by dispersers. Obtaining accurate estimates
176 might still be feasible for species with cupules or other structures that are not removed by seed
177 dispersers.

178 Third, although the focus of this commentary is on pre-dispersal seed predation, it is
179 important to remember that plant performance with potential implications for coexistence is
180 likely to be the result of multiple processes. We know little about the role of other taxa
181 influencing pre-dispersal seed mortality, and even less about the ways in which they potentially
182 enhance or hinder the influence of each other. There is room for both field-based and theoretical
183 work assessing the combined effects of processes such as pollination, seed dispersal, and
184 mortality caused by various groups of pre- and post-dispersal enemies on plant diversity, as well
185 as studies integrating mortality processes at different stages of the plant life cycle (Green &
186 Harms 2018). For example, it is known that feeding by insects in the canopy can affect the
187 vigour of seedlings, and therefore the plant's tolerance to hazards at later stages (Sousa *et al.*
188 2003, Bonal *et al.* 2007). If we focus our efforts too narrowly on one enemy group and/or one
189 specific life stage – as is often the case in work done to date – there is a risk that we miss or
190 greatly underappreciate crucially important interactions.

191

192 CONCLUSIONS – There is ample scope for interesting work on the diversity-enhancing effects of
193 pre-dispersal enemies paralleling work that has been done on post-dispersal enemies. This work
194 would not only be of academic interest but also of potential importance in the context of current
195 environmental changes. With fruiting patterns possibly changing following climate change (see
196 *e.g.* Wright & Calderon 2006), this could lead to disruptions in the pre-dispersal seed predation
197 process. Unless we know the ecological role of this enemy group, we don't know what the
198 consequences are going to be for the diversity of plants in tropical forests.

199

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207

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360 TABLE 1. Summary of data sets on insect seed predation in tropical forest plant communities, as obtained from the literature. Studies
 361 were identified using literature searches (Web of Science and Google Scholar; search terms seed predat* AND insect* AND tropic*)
 362 and through reference lists of relevant publications. The Google Scholar search yielded a large number of studies. These were sorted
 363 according to relevance, and only the top 500 studies were assessed for suitability based on title and/or abstract. Case studies focussing
 364 on single plant species were excluded, since the selection of focal species is likely to be biased towards species with particularly high
 365 predation rates. In studies denoted with an asterisk (*), the focus was not exclusively on pre-dispersal enemies, although it seems
 366 likely (based on sampling methodology and taxa involved) that a substantial proportion of the seed predation will be inflicted by
 367 enemies attacking seeds prior to seed dispersal. In most cases, sampling is unlikely to be exhaustive, and more plant-seed predator
 368 interactions would likely have been detected had sample sizes been larger. Hence, the values of the number and % of attacked species
 369 reported are likely smaller than true values.

370

Source	Focal seed predator group	Geographical region	Method used to assess incidence and rates of seed predation	Type of seeds examined (mature or immature)	Number of plant species studied	Number (and %) of plant species attacked	Proportion of seeds attacked per plant species (min-max) ^a
*Basset <i>et al.</i> 2018	All internally feeding seed predators	Lowland rainforests of Panama (Barro Colorado Island)	Rearing of internally feeding insect seed predators	Freshly fallen mature and immature fruits and seeds collected mostly from the ground	497 ^b	319 (64.2%) ^b	Not reported
*Basset <i>et al.</i> 2018	All internally feeding seed predators	Southern Thailand (forests surrounding the 24-ha ForestGEO plot in Khao Chong)	Rearing of internally feeding insect seed predators	Freshly fallen mature and immature fruits and seeds collected mostly from the ground	357 ^b	255 (71.4%) ^b	Not reported

*Basset <i>et al.</i> 2018	All internally feeding seed predators	Lowland rainforests of Papua New Guinea (seed and fruit samples collected in and around the ForestGEO 50-ha forest dynamics plot in Wanang)	Rearing of internally feeding insect seed predators	Freshly fallen mature and immature fruits and seeds collected mostly from the ground	332 ^b	257 (77.4%) ^b	Not reported
Beckman & Muller-Landau 2011	All insect seed predators	Dry, semi-deciduous forest in Panama (Parque Metropolitano)	Insecticide application	Mature and immature	7	4 (57.1%)	0.03-0.11 ^c
*Ctvrtecka <i>et al.</i> 2014	Internally feeding Curculionidae	Lowland rainforests of Papua New Guinea (two sites in the Madang province)	Rearing of internally feeding insect seed predators	Mature or nearly mature fruits; pre- and post-dispersal	326 ^d	106 (32.5%)	Not reported ^e
Greig 1993	All insect seed predators (main taxa Hemiptera and Coleoptera); most seed predators likely to be external feeders	Lowland rainforests of Costa Rica (La Selva)	Experimental exclusion of insect seed predators; infrutescences monitored throughout development	Mature and immature	5	5 (100%)	0.09-0.87 ^f
Hosaka <i>et al.</i> 2011	All internally feeding seed predators	Dipterocarp forest, Pasoh forest reserve, Malaysia	Rearing of internally feeding insect seed predators; seed dissections	Not reported	3 ^g	3 (100%)	Fruiting season 1: 0.27-0.34 Fruiting season 2: 0.35-0.49

*Janzen 1980	Internally feeding beetles (primarily bruchids)	Lowland dry forests of Costa Rica	Rearing of internally feeding insect seed predators	Ripe or nearly ripe seeds and fruits; collected from parent plant or ground below it	~975	110 (~8.9%)	Not reported
*Jeffer <i>et al.</i> 2018	All internally feeding seed predators (Coleoptera, Lepidoptera, Diptera)	Lowland forests of Panama (8 sites)	Visual examination of dissected seed samples	Freshly fallen mature and immature fruits and seeds collected from the ground	34	15 (44%)	0.018-1 ^h
Nakagawa <i>et al.</i> 2003	Internally feeding seed predators (Lepidoptera, Coleoptera)	Tropical lowland forest in Lambir Hills, Malaysia	Rearing of internally feeding insect seed predators	Seeds collected from seed traps. Maturity stage not mentioned, but likely mature or close to maturity.	1996: 26 1998: 15	1996: 25 (96.2%) 1998: 13 (86.7%)	1996: 0.007-0.143 ⁱ 1998: 0.002-0.492 ^j
Nakagawa <i>et al.</i> 2005	Internally feeding insect seed predators	Tropical lowland forest in Lambir Hills, Malaysia	Rearing of internally feeding seed predators + examination of dissected seeds	Freshly fallen immature and mature seeds and fruits collected from seed traps. ^k	6	6 (100%)	0.235-0.784 ^l
Ramirez & Traveset 2010	All internally feeding insect seed predators	Venezuelan Central Plain (not only forest habitats)	Rearing of internally feeding seed predators	Seeds ready or nearly ready for dispersal; samples taken directly from the parent plant	187	89 (47.6%)	Not reported
*Robertson <i>et al.</i> 1990	All seed-boring insects (Coleoptera, Lepidoptera, Diptera, Hymenoptera)	Mangrove forests at 12 sites in tropical Queensland, Australia	Propagules scored for signs of insect attack (holes, feeding tracks)	Mostly fallen propagules; for some tree species seeds also collected from the plant	12	12 (100%)	0.062-0.803 ^m
*Sam <i>et al.</i> 2017		Lowland rainforests of Papua New Guinea (two sites)	Rearing of internally feeding seed- and fruit-associated Lepidoptera	Mature or nearly mature fruits; pre- and post-dispersal	326 ^d	171 (52.5%)	Not reported ⁿ

		in the Madang province)					
Wesselingh <i>et al.</i> 1999	Internally feeding seed predators (Hymenoptera, weevils)	Two sites in tropical montane forest in Costa Rica (Cordillera de Talamanca)	Visual examination of seeds	Mature seeds	4	4 (100%)	0.082-0.560 ^o
Xu <i>et al.</i> 2015	All pre-dispersal seed predators (insects and vertebrates) leaving feeding marks on seeds.	Mixed evergreen-deciduous broadleaf forest in subtropical China (Dalaoling Nature Reserve, Hubei Province)	Visual examination of seed samples	Seeds at different stages of maturity collected from traps	44	17 (38.6%)	0.002-0.556 ^p

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372 ^aIncludes only the subset of plant species attacked by insect seed predators.

373 ^bData obtained from lead author.

374 ^cTable A1 in *Ecological Archives* E092-185-A1

375 ^dConsidering only species with samples comprising min 50 fruits weighing min 1kg.

376 ^eNot reported, but likely to be low. [“(…) one weevil per 33 individual fruits on average”]

377 ^fSeed predation rates reported in Table 3.

378 ^gSeven species included in study, but intensity of seed predation only recorded for three.

379 ^hSeed predation rates reported in Table 2. *Inga* sp. excluded, and only one entry for *Oenocarpus mapora*.

380 ⁱApproximate seed predation rates inferred from data in Appendix 1, assuming that one insect individual typically emerges from each infested seed. Scolytidae excluded when estimating proportion of seeds attacked, since for this taxon multiple individuals often emerge from each infested seed (pers. obs.).

382 ^jApproximate seed predation rates inferred from data in Appendix 2, assuming that one insect individual typically emerges from each infested seed. Scolytidae excluded when estimating proportion of seeds attacked, since for this taxon multiple individuals often emerge from each infested seed (pers. obs.).

384 ^kPredation rates reported only for mature seeds (but acknowledged in the source article that immature fruits were also commonly attacked by insects).

385 ^lSeed predation rates reported in Table 2.

386 ^mSeed predation rates reported in Table 1. Species-specific means obtained by pooling data from different sites.

387 ⁿNot reported, but likely to be low [“(…) low incidence of seed damage”]

388 ^oSeed predation rates reported in Table 6.

389 ^pSeed predation rates reported in Table 1. Estimates include both insects and vertebrates, but insects were the dominant seed predator group (74.9% of seeds showed signs of damage by insects, 25.1% showed signs of damage by vertebrates)

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