

An entomocentric view of the Janzen-Connell hypothesis

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1 **An entomocentric view of the Janzen-Connell hypothesis**

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20 **Abstract**

21 We may be able to estimate indirectly the role of insects in ecological processes, but without a good
22 knowledge of the identity and life history of the species involved, our conclusions may be rather
23 subjective. In this essay, we explore the implications of ignoring the identity and traits of insects in the
24 context of the mechanistic drivers of the Janzen-Connell hypothesis (JCH). Research inspired by the JCH
25 represents a significant body of ecological literature and proposes an explanation for the coexistence of
26 tree species in diverse tropical forests. Studies that have assessed the role of specific insect species in
27 causing patterns consistent with the predictions of the JCH tend to be biased towards the Neotropics, open
28 forests, palms or leguminous trees, bruchine beetles and leaf-chewing insects. Scrutiny of other study
29 systems is urgently needed before we can make sweeping conclusions about the generality of Janzen-
30 Connell effects induced specifically by insects. Potential engineers of Janzen-Connell effects may include
31 pre and post-dispersal seed predators, ants removing seeds, vectors of phytopathogens such as sap-
32 sucking insects, and insects able to damage meristems or to completely defoliate seedlings. We conclude
33 that Janzen-Connell effects mediated by insects in tropical rainforests appear to be less likely to be driven
34 by contagion of host-specific species from parent trees to seedlings, but more likely via a combination of
35 escape of seeds from pre-dispersal attack, and attack of seedlings by generalist herbivores in the forest
36 understorey, possibly aggravated by transmission of diseases by insect vectors.

37 **Key words:** insect-plant interactions, rainforest, seed, seed predator, seedling.

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39 In 1987, in the first issue of *Conservation Biology*, Edward O. Wilson wrote about the “little things that
40 run the world” – the importance and conservation of insects (Wilson, 1987). Readers of *Insect*
41 *Conservation and Diversity* will no doubt be very familiar with the concept. Sadly, however, this
42 perception is not as widely shared among the rest of the scientific community as it should be, and insects
43 are still comparatively neglected as a prime focus of scientific investigations.

44 For instance, if we look at the Thompson-Reuter impact factors (IF) of specialized scientific journals for
45 2017 (<http://jcr.incites.thomsonreuters.com/JCRJournalHomeAction.action?year=&edition=&journal=#>),
46 the highest ranked journal dedicated to entomology, *Annual Review of Entomology* (IF=13.860), is ranked
47 139th out of 122,271 journals. In comparison, our botanical colleagues fare somewhat better, with the
48 highest ranked journal in plant sciences, *Annual Review of Plant Biology* (IF=18.172), ranked 83rd
49 overall. *Insect Conservation and Diversity* continues to be among the top journals in entomology
50 (IF=2.091; ranked 14th), but overall is ranked 4,549th among the journals evaluated by Thompson-Reuter.
51 There is certainly room for improvement, of course, but in general this reflects the large difference in the
52 scale of endeavour across different scientific disciplines. Part of this challenge may be related to an
53 imbalance in the ratio of funding afforded to invertebrate studies (Leather, 2009).

54 We entomologists are acutely aware of inherent biases in conservation research. Vertebrate studies
55 dominate the field (69% of papers versus 3% of described species) while invertebrate studies lag far
56 behind (11% of papers versus 79% of species: Clark & May, 2002). This taxonomic chauvinism has been
57 commented on and lamented upon many times (e.g. Leather, 2009 and references therein), including in
58 one of our previous editorials (Leather *et al.*, 2008). Moreover, current trends show no signs of
59 improvement (Titley *et al.*, 2017), and the imbalance against insect studies is becoming even more
60 pronounced in tropical countries (Titley *et al.*, 2017), where recent estimates suggest over 25,000
61 arthropod species occurring in just a few hectares of tropical rainforest (Basset *et al.*, 2012).

62 But these issues may not even be the most serious cause for concern. We argue here that the neglect of
63 insects as study organisms has led to serious bias in our understanding of the functional ecology of
64 ecosystems. In other words, ignorance of the identity and role of insects in ecosystems may seriously
65 impede conclusions related to the true contribution that insects make to ecosystem functionality (Weisser
66 & Siemann, 2008). We may be able to estimate indirectly the role of insects in ecological processes, but
67 without a good knowledge of the identity and life history of the species responsible for these processes,

68 our conclusions may be rather subjective. “Knowing the players” is therefore crucial for sound studies of
69 the effects of insects on ecosystem functioning (Schmitz, 2008).

70 This situation is particularly obvious in studies of insect-plant interactions (or should we say in this
71 instance “plant-insect interactions”?), which represents a significant field of ecological research in its own
72 right (Calatayud *et al.*, 2018). Many plant science researchers in this field simply seem to ignore the
73 identity and diversity of the types of insect species doing the work. For instance, given the difficulty in
74 evaluating damage caused by sap-sucking insects, most studies of herbivory (leaf damage) only focus on
75 the action of leaf-chewing insects. This is very evident in studies on herbivory carried out in tropical
76 forests (e.g. Coley & Barone, 1996). Nevertheless, detailed studies have shown that the occurrence of sap-
77 sucking insects on rainforest plants is by no means trivial (Novotny & Basset, 1998; Dem *et al.*, 2013).
78 Since these insects can be vectors of important plant diseases (Denno & Perfect, 2012), they could have a
79 significant effect on rates of mortality of their hosts. In addition, most of the “plant-insect” literature has
80 focused on insects feeding on leaves. Much less is known about the identities and roles of insects
81 attacking other plant parts (e.g., flowers, fruits, roots, stems).

82 Another important issue is the estimation of herbivory caused by leaf-chewing insects in tropical
83 rainforests. Botanists have been keen to measure the area of holes in leaves (review in Coley & Barone,
84 1996) but few, if any, discuss the interpretation of their findings with regard to the identities and life
85 histories of the main species responsible for leaf damage. Total leaf damage rates are often assumed to be
86 correlated with insect species richness, abundance or biomass (e.g., Coley, 1983, discussing the spatial
87 distribution of herbivory). The handful of studies that have, however, considered insect identity and
88 associated variables (abundance, species richness, biomass) all concluded that leaf damage is likely to
89 depend on the feeding behaviour of a few dominant leaf-chewing species and this may complicate the
90 interpretation of results obtained in herbivory studies focusing on community-level patterns (e.g.,
91 Marquis, 1991; Basset & Höft, 1994). We know that the major impact of herbivores on plants,
92 particularly in rainforests, is driven by relatively few insect species, because most of the rest are relatively

93 rare and their action restricted in time (Owen, 1983; Bernays & Graham, 1988). Thus, while overall
94 herbivory rates may be an important correlate of plant fitness, it gives us few clues about the distribution
95 and feeding preferences of the species responsible for the leaf damage.

96 In this essay, we briefly explore the implications of ignoring the identity and traits of insects in the
97 context of another research topic popular among our botanical colleagues, the Janzen-Connell hypothesis,
98 JCH (Janzen, 1970; Connell, 1971). The JCH proposes an explanation for the coexistence of tree species
99 in diverse tropical forests. Seeds are most likely to disperse to sites close to their parent trees, but this is
100 also where they are likely to be most frequently attacked by host-specific enemies such as insects and
101 pathogens that might aggregate near the parent trees. By contrast, seeds and seedlings that do manage to
102 disperse further away from the parent tree are more likely to survive due to escape from enemies. In other
103 words, conspecific negative density-dependent survival results from the proliferation of species-specific
104 herbivores and pathogens on hosts in areas of high conspecific plant densities, giving a negative
105 correlation between relative pest attack rate and distance from parent trees to their nearby offspring
106 (Janzen, 1970; Connell, 1971; Comita *et al.*, 2010; Bagchi *et al.*, 2014).

107 In the seminal paper by Janzen (1970), few examples of insect species responsible for negative density-
108 dependence among rainforest plants are provided, but this information may be gathered from subsequent
109 papers, along with more recent studies (Table 1). Most of the studies concerned with Janzen-Connell
110 effects pay little attention to the identity of insects potentially able to induce such effects (reviews in
111 Clark & Clark, 1984; Hammond & Brown, 1998; Carson *et al.*, 2008; Comita *et al.*, 2014: 63 studies
112 considered). The compilation in Table 1 indicates that most studies that have assessed the role of specific
113 insect species in causing patterns consistent with the predictions of the JCH were performed in the
114 Neotropics (only one study originated from the Old World tropics), in rather open forests, savanna or
115 even open pastures, targeted seeds over seedlings, often included palm or leguminous trees (64 % of
116 cases) and the main species responsible for Janzen-Connell effects were often bruchine beetles. One
117 might be tempted to think that many of these study systems were perhaps selected for the ease of studying

118 large seed crops attacked by noticeable seed predators. What is clear, is that more studies targeting closed
119 tall forests, and trees from other plant families and their seedlings are urgently needed before we can
120 make sweeping conclusions about the generality of Janzen-Connell effects induced specifically by
121 insects.

122 Another bias that is obvious from the studies listed in Table 1 is the almost exclusive focus on chewing
123 insects attacking either seeds or seedlings. The only exception is an influential paper by Janzen in which
124 he reports on the effects of an external-feeding sap-sucking bug on seeds of *Sterculia apetala* (Janzen,
125 1972a). Seed bugs (Lygaeidae and related families) are renowned as potentially important seed predators
126 in the tropics (Slater, 1972 and references therein). Hence, it is also clear that if we are serious about
127 evaluating potential Janzen-Connell effects induced by insects, it is imperative to pay more attention to
128 the guild of externally seed- and fruit-sucking insects in rainforests. Janzen's study on seed mortality by
129 seed-sucking bugs on *Sterculia apetala* also illustrates another potentially important point. Since the
130 externally sap-sucking bug studied by Janzen may transmit a pathogenic fungus to the host tree (Janzen,
131 1972a), the ultimate cause of seed mortality might appear to be caused by a seed pathogen rather than by
132 an insect. This illustrates the need to consider the synergy between insects and pathogens.

133 As discussed by Carson *et al.* (2008), the JCH is ultimately a plant community-level hypothesis, but all
134 the studies reported in Table 1 targeted a single plant species. While research within the framework of the
135 JCH has mostly been conducted on enemies that attack seeds and seedlings that have already dispersed
136 from the mother plant, Janzen (1970) also suggested that coexistence of plant species in tropical forests
137 could also be promoted by pre-dispersal seed enemies (i.e., enemies attacking developing or mature seeds
138 in the canopy). Gripenberg (2018), in stressing the need to pay attention to attack by pre-dispersal seed
139 enemies, reviewed the studies that have assessed the pattern of insect seed predation in tropical forest
140 plant communities. To date, this includes only 15 studies world-wide, from which just two thirds provide
141 hard data about insects. Again, currently available data are so limited that we lack the necessary insect

142 background to discuss adequately the contribution of insects to Janzen-Connell effects in tropical
143 rainforests.

144 What can we gain from knowing the identity and ecology of insects in studies of negative-density
145 dependence in tropical rainforests? Primarily this includes information on patterns of host use
146 (specificity) by specific insect species; information on whether the same insect species tend to feed on
147 adult foliage and seedlings; and spatial patterns of foraging by insects. To address some of these issues
148 briefly, we need to consider the separate effects of insects feeding on seeds versus seedlings.

149 We know that most insects attacking seeds in rainforests are highly host specific (Janzen, 1980; Ctvrtceka
150 *et al.*, 2014; Gripenberg, 2018), in accordance with the expectations of the JCH. What is less well known
151 is the degree of spatial contagion of seed predators near parent trees, which may depend on the ecology of
152 species considered. For example, Janzen (1975b) reported that two species of bruchine beetles are host
153 specific to the seeds of *Guazuma ulmifolia* in Costa Rica, with one being a pre-dispersal seed predator
154 attacking the seeds on the tree, while the other exclusively attacks the mature seeds after they have fallen
155 to the ground. Hence, the identity and ecology of insect species is crucial to fully understand patterns of
156 pre- and post-dispersal seed attack and any resulting effects on plant fitness and patterns of recruitment.

157 Even if the assumptions of host specificity and contagion near the parent trees are met, this does not
158 imply that Janzen-Connell effects related to seeds may be pervasive. Insects need to subsist at minimum
159 densities on their hosts in order to induce significant plant mortality. For example, in the forests of New
160 Guinea 95% of the woody plant species sampled for seed-eating weevil and lepidopteran assemblages had
161 low rates of seed infestation (Ctvrtceka *et al.*, 2014; Sam *et al.*, 2017). Here, a recognition of the main
162 insect species and estimation of their infestation rates in seeds is needed before assessing possible Janzen-
163 Connell effects induced by insects.

164 Overlooking even the higher taxa of insects responsible for seed damage may lead to ambiguous
165 interpretation of results. For example, Bruchinae are often host-specific on seeds of Fabaceae in the

166 Neotropics (Janzen, 1980), whereas they are almost totally replaced by several less host-specific weevil
167 subfamilies in the Old World (Ctvrtceka *et al.*, 2014; Basset *et al.*, 2018). The potential for Bruchinae to
168 induce Janzen-Connell on their fabaceaus hosts is thus much higher than for weevils of the Old World,
169 as suggested by Table 1. Furthermore, botanists pay considerable attention to plant phylogeny in studies
170 of JCH, but they should also take note of plant traits that may explain oviposition patterns of insects
171 attacking seeds, which are not necessarily related to plant phylogeny. One of the most important traits in
172 this regard may be the degree of fleshiness of the fruit (Sam *et al.*, 2017; Basset *et al.*, 2018; C. Dahl *et*
173 *al.*, unpublished data). When assessing the contributions of insects to Janzen-Connell effects, it is also
174 important to have good insights into the feeding ecology of different taxa. Even in relatively well-known
175 Lepidoptera, it can be difficult to separate the seed predator species from pulp eaters or scavengers.
176 Several taxa that are often considered to be scavengers also contain lineages with other life history
177 strategies, such as in the Tineidae (Robinson, 2009), so precise identification of insects reared from seeds
178 or fruits is crucial.

179 If we now turn our attention to seedlings, there are very few community-wide studies of insect herbivores
180 attacking seedlings in tropical rainforests. Twenty years ago, one study in Guyana concluded that free
181 living species attacking seedlings persisted at very low densities, were often generalists, and that Janzen-
182 Connell effects mediated by insects feeding on seedlings were, consequently, unlikely to exist in the
183 system studied (Basset, 1999). We now know that the lack of host specificity (particularly for insects
184 feeding on seedlings) does not necessarily invalidate their potential contribution to plant species
185 coexistence, as negative density dependence may also be generated by the action of generalist herbivores
186 if they tend to be attracted to areas of high conspecific plant density (Lewis & Gripenberg, 2008).

187 Regarding contagion from parent trees, we have noted that insect species responsible for Janzen-Connell
188 effects were often studied in rather open forest or pastures (Table 1), and less so in closed tall forests. In
189 fact, in these forests, where presumably Janzen-Connell effects induce high local diversity of trees
190 (Janzen, 1970; Connell, 1971), contagion of insect herbivores from the parent trees to seedlings has rarely

191 been demonstrated. This may be because the biotic and abiotic conditions experienced in the canopy
192 versus understorey of forests are strikingly different, resulting in different suites of free-living herbivores
193 attacking plants in these two strata. These differences have been observed both at the level of host plant
194 species (e.g., Basset, 2001) and the plant community as a whole (Basset *et al.*, 2015).

195 There may of course be exceptions and they are more likely to involve endophagous insects (stem borers,
196 gallers, miners) than ectophagous insects, because external conditions induced by the forest strata may be
197 buffered to some extent by microclimatic conditions inside the host tissues. Nevertheless, the proportion
198 of host tree species studied that supported the same insect species of either gallers or miners in both the
199 canopy and understorey in one Panamanian wet forest was low and amounted to only 6% (out of 18
200 species: Medianero *et al.*, 2003). Under these conditions, contagion of insect herbivores from parent trees
201 to seedlings is likely to be rather uncommon in closed tall rainforests.

202 Despite claims that in some instances signs of leaf damage can be unequivocally assigned to particular
203 insect species (Barone, 2000; Downey *et al.*, 2018), in our experience it is nearly impossible to do so for
204 the vast majority of the diverse insect species feeding on the leaves of tropical trees and seedlings,
205 particularly in the case of generalist species. This greatly impedes our ability to investigate the causal
206 mechanisms of negative density dependence in seedlings of tropical rainforests. Moreover, one recent
207 study suggested that the amount and categories of herbivore damage on rainforest seedlings may even
208 differ between continents. For example, the percentage of damage on seedlings that could be assigned to
209 insects represented 56%, 78% and 85% of observations in rainforests in Panama, Thailand and Papua
210 New Guinea, respectively (Y. Basset *et al.*, unpubl. data). Identifying the main herbivore species
211 responsible for such variation in herbivory (at least leaf-chewing herbivory) is crucial. And, of course, the
212 degree to which seedlings of different plant species can tolerate differing levels of herbivory before
213 Janzen-Connell effects are triggered is an open question.

214 If we do entertain the idea that at least some insect species are responsible for some examples of negative
215 density-dependence observed in rainforests (review in Comita *et al.*, 2010), then which taxa are most
216 likely to be responsible for these effects? If we consider post-dispersal attack of seeds fallen on the
217 ground, then highly host-specific Bruchinae (Janzen, 1980) and perhaps certain Curculionidae (Pinzón-
218 Navarro *et al.*, 2010) may fit the bill, although many species may only be involved in pre-dispersal attack.
219 We should also not underestimate ants as seed removers in rainforests (Ruzi *et al.*, 2017), and therefore as
220 possible engineers of Janzen-Connell effects. Insect herbivores attacking seedlings in rainforests involve
221 many taxa (Basset & Charles, 2000). Leaf-chewing insects are often represented by Chrysomelidae, leaf-
222 feeding weevils (Entiminae), but Lepidoptera larvae are relatively rare on seedlings (e.g., 6% of the total
223 insect individuals collected in Basset & Charles, 2000). Orthoptera and Phasmatodea are also rather
224 infrequent, at least during day-time censuses (Basset & Charles, 2000). The low incidence of most of
225 these insects on seedlings (Basset, 1999) makes them unlikely candidates to successfully induce Janzen-
226 Connell effects, but exceptions may exist. Further cases of insects notoriously dangerous for the survival
227 of seedlings are worth discussing briefly.

228 First, the action of potential vectors of phytopathogens needs to be quantified and understood. This
229 includes, for example, xylem-feeding and generalist Cicadellinae, which are common as nymphs and
230 adults in the understorey of tropical rainforests, and are able to transmit phytopathogenic viruses (Nielson,
231 1986). Additionally, this may involve adult weevils (for example *Conotrachelus* spp.) or bark beetles,
232 which attack seeds at the larval stage and perform maturation feeding on seedlings as adults (Basset &
233 Charles, 2000). In this situation, they may transmit pathogenic fungi, as for example in the case of Dutch
234 elm disease (Martin *et al.*, 2018). Second, insects damaging meristems may be particularly threatening,
235 such as one erebid moth decapitating seedlings in Costa Rica (Janzen, 1971b). In Panama, this category of
236 damage represents nearly 20% of all observations of seedlings damaged in a community study (Y. Basset
237 *et al.*, unpubl. data). Lepidopterous stem borers may also damage meristems but this group is far less
238 diverse than free-feeding caterpillars, so it may be relatively easy to quantify their effects on particular

239 host species (e.g., Sullivan, 2003). Last, insects able to completely defoliate seedlings are also of concern.
240 This may include outbreaks of host-specific Lepidoptera (Barone, 2000), but this situation is rather rare in
241 tropical rainforests. Large generalist caterpillars such as Saturniidae (Hartnett *et al.*, 2012) may be worth
242 investigating in this context.

243 In conclusion, Janzen-Connell effects mediated by insects in tropical rainforests appear to be less likely
244 by contagion of host-specific species from parent trees to seedlings, but more likely via a combination of
245 escape of seeds from pre-dispersal attack (Lawson *et al.*, 2012), and attack of seedlings by generalist
246 herbivores in the forest understorey, possibly aggravated by transmission of diseases by insect vectors. To
247 collect and identify the culprits of damage is challenging, particularly on seedlings, because generalists
248 may subsist at low densities (Basset, 1999) or specialists may have elusive behaviours. For example,
249 Janzen (1971b), estimated that on average just 10 minutes were necessary for an erebid moth to decapitate
250 one seedling before walking off, rendering any direct census of caterpillars in this study system very
251 difficult. Elegant experiments with insecticide or exclusion of insect herbivores may help us to quantify
252 the action of insect herbivores more effectively (e.g., Bagchi *et al.*, 2014) and those results should be
253 coupled with good old-fashioned natural history observations, or with observations acquired with new
254 technologies. For example, the metabarcoding of the gut of potential insect herbivores (e.g., García-
255 Robledo *et al.*, 2013) or automatic detection of insect activity (e.g., Reynolds & Riley, 2002) on
256 seedlings, particularly at night, appear to be promising opportunities in this context. Further, such studies
257 may be performed at locations where extensive vegetation data, including the basal area, spatial location
258 and seed production of parent trees, may be available, such as in the ForestGEO network of permanent
259 forest plots (Anderson-Teixeira *et al.*, 2015; Basset *et al.*, 2018). New tools, such as DNA barcoding, are
260 now available to assist with rapid and accurate identification of insect species (Miller, 2014), including
261 the BIN clustering algorithm and interim nomenclature system, which facilitates forming putative species
262 concepts and communicating about them (Schindel & Miller, 2010; Ratnasingham & Hebert, 2013).

263 We hope that we may have convinced our non-entomologist readers, perhaps curious about the title of
264 this essay, of the value of paying attention to the identity of insects potentially responsible for Janzen-
265 Connell effects in rainforests, and, to this effect, to collaborate with entomologists. Hopefully, some of
266 our regular readers may also see better scope for collaboration with botanists or forest ecologists
267 regarding this fascinating topic.

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Table 1. Studies (listed in chronological order) in tropical rainforests that linked specific insect species to Janzen-Connell effects.

Plant species	Plant family	Insect species	Insect taxa	Part attacked	Reference
<i>Cassia grandis</i> L. f.	Fabaceae	<i>Pygopachymerus lineola</i> (Chevrolat, 1871)	Bruchinae	Seeds	Janzen, 1971a
		<i>Zabrotes interstitialis</i> (Chevrolat, 1871)	Bruchinae	Seeds	Janzen, 1971a
<i>Dioclea megacarpa</i> Rolfe	Fabaceae	<i>Caryedes brasiliensis</i> (Thunberg, 1816)	Bruchinae	Seeds	Janzen, 1971b
		Unidentified	Erebidae	Seedlings	Janzen, 1971b
<i>Sterculia apetala</i> (Jacq.) H. Karst.	Sterculiaceae	<i>Dysdercus fasciatus</i> Signoret, 1861	Pyrrhocoridae	Seeds	Janzen, 1972a
		<i>Cocotrypes carpophagus</i> (Hornung, 1842)	Scolytinae	Seeds	Janzen, 1972b
<i>Euterpe globosa</i> C.F. Gaertn.	Arecaceae	<i>Caryobruchus buscki</i> Bridwell 1929	Bruchinae	Seeds	Wilson & Janzen, 1972
		<i>Pachymerus</i> sp.	Bruchinae	Seeds	Wilson & Janzen, 1972
<i>Spondias mombin</i> L. <i>Andira inermis</i> (W. Wright) Kunth ex DC.	Fabaceae	<i>Amblycerus</i> sp.	Bruchinae	Seeds	Janzen, 1975a
		<i>Cleogonus</i> spp.	Curculionidae	Seeds	Janzen <i>et al.</i> , 1976
<i>Attalea butyracea</i> (Mutis ex L.f.) Wess.Boer	Arecaceae	<i>Speciomerus giganteus</i> (Chevrolat, 1877)	Bruchinae	Seeds	Wright, 1983; Visser <i>et al.</i> , 2011
		<i>Pachymerus cardo</i> (Fähraeus, 1839)	Bruchinae	Seeds	Wright, 1983; Visser <i>et al.</i> , 2011
<i>Virola surinamensis</i> (Rol. ex Rottb.) Warb.	Myristicaceae	<i>Conotrachelus</i> sp.	Curculionidae	Seeds	Howe <i>et al.</i> , 1985
<i>Copaifera pubiflora</i> Benth.	Fabaceae	<i>Apion</i> sp.	Curculionidae	Seeds	Ramirez & Arroyo, 1987
		<i>Rhinochenus brevicollis</i> Chevrolat, 1871	Curculionidae	Seeds	Ramirez & Arroyo, 1987
<i>Acacia farnesiana</i>	Fabaceae	Unidentified	Microlepidoptera	Seeds	Ramirez & Arroyo, 1987
		<i>Spermologus copaiferae</i> Marshall, 1938	Curculionidae	Seeds	Ramirez & Arroyo, 1987
		<i>Tricorynus herbarius</i> (Gorham, 1883)	Anobiidae	Seeds	Ramirez & Arroyo, 1987
		<i>Stator vachelliae</i>	Bruchinae	Seeds	Traveset, 1990

(L.) Willd.		Bottimer, 1973			
<i>Normanbya normanbyi</i>	Arecaceae	<i>Coccotrypes</i> sp.	Scolytinae	Seeds	Lott <i>et al.</i> , 1995
(W. Hill) L.H. Bailey		Unidentified (two spp.)	Anisolabididae	Seeds	Lott <i>et al.</i> , 1995
<i>Chlorocardium rodiei</i>	Lauraceae	<i>Stenoma catenifer</i>	Stenomatidae	Seeds	Hammond <i>et al.</i> , 1999
(R.H. Schomb.)		Walsingham, 1912	Scolytinae	Seeds+Seedlings	Hammond <i>et al.</i> , 1999
Rohwer, H.G. Richt. & van der Werff		<i>Sternobothrus</i> sp.			
<i>Tabebuia ochracea</i>	Bignoniaceae	<i>Cromarcha stroudagnesia</i>	Pyralidae	Saplings	Sullivan, 2003
(Cham.) Standl.		Solis, 2003			
<i>Cordia alliodora</i>	Boraginaceae	<i>Ischnocodia annulus</i>	Cassidinae	Seedlings	Downey <i>et al.</i> , 2018
(Ruiz & Pav.) Oken		Fabricius, 1781			