Basset, Y., Miller, S. E., Gripenberg, S. ORCID: https://orcid.org/0000-0002-8788-2258, Ctvrtecka, R., Dahl, C., Leather, S. R. and Didham, R. K. (2019) An entomocentric view of the Janzen-Connell hypothesis. Insect Conservation and Diversity, 12 (1). pp. 1-8. ISSN 1752-4598 doi: https://doi.org/10.1111/icad.12337 Available at https://centaur.reading.ac.uk/81044/

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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; Ctvrtecka

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 (Ctvrtecka *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 (Ctvrtecka *et al.,* 2014; Basset *et al*, 2018). The potential for Bruchinae to

168   induce Janzen-Connell on their fabaceaous 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.

268   **Acknowledgments**

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

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