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DOI: <https://doi.org/10.1111/icad.12337>



Basset, Y., Miller, S.E., Gripenberg, S., Ctvrtecka, R., Dahl, C., Leather, S.R. and Didham, R.K. 2019. Entomocentric view of the Janzen-Connell hypethosis. *Insect Conservation and Diversity*.

2 January 2019

An entomocentric view of the Janzen-Connell hypothesis

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Abstract

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

Key words: insect-plant interaction, rainforest, seed, seed predator, seedling

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

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

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

But these issues may not even be the most serious cause for concern. We argue here that the neglect of insects as study organisms has led to serious bias in our understanding of the functional ecology of ecosystems. In other words, ignorance of the identity and role of insects in ecosystems may seriously impede conclusions related to the true contribution that insects make to ecosystem functionality (Weisser & Siemann, 2008). We may be able to estimate indirectly the role of insects in ecological processes, but without a good knowledge of the identity and life history of the species responsible for these processes, our conclusions may be rather subjective. “Knowing the players” is therefore crucial in sound studies of the effects of insects on ecosystem functioning (Schmitz, 2008).

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

Another important issue is the estimation of herbivory caused by leaf-chewing insects in tropical rainforests. Botanists have been keen to measure the area of holes in leaves (review in Coley & Barone, 1996) but few, if any, discuss the interpretation of their findings with regard to the identities and life histories of the main species responsible for leaf damage. Total leaf damage rates are often assumed to be correlated with insect species richness, abundance or biomass (e.g., Coley, 1983, discussing the spatial distribution of herbivory). The handful of studies that have, however, considered insect identity and associated variables (abundance, species richness, biomass) all concluded that leaf damage is likely to depend on the feeding behaviour of a few dominant leaf-chewing species and this may complicate the interpretation of results obtained in herbivory studies focusing on community-level patterns (e.g., Marquis, 1991; Basset & Höft, 1994). We know that the major impact of herbivores on plants, particularly in rainforests, is driven by relatively few insect species, because most of the rest are relatively rare and their action restricted in time (Owen, 1983; Bernays & Graham, 1988). Thus, while overall herbivory rates may be an important correlate of plant fitness, it gives us little clues about the distribution and feeding preferences of the species responsible for the leaf damage.

In this essay, we would like to briefly explore the implications of ignoring the identity and traits of insects in the context of another research topic popular among our botanical colleagues, the Janzen-Connell hypothesis, JCH (Janzen, 1970; Connell, 1971). The JCH proposes an explanation for the coexistence of tree species in diverse tropical forests. Seeds are most likely to disperse to sites close to their parent trees, but this is also where they are likely to be most frequently attacked by host-specific enemies such as insects and pathogens that might aggregate near the parent trees. By contrast, seeds and seedlings that do manage to disperse further away from the parent tree are more likely to survive due to escape from enemies. In other words, conspecific negative density-dependent survival results from the proliferation of

species-specific herbivores and pathogens on hosts in areas of high conspecific plant densities, giving a negative correlation between relative pest attack rate and distance from parent trees to their nearby offspring (Janzen, 1970; Connell, 1971; Comita *et al.*, 2010; Bagchi *et al.*, 2014).

In the seminal paper by Janzen (1970), few examples of insect species responsible for negative density-dependence among rainforest plants are provided, but this information may be gathered from subsequent papers, along with more recent studies (Table 1). Most of the studies concerned with Janzen-Connell effects pay little attention to the identity of insects potentially able to induce such effects (reviews in Clark & Clark, 1984; Hammond & Brown, 1998; Carson *et al.*, 2008; Comita *et al.*, 2014: 63 studies considered). The compilation in Table 1 indicates that most studies that have assessed the role of specific insect species in causing patterns consistent with the predictions of the JCH were performed in the Neotropics (only one study originated from the Old World tropics), in rather open forests, savanna or even open pastures, targeted seeds over seedlings, often included palm or leguminous trees (64 % of cases) and the main species responsible for Janzen-Connell effects were often bruchine beetles. One might be tempted to think that many of these study systems were perhaps selected for the ease of studying large seed crops attacked by noticeable seed predators. What is clear, is that more studies targeting closed tall forests, and trees from other plant families and their seedlings are urgently needed before we can make sweeping conclusions about the generality of Janzen-Connell effects induced specifically by insects.

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

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

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

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

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

Overlooking even the higher insect taxa responsible for seed damage may lead to ambiguous interpretation of results. For example, Bruchinae are often host specific on the seeds of Fabaceae in the Neotropics (Janzen, 1980), whereas they are almost totally replaced by several weevil subfamilies in the Old World that are less host specific (Cvrtecka *et al.*, 2014; Basset *et al.*, 2018). The potential for Bruchinae to induce Janzen-Connell on their fabaceous hosts is thus much higher than for weevils of the Old World, as suggested by Table 1. Furthermore, botanists pay considerable attention to plant phylogeny in studies of JCH, but they should be advised to also take note of plant traits that may explain oviposition patterns of insects attacking seeds, which are not necessarily related to plant phylogeny. One of the most important traits in this regard may be the degree of fleshiness of the fruit (Sam *et al.*, 2017; Basset *et al.*, 2018; C. Dahl *et al.*, unpublished data). Even in relatively well-known Lepidoptera, it can be difficult to separate the seed predator *per se* from the pulp eaters or scavengers. Most of the taxa often considered to be scavengers also contain lineages with other life history strategies, such as in the Tineidae (Robinson, 2009), so precise identification of insects reared from seeds or fruits is crucial.

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

Regarding contagion from parent trees, we have noted that insect species responsible for Janzen-Connell effects were often studied in rather open forest or pastures (Table 1), and less so in closed tall forests. In fact, in these forests, where presumably Janzen-Connell effects induce high local diversity of trees (Janzen, 1970; Connell, 1971), contagion of insect herbivores from the parent trees to seedlings has rarely been demonstrated. This is because the biotic and abiotic conditions experienced in the canopy versus understorey of forests are strikingly different, resulting in different suites of free-living herbivores attacking plants in these two strata. These differences have been observed both at the level of host plant species (e.g., Basset, 2001) and the plant community as a whole (Basset *et al.*, 2015).

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

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

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

First, the action of potential vectors of phytopathogens needs to be quantified and understood. This includes, for example, xylem-feeding and generalist Cicadellinae, which are common as nymphs and adults in the understorey of tropical rainforests, and are able to transmit phytopathogenic viruses (Nielson, 1986). Additionally, this may involve adult weevils (for example *Conotrachelus* spp.) or bark beetles, which attack seeds at the larval stage and perform maturation feeding on seedlings as adults (Basset & Charles, 2000). In this situation, they may transmit pathogenic fungi, as for example in the case of Dutch elm disease (Martin *et al.*, 2018). Second, insects damaging meristems may be particularly threatening, such as one eretid moth decapitating seedlings in Costa Rica (Janzen, 1971b). In Panama, this category of damage represents nearly 20% of all observations of seedlings damaged in a community study (Y. Basset *et al.*, unpubl. data). Lepidopterous stem borers may also damage meristems but this group is far less diverse than free-feeding caterpillars, so it may be relatively easy to quantify their effects on particular host species (e.g., Sullivan, 2003). Last, insects able to completely defoliate seedlings are also of concern. This may include outbreaks of host-specific Lepidoptera (Barone, 2000), but this situation is rather rare in tropical rainforests. Large generalist caterpillars such as Saturniidae (Hartnett *et al.*, 2012) may be worth investigating in this context.

In conclusion, Janzen–Connell effects mediated by insects in tropical rainforests appear to be less likely by contagion of host-specific species from parent trees to seedlings, but more likely via a combination of escape of seeds from pre-dispersal attack (Lawson *et al.*, 2012), and attack of seedlings by generalist herbivores in the forest understorey, possibly aggravated by transmission of diseases by insect vectors. To collect and identify the culprits of damage is challenging, particularly on seedlings, because generalists may subsist at low densities (Basset, 1999) or specialists may have elusive behaviours. For example, Janzen (1971b), estimated that on average just 10 minutes were necessary for an eretid moth to decapitate one seedling before walking off, rendering any direct census of caterpillars in this study system very difficult. Elegant experiments with insecticide or exclusion of insect herbivores may help us to quantify the action of insect herbivores more effectively (e.g., Bagchi *et al.*, 2014) and those results should be coupled with good old-fashioned natural history observations, or with observations acquired with new technologies. For example, the metabarcoding of the gut of potential insect herbivores (e.g., García-Robledo *et al.*, 2013) or automatic detection of insect activity (e.g., Reynolds & Riley, 2002) on seedlings, particularly at night, appear to be promising opportunities in this context. Further, such studies may be performed at locations where extensive vegetation data, including the basal area, spatial location and seed production of parent trees, may be available, such as in the ForestGEO network of permanent forest plots (Anderson-Teixeira *et al.*, 2015; Basset *et al.*, 2018).

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

Acknowledgments

The ideas advanced in this essay were shaped by a project supported by the Czech Science Foundation (GAČR 16-20825S) and a grant from the US National Science Foundation (DEB 0841885).

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Table 1. Selected 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>Pygiopachymerus 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>Euterpe globosa</i> C.F. Gaertn.	Areaceae	<i>Cocotrypes carpophagus</i> (Hornung, 1842)	Scolytinae	Seeds	Janzen, 1972b
<i>Attalea rostrata</i> Oerst.	Areaceae	<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.	Anacardiaceae	<i>Amblycerus</i> sp.	Bruchinae	Seeds	Janzen, 1975a
<i>Andira inermis</i> (W. Wright) Kunth ex DC.	Fabaceae	<i>Cleogonus</i> spp.	Curculionidae	Seeds	Janzen <i>et al.</i> , 1976
<i>Attalea butyracea</i> (Mutis ex L.f.) Wess.Boer	Areaceae	<i>Speciomerus giganteus</i> (Chevrolat, 1877)	Bruchinae	Seeds	Wright, 1983; Visser <i>et al.</i> , 2011
		<i>Pachymerus cardo</i> (Fåhraeus, 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
		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>Acacia farnesiana</i>	Fabaceae	<i>Stator vachelliae</i>	Bruchinae	Seeds	Traveset, 1990

(L.) Willd.		Bottimer, 1973			
<i>Normanbya normanbyi</i>	Areaceae	<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>Iscnocodia annulus</i>	Cassidinae	Seedlings	Downey <i>et al.</i> , 2018
(Ruiz & Pav.) Oken		Fabricius, 1781			
