

## **COMPLEXITIES OF LINKING DEFAUNATION TO TREE COMMUNITY DYNAMICS: CASE STUDIES FROM NATIONAL PARKS IN THAILAND**

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### ABSTRACT

Widespread hunting in tropical forests raises the possibility of major changes to tree populations and communities following the extirpation of seed-dispersing vertebrates. Long-term studies of tree and forest dynamics in national parks, especially Khao Yai National Park, in Thailand provide important case studies and data to address this issue. Some trees, such as the canopy dominant *Choerospondias axillaris*, suffer population decline in over-hunted parks. But such processes must also be placed within longer temporal scale and broader spatial scale contexts; *C. axillaris* appears to depend on episodic forest disturbances for recruitment, and the effects of vertebrate frugivores on the tree's abundance may vary with forest successional stage. *C. axillaris* populations are not self-sustaining in closed canopy forest, even with abundant seed dispersers; yet seed dispersal by deer may be critical for the species to reach open habitats where recruitment is enhanced. Research in Thailand has also suggested that frugivore guilds may contain little redundancy despite their diversity. The tree *Prunus javanicus* is dispersed by a variety of bird and mammal species, but of these only certain primates and hornbills provide high quality dispersal. Moreover, the strength of the effect of frugivore species on tree demography is impossible to predict based on frugivore visitation rates alone. Finally, research has demonstrated that not all frugivores are mutualists; even those that do not destroy seeds outright can function as 'free riders' by precluding removal by more effective dispersal agents. Assessing the impacts of overhunting on tropical tree species and communities remains difficult due to the variety of life history strategies among trees and frugivores.

Keywords: frugivore, Janzen-Connell, long-term research, mutualism, plant-animal interaction, secondary extinction, seed dispersal, seed predation, seedling recruitment

### INTRODUCTION

Hunting is nearly ubiquitous in tropical forests worldwide. Humans have hunted these forests for tens of millennia, driving some animal species extinct (CORLETT, 2007) while practicing more or less sustainable harvest of others (ROBINSON & BENNETT, 2000, and references therein). But the negative impacts of human hunting in tropical countries have increased rapidly in recent decades for a variety of reasons (TUNGITTIPLAKORN & DEARDEN, 2002). Widespread logging has increased accessibility to formerly remote tracts of forest and simultaneously fueled

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demand for wild meat in logging camps (ROBINSON *ET AL.*, 1999). Growing urban centers have driven the expansion of market-based (rather than subsistence-based) hunting (LENZEN *ET AL.*, 2012), while improved transportation networks have allowed wild meat markets to expand dramatically in scale. In many areas, shifts from traditional hunting implements to firearms and wire snares have allowed exploitation rates to skyrocket.

In theory, forest-dwelling people could have positive as well as negative impacts on native vertebrates. Predation by non-human carnivores in other systems can sometimes increase local prey diversity by suppressing the abundance of a dominant herbivore—a phenomenon termed predator-mediated coexistence (PAINE, 1966). Moreover, the swidden agricultural techniques practiced in some areas has been hypothesized to improve habitat quality for large herbivores (NAMGYEL *ET AL.*, 2008). But neither of these mechanisms has been empirically demonstrated for human hunters in tropical forests, especially where large game have been hunted out. The balance of evidence from around the world overwhelmingly demonstrates that forest people have negative or, at best, neutral impacts on native vertebrate abundance and diversity (e.g. TUNGITTIPLAKORN & DEARDEN, 2002). Indeed, unsustainable hunting has led to vast regions that retain structurally intact forest but have lost their large vertebrates (REDFORD, 1992).

The massive and widespread collapse of forest vertebrate populations in many areas could have a variety of impacts on tropical forest ecosystems. Several decades ago, REDFORD (1992) made the prescient observation that many of the large vertebrates that are hunted in tropical forests are frugivorous, and that therefore the myriad tropical tree species in tropical forests that depend on animal-mediated seed dispersal could suffer reduced recruitment in defaunated forests (also see WRIGHT, 2003; STONER *ET AL.*, 2007; MCCONKEY *ET AL.*, 2012). The importance of seed-dispersing animals is often illustrated in the context of the “Janzen-Connell effect”; JANZEN (1970) and CONNELL (1971) independently proposed that large numbers of seeds deposited near their parent trees were likely to attract seed predators and specialized pathogens as well as incur elevated intra-specific competition. Seeds dispersed away from the parent, e.g. by animal vectors, could escape such density-dependent mortality and enjoy increased germination and growth rates.

One way to address the impacts of defaunation on trees is to assess multiple populations simultaneously by looking for shifts in the species composition of the tree community driven by hunting. The theory here is that tree species should vary in their susceptibility to hunting-induced demographic impacts, so that some should incur declines in abundance in overhunted forests while others are unaffected or benefit via reduced competition. In the Peruvian Amazon, tree recruitment was substantially compromised at heavily hunted sites, compared to unhunted sites, with lower recruitment of animal-dispersed species (TERBORGH *ET AL.*, 2008) and particularly those reliant on large-bodied frugivores (NUNEZ-ITURRI *ET AL.*, 2008; TERBORGH *ET AL.*, 2008). However, preliminary results from a recent re-census of two of these plots showed no effect of dispersal mode or seed size on estimated population trend (J. Terborgh, personal communication). In Malaysian Borneo, a recent increase in hunting at Lambir Hills National Park led to reduced recruitment of animal-dispersed tree species (HARRISON *ET AL.*, 2013). However, again these impacts on seed dispersal and sapling demography did not necessarily translate into lower overall abundance or changes in adult tree species composition—population growth rates were indeed reduced in animal-dispersed trees relative to species with abiotic dispersal, but among animal-dispersed species there were no differences between medium- and even large-seeded species (whose frugivores had certainly been extirpated) and small-seeded species which likely retained at least some persistent frugivores (HARRISON *ET AL.*, 2013).

As is so often the case, the picture is substantially more complicated than ecologists had initially predicted; hunting-induced defaunation can alter patterns of regeneration for some tropical trees, but whether and how the species composition of the tree community changes remains difficult to predict.

The issue of “secondary extinctions”, where loss of organisms through direct human impacts (e.g. hunting) leads to knock-on losses in their former interaction partners (e.g. animal-dispersed trees) is of clear concern worldwide. Given the difficulty of measuring secondary extinctions in complex natural systems, many studies have resorted to community models based on food webs or networks of interactions among organisms (e.g. FORTUNA & BASCOMPTE, 2006; SRINIVASAN *ET AL.*, 2007; STANICZENKO *ET AL.*, 2010). These necessarily greatly simplify the complexity of the real world, but must avoid oversimplification that could lead to biased results and poor (or worse, wrong) predictions. Indeed, many of the assumptions on which contemporary interaction network models are based are at odds with our growing understanding of the complexities of species interactions in the real world—we discuss some of these complexities below.

### SOME RESEARCH FINDINGS FROM THAILAND

Research in national parks of Thailand has provided, and continues to uncover, important pieces to the larger puzzle of the ecological consequences of seed dispersal disruption and secondary extinctions. Research on tree demography began in Thailand several decades ago, with the formation of what is now the Mo Singto Forest Dynamics Plot in Khao Yai National Park, a part of the global network of plots established or promoted by the Center for Tropical Forest Science (CTFS), Smithsonian Institution (see [www.ctfs.si.edu](http://www.ctfs.si.edu)). The Mo Singto Plot is 30 hectares in area (500 m × 600 m) and following the standard protocol established by CTFS, has every woody stem >1 cm in diameter at breast height (DBH) measured, mapped, and identified to species (BROCKELMAN *ET AL.*, 2011).

Intensive work on has been carried out on the reproduction, seed dispersal and population dynamics of six species of trees and several species of lianas (also important sources of food for wildlife) on the Mo Singto Plot. We have conducted in-depth studies of one particular tree species, *Choerospondias axillaris* (Roxb.) Burt & Hill (Anacardiaceae), which is an important food source for a wide array of mammals including gibbons (*Hylobates* spp.), squirrels, sambar deer (*Rusa unicolor*), and muntjac (*Muntiacus muntjak*) (CHANTHORN & BROCKELMAN, 2008; BRODIE *ET AL.*, 2009a, b) (Fig. 1). This research has been extended to three other protected areas in Thailand with different assemblages of potentially seed-dispersing mammals. Here we describe the major findings of these studies, as well as those of several other tree species that provide insights on the role of dispersers in forest dynamics and diversity. *C. axillaris* in Thailand is dispersed by several species of mammals including gibbons, sambar, and muntjac. We outline how some of the lessons from these research efforts can be applied broadly to our understanding of seed dispersal ecology and the consequences of defaunation for tropical forest regeneration.

#### *The scale of seed dispersal*

One of the most important lessons from seed dispersal research in Thai national parks is that the importance of seed dispersal for tree demography must be considered within broad

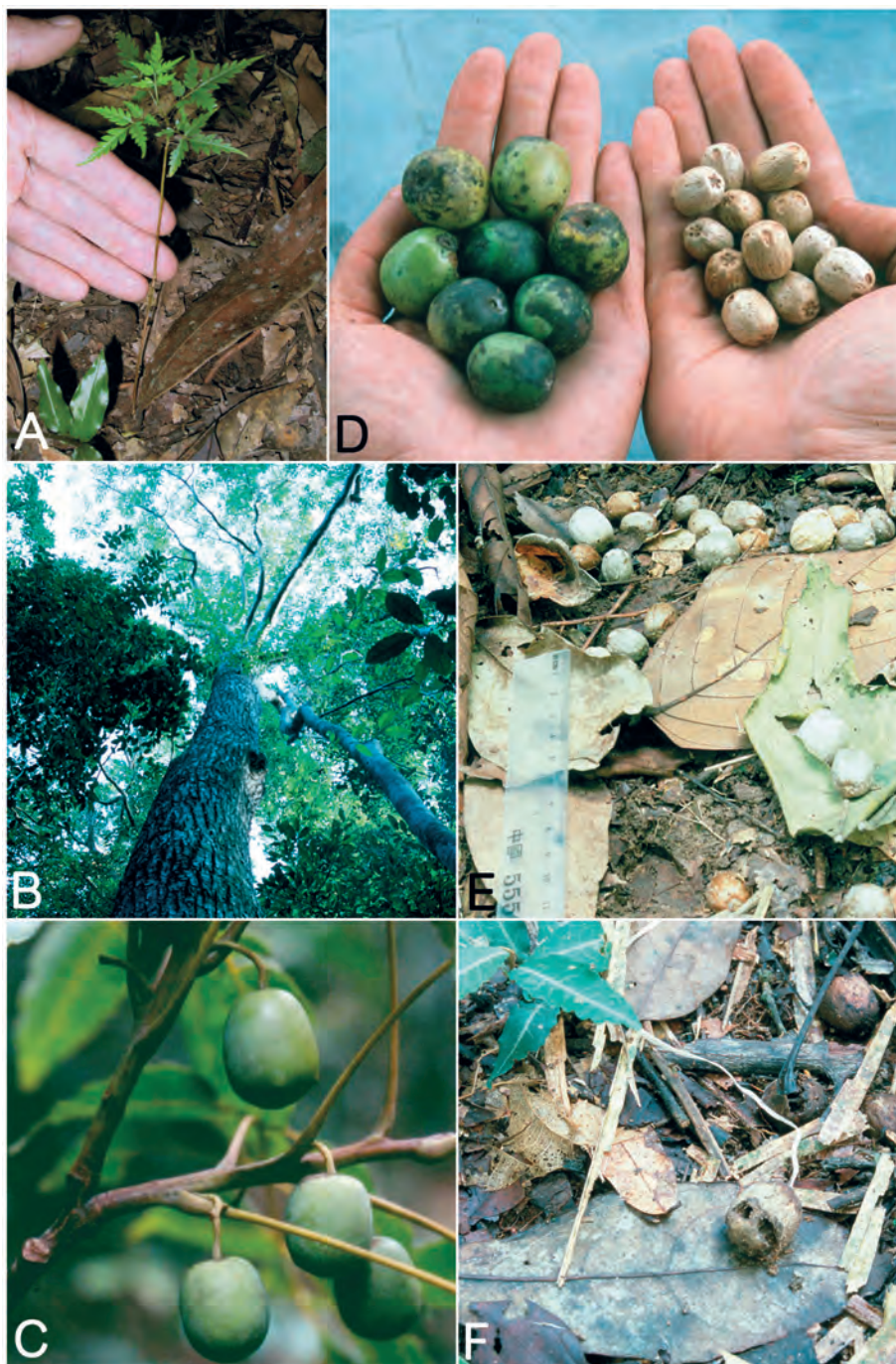


Figure 1. The tree *Choerospondias axillaris* (Anacardiaceae). A, seedling (note the compound leaves); B, trunk of a large tree; C, unripe fruits on a branch; D, ripe fruits and seeds; E, seeds in a pile regurgitated by deer; F, fruit with seeds predated by a squirrel.

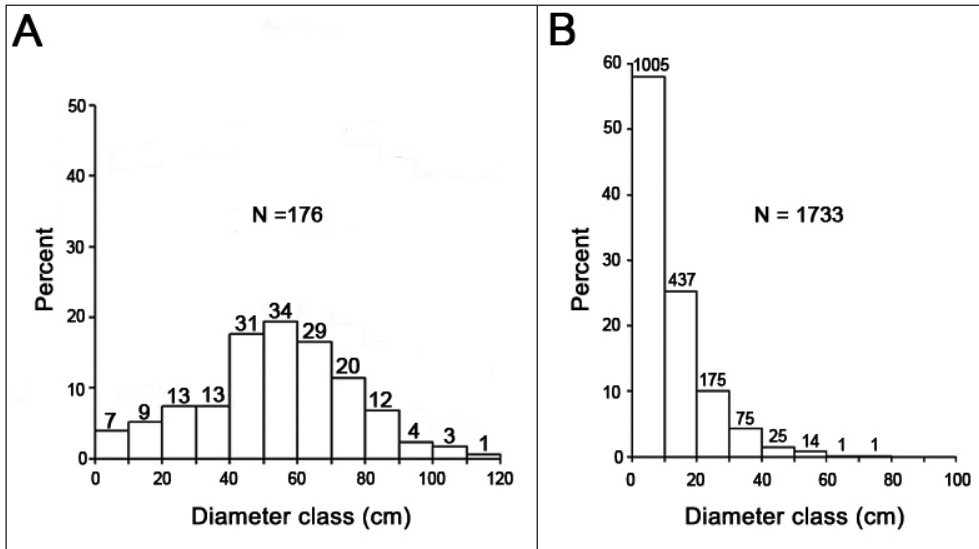


Figure 2. Size (DBH in cm) frequency distributions of two species on the Mo Singto Plot: A, *Choerospondias axillaris*; B, *Nephelium melliferum*.

landscape-level contexts, and over appropriate spatial and temporal scales. It is likely that most tree populations are not in equilibrium—their populations may decline and expand in different places and at different times, creating an intricate mosaic of settings in which seed dispersal takes place.

For a species like *C. axillaris*, dispersal could be particularly important in the early stages of forest recovery from disturbance. The species appears unable to survive for long in old growth forest such as that on the Mo Singto plot. Though growth and survival of adults in the closed canopy of the plot are high, seed germination is hindered—even in the presence of an abundant and diverse frugivore assemblage—and recruitment is extremely low (BRODIE ET AL., 2009a). Germination in canopy gaps is much higher, but recruitment in gaps is still insufficient to maintain abundance of the species (CHANTHORN & BROCKELMAN, 2008). The estimated population growth rate is less than  $\lambda = 1$  in Khao Yai (BRODIE ET AL., 2009a). Analysis of the size distribution of *C. axillaris* individuals on the Mo Singto plot further indicates that the species is probably not sustaining itself (Fig. 2A). A lack of juvenile trees is clearly evident in this unimodal distribution of diameters, indicating poor recruitment of saplings to adults. Contrast this with the diameter distribution of *Nephelium melliferum* Gagnep. (Sapindaceae), a species of wild rambutan tree common on the Mo Singto Plot, which has an inverse J-shape indicating a healthy abundance of young trees (Fig. 2B).

*C. axillaris* is one of the species more common in secondary forest than in old-growth forest, which is consistent with the observation that it has one of the lowest juvenile : adult ratios of all species on the plot (12 juveniles vs. 153 adults of reproductive size in the 2005 census). *C. axillaris* seedlings (Fig. 1A) are relatively common in large grassy areas around the Mo Singto plot, where deer have dispersed the seeds. We believe that the species needs a landscape with rare, episodic catastrophes that destroy the forest and create habitat where

sufficient sunlight can stimulate germination and seedling survival, and animal seed vectors to move seeds into those ephemeral and favorable habitats when they appear.

*C. axillaris* is a large tree (Fig. 1B) that reaches a diameter of 112 cm on the Mo Singto Plot. However, it is not the only large species in the old-growth forest that is having trouble sustaining itself. Other giants that have relatively low juvenile : adult ratios include *Balakata baccata* (Roxb.) Esser (Euphorbiaceae), *Magnolia bailoniii* Pierre (Magnoliaceae), *Cinnamomum ilicioides* Miq. (Lauraceae), *Toona ciliata* M. Roem (Meliaceae), and *Altingia excelsa* Noro. (Hamamelidaceae). Of these, the first three listed are also potentially important producers of fruit for animals, and hence might be affected by the availability of dispersers as well as important for sustaining frugivore populations.

Not all species that can regenerate in highly disturbed habitats such as regenerating swiddens are declining in old-growth forest. One interesting exception is the tree *Aquilaria crassna* Pierre (Thymelaeaceae) which is harvested for aromatic “agarwood” (“*mai hom*” in Thai). This species, moderately common in the park and on the Mo Singto Plot, grows rapidly and readily regenerates in tree-fall gaps on the plot as well as in early secondary forest. A demographic study conducted on the plot by ZHANG *ET AL.* (2008) showed that the population size distribution of *A. crassna* has large numbers of saplings and young trees but relatively low (and declining) numbers of reproductive adults due to widespread poaching for wood. Regeneration of young mostly takes place after adults die or are chopped down by poachers. Seed dispersal appears to be aided by birds and does not seem to be a problem, but it has not been studied quantitatively. Contrary to common belief, this species is not threatened with extirpation in the park, although reproducing adults (those above about 20 cm in diameter) will disappear for many years if the intense poaching now taking place continues.

The implication of these findings, especially for *C. axillaris*, is that both habitat disturbance and regeneration cycles over large spatial and temporal scales and also abundant seed dispersing animals are required to sustain many of the species in the forest. The relatively rapid predicted decline of *C. axillaris* in heavily hunted parks such as Doi Suthep–Pui (BRODIE *ET AL.*, 2009a) would thus not necessarily be offset by a cessation of hunting or a recovery of ungulate populations. Maintenance of *C. axillaris* and other species in such parks may require the protection (or re-establishment) of long-term episodic disturbance cycles and landscape manipulation beyond park boundaries, a management strategy likely beyond the capabilities of many park management authorities.

### ***Proxies for interaction strength***

Interaction strength can be measured in various ways, but a useful plant-centric definition in seed dispersal ecology is the difference in fitness or population growth rate of the plant when its seeds are dispersed as compared to when they are not dispersed (BRODIE *ET AL.*, 2009b). Such a measure allows the quantification of the impacts of frugivores on tree population dynamics and evolutionary fitness, as well as providing a measure of the selection pressure for the development and maintenance of phenotypic traits favoring seed dispersal. However, measurements of fitness responses to seed dispersal are difficult and time-consuming to obtain, and are usually limited to time durations that are short relative to the generation time of the species (BRODIE *ET AL.*, 2009b).

To circumvent these difficulties, community ecologists often resort to proxies of interaction strength. For example, a common assumption in the literature is that the visitation rate of animal mutualists (in this case frugivores) is proportional to their interaction strength (e.g.

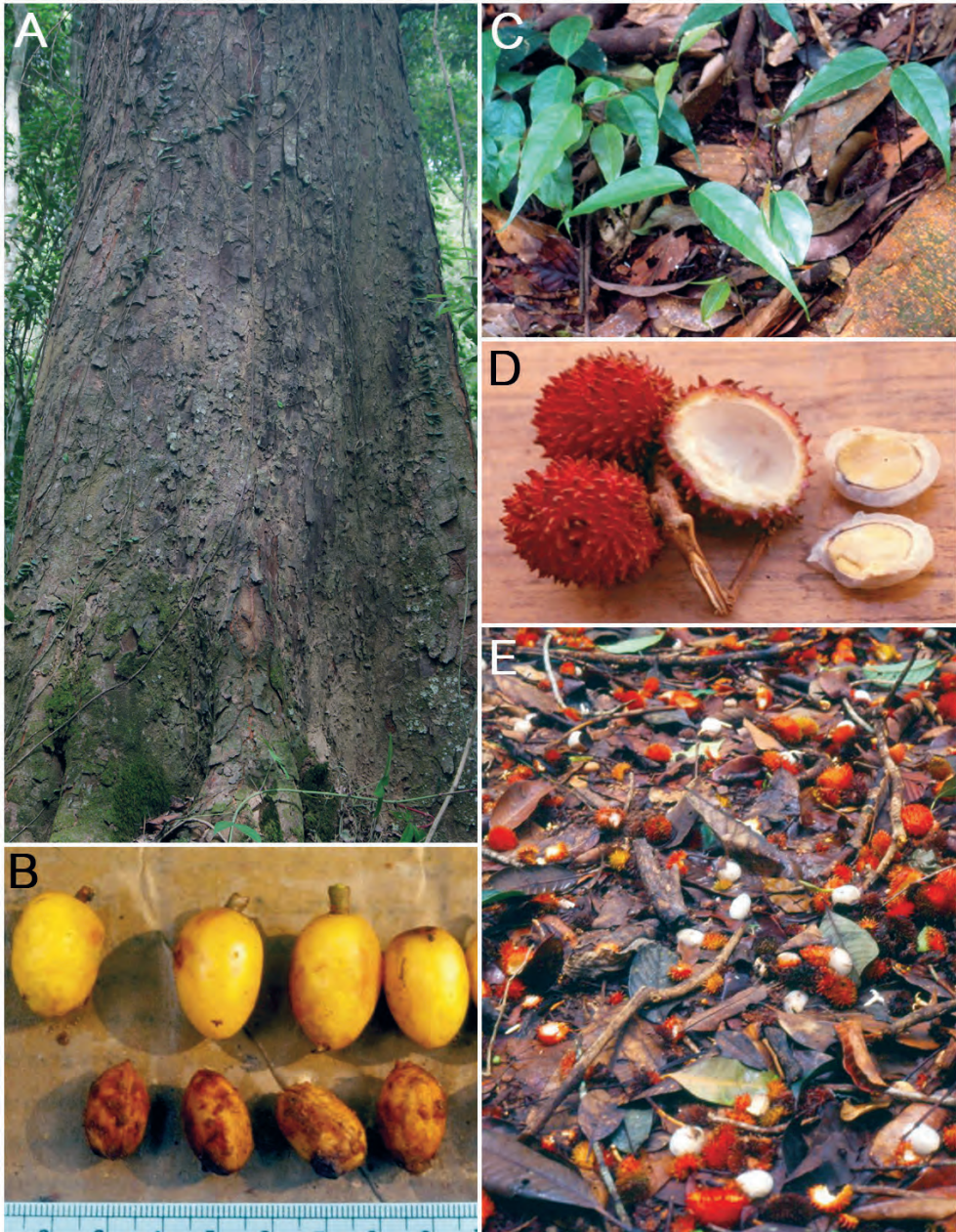


Figure 3. Stages of the trees *Prunus javanica* (Rosaceae) and *Nephelium melliferum* (Sapindaceae). *P. javanica*: A, large tree; B, fruit and seeds (Scale in cm/mm); C, young seedlings at the base of parent tree. *N. melliferum*: D, fruit whole and peeled; E, fruits and seeds dropped by squirrels and monkeys.

VAZQUEZ *ET AL.*, 2005; BASCOMPTE *ET AL.*, 2006). Research in Khao Yai Park shows that this assumption is often not valid. For example, species that take large quantities of fruit from a tree may play little role in dispersing seeds, and in some cases may even have negative effects on the fitness of the tree. Studies of the trees *Prunus javanica* (Teijsm. & Binn.) Miq. (Rosaceae) and *N. melliferum* in the Mo Singto Plot illustrate these points (Fig. 3). Gibbons were one of the least frequent visitors to the large *P. javanica* trees but provided arguably the best seed dispersal, insofar as conferring the greatest benefits to seed germination (McCONKEY & BROCKELMAN, 2011). Northern pig-tailed macaques (*Macaca leonina*) consumed the fruits and spit out larger numbers of seeds (Fig. 3B) but did not carry them as far from the parent tree as did gibbons, which swallowed and defecated the seeds. Bear scats have also been found containing large numbers of *P. javanica* seeds. Often these seeds were deposited in large clumps; this could potentially reduce germination or seedling survival rates through negative density dependence, although secondary dispersers often scatter seeds that were initially deposited together (BRODIE *ET AL.*, 2009b).

In our study of *C. axillaris*, muntjac and sambar removed roughly equivalent numbers of seeds (Fig. 1D, E) but had very different short-term impacts on demography of the tree (BRODIE *ET AL.*, 2009b). Moreover, as mentioned above, interaction strength is likely to vary substantially in different areas or phases of tree population expansion and decline. Interaction strength for all frugivores may be low for a tree like *C. axillaris* in closed-canopy forest, but substantially higher overall (and with more variance among frugivore species) in the context of dispersal to large light gaps and open areas.

It is possible that muntjac are particularly important seed dispersers for *C. axillaris* in Khao Yai because their population density is elevated due to extirpation of tigers (*Panthera tigris*) in the park (LYNAM *ET AL.*, 2006). Predators can alter plant-consumer interactions both by reducing the density of primary consumers or altering the feeding behavior of primary consumers. However, there is mixed evidence for “trophic release” in tropical systems (TERBORGH *ET AL.*, 2001; BRODIE & GIORDANO, 2013), and poor evidence for behaviorally-mediated trophic cascades in any non-insular, large vertebrate system (KAUFFMAN *ET AL.*, 2010).

### ***Complementarity and redundancy among frugivores***

There are usually some frugivorous animals that can persist even in heavily hunted areas. At the very least, small passerines and squirrels may still be found in most forests of Southeast Asia. Small-bodied ungulates such as muntjac appear to still have been present (though very uncommon) in Doi Suthep–Pui in 2004 (BRODIE *ET AL.*, 2009a). So the question becomes whether persistent frugivore species can replace the seed dispersal services of species that have been extirpated or reduced to low abundance. In turn, this depends on whether frugivore species are functionally redundant (playing the same ecological role), or else perform different and “complementary” ecological roles.

Research in Thailand has shown that complementarity among frugivores can be complex. For many plant species it is unlikely that persisting frugivores can simply step in to replace another that was lost to overhunting. Frugivores may differ greatly in seed handling behavior, movement patterns, and ranges. By attracting many frugivore species, tree species hedge their bets in terms of maintaining levels of seed dispersal sufficient for population growth.

For *P. javanica*, squirrels and most bird species provided ineffective seed dispersal, and therefore could not replace the dispersal services of larger seed dispersers such as hornbills and primates. Larger species are precisely the taxa most often lost from overhunted



forests—indeed both primates (BRODIE *ET AL.*, 2009a) and hornbills (ROUND, 1984; TRISURAT *ET AL.*, 2013) have disappeared from several Thai parks. Thus the persistence of *P. javanica* in these parks may be compromised. The larger-bodied, more effective seed dispersers could replace the seed dispersal services of the smaller-bodied species, but this will seldom happen in nature: it is difficult to imagine a hunting scenario that would lead to the extirpation of small and fast-reproducing frugivores but not larger ones with slower life-history strategies. The larger-bodied seed dispersers of *P. javanica* could potentially replace each other to some degree, though even here there is some complementarity in their dispersal services; gibbons providing low quantity but high quality dispersal, macaques dispersing large numbers of seeds with reduced quality to their seed handling, and hornbills visiting irregularly but dispersing seeds over long distances.

### ***Are all frugivores mutualists?***

Plant–animal seed dispersal interactions are considered mutualisms, in that both partners benefit from the interaction. But do they always? Research in Thailand has highlighted that distinguishing whether frugivores are beneficial or detrimental to tree demography can be more complicated than previously appreciated. Clearly, some animals may be both seed dispersers and seed predators. Squirrels, for example, consume and destroy many seeds but also cache or drop others cleaned of their surrounding pulp and cover. Indeed squirrels are known to feed on the unripe fruits of *C. axillaris* and gnaw into the chambers containing the endosperm (unpublished observations; Fig. 1F). Likewise, ungulates may both disperse seeds, which is beneficial to tree fitness (BRODIE *ET AL.*, 2009b), and trample or consume seedlings, which is detrimental to the trees.

But we highlight here a different, and more subtle, form of negative impacts that frugivores can have on tree populations. Given limited fruit production by any given tree species, the proportion of the fruit crop consumed by one animal species becomes unavailable to other species. On their own, gibbons would be considered mutualists for *C. axillaris* since they provide some seed dispersal, even though they do not carry seeds beyond the forest. But in a community context, gibbons could almost be considered “parasites” since they are taking away fruits that could have otherwise received more effective dispersal from ungulates. Clearly such a context-dependent interaction does not fit the classical definition of parasite very well and the term “free rider” may be more appropriate (MCCONKEY & BROCKELMAN, 2011). In a situation analogous to what we describe with frugivores and fruit, a “free-rider problem” in economics arises when parties that benefit by using goods or services without paying for them contribute to depletion of the resources, thereby generating sub-optimal provisioning of goods (CORNES & SANDLER, 1986). The evolution of seed-dispersal mutualisms is considered to be a key to the maintenance of high species diversity and food-web connectivity in tropical forest communities (HOWE & SMALLWOOD, 1982), but there is nothing to prevent other species from taking advantage of the “free” resources intended for dispersers. To some extent fruiting plants can evolve devices such as protective covers, allelopathic chemical defenses, and interannual fruiting variability (KELLY & SORK, 2002) to discourage seed predators, though the extent to which they can exclude free riders remains unclear.

The role of frugivores which feed on fruits of *N. melliferum*, studied by BROCKELMAN & MCCONKEY (unpublished), takes some new and unusual twists. Gibbons visit the trees regularly when they are in fruit and appear to be the main disperser-mutualists for the species, but they consume less than a third of the fruits on average. The rest are taken mainly by

squirrels (*Callosciurus finlaysonii* and *Ratufa bicolor*) and pig-tailed macaques. Every day, the squirrels gnaw the succulent pulp off the seeds and drop them below the tree. Macaque troops visit the trees irregularly, and when they do they feed on large numbers of fruits and seeds, dropping most to the ground below. Sambar and muntjac in the area are aware of the feeding commotion created by the monkeys and each night they consume the bonanza of seeds and fruits on the ground; not a single one is left by the following morning (Fig. 3D, E). The relatively soft seeds of *N. melliferum* are readily crunched up by the jaws of deer, which makes them seed-predators in the case of this tree species; it also makes the squirrels and monkeys seed-predators in an indirect sense because they subsidize the diet of the deer. The somewhat beneficial relations between monkeys and deer (and perhaps rodents on the ground) has been termed “gleaning” (NEWTON, 1989; MAJOLO & VENTURA, 2004; TSUJI *ET AL.*, 2007). The deer do not reciprocate the benefit provided by monkeys and squirrels as far as we know. From the sum of these observations, we must be very careful about necessarily equating “frugivore” with “seed disperser,” as is currently common. To say that squirrels, monkeys, gibbons and deer lack redundancy in this case is an extreme understatement.

### ***Seedling survival is a vital link***

The survival of seedlings, especially in the first year of life, is a complex function of the placement of seeds by dispersers, the abundance of terrestrial herbivores, and the adaptations of the plant to discourage herbivores from consuming leaves. In the case of *P. javanica*, MCCONKEY & BROCKELMAN (2011) found that seeds that were poorly dispersed and simply dropped under the tree germinated rapidly and formed a dense carpet of seedlings (Fig. 3C) which was soon grazed and eliminated by herbivores (probably mostly deer). Those deposited farther from the tree had higher chances of survival. A similar relation may also hold true for *N. melliferum* (unpublished observations). *Nephelium* seeds germinate very rapidly in the early wet season when the trees fruit and the seedlings grow very rapidly, reaching about 40 cm in height in the first year. Seedlings protected by wire cages that excluded mammals (but not insects) all survived well, but were nipped off by deer when they grew out of the tops of the cages (Fig. 3F). Unlike *Choerospondias axillaris* seedlings, *Nephelium* seedlings survive well in the partial shade of the old-growth forest canopy. Despite the depredations of the abundant deer in Khao Yai Park, the species maintains a relatively high density in its apparently optimal environment on the Mo Singto Plot. Its efficient dispersal by gibbons is a key to its survival; the loss of gibbons would be expected to change its fate for the worse. An issue of concern, however, is evidence that seedlings may be responding negatively to the increasing dryness caused by climate warming. Because *N. melliferum* is an important fruit species for all the mammals that depend on it, its loss could be a serious blow to the survival of some species, and this could have effects which ripple throughout the highly connected forest community.

Our final example illustrates the diversity of plant life histories and dispersal biology. Large trees of *Cinnamomum subavenium* Miq. (Lauraceae) can be easily located by the dense populations of large seedlings that are massed around the trunk (CHANTHORN *ET AL.*, 2013). According to lessons learned from the other tree species, these seedlings should not be able to survive in large numbers—the abundant seedlings should attract herbivores that destroy the seedlings. The leaves of *C. subavenium*, however, as with many other species in its family, are protected by toxic defensive compounds (KUO *ET AL.*, 2008; NENAAH & IBRAHIM, 2011). The cost of this crowded condition seems to be frequent infection by a fungus, a new species of *Laurobasidium* or *Exobasidium* (Exobasidiaceae) that enters the phloem of injured seedlings



Figure 4. A, *Nephelium melliferum* seedlings growing in a cage designed to exclude mammal grazers; *Prunus javanica*: B, seedling; C, fungal parasite attacking a tree; D, fungal parasite attacking a small sapling.

and causes out-pouching of the tissues into long finger-like processes that are plainly visible (CHANTHORN *ET AL.*, 2013) (Fig. 4). Infected seedlings have high mortality; however, it is unclear if the fungus actually regulates the density of seedlings of larger stages of the tree. The succulent fruits of *C. subavenium* are consumed by gibbons, bears, birds and other species, but we still do not know what the important dispersal agents are. Another puzzling aspect of

the behavior of this tree species is its mast fruiting: many years go by between rare fruiting years (BROCKELMAN, SUWANVECHO & NATHALANG, unpublished). Such behavior is thought to be an adaptation to overwhelm and satiate populations of seed predators (particularly insects) (JANZEN, 1970; JANZEN, 1971; KELLY & SORK, 2002), but both seeds and seedlings of *C. subavenium* appear to be protected against predators. Many other species on the Mo Singto plot have irregular fruiting, and most highly preferred species are not available more than one year out of two or three (BROCKELMAN, 2011). Much further research will be needed to solve these puzzles.

## CONCLUSIONS

Long-term research on tree dynamics, combined with observational and experimental studies of seed dispersal, have provided strong contributions to the fields of plant ecology and conservation biology. For example, they have improved our understanding of how tree communities may respond to defaunation induced by overhunting. To conclude, we highlight several important messages that have emerged from work in Thailand.

- 1) Loss of frugivores may not only reduce tree recruitment in a particular environment, but may also reduce trees' ability to colonize new habitats and expand their ranges. It may be that different frugivore species are involved in these different phases of the plant population cycle. Such nuances are important to consider in the context of climatic changes, where expansion rates of many tropical tree populations are predicted to be too slow to keep up with rising temperature (CORLETT, 2012; CORLETT & WESTCOTT, 2013).
- 2) Frugivores may not all be effective dispersers, some may even function as free riders if they make the seeds available to seed predators or other agents of mortality, or if they reduce the number of seeds available to more effective dispersers.
- 3) Seed dispersal must be considered at the landscape scale, over long time periods, and across the course of forest disturbance cycles and gap-phase dynamics. This is true for all tree species, but particularly for taxa such as *Choerospondias axillaris*, which are essentially pioneer species that persist into old growth forests and thereby are likely to require periodic large-scale disturbance events, in conjunction with animal-mediated seed dispersal, to sustain their populations. BAKER *ET AL.* (2005) have provided strong evidence for long term cycles of disturbance in another CTFS plot in Huai Kha Khaeng Wildlife Sanctuary, western Thailand.
- 4) Overhunting of animals not only reduces short-term population growth rates for some tree species, it can also limit trees' colonization potential. Colonization of distant or isolated fields will have to be aided by species like sambar that can travel to open fields to graze and bed down. This option may now be closed to Thai protected areas that are fragments surrounded by permanent non-forest. Better forest management may restore areas suitable for tree colonization. Control of hunting, in some instances augmented by frugivore reintroductions, may be necessary to promote long-term population persistence of many trees (BRODIE & ASLAN, 2012).
- 5) Research on a number of tree species in the Mo Singto Plot has clearly shown that species of trees differ greatly in their life histories, and that frugivores have different roles to play in

the lives of different species of trees. So far it has proved impossible to generalize from one species of tree to another, as each one has a distinctive life history and set of relationships with animal species. Were this not the case, such high tree species diversity might not have evolved in tropical forests.

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