

CHAPTER TWELVE

The role of trophic interactions in community initiation, maintenance and degradation

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The generality of the role of trophic cascades in creating trophic structure is still in debate (Strong 1992; Polis *et al.* 2000; Holt 2000). In part this is because spatial (van Noughys & Hanski 2002) and temporal effects (Dyer & Coley 2002; Dyer & Letourneau 2003) make it difficult to pinpoint patterns in the impact of intertrophic effects and cascades on community structure. For example, predators may exert effects at some times but not others (Sinclair 2003), and in some locations but not others (van Noughys & Hanski 2002). Sinclair (2003) and Sinclair and Krebs (2002), working with vertebrates (hares, lynx, predatory birds and others), found that predators regulated their prey populations at high but not low densities in the boreal forest of Canada, and that this effect did not cascade down to plant populations.

To date, support for the existence of trophic cascades and their role in influencing trophic structure comes primarily from biologically simple ecosystems with two or three interacting organisms and trophic levels (see the recent volume by Tscharntke and Hawkins 2002). Although there are suggestions in the literature (Tscharntke & Hawkins 2002) that it will be difficult to find evidence in support of strong trophic cascades in high-biodiversity terrestrial systems with complex food webs, Terborgh and co-workers have found correlations that support their occurrence in predator–herbivore–plant systems involving both vertebrates and invertebrates (Terborgh 1992, Terborgh *et al.* 2001). Letourneau and Dyer (1998) also experimentally reproduced top-down effects for four trophic levels (soil nutrients, a plant, insect herbivores and insect predator) in Costa Rica. Recognition of strong multitrophic interactions in high-diversity terrestrial systems may also have been limited because work to date has not included appropriately scaled studies with large vertebrate herbivores and their predators (Persson 1999). Furthermore, most studies have simplified complex food webs into simpler food chains in their attempt to understand the nature of the system (Pace *et al.* 1999).

To explore how spatial and temporal scales and long-term dynamics may affect both the functioning of multitrophic interactions and our ability to detect their impact on community structure, I consider one multi-species trophic interaction and trophic cascade in a complex food web in a terrestrial tropical system. As documented to date (Fragoso 1994; 1997a; Fragoso *et al.* 2003; Silvius 2002; Silvius & Fragoso 2002; 2003), the system consists of the palm *Attalea maripa* (formerly *Maximiliana maripa*, revised by Henderson 1995), its fruits and seeds, two obligate invertebrate herbivores of *A. maripa* seeds, a wasp parasitoid of at least one and probably both of the invertebrate herbivores, a large vertebrate herbivore, and a number of omnivorous vertebrate species that feed on the fruits and seeds and that prey on the invertebrate herbivores. I describe the key role of seed dispersal by tapirs (*Tapirus terrestris*) in allowing *Attalea* to escape its predators, and subsequent local regulation by a multi-level trophic system, in which the ecological importance of each interaction shifts through time. I further consider how the interactions between organisms in the same and different trophic levels can affect the diversity and abundance of different species, and speculate on how these interactions can initiate community formation, biodiversity patterns, trophic organization, community degradation and death. Because the interactions are focused on seed dispersal and seed predation, they help set patterns of diversity among tropical forest tree species, and may represent an alternative or complementary scenario to explanations based on canopy disturbance and gap dynamics. I compiled and correlated data from studies conducted over 16 years at Maracá Island Ecological Reserve in tropical rainforest in the state of Roraima, Amazonian Brazil (Fragoso 1994; 1997a, b; 1998a, b; 1999; Fragoso & Huffman 2000; Fragoso *et al.* 2003; Silvius 1999; 2002; Silvius & Fragoso 2002; 2003).

The system

Producer trophic level

Attalea maripa

This palm forms the producer trophic level of the system. It grows to 30 m in height and reaches the canopy or sub-canopy of old-growth forests (Fragoso 1997a). It occurs in a clumped distribution with high-density patches containing 12–24 trees per 0.25 ha (Fragoso 1998b). Within patches *Attalea* co-occurs with many other tree species (Milliken & Ratter 1989). *Attalea* also occurs in patches in savannas, riverine forests and secondary forests (Fragoso *et al.* 2003). Within the forest matrix, palm patches range from less than a hectare to about 10 hectares in extent, although most are probably between half a hectare and 2 hectares; patches are separated by hundreds to thousands of metres of palm-free forest (Fragoso *et al.* 2003). Adult *Attalea* also occur as solitaires. *Attalea* fruiting is synchronized within climatic regions (J. M. V. Fragoso, personal observations). In the northern part of Roraima most trees flower from January to March and ripe

fruit falls en masse from April (peaking in June) to October (Fragoso 1998a). Adult trees produce one to three infructescences each containing from a few hundred to more than 2500 fruits (Fragoso 1998b; Silvius & Fragoso 2002). Mature fruits are yellowish-green, oval-shaped and 4 to 7 cm long. A slightly sweet soapy-tasting fleshy pulp with some fibres surrounds a thick woody endocarp (3 to 6 cm length) that generally contains one and occasionally two or three seeds (Fragoso 1994; Silvius 2002). Ripe fruits drop naturally below parent trees, or are dropped or spat out by arboreal herbivores (frugivores; e.g. primates, parrots, macaws) after pulp has been consumed (Fragoso 1997a). Pulp-free seeds can remain dormant for at least 14 months (J. M. V. Fragoso, unpublished data).

Herbivore trophic level

Pachymerus cardo (Fåhraeus) and *Speciomerus giganteus* (Chevrolat)

These bruchid beetles specialize on *Attalea* seeds, although they are not confined to the genus (Delobelle *et al.* 1995; Silvius 1999). They appear to be the dominant representatives of the herbivorous trophic level supported directly by *Attalea* fruits and seeds (Fragoso 1997a; Fragoso *et al.* 2003; Silvius 2003; Silvius & Fragoso 2002). Signs of vertebrate or insect herbivory on the leaves of seedlings or adults are not obvious (personal observations). It is during the larval stage that beetles feed on *Attalea*. Females can lay 1–30 eggs on an endocarp, and oviposit preferentially on endocarps whose pulp has been incompletely consumed by frugivores (Silvius & Fragoso 2002). However, they eventually lay eggs on all fruits and endocarps on the soil surface within palm patches (Fragoso 1997a). Upon hatching (6–7 days), first-instar larvae burrow through the remaining pulp and woody endocarp and take up residence in the endosperm (Silvius 1999). They consume the endosperm over a 3- to 12-month period (possibly up to 2 years; K. Silvius, personal communication), after which one adult beetle (occasionally two or three, in multiple-seeded endocarps) emerges from each endocarp, although many first-instar larvae may have entered each seed. Up to 97% of seeds remaining on soil surfaces within 30 m of parent trees are consumed by beetles (Fragoso 1997a), as are almost all seeds within a palm patch (K. Silvius, personal communication). Adult beetles oviposit on endocarps at night (J. M. V. Fragoso, unpublished data). In forest, eggs are laid only on fallen fruits.

Tapirus terrestris (Linnaeus) and other vertebrate herbivores

Lowland tapirs (*Tapirus terrestris*) eat the pulp of intact freshly fallen *Attalea* fruits; although they ingest the seeds, they do not consume them and the seeds pass intact and viable through the digestive tract (Fragoso 1997a; Fragoso & Huffman 2000). Tapirs thus belong to the herbivore trophic level, which includes animals that feed only on the pulp of the fruits as well as those that feed on seeds. Tapirs are large (250 kg) and can ingest many fruits at one time; up to 210 fruits have been found in one faecal pile (Fragoso & Huffman 2000). Thousands of viable seeds become aggregated at tapir latrines in upland and wetland areas

(Fragoso 1997a). The immersion of endocarps in faeces prevents beetles from accessing and killing seeds (Fragoso *et al.* 2003). The long-distance movement of endocarps several kilometres beyond *Attalea* patches by tapirs makes it difficult if not impossible for beetles to find these seeds (Fragoso *et al.* 2003). Nothing is known about how far beetles disperse, but they appear to be weak flyers with restricted movements, as they are never captured in light traps or by other capture methods that intercept insect movements (Fragoso *et al.* 2003). Thus, seed-handling by tapirs ensures the survival of seeds that would otherwise have been killed by beetles. This interaction is best described as a mutualism between *Attalea* and tapirs, and exemplifies what Bronstein and Barbosa (2002) classify as a protective mutualism, where a species deters other species in the same trophic level from negatively affecting the producer species. Endocarps are secondarily dispersed from latrines by rodents and many of these seeds eventually germinate and create high-density patches of seedlings, saplings and probably adult palms (Fragoso 1997a). Tapirs mediate the interaction between *Attalea* palms, beetles and rodents, and are responsible for initiating new *Attalea* patches.

Other vertebrate species in this trophic level include at least five primate, three macaw, two parrot and four ungulate species and potentially a number of marsupials, armadillos and carnivores (Fragoso 1997a, and personal observations); however, these animals, with the possible exception of macaws and parrots, move seeds only one metre to tens of metres from parent trees (Fragoso 1997a). Because the seeds remain within a conspecific patch they are accessible to beetles for egg-laying and consumption (Fragoso 1997a; Silvius & Fragoso 2002). The scarce amounts of faecal matter produced per defecation by other fruit eaters that swallow fruits and defecate seeds, such as spider monkeys (*Ateles belzebuth* É. Geoffroy; K. Silvius, personal communication), are insufficient to cover and protect the large *Attalea* endocarps.

Predator trophic level one (exclusively)

Parasitoid

A potentially important member of the first predator trophic level is an unidentified braconid wasp whose larvae parasitize beetle larvae (Silvius, 1999; 2002). This parasitic wasp may be an obligate predator of *Pachymerus* and *Speciomerus* beetle larvae. Adult wasps lay their eggs inside *Attalea* endocarps that contain beetle larva. As wasp larvae mature they consume their beetle larval host. Once the beetle larva is consumed the wasp larva pupates inside the endocarp and two to five or more adult wasps eventually emerge (K. Silvius, unpublished data).

Omnivores: trophic levels predator one and two, and herbivore

Tayassu pecari (Link)

One of the more important vertebrates in the system may be the white-lipped peccary (white-lips, *Tayassu pecari*). These large ungulates (up to 50 kg) occur in herds of 40–400 and perhaps thousands of individuals (Fragoso 1998a; Kiltie &

Terborgh 1983; Mayer & Brandt 1982). Although omnivorous, white-lipped peccaries forage extensively on *Attalea* endocarps (Fragoso 1999), consuming bruchid larvae in the endocarps (Silvius 2002), and also occasionally consume endosperm (Fragoso 1994; 1999). These animals simultaneously belong to the herbivore and first predator trophic levels. To the extent that they encounter and consume wasp larvae and adult wasps, white-lipped peccaries (and the other omnivores described below) also constitute a second predator trophic level. White-lipped peccary populations fluctuate from very high to very low densities at intervals of 10 to 15 years (Fragoso 1997b, 2004). At low densities white-lips open few *Attalea* endocarps and usually only those encountered incidentally in wetland tapir latrines when they are foraging for other items (Fragoso 1994; and unpublished data). As the population increases they begin foraging on endocarps around a few to eventually all parent trees and patches (K. Silvius, unpublished data). They also uproot and kill hundreds of seedlings (Kiltie & Terborgh 1983; Silman *et al.* 2003; Fragoso, unpublished data).

Rodents

Agoutis (*Dasyprocta leporina* Linnaeus) are large rodents (3 to 5 kg) that feed on endosperm and beetle larvae as do Amazon red squirrels (*Sciurus igniventris* Wagner) and smaller rodents such as spiny rats (*Proechimys* sp.; Silvius 2002). These animals also simultaneously belong to the herbivore and first predator trophic levels. Squirrels may be the only vertebrate species that specializes on *Attalea* and other palm endocarps in this system; however, they regularly consume both endosperm and beetle larvae (Silvius 2002). As is the case for white-lipped peccaries, these rodents may also consume wasp larvae and thus influence wasp population dynamics as level-two predators. White-lipped and collared (*Tayassu tajacu* Linnaeus) peccaries, agoutis, squirrels, smaller rodents, deer and other terrestrial herbivores also consume the pulp from fallen fruits and are thus also members of the herbivore trophic level (Fragoso 1997a). The multiplicity of trophic levels to which these vertebrates belong indicates that they probably mediate interactions between one another in various ways.

Next I consider the nature of the interactions between *Attalea* palms herbivorous beetles, parasitic wasps, predatory white-lipped peccaries and rodents across time and space in an attempt to understand how multi-trophic interactions may contribute to community initiation, structure and dynamics. I also consider how these interactions influence one another under a scenario of *Attalea* patches transitioning from formation through to maintenance, degradation and death. Figure 12.1 depicts the type and direction of interaction and the trophic-level placement of the species under consideration.

To determine whether the multitrophic interactions described in Figure 12.1 remain constant during all life phases of an *Attalea* patch, I classified *Attalea* patches into different stages (phases) of patch development: birth, growth,

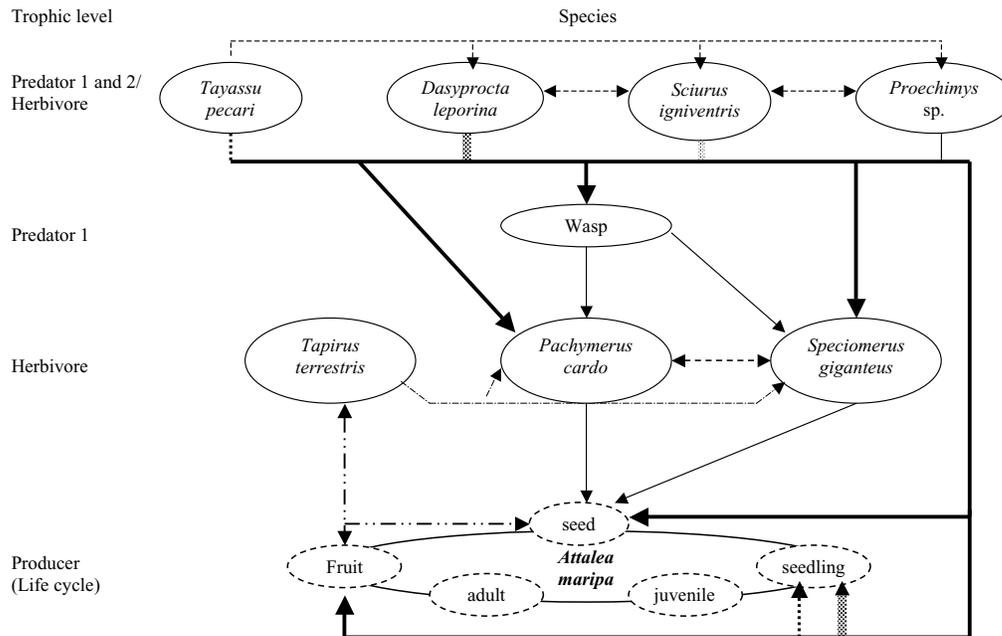


Figure 12.1 Trophic levels of nine species forming a food web, and the direction of consumption, in an Amazonian tropical forest. Additional frugivores (not shown) consume the fruit pulp. Legend: predation (one species) —, predation (several species) —, interference — —, cooperation ···· and competition — · —. The arrowhead indicates the direction of the interaction; two arrowheads pointing in opposite directions on a single line indicate mutualism or competition. The point of influence of an animal species in the top row of the figure occurs where its line-pattern departs from the thick solid line that almost encircles the figure. When the exit line is also black and thick it indicates that all the top row animal species affect a taxon or plant part.

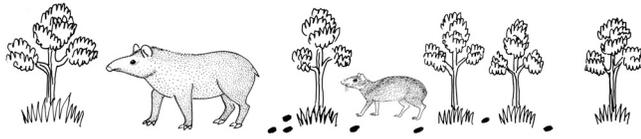
expansion, decline and death, based on long-term work by Fragoso (1994; 1997a; 1998a; 1999), Fragoso and Huffman (2000) and Fragoso *et al.* (2003).

Phases in *Attalea* patch development

Phase 1

All phases and constituent organisms can be viewed in Figure 12.2. In Phase 1, tapirs disperse *Attalea* seeds into an area without adult *Attalea*, dominated by adults of other tree species (Fragoso *et al.* 2003). Rodents re-disperse these endocarps a few to hundreds of metres beyond the arrival points (Forget & Milleron 1991; Forget *et al.* 1998; Fragoso 1997a; Wenny 1999). Because some *Attalea* seed predators (e.g. white-lipped peccaries) locate their prey by searching for adult palms (Fragoso 1997a), and others such as agoutis (Silvius & Fragoso 2003) are territorial, there will be few seed predators at the arrival points at this time (Fragoso *et al.* 2003). Without predators almost all seeds survive (Fragoso *et al.* 2003). Many

Phase 1 (seed dispersal)



Phase 1: Seedlings



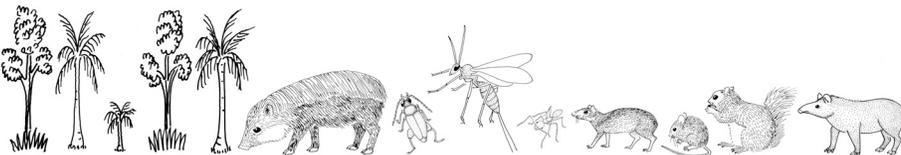
Phase 2: First Fruit



Phase 3:



Phase 4:



Phase 5:

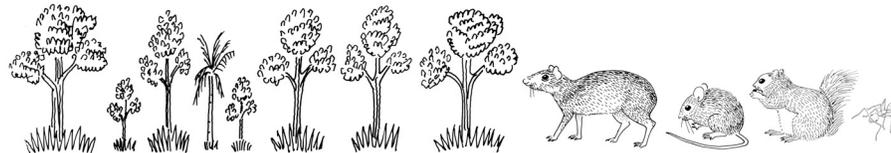


Figure 12.2 An illustration of the organisms involved in five phases of *Attalea maripa* patch formation, maintenance and death. The number of individuals of a plant type represents their numerical importance in that phase relative to other plants, while individual size (largest) indicates a dominant or driver animal species. Species in order of appearance are: dicotyledonous trees, tapir (*Tapirus terrestris*), *Attalea maripa* seeds, agouti (*Dasyprocta leporine*), *Attalea* seedlings and adults, bruchid beetle (*Pachymerus cardo* and *Speciomerus giganteus*), rat (*Proechimys* sp.), squirrel (*Sciurus igniventris*), braconid wasp sp., and white-lipped peccary (*Tayassu pecari*).

germinate, establish seedlings and reach maturity (Fragoso 1997a). At this time the *Attalea* patch should exhibit a truncated age distribution because of an abundance of seedlings and saplings, and a lack of adult palms. High recruitment levels should continue until slightly beyond the appearance of the first fruit-producing adult trees. This may take 10 to 20 years based on *Attalea* recruitment from seeds to adults following deforestation at nearby ranches (Fragoso, personal observation).

At this stage the *Attalea* population is most likely to be controlled by soil fertility, light and water levels in conjunction with positive interactions with herbivores (tapirs and rodents). Since herbivorous beetles and other seed-eating organisms do not occur in the area or occur at very low densities, they have little or no influence on *Attalea* (Fragoso 1997a; Fragoso *et al.* 2003). Similarly, with no fruit-producing palms, white-lipped peccaries, the other potential herbivorous influence on seeds, are unlikely to be visiting the area (Fragoso 1998a), unless some other tree species is producing fruit or seeds (Silvius 2002). This *Attalea* population is regulated by bottom-up, pre-producer-level trophic elements.

Phase 2

The first *Attalea* palms produce fruit. Assuming that intraspecific competition is stronger than interspecific competition, and that *Attalea* trees affect soil nutrient levels differently from dicot species, fruit production per tree should be high, as the soil nutrient levels will be higher than for sites where *Attalea* has been long established. Both assumptions need to be tested, but support comes from the observations that (1) *Attalea* seedlings and saplings establish and grow under the closed forest canopy in the absence of disturbance, and (2) palms release large amounts of slow-decaying litter that physically prevents nearby seedling establishment and may contribute few nutrients to the soil. Seed survival and recruitment into all age classes, including adults, continues to be high (Fragoso 1997a). However, demographically the population is still dominated by younger plants (a reverse J curve with very few adults). A few bruchids will have discovered the first *Attalea* fruits and they will have infested a few endocarps. These beetles will show high egg-laying rates per female because of low intraspecific competition for seeds (Wright 1983; 1990). Bruchid egg, hatching, larval survivorship and recruitment rates to the adult stage will be very high, although their density remains low. Low beetle-larvae densities mean few to no parasitoids can be supported, and this species has yet to colonize the area. The system is still regulated by bottom-up trophic forces, meaning that *Attalea* productivity is dependent on soil nutrients and light levels. Competition with other palm species is probably low, since the other arborescent species in the area, *Astrocaryum vulgare* (Giseke) and *Oenocarpus bacaba* (Martius), occur at low densities (Fragoso, unpublished data). The population density of bruchid beetles is still too low to affect seed survivorship and population recruitment.

The community structure of the area will have changed as new frugivorous, granivorous and grubivorous (larvae feeders; as per Silvius 2002) species arrived or increased in density in response to the new abundance of *Attalea* fruits, seeds and beetle larvae. White-lipped peccaries, as well as various primate, bird and invertebrate species that feed on fruit pulp or seeds may now have located the new palm patch; however, their visits to the area should still be infrequent, especially for white-lipped peccaries since they tend to forage in traditional feeding areas dispersed over a home range 100 to 200 km² in area (Fragoso 1998a; 1999; Carrillo *et al.* 2002; Keuroghlian 2003). Hence, at this stage the palm and the bruchid beetle populations are relatively unaffected by a predatory trophic level (white-lipped peccaries). Rodents such as agoutis, squirrels and smaller rats (e.g. *Proechimys*) should now be more common in the area, be feeding on *Attalea* fruit and seeds, and have begun feeding on beetle larvae. However, these animals continue to occur at low densities and this coupled with their territorial behaviour suggests that they would have a weak effect or none on the *Attalea* population. Squirrels will probably not establish many territories in the area, because of the lack of a year-round source of palm endocarps, and agoutis will still prefer to feed on alternative food sources, as *Attalea* is not a preferred food (Silvius 2002; Silvius & Fragoso 2003). The *Attalea*-dominated producer trophic level now regulates the diversity and abundance of the animal species in higher trophic levels.

Phase 3

Attalea fruit and seed production per tree and patch continues to be high, and I posit that the seed population is in a state of dynamic equilibrium. Thus, the number of seeds consumed by predators and recruiting into older plants is approximately equal. At this stage the *Attalea* population and animal species at higher trophic levels continue to be regulated by *Attalea*-dominated bottom-up relationships but the system is beginning to flip into another state (*sensu* Holling 1986), from one controlled by the producer trophic level, to one regulated by a dominant herbivore, the bruchid beetle. In this phase female beetles may lay up to 30 eggs per endocarp; most of these hatch and many larvae penetrate individual endocarps (Silvius & Fragoso 2002). The endocarp population attains a beetle larvae infestation rate of 90% or more, and most multiple-seeded endocarps support more than one larva. The number of eggs laid by wasps per beetle larva per endocarp is now high but wasp infestation of the endocarp/beetle larvae population remains at medium levels; however, wasp survival and recruitment rates into adulthood should be very high. Beetle recruitment rates between life stages are at medium levels owing to high predation by vertebrates, wasps and perhaps fungus (Silvius 2002; Fragoso unpublished data). High densities of larvae-infested seeds have led to more visits by white-lipped peccaries to the patch (Fragoso 1998a; 1999), and concomitant higher rates of beetle-larvae consumption.

White-lipped peccaries, members of the second predator trophic level, have begun to exert a regulating influence on the larvae population and are competing with wasps for the larva resource, potentially limiting wasp populations. The various rodent species may also have experienced population increases.

The local adult tree community has shifted from one with high species diversity to a lower-diversity system dominated by adult *Attalea* palms (Milliken & Ratter 1989; Fragoso *et al.* 2003). The species diversity and abundance of vertebrates and invertebrates in the community is high, owing to the diversity and abundance of food types available (*Attalea* fruit pulp and seeds, beetle eggs on seeds and fruits, and bruchid larvae, pupae and wasp larvae in endocarps). A diversity of insect species feed and/or lay their eggs on *Attalea* pulp, and insect predators hunt in the fruit patches (Silvius & Fragoso 2002; K. Silvius, personal communication); because of the sheer abundance of the resource, many individuals and species can be supported; because the resource is ephemeral, it is unlikely that one species can dominate it. At this point tapirs ingest fruits at the patch and initiate the creation of new *Attalea* patches far from the present patch. Seed survival within the parent palm patch is low but sufficient to maintain its structure and extent. The palm population now exhibits a reverse J age distribution curve.

Phase 4

The numerical dominance of *Attalea* trees is declining as adults senesce and recruitment falls, and diversity of other tree species in the understorey is increasing. *Attalea* trees are still producing fruit, but seed predation by beetles (before and after short-distance dispersal) is very high (Fragoso 1997a; Fragoso *et al.* 2003; Silvius & Fragoso 2002). Seedling mortality rates are also high because of intense soil-rooting and trampling by peccaries (Cintra 1997; Fragoso unpublished data; Silman *et al.* 2003). Primary short-distance seed dispersal by vertebrates is low and too few seeds are surviving to maintain the recruitment rates necessary for patch maintenance. The population has an age structure with more adults than saplings and seedlings. This phase probably lasts for a long time, determined by the lifespan of the palm.

The bruchid beetle, a member of the first predator trophic level, now dominates the herbivorous trophic level and controls the palm. Female bruchid beetles continue to lay up to 30 eggs per seed; however, many of these are consumed by ants before hatching (K. Silvius, personal communication). Egg-survival rates per seed are still high enough to maintain 95% to 100% seed-infestation rates (Fragoso 1997a). A high density of beetle larvae continues to attract a diversity and abundance of grubivorous species such as parasitic wasps, white-lipped peccaries, agoutis and other rodents (Fragoso 1997a; Silvius 2002; Silvius & Fragoso 2002). Wasp-larvae infestation of beetle larva is at its highest levels, with a high number of wasp eggs laid per beetle larva and over the larvae-endocarp

population. The vertebrate community attains its highest diversity and abundance, and the frequency of visits by white-lipped peccaries to the area is at its peak. Consumption of larvae by these organisms is at its highest level (Silvius 2002; Silvius & Fragoso 2002). The herbivore trophic level (beetle larvae) is now strongly influencing the dynamics of adjacent trophic levels (up and down), and may eventually cause the collapse of the *Attalea* population. However, members of the predator trophic levels, especially white-lipped peccaries and wasps (first predator level), exert a strong negative influence on the beetle population (Fragoso & Silvius unpublished data), and probably introduce non-linear dynamics into the system, in contrast to the linearity we have described up to this point. For example, if the white-lipped peccary population is at a high or increasing point in its cycle (Fragoso 1997b; Fragoso, 2004), they may exert enough negative pressure on the beetle population to negate or eliminate their effect on the *Attalea* population. However, if the white-lips are at a low point in their population cycle, wasps are released from competition with and predation by white-lips and may exert control of the beetle population. Thus, community assembly and disassembly depends not only on internal factors, but on an externally controlled population fluctuation – two patches will not follow the same trajectory if they are established at different times in the population shift of white-lipped peccaries. If predation pressure is too low to reduce the beetle population, the *Attalea*-population size begins to decline. At this point the community of species supported by beetles has peaked in diversity and abundance. The seeds that are surviving at high rates are those that were swallowed by tapirs and dispersed to their latrines.

Phase 5

Rodents, organisms belonging to the first and second predator trophic levels, are now driving the *Attalea* system. Adult *Attalea* palms are now rare or non-existent in the area. If a few palms occur they appear as solitaires. The area is now dominated by other tree species. *Attalea* fruit and seed production is non-existent or a tiny fraction of that in phases 2 to 4. If a few fruits and seeds are available rodents quickly find and eat them, or eat the fruit pulp and quickly cache the seed for later consumption and before beetles can lay eggs on them. Most if not all the cached seeds will be found and eaten. Quick seed removal translates into few if any beetle eggs being laid, and few larvae attaining adulthood. The few beetles that do lay eggs should lay high numbers per endocarp, but predation by ants (Silvius & Fragoso 2002) and death due to handling by rodents should also be very high, negating the effects of high levels of egg-laying. Low to no egg survival results in proportionally low endocarp-infestation rates. The low survival rate translates into very few to no adult beetles and eventually local beetle extinction. The few adult beetles to emerge from endocarps will either die or disperse long distances at low frequencies in search of fruit-producing

Attalea patches in phases 2 to 4. This dispersal probably occurs through self-propelled flight.

With few beetles, the wasps and ants die out, or the ants switch to alternate foods. The tapirs, primates, peccaries, deer, macaws, parrots, rodents and other vertebrates stop visiting the area, or if they continue they do so because of another tree species whose fruit, seeds or grubs colonized the region. The timing of white-lipped-peccary foraging visits to the area will now coincide with the fruiting phenology of the new dominant tree species. The area may also now support a more diverse adult tree community. Rodents thus deliver the final death-blow to the *Attalea* and beetle population. Some evidence indicates prey population collapse occurs when a species is a secondary prey item for a predator sustained by alternative food items (Sinclair & Krebs 2002), as larvae are for white-lipped peccaries, and as they become for rodents, but not for wasps. How long the area remains uninhabited by *Attalea* is unknown. This may be as short a time as it takes for a new generation of adult palms to arise from the local seed bank (*Attalea* seeds may remain dormant for over 14 months) or to be moved into the area by tapirs from an *Attalea* population in an earlier phase of development.

Patterning in tropical multitrophic interactions

The model I present above is based on empirical evidence collected during 16 years of study at Maracá Island Ecological Reserve, Amazonian Brazil, and on some speculation. Important components of the model are colonization and extinction dynamics driven by interactions between organisms belonging to different trophic levels. Initially, spatial expansion and numerical growth of a new plant (producer) population is limited by physical parameters. However, this situation is temporary. When individuals in the producer trophic level begin reproducing and attain high group reproductive output, herbivorous species (beetle larvae, rodents, white-lipped peccaries and other seed- and fruit-eating organisms) are attracted to the region. The upper trophic levels of the system are regulated by the producer trophic level at this stage. The system eventually flips to one regulated by the herbivore (beetles) trophic level owing to the growth of the herbivore population, a top-down effect. An increased density of herbivores attracts species in the next trophic level up, predators (white-lipped peccaries; predators with respect to this system, but omnivores in terms of overall diet), and increases the density of the resident omnivore population (rodents: omnivores with respect to this system, frugivore-granivores in terms of overall diet). The rate of visits by one member of the top predator trophic level (white-lipped peccaries), discovery of the beetle population by strict parasitoids, and an increase in the resident population of omnivores (rodents) lead to control of the system by the first and second predator trophic levels, so that the system is now controlled by top predators. Population and community regulation of the system is fluid, however, and the organism or trophic level that drives it depends

on the population dynamics of and interactions among other organisms. The succession in dominance appears to be linear with succeeding species taking control in a time-lagged fashion. The speed at which this happens will depend on the rate at which different species locate the palm patches, which will in turn depend on their searching behaviour (for large species like white-lipped peccaries and tapirs) and their dispersal pattern (for smaller or territorial species such as insects and rodents). The species driving the system at any one time is dependent on the maturity of the plants, the abundance of the herbivores, and the abundance and diversity of the predators.

Non-linear dynamics are introduced to the system when the population dynamics of a driver species are not linked to the system. For example, the population fluctuations of white-lipped peccaries appear to be driven by factors operating at larger spatial scales than *Attalea*-patch dynamics and at longer time scales than those of animals restricted to *Attalea* patches. This component of white-lipped peccary ecology may introduce non-linearity into the succession-dominance pattern of the *Attalea* community. Short-term environmental fluctuations can be tracked through rapid reproduction by small-bodied species; however, large-bodied, long-lived vertebrate species such as peccaries cannot track these changes, making their populations less responsive to the environment (Sinclair 2003). White-lipped peccaries are long-lived mammals (Walker 1999). White-lipped peccary populations respond to factors unrelated to the dynamics of the *Attalea* community (Fragoso 1997b; 2004). As their population nears a high point in its cycle, more beetle larvae and/or *Attalea* endocarps will be eaten; therefore white-lips will have a severe negative effect on the larval population. This effect eventually cascades down and up to other trophic levels, potentially increasing seed survivorship in following years or reducing the population of parasitic wasps. Synergy with palm reproductive phenology, another non-linear, decoupled factor in the system, can intensify the effect of the white-lips: if a year of high white-lip predation is followed by a year of low fruit production, then local beetle populations may be strongly impacted. However, when white-lipped peccaries are at low or medium population densities, their influence on the system is minor (Fragoso 1994, unpublished data). At this time most endocarps beneath parent trees remain untouched by white-lipped peccaries, and larvae continue to drive the system. Under this scenario most endocarps produce at least one adult beetle, and over 90% of endocarps in palm patches produce beetles. In this case the beetle-larvae population has outgrown any regulatory effect that wasps may have, and most larvae become adult beetles. Since the wasp-parasitoid generation time is probably much shorter than that of white-lipped peccaries their populations can react more quickly to this abundance of food, eventually growing to a level that begins reducing the beetle population (van Noughys & Hanski 2002). Even in the absence of white-lipped peccaries, non-linearity can be introduced by fluctuations in fruit production.

White-lipped-peccary population density appears to fluctuate at intervals of approximately 20–30 years between high or low points (Fragoso 1997b; Fragoso, 2004; Silman *et al.* 2003). During these intervals, a few highs and lows in beetle and wasp populations may have occurred, but we do not know how long individual beetles and wasps can live. In captivity white-lipped peccaries can live 12 to 15 years (Eisenberg 1989), begin reproducing at about 1 year of age, and bear one litter of 1–4 young (normally two). We also know that agoutis live 2–3 years, reproduce once to twice per year and may bear two young but only one survives (Silvius & Fragoso 2003; Smythe 1978). We do not know how long an adult bruchid beetle survives, but we do know that eggs laid on an endocarp take approximately 6–7 days to hatch, that first-instar larvae probably take a few days to penetrate to the endosperm, and the beetles remain as larvae from 3 months to a year (and sometimes up to 2 years) before pupating within the endocarp and emerging as adults (Silvius 2002). Assuming that like many beetles the adults begin searching for mates soon after emergence and reproduce within the same year, then we see that the beetles have a very short generation time, and in comparison to the other organisms described above, an extremely high reproductive output. Following a similar logic for a small invertebrate parasitoid of the beetles, we would predict them to have very high reproductive outputs; for example, we know that 4 to 19 wasps may emerge from one endocarp (J. M. V. Fragoso, personal observations), suggesting that a female lays many eggs at one time. Interrelating this information leads to the prediction that wasp population growth tracks the beetle larvae in a time-lagged way. However, the wasps may eventually exert a strong predation pressure on the beetle population, which begins to decline. Since white-lips are decoupled from the system, their population dynamics are unaffected by those of *Attalea*, beetles and wasps, but they can strongly influence the beetles and wasps during high points in their population fluctuations. These population-level interactions produce time-lagged responses from the various trophic levels, and these may be linear or non-linear depending on whether a strongly interacting organism is coupled or decoupled from the system.

Van Noughys and Hanski (2002), working with a more limited set of organisms, no vertebrates and fewer trophic levels, observed that populations of two parasitoid species of a herbivorous insect fluctuated in response to the population of their prey species. They also found that the dynamics of one interacting pool of organisms were decoupled from other spatially distinct pools. The parasitoids depressed the population of their prey, eventually causing the local extinction of the herbivore. These observations are very similar to what we predict to occur in the *Attalea* system for beetle and wasps.

Large mammals because of their size can have major impacts on the physical structure of habitats, rates of ecosystem processes and the diversity of communities (Sinclair 2003). For this reason many researchers have suggested that large

mammals can exert significant influence on other elements of the communities to which they belong (see Terborgh *et al.* 2001). There is debate as to whether top predators are capable of exerting strong negative influences on their prey species (Wright *et al.* 1994; Terborgh *et al.* 2001); but several studies show that rodent populations in areas without predators can exist at very high densities (e.g. Adler 1994; 1998; Terborgh *et al.* 2001). On islands without predators rodent populations were 35 times as great as those on adjacent mainland areas of the Guri impoundment in Venezuela (Terborgh *et al.* 2001). On islands without predators and with high populations of terrestrial herbivorous vertebrates, the herbivores' plant-food species declined significantly, and the plant community transitioned into one dominated by species that were not preferred by the herbivores. Terborgh *et al.* (2001) observed a correlation between a lack of predators and possible cascading effects down into lower trophic levels. They did not consider interactions between invertebrates, between vertebrates and invertebrates, and between producers and all of the others. Nor did they consider how the suite of interactions and their outcomes could change with time. The assumption of their study is that the effect of predators, and the other organisms, is constant through time and space, with the only important variable being the presence or absence of a 'key' organism, in their case one that produced significant 'top-down effects'.

Terborgh and colleagues' model differs from the one presented here in that the *Attalea* model is dynamic and the strength or type of outcomes from interaction between species and trophic levels exhibits fluidity in both linear and non-linear fashions. In other words, a key species at one time (e.g. white-lipped peccaries) may be a passive 'rider' or even completely lacking at another time (or place). This temporarily missing or weakly present element may not be unusual in such systems, as long as their influence or a similar one returns to the system before it flips completely into another ecological state. Thus, I predict that the strength of top-down or bottom-up effects is a function of sampling time and spatial scale and location of the study. In effect, one should consider the stage of assembly of the local community when isolation occurred; differences in these stages, and the organisms that were most strongly affecting community processes, may be partially responsible for the sharp differences in community structure found on the Guri islands after several decades of isolation. Also important is whether the population is viewed from the context of metapopulations or single populations (van Noughys & Hanski 2002). In non-island situations, where populations are not separated from one another by impermeable barriers (e.g. extensive water bodies for terrestrial species), long-distance dispersal eventually occurs between areas, and this re-sets relationships and the importance of different trophic levels. Thus there can be no constancy in top-down or bottom-up effects even within one location.

In conclusion, the discussion of whether cascades occur in high-diversity terrestrial systems, and whether they affect community structure, may benefit from

a shift in our perspective on trophic interactions. If we view them as short-lived, variable and dynamic, we may see that cascades often exist at one location and time, but that they may be different from those occurring at the same location at a different time, or a different location at the same time, still with the same organisms. The pattern of interactions is driven by different species depending on who is at a population high, and on the scale of measurement of the study. For example, white-lipped-peccary population highs occur at intervals of 20–30 years, and thus they drive the system at this scale. Beetles drive the system at the 8-year scale and wasps at the 6-year scale, based on a logic of longer lifespans described above. Because agoutis and squirrels can switch their diet their populations are unlikely to be driving the system. But if their populations explode (as in the Guri dam case) then the potential is there for them to be drivers.

Acknowledgements

This paper is dedicated to the memory of John F. Eisenberg, whose insatiable curiosity stimulated much of the research and speculation about both plants and animals contained in this paper, and to C. S. 'Buzz' Holling, who introduced me to large-scale, lumpy approaches to ecology. I thank Kirsten M. Silvius for letting me know when my logic was unsound, and for critical reviews, thoughtful suggestions and insight into the functioning of the *Attalea* system. Without Michelle Pinard's graciousness this paper would not have been published. I also thank Jerome Chave and Dan Wenny for their quick and meaningful reviews.

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