Linking plant mediated nutrition cycle to seed disperser activities

Seed dispersal can play important roles in how plants are spatially distributed at different scales. While some processes may remain important across scales, others may be prominent only at particular spatial scale.

Seed dispersers such as frugivorous birds or mammals can carry seeds away from their parent tree and deposit them elsewhere. How these dispersers select these resources are complex and mediated through both plant and animal traits (*I will have some question here*).

Once the seeds are dispersed, they can establish them as seedlings if both the habitat is suitable and they escape seed predation. Thus, only a proportion of seeds are likely to become seedlings. While, the rest are not successful, some of them can still contribute their nutrition to the seedlings through decomposition. Such processes are likely to happen at small spatial scales.

Seeds, once deposited are in the neighborhood of adult trees. Adult trees can impact seed mortality by attracting seed predators. As, seed disperses fail to consume fruits, they would drop near the parent tree and attract predators. However, these fruits are also rich in nutrients. As they decompose, fruits can provide essential nutrient like phosphorous to seedlings. If the neighboring adult trees are leguminous plants, seedlings may further benefit from nitrogen fixation. Such processes are likely to occur at larger scales.

Thus, seed dispersers can play important role in how plants are spatially distributed. While they can effectively carry seeds, their failure to do so can also trigger other ecological processes that can have important impacts.

I, therefore plan to study how dispersers can influence seedling recruitment by influencing both their mortality through predation and survivability from nutrient cycling.

Nutrients

Predators

Trees

Dispersers

Seedling

Seeds/Fruits

Fig: A schematic describing how seed dispersal by animal seed dispersers can influence seedling fate. Dispersers can bring seeds to the right habitat. However, not all seeds will germinate. While some are predated, others can decompose to provide soil nutrients. These are small scale processes (dashed rectangle). Dispersers can also play important role in shaping the neighborhood of seedlings. The neighboring adult trees can influence seedlings by attracting predators or influencing the nutrient cycles. One major way this can happen is through fruits that failed to disperse. These are mostly larger scale processes (solid rectangle).

I therefore predict that

1. Disperser moves searching for fruits that provide maximum reward per unit effort. Fruit rewards would be trait based, that matches disperser traits. For instance, large birds looking for larger fruits. I therefore predicted that the spatial pattern of trees on large scale would match disperser movement. (This is based on the disperser-tree interaction, the dashed arrow)
2. On contemporary time scale, disperser defecates and deposit seeds (seed rain). Such shadows can occur under roosting, nesting or feeding sites. These spatial scales are smaller. I therefore predicted that at smaller scale, pattern of seed shadow should match disperser roosting, nesting or feeding activities.
3. Some seeds would decompose and fail to germinate. Such seed pools would be replenished with fruits falling from nearby adult trees. I predict that the decomposing seeds will add important and limiting nutrient like phosphorous that can play vital roles. These processes are small scale.
4. Additional net benefits can be accrued in the neighborhood of adult plants. These benefits can be gradated. I predict that if the adult plants are conspecific, seeds are likely to be predated. If adult neighbors are mostly heterospecific, seeds can benefit from adult trees adding fruit nutrients to soil. Additional benefits can come in the neighborhood of leguminous plants. These processes happen at larger scales

**Iteration 2**

Tropical forests are rich in biodiversity, with multiple interactions like competition, mutualism and predation shaping the communities. Among, community members, there can be species that play important roles in maintaining biodiversity and ecosystem functions. Tropical trees are among the important members of tropical communities. They can provide nutrition to animals, and maintain critical nutrient cycles. Few species of tropical trees can have significant roles. For instance, tropical palm trees constitute a large portion of the plant community. Studies have shown palms limit seed recruitments under it through limiting light. But, at the same time it contributes resources to the frugivore guild. But little is known about their contribution to nutrient cycling. Palm fruits and leaves can be particularly rich in phosphorous, a limiting resource in tropical forests. Therefore, palms can create these small nutrient hotspots around them where shade-tolerant and phosphorous limited species can particularly thrive.

Likewise, leguminous plants are equally abundant in tropical forests and influence plant and animal communities through the before mentioned ways. However, not much is known on their role on light limitation or food resources to frugivores. It is likely that they may not significantly limit light if they were canopy plants. On the other hand, animals might avoid these fruits for their toxic chemical content.

In this study, I would be looking at the ecological roles of these two important tropical plant groups.

1. I particularly hypothesize that frugivores prefer palms and avoid leguminous plants relative to their abundance and habitat use. I therefore predict that the seed rain would have more palm seeds and fewer leguminous seeds than expected from disperser’s habitat use. I also predict that seed diversity around the palm trees would be higher compared to random locations. I predict the opposite for leguminous plants.

Study design:

For this, I plan to estimate habitat use by potential dispersers, and calculate if the seed rain generated by them is as expected or not. This spatial coverage potentially can inform seed rain hotspots in the entire study area.

1. Palm and legume litter will supply nutrients at small scales through litter fall. I therefore predict nutrient hotspots around them compared to random locations.

Study design:

For this study, I plan to estimate litter quality and quantity from under the palm, legumes and controls. This spatial coverage can potentially inform nutrient hotspots in the study area at a small scale.

1. Seedling will establish, survive and grow significantly in these hotspots. Therefore, I predict under controlled conditions, these responses will be higher than otherwise. I particularly predict that phosphorous limited seedlings will have better responses in controlled conditions under palm. Likewise, I predict nitrogen limited seedling will have better responses in controlled conditions under legumes.

Study design:

For this study, I plan to do green house experiments where I will simulate soil conditions under palm and legumes and random locations, controlling for light limitation and predation. This can inform, if these seed rain and nutrient hotspots are viable for some species depending on their competitive and stress enduring abilities.

**Iteration 4**

Seed dispersers play vital role in generating a seedscape. Several factors can influence their functions, that can vary across scales. For instance, the movement of the dispersers after a feeding bout can create a spatial seed shadow around the parent tree. The decision to move in a particular way itself would depend how other resources are distributed in space and time. However, there is a dearth of literature that integrates animal movement with different stages of seed dispersal.

Seed arrival plays a critical role in the emerging seedscape. Plants can be limited by where, when and how many seeds arrive. As seeds move using their biotic disperser, they may or may not reach particular locations depending on animal habitat selection. Seeds may also not reach particular sites if the fruiting plants did not produce enough seeds. Thus, seed arrival depends on both on the number of seeds available to be dispersed and the animal decision to go to particular locations.

Post arrival, seeds further go through other biotic interactions. Seeds can be predated, attacked by pathogens, or moved further by secondary disperser. These processes again will depend on factors such as seed availability and predator or pathogen choices. Predators (or pathogens) can simply choose based on the availability of seeds, as they move randomly through the habitat. Or else, their choices can be contingent on other seed properties, such as size, nutrition quality etc. These processes can strongly influence how seedlings eventually recruit to saplings.

Defaunation of tropical forests can influence these processes by affecting animal densities and their movements. In hunted forests, there may not be enough dispersers. The remaining individuals may move in manners to reduce risk of hunting. Likewise, large seed predators can be selectively hunted, leaving fewer seeds removed from near the parent tree. This in turn can cause increase pathogen attack on seeds as they respond to increased densities of fruits.

Here, I look to integrate animal behavior and movement with how and where seeds arrive, removed, predated and then recruited as seedlings.

**Null hypothesis 1**: Seed dispersers choose fruits based simply on their availabilities, and then deposit them randomly in the landscape

**Alternate hypothesis**: Fruits are chosen not only based on their availabilities, but also other traits such as size and nutrition quality. Animals move non-randomly while foraging for them

**Prediction**: I therefore predict that the seedscape generated will be non-random and determined by the combined effect of fruit availabilities, traits and animal movement

**Method:** Not quite sure currently, but dispersers carry most seeds only up to few meters (<15 m) from the parent tree. Therefore, the movement decisions dispersers take immediately after a feeding bout are crucial. If in a study plot, I visually observe the movement decisions of dispersers (primates, birds) after they feed and quantify it, it can be informative. These movements can be compared to a null model where animals moved from one abundant resource to another (regardless of other fruit traits). I plan to use resource selection functions that I am learning in Taal’s class. In a simulated model, I can assume animals moved randomly after they fed on a fruiting tree. I can use this movement and the gut retention time to generate an expected seed shadow around the parent tree. This can be then compared to the actual movement data and the observed seed shadow around the parent tree.

**Null hypothesis 2:** Seed predators choose seeds based simply on their availabilities, and they randomly forage in their habitat

**Alternate hypothesis:** Seeds are chosen not only on their availabilities, but also other traits like size and nutritional qualities.

**Prediction:** I predict that the seedling scape generated will be non-random

**Method**: Since we are interested in how seed predators like rodents chose seeds, we can use camera traps around natural as well as experimentally laid out seed plots. Seed predation should be higher in areas of high activity/occupancy. I also plan to conduct field experiments to test how pathogens attack seeds/seedlings and if there is an increased density mediated mortality of seedlings in hunted forests.

**Null hypothesis 3:** There is an increased negative density mediated mortality of seedlings in hunted forest

**Alternate hypothesis:** Rather, increased intraspecific competition for resources play a stronger role in hunted forest

**Prediction:** I predict that if predation is controlled for in both intact and hunted forests, seedlings will have poorer growth/survival in hunted forest as they increasingly compete for limited resources.

**Method**: Nutrition addition and pathogen exclosures can be used to tease this apart. If nutrition addition plays a stronger role, adding nutrition can significantly increase seedling growth and survival. If pathogen attack is more important, excluding them can significantly increase growth. This has to be done in both faunally intact and hunted forests.

**Iteration 6**

Tropical forests are among the richest ecosystems of the world. Researchers have long attempted to explain this rich biodiversity. Both abiotic and biotic factors play important roles in tropical forests. It is now recognized that sunlight can play important roles in different life stages of a tropical forest, and plants have developed strategies to adapt to variable supply of this resource.

As most of the sunlight is intercepted by the canopy of mature trees, many plants have evolved seeds, seedlings and saplings that can tolerate low level of sunlight. Such seeds are large with sufficient resources that can withstand stressful conditions and produce longer seedlings. Likewise, the saplings of these plants have thick leaves. On the other hand, some plants have developed strategies to take advantage of the ephemeral sunlight when it reaches the forest ground. Such plants have smaller seeds and can form seed banks in the soil. When the seedlings germinate, they can grow faster and the saplings generally have leaves with higher nutrient qualities.

These strategies play important roles, particularly when the canopy opens up and forms gaps. Tropical forest gaps are an important part of the ecosystems. It leads to changes in the immediate surrounding. There is higher incidence of sunlight and higher temperature. However, studies so far did not find a significant difference in nutrient qualities, attributing with the very dynamic nature of their cycles.

Gaps also influence biotic interactions. Gaps may affect different guilds of dispersers differentially. Gaps may not possess significant predation risk to larger birds and animals, but at the same time may not offer large foraging benefits as they lack large fruiting trees. But smaller animals and birds use forest gaps, particularly if there is proliferation of under-storey fruiting shrubs. However, they also face considerable predation risk in gaps as the canopy opens up. Thus, a disperser’s decision to venture into a gap can be decomposed into multiple components- the probability of coming to the edge of the gap and the probability of venturing into the gap itself. While the former may not significantly vary with different functional guilds, the latter can. This can significantly influence seed arrival patterns.

Moreover, gaps are suitable habitats for lianas. Rodents, important seed predators may use gaps as they seek covers in lianas that proliferate in these gaps. Such lianas themselves can have important direct interactions with seedlings and saplings. They can compete with them for soil nutrients and sunlight. Studies have shown, a large proportion of seeds that arrive in gaps belong to lianas. As such, lianas may benefit in gaps from such arrival events.

With this background information, I plan to ask **‘What roles canopy gaps in tropical forest play in tree communities and how does seed and seedling traits mediate this role?’**

I specifically have the following hypotheses and predictions. I also state alternate expectations if any of the predictions fail.

**Overall these results will play inform how the seed and seedling community is assembled in tropical forest plants under the influence of spatially and temporally varying habitats as gaps**

**Hypothesis 1**: Large animals and birds avoid forest gaps due to lack of food, perches and cover. However smaller birds and animals may still use them as they feed on under storey light demanding fruiting plants. However, both groups use the edges of gaps equally.

**Prediction:** As seed size and disperser body size are positively correlated, I expect that few larger seeds than smaller seeds would arrive in forest gaps. Thus, recruitment of large seed seedlings in gaps is dispersal limited. But I expect no significant differences in seed sizes that arrived at the edges of the gaps.

*However, if this prediction fails, then recruitment of large seeds is limited by post dispersal life history stages*

Also, as gaps may still present predation risks to smaller birds and animals, I also predict that the arrival of smaller seeds in gaps is fewer than expected based on the abundances of fruiting trees surrounding the gaps.

*If this prediction fail, arrival of smaller seeds is simply based on how many fruiting plants are available around*

**Method:** In order to look at the variation of gap use by different functional groups of dispersers, I plan to quantify their daily movements around gaps, which is important for dispersing seeds. I plan to use techniques from movement ecology that can quantify the effect of gaps as attractors or repellants. For this, I plan to have two response variables- **intensity of habitat use** around the gap. This is a static response. I expect intensity of gap use to decrease with increase in body sizes. For gap edges, I do not expect a significant pattern. In the forest interior away from gap edges, I expect intensity of habitat use to increase with body sizes. For this, I plan to use line transects radially pointing out from the gap center. I expect to see fewer large vertebrates during sampling near the gaps, but no significant differences for smaller vertebrates.

*(The other response variable could be* ***daily movement pattern*** *of an important group of dispersers, the white-face capuchin monkeys. This is a dynamic response. For these large vertebrates, gaps will act as points of repulsion, and they would move away from them once they were close to these gaps. Again, availability of fruiting trees near gaps can alter this expectation, and I have to take that in account. I was reading about resource selection function, which is the probability of a resource being used when its available. I think I can test gaps as resources and model their use based on other covariates.*

*I looked up the movebank database and found capuchin monkey movement data, but they are from 2014 and may not be applicable as gaps form and close every year.)*

In order to quantify seed arrival, I plan to set up seed traps in gaps, both at the center and the edges.

In order to quantify if seed arrival is different from expected, I plan to model arrival as the function of abundances of fruiting trees around a certain area about a gap and animal movement (or habitat use). If arrival was a random process, this would simply be a function of fruiting plant abundances and random use of gaps by animals. (*I think this can be used to test the relative strength of each component? If one is held constant to the observed value (say fruiting plant abundances) and the other is randomized, the deviation from the observed pattern can indicate how much non-random use of habitats matter? For instance, I observe that large birds use the gaps with an intensity 0.3, however if their uses were random it should be 0.5 in the gaps and 0.5 at the edges. Seed arrival then could be modelled as some function of intensity in use and abundances to find how much it varies with habitat use changes when abundances of trees is held constant.)*

**Hypothesis 2:** While gaps are unfavorable habitats for specialist soil pathogens due to higher temperature and increased sunlight, they attract generalist seed predators like rodents

**Prediction**: I predict that small seeds that are more vulnerable to pathogen induced mortalities, escape in gaps while large seeds that are preferred by vertebrate predators are predated upon. Thus, recruitment in gaps is post dispersal seed number mediated.

*If this prediction fails, recruitment of large seeds in gaps is limited by seedling stage*

**Method**: To test the prediction that small seeds are more vulnerable to pathogens than larger seeds, conditional that pathogens are present in gaps, I would perform a greenhouse experiment where I would grow seeds/ seedlings of different sizes in soil taken from gaps. I expect to see no significant differences in mortalities due to lack of significant pathogen activities in gaps. On the other hand, I plan to use fungicide in field and use seeds/ seedlings of different sizes. I expect to find higher predation of rodents in gaps in these treatments.

**Hypothesis 3:** The highest proportion of seeds that fall in gaps belong to lianas and contribute significantly towards their regeneration

**Prediction:** I predict that, due to low pathogen activities, liana seeds and seedlings suffer fewer mortalities. Also, as liana seeds are small, they suffer fewer rodent mediated mortalities. Thus, dispersal contributes significantly to liana establishment in gaps.

**Method:** To test whether liana seeds/seedlings suffer fewer pathogen related mortalities than tree seeds/seedlings, I plan to perform a green house experiment. In this experiment, I would grow seeds/ seedlings from lianas and trees in soil taken from gaps. *Any difference in survival between them will support/ did not support the predictions*.