Agent based model description for bark beetle/pine tree system

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Introduction

The western pine beetle, aka WPB, (*Dendroctonus brevicomis*) is a species of bark beetle that is capable of attacking and killing live trees. In the Sierra Nevada yellow pine/mixed-conifer region of California, WPB has been implicated in the deaths of many if not most of the 120+ million trees killed in the 2012 to 2016 hot drought– perhaps the most severe such event in at least 1200 years.

The hottest, driest sites in the Sierra Nevada range were the most susceptible to WPB-induced tree mortality, as were areas with high tree density. Trees are more likely to be water stressed in hot, dry conditions, making them less able to defend against insect attack. High tree density can exacerbate this water stress due to increased local competition for a limited water resource, but high tree density may also directly affect the behavior of the WPB and facilitate their spread. For instance, greater tree density implies a shorter dispersal distance is necessary for the WPB to attack a new potential host. Alternatively, conspecific communication between WPB individuals may be enhanced in denser stand conditions because the plume of chemical communication signals that the WPB produce are be less likely to be dissipated by the wind. Thus, it is unclear exactly how the physical arrangement of trees in the forest affects the spread of WPB, or what scale of tree density is most relevant for understanding their behavior.

We propose to use an agent-based model (aka an individual-based model) to simulate the behavior of the WPB in different forest stand structural conditions. By simulating the activity of biological phenomena at the scale of their interactions– individual beetle agents making decisions about which potential host trees to attack, and having those agents follow simple rules parameterized by what is known about their life history, we can assess the effect of those life history characteristics and the environmental conditions (e.g., forest structure) on the broader patterns of tree mortality that emerge from the local-scale individual interactions.

Main question

How does the spatial arrangement of host trees (including overall density trees as well as their dispersion) in the forest affect the patterns of tree mortality resulting from bark beetle attack?

The model

Each time step represents an opportunity for beetles to move to a neighboring cell. Let's say 10 minutes? That makes 144 time steps per day. The beetle in one cell will move to one of that cell's 8 neighbors with some probability. That probability is determined by a combination of the pheromone communication by beetles that have successfully attacked trees and some indicator of each tree's susceptibility (based on their perceived ability to defend against attacks). With some probability, the beetle will decide not to move and will instead search within some radius and land on a tree within that radius. Depending on how choosy the beetle is, it will land on a random tree or it will land on a tree that is perceived to be weakened (by water stress, for instance). The beetle will attack the tree and, if successful, contribute to the pheromone output of the tree. If not successful, the beetle will die. If at any point there are more than K beetles within a given tree, then all the beetles within that tree reproduce. Offspring develop within the tree for some number of time steps equivalent to 6 to 8 weeks and then emerge to find their own hosts leaving the original host tree to die.

The model comprises four main parts: the environment in which the agents interact, the WPB agents, the ponderosa pine tree (hosts for the WPB) agents, and an environment that describes the phereomone field present during the current time step, and an environment that describes the tree susceptibility field.

The software

The MASON (multi-agent simulation of neighborhoods… or networks… or something) framework (https://cs.gmu.edu/~eclab/projects/mason/) is implemented in Java and it is designed to be very fast (unlike some other agent-based model frameworks). For instance, rather than track 10,000 trees times 10,000 beetles per tree, we track only the beetles that are currently dispersing and then collapse all of the beetle agents that successfully attack a tree into a set of attributes of the tree itself: the number of beetles in the tree, the mean choosiness value of the beetles in the tree, and the standard deviation of choosiness of beetles in the tree. Then, when the next generation of beetle agents needs to be created, the total number and *their* attributes can be defined based on these attributes from the tree.

We build on the HeatBugs program (https://github.com/eclab/mason/tree/master/mason/sim/app/heatbugs) to simulate agents moving in response to a pheromone cue.

Some possible computational constraints

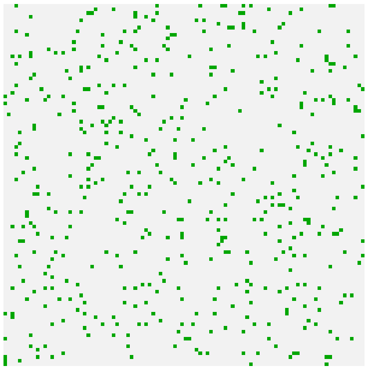
We have some data on extent of tree mortality in 36 different ~40 hectare forest stands (~100 acres each). Each of these stands has ~10,000 trees in it, and perhaps 10,000 beetles might attack a single tree at once. Thus, there are a lot of "agents" to keep track of, which may require some workarounds to build a model within some constraints defined by the computational power we have available.

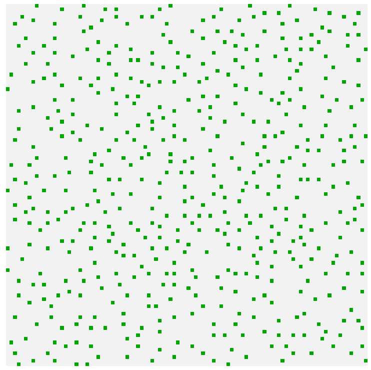
General life history

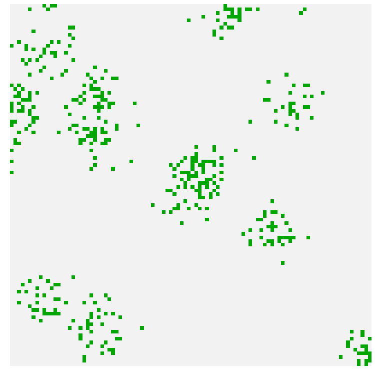
An adult beetle flies to a potential host tree. The beetle determines whether or not to attack the tree based on how well-defended the tree is and how many other beetles are locally available that can be called in to cooperatively attack the tree. If the beetle decides to attack, it bores into the bark and starts releasing aggregation pheromones that signal to other beetles that a suitable host has been found and that they should come and also attack the tree. If enough beetles arrive to the tree, the tree's defenses are overwhelmed and the attack is successful. For the western pine beetle, attack densities anywhere from 100 to 300 attacks m^{-2} have been reported. A cylindrical tree with 40m of trunk and a diameter of 50cm (a fairly large tree) represents approximately 100 m^2 of attack surface so perhaps (on the order of) 10,000 beetles may attack a single tree in order to kill it. If not enough beetles arrive to the tree, all the beetles die. Once enough beetles have arrived to the tree to ensure a successful attack, the aggregation pheromones that the beetles release begin to act as an anti-aggregation pheromone and it wards off additional beetles. This ensures that too many beetles don't lay their eggs inside the tree and compete strongly amongst each other for the phloem resources. If the attack is successful, beetles will mate and lay their eggs inside the inner bark where they develop for 6 to 8 weeks. The development time is temperature dependent (warmer temperatures speed up development) and there are some mechanisms in place that synchronize development speed amongst individual eggs/larvae/pupae. The next generation of adult beetles emerge from the inner bark and disperse to a new potential host, leaving the original host tree to die.

The environment

The environment will be an n x n grid, where each cell is either occupied or not occupied by a ponderosa pine tree host. Each cell can also have an environmental condition that affects the tree's total amount of resin (their inherent vigor and their water stress).







Necessary global variables

Pheromone spatial decay kernel: The decay rate of the effectiveness of the pheromone eminating from each tree. The greater the decay constant, the closer a beetle has to be to a tree to experience the same degree of aggretation or anti-aggregation effect.

Rate of beetle immigration to the study area: Some number of beetles enter the study area. This number will also be used to seed the study area in the initialization step.

Rate of beetle emigration from the study area: With some non-zero probability, beetles will seek trees outside of the study area and will no longer affect the trees in the study area. I think this is a more appropriate choice than using a toroidal surface (where the beetles can move off the left hand side of the environment and reappear on the right hand side)

Total fat store for each beetle: Dictates total distance they can fly

Mean per-capita population growth rate for beetles: Determines how many new beetles result in the next generation when N_t beetles have successfully colonized a tree. Goes into the logistic equation.

Optional global variables

Demographic stochasticity of total resin value (overall vigor) of trees: Represents the standard deviation of the distribution from which the individual tree vigor values are drawn. Note that the value for the intrinsic tree vigor will be part of the calculation of the total resin value along with the tree size as well as the environmental characteristics of the cell that it occupies.

Strength of tree crowding effect: How much does the tree crowding variable for each tree affect that tree's total resin reserves?

Strength of water stress environmental variable effect: How much does the water stress environmental variable for each tree affect that tree's total resin reserves?

Strength of interaction between environmental variable and tree crowding effect: How much does the interaction between crowdedness and the environmental stressor variables matter? Okay to set this at 0 to start implying there is no interaction (i.e., just an additive effect) of tree crowding and environmental water stress.

The agents

Tree

Necessary tree properties

Location: (x, y) coordinates of the tree

Alive or dead: Is the tree alive? Only available for attack if it's alive.

Tree size: Some measure of size. Diameter at breast height is typical (approximate range is 10 to 60 cm). Height might be better, since that's what we can measure using the drone. These are mostly interchangeable though. The key is that the tree size is part of what determines other characteristics: namely, the carrying capacity of the tree, the maximum total resin reserves for the tree, and

Maximum amount of resin reserves for the tree: A measure of the tree's inherent vigor. A big, healthy tree has lots of resin reserves that it can use to defend against many attackers. A water stressed tree cannot muster the resin required to ward off attackers. This will also essentially be the carrying capacity, K, for the logistic growth of the population of beetles that successfully attacked the tree

Pheromone total: The amount of chemical signal the tree is giving off as a combination of the water stress it is experiencing as well as the number of beetles that have currently successfully attacked it.

Optional tree properties

Total amount of resin reserves remaining in the tree: Physically expelling attacking beetles by flushing beetle bore holes with resin is the key defense mechanism of the tree. But this resin reserve is a limited resource that is tapped each time the tree fends off an attacking beetle. When this resin reserve reaches zero, the tree can no longer defend against attackers. If this property is not included, then the resin reserves implicitly "recharge" as beetles attempting to attack die. If this property is included, then we can fine tune the degree to which the resin reserves recharge in future time steps after attacks by beetles (from a downward ratcheting loss of resin to a rapid recharge)

Host versus non-host: The only suitable host for WPB is the ponderosa pine tree (*Pinus ponderosa*). It will be simplest at first to have all trees in the environment be ponderosa pine, but having an ability for some trees to not be ponderosa may allow some interesting iterations of the model in the future (expected dissipation of the pheromone plume based on proximity to a tree of *any* species, not just a host species, to account for wind dynamics around all trees). Additionally, with a random dispersal of beetles to a new tree, some fat stores will be used up by landing on a non-host. This could be important if we dive into random versus chemical-mediated dispersal.

Number of beetles successfully attacking: The number of beetles that have successfully attacked the tree and whose eggs are developing inside of it.

Average choosiness of successfully attacking beetles: The mean value of the choosiness of all of the beetles that successfully attacked the tree. This can be used to randomly generate new choosiness values for the next generation of beetles that emerge from the tree.

Standard deviation of choosiness of successfully attacking beetles: Standard deviation of choosiness of all beetles that successfully attacked the tree. This can also be used (along with the mean, above) to randomly generate new choosiness values for the next generation of beetles that emerge from the tree.

Western pine beetle

Necessary western pine beetle properties

Fat stores: The total remaining amount of fat stores in each individual. This total dictated how far the beetle can fly, and also affects how likely they are to stop and land on a tree (i.e., whether they have the luxury to try to find a more suitable host or whether they need to settle for the tree they are on)

Time steps left to live once on a tree: How many time steps will the beetle live for once it has decided to land on and attack a tree? A beetle can only stay and try to attack a tree for a limited period of time before the tree ultimately succeeds in keeping the beetle out. The life expectancy of the beetle will play a role in whether any given tree's defenses are successfully overwhelmed. That is, we can assess in each time step the total number of beetles that successfully colonized each tree and if it is above some threshold number then the tree will die.

Optional western pine beetle properties

Choosiness: How discriminating is each beetle in deciding whether to initiate attack on a given tree depending on the pheromone output of that tree? A super choosy beetle will be less likely to respond to the pheromone cue and stop to go to the nearest tree. A non-choosy beetle will be highly responsive to the pheromone field.

Initialization

1. Set up the world.
    - Populate with some number of trees in some physical arrangement (random, clustered at different scales, evenly spaced)
    - Assign a tree size to each tree (could come from data)
    - Assign a maximum resin level to each tree based on its size, the environmental variable at that cell (*optional*), the tree's crowding variable (*optional*), and some demographic stochasticity (*optional*)
    - Set the remaining resin level for each tree to the maximum resin level
    - Assign each tree's pheromone output to 0
    - Assign each tree's current number of beetles to 0
    - Update the pheromone field environment based on the pheromone output of all trees and some diffusion range (will start at 0 for the whole environment because there are no successfully attacking beetles)
    - *Optional*: Add an environmental variable to each cell that will dictate the kind of water stress experienced by a tree there (e.g., long-term climatic water deficit for a site, average temperature/precipitiation)
    - *Optional*: Assign a tree crowding variable to each tree based on some local measure of crowding (e.g., voronoi polygon area, number of neighbors within X distance)
    - *Optional*: Assign the mean choosiness of each tree's population of beetles to 0
    - *Optional*: Assign the standard deviation of choosiness of each tree's population of beetles to 0
2. Diserpsal of immigrant beetles to the study area
    - Randomly disperse the immigrant beetles into the environment
    - *Optional*: For each of these beetles, reduce their total fat stores an amount proportional to how far from the edge of the study area the tree is that they landed on. That is, if they had to fly further to get to a tree in the center, that should be reflected in a more decreased fat stores

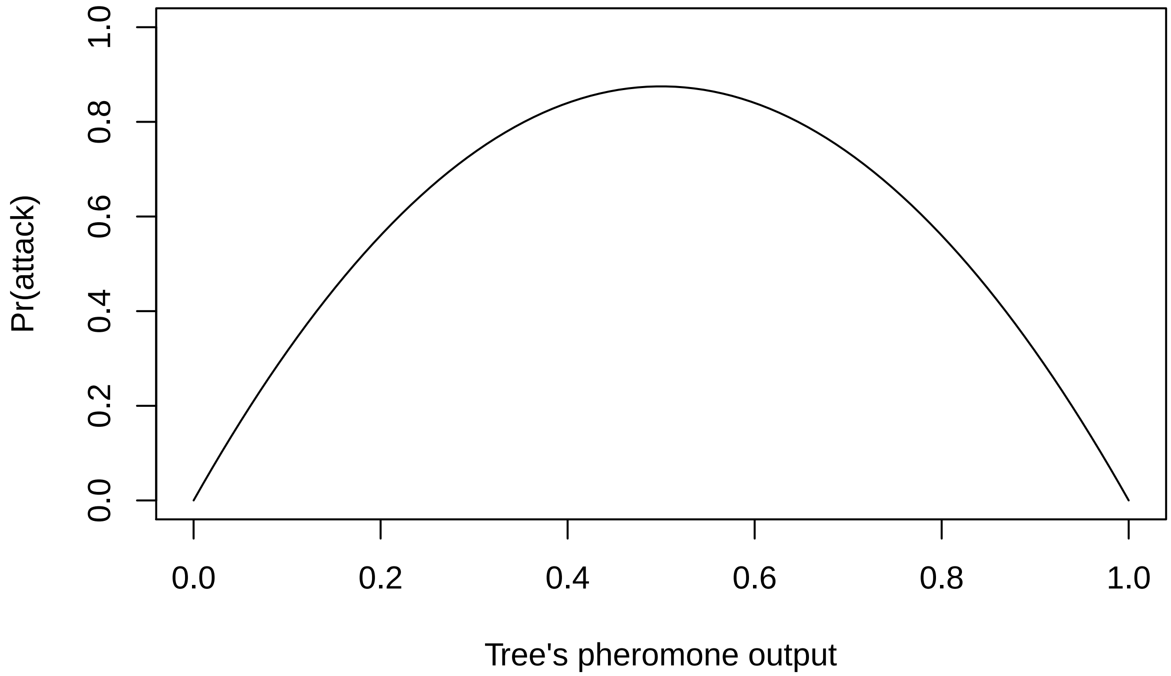
Beetle movement decision process

Each time step, a dispersing beetle will: a) die, b) move to a neighboring cell, or c) decide to stop and search for a nearby tree to land on and attack

1. Can the beetle fly further? If the beetle has no remaining fat stores, it cannot fly any further and it dies.

2. Which neighboring cell has the best pheromone field characteristics?

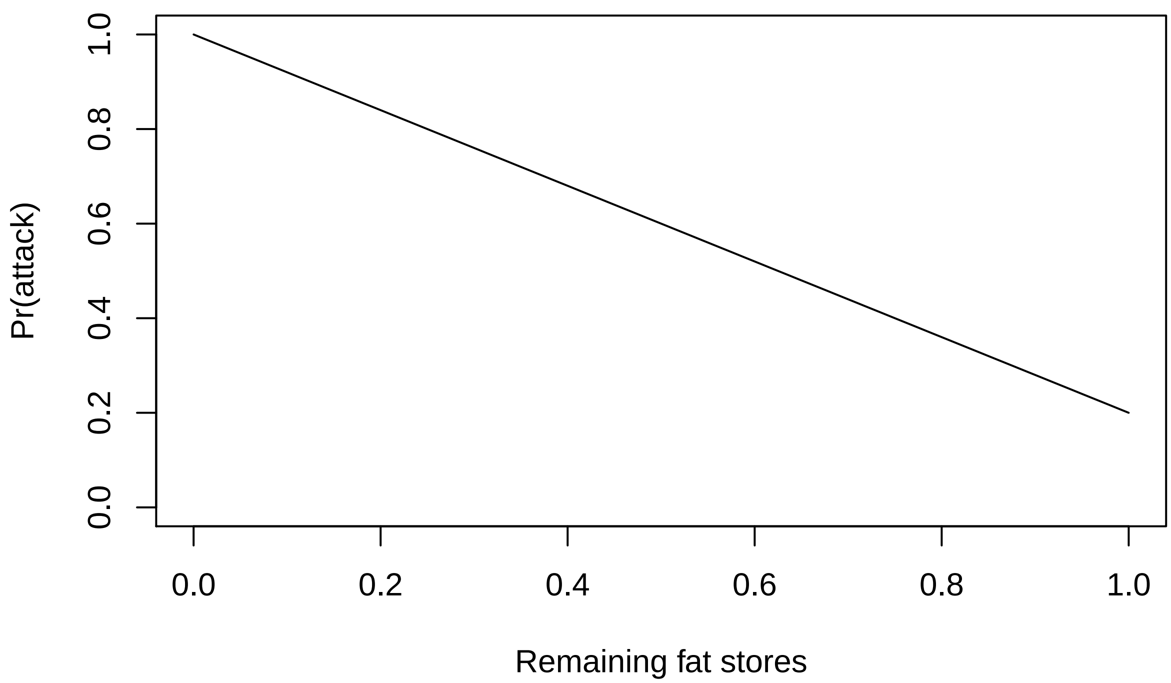
    - No pheromone levels in any cell? Move to a neighboring cell at random.
    - Detectable pheromones in the 8 neighboring cells? Move to the cell with the most favorable characteristics– not too weak, not too strong.



- At an edge of the environment? If the beetle moves off the edge, we stop tracking it (effectively it dies). The beetle may implicitly "re-enter" via the global immigration rate variable.

3. Does the beetle stop and land? The beetle will stop and land on a tree to attack with some probability based on some baseline probability as well as:

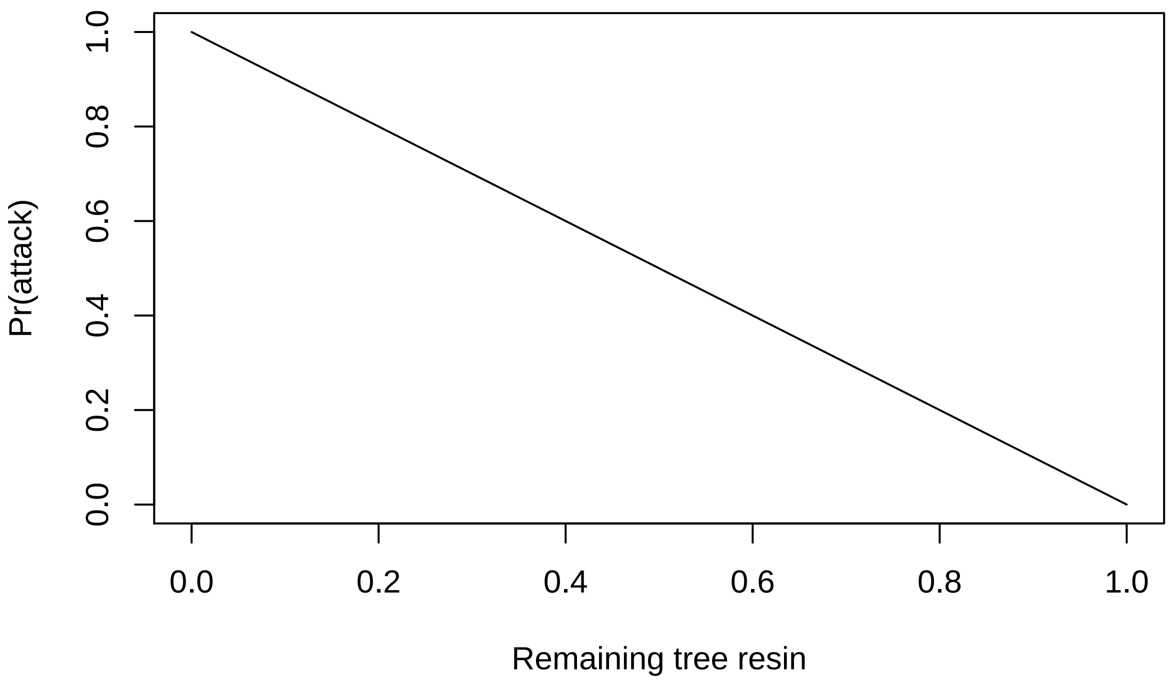
   - The beetle's current fat stores (more likely to attack if fat stores are low).



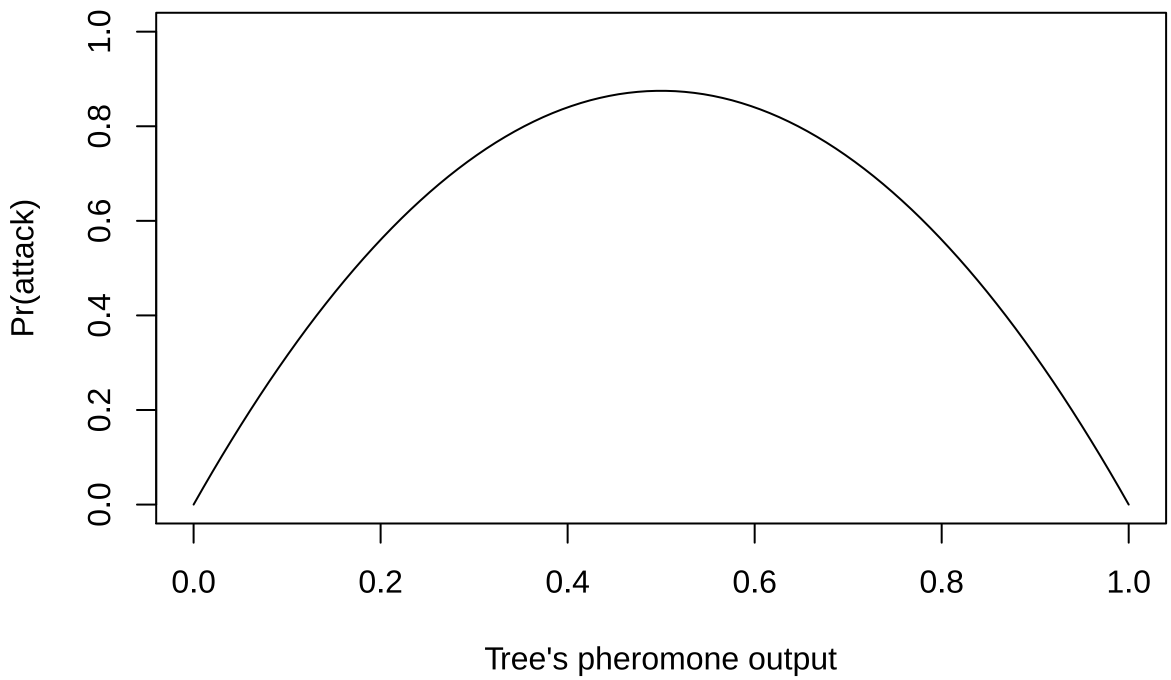
Beetle attack decision process

1. Beetles decide which tree to attack with some probability based on:

- Totally random tree within some search radius (if a tree exists there).
- *Optional*: How choosy the beetle is. A more choosy beetle is more discriminating about which trees it will try to attack and will only attack trees that are weakened. In this model framework, "weakened" might be best assessed as the maximum resin value of a tree, which incorporates both the inherent tree vigor (bigger trees more vigorous, some demographic stochasticity (*optional*), water stress (*optional*), crowding effects (*optional*)). Use maximum resin level of each tree to not confound the effect of
- *Optional*: The tree's current level of resin (the tree's current vigor; beetle is more likely to attack if tree has low resin reserves).



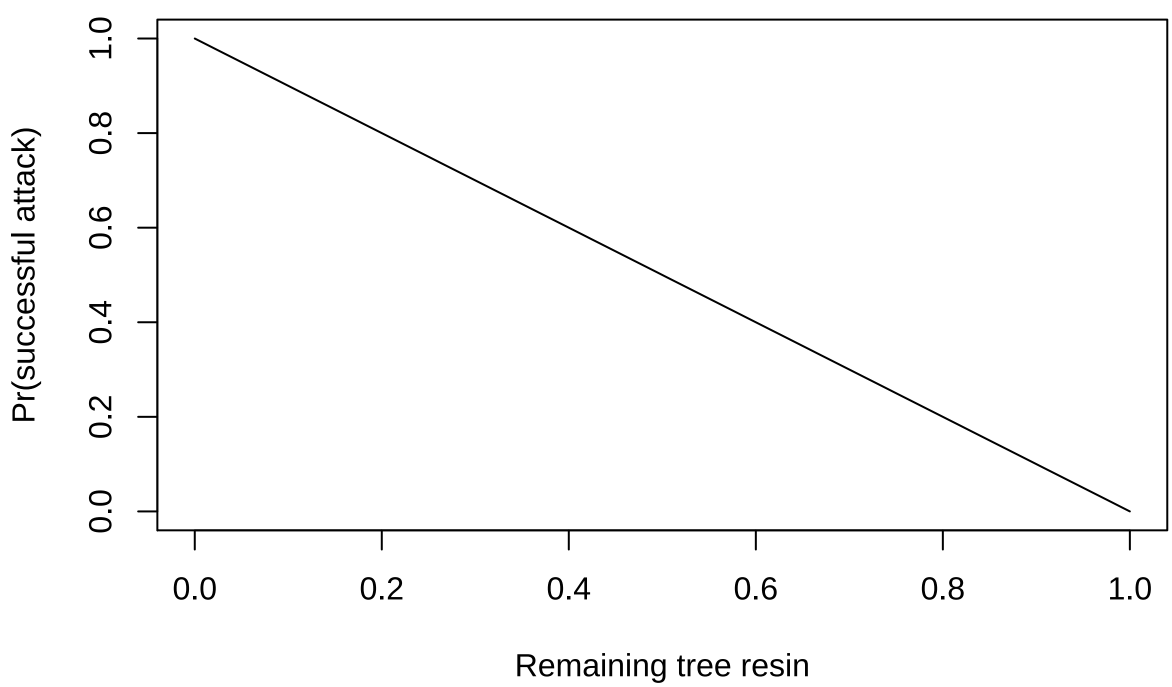
- *Optional*: A unimodal effect of the pheromone output from the tree. Currently, the pheromone effect is only incorporated into the beetle movement behavior. Optionally, we could also incorporate the pheromone level into the attack decision process (which tree to land on, whether to attack the tree)



2. *Optional*: Determine whether the attack is successful.

   In the default case, we let each beetle's maximum possible lifespan in the tree determine whether the attack is successful or not. That is, if the beetle attacks, we assume that it is working at the tree for some limited amount of time (timer starts once the beetle lands). If enough beetles are simultaneously working at the tree, then all those beetles are "successful" and reproduce. If any given beetle's lifespan runs out before enough conspecifics join in on the attack, then that beetle's attack is "unsuccessful" and it doesn't live to reproduce.

   Optionally, we can flip a weighted coin to decide whether the beetle is successfully able to attack the tree. This would be a function of the tree's total resin level plus some noise.



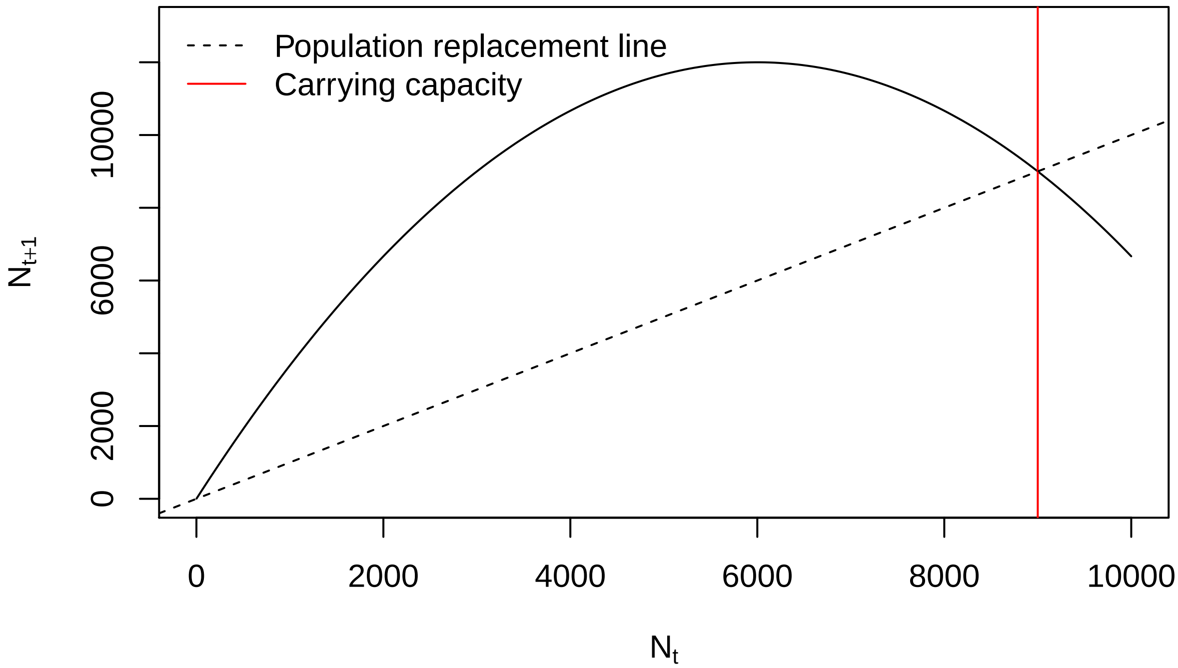
3. In the event of a beetle attack (or a "successful" beetle attack if we are implementing the optional item above), update some tree, beetle, and pheromone field characteristics.
   - When the beetle lands, start its life expectancy countdown. The beetle has only a limited amount of time to attack the tree before it dies– if the beetle is joined by enough conspecifics in that time period, then all the beetles are successful.
   - Add 1 to the tree's total number of successfully attacking beetles attribute
   - Update the tree's total pheromone output (plus 1 beetle's worth)
   - Update the pheromone field for each cell based on the pheromone output for each tree (governed by the number of attacking beetles), the diffusion of that pheromone field around each tree (goverend by the global pheromone spatial decay kernel), and the summation of overlapping diffused pheromone values
   - *Optional*:Update the tree's "mean choosiness of successfully attacking beetles" attribute and "standard deviation of choosiness of successfully attacking beetles" attribute. This can be done using the Welford algorithm in order to update these population values as each new beetle arrives.
   - *Optional*: Update the tree's resin reserves (substract 1 beetle's worth unless it's already 0)
   - *Optional*: Adjust the pheromone field to allow for some evaporation of pheromones in cells that are distant from any tree (whether or not that tree is giving off pheromones itself). This would mimic the wind effect on the pheromone plume in dense versus sparse stands, regardless of what species of tree is present. That is, all trees interrupt the wind and enhance bark beetle communication by allowing the pheromone plume to sit undisturbed.
4. Time step increments to the next movement period

Tree dynamics

1. If a tree is ever occupied by more beetles than it's maximum resin level, then the tree dies and all the beetles within it reproduce.
   - Keeping track of the remaining lifespan of each beetle makes this possible relatively easily. Beetles stay "attacking" a tree until their lifespan runs out. If enough beetles in "attacking" status are on a particular tree, then the tree's defenses are overwhelmed. As the beetle's the lifespan runs out, it dies and can no longer contribute to overcoming the strong Allee effect.
2. If a tree is successfully overwhelmed by mass attack, the beetles develop inside for some number of days (~42 to 56 days). *Optional*: We could also make this development time related to temperature (develop for some amount of cumulative degree days) by having a time series of temperatures associated with the time step progression.
3. Next generation of adult beetles is generated from the tree after development.
   - When the beetle eggs within a tree have fully developed into the next generation of adults, they emerge from each tree as new agents
   - The number of new beetle agents is defined by a population growth equation that can take the "carrying capacity" of the tree into account. If too many beetles happened to land on a given tree and the anti-aggregation phereomone wasn't strong enough to deter them, then the average fitness of all individuals in the tree decreases. If the anti-aggregation phereomone worked properly, beetles should have mostly avoided colonizing a tree that had too many beetles in it.
   - A logistic growth equation seems reasonable:

$$N_{t+1} = N_t + rN_t \left(\frac{K - N_t}{K} \right) \tag{1}$$

   Here, N_{t+1} is the number of adult beetles emerging from the tree, r is the maximum population growth rate (if $r > 0$ then the population is growing), K is the carrying capacity of the tree defined as the maximum resin reserves. It is possible that more beetles colonize the tree after resin reserves are depleted, which would begin to suppress the growth rate of the resident beetle population.



Some final thoughts

There are lots of potential future directions for this framework, especially:

- Incorporating water stress and tree crowding stress (and their interaction) on the total resin reserves for each tree which would help to test one of the hypotheses for why greater tree density leads to greater proportional mortality (lower average vigor per tree makes each more susceptible to attack)
- Incorporating evaporation of the pheromone plume when it is far from any tree, which would help to test one of the hypotheses for why greater tree density leads to greater proportional mortality (large gaps between trees in sparser forests allow wind to disperse the pheromone cloud which would otherwise aid the mass attack behavior of beetles)
- Incorporate the evolutionary dynamic of selection for choosiness into the simulations. That is, assign a choosiness value to each beetles which dictates which local tree a beetle will attack (a choosy beetle attacks trees with lower maximum resin reserves; a non-choosy beetle attacks random trees within the search radius). Let this value carry over into the population of beetles that successfully overwhelm a tree's defenses and live to reproduce. This way, the choosiness of each beetle that is part of a successful mass attack will help dictate the choosiness of the adults that emerge from the tree in the next generation.
- Incorporate the pheromone field into other parts of the model besides the movement behavior (e.g., the decision to initiate attack or not)

If this approach to simulate beetle movement in each time step is totally infeasible, I still see a path forward to working with daily time steps and instantaneous dispersal to a new tree. This would significantly cut down on the number of moving parts I think (144 time steps per day to 1 time step per day; no need to track individual beetle movement). Each tree would be assigned an intrinsic pheromone value based only on the number of beetles currently attacking it, but would also have a "realized" pheromone value that would include the additive effect of pheromone production from nearby trees. Then, during each daily movement, each beetle agent would instantaneously disperse to a tree with a probability representing a joint function of how far away each tree is (more likely to disperse to close trees) and how favorable the "realized" pheromone output is for each tree. There'd be no need to have a pheromone "field" (unless it makes it easier to calculate the "realized" pheromone output for each tree). This might make it more difficult to add in a separate effect of pheromone-mediated movement as well as pheromone-mediated attack decisions.