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Mission Monteverde: Mathematical Rainforest Modeling

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Abstract: The tropical rainforest is one of earth's most diverse and dynamic ecosystems. Tree or branch falls in the forest can open gaps in the canopy, allowing light to reach the forest floor. Pioneer plants are adapted to take advantage of these conditions, sometimes emerging many years after being deposited as seeds. Light conditions change as the gap closes, impacting rates of growth and reproduction.

For the past 30 years, sizes and reproductive outputs of individuals of 6 pioneer plant species have been measured along 5 transects in the Monteverde Cloud Forest Preserve in Monteverde, Costa Rica. Each 500 m transect was chosen to be representative of different conditions in some part of the cloud forest.

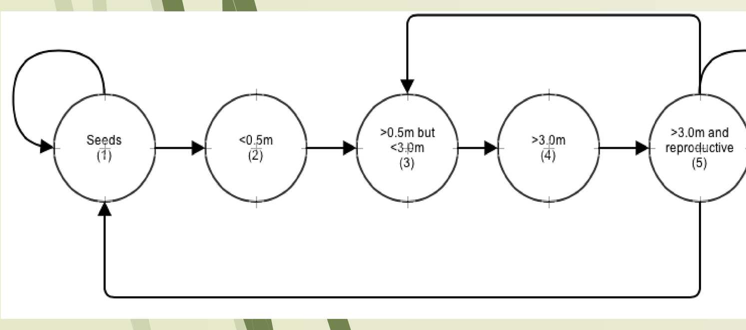
To model the pioneer plant demographics, we classified canopy gaps by age and size and developed a matrix population model that accounts for the differing gap environments. We also created a stochastic matrix model of gap formation and evolution to simulate the dynamics of rainforest canopy gaps. Combined, these models will allow us to simulate pioneer plant population dynamics in the changing forest environment, and to explore how reproduction and growth rate parameters, such as seed predation rates, impact pioneer population dynamics.




a) Clouds rolling through the canopy of the cloud forest. b) Pioneer plant species *Cecropia polyphlebia*. c) A canopy gap lets increased amounts of light into the forest floor. d) Pioneer plant species *Urera elata*.

Introduction: In the 1950's Quakers looking to flee the Korean War draft settled in Monteverde, Costa Rica. They established simple lives, centered around cheese and dairy production. Recognizing the land above them as a valuable water source, they did their best to protect it. Twenty years later through the efforts of The Tropical Science Center and visiting scientists land was purchased and the Monteverde Cloud Forest Preserve was founded.

Our data is from five 500 meter long transects of land that represent the variety of terrains and environments in the preserve. The six focal plant species, *Urera elata, Witheringia meanthia, Phytolacca rivinoides, Cecropia polyphlebia, Bocconia fructescens*, and *Guettarda poasana* are representative of the diverse nature of the pioneer plant species found in Monteverde. Plants that land within two meters of either side of the transect are accounted for in the data and their height, diameter at breast height (DBH), density of the canopy above the plant and seed production (if appropriate). Gaps near enough to the transect to affect light conditions of the plants on the transect were measured and the area of the gaps was calculated for later classification.



Plant Classification Scheme: To organize plant data, species were classified into size classes based on the height of the plant. The figure to the left is a simplified life cycle diagram for the plant *Urera elata*, displaying some possible transitions from size class to size class.

Gap Classification Scheme:

Canopy gaps are classified into 9 stage classes based on the size and age of the gap (see figure 1). Each 500m transects is divided into 5,000 1/10m intervals. Each interval is classified in a stage class based on the stage class of the gap that overlaps the interval. Gaps take multiple years to regrow into mature forest, hence an interval may be in one stage class for multiple time steps.

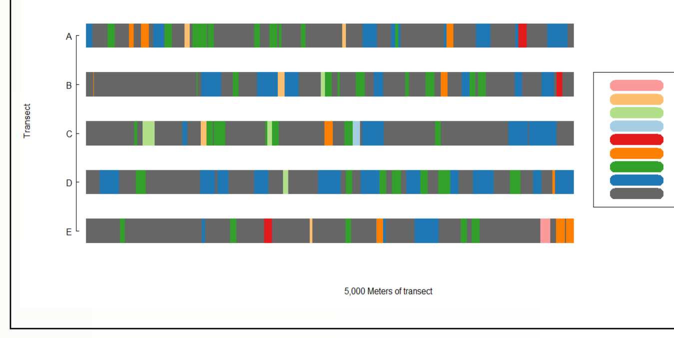
Stage Class	Size (m²)	Age (yr)
1	<5	≤ 1
2	5 - <20	≤ 1
3	20 - <80	≤ 1
4	≥ 80	≤ 1
5	<5	>1 - <2
6	5 - <20	>1 - <5
7	20 - <80	>1 - <10
8	≥ 80	>1 - <15
9 (mature forest)		

Figure 1: Gap classification scheme as determined by gap size and age

Time t: 9999999999111111999922222222222111111999999999911999
Time t+1:1119999999555555999966666666661555559999999999955999

Figure 2: Example of a theoretical gap classification for a 5m long transect

Within the model, each interval is projected forward from its initial gap into its appropriate size class during its building phase years. The 5,000 intervals are combined into a matrix where the rows are the years from 1983-present and the columns represent the 5,000 intervals on the transect. For instance, figure 2 is an example of a 5 meter long transect and represents how gap classification sizes can change between two years.



Snapshot of the forest in 2013: This figure represents the gap data for all 5 transects in 2013. Each color represents a different gap classification (1-9) with 9 signifying mature forest. This figure specifically indicates the variety of gap sizes that are present as the transects progress.

$$\underset{\text{class in time t+1}}{\begin{bmatrix} & \overset{\text{class in time t}}{1} & 2 & 3 & 4 \\ 1 & f_{1,1} & f_{1,2} & f_{1,3} & f_{1,4} \\ 2 & f_{2,1} & f_{2,2} & f_{2,3} & f_{2,4} \\ 3 & f_{3,1} & f_{3,2} & f_{3,3} & f_{3,4} \\ 4 & f_{4,1} & f_{4,2} & f_{4,3} & f_{4,4} \end{bmatrix}} * \underset{\text{time t}}{\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}} = \underset{\text{time t+1}}{\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}}$$

Transition Probability Matrix: After organizing the data, R code was written to extract transitional probability matrices (where each entry displays the probability that something in class x at time t will end up in class y at time t+1). The transitional probability matrix is multiplied by the column vectors holding the population at time t to project the population at time t+1.

Ben and Grace in the Monteverde Rainforest Preserve, July 2014

Transition Probability Matrices:

Figure 3 is the transition probability matrix for *Urera elata* calculated from all of the present *Urera* transitions in the data set. The zero probabilities in row one (blue entries) are due to the fact that only mature plants are able to produce seeds, so no transitions are present there. The red entry (1, 5) holds the average number of seeds one mature *Urera* will produce per season. Note the general linear trend of small size classes to larger size classes. The NaNs in column one are due to a lack of configuration of the seed data.

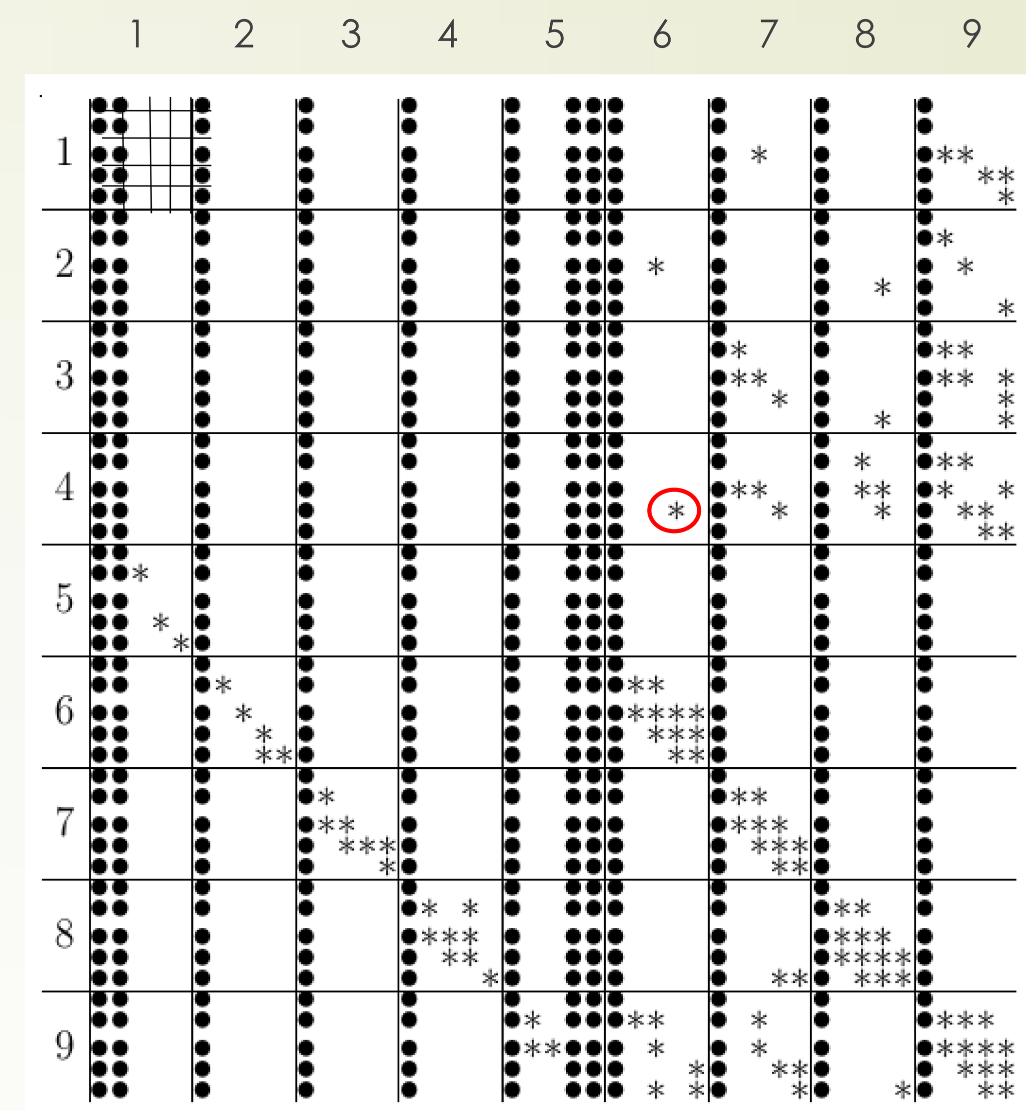
	[,1]	[,2]	[,3]	[,4]	[,5]
[1,]	NaN	0.000	0.000	0.000	10607.540
[2,]	NaN	0.369	0.079	0.008	0.000
[3,]	NaN	0.232	0.653	0.076	0.043
[4,]	NaN	0.004	0.102	0.807	0.188
[5,]	NaN	0.000	0.005	0.092	0.758

Figure 3: Transition probability matrix for *Urera elata*.

	[,1]	[,2]	[,3]	[,4]	,5]	[,6]	[,7]	[,8]	[,9]
[1,]	0.009	0.013	0.006	0.008	0.017	0.008	0.003	0.002	0.010
[2,]	0.000	0.032	0.027	0.000	0.009	0.019	0.013	0.010	0.013
[3,]	0.000	0.012	0.002	0.000	0.017	0.009	0.011	0.008	0.014
[4,]	0.012	0.013	0.008	0.000	0.014	0.011	0.015	0.005	0.010
[5,]	0.979	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
[6,]	0.000	0.931	0.000	0.000	0.035	0.738	0.000	0.000	0.000
[7,]	0.000	0.000	0.958	0.000	0.027	0.014	0.894	0.000	0.000
[8,]	0.000	0.000	0.000	0.992	0.040	0.007	0.003	0.950	0.000
[9,]	0.000	0.000	0.000	0.000	0.840	0.195	0.062	0.026	0.953

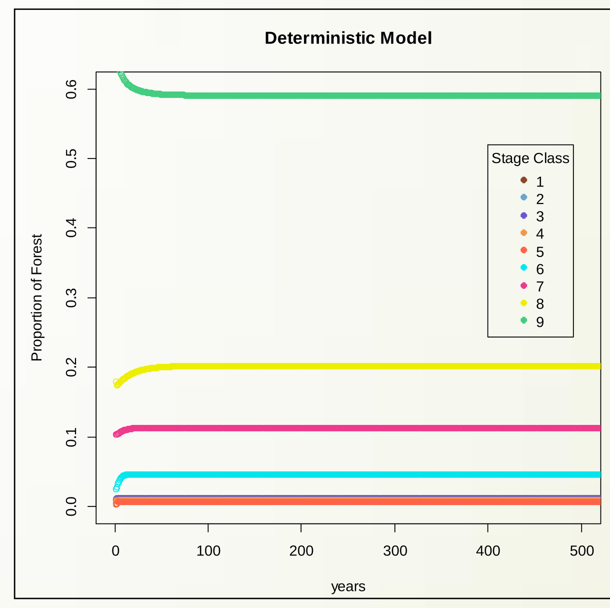
Figure 4: Transition probability matrix for gap structures.

Figure 4 is the overall transition matrix that represents the changing rainforest gap structures. Based on our initial classification, there are some expected patterns (noted in red) in the matrix such as a high probability of transitions from gap classes 1 to 5, 2 to 6, 3 to 7 and 4 to 8, along with a large portion of mature forest 9 remaining as 9. There are also high probabilities (noted in blue) that gap 6 will remain 6, 7 remain 7 and 8 remain 8 due to those structures remaining in their classification for multiple years before returning to mature forest.



Key:
● NA
* Transition probability
(blank) Insufficient data
◯ Example probability of a plant in size class 4 in gap class 6 transitioning to a plant in size class 4 gap 4 after 1 time step

Mega-matrix model: The mega-matrix model accounts for both gap and plant dynamics. The size of the matrix is determined by the number of gap classes (constant 9) multiplied by the number of plant classes (4, 5 or 6). The mega matrix format allows a plant transition matrix to exist within each gap transition. In the mega-matrix above for *Urera elata*, there are columns of NAs that are due to the lack of fecundity data. Also, at this point there is insufficient data to see all possibly transitions, but this mega matrix model provides direction for how our data could be represented in the future.



Deterministic Model: The graph to the left represents the deterministic model for gap structures created from the data set. In the graph, the probabilities are projected forward 500 years.

Future Direction: Future work with this project will attempt to incorporate plant fecundity data into the mega matrix model, enabling the model to be projected forward in time which would giving the liberty to make predictions about the pioneer plant population dynamics in a changing forest environment. One of the pioneer plant species, *Urera elata*, is capable of undergoing reverse transitions (a transition from a larger size class to a smaller size class). This is a pattern that would be interesting to explore further. Once the mega matrix model is more complete, we would like to compute elasticities. This will allow us to identify which transitions are the most important in determining population growth and deterioration.

The team at the Monteverde Rainforest Preserve on completion of a week of data collection, July 2014

A happy little Capuchin monkey

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