

Evolution of vegetation structure

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Goal

To explore how evolutionary diversification through endogenous selection on tree architecture depends on ecological conditions.

Background and motivation

Trees and plants are of key importance for upholding the world's biodiversity, as they provide habitats and serve as a source of food for a great number of different animals. An exceptional case of plant biodiversity is reported by Wright (2002), who found that a tropical rain forest in Ecuador supported 1104 tree species in an area as small as 0.25 square kilometers. Understanding the principles that underpin the emergence of such remarkable diversity is of tremendous importance if we are to preserve our world's ecosystems for future generations.

Trees prominently differ in the architecture of their stems and crowns. In a landmark study, Iwasa et al. (1985) derive evolutionarily stable tree heights and crown shapes by analyzing competition for light. A key finding of that study is that trees invest large amounts of energy into tall trunks, something that can only be understood in the context of their competition with other trees. When growing in solitude or among kin, trees save the effort of producing tall trunks and enjoy higher fitness. Similarly, crown shape depends on how other trees shape the light environment. A further interesting result reported by Iwasa et al. (1985) is that a polymorphic evolutionary equilibrium is reached when a canopy is thin enough, consisting of trees with equal fitness but different heights (Falster and Westoby 2003).

Niklas (1992) describes a detailed tree-architecture model in an evolutionary context. The trees in his model have branches, in contrast to the simple geometric objects and functions usually examined in ecological tree models. Niklas explores the evolution of tree architecture under optimizing selection, maximizing light interception, mechanical stability, and reproductive capacity. While this yields insights into important factors determining tree architecture, the definition of fitness in this model is statically prescribed rather than dynamically derived from an underlying ecological model. The focus on optimizing selection neglects the endogenous environment that is created by the trees themselves, and thereby prohibits the emergence and coexistence of different tree types through frequency-dependent interactions.

While the studies by Iwasa et al. (1985) and Niklas (1992) were major leaps forward, neither account for the process of ontogenetic growth from seedlings to large trees. As tree architectures that are competitively superior in early phases of vegetative growth need not do as well during later phases, the ontogenetic growth process potentially has important evolutionary implications. A first inroad into understanding these implications has been provided by Yokozawa et al. (1996), who studied the coexistence of conic-canopy plants (conifers) and spheroidal-canopy plants (hard-

woods). However, no study to date has considered the evolution of tree architecture in an ecologically realistic model of growing plants.

Research questions

The aim of this research project is to understand the evolution of tree architecture in an ecologically realistic vegetation model that explicitly incorporates ontogenetic growth. I propose two main research questions:

- What is the optimal architecture for a tree growing in solitude, or in a group of genetically identical trees?
- What is the stable monomorphic or polymorphic evolutionarily stable strategy in a given environment?

Explicit consideration of external environmental factors such as wind, fire, grazing, and light will be essential in answering these questions. My focus will initially be on wind and light, since these factors most clearly affect trees differentially depending on their architecture.

Methods and work plan

Metapopulation dynamics

I will investigate a spatially implicit metapopulation model of competing trees. The ecological dynamics will describe a structured population and the evolutionary dynamics will be explored using adaptive dynamics techniques and the canonical equation (Dieckmann & Law 1996; Geritz et al. 1998).

As a first approximation, trees will be assumed to have simple geometric shapes consisting of a spheroidal crown, whose top is attached to the tip of a conical trunk. Each tree will be characterized by three adaptive phenotypic traits: the trunk's apex angle, the relation of crown width to crown height, and the proportion of energy available for growth invested into the crown as opposed to the trunk.

The model comprises two coupled components, with the first describing the age distribution of stands and the second describing the size distribution within stands. Stands only interact through random seed dispersal. Seeds enter a common seed pool and are then redistributed randomly among stands. There is no horizontal structure within stands, meaning that trees are interacting through a "mean field". No edge effects exist in or between patches. Stands are destroyed and regenerated with new saplings according to a probabilistic rate depending on patch age.

A stand's size structure is governed by a diffusion equation describing the vegetation density $n(m, a)$ at age a and plant mass m ,

$$\frac{\partial n(m, a)}{\partial a} + \frac{\partial}{\partial m} [g(m, a)n(m, a)] = -d(m, a)n(m, a),$$

where $g(m, a)$ is the mean growth rate and $d(m, a)$ is the mortality rate. A numerical discontinuous Galerkin method implemented in Matlab will be used for solving this equation.

The physical properties of trees will be modeled with simple relations that try to capture the most important features. Using the three adaptive traits mentioned above, we will try to describe trees as realistically as possible. This project will therefore build on ongoing work by Daniel Falster from Macquarie University in Sydney, Aus-

tralia, former participant in IIASA's YSSP, to make full use of insights derived from his earlier work. By starting from the model he designed, a great deal of effort can be saved.

Light environment

Once the distribution $n(m, a)$ is known, we can calculate the average biomass density at any height. We obtain the light intensity at canopy depth d through the Beer-Lambert law $I(d) = I(0)\exp(-kF(d))$, where $F(d)$ is a patch's accumulated leaf area above depth d , and k describes the extent of light attenuation through leaves. The light intensity above the canopy at depth 0 is $I(0)$ (Prentice et al. 1990). The actual energy intake derived from light interception depends on a tree's photosynthetic rate, which grows linearly with light intensity when the latter is small and is saturated at high light intensities. The sun will be modeled as having an annually varying angle α above the horizon, with light intensity diminishing at small angles. By averaging light interception over the distribution of angles corresponding to a climate zone, the effective annual light interception can be estimated. As a start, just keeping the sun fixed at a given angle should yield interesting results.

Self-shading will be added to the mean-field shading of a stand to study the effects of crown architecture. A two-dimensional ellipse is easier to integrate than a three-dimensional spheroid, and therefore preferable for describing crown shape. We need to determine the distance travelled by light inside the spheroid, and this can be found by basic linear algebra. The leaf distribution within a crown is assumed to be uniform, so that the accumulated leaf area is proportional to this distance. Knowing the light intensity at many points in the ellipse, we can approximate light intensity within the whole ellipse. The distance from an interior point to the edge of the ellipse trivially scales with the size of the ellipse, so that distances can be computed in advance independent of crown sizes.

Only crowns will be shading, not trunks. The light angle is important for how crowns are shaped, as it alters self-shading. In northern boreal and sub-boreal forests conifers are successful, whereas on the African savannah acacias are successful. The maximizing of light interception helps explain these patterns.

Energy allocation

Energy gained from photosynthesis will be allocated to different physiological functions. First, a portion of energy intake will be used for maintenance. The allocation to maintenance depends on the mass of leaves. What is left will be used for reproduction and growth. The relative proportion of growth energy directed to the crown as opposed to the trunk is described by the adaptive trait r which is one. In the model by Daniel Falster, the mass of sapwood, bark, heartwood, and fine roots are all related to the mass of leaves through fixed equations depending on traits r .

A complicating factor is that the energy allocation of trees may vary throughout their lifetime, so more realistically r should depend on tree biomass. The pipe model (Shinozaki et al. 1964 a,b) states that the cross-section of a tree's stem at any height above ground is proportional to the accumulated weight of its leaves situated above that height. This will guide us in devising, as an extension, a more realistic time-dependent model of energy allocation.

Disturbances

Breakage of branches and removal of leaves will occur when trees are affected by wind and grazing. Since we do not explicitly model branches and leaves, we will account for breakage through its secondary effects. There are three essential ways to do this: increased maintenance cost, reduced leaf area density, and increased mortality risk. Grazing implies the investment of energy into producing leaves that will be of no use. Assuming that grazing primarily affects low leaves, it can be described by reducing light intensity at low heights.

Wind affects trees through the breakage of branches and defoliation, as well as through the breakage of entire trees and the removal of stands. Ignoring the effects of turbulence, the wind strength can be thought of as decreasing exponentially with a stand's biomass at a certain height. Knowing the horizontal wind strength at every vertical point, we can approximate the defoliation rate and the breakage rate of branches. Reasoning as in the case of grazing, wind can be simulated as a light filter. This filter will depend on a stand's biomasses at different heights, so that light intensity will decrease more on those horizontal levels on which biomass is low. For the mortality rate resulting from entire trees breaking in a storm, the distance from the ground to their centers of mass is important. A tree with a height deviating greatly from those in its stand will experience a higher breakage risk than other trees, elevating its instantaneous mortality rate.

Catastrophic events like storms and fires will occasionally wipe out entire stands, thereby decreasing the mean disturbance interval in the metapopulation.

Possible extensions

After the successful completion of the proposed tasks, many extensions are possible. For example, instead of using a spheroid, a crown can be shaped like a cylinder, a cone, or according to a profile defined by a function-valued trait. Likewise, a trunk can be modeled as a cylinder or be shaped according to another function-valued trait. However, trunk shapes are less interesting than crown shapes, because the former largely depend on the mass distribution within crowns.

Relevance and link to EEP's research plan

This research project relates directly to EEP's research project on Evolving Biodiversity. It is aimed to yield new fundamental insights in the theory of plant evolution and ecology, and is expected to strengthen EEP's participation in the international collaboration on Evolutionary Ecology Vegetation Models (EEVMs). The anticipated results may furthermore be of interest to researchers working with dynamic global vegetation models.

Expected output and publications

I expect the results of this project to be part of my PhD dissertation; they will also be published as a co-authored research article in an international scientific journal.

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