Ecological disturbance maintains and promotes biodiversity in an artificial plant ecology

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Abstract

A model of plant growth, competition and reproduction in three dimensions was constructed using L-systems to simulate plant growth, ray tracing to simulate sunlight and shading, and a steady-state genetic algorithm to simulate evolution by natural selection. Simulated plant growth conformed to expected trade-offs between, for instance, growing up and growing out. Simulated cohorts exhibited conventional population-level phenomena such as obeying the self-thinning law. Competition between species was simulated under various disturbance regimes. Undisturbed, a K-selected type of plant species dominated at equilibrium. However, under certain disturbance regimes, diverse life-history strategies were able to coexist at equilibrium, and even speciate.

Competition for light is probably the most important environmental influence on plants. Successful plant life-history strategies maximize light capture (amongst other things) despite the presence of competing plants. As it is often too difficult to measure local interactions between individual plants, most ecological studies take a population-level perspective. The local interactions that give rise to population-level phenomena are acknowledged, but their role in competition is often ignored.

Understanding how plant-plant interactions affect the evolution of plant life-history strategies is made more difficult by the fact that plant structure is far more developmentally plastic than that of most animals. Plant morphological plasticity is largely in response to heterogeneity in the local light environment. Of course, just as light availability influences a plant's structure, so a plant's structure affects its ability to capture light. The intimate, reciprocal relationships between a plant's current morphology, the structure of its local environment (including competing plants), its resultant ability to capture light, and any subsequent changes to its structure are highly complex. However, it is exactly these relationships that drive plant growth and determine the fitness of competing life-history strategies.

Understanding plant competition for light in terms of processes taking place at and below the level of individual plants could provide a unifying account for well-characterized population-level phenomena. This type of individual-level understanding could improve our insight into the role of natural selection in shaping plant life-history strategies. Unfortunately, analytic models at the high-resolution required to achieve this are currently intractable. Here we resort to numerical methods, in particular the use of individual-based models.

1. Method

The life-history strategy of each plant was represented by a set of values used to parameterize a simple L-system (a rule re-writing system used to model plant development; Lindenmayer 1968). These values included branching angles and probabilities, branch strength, and age of onset of reproduction. By varying these parameters we explored a wide range of different plant life-history strategies—from what could be thought of as K-selected plant species (e.g., oak trees) to r-selected plant species (e.g., grasses). A plant's growth was simulated in 3-D by applying the parameterized L-system rules to a seed, and repeatedly applying the same set of rules to all elements of the resultant plant structure in parallel.

We have attempted to model the most important processes involved in plant development (shading, photosynthate production, transport and consumption, leaf and branch shedding, reproduction, and death) in the most basic, and wherever possible, principled manner. Sunlight was simulated using a ray tracing approach which calculated the degree of shading experienced by each of a plant's leaves. The photosynthate production of each leaf varied inversely with degree of shading. Photosynthate transport was simulated using a simple diffusion algorithm that slowly propagated photosynthate from leaves (where it is synthesized) throughout the plant. This enabled us to model plants that were developmentally plastic in response to variation in shade such that they "foraged for light". Leaf and branch shedding was simulated as resulting from over-shading and over-loading, respectively. Once a plant reached it's reproductive age, it began to produce seeds at each branch apex. Seed production was modelled as proportional to the amount of photosynthate present at the apex. Plants with no leaves were considered dead.

In many cases, we were interested in modelling a single plant or a single-species cohort. However, in some cases, we were interested in modelling life-history strategy coevolution directly. For these purposes we considered a plant's set of life-history strategy parameters to constitute its genome. Each plant seed contained a copy of its parent's genome subject to a small chance of mutation (reproduction was thus asexual). By applying a steady-state genetic algorithm to a population of plants, we could simulate the heritable variation and competition for a scarce resource (light) necessary to implement a process analogous to evolution by natural selection.

2. Results

First, we explored the parameter space, varying each parameter in order to assess its impact on maximum attained height and effective leaf area (each taken to be rough indicators of plant fitness). We were, of course unable to explore the entire parameter space. However, these preliminary simulations allowed us to ascertain that various expected developmental trade-offs were indeed present. Higher branching angles can increase effective leaf area (by reducing self-shading) but at the expense of reduced plant height and reduced stability. Laying down stronger tissue can reduce branch shedding and thus increase effective leaf area, but at the result of slower growth rate. Increasing age of reproductive onset can increase overall life-time seed production, but at the expense of higher risk of death before reproduction.

By simulating cohorts of plants, we were able to confirm that population characteristics such as density, size distribution and skewness conformed to results from natural plant populations. In particular, model cohorts obeyed the self-thinning law (Yoda et al., 1963), where plant communities evidence a log-log relationship between biomass and density with an exponent of $-3/2$. Our simulated cohorts (when they achieved canopy closure) all achieved exponents between -1.6 and -1.3. It is interesting that these population-level phenomena resulted solely from simulating the competition for light.

By simulating communities comprising multiple species, we were able to explore the capacity for a plant ecosystem to maintain multiple life-history strategies. Here we explored competition between a single tree-like species (K) that could be considered to represent K-selected species, and a single grass-like species (r) that could be considered to represent r-selected species. In an undisturbed environment, K dominated, eventually driving down numbers of r. However, when random ecological disturbance was simulated by sporadically removing any plant within a certain radius of a randomly chosen location, the balance between the two species altered. High or medium rates (0.5 to 5 units of area per iteration) of small disturbances (0.5 units of area per disturbance) led to increased numbers of both r and K. This type of disturbance weeded plants at random, preventing the formation of an unbroken canopy and promoting the growth of young plants. Increasing the size of the disturbances (to 50 units of area per disturbance) led to increased numbers of r, as this species is more able to quickly exploit newly cleared areas, and sometimes drove K to extinction.

Implementing genotypic mutation allowed us to explore the extent to which the life-history strategies of r and K would change over coevolutionary time as a result of their competition for light. The prohibitive length of coevolutionary simulation runs ensured that these explorations were, by necessity, preliminary. We ran 25 replicate simulations, comparing the genotypes of the initial seed population with that of their descendants 6000 iterations later (the equivalent of 100 generations for K), using K-means clustering to detect speciation. There was evidence of selection having acted on the genotypes, as variation within a genotypic cluster was smaller after 6000 iterations. Results also suggested a tendency for r to speciate, forming a third grass-like species with increased reproductive allocation (although the action of evolutionary drift may have been enough to account for the evidence of a third genotypic cluster).

3. Conclusions

Using an individual-based model at a high resolution, we were able to demonstrate that ecological disturbance has an effect on the evolution of plant life-history strategies. Although the model neglects many aspects of plant growth and development, the system evidenced realistic phenomena at both the individual and population level, and demonstrated the competitive coexistence of at least two species. No doubt many aspects of plant biology so far excluded from the model have implications for diversity. However, the current simulation suggests that the impact of competition for light on plant growth and development alone is capable of maintaining and promoting the diversity of plant life-history strategies.

References

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