

An evolutionary model of plant succession

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Goal

To investigate the evolutionary origin of coexisting growth strategies in environments with repeated disturbance.

Background and motivation

While all plants use the common resources of light, water, and nutrients for growth, there is great diversity among species in rates of use and mix of inputs (Westoby 1998). Much of this diversity is thought to reflect the evolutionary diversification of a few key traits in response to frequency-dependent resource competition (Niklas 1997, Westoby et al. 2002). In particular, the evolution of plant height is driven by the need for securing light capture. Taller plants shade shorter plants (but not vice versa), with the asymmetry of this interaction favouring additional expenditure on stems (Givnish 1982, Iwasa et al. 1985). By growing taller than surrounding vegetation, plants thus accrue a significant fitness advantage.

Traditionally, competition for light has been seen to favour evolution of greater height at maturity (reviewed in Falster and Westoby 2003). More general models also describe the evolution of larger adult body sizes if body size confers an asymmetric competitive advantage (Law et al. 1997, Kisdi 1999). However, in environments with frequent disturbance (removal of established individuals by wind, fire, or grazing), selection should also favour the evolution of rapid growth rates and early maturation. Following a disturbance, rapid height growth ensures access to light without requiring a large investment in support structures. Consequently, there may be strong selection for traits that maximise height growth rate, and thereby resource acquisition, in vegetation undergoing frequent disturbance.

Several traits can facilitate rapid height growth. Among species regenerating from seed, these include low leaf mass per area (Reich et al. 1992), low stem tissue density (Enquist et al. 1999), branching patterns emphasising vertical extension (Horn 1971, Pacala et al. 1996), and narrow stem diameters (Falster and Westoby 2005). The same leaf and stem traits that facilitate rapid height growth make fast-growing species inefficient, in the sense that a greater proportion of fixed biomass is lost via respiration, tissue turnover or through mechanical instability leading to mortality (Smith 1976). Low efficiency results in decreased longevity and low shade tolerance (Loehle 1988, Condit et al. 1996), preventing fast-growing species from monopolising environments. Low efficiency should also limit size at maturity (Smith 1976), so that fast-growing species tend both to have shorter asymptotic heights and to be shorter-lived (e.g., Falster and Westoby 2005). The full range of strategies may be found at a single locality. Fast-growing species exploit post-disturbance conditions, but are gradually replaced by slower-growing, progressively taller strategies. This temporal partitioning of access to light, known as succession, is a conspicuous feature of most vegetation types.

Even though ecologists have incorporated successional dynamics into models of vegetation growth (Shugart 1984, Huston and Smith 1987, Pacala et al. 1996, Moorcroft et al. 2001), models accounting for the evolutionary origin of rapid height growth and the diversification of strategies along the successional axis are yet to be developed. Meanwhile, there have been significant advances in techniques used for modelling phenotypic trait evolution under frequency-dependent resource competition (review by Dieckmann 1997). Of particular interest are studies outlining how competition between individuals can promote strategy diversification through evolutionary branching (Geritz et al. 1998, Dieckmann and Doebeli 1999, Kisdi 1999). The aim of this project is to integrate state-of-the-art evolutionary models with models of vegetation dynamics, in order to understand the evolutionary origin of coexisting growth strategies in environments with repeated disturbance.

Research questions

Plants will be considered to differ in two phenotypic traits, (a) a growth trait, indicating higher or lower mass-based growth rates; and (b) a maturation trait, indicating the height at which plants switch from allocation towards growth to production of seeds. The implications for evolutionary dynamics will then be investigated, with the following questions asked.

When strategies are allowed to evolve in one trait only:

1. Is there an evolutionarily singular strategy?
2. Will an initially monomorphic population undergo evolutionary branching?
3. Can multiple strategies coexist in an evolutionarily stable coalition?
4. How does this depend on the values of the other (fixed) traits?

When both traits are allowed to evolve simultaneously:

5. Does this lead to an increase in the number of coexisting branches?
6. Do the dynamics lead to correlated evolutionary divergences (are the height and growth traits correlated across branches?), or is any combination of the two traits possible?

These analyses will then be repeated considering different and additional growth traits, resulting in different and additional trade-offs (as described in the next section). Outcomes will be compared qualitatively:

7. Are all traits correlated, or only some?

Analyses will be carried out for a variety of environmental and spatial configurations. Here I am interested in what features the answers to questions 1-7 depend on:

8. How do environmental parameters, such as disturbance frequency and site productivity, affect evolutionary outcomes?
9. Considering patch connectivity, does a metapopulation structure increase phenotypic diversity compared to a single-patch model? Under what conditions do the results of a metapopulation model converge to those of the single-patch model?

The primary objective during my stay at IIASA is to address questions 1-4. Time permitting, also the remaining questions will be pursued.

Methods and work plan

Evolutionary model

Phenotypic trait evolution will be modeled using the adaptive dynamics framework (Dieckmann and Law 1996, Metz et al. 1996, Geritz et al. 1998). Central to this ap-

proach is the calculation of invasion fitness: the per capita rate of population growth for a given strategy in the environment set by the resident strategies (Metz et al. 1992). If, for a given strategy, invasion fitness is greater than zero then a mutant with this strategy has a chance to invade. Evolution can then be tracked by calculating the invasion fitness of mutant strategies adjacent to the resident. The key question is whether an initially monomorphic population can become dimorphic, which can be assessed using pairwise invasibility plots (Geritz et al. 1998). Analogous techniques are then used to model evolution in a dimorphic populations (Dieckmann and Law 1996, Metz et al. 1996).

Evolution will be considered both within a single patch and within a metapopulation (multiple patches linked by dispersal). For plants growing under repeated disturbance, invasion fitness is given by the cumulative number of mutant seeds produced by a single mutant seed throughout the entire period between disturbances. This number has to be averaged over all possible lengths of such periods in the single-patch model or over all patches of the metapopulation. Several assumptions help simplify calculations (Geritz et al. 1998). The population size of each patch is assumed to be sufficiently large such that mutants experience the local environment as determined by residents, but residents are not significantly affected by the mutant. In addition, evolutionary dynamics are assumed to be slow relative to ecological dynamics. For the metapopulation, the framework of Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001) will be employed. The number of patches is assumed to be large (infinite), with each patch following the same local growth model, but with differences in patch states arising from local catastrophes wiping out a patch's population at different times. These assumptions simplify fitness calculations by removing patch-level stochasticity, a dependence on initial spatial configurations, and the complexities of differential dispersal among patches.

The single-patch model requires an assumption about seed dormancy (related to delayed germination), while the metapopulation model requires an assumption about dispersal rates (related to connectivity between patches). Since many aspects of these two models are formally analogous (in each model, for example, seed output must be weighted with a probability density function for the duration of disturbance-free growth), formal links between the results of single-patch and metapopulation models will be sought.

Local-growth model

The purpose of the local-growth model is to determine the trajectory of growth for a patch containing only individuals expressing the resident strategies, based on the number of resident seeds arriving and on their trait values, and subsequently, for a mutant seed arriving at a given time since the last disturbance occurred. At any moment, the local environment in a patch will be characterised by a single number: the time since last disturbance. We call this the successional state. For each successional state, the local growth model provides vectors describing, first, the rates at which seeds are produced by each resident and, second, the height distribution of each resident.

Space will not be considered explicitly. Within each patch, individuals will be assumed to experience each other equally (mean-field assumption). At a later stage after this summer project, deterministic approximations of spatial processes and patterns occurring within each patch (Dieckmann et al. 2000, Law and Dieckmann 2000) may be used.

The local growth model will be adapted from existing models of vegetation (e.g., Friend 1997, Moorcroft et al. 2001, Woodward and Lomas 2004). While these model the dynamics of plant growth in a simplified manner, they account for the dependencies of production on climate and basic physiology, thereby providing realistic cost-benefit curves.

Traits and trade-offs

Evolution of three growth traits will be considered, each capturing a different type of trade-off thought to be important in structuring vegetation:

1. The first trade-off occurs between leaf mass per area (LMA) and leaf longevity (Wright et al. 2004). High LMA results in greater light capture per unit of biomass, and thus faster height growth, but also in shorter leaf life spans and higher tissue turnover.
2. The second trade-off occurs between wood density and the risk of mortality due to structural instability or attack by pathogens (Moorcroft et al. 2001). Lower density increases the economy of growth at the expense of expected longevity.
3. The third trade-off occurs between vertical growth and the efficiency of light interception, through differences in branching architecture (Niklas 1994). Here a topological branching model (or L-system) can be used to translate mass-based growth rates into predictions about vertical and lateral extension and the distribution of foliage (e.g., Niklas 1994, Prusinkiewicz and Rolland-Lagan 2006).

Schedule

Development of the local growth model will begin during May, prior to arrival at II-ASA. The primary focus in June will be on the development of a simple evolutionary model, with single-trait evolution in a single patch. This will be followed by the development of the full evolutionary model throughout July and pursuit of the research questions as outlined above.

Relevance and link to EEP's research plan

This research continues to extend applications of adaptive dynamics theory to specific ecological systems. There are links with EEP's previous work on adaptive dynamics, adaptive speciation, and on spatially explicit evolutionary models. In the longer term, evolutionary submodels might be incorporated into existing "dynamic vegetation models" used to predict the response of terrestrial biosphere to global change. By highlighting this potential, my project will strengthen the profile of EEP among a broader audience of researchers working in ecology and ecosystem science.

Expected output and publications

This work is intended for publication as a co-authored research article and will also be included in my PhD thesis. Results will be presented at a meeting of the ARC-NZ Research Network for Vegetation Function on "Vegetation Schemes in Earth System Models" in September 2006.

References

- Condit, R., Hubbell, S.P. and Foster, R.B. (1996). Assessing the response of plant functional types to climate change in tropical forests. *Journal of Vegetation Science*, 7: 405-416.

- Dieckmann, U. (1997). Can adaptive dynamics invade? *Trends in Ecology and Evolution*, 12: 128-131.
- Dieckmann, U. and Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, 400:354-357.
- Dieckmann, U. and Law, R. (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34: 579-612.
- Dieckmann, U., Law, R. and Metz, J.A.J. (2000). *The geometry of ecological interactions: Simplifying spatial complexity*. Cambridge University Press, Cambridge, U.K.
- Enquist, B.J., West, G.B., Charnov, E.L. *et al.* (1999). Allometric scaling of production and life-history variation in vascular plants. *Nature*, 401: 907-911.
- Falster, D.S. and Westoby, M. (2003). Plant height and evolutionary games. *Trends in Ecology and Evolution*, 18: 337-343.
- Falster, D.S. and Westoby, M. (2005). Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession. *Oikos* 111: 57-66.
- Friend, A.D., Stevens, A.K., Knox, R.G. and Cannell, M.G.R. (1997). A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling*, 95: 249-287.
- Geritz, S.A.H., Kisdi, E., Meszén, G. *et al.* (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12: 35-57.
- Givnish, T.J. (1982). Adaptive significance of leaf height in forest herbs. *American Naturalist*, 120: 353-381.
- Gyllenberg, M. and Metz, J.A.J. (2001). On fitness in structured metapopulations. *Journal of Mathematical Biology*, 43: 545-560.
- Horn, H. (1971). *The adaptive geometry of trees*. Princeton University Press, Princeton, New Jersey.
- Huston, M. and Smith, T. (1987). Plant succession: Life history and competition. *The American Naturalist*, 130: 168-198.
- Iwasa, Y., Cohen, D. and Leon, J.A. (1985). Tree height and crown shape, as results of competitive games. *Journal of Theoretical Biology*, 112: 279-298.
- Kisdi, É. (1999). Evolutionary Branching under Asymmetric Competition. *Journal of Theoretical Biology*, 197: 149-162.
- Law, R., and Dieckmann, U. (2000). A dynamical system for neighborhoods in plant communities. *Ecology*, 81: 2137-2148.
- Law, R., Marrow, P. and Dieckmann, U. (1997). On evolution under asymmetric competition. *Evolutionary Ecology*, 11: 485-501.
- Loehle, C.F. (1988). Tree life history strategies: The role of defenses. *Canadian Journal of Forest Research*, 18: 209-222.
- Metz, J.A.J., Geritz, S.A.H., Meszén, G. *et al.* (1996). Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. pp. 183-231 *In*: S. J. van Strien and S. M. Verduyn Lunel, eds. *Stochastic and spatial structures of dynamical systems*, Amsterdam: North Holland.

- Metz, J.A.J. and Gyllenberg, M. (2001). How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 268: 499-508.
- Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. (1992). How should we define 'fitness' for general ecological scenarios? *Trends in Ecology and Evolution*, 7: 198-202.
- Moorcroft, P.R., Hurtt, G.C. and Pacala, S.W. (2001). A method for scaling vegetation dynamics: The ecosystem demography model (ED). *Ecological Monographs*, 71: 557-585.
- Niklas, K. (1994). *Plant Allometry: The scaling of form and process*. University of Chicago Press, Chicago.
- Niklas, K.J. (1997). *The evolutionary biology of plants*. University of Chicago Press, Chicago.
- Pacala, S.W., Canham, C.D., Saponara, J. *et al.* (1996). Forest models defined by field measurements - estimation, error analysis and dynamics. *Ecological Monographs*, 66: 1-43.
- Prusinkiewicz, P. and Rolland-Lagan, A.G. (2006). Modeling plant morphogenesis. *Current Opinion in Plant Biology*, 9: 83-88.
- Reich, P.B., Walters, M.B. and Ellsworth, D.S. (1992). Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, 62: 365-392.
- Shugart, H.H. (1984). *A theory of forest dynamics: The ecological implications of forest succession*. Springer-Verlag, New York.
- Smith, C.C. (1976). When and how much to reproduce - The trade-off between power and efficiency. *American Zoologist*, 16: 763-774.
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199: 213-227.
- Westoby, M., Falster, D.S., Moles, A. *et al.* (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33: 125-159.
- Woodward, F.I. and Lomas, M.R. (2004). Vegetation dynamics - simulating responses to climatic change. *Biological Reviews*, 79: 643-670.
- Wright, I.J., Reich, P.B., Westoby, M. *et al.* (2004). The world-wide leaf economics spectrum. *Nature*, 428: 821-827.