

Evolutionary ecology of plant-plant interactions

An empirical modelling approach

Christian Damgaard

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Christian Damgaard
Department of Terrestrial Ecology
National Environmental Research Institute
Vejlsovej 25
DK-8600 Silkeborg
www.dmu.dk

AARHUS UNIVERSITY PRESS
Langelandsgade 177
DK-8200 Aarhus N
Fax +45 89 42 53 80
www.unipress.dk

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Preface

Evolutionary ecology

Evolutionary biology and ecology share the goals of describing variation in natural systems and understanding its functional basis. Within this common framework, evolutionary biologists principally describe the historical lineage-dependent processes, while ecologists focus on the contemporary processes. This difference is summarised in the commonly used truism that evolutionary time scales are longer than ecological time scales. Evolutionary ecologists try to integrate the two approaches by studying variation at all levels, from variation between individuals to variation among communities or major taxonomic groups.

Traditionally the mathematical formulation of evolutionary and ecological problems has differed in one important aspect, which is the description of individuals. In evolutionary or population genetic models an individual plant is expressed relatively to the total size of the population as a frequency, whereas individuals in ecological models are counted in absolute numbers or per area as a density. Mathematically it is easier to work with frequencies. However, for many ecological problems mathematical models expressed in frequencies are too degenerated to provide suitable solutions. For example, it is a well known fact that in a world with limited resources all population growth has to stop at a certain point, however, this fact cannot be expressed in a traditional population genetic model, which implicitly assumes permanent exponential growth.

Integrating ecological data and mathematical modelling

Evolutionary biology has since long been a quantitative scientific discipline. However, there has been a strong tradition in plant ecology to describe different plant communities and succession processes in a qualitative way. Possibly due to the obvious importance of plasticity and the spatial setting, which only lately has started to be incorporated in the ecological models, many field ecologists have felt that mathematical modelling have had little to offer in their attempt to understand the dynamics of plant communities. As a consequence of the lack of communication between field ecologists and mathematical modellers, many ecological studies have been inappropriately analysed with standard linear models and, on the other hand many mathematical modellers have tended to examine parameter space rather than ecological data.

However, there has been a growing interest to make simple and at the same time more biologically realistic plant ecological models, and due to the powerful computers it is now possible to fit ecological data to such simple ecological models with biological meaningful parameters. This will allow a more rigorous testing of various ecological hypotheses and the development of quantitative ecological predictions. Such predictions are highly demanded both by the public, e.g., in conservation management and risk assessment of genetically modified plants, and in order to advance the scientific field of plant ecology (Keddy 1990, Cousens 2001).

It seems that the dialog between ecologists and mathematical modellers, which have proved so fruitful in other areas of ecology, is now also beginning to develop in plant ecology. It is my hope that this monograph will further strengthen the bond between plant ecology and modelling.

Outline of monograph

This monograph will discuss and develop concepts and simple empirical models that are useful in the study of quantitative aspects of the evolutionary ecology of plant – plant interactions and the statistical analysis of plant ecological data. Special attention will be paid to the consequences of the sedentary life form of adult plants and the subsequent strong interactions between neighbouring plants. The monograph will provide an overview of different evolutionary and ecological empirical plant population models and provide conceptual links between different modelling approaches, e.g., spatial individual-based or plant size explicit modelling and the equilibrium conditions of mean-field models. The biological information underlying the discussed models will be summarised. However, it is not the scope to present a full discussion of the biology of plant – plant interactions, which have been treated extensively by other authors (e.g., Harper 1977, Grime 2001, Silvertown and Charlesworth 2001).

The consequences of a sedentary life history with strong interactions with neighbouring plants will be introduced in chapter 1. Single-species competitive plant growth models will be described in chapter 2, where the growth of individual plants is modelled with increasing complexity as functions of plant size, plant density, and the spatial distributions of plants. In chapter 3, models describing the demography of a single plant species, including mortality, reproduction, seed dispersal and dormancy will be discussed and linked to different population growth models and equilibrium conditions. After ecological concepts and models are

introduced in the single-species case, modelling of the interactions between species will be introduced in chapter 4, where emphasis will be on equilibrium conditions and how to predict the probability of different ecological scenarios as a function of the environment. The on-going discussion on the ecological success of different plant strategies will be introduced and put into a modelling context. In chapter 5, the genetic analysis of population structure will be introduced and the effect of inbreeding and finite population sizes on the genetic variation will be discussed. In chapter 6, one-locus sex asymmetric and density-dependent mixed-mating selection models, which are particularly relevant for plant populations, will briefly be introduced, after which the measuring of natural selection will be discussed. In chapter 7, different genetically and ecologically based hypotheses on the evolution of plant life history will briefly be discussed. Finally, in the appendices there is a list of the parameters with a fixed usage in chapters 2-4 (A), an introduction to linear regression technique (B), Bayesian statistics (C), and the stability analysis of discrete dynamic systems (D). Mathematica notebooks exemplifying the methodology introduced in this monograph may be downloaded from my webpage.

This monograph was written as a part of my doctoral thesis at Aarhus University, where I present my scientific contributions over the last decade in a coherent way. Consequently the monograph is a reflection of my views on the issues rather than a balanced account of the field and the cited references are somewhat biased towards my own production.

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