From Plant Traits to Vegetation Structure

Plant community ecology has traditionally taken a taxonomical approach based on population dynamics. This book contrasts such an approach with a trait-based approach. After reviewing these two approaches, it then explains how models based on the Maximum Entropy Formalism can be used to predict the relative abundance of different species from a potential species pool. Following this it shows how the trait constraints, upon which the model is based, are necessary consequences of natural selection and population dynamics. The final sections of the book extend the discussion to macroecological patterns of species abundance and conclude with some outstanding unresolved questions. Written for advanced undergraduates, graduates and researchers in plant ecology, Bill Shipley demonstrates how a trait-based approach can explain how the principle of natural selection and quantitative genetics can be combined with maximum entropy methods to explain and predict the structure of plant communities.

BILL SHIPLEY obtained his PhD in plant ecology from the University of Ottawa in 1987 and now teaches plant ecology and statistics at the Université de Sherbrooke (Qc) Canada. He is author of over 70 peer-reviewed papers in ecology and statistics and *Cause and Correlation in Biology: A user's guide to path analysis, structural equations, and causal inference* (Cambridge University Press, 2000).

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Chance and selection in the assembly of ecological communities

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À Lyne, qui garde mes pieds sur terre
quand ma tête est dans les nuages.

Contents

Preface

"If you can look into the seeds of time, and say which grain will grow and which will not, speak then to me."

Banquo, from Shakespeare's Macbeth

Perhaps this book is my attempt to hold a conversation with Banquo? He would be a fierce critic of the scientific stature of plant ecology, judging from this quote, and I doubt that I could get him to speak at all. He demands, not only predictive ability, but a very fine-grained level of predictive ability. In this book I attempt to develop a predictive theory of plant community assembly. By "predictive" I mean that the theory should be able to quantitatively tell us the relative abundance of each species in the local community under natural field conditions and based on information that can be collected in practice. By "theory" I mean a formal method of both performing such predictions and also of being able logically to deduce why such predictions actually hold in nature based on known biological processes – in this case, the process of natural selection.

I warn you at the outset that the predictive theory presented in this book would not satisfy Banquo even if it were to succeed. Such fine-scale predictive ability – being able to "say which grain will grow and which will not" – is likely forever beyond our grasp. The reason for this is explained in Chapter 2. We must remain forever mute before Banquo. However, this does not mean that macroscopic properties of plant to communities must remain forever beyond our grasp. We might be able accurately to predict such aggregate properties as the relative abundance of various species even if we can never say what will happen with every seed. In fact, counterintuitive as this might sound, such inherent unpredictability at a fine scale might even help us to predict such macroscopic properties. This is the message of Chapters 4 to 7. On reflection then, my conversation cannot be with Banquo but rather with you, the reader.

So who are you? I find it easier to write if I can imagine the person to whom I am speaking and then simply write down the conversation. Let me tell you who I imagine you to be. You are a graduate student of ecology, or perhaps an advanced undergraduate student, who is interested in how ecological communities are formed. No? Then you are a more seasoned researcher in plant ecology who is looking for a new perspective on a question as old as our science. That's not you either? Then you are an animal ecologist, or maybe an ecologist without any taxonomic preference, who is looking for a *really* new perspective on the same old question. If this is who you are then I dearly hope that you will apply these ideas to your own subject area. Perhaps your interests are more theoretical? If so you will also find some new theoretical developments that might interest you. In case you are *not* a theoretical ecologist I hasten to add that explicitly mathematical developments have been separated from the main text by placing them inside boxes. You can certainly read the text – if you want – without wading through these boxes. You will have to endure some equations but you will not need any mathematics beyond basic algebra, some introductory calculus, and the rudiments of statistics. Although not a user's manual, you should find enough practical information (including some code in the *R* language) to be able to apply the ideas of this book to real field data.

Ideas are only scientific ones when they are made public. Public ideas (memes) are ones that travel from brain to brain. Each passage through some grey matter changes the idea, sometimes profoundly but usually only subtly, and this gradual change makes it very hard to say where an "idea" originates or even if two people are thinking about the same "idea". The ideas in this book are no exception. I am constantly surprised when I find one of my own apparently original ideas written, long before I ever thought it, in the writings of people who have influenced me. Properly chastened, such surprises remind me both of how much I owe to others and also of how few original ideas I actually have. I have tried to properly credit such borrowed ideas but, just to be sure, I want to acknowledge my debt to the following people who have each influenced my thoughts on the subject: Robert van Hulst, Paul Keddy, Rob Peters, Martin Lechowicz, Len Lefkovitch and Éric Garnier. Grégory Sonnier (a current PhD student) has been working hard to find new ways of empirically testing many of the ideas in this book. Some of his interesting results have not been included in this book since they have not yet been published, but they have undoubtedly influenced me as well. If anyone notices that I have not properly

acknowledged the ideas of others I can only ask that they let me know so that I can properly pay my debts.

Bernard Colin, Robert van Hulst, Martin Lechowicz, Dany Garant, Roderick Dewar, Bruce Glymour, Daniel Laughlin, Rafael Otfinowski and Grégory Sonnier have read and commented on some of the chapters. Thank you all.