What is a “plant community”? Is it a set of interacting species growing at their environmental optima (Clements 1916)? Is it a random selection from a broader species pool, each behaving idiosyncratically (Gleason 1927)? Is it a group of species each of which represents a particular functional type as defined by particular, morphological or physiological traits (Warming and Vahl 1909): Do species in a community represent strategic “solutions” and “trade-offs” constrained by natural selection (Grime 1974)? Or, as Bill Shipley writes in From Plant Traits to Vegetation Structure, (pp. 17-18), “What do you see when you stand in a forest?...[P]lants belonging to different species...or [a set of] plants possessing different traits? And once one has settled on a definition of a plant community, the next important question is how such a community comes to be, or, in the ecological jargon du jour, how it is assembled. Shipley dispenses with definitions quickly and then
uses statistical models to illustrate why trait-based models of community assembly can have more explanatory power than species-based models of community assembly.

In this clearly written book, Shipley first argues that different species are associated with different environments because of different demographic processes (births, deaths, dispersal). These demographic processes in turn are not caused by species identity but rather are a function of morphological and physiological traits that are subject to natural selection. Therefore, plant communities are best seen as groups of species that have traits (or “strategies”) that are successful in their local environments. Thus, community assembly can be viewed as a process of filtering: the end result of a set of (species with) traits that pass through an environmental filter. The key challenge, and the focus of the bulk of From Plant Traits to Vegetation Structure, is to turn this clear, but qualitative, link between traits and environment into a quantitative framework that can be used to link species that have particular traits to the environment. Shipley has been working on this problem for the better part of 30 years, and his keen insights and engaging style of writing lead the reader easily through a very dense body of theory, models, and data.

Shipley begins this journey with an analogy: the process of community assembly is “nature-as-a-biased-die” (p. 2). The world we see is the result of constantly throwing dice. The face of each die is a species, but the dice are loaded – the traits of each species bias the dice. These biases are expressed differently in different environments, or to continue the analogy, on different gambling tables. Because the environment is constantly changing, the biases are also constantly changing, and the dice need to be re-rolled just to stay in the game (cf. Van Valen 1973). So, consider the dynamics of community assembly as equivalent to playing craps with biased dice. Developing a quantitative model of this endless crooked game requires extensive use of probability theory and statistical mechanics.

The central two chapters of the book (and nearly 120 pages) take the reader through probability theory, Bayesian statistics, information theory, and the “Maximum Entropy Formalism”. Although the mathematics are formidable, the verbal explanations carry the reader along to the central idea: to “find the distribution of relative abundances of species [in a given community] from a [broader, regional] species pool that maximizes the relative entropy [or degree of uncertainty] subject to community-aggregated trait values” (p. 133). Chapter 4 focuses on the details of quantifying relative entropy – the throwing of the dice. Chapter 5 continues by incorporating traits as constraints on assembly – the biases of the dice. Both chapters include helpful computer code snippets in the R language that illustrate how to maximize entropy and simulate crooked craps. (It is somewhat annoying that the code was typeset without any attention to line-breaks. Thus, the important comments (prefaced by the # sign) are broken across lines, and if a reader simply scanned or typed the code as written, it would fail to run because the R interpreter would try to execute fragments of comments.)

A brief 12-page detour lets the reader view an empirical example of community assembly based on data collected during secondary succession after some French vineyards were abandoned (Shipley et al. 2006). The results of the confrontation of Shipley’s model with Shipley’s data are encouraging but limited in scope. The scope would be expanded if more data were available or brought to bear on the problem. Shipley asserts that this dataset is the only one available to actually test whether or not his models actually work. I suspect that combining ecological studies with trait data in floras and emerging databases would yield more chronosequences of vegetation composition, traits associated with the species, and reasonable species pools – at least as reasonable Shipley et al.’s dataset, which itself was not collected to address this model..

The strength of the empirical example is that Shipley et al. (2006) had detailed information on the species pool, the actual species in the sample, and their functional traits. In most cases, however, the composition of the species is not known. One needs precisely that information to determine the relative abundance of species in a given environment that results from filtering of traits! However, we can use the
data we do have on traits and environmental filtering to forecast a species abundance distribution (SAD). A SAD illustrates the expected number of species with \( n \) individuals (on the y-axis) as a function of the number of individuals \( (n) \) per species (on the x-axis). Constructing a SAD requires no information on the identity of each species. In contrast, a relative abundance distribution illustrates the number of species having a proportion \( p \) of all individuals (on the y-axis) against \( p \) (on the x-axis), and does require information on the identity of each species. Chapter 7 explores the application of the Maximum Entropy Formalism to SADs. Although this chapter, as Shipley himself notes (p. 213-214), is not cleanly linked with the rest of the book, it does illustrate well the generality of the maximum entropy approach.

Ecologists have spent decades looking at SADs and constructing and endlessly debating complex models and ecological explanations for the predictions of these models (the current “niche-versus-neutral” debate is only the most recent salvo; see Leibold and McPeek 2006). But SADs are a special case of a general set of “abundance distributions” – including not only relative abundance distributions but also distributions of income, classes of star types, molecules of gasses, and bits of information – that can be analyzed with a common set of equations (Rostovtsev 2005). To me, bringing this paper to the attention of ecologists and expanding on this insight is one of the most important messages of this book. The observation that ecological phenomena are part of a larger, mathematically unifiable framework should encourage ecologists to look beyond the idiosyncracies of individual species or particular ecosystems and towards more general rules that can be used to understand natural phenomena.

Overall, From Plant Traits to Vegetation Structure provides a quantitatively strong and pleasantly readable treatment of contemporary ecological theories of community assembly. Nonetheless, despite an awareness that natural selection works on traits, a longer view of evolutionary dynamics is rarely evident. The emerging field of community phylogenetics (Cavender-Bares et al. 2009) seeks to link evolutionary history with community assembly. Closely-related species often have similar traits, and recent work illustrates that traits with strong phylogenetic (and hence species-linked) signals are filtered similarly along environmental gradients (Pillar and Duarte 2010). Although Shipley does not apply the Maximum Entropy Formalism in this evolutionary framework, the generality of the model provides some cause for optimism. The time spent reading From Plant Traits to Vegetation Structure will be time very well spent in preparing for the next generation of models of community assembly.

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Literature Cited


