

ONE

THE MODEL AS MONSTER

One of the most enduring popular images of science is that of the cinematic mad scientist, scouring a graveyard for body parts from which to build a monster. Dr. Frankenstein is faced with two formidable tasks. First, he and his hunchbacked assistant must gather all of the pieces needed to build a living monster (usually while evading the local constabulary). Even more daunting, he then must find some way to animate the collection of unliving body parts—he must make the monster walk.

Dr. Frankenstein might seem to be a strange role model for scientists, but his method is perhaps a compelling model of reductionist science. In reductionist science, scientists study the various parts of a larger scientific problem or system in the hope that once they understand how all of the pieces work they will be able to put them together and achieve a mechanistic understanding of the whole. Although reductionist approaches are used widely and successfully in many branches of science, including ecology, some critics have claimed that ecological systems are so complex that the reductionist goal of constructing a satisfactory understanding of complex ecological systems from its parts is so difficult so as to be practically unachievable, as well as philosophically unsound (e.g., Peters 1991, Rigler and Peters 1995, Bormann 2005).

In some ways, the task of reductionist science is even more difficult than Dr. Frankenstein's. Most often, a scientific field is not coordinated

by a single person—it is as if we have dozens of hunchbacks scouring the countryside for body parts, but no scientist (mad or otherwise) to coordinate the monster-building. Further, unlike Dr. Frankenstein, we don't usually have an explicit plan for animating the parts into a working theory. Although most of ecological science is reductionist in character, scientists rarely explicitly assess whether a reductionist approach to a particular ecological problem is feasible: Can we collect all the parts needed to build a mechanistic understanding of the problem? Can we animate them into a working whole? If these *are* feasible problems, what parts do we need, and how do we best integrate them into a working theory? Here, I explicitly consider what would be required to build a mechanistic understanding of one specific ecological problem: that of predicting the distribution and abundance of freshwater unionoid mussels (Fig. 1); I then assess the feasibility of this enterprise.

This exercise could be done with any group of organisms. I chose unionoid mussels as an example because they are important in conservation and freshwater ecology—thus, there is a specific interest in understanding the factors that limit the distribution and abundance of this particular group of organisms; and because there is no reason to think that unionoids are unrepresentative of the many other groups of organisms that ecologists try to understand or manage; and also because I enjoy working with the group and am familiar with the literature on these animals.

Our current understanding of unionoid ecology is inadequate in three important ways: (1) studies of single factors have not yet led to an adequate understanding of the importance of *any* single factor in nature, even for those factors that have received much study (e.g., habitat, fish hosts); (2) some factors (e.g., food) have not even been seriously considered as controls on natural populations; and (3) the simultaneous influence of multiple controlling factors, although probably important in nature, has not been seriously considered by unionoid ecologists. That is, both Igor¹ and Dr. Frankenstein have work to do. These problems are not unique to unionoid

1. Although popularly known as “Igor”, the hunchbacked assistant had different names in the various Frankenstein films: “Fritz” in *Frankenstein* (1931), “Ygor” in *Son of Frankenstein* (1936), and “Igor” in *Young Frankenstein* (1974). He didn't appear at all in Mary Shelley's novel. I'll call him Igor.

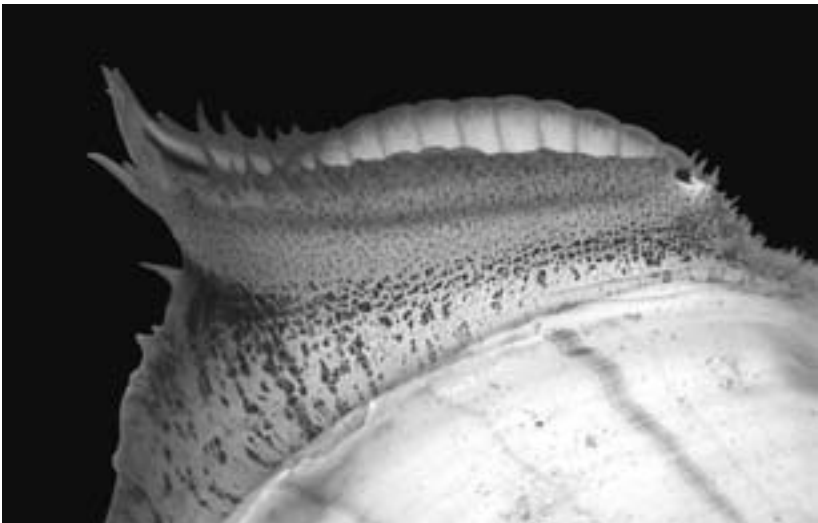


FIGURE 1. Unionoid mussels. Top: Shells of a mixed-species assemblage, showing the lustrous mother-of-pearl for which these animals were prized. Bottom: A gravid female of *Lampsilis cardium* displaying a lure to attract hosts for her larvae. From Chris Barnhart (<http://courses.missouristate.edu/mcb095f/gallery>).

ecology—I do not believe that there is anything especially pathological about unionoid ecology—but are common to many areas in ecology.

Before proceeding, I want to be clear about what, in my view, would constitute a satisfactory theory of mussel distribution and abundance. Ecology is often said to be concerned with predicting the distribution and abundance of organisms, and I take that goal literally. That is, I think we should strive to make quantitative predictions about the probability of occurrence or abundance of individual species based on environmental and biological variables. An adequate theory should be able to do this well; that is, the theory predictions should be close to actual values of these variables in the field.

Ecologists sometimes seem content to reach alternative goals. For instance, I have the impression that some ecologists would be satisfied if we could just list the factors that determine distribution and abundance of organisms. That is, instead of producing an equation of the form

$$Abundance = 0.15 + (0.5 \times food - 1.66 \times predation)^{-|temperature-20|}$$

they would be happy to say that

$$Abundance = f(food, predation, temperature)$$

Alternatively, much of contemporary ecology is focused on understanding individual processes (e.g., predation, disturbance, competition). This focus has been very fruitful in making generalizations across study systems, and I do not question its value. Nevertheless, both science and society often have compelling needs to know the actual distribution or abundance of individual species. Species, and the ecosystems in which they live, are subject to the integrated, simultaneous influences of multiple processes (cf. Greene 2005). Isolated studies of individual processes or a vague outline of the equation that describes the control of distribution and abundance will not meet the intellectual or practical goals that ecologists and society have set for our discipline. Therefore, I insist that, whatever the value of reaching any other goals, a literal, quantitative prediction of the distribution and abundance of individual species is properly a central goal of ecology.

The objectives of this book are to assess the feasibility of producing such a theory to predict the distribution and abundance of unionoid mussels and, to the extent possible, rough in parts of that theory. I see three

possible conclusions of this assessment: (1) we can produce a mechanistic theory (following the reductionist model) that adequately predicts the distribution and abundance of unionoid mussels; (2) we can't produce an adequate mechanistic theory, but we can devise some sort of acceptable alternative that provides useful predictions of unionoid distribution and abundance; or (3) we can't produce adequate predictions by any means and must abandon the problem as scientifically intractable.

I will begin by considering individually the pieces that I think are probably necessary for a working theory of unionoid distribution and abundance, reviewing what we know and what we might ultimately need to know about each part. There are many ways in which to divide up and define these parts, but I will use a five part structure that seems natural to me. The five pieces that I think might be needed to predict unionoid distribution and abundance are dispersal, habitat, fish hosts, food, and predation. Except for the piece on fish hosts, which is needed to account for the unionoids' peculiar parasitic life history, these pieces probably are needed to explain the distribution and abundance of any kind of organism. After I review each of these pieces, I will discuss various ways in which they might be put together. Finally, I will assess our prospects for actually collecting all of the necessary pieces and integrating them into a working theory, a central goal of unionoid ecology.