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Introduction

In this short Element, I consider three questions.

- What are ecological models?
- How are they tested?
- How do ecological models inform environmental policy and politics?

Ecology is a remarkably diverse discipline since it includes physiological, behavioral, population, community, landscape, ecosystem, and evolutionary ecology. It frankly raises the question: In what sense are they all ecology (Cooper, 2003, ix–xiv)? For example, one might argue that ecosystem ecology is really just biogeochemistry – it isn't biology at all. Due to space, my examples of models can only pull from a few of these areas, but I think they are representative of the work that goes on in the science of the struggle for existence. Additionally, in order to understand contemporary ecological models, you must understand many models that appeared in the 1920s through to the 1990s (Kingsland, 1995). So, I pay special attention to this period although I include a variety of more recent models as well.

Ecological models are very often mathematical. I have tried to do justice to the models, which means including some of the mathematics. But, I have also tried to circumnavigate the math when I can. The tool I use to do so are *Technical Discussions*. Therein, I add details that can be skipped if you don't want them. I expect my reader to be either the ecologically curious philosopher or philosophically curious ecologist. Both constituencies are interested in learning about the issues that animate the other, even if I cannot fully explore those issues and thus satisfy those curiosities. Ecologists will find the models familiar, but hopefully the philosophical discussions will aid them in critical reflecting on their scientific practice. Philosophers will find the philosophy familiar, but the models less so and hopefully they push those conceptual issues further in new directions.

To warm you up, consider this. Models involve idealizations, simplifications, distortions of the truth, and the like. If science is searching for the truth, you would think they have no place in sciences like ecology. But they *do*. That is what this Element is about.

1 What Are Ecological Models?

If you leaf through any recent issue of *Ecology*, *Ecology Letters*, *Trends in Ecology and Evolution*, *Journal of Ecology*, among others, you will find reams of models.[1] Ecology includes a lot more than model-building, but it is central to the science. For example, modelers Sarah Otto and Troy Day analyzed the content of the journals *Evolution*, *Ecology*, and *American Naturalist* for the year 2001 (Otto and Day, 2011, 1–2). With regard to *Ecology*, they found that, of 274 articles, 100 percent used models if we include phylogenetic and statistical ones, 35 percent used models to predict results, and 33 percent explicitly present the model equations. That is a lot of models.

Increasing attention has been given by philosophers to the role of models and modeling in science (Bailer-Jones, 2009; Pincock, 2011). Here are two issues concerning the nature of models that have occupied them. First, the term "model" is applied to many different things, including mathematical structures, graphs, computer simulations, and organisms. What are models? Second, in some sciences we talk about theories, but in others we talk of models. This raises the question: How are models and theories related? Ecologists like Richard Levins claim theories just are a "cluster of models" (Levins, 1966, 431). In this section, we will consider both of these questions.

1.1 Metapopulation Models

In order to help us think about what ecological models are, let's begin with an example used throughout the section.[2] Let's consider some metapopulation models from population ecology (Levins, 1969; Levins and Culver, 1971; Lande, 1987; Gotelli, 1991).[3] A metapopulation can be thought of as a "population of populations" that are subdivided spatially into patches, but are connected by immigrating and emigrating organisms. Let P be the proportion of occupied population patches where $0 \leq P \leq 1$. If $P = 1$, then all patches are occupied, and if $P = 0$, then extinction (at least regionally) has occurred. Thus, $(1 - P)$ is the proportion of unoccupied patches. All metapopulation models have this form,

$$\frac{dP}{dt} = \text{immigration rate} - \text{extinction rate}$$

Let c be probability of local colonization, and e be the probability of local extinction.[4] The simplest metapopulation model assumes an "island–mainland"

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[1] And note, these are not journals like *Theoretical Ecology* and *Theoretical Population Biology* where you expect a lot of models.

[2] Due to space, I focus on mathematical models. However, ecology also uses material models as well – see Griesemer (1990a, 1990b); Odenbaugh (2010), Weisberg (2012) for further discussion.

[3] For a presentation of metapopulation models, see Gotelli (1995, ch. 4) and Rockwood (2015, ch. 5).

[4] By local probability, we are considering the probability of colonization or extinction of a patch. We will then consider the immigration or extinctions rates more generally.

structure of immigration. Colonists always come to a patch from some external source sometimes called a "propagule rain." Let's also assume that the extinction rate is independent of regional occurrence of the species. That is, the probability of extinction is wholly unaffected by how many patches are occupied. We then have,

$$\frac{dP}{dt} = c(1 - P) - eP \tag{1.1}$$

Next, let's suppose our metapopulation is not changing; it is at an equilibrium, and so $dP/dt = 0$.

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Just because a system is at equilibrium does not imply it is a *stable* equilibrium. Suppose we have a model of the form,

$$\frac{dP}{dt} = F(P)$$

We find the equilibria by setting $dP/dt = 0$ and solving for $\hat{P}$. But, we haven't determined if the equilibrium is stable. To determine if the equilibrium is stable, we define $P = \hat{P} + p$ and find $dp/dt \approx \lambda p$, which is,

$$\lambda = \left.\frac{dF}{dP}\right|_{P=\hat{P}}$$

The equilibrium is stable if λ, is negative and it is unstable if λ is positive (Hastings, 1997, 91). The rate of return (or away) is determined by λ. Things are more complicated when the model has two or more variables of course.

The equilibrium metapopulation $\hat{P}$ is,

$$\hat{P} = \frac{c}{c + e}$$

Even when c is small and e is large, $P > 0$. Thus, the metapopulation always persists since the immigration rate is always positive given immigrants are always entering from the source.

We can revise our model (1.1) by assuming internal colonization. This means colonists come from other patches rather than a mainland. There is no external source, only an internal one. Specifically, we assume that when P is large, the immigration rate is low because there are few places to immigrate. But, when P is small, the immigration rate is also low because there are few sites from which colonists can be found. We thus alter the immigration term from $c(1 - P)$ to $cP(1 - P)$. Thus, we have,

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$$\frac{dP}{dt} = cP(1 - P) - eP \tag{1.2}$$

At equilibrium,

$$\hat{P} = 1 - \frac{e}{c}$$

The metapopulation avoids extinction when the immigration rate is greater than the extinction rate; otherwise, it goes extinct. It also entails that, if the rate of extinction is non-zero, then the there must be habitats unoccupied.

Both (1.1) and (1.2) assume that the extinction rate is independent of how many patches are occupied. But, we might think immigrants could prevent a patch from extinction. We thus replace eP with $eP(1 - P)$. This is termed the “rescue effect.” Thus, (1.1) can be amended with a propagule rain and rescue effect,

$$\frac{dP}{dt} = c(1 - P) - eP(1 - P) \tag{1.3}$$

At equilibrium, we have,

$$\hat{P} = \frac{c}{e}$$

As with (1.1), the persistence of the metapopulation is assured and all patches are occupied when $c > e$. Finally, we can suppose immigration and extinction are dependent on regional occurrence,

$$\frac{dP}{dt} = cP(1 - P) - eP(1 - P) \tag{1.4}$$

With (1.4), there is no simple equilibrium. If $c > e$, then $cP(1-P) > eP(1-P)$ and the metapopulation increases until all patches are occupied. If $c < e$, then $cP(1-P) < eP(1-P)$ and the metapopulation decreases until extinct. If $c = e$, then we have a neutral equilibrium.[5]

As one more final refinement, consider the work of Russell Lande (1987). Suppose a fraction $(1 - h)$ of patches are unsuitable, and thus cannot be colonized. Thus, h is the fraction that are suitable. Therefore, the colonization rate of empty patches is $cPh(1 - P)$. Assuming internal immigration and no rescue effect, we have,

$$\frac{dP}{dt} = cPh(1 - P) - eP \tag{1.5}$$

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[5] A neutral equilibrium is one where, if the system is displaced from x^*, it does not return to x^*, but remains at the new equilibrium.

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At equilibrium,

$$\hat{P} = 1 - \frac{e}{ch}$$

Thus, $\hat{P} > 0$, if $1 > e/ch$ and $h > e/c$.

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Let P^* be the fraction of habitat originally occupied and h_0 be the original amount of suitable habitat. Our equilibrium for (1.5) is,

$$0 = ch(1 - P) - e$$

We can substitute these values in the equation and rearrange the terms,

$$\frac{e}{c} = h_0(1 - P^*)$$

Since the metapopulation can persist if $h > e/c$,

$$h > h_0(1 - P^*)$$

This is termed "Levins's rule." Metapopulation survival occurs if the remaining number of patches following habitat reduction is greater than the number of empty although suitable patches prior to the reduction.

Carlson (2000) applied Levins's rule to the woodpecker *Dendrocopos leucotos* in Sweden and Finland. He determed that $h_0 = 0.66$ and $P^* = 0.81$. Thus, $h > 0.125$ for the metapopulation to survive. However, he determined $h < 0.12$, which was confirmed by the fact that the populations have been declining rapidly.

Our simple metapopulation models are based on a variety of assumptions. Here are some noteworthy ones.

- The probabilities of immigration and extinction are influenced by the number of occupied patches, but not by their spatial arrangement.
- The local probabilities of immigration and extinction are constants since they do not change with time.
- There are a large number of homogeneous patches.

For actual metapopulations, they are all probably *false*. Spatial arrangement clearly matters, since, the closer an occupied patch is to an unoccupied one, the more likely colonization will occur. Probabilities of colonization and extinction surely change over time. Additionally, the patches differ in their quality, which affects extinction rates.

1.2 What Are Models?

Ecologists use the term “model” in myriad ways, as mentioned earlier. Mathematical structures, graphs, computer simulations, organisms, among others, are all called ‘models.’ One might infer there is no unified account of what models are, but, we can resist this inference. Here is a working definition of the term:

> Models are representations that abstract and idealize.

Let’s unpack it.

First, models have intentional content – they are about what they represent. There are many different kinds of representations; for example, words, pictures, and so on. Models represent their objects by attributing properties to them – by representing them as being a certain way. A model may have an intension, but no extension (or no referent). The intentional content of models can be understood in terms of accuracy conditions – the content of a model is the way the world would have to be for the model to have a referent. A model has this content even in cases in which the world isn’t this way, and thus fails to have a referent. The accuracy conditions of ecological models are often truth conditions, since they are equations that describe ecological systems truly (or not).[6]

Second, models represent their objects by abstraction: they represent their objects by attributing to them a proper subset of the properties that may be so attributed. Suppose I draw a picture of my son Everett, niece Sadie, and nephews Caleb and Jack using a graphite pencil. My drawing does not represent Everett, Sadie, Caleb, and Jack as monochromatic. Rather, my drawing simply does not represent the colors of their clothes, hair, and so on.

Third, models represent their objects by idealization: they represent their objects by attributing to them properties they lack (think of a caricaturist’s drawings). Lots of representations misrepresent their referents, of course. The history of science is chock full of false theories and models. But models are not merely false. Their idealizations are also *useful* (and they might even be approximately true).[7] Successful representation sometimes requires the attribution of

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[6] Truth conditions are a subset of accuracy conditions. For example, pictures may be more or less accurate, but we might not think they express propositions that are true or false. For more on depiction, see Kulvicki (2013).

[7] Idealizations can be useful for one purpose and not for another. Really simple population growth equations in population ecology or single locus, two allele models in population genetics are often of little use predictively. But, they are of great value pedagogically, since they help students learn how to build and evaluate models. Anchoring model evaluation to the purposes for which they are built or deployed is crucial (Odenbaugh, 2005; Parker, 2009).

properties not had by the object represented.[8] Thus, the intension of the term 'model' is abstract, idealized representation. The extension of the term, however, consists in a variety of things that have those properties. That is, objects as diverse as phase spaces, computer code in R, and *Tribolium castaneum* are all objects denoted by the term 'model'.

Our working definition fits metapopulation models very well. First, our models are representations – they represent populations of populations as having various properties like habitat patches where they reside, probabilities of colonization and extinction, and so on. Second, the models abstract from those metapopulations. For example, organisms in those populations compete with one another and our models are silent on this score. They do not say that they don't compete. Rather, they simply do not describe intraspecific competition at all. Third, the models idealize those metapopulations too. They assume that patches are homogeneous, the spatial distribution of patches does not matter, the probabilities of local colonization and extinction are constants, among others. These are all false assumptions, but which provide us with useful analytically tractable equations for thinking about spatial ecology.

Modelers talk of models being built from "assumptions." Sometimes they talk of models "assuming" this and that. Assumptions are the propositions that characterize the model. Mathematician Edward Bender puts it this way,

> Definitions of the variables and their interrelations constitute the *assumptions* of the model. We then use the model to *draw conclusions* (i.e., to make predictions). This is a deductive process: *If the assumptions are true, the conclusions must also be true*. Hence a false prediction implies that the model is wrong in some respect. (Bender, 1978, 4)

This is a shorthand for talking about the structure of models (see Sorensen, 2012).

In this Element, we will discuss mostly mathematical models. Modelers describe models as having variables, parameters, and laws. The variables of a model are those properties that can change. In our metapopulation models, the variable P is the frequency of occupied patches. The parameters of the models are those properties that cannot, or at least do not, change. The parameters in the metapopulation models are c, e, and h. Of course, in the actual world, these

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[8] For discussions of idealization and abstraction see (McMullin, 1985; Cartwright, 1994; Morrison, 2015; Potochnik, 2017; Weisberg, 2012). One might argue that successful models abstract but rarely idealize (Strevens, 2008). For example, it is common in evolutionary genetics to suppose we have an infinite population size that would clearly be an idealization ignoring random genetic drift. However, we could also describe this as assuming a sufficiently large population such that drift can be ignored (Strevens, 2017). For our purposes, we will assume models in ecology abstract and idealize.

properties might change over time, but, in our model, we simplify by supposing they don't. Finally, the laws of the model are laws of "succession" or "coexistence." The former tell us how a system changes over time. For example, $dP = c(1 - P) - eP$ is a law of succession. Laws of succession can be deterministic or stochastic. If deterministic, then, given values of c, e, and h and P at a time, there is there is a one value of P possible for any given time. Similarly, if stochastic, then, given the same conditions at a time, it is possible for P to have more than one value at any later time. Likewise, they can be continuous or discrete. A function is continuous with respect to any interval if it can take any value in the interval; otherwise, it is discrete.[9] The laws of coexistence tell us what values of the properties (e.g., variables and parameters) can be jointly occupied by the system. For example, the equilibrium $\hat{P} = c/(c + e)$ is such a law.

This notion of a 'law' is not the same as discussed by philosophers of science and metaphysicians. First, the laws in ecologist's models are simply generalizations. They need not be exceptionless generalizations that support counterfactuals, as philosophers sometimes put it. And, they may be false. Second, philosophers of biology are divided over what laws are and whether biology has them. Some argue biology has no such laws since biological generalizations are mathematical truisms (Sober, 1997), true counterfactual-supporting generalizations that have exceptions (Brandon, 1997), or that they are the contingent products of evolutionary history and false in some circumstances (Beatty, 1997). Others argue that physical and chemical generalizations have exceptions and are contingent; hence, physics, chemistry, and biology are in the same boat (Cartwright, 1983).[10]

A very popular view of models is what I call the "similarity view" (Hesse, 1966; Giere, 1988; Weisberg, 2012). This view says that a representational device represents an object (if it does) that is similar in certain degrees and respects to the object. In the case of mathematical models, we have a set of equations that refer to a mathematical structure. This mathematical structure when interpreted is then similar in certain respects in certain degrees to the object. It it this interpreted mathematical structure that is the model.[11] Thus,

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[9] It is worth noting that this is an idealization in ecology, since population size is not continuous. But, for some populations, this is approximately true.

[10] In ecology, there is rich debate over ecological laws among philosophers and ecologists (Cooper, 1998; Lawton, 1999; Weber, 1999; Turchin, 2001; Berryman, 2003; Colyvan and Ginzburg, 2003; Mikkelson, 2003; Lange, 2005; Linquist et al., 2016).

[11] The similarity view is related to the semantic view of theories (Beatty, 1980; van Fraassen, 1980; Beatty, 1982; Suppe, 1989; Thompson, 1989; Lloyd, 1994). For an analysis of the equilibrium model of island biogeography using the semantic view of theories, see Castle (2001). For an

model (1.1) refers to the unit interval $[0, 1] = \{x \mid 0 \leq x \leq 1\}$. This mathematical structure may be similar to the Bay checkerspot butterfly's (*Euphydryas editha bayensis*) patch occupancy (Harrison et al., 1988). This butterfly lives in discrete patches that are organized in a metapopulation. Adult butterflies appear in the spring and females lay their eggs on *Plantago erecta*. This host provides food for capterpillars, which feed for a few weeks, and then go into a summer diapause. They return to feeding in December until February, and then build cocoons. *P. erecta* live in Northern California on soil rock outcroppings. The butterfly and host can go out of synchrony with extreme weather like droughts, which lead to local extinctions. However, other patches provide available colonists to immigrate to new hosts in the old patches.

The similarity view faces a problem, which I call "Hughes' worry" (Odenbaugh, 2015, 2018). This problem was first posed by R. I. G. Hughes (1997). Consider our model (1.1) again, $dP/dt = c(1 - P) - eP$. The variable P represents the proportion of patches occuped, c is the probability of local immigration, and e is the probability of local extinction. An object can have a probability of immigration or extinction only if it can immigrate or go extinct. Mathematical objects like real numbers certainly cannot immigrate or go extinct. So, they cannot have properties like a probability to immigrate or go extinct (even if they can have probabilities). Mathematical objects and metapopulations cannot share the properties like *probability to immigrate* and *probability to go extinct*. Therefore, they cannot be similar with respect to those properties. But this implies that the similarity view is incorrect.

One response is that we should we think of the data (e.g., the metapopulation) as a mathematical structure too. If right, then, certainly, mathematical structures can share properties. For example, the numbers 2, 3, 5, 7, 11, 13, 17, 19, 23 and 29 all have the property of *being prime*, but we still have the same problem we started with – how can can the data structure be similar to the metapopulation?[12]

My own view of models is a deflationary one (Downes, 1992; Callender and Cohen, 2006; Suárez, 2010, 2015). Many philosophers of science think

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overview of the received view, the semantic view, and models as mediators in the context of biology, see Odenbaugh (2010).

[12] Here is one way to represent data mathematically. A relational structure is a set of objects D with relations R on them; $M =< D, R >$. Let that be our model. Additionally, suppose the data as a relational structure $M^* =< D^*, R_i^* >$. There might be an isomorphism between M and M^* that is a function f such that $< o_1, \ldots., o_n > \in R$ if, and only if, $f(o_1), \ldots, f(o_n) > \in R^*$. But, at best, we have shown that there is a second-order relation of isomorphism between the two relational structures. There is no R or R^*, respectively such that an element of D and D^* both have it. Therefore, even if here are mappings between interpreted relational structures, these are not the relevant shared spatiotemporal properties between mathematical and concrete objects.

a special account of representation is needed for models (Giere, 1988; Hughes, 1997; van Fraassen, 2010). This isn't wrong *per se*. However, if the above argument is sound, then it is unnecessary. Following Callender and Cohen (2006), there are fundamental and derived representations (Grice, 1991). The latter are explained in terms of the former. For example, the meaning of utterances and inscriptions are explained in terms of mental states, which in turn are explained in terms of something more fundamental (insert your favorite naturalistic theory of mental representation). Deflationists deny we need a tailored account of scientific representation for models. We simply deploy those general accounts of representations found in cognitive science, cognitive psychology, linguistics, and so on (Cummins, 1989; Sterelny, 1990). This is consistent with there being different types of representation, which there are of course. For example, pictures and words represent in distinctive ways (Goodman, 1968), but these differences are orthogonal to the model/non-model distinction.

The similarity view departs from deflationism in two ways. First, it supposes that models are a special *sui generis* form of indirect representation.[13] Second, the representations are not true of or satisfied by objects, but are aspectually similar to the represented. We don't need to make either supposition.

Why accept deflationism? First, scientific representations are constructed from ordinary representational tools like languages, diagrams, among others. Second, the features that make scientific representation seem distinct from other forms of representation are actually found in them too. Models are representations that involve abstraction and idealization, but these are found in other types of representation. As we saw, a graphite pencil drawing does not represent colors of objects. In language, we presuppose sharp boundaries where there are none between things. Third, philosophers like Giere (1988, 1999, 2010), Hughes (1997), and van Fraassen (2010) already employ a deflationary framework construing representation in terms of intentions and interpretation.

As is customary in cognitive science and the philosophy of mind, we can distinguish between representational vehicles and representational contents (Dretske, 1997). Representational vehicles are the objects, events, or properties that do the representing. Representational contents are the properties the vehicles represent objects as having. Scientists use various vehicles to represent the world, including concrete objects, equations, graphs, pictures, and so on

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[13] A representation x is indirect if x represents y, which in turn represents z rather than x directly representing z. Representation is not a transitive relation, and so x does not represent z. On the similarity view, equations represent mathematical structures that represent and are similar to ecological systems. For deflationists, the equations directly represent systems, ecological and otherwise. Although it is common, it is a misconception to think that similiarists define representation in terms of similarity.