



## Island Biogeography and the Multiple Domains of Models

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**Abstract.** This paper adopts a symmetrical approach to controversies over R.H. MacArthur and E.O. Wilson's equilibrium model of island biogeography, in order to show how different interpretations of the model depend upon different philosophical understandings of the application of models and theories. In particular, there are quite distinct domains to which the model could apply; in addition, some equivocation among these domains is important to the model's success. Therefore, apparently inconsistent interpretations, interpretations that fit into roughly instrumentalist, realist and rationalist conceptions of science, may be mutually supporting in practice. Descriptions of scientific practice, then, should not adjudicate among these interpretations, but should instead recognize ways in which successful models translate among domains, and in so doing can become realistic, instrumentally successful, or rationally established. As complex social objects, models can afford complex representational relations.

**Key words:** domains, idealization, island biogeography, realism

[The scientist] must appear an unscrupulous opportunist: he appears a *realist* insofar as he seeks to describe a world independent of acts of perception; an *idealist* insofar as he looks upon concepts and theories as free inventions of the human spirit ...; a *positivist* insofar as he considers his concepts and theories justified *only* to the extent to which they furnish a logical representation of the relations among sensory experiences. He may even appear a *Platonist* or *Pythagorean* insofar as he considers the viewpoint of logical simplicity an indispensable and effective tool of his research.

Albert Einstein (1970, p. 684)

### Introduction: Domains of applicability

Some of the central debates in philosophy of science are about the objects and domains to which scientific theories and models can or should be expected to apply. Realists and instrumentalists, for example, disagree over whether

theories can be expected to describe hidden structures or merely account for data. Although such debates are often well-removed from scientific practice, working out the referents of scientific theories is not only a project for philosophers: scientists implicitly, and sometimes explicitly, engage in such interpretation, because debates about particular theories and models can importantly include debates about domains to which they should be applicable. The “domains” I have in mind here depend upon conceptual divisions, rather than strictly empirical ones. They are different structures or objects to which theories or models might apply: aggregate data or underlying formations, the natural world as we find it, laboratory phenomena, or strongly idealized worlds. Theories might also have correlated domains in the sense that they only apply to marine ecosystems, or to terrestrial life, but those domains are not at issue here.

In this paper I explore some interpretations, mostly by biologists, of Robert H. MacArthur and Edward O. Wilson’s equilibrium model of island biogeography (IB). I use the long-running controversy around this important model to display distinct domains to which it could apply, and some equivocation or uncertainty about to which it does and should apply. While to the philosopher this might look like inconsistency or lack of thoroughness, some such equivocation is crucial to the success of models like IB – especially in disciplines like ecology, in which fieldwork in a messy natural world is important. Typically, theories and models must gain legitimacy from their being counted true of idealized domains but also from being attached to the natural world. That is, neither the natural world nor a heavily idealized world can serve as the grounding for an ecological model. And even experimental data can fail to legitimate a model, if the experimental systems producing the data are artificial and uninteresting. Therefore, apparently incoherent interpretations of IB may be mutually supporting in practical terms, each giving the model justification that the others cannot provide: it is because IB has rational appeal that it can be deemed approximately true of some natural or experimental system, and vice versa. The debate over MacArthur and Wilson’s model and its interpretation, then, shows that standard universalizing philosophical approaches to science miss something important when they idealize or purify interpretations, because those interpretations are not in all ways independent. Philosophers’ reconstructions fail to recognize that the practice of science can depend upon what Einstein calls “unscrupulous opportunism.” Whether the model is successful, or even true, depends on whether it applies to multiple domains. What those domains are, and what the demands for application are, depend on ecologists’ construction of the goals and aesthetics of research for their field.

Because the central problem for mainstream philosophy of science concerns the relation of theory to evidence, philosophers have a tendency to run these different domains together.<sup>1</sup> This results in a lack of attention to disciplinary choices about what types of evidence to consider, and ignores the way in which those choices are intimately bound up with choices about interpretation of theories, and choices about what type of science is at issue. If we run all domains together in the case of IB, we fail to see that ecologists don't agree on their status, and that nothing other than a disciplinary decision need force their agreement. For some ecologists, data from the natural world is the only relevant data, because a fully natural world is the proper object of study. For others, natural world data is too messy to support what they see as genuinely theoretical work, and therefore experimental data is needed to translate between theoretical concerns and the natural world. And for some ecologists, adequacy to an appropriate ideal world is most of what is needed to legitimize a model. These judgments interweave empirical, epistemic, and even metaphysical considerations, with conceptions of ecology and of ecological research.

Beyond ecologists' implicit philosophizing on IB, there have been at least two discussions of the model in philosophical contexts.<sup>2</sup> Kristin Shrader-Frechette argues that for the purposes of conservation, IB does not work well (Shrader-Frechette and McCoy 1993; Shrader-Frechette 1995). But in the course of her discussion, Shrader-Frechette makes more global claims about IB and about the value of experiments, and hence a more absolute evaluation of the model. Yrjö Haila also wades into the debate, arguing that IB should be interpreted as an abstract model the value of which lies in its truth to an ideal world (Haila 1986; Haila and Järvinen 1982). Both of these cases are, then, interventions into the debate over the model. Though it might be an effect of this paper to support one or another side of the controversy around IB, that is not one of my goals here; instead I attempt to keep the viability of each interpretation at least as open as participants do. While there can be excellent reasons for philosophers to intervene in a scientific debate, that intervention often removes the perspective that allows one to understand the debate as a whole, as a piece of scientific practice.

### **Island biogeography**

What determines the number of species of a given taxon on an island? In the 1960s MacArthur and Wilson (1963, 1967) put forward a stochastic model to address this question, the equilibrium model of island biogeography. It built on the work of Preston (1962) and some well-known generalizations (Haila and Järvinen 1982; Williamson 1988) – Quammen's (1996) recent

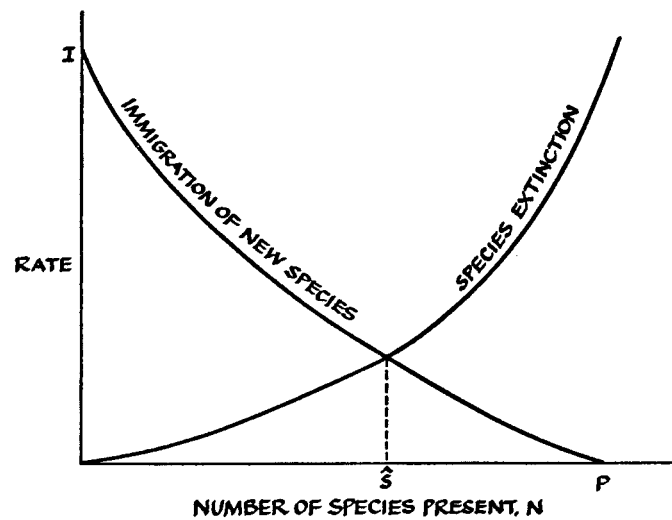


Figure 1. Equilibrium model of a biota of a single island (From MacArthur and Wilson 1967).

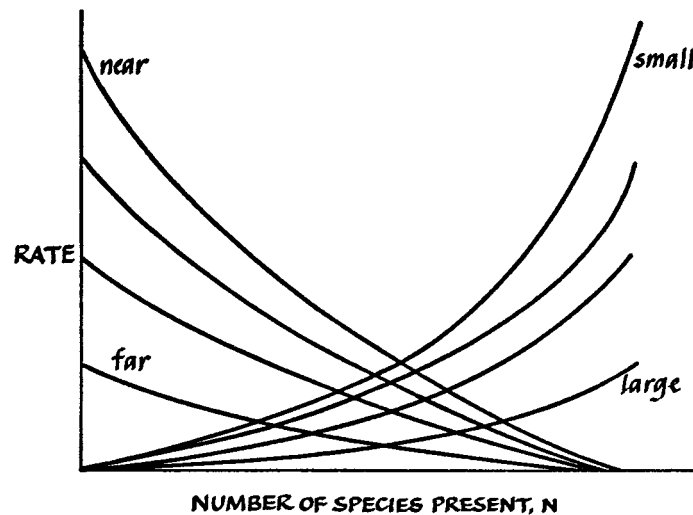


Figure 2. Equilibrium models of biotas of several islands of varying distances from the principal source area and of varying size (From MacArthur and Wilson 1967).

journalistic description of IB and related biology is an excellent and enjoyable general account. The model, as originally formulated, brings three key variables to play in determining immigration and extinction rates: distance from sources of colonists, number of species, and area. These relationships alone allowed MacArthur and Wilson to draw curves such as Figures 1 and 2. The points at which immigration and extinction curves cross is the equilibrium

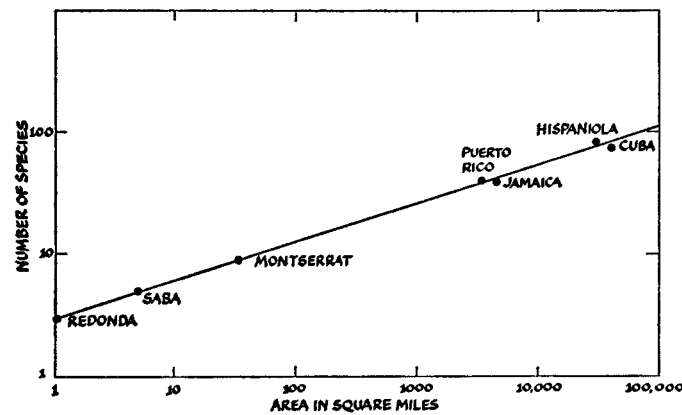


Figure 3. The area-species curve of the West Indian amphibians and reptiles (from MacArthur and Wilson 1967).

point at which extinctions are balanced by new colonizations, a point which should be relatively stable.

MacArthur and Wilson importantly assume that an organism's niche is plastic. Survival is not dependent upon the availability of a particular niche, but is dependent upon the total amount of competition: they adopt a picture of diffuse competition in which all of the organisms in question can be thought of as competing with each other. For the purposes of the model, then, the community on an island is simply a relatively homogeneous and unstructured collection of organisms – for example there is no orderly succession or pattern of organisms or communities replacing one another. And there are no individualistic features of islands, features that might contribute to particular habitats.

MacArthur and Wilson's 1967 book *The Theory of Island Biogeography* presents evidence for IB in the form of some striking species-area curves, such as Figure 3, showing the basic species-area relationship (distance from sources of colonists is generally thought to be a less important variable). Those figures were almost too striking, because this basic portion of the equilibrium model has been the limit of many researchers' interest in IB, even though MacArthur and Wilson's book goes further. Drawing from Preston (1962), species abundances on a group of similar islands could be approximated by the curve  $S = CA^z$  ( $S$  is the number of species represented,  $C$  is a constant representing something like "biological richness,"  $A$  is area of the island, and  $z$  is a parameter that is relatively stable across regions and taxa, approximately equal to 0.27). The authors also developed a number of other relationships and concepts, some of which have become important in theoretical ecology. Yet as Haila (1986) points out, often IB and its most simple

graphical representations have been equated, making much work on the model curve-fitting exercises; this has been possible, Haila claims, because of IB's status as a signifier of interesting ecology. In Star and Griesemer's (1989) terms, IB is a "boundary object" used to attach empirical ecology to theoretical issues: the vast majority of the recent articles that make reference to IB do so to frame biogeographical data, usually data that does not quite fit the model's predictions.

An aside on IB as a model: Although models and theories are typically treated as distinct types of objects, this is not a clean distinction, especially in biology. The people who create such objects as IB are referred to both as modellers and as theoreticians, even when they are not trying to apply the theory or model to any particular subject matter. If we adopt a more fine-grained taxonomy, we can finesse the difference by seeing IB as a theoretical model, as opposed to a simulation model (computerized or other) or an analog model (like a wind tunnel). It is theoretical in the sense that it is often considered in the abstract, but is a model in the sense that it uses the tools of the modeller, and is an attempt to produce an image of a particular type of process.

#### **"Naive" realism: Natural history tests**

The history of testing IB is perhaps surprising, because attempts to extend the model empirically have often given way to attempts to demonstrate IB's most basic and apparently truistic claims. For example, it has proven difficult to demonstrate that islands are in approximate equilibrium. And Daniel Simberloff (1983) points out that most researchers do not even specify a null hypothesis: what amount of fluctuation in numbers is allowed for in a stable equilibrium?

The model was put forward as explaining a correlation between species numbers and areas of islands. Unfortunately, although it is agreed that species numbers generally increase with area, the relationship between the two has become less clear and consistent than MacArthur and Wilson found. In their study of 100 sets of data on species and area, Connor and McCoy (1979) do not find a consistent shape of the best-fit species-area curves, though IB's power function  $S = CA^z$  fits data more frequently than do other proposed functions. Recent studies have continued in the same vein: IB's curve fits a considerable amount of data reasonably well, but by no means all of it (e.g. Williamson 1988).

More important than the shape of the curve is the variation in species numbers that is not explained by area. While some studies show that area is a reasonably good predictor of species numbers, many point to other variables

as more important (see Gilbert 1980; Brown and Dinsmore 1988). In addition, area is correlated with other variables that might account for diversity, such as number of habitats, which sometimes accounts for more variability than does area (Johnson and Simberloff 1974).

An alternate natural history approach to testing IB is to follow the colonization of a new island. This can only rarely be done, but there is one prominent example. In 1883 the Indonesian island of Krakatau was destroyed by a volcanic eruption, and the remaining fragment, Rakata, was thoroughly sterilized by a thick layer of hot pumice and ash; for biogeographical purposes it was essentially a new island in August of 1883. MacArthur and Wilson made use of census data on Rakata to argue that equilibrium was quite quickly reached (25 to 36 years after the eruption) and that there was turnover of the species at equilibrium, though they recognized that other patterns in the colonization pattern did not match their predictions.

Bush and Whittaker (1991) argue that IB does not predict the right overall patterns at all, because immigration and extinction curves are not all monotonic, and for the taxa they studied there was no indication that equilibrium had been reached at any time over the past century. Rakata has undergone successional changes, from grasslands toward mature forest, and new colonists today tend to be either species that can compete in a dense forest, or that can take advantage of a forest gap opened up by a falling tree. Colonizing ability accounts for other patterns: early colonists were wind- or sea-dispersed, whereas animal-dispersed species have tended to be more recent. Bush and Whittaker's more fine-grained look at the changes in the flora and fauna of Rakata suggests that IB's abstract approach leaves out an enormous portion of the history of the island, perhaps most of what might be interesting to a field ecologist.

The use of species-area curves and data from new islands such as Rakata to test IB implicitly gives the model its most traditional interpretation, an interpretation as a hypothetical description of the natural world. Because of the discrepancy between the simplicity of IB and the complexity of ecosystems as ecologists choose to understand them, it has been relatively easy to see IB as failing to describe this domain. Most ecologists and biogeographers today, well-trained into an understanding of Popperian hypothesis-testing as the norm of science, see IB as a failed hypothesis, or, at best, a hypothesis only very approximately true.

Daniel Simberloff has been most prominent in promoting a Popperian and straightforwardly realist approach to IB. In an early critique of IB he explicitly turned it into a falsifiable hypothesis, perhaps in order to refute it (1976; see also Gilbert 1980). As a result of the work by Simberloff, his colleagues, and their students, consensus may be emerging that as a hypothesis about the

naturally occurring islands, IB is not a success. Shrader-Frechette and McCoy (1993) are in the mainstream in calling IB a “hypothesis,” and arguing that it is not adequate for the purposes of ecology or environmental planning; what is needed is more “autecological” knowledge, knowledge of particular ecosystems and organisms (see also Shrader-Frechette 1995).

### **Instrumentalism: The design of nature preserves**

There is another approach to the domain of natural history data. Nature preserves are habitat islands, and therefore it has been argued that IB could be useful in the design of nature preserves, by predicting the number of species preserved in a given conservation area (e.g. Diamond 1975; Lovejoy and Oren 1981; Terborgh 1974). Despite the poor results from tests of IB in nature, it is possible that the model describes some aggregate states reasonably well, because a number of different factors acting together and in opposition to each other might mimic IB’s picture. If the model does not meet criteria for realistic correspondence it might still be empirically adequate to a restricted set of data, or good enough for the purpose of conservation. This is a more blunt form of instrumentalism than is typically discussed in philosophy of science, because it accepts not only that the model *may* not describe the natural world accurately, but that it *fails* to do so – and yet is still valuable.

The central argument for interpreting IB instrumentally stems from the urgency of the conservation effort. The alternatives to its use in planning for preserves – mainly detailed study of endangered organisms and habitats – may be too expensive and time-consuming given the circumstances (Soulé 1980). In response to this argument, Boecklen and Gotelli (1984) analyze species-area relationships from published data, mostly the same 100 studies used by Connor and McCoy (1979). Boecklen and Gotelli show that area explains approximately half (49%) of the variation in species diversity. More striking, and used to great rhetorical effect, are the confidence intervals that they draw around specific predictions: in the worst case chosen the data apparently allows for an interval of ten orders of magnitude in an extinction coefficient (data of Soulé et al. 1979); that means that for the Nairobi National Park, at a confidence level of 95%, one can predict only that between 0.5 and 99.5 percent of faunal species will disappear in a space of 5000 years. Most of the predictions fare considerably better than that, but Boecklen and Gotelli’s overall conclusion, in combination with a number of other arguments, has cast doubt on whether IB has any predictive power at all for conservation practice. So while conservation biologists are willing to *consider* the possibility that IB is empirically adequate – instrumentalism is a permissible interpretive strategy – many are quick to reject



that possibility or to demand higher levels of precision than the model can provide. Empirical adequacy, then, does not seem to be a strong option for IB.

### **Metaphysical realism: Experiments**

A model or theory “abstractly corresponds” when it describes processes, forces, or objects that can be, at least in principle, separated from each other, and from the rest of messy nature. That is, abstract correspondence is what the scientific realist assumes a description does if it “carves nature at its joints” (e.g. Boyd 1979). The point of many experiments is apparently to identify, display, or realize those joints, showing that they are in fact separable; experimental results, then, fall into a third approach to the applicability of IB, and another distinct domain of data.

An experimental system is not nature. Instead it is a crafted, constructed, and designed environment and set of interactions, interesting and useful precisely because the messiness of nature has been excluded (e.g. Hacking 1983; Knorr-Cetina 1983). Experiment is a surrogate for nature which can allow one to materially realize some of the abstractions of scientific theories and models. At the experimental level IB has had some measure of success, though certainly not universal success. Almost all experiments show enough variability to indicate that IB misses important factors of experimental systems. Some studies do not show the area or distance effects predicted by IB. Most studies do not show smooth changes in species abundance, suggesting succession effects.

Experimental tests of IB either use small natural islands (e.g. Simberloff and Wilson 1970; Rey and Strong 1983), or artificial substrates to represent islands (e.g. Cairns et al. 1969; Schoener 1974a, b; Have 1987). The best-known test was done in the late 1960s by Daniel Simberloff and E.O. Wilson, who fumigated six mangrove islands in the Florida Keys, and then periodically censused the islands for arthropods.<sup>3</sup> Their data showed that the number of species on all but one of the islands returned to their pre-fumigation levels within a year, and stayed at those levels for the following year. The compositions of species at the end of the first year were different from pre-fumigation compositions, supporting MacArthur and Wilson’s stochastic model, though the islands were apparently drifting toward their original state.

Simberloff (e.g. 1976) later directly questioned the extent to which his experiment supported IB, pointing to such problems as the difficulty of extrapolation from such small islands limited in diversity of habitats, the difficulty of determining statistically what the results showed, the likelihood of many missed immigrations and extinctions when both occurred between censuses,

and, given the proximity of these mangrove islands, the lack of distinction between real colonizations and more fluid movements of insects. These and similar problems are faced by most experimental studies of IB.

For the experimentalist a model is true not only when it describes nature as we see it, but when it describes separable forces or processes of nature. There are two requirements for truth or correspondence embedded here: the first is that the model be realized sufficiently clearly or well; the second is that the experimental system is sufficiently natural or analogous to nature (Brandon 1994). These requirements leave plenty of room for disputes. For example, Arne Have's study of plastic cylinders as stand-ins for islands showed considerable unexplained variability but he could interpret them optimistically (Have 1987). Rey and Strong's study of marsh grass islands, on the other hand, showed similar unexplained variability but were interpreted pessimistically (Rey and Strong 1983; Strong and Rey 1982). The early Simberloff saw mangrove islands as acceptable representations of more substantial islands. The later Simberloff (1976 and on), closer to the demanding, strict, and empirical end of the realist continuum, questioned the extent to which any small experimental island, either natural or artificial, could stand in for real islands. Likewise, Shrader-Frechette and McCoy (1993) call all experimental tests "short-cuts," and claim that these tests cannot confirm IB – they apparently see natural history data as the only legitimate domain for ecological models. Even an experimental system which perfectly matched IB's predictions would not necessarily be interpreted as confirming IB, because of the distance between the system and the natural world.

### **Rationalism: Theoretical elaborations**

Probably the most interesting interpretive work – certainly the most explicitly interpretive – done on IB has been done by a few of its proponents pointing to its success in completely ideal worlds, and drawing its usefulness out of that success.<sup>4</sup> Yrjö Haila and Olli Järvinen, for example, argue that the fact that IB is a strong idealization is not a problem for the model, but is rather an opportunity for ecology: IB provides the opportunity to identify variables that affect biogeographical distributions of species (Haila and Järvinen 1982). We should accept IB not as a strict hypothesis but as an *analytic model*, which describes in a systematic way the consequences of thinking stochastically about immigration and extinction equilibria on islands. Haila and Järvinen claim that most ecologists see IB as a hypothesis because of the strength of Popperian hypothesis-testing as an ideology of good science. But if IB is an analytic model then it is not a hypothesis to be tested.

IB assumes that all of the organisms being considered are essentially identical, and, except for their areas and distances from the source of colonists, all of the islands being considered are essentially identical and are identical with themselves through time. Although it might be possible to approximately realize these assumptions experimentally, they are obviously false of all interesting natural systems. Therefore, “it ought to be regarded as a conceptual framework that offers novel insights into the processes determining the structure and dynamics of insular populations and communities and helps to analyze such patterns” (Haila and Järvinen 1982, p. 266). This is rationalism in a Bachelardian sense. The model is taken as an object whose reference to empirically given reality is secondary. What is essential is that it makes sense of an ideal world, one which may not even be materially realizable. On this view the important qualities of such models center around consistency and lack of *ad hocness*. They should adopt a reasonably consistent *level* of abstraction, not including or excluding arbitrarily chosen details. In addition, the parts of the model should have obvious physical or biological interpretations, which appear roughly right at the model’s level of abstraction (see e.g. Maynard Smith 1973; Levins 1966).

The position that IB is an analytic model makes space for the activity of modelling by taking seriously the idea that the model is an object of study in itself, though perhaps one whose value consists in what it teaches us about other objects. It is no surprise, then, that some of the other people who hold it are modellers. Christian Wissel, who has done recent work reformulating IB (Wissel and Maier 1992), says that, “the main aim of ecological models is to *contribute* to a better understanding of ecological systems,” and “models are intellectual *instruments* for thinking people, not crutches for the thoughtless” (Wissel 1992, emphasis added). Although he means by these claims something broader than would Haila and Järvinen, Wissel notably avoids claiming that ecological models map or correspond to ecological systems. Similarly, James H. Brown says:

The value of [IB] has been largely heuristic. It has been tested repeatedly, often rejected, and not yet to my knowledge proven to be both necessary and sufficient to account for the diversity of a single insular biotas. Nevertheless, the theory provides an exceptionally useful conceptual framework for investigating patterns of species diversity and the underlying mechanisms which produce these patterns. (Brown 1981, p. 882)

Michael Begon and Martin Mortimer, in a textbook on modelling in population ecology, say that “mathematical models *do* have an essential role to play. Time and again they crystallize our understanding of a topic, or actually tell us more about the real world than we can learn directly from the real world

itself” (Begon and Mortimer 1986, p. vii). Correspondence with the natural world is conspicuously absent.

The ideal realm has both higher and lower status than does the natural world. It has higher status because it can be exactly described and behaves predictably: science’s greatest achievements come from elegant constructions of ideal worlds. But at the same time the ideal realm has lower status than the natural world because the latter is paradigmatic reality, and therefore the ideal realm is most clearly unreal exactly when it is placed in opposition to nature (Austin 1962; Sismondo 1997).

### **Norms, interpretations, and the construction of success**

Given all of the criticisms of IB, what is its status? Although it has been more or less rejected as an adequate description, either realistic or instrumental, of species distributions, IB’s chances of being considered abstractly realistic have looked and perhaps continue to look better. It might have turned into a model describing important yet submerged biogeographical tendencies, tendencies whose contribution to observed distributions is hidden by the mass of messy features of the biological world. Yet many ecologists have not drawn that conclusion, preferring to see inconsistent experimental results as evidence of weakness. Criticism of IB’s connection to empirical data has been intense, as some of the uncommonly strong language illustrates. Boecklen and Gotelli give an article the title: “Island Biogeographic Theory and Conservation Practice: Species-Area or Specious-Area Relationships?” and Gilbert gives his review of the literature the title: “The Equilibrium Theory of Island Biogeography: Fact or Fiction?” Strong language can be found on both sides. Jared Diamond says: “The sheer diversity of Mr. Simberloff’s targets – not only competition and the MacArthur-Wilson island biogeography theory but also character displacement, cladistic analyses, coevolution, conservation strategies, and comparative observational methods in ecology – reveals that his is a scattergun attack” (quoted in Woodbury 1988).

To some extent the debate over IB has been part of a larger debate over interspecific competition (e.g. Connell 1983; Lewin 1983; Roughgarden 1983; Sloep 1993). MacArthur was a key proponent of the idea that there is strong competition between and not just within species, on both evolutionary and ecological timescales. In IB this idea is important; it is the assumption that the resources of the island are evenly divided among the organisms. Simberloff, his colleagues, and their students – the “Tallahassee Mafia,” standing in opposition to Ivy League MacArthurians (Lewin 1983) – have been stridently opposed to the many different manifestations of the hypothesis of competition, and their opposition has proven productive of

controversy and careers. But while the debate over interspecific competition has undoubtedly been important to the production of articles criticizing IB, it is only a part of the story. Much skepticism about IB has apparently little to do with the competition hypothesis and more to do with norms of research (e.g. Cox and Moore 1993; Bush and Whittaker 1991; Williamson 1989; Gilbert 1980).

MacArthur, Wilson, and other articulators of the model do not *believe* their levelling assumptions (the assumptions that treat all relevant organisms and environments as the same) even when they are interpreting IB as a hypothesis to explain observed species distributions (e.g. MacArthur and Wilson 1963). Instead, supporters of the model implicitly claim that their pictures of immigration and extinction are as good as one can hope to devise without descending into a much more detailed account of empirical data. This characterization points to a straightforward way in which successful representation can be embedded in a social context. An abstract representation is approximately true if researchers are unable or unwilling to disentangle the details effaced by abstraction. Therefore the success of IB in representing nature depends in part upon lifestyle and labor issues: to the extent that ecologists are interested in and able to gather more detailed causal information they will find IB unsatisfactory. Even though there are occasional complaints that mathematical ecology dominates too many journals, fieldwork and experimentation are still central to ecology as a discipline, and most ecologists see their detailed knowledge of organisms, niches and ecosystems as part of their professional identities. Ecologists work on patchy systems and are interested in the properties of patches. Therefore, as a uniform model of biogeographical distribution IB does not match some of the norms of ecological research. This may go some way to explaining why opposition to IB has been so strong, and why the call for more “autecological” study – this prominent word itself indicates a normative conception – is the counter to and reverse of it. This is not to say that ecology is an anti-theoretical discipline, but only that there are pressures to keep the level of abstraction of theoretical ecology low. Here, for example, is one biogeographer commenting on IB and similar work: “[A]re there general laws in biogeography? ... I suspect that many existing general biological laws, including MacArthur and Wilson’s (1967), result from constraints imposed by non-biological laws on biological variation, and that as a consequence, they are of biological interest only as constraints” (Hengeveld 1990, p. 9).

Prominent norms of research and styles of work in ecology made for strong opposition to IB. But competing norms have contributed to its persistence. Modelling is itself a specialty within ecology. For modellers, IB’s rational appeal, the fact that it has to be true of its idealized organisms,

is its justification. Modellers tend to accept that their constructions are not strictly true of the material world, but adopt a different aesthetic for judging them, centered around their being non-ad hoc descriptions of appropriate ideal worlds. A model should also make good qualitative predictions, but that requirement is at least temporally secondary to other aesthetic considerations (see Salt 1983). Simon Levin, dipping into such issues, says:

Certainly the naturalist may regard as curious the things the theoretician finds interesting. This is reasonable; there is, after all, no accounting for taste. The field biologist should, however, recognize that much of what he chooses to examine may be thought equally obscure by the theoretician. Not every just-so story of natural history is of obvious cosmic importance, and when global significance is removed as a factor and only intellectual value remains, models are intrinsically neither more nor less interesting than membracids. To the theoretician, models are a part of the real world. In studying the logical consequences of assumptions, the theoretician is discovering, not inventing, and is spiritually akin to the natural historian. (Levin 1981, p. 866)

The fact that there are competing norms does not simply turn the debate into one over the relative merits of theory and empiricism. The autecologists' position that interspecific competition is relatively unimportant is as theoretical a claim as the modellers' position. The debate does not even neatly split the mathematicians from the natural historians. Roughgarden suggests that it might so split when he says that he hopes that "the extreme antagonism in the rhetoric about theory doesn't reinforce the inherent disinclination people have to learn all that math that is so necessary in the study of ecology" (quoted in Lewin 1983). Yet many of the protagonists do not fit neatly into one or another camp. Wilson portrays himself as an unmathematical naturalist, an expert on ants (1994). MacArthur, while an excellent mathematician, had also done careful empirical work with warblers, which Evelyn Hutchinson made sure to point out: "Robert MacArthur really knew his warblers" (Hutchinson 1975). Simberloff came to biology from mathematics. And almost all of the opponents of IB display a sophistication about statistics that suggests comfort with formalism. For this reason it is more useful to see the debate as produced by the competition between norms of ecological research.

As I have already mentioned, Haila identifies another reason for IB's persistence. Perhaps because of its theoretical attractions IB became a signifier of good ecology, and thus many empirical studies make reference to it, organizing and situating data (both positively and negatively) with respect to it. The model is a boundary object that gives shape to a large quantity of empirical work. Although in the process IB might sometimes be given simplistic interpretations, we can choose to see these interpretations more

positively: the model helps to structure ecologists' worlds of work. Seeing IB as a boundary object allows us to accept that it can have multiple uses and interpretations.

### **Conclusions: On travelling between domains**

There are distinct domains or realms of applicability, in which the model has differing levels of success. If this were a folk tale we might be satisfied for the model to settle down in its ideal realm where its success is perfect, or nearly so, and live happily ever after: IB would be the traveller who discovers that he is the king in the land of his birth, itself a realm of fables in this case (see Cartwright 1991). Few scientists, though, would be comfortable with a model or theory whose only clear applicability is to an ideal domain; after all, they work hard to distinguish theorizing from the telling of fables.

One of the easiest lessons to take from this is the perhaps obvious point that at least the four interpretive strategies that I identified here are already present in science, and are all, in context, potentially legitimate. If we take scientific practice at face value, then we should accept that models are things constructed and manipulated in many different contexts and by many different actors. While one or another scientist may be adamant in the adoption of an interpretive position, the community taken as a whole is at least sometimes more tolerant, when an important object like IB is at stake. Given that the choice of interpretive positions depends in part upon a choice of norms or aesthetics of research, it is extremely unlikely that there could be a single epistemically privileged relationship between models and nature. Ecology might eventually become a science like economics, which emphasizes ideal domains over empirical ones. Or it might become more like one of the medical sciences, which emphasizes detailed knowledge of interactions and processes.

But that point can be pushed considerably further. Not only are there multiple legitimate interpretive strategies, but we should *expect* solid models to have multiple interpretations. In rich fields some travelling among domains is almost certainly desirable for successful models. On the one hand legitimacy comes from conceptual rigor, success in the ideal domain. On the other hand, there are demands that models take hold of the material world. In its strongest form this taking hold of the world consists in explaining the details of natural formations, by addressing natural history data. In the current climate, strong legitimacy for IB could also come from its successful use in designing nature preserves, or otherwise protecting threatened species in particular habitats. A less firm source of legitimacy in ecology – though not in other disciplines – comes from taking hold of the world experimentally; this

is less firm because experiments can be easily seen to stand in a troubled relation to nature. In this middle ground of experimental systems, an ecological model's success depends both upon its coherence with experimental results and upon the systems' being deemed natural enough – or interesting enough in their own light. An abstract object like IB should be expected to have difficulties on both counts. To the extent that IB has succeeded experimentally, it is *because* of success in the ideal domain, which has allowed it to become a model that structures and justifies empirical work, and allows experimental variability to be interpreted optimistically. The simultaneous demands that models have conceptual rigor and take hold of the material world can result either in compromise or in multiple interpretations. In a science like ecology, where it is perceived that there is massive variability in the subject matter, compromise tends to be difficult, because of the difficulty of finding a level of abstraction at which models can be seen as both empirically adequate and mathematically or conceptually tractable. We should simply not expect uniform understandings of successful models. Taking models as boundary objects suggests the partiality of unifying interpretations of science in terms of such categories as instrumentalism, realism, and rationalism. Models are complex social objects, and therefore can afford complex representational relations.

Typically, then, models are objects that should travel among domains. A model that only referred to the natural world would likely do little work; one that only referred to aggregate data would likely be intellectually unsatisfying; one that only referred to experimental or ideal domains would likely lack legitimacy. Models are useful and interesting precisely because they potentially translate among our interests in the ideal, the experimental, the pragmatic, and the natural. Therefore, simple philosophers' slogans, such as that science "reads the book of nature" (Kosso 1992) or "cuts nature at its joints" (Boyd 1979) are misleading, because nature is not an unproblematic object of scientific models and theories: nature is instead a construal of one or more domains to which they can apply.

Debates over idealized models show how truth and falsity depend in a straightforward way on community decisions and expectations. We might, then, say that truth is socially constructed. There is a sense in which this is right, but it is important to distinguish this sense of the social construction of truth from others. This construction of truth is a very mundane and deflationary one, because we don't have to do any particularly interesting metaphysics in order to see it. Whether a model is true but quite abstract, or interesting but false depends upon what work the scientific community wants it to do. Social constructivist studies of science, by not distinguishing among many different senses and techniques of "construction," sometimes appear to



adopt a mystical understanding of the dependence of truth on the social world (Sismondo 1996).

Therefore, in arguing that the truth or falsity of theories and models is context-dependent, I want to show the flexibility of truth, even truth as correspondence. What idealized scientific theories and models correspond to can be as much at issue as judgments of correspondence. Although some models are undoubtedly false under any reasonable interpretation, IB is not. Too simple an application of the language of truth and falsity does not do justice to the complex representational relationships that theoretical models have. For this sort of object truth and falsity are relative to levels of abstraction – and what gets to count as an acceptable level of abstraction may be at issue in a scientific community. Therefore from an outsider's perspective it does not make sense to say that it is right or wrong, or true or false, in an absolute sense. Instead its rightness or wrongness depends upon what the community decides gets to count as being right or wrong in particular circumstances, what the community wants the object to do.

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### Notes

<sup>1</sup> See, for example, the essays in Boyd et al. (1991), an exemplary reader in the philosophy of science. With very few exceptions, those essays do not recognize the artificiality of experimental systems, or the selectiveness with which natural world data is allowed to bear on theories. Thus standard domains of evidence for any given theory are treated as fully natural.

<sup>2</sup> Peter Sloep (1993) also discusses the controversy over interspecific competition, which is closely connected to the one IB. Although my description of the controversy over IB supports Sloep's conclusion that some universalizing philosophical positions are wrong as descriptions of scientific practice, those positions have been useful to participants, useful in articulating domains for which the model does and does not succeed, and hence need not be completely abandoned, as Sloep recommends.

<sup>3</sup> The experiment was a feat of organization, requiring, for example, the temporary erection of Christo-like tents over the islands for the fumigation. Its importance recognized by the 1971 Mercer Award of the Ecological Society of America. The work is nicely described in Wilson's autobiography, *Naturalist* (1994).

<sup>4</sup> I choose some realist language – saying that IB is true of an ideal world – to describe this interpretive position for a number of reasons. Given IB's limited empirical successes,

instrumentalist language, philosophy of science's favorite alternative, would be misleading. In part I am following Haila and Järvinen (1982), who believe that IB attempts to describe "essences" of biogeographical processes, even if they are unrealizable essences. Thinking in terms of essences also marks the continuity of this rationalist position with the metaphysical realism I describe above.

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