



Complexity and Verisimilitude: Realism for Ecology

GREGORY M. MIKKELSON

*Department of Philosophy and School of the Environment
McGill University
845 Sherbrooke Street West
Montreal, Quebec
Canada H3A 2T5
E-mail: gregirt.mikkelson@mcgill.ca*

Abstract. When data are limited, simple models of complex ecological systems tend to wind up closer to the truth than more complex models of the same systems. This greater proximity to the truth, or “verisimilitude”, leads to greater predictive success. When more data are available, the advantage of simplicity decreases, and more complex models may gain the upper hand. In ecology, holistic models are usually simpler than reductionistic models. Thus, when data are limited, holistic models have an advantage over reductionistic models, with respect to verisimilitude and predictive success. I illustrate these points with models designed to explain and predict the numbers of species on islands.

Key words: biodiversity, biogeography, ecology, holism, instrumentalism, parsimony, prediction, realism, reductionism, verisimilitude

Introduction

Ecology, at 135 years of age, is still a relatively young science.¹ The philosophy of ecology is of course much younger still, and remains strikingly underdeveloped, despite repeated calls for more work on the subject.² Nevertheless, a few landmarks already exist. Two decades ago, Saarinen (1982) assembled a rich collection of essays by ecologists, evolutionary biologists, and philosophers. About a decade later, three more books appeared, each offering a different analysis of problems and prospects for ecological science (Peters 1991; Allen and Hoekstra 1992; Shrader-Frechette and McCoy 1993).

Together, these four books convey a remarkable diversity of viewpoints. Much of the diversity results from assuming different stances toward familiar philosophical issues. For example, Simberloff (in the 1982 anthology) argued strongly for reductionism, beseeching fellow ecologists to explain higher-level properties – such as those of whole communities and ecosystems – by reference to lower-level details about their component species. Allen and

Hoekstra espoused the opposite point of view, favoring explanations pitched at higher, rather than lower, levels in the ecological hierarchy. They also took a stand on the realism-instrumentalism issue, siding firmly with the latter.³

In this paper, I shall present a realist alternative to the instrumentalism propounded by Allen and Hoekstra. I will also show how this alternative framework can be used to adjudicate between reductionism and holism in specific cases. The framework relies heavily on the concept of proximity to the truth, or “verisimilitude”. The verisimilitude concept has played an important role in discussions of realism about theories (Laudan 1981; Brown 1985).⁴ Another, and perhaps better-known, bone of contention in the realism-instrumentalism debate is realism about “unobservable” entities (Hacking 1980). In this paper I will not engage in that part of the debate. However plausible anti-realism about atoms and other micro-physical objects may be for some people, the existence of such macroscopic and operationally-defined entities as ecosystems, communities, and populations does not lend itself to the same kind of doubt.

The instrumentalism of Allen and Hoekstra stems, in part, from their emphasis on the necessary contrast between the complexity of ecological systems, and the relative simplicity of models designed to explain the behavior of such systems. However, the realist framework presented below easily accommodates this contrast. In fact, it helps to justify it. I shall illustrate the relationship between complexity (both ontological and epistemological) and verisimilitude with an example from island biogeography. This example demonstrates the kind of link between predictive success and verisimilitude that anti-realist philosophers and scientists have oppugned.

With a second island-biogeographical example, I will support a general point made by Levins and Lewontin (1982). In their retort to Simberloff, these authors argued that higher-level properties such as food-web structure often, but not always, do better than lower-level ones such as physiological characteristics, at explaining phenomena like the numerical response of a primary producer to an increase in nutrients (for instance).

Distance from the truth

The vast majority of scientists are, consciously or unconsciously, meta-physical and epistemological realists. That is, we believe that there is an objective universe that exists independent of us and our observations [and] . . . that we are making successively closer approximations to the truth, although we can never be certain that we have ever actually arrived at the truth. (Scheiner 1993: 3)

Science is not about truth and reality, it is about organizing experience and predictive power. (Allen and Hoekstra 1992: 13)

As the passages above indicate, philosophers of science are not the only ones who become exercised by the question of whether scientific theories aim at the truth. Sometimes, ecologists do as well. As in philosophy, those inclined to answer the question negatively tend to characterize theories as nothing more than instruments for prediction. But can a theory be a reliable instrument for prediction without also being a reliable guide to the truth?

In their important book on the state of ecological science, Allen and Hoekstra (1992) argued that ecological models not only can, but must, achieve predictive success without approaching any kind of underlying truth. Ecological systems, compared to the systems studied in other sciences, are very complex. One aspect of this complexity is caricatured by the platitude, “everything is connected to everything else”. To put it more mildly, the sheer number of causal factors affecting any ecological system is undoubtedly quite large. Allen and Hoekstra rightly pointed out that models of such systems must ignore most of these factors. And they correctly observed that some of these models nevertheless yield successful predictions. However, when they concluded from these facts that “truth and reality” have nothing to do with predictive success in ecology, they went too far.

The truth comes in many forms, after all. To consider simple ecological models “unrealistic”, as Allen and Hoekstra did, is to focus exclusively on one kind of truth: the truth about the sheer *number* of factors affecting a system of interest. However, a more useful kind of truth is about *how* those factors affect the system. Simple models often (but not always) turn out to be closer to this kind of truth than more complex rivals. Furthermore, proximity to this kind of truth leads to predictive success.

How should proximity to the second kind of truth be defined? At least one general definition of verisimilitude (Popper’s original one) has been shown to be unworkable (Niiniluoto 1998). But many others exist, some of which are “natural” choices for particular purposes (Kieseppä 1996). For example, consider a hypothesis *H*, asserting that a given coin is unbiased – that is, will land heads with a probability of 0.5. If, in fact, the coin is biased such that the true probability of heads is 0.55, then by one obvious measure, *H* is 0.05 units away from the truth. Unlike *H*, most scientifically interesting models can deviate from the truth in more than one relevant respect. Such cases call for a measure of verisimilitude that collapses these respects into a single value.

Below, I shall consider standard probabilistic models about the effects of different causal factors on island biodiversity (that is, number of species). Such models can deviate from the truth in several relevant respects. For instance, a model could posit a strong effect of island area on diversity,

whereas in truth area exerts only a weak effect. The same model might be more accurate with respect to the influence exerted by isolation from the mainland. The Kullback-Leibler distance, a standard measure of distance from the truth, collapses all of these respects into a single value:

$$\text{Distance from the truth} \equiv \sum_{S=0}^{\infty} p(S) \log \left[\frac{p(S)}{\hat{p}(S)} \right],$$

where S is number of species, $p(S)$ is the true probability that a randomly-chosen island contains S species, and $\hat{p}(S)$ is the probability asserted by the model under consideration.^{5,6}

Parsimony, and prediction

Over the past many decades, ecologists have uncovered a vast number of factors, each of which actually influences the number of species on some island, and all of which potentially influence the number of species on any island (Rosenzweig 1995). These include the following:

- 1) Area of the island,
- 2) Isolation from the mainland,
- 3) Latitude,
- 4) Habitat diversity (often highly correlated with maximum elevation),
- 5) Frequency and severity of disturbance,
- 6) Productivity,
- 7) Evolutionarily contingent properties of individual species in the mainland biota, and
- 8) Time since island formation.

The most robust relationship between any single factor and island diversity is the species-area relation, $S \approx cA^z$, where S is diversity, A is area – say, in square kilometers – and c and z are parameters (Figure 1). Like area, other variables also tend to be related to diversity in the form of power laws: *ceteris paribus*, $S \propto bX^y$, where X is the value of a given other variable.⁷ Thus, a model of the effects of both area and isolation would be $S = cA^zI^y$, where I is isolation, say, in kilometers.

With limited data, simple models that ignore most factors influencing diversity often end up closer to the truth than models that take into account more of those influences.⁸ In order to illustrate this, I performed a computer simulation.

- 1) As a first step, I stipulated that diversity is affected by area, isolation, and other unknown factors, exactly as follows:

$$S = 1.0A^{0.40}I^{-0.10}e^{\epsilon},$$

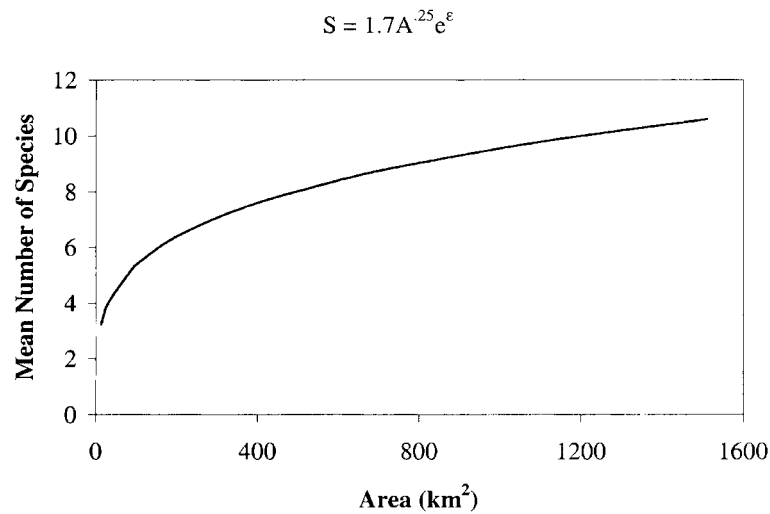


Figure 1. Estimated species-area curve for bats in the Lesser Antilles (Data from Griffiths and Klingener 1988).

except that each value of S is rounded to the nearest integer. (Species richness is of course a discrete variable.) ϵ is a random variable, distributed normally with a mean of zero and a variance of 0.2, that represents the effects of unknown causes.

- 2) I then assigned values of area (km^2) and isolation (km) to each of 10 imaginary islands, by random draw from the following independent lognormal distributions:

$$\log(A) \sim N(5, 1.3); \log(I) \sim N(6.4, 0.3).$$

For the sake of plausibility, I based these distributions on the areas and isolations of the Lesser Antilles chain of islands in the Caribbean Sea.

- 3) I used the “true” relationship given in step 1, along with a random-number generator for ϵ , to assign diversities to each of the islands.
- 4) “Forgetting”, for the moment, the true relationship given in step 1, I used the “observed” data generated in steps 2 and 3 to estimate the parameter values of two models: $S = cA^ze^{\epsilon}$, and $S = cA^zI^ye^{\epsilon}$.⁹
- 5) Finally, I repeated steps 2, 3, and 4 100 times. Table 1 presents one of these 100 “Monte Carlo” trials.

In “reality”, then, area has a positive, and isolation a negative, effect on diversity. One might assume, therefore, that a model invoking both factors will be closer to the truth than a relatively simpler model invoking only area. In the preceding section, I acknowledged one crude sense in which the more complex model is closer to the truth. However, I also claimed that there is a

Table 1. Diversity determined by area, isolation, and unknown factors

Island	Area (km ²)	Isolation (km)	Diversity (spp)
1	104	475	4
2	198	644	5
3	135	425	4
4	444	735	8
5	237	912	6
6	218	646	5
7	83	769	4
8	141	409	5
9	452	730	5
10	47	551	3

more important sense in which the simpler model may be closer to the truth. The reason stems from the fact that ecological models usually do not specify their parameter values; such as c , z , and y ; at the outset. Rather, the models have to be “parameterized”: their parameters must be estimated empirically. “Residual variation”, caused by unmeasured, unmodeled causal influences, can throw off parameter estimates. Such variation tends to cause more trouble for complex models than for simple ones (Forster and Sober 1994).

The simulation illustrates this phenomenon well. Given the data listed in Table 1, the best-fit species-area-isolation model is $S = 0.5A^{0.31}I^{0.10}e^{\epsilon \cdot 10}$. According to this model, isolation has a *positive* effect on diversity. This is, of course, biologically quite unreasonable. The number of species dispersing from the mainland should *decline* with isolation, thus reducing the immigration rate to, and in turn the diversity of, the island. Furthermore, I *stipulated* that isolation does, in “fact”, have a negative effect on diversity. The unreasonableness of the parameterized species-area-isolation model is reflected in the fact that it is further from the truth than the best-fit species-area model, $S = 0.9A^{0.32}e^{\epsilon \cdot 11}$. The Kullback-Leibler distance of the species-area-isolation model is 0.63, while that of the species-area model is only 0.61. Most of the other 99 random samples produced qualitatively identical results: in 72 out of 100 samples, the species-area model was closer to the truth than the species-area-isolation model. Average distance from the truth for the two models was 0.22 and 0.35, respectively.

In general, the more complex species-area-isolation model is more sensitive than the simpler species-area model, not only to the “signal” regarding

the effects of the area and isolation on diversity, but also to the “noise” caused by other variables (represented by ϵ). Because of this, whether the species-area-isolation model ends up closer to the truth than the species-area model depends on the ratio of signal to noise. This ratio depends, in turn, on how much of an effect the unknown causes have, and on the number of data used to parameterize the models. If such data are sampled at random with respect to the unmeasured variables, then the effects of those variables tend to cancel out as the sample size increases. Thus, as more data are collected, the ratio of signal to noise increases, and the relative performance of more complex models improves (Forster and Sober 1994).¹² This tendency provides additional justification for a point made by Levins (1966): “The difference between legitimate and illegitimate simplifications depends not only on the reality to be described but also on the state of the science” (421).

However, the relative advantage of complex models increases with sample size only to the extent that the true underlying relationship between species diversity and the independent variables does not change. One can imagine any number of reasons why it could be otherwise, not only for island biogeography but for other types of ecological system as well. For example, perhaps global warming will substantially alter the numbers of species that can be supported on many islands. In that case, diversity models for those islands will have to be reparameterized. Again, during the early stages of this process – before sample sizes become large enough to favor complex models decisively – simpler models may be closer to the truth. This does not mean that simpler models *will* necessarily be closer to the truth. They will be, only if the biases engendered by their simplistic assumptions are not too severe.

Among samples of 10 islands, not only does the simpler species-area model tend to wind up closer to the truth than the more complex species-area-isolation model, but the simpler model tends to yield more successful predictions. This is true on a variety of definitions of predictive success. One common definition is in terms of “log-likelihood”. Intuitively speaking, if two hypotheses attribute different probabilities to a given event, and that event subsequently occurs, then the hypothesis that originally attributed the higher probability to the event has more successfully predicted it. For our purposes, the predictive success of a given hypothesis with respect to a given island is

$$\text{Predictive success} \equiv \log[\hat{p}(S)].$$

Here, S is a datum that was not used in the initial parameterization of the models. For instance, it could be the diversity of an 11th island randomly sampled from the same general class of islands as the first 10.

Predictive success, so defined, is negatively correlated with Kullback-Leibler distance, our measure of distance from the truth.¹³ Laudan (1981) complained that predictive success has no obvious connection to verisimilitude. The correlation just mentioned is that missing connection, and it justifies interpreting predictive success as evidence of verisimilitude.¹⁴

Holism and reductionism

The above framework can also help adjudicate between holistic and reductionistic models of a given domain. I mean “holistic” and “reductionistic” as relative terms, referring to models that invoke entities and processes at relatively higher vs. lower levels of organization. The higher-/lower-level distinction is most clear when one group of entities and processes (the lower level) comprise the parts of a larger system (the higher level). As I mentioned above, Simberloff (1982, like such evolutionary biologists as Williams 1966) advocated a reductionist methodology favoring lower- over higher-level explanations. Allen and Hoekstra (1992), on the other hand, favored higher-level explanations. In contrast to all of these authors, Levins and Lewontin (1982) offered a more open-minded approach in which the phenomena at hand, rather than methodological *a priori*’s, direct scientists to adopt one or the other approach.

One reason that holistic models are sometimes better than reductionistic ones is that holistic models are often simpler. Simplicity, of course, affords “pragmatic” advantages such as ease of computation. But, as we saw above, in some circumstances it also provides an epistemic advantage. Furthermore, the advantage enjoyed by a simple model is greater, the larger the difference between the number of causal factors invoked by it, and the number invoked by its more complex rival (Forster and Sober 1994).

Consider, then, the following situation. As in the preceding section, we start with data on 10 islands. In this case, however, the data include not only overall diversity on each island, but also the identities of the species there. Suppose further that the 10 islands together contain 17 species (the number of bats in the Lesser Antilles, according to Griffiths and Klingener 1988). Let us maintain the same ultimate goal as before: to explain island diversity. How would the species-area model encountered in the previous section fare against a more reductionistic approach that incorporates the extra information about species identities?

One approach, that is more reductionistic than the species-area approach, would be to use the observed data to estimate 17 different “incidence functions” – one for each species. An incidence function is a relationship between the area of an island and the probability that a given species occurs on the

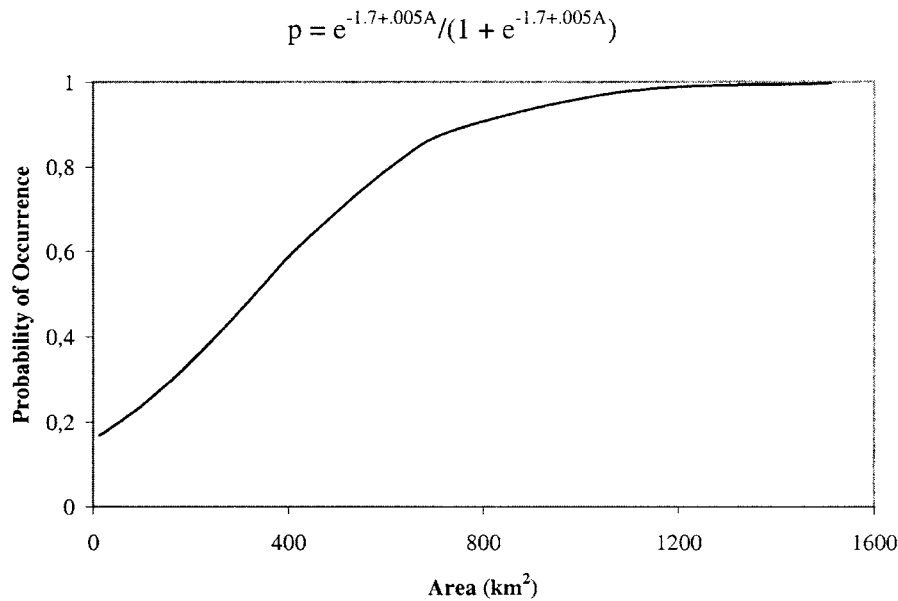


Figure 2. Estimated incidence function for the Antillean bat, *Ardops nichollsi* (Data from Griffiths and Klingener 1988).

island (Hanski 1992; Figure 2). One way to estimate such functions is to use logistic regression to parameterize the following kind of model:

$$p = \frac{e^{\beta_0 + \beta_1 A}}{1 + e^{\beta_0 + \beta_1 A}},$$

where p is the probability that a given species occurs on a given island, and β_0 and β_1 are parameters estimated from the data. Applying this method to 17 species would thus entail estimating 34 different parameters.

This 34-parameter incidence-function model would be vastly more complex than the three-parameter species-area model (c , z , and ϵ being three). The results of the previous section suggest that even if true incidence functions had generated the observed data, the species-area model would nevertheless end up closer to the truth, given data from just 10 islands. In fact, we should expect the species-area model to have even more of an advantage against an incidence-function model than it enjoyed against the species-area-isolation model. The difference in complexity in the present case is much greater – 31 parameters, as oppose to just one (the presence or absence of an isolation effect). Preliminary simulations confirm these intuitions, as well as the expectation that with expanded sample size (e.g., 100 rather than 10 islands per sample), the incidence-function model does better.

Despite its reputation as a holistic science, ecology can be just as reductionistic as physics. The only difference is in the scale of the entities involved. An atomic physicist might imagine that the best way to understand the behavior of a given molecule is via detailed knowledge of the particular atoms that make it up. Likewise, a population ecologist might think that the only way to understand communities is by learning as much as possible about the particular species populations that constitute them.

Such reductionistic strategies have and will continue to shed light on the respective explananda of both physics and ecology. However, they also have their limits (Wimsatt 1982). For one thing, it is impossible to study all of the species in any sizable community. Luckily, several papers (e.g., Heatwole and Levins 1972; Brown et al. 2001) have demonstrated that higher-level properties such as species richness and food-web structure are often fairly insensitive to changes in, and thus more stable than, species composition. In this section, I have presented another reason for sometimes preferring holistic models: in certain circumstances, they are closer to the truth than more complicated, reductionistic models. In such contexts, holism promises “hard-core” epistemic advantages, in addition to more pragmatic ones.

Conclusion

In this paper, I have taken a realist approach to ecological science. In order to motivate this approach, I introduced a distinction between proximity to two different kinds of truth. I traced Allen and Hoekstra’s (1992) instrumentalism to their focus on the less important of these two: the truth about the sheer number of factors affecting an ecological system. I then introduced a measure of distance from a more important kind of truth: about how those factors affect the system. I applied this measure (the Kullback-Leibler distance) to two models of island diversity. In the circumstances prescribed, the simpler model tends to end up closer to the truth after parameterization – even though the more complex model includes more of the factors that genuinely affect diversity. This kind of proximity to the truth, or verisimilitude, is correlated with predictive success.

Thus, a realist framework meets two challenges posed by anti-realists. First, it explains why simple models of complex systems are sometimes better than complex models of the same complex systems (Forster and Sober 1994). This realist explanation obviates what appears to be Allen and Hoekstra’s main reason for resorting to instrumentalism. The realist framework also indicates a strong connection between verisimilitude and predictive success. This connection eliminates a motive for anti-realism offered by Laudan (1981).

I also discussed a different pair of models, one of which is both simpler and more holistic than the other. I argued that in situations of limited data, we should expect the reductionistic model to end up further from the truth – even if reality is just as complicated as the more complex, reductionistic model purports. This argument gainsays the idea that explanations of communities and ecosystems should always invoke lower-level details about the species populations that compose them.

Simberloff (1982) has been the most vocal advocate of “population-reductionism” in ecology. But perhaps my critique of this kind of position applies more directly to allegations made by Sterelny and Griffiths (1999). In the ecology chapter of their fascinating book, they “rather skeptically consider the idea that the structure and dynamics of communities can be explained by ecological theories that abstract away from the particular species that inhabit them” (257). The scope of the present paper does not allow me to go into the details of their argument(s). Suffice it to say that species diversity is perhaps the most fundamental aspect of community structure, and changes therein the most basic of community dynamics. Above, I argued that under plausible conditions, a species-area model of diversity should end up closer to the truth than an incidence-function model. Furthermore, species-area models “abstract away from the particular species that inhabit” islands – to a much greater degree than do incidence-function models. The former treat all species as equivalent, while the latter track differences between them. My argument, along with the species-area model’s status as perhaps the best-confirmed generalization in the history of ecology,¹⁵ would thus seem to refute Sterelny and Griffiths’ skepticism.

Acknowledgements

Thanks to David Castle, John Huss, Paul Jeffries, Hilary Mackie, Jerry Mikkelsen, Jeff Mikkelsen, Bob Oliver, Sherri Roush, Kim Sterelny, and Tom Williams for comments on written drafts of this paper; to audiences at the University of Texas, Texas Tech University, McGill University, and Oregon State University for comments on spoken versions; and to Deborah Mayo and my fellow participants in her NEH seminar for furthering my understanding of probabilistic reasoning.

I wrote the bulk of this paper during my employment at Rice University.

Notes

¹ Haeckel (1866) coined the term “ecology”.

² See, for instance, Ruse (1988).

³ Although Peters’ book differs substantially from Allen and Hoekstra’s, both works are anti-realist and anti-reductionist. Shrader-Frechette and McCoy, on the other hand, followed Simberloff in espousing reductionism. (It is not clear to me whether their position(s) qualify as realism, instrumentalism, or neither.)

⁴ The verisimilitude concept is also akin to the “similarity” or “isomorphism” between model and world invoked by proponents of the semantic view of scientific theories.

⁵ See Burnham and Anderson (1998) for a motivation of the Kullback-Leibler distance as a measure of distance from the truth.

⁶ The causal factors influencing diversity do not appear in this expression. However, a continuous, non-negative variable X (such as area or isolation) would appear in the following equivalent version:

$$\text{Distance from the truth} \equiv \sum_{S=0}^{\infty} \int_{X=0}^{\infty} f(X)p(S|X) \log \left[\frac{p(S|X)}{\hat{p}(S|X)} \right] dx,$$

where $f(X)$ is the true probability density that X has a given value on a randomly-chosen island. This expression could be expanded to account for any number of factors under investigation.

⁷ See, for instance, Wilcox (1978) on the influences of area, isolation, latitude, elevation and time since island formation.

⁸ Of course, invoking the optimal *number* of factors is far from the only desideratum affecting a model’s proximity to the truth. Two others deserve mention here: *which* factors are invoked, and the general kind of *relationship* assumed (e.g., power law, linear equation, etc.). Here, I assume that both models are on the mark in these respects. In actual cases, however, simple models run a greater risk of leaving out important variables, while complex models are more prone to including irrelevant factors.

⁹ I.e., I applied standard linear regression to the natural-log-transformed “data”.

¹⁰ In this model, ϵ is normally distributed, with an estimated variance of 0.14.

¹¹ Estimated variance of $\epsilon = 0.15$.

¹² I confirmed this via another simulation, exactly like the one described above, except with an expanded sample size of 100 islands. The more complex species-area-isolation model ended up closer to the truth in 90 out of 100 of these larger samples. The average Kullback-Leibler distance of the species-area-isolation model was 0.022; that of the simpler species-area model, 0.091.

¹³ Other plausible definitions of predictive success and verisimilitude also entail a correlation between the two. For example, in the coin-tossing example from above, one could define distance from perfect predictive success as $|B - \hat{p}|$. Here, B represents the outcome of a given coin toss (1 if heads, 0 if tails), and \hat{p} is the probability of heads asserted by a given model or hypothesis. (In the example above, \hat{p} was 0.5.) $|B - \hat{p}|$ is correlated with the measure of distance from the truth implied above for tossed coins: $|p - \hat{p}|$, where p is the true probability of heads.

¹⁴ Leave-one-out cross-validation is one particularly robust way to compare the predictive success, and thus the verisimilitude, of different models (Browne 2000).

¹⁵ While c tends to differ quite a bit from case to case, two other aspects of the species-area “law” are fairly consistent: the power-law form of the relationship, and, for islands that have

reached equilibrium between colonization and extinction, the z value (0.25–0.45; Rosenzweig 1995).

References

- Allen, T.F.H. and Hoekstra, T.W.: 1992, *Toward a Unified Ecology*, Columbia University Press, New York, NY.
- Brown, J.H., Morgan Ernest, S.K., Parody, J.M. and Haskell, J.P.: 2001, 'Regulation of Diversity: Maintenance of Species Richness in Changing Environments', *Oecologia* **126**, 321–332.
- Brown, J.R.: 1985, 'Explaining the Success of Science', *Ratio* **27**, 49–66.
- Browne, M.W.: 2000, 'Cross-Validation Methods', *Journal of Mathematical Psychology* **44**, 108–132.
- Burnham, K.P. and Anderson, D.R.: 1998, *Model Selection and Inference: A Practical Information-Theoretic Approach*, Springer, New York, NY.
- Forster, M.R. and Sober, E.: 1994, 'How to Tell When Simpler, More Unified, or Less *Ad Hoc* Theories will Provide More Accurate Predictions', *British Journal for the Philosophy of Science* **45**, 1–35.
- Griffiths, T.A. and Klingener, D.: 1988, 'On the Distribution of Greater Antillean Bats', *Biotropica* **20**, 240–251.
- Hacking, I.: 1980, 'Experimentation and Scientific Realism', *Philosophical Topics* **13**, 71–87.
- Hanski, I.: 1992, 'Inferences from Ecological Incidence Functions', *The American Naturalist* **139**, 657–662.
- Haeckel, E.: 1866, *Generelle Morphologie der Organismen: Allgemeine Grundzüge der Organischen Formen-Wissenschaft, Mechanisch Begründet durch die von Charles Darwin Reformirte Descendenz-Theorie*, Reimer, Berlin, Germany.
- Heatwole, H. and Levins, R.: 1972, 'Trophic Structure Stability and Faunal Change during Recolonization', *Ecology* **53**, 531–534.
- Kieseppä, I.A.: 1996, *Truthlikeness for Multidimensional, Quantitative Problems*, Kluwer, Boston, MA.
- Laudan, L.: 1981, 'A Confutation of Convergent Realism', *Philosophy of Science* **48**, 19–49.
- Levins, R.: 1966, 'The Strategy of Model Building in Population Biology', *American Scientist* **54**, 421–431.
- Levins, R. and Lewontin, R.: 1982, 'Dialectics and Reductionism in Ecology', in E. Saarinen (ed.), *Conceptual Issues in Ecology*, D. Reidel, Boston.
- Niiniluoto, I.: 1998, 'Verisimilitude: The Third Period', *British Journal for the Philosophy of Science* **49**, 1–29.
- Peters, R.H.: 1991, *A Critique for Ecology*, Cambridge University Press, New York, NY.
- Rosenzweig, M.L.: 1995, *Species Diversity in Space and Time*, Cambridge University Press, Cambridge, England.
- Ruse, M.: 1988, *Philosophy of Biology Today*, State University of New York Press, Albany, NY.
- Saarinen, E. (ed.): 1982, *Conceptual Issues in Ecology*, D. Reidel, Boston, MA.
- Scheiner, S.M.: 1993, 'Introduction: Theories, Hypotheses, and Statistics', in S.M. Scheiner and J. Gurevitch (eds), *Design and Analysis of Ecological Experiments*, Chapman and Hall, New York, NY, pp. 1–13.
- Shrader-Frechette, K.S. and McCoy, E.D.: 1993, *Method in Ecology: Strategies for Conservation*, Cambridge University Press, Cambridge, UK.

- Simberloff, D.: 1982, 'A Succession of Paradigms in Ecology: Essentialism to Materialism and Probabilism', in E. Saarinen (ed.), *Conceptual Issues in Ecology*, D. Reidel, Boston.
- Sterelny, K. and Griffiths, P.: 1999, *Sex and Death: An Introduction to Philosophy of Biology*, University of Chicago Press, Chicago, IL.
- Wilcox, B.A.: 1978, 'Supersaturated Island Faunas: A Species-Age Relationship for Lizards on Post-Pleistocene Land-Bridge Islands', *Science* **199**, 996–998.
- Williams, G.C.: 1966, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, Princeton University Press, Princeton, N.J.
- Wimsatt, W.C.: 1982, 'Reductionistic Research Strategies and Their Biases in the Units of Selection Controversy', in E. Saarinen (ed.), *Conceptual Issues in Ecology*, D. Reidel, Boston.