Appendix 4.4

The following material is Appendix 4.4 for Chapter 4 of: Fowler, C.W. 2009. Systemic Management: Sustainable Human Interactions with Ecosystems and the Biosphere. Oxford University Press

1 The Bayesian interpretation of selective extinction and speciation

To appreciate the interpretation of species frequency distributions (Fig. 1.4) as Bayesian integrators of complexity, consider the following scenario.

Imagine a statistician being asked to undertake a Bayesian analysis to address management questions plagued by conflict, complexity, and uncertainty. In such an approach a computer model that mimics a species could be repeatedly used to try alternative parameters relating to a specific management question. With such models, we could, for example, address the question of how much biomass (or alternatively how many individuals) might optimally be removed from a resource species. Such a statistician could start with a population model of a consuming species, with a set of randomly chosen values for population parameters (e.g., density dependence, age specific mortality, and birth rates, etc.). Consumption rates would be included as part of the model and the behavior of the model would be compared with empirical data. Such data could include the population dynamics of observed consumer species from field studies. Models that do not conform to reality (especially those that result in extinction) would indicate that the respective parameter combination is unrealistic and they would be given low probability.

However, a simple population model is insufficient; there are dynamics of interactions to take into account. The population model, therefore, could be embedded in an ecosystem model. Additional people would be hired to contribute to the exercise. The enlarged team would build models that would be based on parameters and measures of the environment and other species with which the focal species interacts. There would be population models of the other species embedded in the overall model. Producing such models would require accumulation of a great deal of information. Various interactions would be included, but of special importance would be the predator-prey interaction and processes related to consumption rates, and competition. To achieve as much realistic representation as possible, resource populations would be represented in the model to incorporate responses to consumers, especially for the focal species (primarily its consumption rates, still one of the main focuses of the exercise).

Numerous applications of the model would be tried with different parameter combinations. Consumption rates corresponding to model formulations (parameter combinations) exhibiting population dynamics in which levels of less than one organism (extinction) for the consumer species would not be viable options, nor would be other parameters in combinations resulting in extinction. Such combinations of parameters would be rejected as unrealistic. Similarly, parameter combinations that resulted in model behavior showing population variation higher than observed would be rejected or given low weight. Other combinations of parameters would be rejected on the bases of other unrealistic behavior, including such things as unrealistic fluctuations in the age structure of the consuming species population or unrealistic birth rates.

Critics of such an approach might point out that various factors, processes, dynamics or interactions were not taken into account and the model should be expanded to incorporate at least some of them. Further enlargement would account for greater complexity (including more species of competitors, other species in food chains, and more of their interactions with their environments), all matters of ecological mechanics, but never, of course, all of them.

However, a different level of complexity, another realm of consideration, is still missing entirely. Further review in attempts to publish the results in early phases of such a study could easily bring out the fact that evolutionary dynamics were not included. This would extend the level of consideration beyond (but would include as fundamentally important) early attempts to consider ecological mechanics. Evolutionary biologists would be added to the team and the population model might be made to have at least a few parameters that are subject to various elements of selection. Individual organisms could be added to the model (after hiring on experts in individual-based modeling) and individuals in the model would be made subject to selective mortality and reproduction. Coevolutionary biologists (especially those interested in employment and joining the elite project) might find fault with this situation if it is not extended to the other species in the system and all of their interactions, both with other species and their interactions with their environments.

The complexity of such a model would probably prohibit the analysis on all but the largest of existing computers in view of the number of iterations required to sample the parameter space at the heart of the original question. The data required for such an exercise, and estimating the variance of these data, would be prohibitively difficult to obtain. What started as a one person exercise now requires a major team and budget and the politicians involved speak highly of the progress and economic stimulus it represents. However, even unskilled critics would be able to find fault with various parts of the model. It would never be clear whether or not the correct model formulation had been chosen. But because of its complexity and the volume of information used, it would be seen as an honest and well intentioned effort from which something should be learned, in spite of the costs (perhaps because of the costs) and in spite of the fact that consideration of elements, molecules, chemistry, hormones, behavior, and atomic particles has not yet been entertained.

At this point a new set of issues might arise. Perhaps they would originate with the addition of a new, relatively uneducated, or inexperienced, member of the growing team of experts, all brought to bear on the original question. Someone might suggest that the models of individual organisms embedded in the larger model should account for the fact that individual organisms in reality are made up of cells, molecules, atoms, tissues, organs, and have behavior, and interact with each other as well as the individuals of other species. Pheromones are part of both interspecific and intraspecific interactions. The physical environment might be recognized as inclusive of astronomical factors influencing day length, tidal cycles, and weather associated with the movement of the sun and moon. Carbon dioxide, oxygen, nitrogen, and all of the other elements would be brought into the model. To adequately integrate (account for) such factors would require more than had been anticipated at the outset of such a project.

In the frustration of the realization that no model can be so complex as to fully represent reality (or even the whole of such a complex system), one of the seasoned members of the team might realize that to account for certain aspects of reality, the model would have to be physical, much like hydrological models or airplanes used in wind tunnels. In contemplating the fanciful world of what a Bayesian analysis would be if it were based on physical models, the newly arrived naive team member might stimulate a brainstorming mode of thinking, noting that it would be interesting to know what it would be like if an extra-terrestrial with the capacity to introduce billions of genetically engineered species might do as a Bayesian exercise with physical species rather than computer models. After all, they would be injected into a world with all of the factors and processes about which the critics were concerned.

Upon hearing the query, a paleontologist (recently added to the team to help account for long time frames and extinction processes) might react to this hypothetical prospect with the suggestion that they consider what has happened through the processes of selective extinction and speciation as just that: trial-and-error production and testing of species as a Monte Carlo process resulting in a natural Bayesian integration process. The results of the process would be represented in the species frequency distributions among the sets of species found in nature. These would correspond to the probability distributions from conventional Bayesian analysis. This would also take into account that species are made up of individuals because the physical models of species would be made up of physical individuals (with cells, physiological processes, environmentally influenced genetic design, and subject to selective mortality and reproduction).

Further consideration of this possibility would reveal that the "data" ordinarily used in Bayesian integration would be the complex of real factors and conditions to which species (as physical Bayesian integration models) are exposed. In Bayesian approaches, the probabilities with which statisticians work are the probabilities of the models given the data (rather than probabilities of the data given the model for conventional frequentist statistics). The integration represented by species frequency distributions are probabilities of species characteristics given the reality to which they are exposed and the reality of what they are composed, along with all interrelated processes over all scales of time and space. This reality, of course, is impossible to sample completely, to study for full understanding or explanation, or to represent in models adequately. But the probability of that reality is one (1.0—a critical assumption: reality exists; Appendix 1.1). The sciences that study particular phenomena are only conceptual models of pieces of reality.

A frequentist statistician in the group might lean back in his chair, after witnessing this history, and wonder to himself if his Bayesian oriented friends hadn't just come full circle to join him in a frequentist approach with data from direct observations at the species level—with direct practical application if the observations dealt with a specific issue of importance to management. The term "useful reductionism" might enter his mind.

The Bayesian approach to statistical parameter estimation (system characterization) uses computer models. These artificial models of natural systems are constructed with parameters that are allowed to vary randomly in numerous applications of the model (often hundreds of thousands or more). Such a model is compared to the real world by assessing the characteristics and behavior of the model against data. Those parameter combinations that fail to produce realistic "simulation" or representation of the system are discarded (or given low weight). Among the parameter combinations that work, some are more realistic than others and are given higher weight. The probability that a particular parameter value is realistic is measured primarily on the basis of the frequency with which it resulted in acceptable models. Parameter combinations are evaluated on the basis of preselected criteria and weightings based on knowledge of the real system. Frequency distributions of values for each parameter are thus produced based on the number of times (portion of trials) specific values resulted in acceptable models.

Part of the parallel or analogy to be drawn between selective extinction and speciation on the one hand, and Monte Carlo (randomized experimental) aspect of Bayesian statistics on the other, involves the trial-and-error nature of both. A variety of models (parameter combinations) are involved in Bayesian analyses; a variety of species (and combinations of DNA coded characteristics) are involved in natural selection at the species level. The trial-and-error aspects of selective extinction and speciation were developed in Chapter 3 and its appendices.

In nature, species take the place of computer models (are analogues of computer models but are real rather than abstract). Species are actual physical entities with a DNA code rather than models with a computer code as used in Bayesian analyses. Rather than being tested against data collected by human observers from the real world, species are tested against the real world itself. This testing is carried out, therefore, in the full spectrum of complexity and not subject to the error of measurement inherent in data nor errors and inadequacies in the specification of models. Those combinations of code (DNA) that do not meet the criteria for success in nature are removed (rejected) as the species that contain them go extinct, just as certain parameter combinations for Bayesian models are rejected as unrealistic. Thus, the genetic code of extinct species is not represented among species to be duplicated for further testing within the constraints of nature. Within species are individuals and individuals undergo a similar trial-and-error process of natural selection. Thus, evolution is taken into account as one of the characteristics or processes of relevance for the physical Bayesian models we call species.

Thus, existing species are nature's trial-and-error models of success, as tenuous as each one is. These successes are determined as functions of *all* the factors to which they are exposed plus their history of such exposure and the variable circumstances involved (Fig. 1.4). Therefore the probability distribution represented by species frequency distributions (examples of which were shown in Chapter 2) present extremely useful information. In part, this information is in code form (DNA) in parallel with the computer code used in Bayesian models. Thus, species frequency distributions, as probability distributions, reflect the constraints known to operate in natural systems. In other words, existing species represent an integration of all factors in their environment. They are products of natural selection brought about by these factors, including selective extinction and speciation. They represent information of practical use, or guidance, for systemic management as developed in this book.