

Parameter identifiability, constraint, and equifinality in data assimilation with ecosystem models

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One of the most desirable goals of scientific endeavor is to discover laws or principles behind “mystified” phenomena. A cherished example is the discovery of the law of universal gravitation by Isaac Newton, which can precisely describe falling of an apple from a tree and predict the existence of Neptune. Scientists pursue mechanistic understanding of natural phenomena in an attempt to develop relatively simple equations with a small number of parameters to describe patterns in nature and to predict changes in the future. In this context, uncertainty had been considered to be incompatible with science (Klir 2006). Not until the early 20th century was the notion gradually changed when physicists studied the behavior of matter and energy on the scale of atoms and subatomic particles in quantum mechanics. In 1927, Heisenberg observed that the electron could not be considered as in an exact location, but rather in points of probable location in its orbital, which can be described by a probability distribution (Heisenberg 1958). Quantum mechanics lets scientists realize that inherent uncertainty exists in nature and is an unavoidable and essential property of most systems. Since then, scientists have developed methods to analyze and describe uncertainty.

Ecosystem ecologists have recently directed attention to studying uncertainty in ecosystem processes. The Bayesian paradigm allows ecologists to generate a posteriori probabilistic density functions (PDF) for parameters of ecosystem models by assimilating a priori PDFs and measurements (Dowd and Meyer 2003). Xu et al. (2006), for example, evaluated uncertainty in parameter estimation and projected carbon sinks by a Bayesian framework using six data sets and a terrestrial ecosystem (TECO) model. The Bayesian framework has been applied to assimilation of eddy-flux data into simplified photosynthesis and evapotranspiration model (SIPNET) to evaluate information content of the net ecosystem exchange (NEE) observations for constraints of process parameters (e.g., Braswell et al. 2005) and to partition NEE into its component fluxes (Sacks et al.

2006). Verstraeten et al. (2008) evaluate error propagation and uncertainty of evaporation, soil moisture content, and net ecosystem productivity with remotely sensed data assimilation. Nevertheless, uncertainty in data assimilation with ecosystem models has not been systematically explored.

Cressie et al. (2009) proposed a general framework to account for multiple sources of uncertainty in measurements, in sampling, in specification of the process, in parameters, and in initial and boundary conditions. They proposed to separate the multiple sources of uncertainty using a conditional-probabilistic approach. With this approach, ecologists need to build a hierarchical statistical model based on the Bayesian theorem, and to use Markov chain Monte Carlo (MCMC) techniques for sampling before probability distributions of interested parameters or projected state variables can be obtained for quantification of uncertainty. It is an elegant framework for quantifying uncertainties in the parameters and processes of ecological models.

At the core of uncertainty analysis is parameter identifiability. When parameters can be constrained by a set of data with a given model structure, we can identify maximum likelihood values of the parameters and then those parameters are identifiable. Conversely, there is an issue of equifinality in data assimilation (Beven 2006) that different models, or different parameter values of the same model, may fit data equally well without the ability to distinguish which models or parameter values are better than others. Thus, the issue of identifiability is reflected by parameter constraint and equifinality. This essay first reviews the current status of our knowledge on parameter identifiability and then discusses major factors that influence it. To enrich discussion, we use examples in ecosystem ecology that are different from the one on population dynamics of harbor seals in Cressie et al. (2009).

CURRENT STATUS

Data assimilation is in the infant stage in ecosystem ecology but gradually is becoming a more active research subject due to increased data availability from observational networks. Uncertainty analysis with data assimilation has been conducted in a limited number of studies in the past few years (Xu et al. 2006, Verstraeten

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et al. 2008). However, parameter identifiability in association with uncertainty analysis has not been much explored at all. That is not because it is not an issue for data assimilation with ecosystem models but because this issue has not been well formulated to rise to the top of the research agenda in the community.

In reality, the number of identifiable parameters in any process-based ecosystem models is extremely low, particularly when only NEE data from eddy-flux networks are used in data assimilation. For example, Wang et al. (2001) showed that only a maximum of three or four parameters could be determined independently from the CO₂ flux observation. Posterior standard deviations were reduced in seven out of 14 BETHY C₄ plant model parameters and in five out of 23 BETHY C₃ plant model parameters relative to prior standard deviation of parameters (Knorr and Kattge 2005). When six data sets of soil respiration, woody biomass, foliage biomass, litter fall, and soil carbon content were used for parameter estimation, four out of seven carbon transfer coefficients at ambient CO₂ and three at elevated CO₂ can be constrained (Xu et al. 2006). The parameter identifiability is a ubiquitous issue in data assimilation with ecosystem models.

Most of the published studies on data assimilation with ecosystem models avoid the issue of parameter identifiability by using simplified ecosystem models with a very limited set of parameters and/or prescribing many of the parameters in the models. Williams et al. (2005), for example, used a simple carbon box model with nine parameters and five initial values of carbon pools to be estimated from eddy-flux data using ensemble Kalman Filter. Braswell et al. (2005) used a three-carbon-pool model and estimated 23 parameters while initial values of the leaf carbon pool and soil moisture content were prescribed. Luo and his colleagues prescribed partitioning coefficients of photosynthates into plant pools, initial values of pool sizes, and parameters that describe carbon flows into receiving pools in the inverse analysis with six data sets from a forest CO₂ experiment (Luo et al. 2003, Xu et al. 2006). They only estimated seven transfer coefficients from the plant and soil carbon pools based on the rationale that the coefficients are among the most important parameters in determining ecosystem carbon sequestration (Luo et al. 2003). None of the studies has used comprehensive ecosystem models for data assimilation because of the difficulty in identifying hundreds of parameters against limited sets of data. In short, the issue of parameter identifiability in data assimilation has not been explicitly addressed although equifinality is a serious problem in ecosystem modeling (Medlyn et al. 2005). A Bayesian framework described by Cressie et al. (2009) is useful for examining causes of equifinality or parameter identifiability as related to uncertainty in measurements, data availability, specification of model structure, and optimization methods.

FACTORS THAT INFLUENCE PARAMETER IDENTIFIABILITY IN ECOSYSTEM MODELS

Many factors influence parameter identifiability in ecosystem models, such as data availability, model structures, optimization methods, initial values, boundary conditions, ranges, and patterns of priors. Since none of the factors has been explicitly examined in the literature of ecosystem research, the following discussion is mainly derived from our own studies on data availability and compatibility, model structures (E. S. Weng and Y. Q. Luo, *unpublished data*), and optimization methods.

Data availability and compatibility.—It is a common sense that we have to collect relevant data to address a specific scientific issue. For example, we measure mineralization rates to examine nitrogen availability. To characterize ecosystem carbon cycling, we have to collect carbon-related data, such as photosynthesis, respiration, plant growth, and soil carbon content and fluxes.

Recently, eddy-flux networks have been set up worldwide and offer extensive data sets that record net ecosystem exchange of CO₂ (NEE) between the atmosphere and ecosystems. These data sets hold great promises for understanding the processes of ecosystem carbon cycling. Several studies have been conducted on NEE data assimilation to improve predictive understanding of ecosystem carbon processes (Braswell et al. 2005, Williams et al. 2005, Wang et al. 2007). However, it has not been carefully evaluated how different data sets constrain different model parameters.

L. Zhang, Y. Q. Luo, G. R. Yu, and L. M. Zhang (*unpublished manuscript*) recently conducted a study to evaluate parameter identifiability using NEE and biometric data in three forest ecosystems in China. Biometric data in their study include observed values of foliage biomass, fine-root biomass, woody biomass, litter fall, soil organic carbon, and soil respiration. Three experiments of data assimilation were conducted to estimate carbon transfer coefficients using biometric data only, NEE data only, or both the biometric and NEE data.

Biometric data were effective in constraining carbon transfer coefficients from plants pools in leaves, roots, and wood, whereas NEE data strongly constrained carbon transfer coefficients from litter, microbial, and slow soil pools. It indicated that measurements of foliage, fine-root, and woody biomass provided information on C transfer from plant to litter pools. NEE data provided the information of C transfer among litter, microbial biomass, and SOM pools, from which CO₂ was released. In addition, the NEE data set has a much larger sample size than those of biometric data sets. As a result, biometric data sets provided less information than the NEE data set in constraining parameters. When NEE data without gap-filled points were used, the transfer coefficients from litter, microbial, and slow soil carbon pools were much less constrained.

Parameter identifiability is also dependent on relevance of data. In a data assimilation study with a mechanistic canopy photosynthesis model, two activation energy parameters for carboxylation and oxygenation cannot be constrained by NEE data. To constrain those parameters, we need measurements of enzyme kinetics along a temperature gradient. In general, different kinds of data constrain different parameters. However, magnitudes of measurement errors were not found to considerably influence parameter identifiability. We also need to evaluate information content of different length, frequency, and quality of measurement data in constraining different parameters.

Model structures.—Model structure is a main source of uncertainty (Chatfield 1995). We have a tendency to incorporate more and more processes into models to improve fitness between simulated and observed data. Complicated models may integrate more process knowledge but make more parameters less identifiable given certain data sets. We conducted a data assimilation study to evaluate parameter identifiability when carbon pools vary from three to eight among models. The eight-pool model has foliage, woody, roots, metabolic litter, structural litter, microbial, slow soil carbon, and passive soil carbon pools. We lumped together plant pools, litter pools, and soil pools in different combinations to construct four other models with pools ranging from three to seven. Nine data sets (i.e., foliage biomass, woody biomass, fine-root biomass, microbial biomass, litter fall, forest floor carbon, organic soil carbon, mineral soil carbon, and soil respiration) from the Duke CO₂ experiment site (North Carolina, USA) constrain the three-pool model best. Transfer coefficients from passive soil carbon pool and microbial pool could not be identified in seven or eight pool models. Thus, introduction of additional processes in modeling may reduce parameter identifiability.

Optimization methods.—Many papers and books have been published on methods for local and global optimization. We have evaluated different optimization methods for parameter identifiability by comparing conventional and conditional Bayesian inversions. The conditional Bayesian inversion sequentially identifies constrained parameters in several steps. In each step, constrained parameters were obtained. Their maximum likelihood estimators (MLE) were used as priors to fix the parameter values at MLE in the next step of Bayesian inversion with decreased parameter dimensionality. Conditional inversion was repeated until there was no more parameter to be constrained. This method was applied with a physiologically based ecosystem model to hourly NEE measurements at Harvard Forest (Petersham, Massachusetts, USA). The conventional inversion method constrained six out of 16 parameters in the model while the conditional inversion method constrained 14 parameters after six steps.

The conditional inversion resulted in more constrained parameters for two reasons. First, parameter

dimensionality decreased during conditional Bayesian inversion, resulting in less difficulty in finding the optimized parameter values. Second, parameter identifiability is altered due to increased differentiability against NEE data once some other parameter values are fixed within the steps of conditional Bayesian inversion.

In summary, parameter identifiability is a critical but complex issue that needs to be carefully addressed in the future. The hierarchical Bayesian modeling described by Cressie et al. (2009) is a promising approach to explore different factors in influencing parameter identifiability or equifinality.

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The importance of accounting for spatial and temporal correlation in analyses of ecological data

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I congratulate Cressie, Calder, Clark, Ver Hoef, and Wikle for their insightful overview on hierarchical modeling in ecology. These authors are all experts in this field and have contributed to many of the advances that have been made in the field of ecological modeling. Spatial and temporal correlation is a major theme in Cressie et al. (2009). Below I expand on these ideas, discussing some of the advantages and disadvantages of accounting for spatial and/or temporal correlation in analyses of ecological data. While much of the focus in this discussion is on spatial statistical models, similar problems occur when temporal or spatiotemporal correlation is ignored.

AN EXAMPLE OF A STATISTICAL MODEL THAT ACCOUNTS FOR SPATIAL CORRELATION

Unless data are observed within a very specific experimental design, ecological data are often correlated. As an example, consider the problem of estimating stream sulfate concentrations in the eastern United States. We consider data collected as part of the EPA's Environmental Monitoring and Assessment Program (EMAP). The sample sites were mainly located in Pennsylvania, West Virginia, Maryland, and Virginia. For more details about this example and the issues described below, see Irvine et al. (2007).

The response $\mathbf{Y} = [Y_1, \dots, Y_n]'$ is stream sulfate concentration at each of the n stream sites. In this simplified example we consider four predictors $[\mathbf{X}_1, \dots, \mathbf{X}_4]$ which are geographic information system (GIS) derived covariates of the percentage of landscape covered by forest, agriculture, urban, and mining within

the watershed above each stream site. To investigate the relationship between these covariates and the response, we might first consider a standard multiple regression model for $i = 1, \dots, n$ given by

$$Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i3} + \beta_4 X_{i4} + \varepsilon_i \quad (1)$$

where X_{ij} is the i th observation from the j th predictor and the error terms ε_i are independent normally distributed random variables with mean 0 and variance σ^2 . If we follow through with this analysis, we might find that various predictors have statistically significant effects, and we might provide some estimate of the variance, σ^2 . We might also undertake some form of model selection to determine which covariates best explain observed patterns of stream sulfate concentration. However, what if, after accounting for all available covariates, the errors are not independent? What if there is remaining spatial correlation, such that observations that are in close proximity in space are related, and that these predictors haven't fully accounted for such correlation? In this case, we can learn a lot from modeling the nonindependent errors.

As an alternative to a multiple regression model with independent errors, we might consider a spatial regression model where the errors are assumed to be spatially correlated. In this case, we could use the model in Eq. 1, but now would assume that the errors, ε_i , for stream sites close to one another are more similar than the errors for stream sites that are far apart. In mathematical terms, the independent error model assumes $\boldsymbol{\varepsilon} \sim \mathcal{N}(\mathbf{0}, \sigma^2 \mathbf{I})$ where \mathbf{I} is the $n \times n$ identity matrix and $\mathbf{0}$ is a vector of length n , and the spatial regression model assumes $\boldsymbol{\varepsilon} \sim \mathcal{N}(\mathbf{0}, \sigma^2 \boldsymbol{\Sigma})$ where $\boldsymbol{\Sigma}$ is an $n \times n$ correlation matrix. This model goes by many names in the literature and is a type of general (or generalized) linear model. For our stream sulfate problem, we might adopt a model for the covariance matrix $\boldsymbol{\Sigma}$ (see e.g., Schabenberger and

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Gotway 2005) and conclude that observations that are less than 200 km apart are related. This might lead us to think about the biological and physical processes that could lead to this correlation; such research avenues might suggest additional covariates that should be included in our model.

DISADVANTAGES OF IGNORING SPATIAL CORRELATION

What could go wrong if we use the independent error model (Eq. 1) instead of a spatial regression model when the latter is the appropriate model? Plenty. There is a long history of research that demonstrates the many disadvantages of ignoring spatial correlation. Some of the highlights and relations to ecology are described here.

One key issue is sample size. If an independent-error model is adopted (Eq. 1) but the model errors are not independent, then the “effective sample size” will be smaller than the number of observations collected (Schabenberger and Gotway 2005:32). Effective sample size decreases as the correlation between observations increases. If an independent-error model is adopted but the data are correlated, standard errors can be underestimated. For example, when the independent-error model is used and maximum likelihood estimates of the regression coefficients β_1, \dots, β_4 in Eq. 1 are obtained, the parameter estimates will be unbiased but the standard errors of these estimates can be too small (Schabenberger and Gotway 2005:324). In ecology this underestimate of uncertainty can be critical: a covariate may be deemed to be important only because an inappropriate model is selected.

In the area of model selection, Hoeting et al. (2006) showed that ignoring spatial correlation when selecting covariates for inclusion in regression models can lead to the exclusion of relevant covariates in the model. Ignoring spatial correlation in model selection can also lead to higher prediction errors for estimation of the response.

The drawbacks described above were based on research for non-Bayesian spatial modeling. In addition to those drawbacks, non-Bayesian spatial models can lead to underestimation of uncertainty. For example, traditional estimation methods for the spatial regression model assume that the covariance matrix Σ is fixed even when the parameters in the model for Σ are estimated. This leads to estimates of standard errors that do not account for the uncertainty in all parameters.

Spatial correlation also plays a factor in sampling design. Cressie et al. (2009) made an important point that hierarchical models allow for direct incorporation of the sampling design in the modeling. The advantages of a sound sampling design cannot be overemphasized. Too many ecological studies involve sites selected for convenience. When the goal of an analysis is to provide a map or some other inference across a sampling area, then additional considerations should be made when designing the study. It has been shown in a number of contexts that a cluster sampling design is appropriate for

spatially correlated data (e.g., Zimmerman 2006, Irvine et al. 2007, Ritter and Leecaster 2007). A cluster design includes some observations observed at close distances as well as sampling coverage over the entire sampling area. Xia et al. (2006) proposed methodology that produces an optimal design for spatially correlated data where the optimization and subsequent design depends on the goals of the study. For example, a design which emphasizes accurate estimation of the regression coefficients in Eq. 1 will be different than a design which emphasizes accurate estimation of the degree of spatial correlation. While such informed design is not always possible, even cursory consideration of these ideas should lead to improved sampling designs and thus more accurate models.

ADVANTAGES OF BAYESIAN SPATIAL AND SPATIOTEMPORAL HIERARCHICAL MODELS

Numerous examples demonstrate the advantages of accounting for spatial and/or temporal correlation in Bayesian hierarchical models for ecological problems. In the area of species distribution, a series of papers by Gelfand and coauthors (Gelfand et al. 2005, 2006, Latimer et al. 2006) developed a complex hierarchical modeling framework that led to new insights into the spatial distributions of 23 species of a flowering plant family in South Africa. These authors showed that accounting for spatial correlation facilitated the assessment of the factors that impact species distributions, produced accurate maps of species occurrence, and allowed for honest assessment of uncertainty. This work is a particularly good example of the advantages of a Bayesian analysis. The Bayesian paradigm allows for in depth exploration of a virtually unlimited set of results through careful thought and collaboration between ecologists and statisticians. One warning, however, is that the South African species distribution analyses were complex and required many person-hours to produce results. While this work is a terrific example of the possibilities of a Bayesian analysis, it is also an example of the complexities involved in doing such a careful analysis.

In the area of disease ecology, Waller et al. (2007) considered the county-specific incidence of Lyme disease in humans for the northeastern United States. They examined a suite of models ranging from a standard least-squares independent-errors regression model to a hierarchical Bayesian model that accounted for spatial correlation among counties. The inclusion of spatial and temporal components in the model led to new insights into the spread of Lyme disease over space and time and produced maps showing disease trends over space and time. The Bayesian model also allowed for natural incorporation of missing data; the model provided estimates for sites where the predictors were known but the response (Lyme disease counts) was unknown. This work led to new insights into the factors that might contribute to the spread of Lyme disease.

In the area of wildlife disease, Farnsworth et al. (2006) used spatial models to link spatial patterns to the scales over which generating processes operate. They developed a Bayesian hierarchical model to relate scales of deer movement to observed patterns of chronic wasting disease (CWD) in mule deer in Colorado. The Bayesian hierarchical model allowed for investigation of the effects of covariates observed at different scales; covariates for individual deer (e.g., sex and age) and covariates observed across the landscape (e.g., percentage of low-elevation grassland habitat) were included in the model for the probability that an individual deer was infected by CWD. The modeling framework also facilitated a comparison of models for CWD across different scales of deer movement via a model for the unexplained variability in the probability that an individual deer was infected by CWD. The model with the strongest support suggested that unexplained variability has a small-scale component. This led the authors to suggest that future investigations into the spread of chronic wasting disease should focus on processes that operate at smaller, local-contact scales. For example, deer congregate in smaller areas during the winter and disperse across the landscape during the summer; thus CWD may be spread more easily during the winter months.

Hooten and Wikle (2008) considered the spread of an invasive species over time and space. They demonstrated that many insights can be gained via a spatiotemporal model that incorporates a reaction–diffusion component to model the spread of the invasive Eurasian Collared-Dove in the United States. This paper demonstrates another strength of the Bayesian approach as it allows for a natural incorporation of partial differential equation models, long used in mathematics but typically not parameterized to allow for process and data error. The Hooten and Wikle model allows for uncertainty and nonlinearity in the diffusion model (process error) as well as an error term that allows for both observer error and small-scale spatiotemporal variability (data error). The analyses provided a series of maps estimating the extent of the Eurasian Collared-Dove invasion over time for the southeastern United States. The authors concluded that there is remaining variability associated with the rate of species invasion and not attributable to human population. This remaining variability has an estimated spatial range of 1/10 the size of the United States. Such conclusions allow biologists to do a targeted search for other factors that might contribute to the spread of this invasive species.

CHALLENGES AND EDUCATION

All of the spatial and spatiotemporal modeling cited in the previous section involved close collaboration between ecologists and statisticians. While such collaborations advance the fields of statistics and ecology, statisticians need to develop more approachable interfaces to allow scientists to apply complex Bayesian

hierarchical models. As the field of Bayesian hierarchical modeling has matured, software packages such as WinBUGS (*available online*)² have made it possible for non-experts to implement the Markov chain Monte Carlo methods required for estimation and inference in many Bayesian hierarchical models. However, much more work needs to be done in this area, particularly for the more complex models that account for spatial and/or temporal correlation.

In addition, a push for more modern statistical education in ecology and other sciences is needed. In the meantime, where can an ecologist learn more about statistical models to account for spatial and/or temporal correlation? An introduction to these issues with an ecological focus is given in the book by Clark (2007). Waller and Gotway (2004) focus on spatial statistics in public health. Books that require a higher-level understanding of statistics but that are still quite accessible include Banerjee et al. (2004), which focuses on Bayesian hierarchical models for spatial data, and Schabenberger and Gotway (2005), which provides a broad overview to statistical methods for spatial data. Both these books include sections on spatiotemporal modeling. Other overviews of spatiotemporal models with an ecological focus include Wikle (1993) and Wikle et al. (1998).

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² (<http://www.mrc-bsu.cam.ac.uk/bugs>)

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Hierarchical Bayesian statistics: merging experimental and modeling approaches in ecology

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INTRODUCTION

This is an exciting time in ecological research because modern data analytical methods are allowing us to address new and difficult problems. As noted by Cressie et al. (2009), hierarchical statistical modeling provides a statistically rigorous framework for synthesizing ecological information. For example, hierarchical Bayesian methods offer quantitative tools for explicitly integrating experimental and modeling approaches to address important ecological problems that have eluded ecologists due to limitations imposed by classical approaches. Fruitful interactions between ecologists and statisticians have spawned dialogue and specific examples demonstrating the utility of such modeling approaches in ecology (e.g., Wikle 2003, Clark and Gelfand 2006a, b, Ogle and Barber 2008), and I applaud Cressie et al. for introducing ecologists to some of the fundamental statistical and probability concepts underlying hierarchical statistical modeling. Readers are also referred to Ogle and Barber (2008) for a more in-depth treatment of the hierarchical modeling framework, fundamental probability results, and examples that illustrate the advantages of this approach in plant physiological and ecosystem ecology.

Hierarchical statistical modeling approaches are promising for addressing complex ecological problems, and I imagine that in the next 10–20 years, these approaches will be commonly employed in ecological data analysis. However, application of these approaches requires appropriate training, but training opportunities in hierarchical modeling methods that integrate experimental and/or observational data with models are lacking (Hobbs and Hilborn 2006, Hobbs et al. 2006, Little 2006). Thus, overview papers such as those by Cressie et al. (2009) and Ogle and Barber (2008) are expected to stimulate interests and motivate new curriculums that deliver training in modern, model-based approaches to data analysis. Cressie et al. discuss several strengths and limitations of hierarchical statistical modeling, but no single topic is treated in great detail. Thus, I expand upon the importance of the “process model” because I see this as a key element of hierarchical statistical modeling that facilitates explicit integration of experiments (data) and ecological theory (models).

EXPERIMENTAL VS. MODELING APPROACHES

Ecologists generally take one of two approaches to tackling scientific problems: experimental vs. modeling (Herendeen 1988, Grimm 1994). Perhaps the most common approach is to couch a study within an experimental or sampling design framework that “controls” for sources of variability, followed up by standard, frequentist-based hypothesis testing (Cottingham et

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al. 2005, Hobbs and Hilborn 2006, Stephens et al. 2007). Alternatively, one may employ mathematical or simulation models that may have weak ties to experimental data and that are often used for hypothesis generation, parameter estimation, or prediction (Pielou 1981, Rastetter et al. 2003). Rarely are these two approaches combined in such a way that considers all relevant information (e.g., data), preserves sources of variability introduced by the experimental or sampling design, formalizes existing knowledge about the ecological system through quantitative models, and simultaneously allows for hypothesis testing, hypothesis generation, and parameter estimation.

Although the experimental approach can yield important insight into the behavior of ecological systems, it is a “slow” learning process that forces the experimentalist to design a study to fit a relatively restrictive analysis framework (Little 2006). For example, a particular study may yield multiple types of data representing different biological processes operating at diverse temporal and spatial scales. As Ogle and Barber (2008) note, however, the data are often treated in a piece-wise fashion where different components of the data are analyzed independent of each other despite the fact that all/most data arise from interconnected processes. Moreover, data analysis tends to proceed via simple analysis of variance (ANOVA) or regression methods (Cottingham et al. 2005, Hobbs and Hilborn 2006) that assume linearity and normality of responses (e.g., data) and parameters (e.g., treatment effects, regression coefficients). Depending on the context, more sophisticated analyses in the form of hierarchical statistical modeling may be applied. It should be noted that most hierarchical modeling methods can be implemented within different frameworks such as Bayesian or maximum likelihood. Examples include repeated-measurement or longitudinal data models (Lindsey 1993, Diggle et al. 2002), multilevel models (Goldstein 2002, Gelman and Hill 2006), or, more generally, linear, nonlinear, or generalized linear (for non-Gaussian data) mixed-effects models (e.g., Searle et al. 1992, Davidian and Giltinan 1995, Gelman and Hill 2006). Such hierarchical modeling methods, however, are often not employed by ecologists even though the data structure may call for such methods (e.g., Potvin et al. 1990, Peek et al. 2002).

Cressie et al. (2009) point out an important shortcoming of non-hierarchical, classical analyses such as ANOVA and regression. That is, these methods assume that “the uncertainty lies with the data and is due to sampling and measurement.” The hierarchical versions that include random effects, however, allow for additional sources of uncertainty due to, for example, temporal, spatial, or individual variability that is separate from measurement error. When considering real ecological systems, especially in field settings, a large fraction of the unexplained variability may be due to process error. Process error exists for two primary and

interrelated reasons. First, other influential factors (e.g., covariates) that vary by, for example, individual (or “subject”), time, or location, are often not measured or not considered in the analysis. Second, it is impossible to define a statistical or mathematical model that describes the ecological system exactly. Importantly, classical data analysis approaches may be inappropriate in many settings because ecological systems give rise to multiple sources of uncertainty and involve multiple, interacting, nonlinear, and potentially non-Gaussian processes.

On the other end of the spectrum lies the modeling approach. The application of process models in ecology has a rich history stemming back to, for example, theoretical models in population and community ecology (see reviews by Getz 1998, Jackson et al. 2000) to ecological systems modeling (Patten 1971, Jørgensen 1986) such as terrestrial ecosystem models (see reviews by Ulanowicz 1988, Hurtt et al. 1998). Process models can range from simple, empirical equations for reconstructing observed patterns to detailed formulations representing underlying mechanisms and interactions. Thus, they can take on many different forms including, for example, stationary and lumped parameter models to deterministic or stochastic differential equation models (e.g., Jørgensen 1986, Gertsev and Gertseva 2004). Such models are often applied for heuristic purposes, and the process of going from a conceptual model to a set of mathematical equations or computer code forces one to quantify existing knowledge, thus improving one’s understanding of the ecological system (Grimm 1994, Rastetter et al. 2003).

Ecological process models have been used in different capacities. Some are employed as tools for gaining inductive insight about an ecological system based on the mathematical structure and behavior of the model (e.g., stability analysis; Getz 1998). When used in this capacity, the models are generally evaluated independent of actual data. Other applications use models to make predictions about an ecological system, and the predictions may be compared against data as a form of model validation (Jørgensen 1986, Jackson et al. 2000). Ogle and Barber (2008) note that the functional forms and parameter values defining such models are often derived from empirical information, but a model of even moderate complexity is rarely rigorously fit to data. For more detailed models, parameter values are commonly obtained via “tuning” so that the model adequately fits a particular data set or, more often, a summary of such data (e.g., sample means). This approach is frequently referred to as “forward modeling,” and comparatively little emphasis is placed on rigorous statistical quantification of parameter and process uncertainty.

Thus, both ecological process modeling and hierarchical statistical modeling are not new. The new and exciting aspect of hierarchical statistical modeling—and especially hierarchical Bayesian modeling as presented by Cressie et al. (2009) and Ogle and Barber (2008)—is the explicit integration of data obtained from exper-

imental and/or observational studies with process models that encapsulate our understanding of the ecological system. This approach facilitates model-based inference and permits us to break free from the relatively restrictive framework of classical hypothesis testing and design-based inference. In particular, it allows us to acknowledge a richer understanding of the ecological system(s), and the process model itself embodies a suite of hypotheses about how the system behaves (e.g., Hobbs and Hilborn 2006). The hierarchical Bayesian framework enables simultaneous analysis of diverse sources of data within the context of an ecological process model or models, thereby providing a very flexible approach to data analysis. I see such flexibility as a major strength of this approach because it can accelerate our ability to gain new ecological insights and develop and test new hypotheses.

INTEGRATION OF EXPERIMENTS AND MODELS

In the previous section, I refer to the “process model” as a mathematical or simulation model that can be developed and applied independently of the hierarchical statistical model. This terminology is different from that in Cressie et al. (2009), and for clarity, I will refer to the “process model” as defined in their paper (i.e., $[E|P_E]$, their Eqs. 1 and 2) as the “probabilistic process model.” The probabilistic process model is a key element of the hierarchical modeling framework because it provides a direct link between the data and the ecological process model. Cressie et al. use the harbor seal haul-out example to nicely illustrate aspects of hierarchical statistical modeling, but the process model that they employ is highly empirical as it simply describes the log of expected seal counts as a linear function of three covariates and their squared terms. As an ecologist who works with diverse and “messy” data describing complex processes, I feel that their example does not sufficiently illustrate the strengths of the process model. This is what I emphasize here, and my intention is to provide a conceptual overview that is accessible to ecologists who may not have a strong background in ecological modeling, statistical modeling, or probability theory.

Let us begin by considering the right-hand side of Eqs. 2 and 4 in Cressie et al. (2009), where $[D|E, P_D]$ is the data model, $[E|P_E]$ is the probabilistic process model, and $[P_D, P_E]$ is the parameter model (i.e., prior). For the data model, one can think of an observed quantity (i.e., data) as “varying around” the true quantity (i.e., latent process) plus observation or measurement error. For the probabilistic process model, one can think of the true or latent process—something that we can never observe directly—as varying around an expected process plus process error. For both models, the error terms are described by probability distributions that quantify variability in the measurement and process errors. Note that the errors do not have to be additive; for example, one could assume multiplicative errors, but a log

transformation would result in additive errors. Once we have accounted for variability in the data explained by the latent processes, then the remaining variability is expected to reflect measurement errors. It is often reasonable to assume that these errors are independent; however, there are situations where knowledge about the measurement process indicates that dependent errors may be more appropriate (e.g., Ogle and Barber 2008).

Conversely, the process errors are likely to exhibit greater “structure” such that they may be correlated in time or space (e.g., Wikle et al. 1998, Wikle 2003); they may also describe random effects reflecting uncertainty introduced at various levels associated with data collection (e.g., Clark et al. 2004). It is often the case that these effects are nested (e.g., individual effects nested within plot, plot effects nested within site, and overall site effects). In most settings, structured process errors are appropriate and follow from the experimental or sampling design. Moreover, incorporation of structure is often necessary for separating measurement and process errors, thereby avoiding identifiability problems. Alternatively, random effects describing, for example, individual or group effects can be directly incorporated into the ecological process model (Ogle and Barber 2008), and process model parameters (P_E) may be modeled hierarchically. For example, Schneider (2006) assumed that the parameters in a differential equation model of plant growth differed between plots (q). They observed several plots composed of single genotypes (g) and modeled the plot-specific parameters (P_{Eq}) as coming from a population described by genotype-specific parameters ($P_{Eg(q)}$). The decision to incorporate random effects into the processes errors vs. the process parameters (or both) will depend on the problem at hand and on one’s assumptions about the process model.

Let us return to the probabilistic process model as describing how the latent process(es) vary around an “expected process” plus process error. The expected process is the ecological process model, and specification of this component can be the most challenging part of assembling a hierarchical Bayesian model. However, this is where the vast knowledge accumulated by “ecological modelers” can be incorporated. It is at this stage that one formalizes their understanding of the ecological system into a consistent set of mathematical equations, yielding a model for the expected process. In constructing this model, one is challenged with balancing detail with simplicity such that important components, processes, and interactions are incorporated in such a way that pieces of the model can be directly related to observable quantities. Simplicity is also key because it is important that one understands the model’s behavior with respect to how model outputs are affected by functional forms (or specific equations) and parameter values in these equations.

The goal is to arrive at a process model or set of process models—representing alternative hypotheses

about the system—that can be rigorously informed by data. One may choose to define an empirical process model that essentially describes a more traditional ANOVA or linear regression model, but such a model will provide limited insight into underlying mechanisms. Conversely, I advocate using models that reflect hypothesized nonlinearities and interactions and that may represent processes operating at different biological, spatial, or temporal scales. The hierarchical statistical modeling framework, and especially the hierarchical Bayesian framework, can accommodate this complexity by simultaneously considering data collected at different scales that are directly related to model inputs (e.g., parameters) and/or model outputs. Of course, the scientific objectives of a particular study should dictate the structure of the process model in the same way that the objectives lead to a particular experimental or sampling design, but neither should determine the objectives, as is often the case in classical, design-based inference.

In summary, the above discussion highlights the fact that data obtained under an experimental design framework can be analyzed in a hierarchical statistical modeling framework that integrates all relevant data with process models constructed to capture key ecological interactions and nonlinearities. In particular, I find that the hierarchical Bayesian approach provides the most straightforward method for integrating diverse data and process models. Although parameter estimation is often the goal of hierarchical Bayesian modeling, hypothesis testing can also proceed by evaluating posterior distributions of parameters describing hypothesized relationships or responses. More importantly, hypothesis testing and parameter estimation can occur within the context of process models that embody our understanding of the ecological system.

I consider the strengths of hierarchical statistical modeling, and hierarchical Bayesian modeling in particular, to significantly outweigh the limitations because these methods can bring together all sources of information to bear on a particular problem, thereby accelerating our ability to study and learn about real ecological systems. The primary issues that the field of ecology faces with respect to this exciting and powerful approach to ecological data analysis is adequate training and education. In the absence of sufficient training, these methods may be underutilized, misunderstood, or incorrectly applied.

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Bayesian methods for hierarchical models: Are ecologists making a Faustian bargain?

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It is unquestionably true that hierarchical models represent an order of magnitude increase in the scope and complexity of models for ecological data. The past decade has seen a tremendous expansion of applications of hierarchical models in ecology. The expansion was primarily due to the advent of the Bayesian computational methods. We congratulate the authors for writing a clear summary of hierarchical models in ecology.

While we agree that hierarchical models are highly useful to ecology, we have reservations about the Bayesian principles of statistical inference commonly used in the analysis of these models. One of the major reasons why scientists use Bayesian analysis for hierarchical models is the myth that for all practical purposes, the only feasible way to fit hierarchical models is Bayesian. Cressie et al. (2009) do perfunctorily mention the frequentist approaches but are quick to launch into an extensive review of the Bayesian analyses. Frequentist inferences for hierarchical models such as those based on maximum likelihood are beginning to catch up in ease and feasibility (De Valpine 2004, Lele et al. 2007). The recent “data cloning” algorithm, for instance, “tricks” the Bayesian MCMC setup into providing maximum likelihood estimates and their standard errors (Lele et al. 2007). A natural question that a scientist should ask is: if one has a hierarchical model for which full frequentist (say, based on ML estimation) as well as Bayesian inferences are available, which should be used and why? This can only be

answered based on the philosophical underpinnings. The convenience criterion, commonly used to justify the use of Bayesian approach, no longer applies, given the recent advances in the frequentist computational approaches. Although the Bayesian computational algorithms made statistical inference for such models possible, it is not clear to us that the Bayesian inferential philosophy necessarily leads to good science. In return for seemingly confident inferences about important quantities in the face of poor data and vast natural uncertainties, are ecologists making a Faustian bargain?

We begin by stating our reservations about the scientific philosophy advocated by the authors. The authors claim that modeling is for synthesis of information (Cressie 2009). Furthermore, they claim that subjectivity is unavoidable. We completely disagree with both these statements. In our opinion, the fundamental goal of modeling in science is to understand the mechanisms underlying the natural phenomena. Models are quantitative hypotheses about mechanisms that help us connect our prospective understandings to observable phenomena. Certainly in the sociology of the conduct of science, subjectivity often enters in the array of mechanisms hypothesized. However, good scientists are trained rigorously toward considering as many alternative explanations as imagination allows, with the ultimate filters being consistency with observation, experiment, and previous reliable knowledge. Introducing more subjectivity into the process of acquiring reliable knowledge introduces confounding factors in the empirical filtering of hypotheses, and so as scientists, we should be striving to reduce subjectivity instead of increasing it. Just because there is subjectivity in hypothesizing mechanisms, it does not give us a free

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pass to introduce subjectivity in testing those mechanisms against the data.

Obtaining hard, highly informative data requires substantial resources and time. Can expert opinion play a role in inference? Eliciting prior distributions from experts for use in Bayesian statistical analysis has often been suggested for incorporating expert knowledge. However, eliciting priors is more art than science. Aside from this operational difficulty, a far more serious problem is in deciding “who is an expert.” In the news media, “experts” are available to offer sound bites favoring any side of any issue. As scientists, we might insist that expert opinion should be calibrated against reality. Furthermore, the weight the expert opinion receives in the statistical analysis should be based on the amount and quality of information such an expert brings to the table. Bayesian analysis lacks such explicit quantification of the expertness.

We do believe that expert opinion can and should be brought into ecological analyses (Lele and Das 2000, Lele 2004), although not by Bayesian methods. Recently, Lele and Allen (2006) showed how expert opinion can be incorporated using a frequentist framework by eliciting data instead of a prior. The methodology suggested in Lele and Allen (2006) automatically weighs expert opinion and hard data according to their Fisher information about the parameters of the process. The expert who brings in only “noise” and no information automatically gets zero weight in the analysis. Provided the expert opinion is truly informative, the confidence intervals and prediction intervals after incorporation of such opinion are shown to be shorter than the ones that would be obtained without its inclusion. It is thus possible to incorporate expert opinion under the frequentist paradigm.

Hierarchical models are attractive for realistic modeling of complexity in nature. However, as a general principle, the complexity of the model should be matched by the information content of the data. As the number of hierarchies in the model increases, the ratio of information content to model complexity necessarily decreases.

Unfortunately expositions of Bayesian methods for hierarchical models have tended to emphasize practice while deemphasizing the inferential principles involved. Potential consequences of ignoring principles can be severe when such data analyses are used in policy making. In the following, we discuss some myths and misconceptions about Bayesian inference.

“Flat” or “objective” priors lead to desirable frequentist properties.—Many applied statisticians and ecologists believe that flat or non-informative priors produce Bayesian credible intervals that have properties similar to the frequentist confidence intervals. This idea has been touted by the advocates of the Bayesian approach as an important point of reassurance. An irony in this claim is that Bayesian inference seems to be justified under frequentist principles. However, the claim is plain

wrong. The Bayesian credible intervals obtained under flat priors can have seriously incorrect frequentist coverage properties; the actual coverage can be substantially smaller or larger than the nominal coverage (Mitchell 1967, Heinrich 2005; D. A. S. Fraser, N. Reid, E. Marras, and G. Y. Yi, *unpublished manuscript*). A practicing scientist should ask: Under Bayesian inferential principles, what statistical properties are considered desirable for credible intervals and how does one assure them in practice?

Non-informative priors are unique.—Many ecologists believe that the flat priors are the only kind of distributions that are “objective” priors. In fact, in Bayesian statistics the definition of non-informative prior has been under debate since the 1930s with no resolution. There are many different types of proper and improper distributions that are considered “non-informative.” We highly recommend that ecologists read Chapter 5 of Press (2003) and Chapter 6 of Barnett (1999) for a non-mathematical, easily accessible discussion on the issue of non-informative priors. For a quick summary, see Cox (2005). Furthermore, it is also known that different “non-informative” priors lead to different posterior distributions and hence different scientific inferences (e.g., Tyul et al. 2008). The claim that use of non-informative priors lets the data speak is flatly incorrect. A scientist should ask: Which non-informative priors should ecologists be using when analyzing data with hierarchical models?

Credible intervals are more understandable than confidence intervals.—The “objective” credible intervals (i.e., formed with flat priors) do not have valid frequentist interpretation in terms of coverage. For subjective Bayesians, the interpretation of the coverage is in terms of “personal belief probability”. Neither of these interpretations is valid for the “objective” Bayesian analysis. A scientist should ask: What is the correct way to interpret “objective” credible intervals?

Bayesian prediction intervals are better than frequentist prediction intervals.—Hierarchical models enable the researcher to predict the unobserved states of the system. The naïve frequentist prediction intervals, where estimated parameter values are substituted as if they are true parameter values, are correctly criticized for having incorrect coverage probabilities. These intervals can be corrected using bootstrap techniques (e.g., Laird and Louis 1987). Such corrected intervals tend to have close to nominal coverage. It is known that “objective” Bayesian credible intervals for parameters do not have correct frequentist coverage. A scientist should ask: Are prediction intervals obtained under the “objective” Bayesian approach guaranteed to have correct frequentist properties? If not, how does one interpret the “probability” represented by these prediction intervals?

As sample size increases, the influence of prior decreases rapidly.—For models that have multiple parameters, it is usually difficult to specify non-informative priors on all the parameters. The Bayesian

scientists put non-informative priors on some of the parameters and informative priors on the rest. Dennis (2004) showed that the influence of an informative prior can decrease extremely slowly as the sample size increases when there are multiple parameters. We point out that the hierarchical models being proposed in ecology sometimes have enormous numbers of parameters. A scientist should ask: How does one evaluate the influence of prior specification on the final inference?

The problem of identifiability can be surmounted by specifying informative priors.—By definition, no experimental data generated by the hierarchical model in question can ever provide information about the non-identifiable parameters. If this is the case, then how can anyone have an “informed” guess about something that can never be observed? Furthermore, as noted above such “informative” priors can be inordinately influential, even for large samples. A scientist should ask: How exactly does one choose a prior for a non-identifiable parameter, and in what sense is specifying an informative prior a desirable solution for surmounting non-identifiability?

Influence of priors on the final inference can be judged from plots of the marginal posterior distributions.—The true influence of the priors on the final inference is manifested in how much the joint posterior distribution differs from the joint prior. In practice, however, influence of priors is judged by looking at the plots of the marginal priors and posteriors. The marginalization paradox (Dawid et al. 1973) suggests that the practice could fail in spectacular ways. A scientist should ask: How should one judge the influence of the specification of the prior distribution on the final inference?

Bayesian posterior distributions can be used for checking model adequacy.—Cressie et al. (2009) correctly emphasize the importance of checking for model adequacy in statistical inference. They suggest using goodness of fit type tests on the Bayesian predictive distribution. A scientist should ask: If such a test suggests that the model is inadequate, how does one know if the error is in the form of the likelihood function or in the specification of the prior distribution?

Reporting sensitivity of the inferences to the specification of the priors is adequate for scientific inference.—Cressie et al. (2009), as well as many other Bayesian analysts, suggest that one should conduct sensitivity of the inferences to the specification of the priors. In our opinion, it is not enough to simply report that the inferences are sensitive. Inferences are guaranteed to be sensitive to some priors and guaranteed to be non-sensitive to some other priors. What is needed is a suggestion as to what should be done if the inferences are sensitive. A scientist should ask: If the inferences prove sensitive to the particular choice of a prior, what recourse does the researcher have?

Scientific method is better served by Bayesian approaches.—One of the most desirable properties of a scientific study is that it be reproducible (Chang 2008).

The frequentist error rates, either the coverage probabilities or probabilities of weak and misleading evidence (Royall 2000), inform the scientists about the reproducibility of their results. A scientist should ask: How does one quantify reproducibility when using “objective” Bayesian approach?

In summary, we applaud the authors for furthering the discussion of use of hierarchical models in ecology. While hierarchical models are useful, we cannot avoid questioning the quality of inference that results from hierarchy proliferation. Royall (2000) quantifies the concept of weak inference in terms of probability of weak evidence where, based on the observed data, one cannot distinguish between different mechanisms with enough confidence. We surmise that the probability of weak evidence becomes unacceptably large as the number of unobserved states increases. We feel that scientists should be wary of introducing too many hierarchies in the modeling framework. Furthermore, we also have difficulties with the Bayesian approach commonly used in the analysis of hierarchical models. We suggest that the Bayesian approach is neither needed nor is desirable to conduct proper statistical analysis of hierarchical models. The alternative approaches based on the frequentist philosophy of science should be considered in analyzing the hierarchical models.

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Shared challenges and common ground for Bayesian and classical analysis of hierarchical statistical models

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Let me begin by welcoming the paper by Cressie et al. (2009) as an insightful overview of hierarchical statistical modeling that will be valuable from both Bayesian and classical perspectives. Statistical conclusions hinge on the appropriateness of the mathematical models used to represent hypotheses, and Cressie et al. explain many merits of hierarchical models. My comments will highlight the shared challenges and common ground of Bayesian and classical analysis of hierarchical models; give a likelihood theory complement to Cressie et al.'s explanations of their merits; summarize methods for maximum likelihood and “empirical Bayes” estimation and incorporation of uncertainty; and explore some of the claims of Bayesian advantages and classical limitations.

Both Bayesian and classical analyses can and must address the inherent challenges of inference and prediction from noisy data, including comparing models, selecting a best model or combination of models, deciding if a model is acceptable at all, avoiding overfitting and statistical “fishing” or “data dredging,” and incorporating uncertainty. In practice, an appropriate modeling framework trumps many other issues, including choice of Bayesian or classical analysis.

The difference between Bayesian and classical philosophies is that Bayesian analysis uses the mathematics of probability distributions for model parameters, P as defined by Cressie et al., while classical analysis does

not. It is generally agreed that Bayesian analysis must define “probability of P ” as “degree of belief for P ” (or “subjective probability of P ” or other synonymous terms), whereas classical “probability” refers to a frequency of outcomes over a long run (O’Hagan 1994). Bayesian analysis makes “probability” statements about hypotheses, given data, that are formally weighted degree-of-belief comparisons, while classical analysis makes statements about frequencies with which different hypotheses would have produced the data and, in some approaches, hypothetical unobserved data. Classical analysis encompasses much more than Neyman–Pearson and/or Fisher hypothesis testing (which have been critiqued for both their actual logical limitations when correctly interpreted and their potential for misinterpretation; see Mayo and Spanos [2006] for extensions of NP logic). For example, model comparison using Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) takes a classical approach to parameters. While Bayesian and classical approaches are philosophically different, one can interpret results from them in tandem (Efron 2005).

It is worth emphasizing that choosing a hierarchical model is separate from choosing a Bayesian or classical approach for parameters. In a hierarchical model, one has parameters (P , either Bayesian or classical) that define the distribution of unknown ecological states (E) that define the distribution of data (D). I will call E the latent variables and/or random effects, which are among the many names for random variables whose values are not directly known but in theory define relationships among data values, to emphasize that hierarchical models are mixed models (McCulloch and Searle

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2001); as Cressie et al. point out, their example uses a generalized linear mixed model. Having at least one E level make a model hierarchical. Treating the parameters, P , with degree-of-belief probability makes an analysis Bayesian. Cressie et al. illustrate a general route to a Bayesian analysis. A general route to a classical analysis would typically include maximum likelihood estimation of P under various models, with comparisons and estimates of uncertainty made by likelihood ratios (Royall 1997), likelihood ratio hypothesis tests and confidence regions, AIC, parametric or nonparametric bootstrapping, or other approaches.

Why are hierarchical models such a good idea for either Bayesian or classical analysis? Cressie et al. explain the sensibility of conditionally nested hierarchies of probability models in terms of ecological and sampling processes. A complementary view is that the likelihood of the parameters, $P = (P_D, P_E)$, given D , is the integral of Cressie et al.'s Eq. 1 with respect to E :

$$L(P_D, P_E) = [D|P_D, P_E] = \int [D|E, P_D][E|P_E]dE. \quad (1)$$

This states that the probability of D given P is the sum over all possible E values of the probability of (i) those E values given P_E and (ii) D given P_D and those E values. This likelihood is the “[data | parameters]” mentioned by Cressie et al. (2009). The asymptotic (as the amount of data increases) behavior of this likelihood guarantees convergence to the best P , a Gaussian shape for L , and other properties (McCulloch and Searle 2001). By “best” P , one can mean either the “true” P or the P that minimizes the theoretical Kullback-Leibler discrepancy (Burnham and Anderson 2002). Likelihood asymptotics give a theoretical bedrock for both Bayesian and classical analysis. Thus, a more formal appeal of hierarchical models is that they often define appropriate likelihoods for P , which drive the soundness of results from either Bayesian or classical analysis and often make the two approaches yield similar conclusions.

What do I mean by saying that a good model trumps many other considerations? Given a choice between Bayesian analysis of a set of appropriate models and classical analysis with a set of plainly inappropriate models, or vice versa, I'll usually take the one with the appropriate models and then judge the pros and cons of the analysis. Recently, such a choice has led to a common pragmatic appeal of Bayesian analysis: for many people it is currently the easiest framework for analyzing a hierarchical model. With time, I suspect that advances in software and algorithms will move us closer to being able to match any model structure to any analysis approach. Then one will be able to choose a set of hierarchical models based on the ecology and conduct either a Bayesian or classical analysis based on scientific goals.

How would one obtain maximum likelihood results for a hierarchical model such as Cressie et al.'s seal example, so one can use likelihood ratios or AIC, for example? For relatively simple models, generalized

linear mixed model software can accomplish this. For more general models, one can use numerical integration of (1) via either grid-based (Efron 1996) or Monte Carlo integration approaches, reviewed by de Valpine (2004). The latter include Monte Carlo expectation maximization, Monte Carlo Newton-Raphson iterations, “direct” Monte Carlo integration with importance sampling, sequential Monte Carlo integration (“particle filters”), iterated Monte Carlo likelihood ratio approximations, and Monte Carlo kernel likelihood approximations (de Valpine 2004). More recent approaches include iterated particle filtering (Ionides et al. 2006) and data cloning (Lele et al. 2007). Each approach has pros and cons, just as Monte Carlo simulation of Bayesian posteriors can be done with relatively efficient or inefficient flavors of Markov chain Monte Carlo (MCMC) algorithms, with the best choice depending on the specific problem. Monte Carlo kernel likelihood (MCKL) uses the full Bayesian posterior, an appealing feature for those who want to compare Bayesian and maximum likelihood results.

Most of these algorithms use calculations that omit a part of the likelihood known as the “normalizing constant,” which must be estimated as a separate step. This problem is mathematically identical to estimating the marginal likelihood used in Bayes Factors after simulating an MCMC posterior sample (de Valpine 2008). In summary, maximum likelihood and normalizing constant algorithms are highly feasible for many hierarchical models, but current software makes Bayesian analysis more easily available for some models.

To a newcomer, the terminology that “empirical Bayes” is a “non-Bayesian” analysis may seem baffling. Typically, the empirical Bayes parameters would be the maximum likelihood estimates, sometimes called the “plug-in” parameters (Cressie et al. 2009). They do not require degree-of-belief probabilities and so are not Bayesian. The confusing distinction is illustrated by contrasting Efron (1986), who discussed empirical Bayes as a frequentist method, and Little (2006), who called it Bayesian in a “broad view” that encompasses “a large class of practical frequentist methods with a Bayesian interpretation.”

Another potential confusion is that some purported contrasts of Bayesian and classical results are confounded with contrasts of hierarchical and nonhierarchical models, respectively. Empirical Bayes has its roots in the estimation of E (not P): if a hierarchical model is appropriate, then using the conditional distribution of E given D for maximum likelihood P (empirical Bayes) or a posterior for P (Bayes) can be better than using a nonhierarchical maximum likelihood approach for E for each unit of D (Morris 1983). Some contrasts use a nonhierarchical model for the classical side and a hierarchical model for the Bayesian (or empirical Bayes) side. This issue is reflected in Cressie et al.'s (2009) reference to a nonhierarchical analysis as the “usual

likelihood analysis” and in examples in Carlin and Louis (2000) and elsewhere.

How can we compare Bayesian and classical approaches? Some have proposed frequentist (classical) evaluation of Bayesian analysis (Morris 1983, Rubin 1984, Robins et al. 2000). That is, the performance of Bayesian analysis that treats parameters (P) with subjective probability can be evaluated based on the frequencies of outcomes over a “true” distribution of hypothetical data, such as coverage of a “true” P or E value by a credible region, which is naturally related to P -value concepts (not to be confused here with model parameters P). The motivation from a Bayesian view is that “frequency calculations are useful for making Bayesian statements scientific, ... capable of being shown wrong by empirical test” (Rubin 1984). Cressie et al. (2009) appeal to this frequentist justification of “accurate” credible intervals, and such accuracy is driven by the likelihood. The common ground that all models should be scientifically rejectable using the same performance currencies seems valuable. In contrast, a “pure” Bayesian would eschew any model testing based on frequencies of hypothetical, unobserved data.

How do Bayesian and classical analyses of hierarchical models each “incorporate uncertainty,” and how justified are the statements of Cressie et al. (2009) that the Bayesian approach “captures the variability in the parameters [P]” while plug-in estimates “do not account properly for the variability,” and that frequentist incorporation of uncertainty is limited in complexity? Frequentist thinking has long recognized that estimated parameters by definition give an optimistic picture of model fit, and one must account for this in inference and prediction. Cressie et al. mention quadratic likelihood approximations, bootstrapping and cross-validation. One could extend this list by including profile likelihoods, AIC, bootstrapping in empirical Bayes (Efron 1996), generalized cross-validation, generalized degrees of freedom to account for over-fitting due to model selection (Ye 1998), general covariance penalties (Efron 2004), and more. Nevertheless, in many situations a Bayesian posterior sample will be the easiest picture of uncertainty in P one can quickly generate, and indeed the only feasible picture for relatively complex models. Since neither approach is inherently superior at incorporating uncertainty, and since this topic touches the core of much statistical research, the pragmatic boundaries between approaches are likely to change with time.

Although a Bayesian picture of uncertainty is valuable and practical, it is not necessarily better for all purposes than even simply “plugging-in” the maximum likelihood estimate for P . For example, it turns out that using posterior predictive intervals to test overall model fit can be too conservative in the sense that they are guided by the same data used to evaluate the model, so the model is not rejected as often, in a frequency sense, as intended by the analyst (Bayarri 2003, Gelfand 2003). Robins et al. (2000) compared seven classical and “Bayesian” P

value approaches for model assessment. Maximum likelihood (“plug-in”) P values were *more accurate* than posterior predictive P values. The best approaches were newer ones developed by Bayarri and Berger (2000), who also concluded that the P value from maximum likelihood estimates “seems superior” to the posterior predictive P value, “which would seem to contradict the common Bayesian intuition that it is better to account for parameter uncertainty by using a posterior than by” plugging in the maximum likelihood estimate.

The related topics of model selection and model validation or criticism are more important than ever with the Pandora’s box of computational model-fitting opened: we can fit a huge range of models to data—a good problem to have—but must avoid being misled by them. O’Hagan (2003) reviewed Bayesian “model criticism” starting from a “growing unease that the power of HSSS [hierarchical] modeling ... was tempting us to build models that we did not know how to criticize effectively.” To give ecologists context about using DIC for model selection (Cressie et al. 2009): Spiegelhalter et al. (2002) presented DIC “tentatively” on “somewhat heuristic” grounds that were motivated by classical theory. It is also motivated pragmatically by using only information available from MCMC output. AIC is defined for a hierarchical model in terms of the likelihood (1) and parameters, P , and BIC is an asymptotic estimate of a Bayesian marginal likelihood, but neither is available simply from MCMC output (de Valpine 2008). The discussants of Spiegelhalter et al. (2002) largely praised the DIC but raised many cautions and questions about its performance. These fields are sure to see both Bayesian and classical advances.

What should ecologists make of Cressie et al.’s claims that Bayesian methods incorporate information “in a coherent fashion” and give a “conceptually holistic approach to inference”? Based on other Bayesian usages of incorporating information “coherently” (Carlin and Louis 2000, Efron 2005), the first claim seems to refer largely to formulating a likelihood function that includes data related by random effects or from multiple sources (studies or sampling procedures), so it is really a feature of hierarchical models more than of Bayesian analysis. I interpret at least an aspect of the second appeal to refer to the handy practical situation that once you have a posterior sample of all P and E dimensions at your fingertips, much of the rest of your analysis involves summarizing it in various ways without worrying about breaking Bayesian rules. I think this is in part a valuable, practical view, and in part overoptimistic. I have already given the examples that calculating marginal likelihoods for model comparisons requires additional computations; that many conceptually meaningful P values for model criticism can be defined; that model selection will see further development; and that the easily generated posterior predictive intervals may represent over-fits to the data. As an example of a more advanced approach, Cressie et al. (2009) mention cross-validation, a form of

which was recently used to criticize a Bayesian population model for conservation (Snover 2008).

The above variety of considerations illustrate that a thorough Bayesian analysis, beyond just a posterior, can lead to a fairly complicated set of results requiring careful judgment. This seems not very different from the situation in classical analysis that structured probability models define likelihoods, which provide a theoretical core connecting related analyses. An example of how the beguiling unity of treating both random effects and parameters as Bayesian “parameters” led to mistakes in justifying and using state-space fisheries models is explained by de Valpine and Hilborn (2005).

Cressie et al. (2009) give an example of the practical appeal of posterior probability summaries, such as 95% credible intervals, for an E value. Credible intervals are informative, but it is useful to note that such claims about their interpretation revolve around the contrast between degree-of-belief and frequency “probability.”

I will touch briefly on some other aspects of hierarchical model analysis set up by Cressie et al. While the challenge of generating sound MCMC results varies greatly between problems, I do not see computational convergence as a major concern for the overall approaches. For full Bayesian analysis, a practical way to assess the computational error for posterior summaries is the Moving Block Bootstrap (Mignani and Rosa 2001). The subjectivity of Bayesian priors seems to me a more serious issue, but not for the most commonly mentioned reasons. A more subtle problem than sensitivity to prior parameters is that there is no such thing as a universally flat prior, because flatness depends on the parameterization of the model. Flat priors for σ^2 , σ , or $1/\sigma^2$ will all give different results, as will flat priors for λ (population growth rate) or $\log(\lambda)$ in a population dynamics model. In many cases, the difference in results may be small, but nevertheless considering this issue should be a standard step in applications. Finally, while I appreciate the contrast between “curve fitting” and “formal statistical modeling” (Cressie et al. 2009) as a gentle warm-up to the rationale for hierarchical models, the distinction seems limited. Even in a hierarchical model, one is estimating, or “fitting,” parameters of “curves” as reflected by the “smooth curve” language of Cressie et al.’s seal example; the advantage is doing so with a better model.

In summary, hierarchical models are an excellent framework for analyzing data, and Cressie et al. should go a long way towards helping ecologists adopt them. Learning to formulate and interpret hierarchical models involves learning to think clearly about stochastic relationships among variables in complex systems. Likelihood theory represents a major common ground for most Bayesian and classical analysis methods and is the reason they often give practically similar insights. Both classical and Bayesian approaches have pros and cons for pragmatism, performance, and interpretation. My comments are not intended to tally points in a debate, but rather to emphasize that inference and

prediction from noisy data are very hard problems. Bayesian parameter distributions can give useful accountings of uncertainty in many contexts. However, some claims of Bayesian advantages based partly on appeals to intuition do not hold up to theoretical analysis, even if the intuitions have real merits.

While Bayesian approaches are practical for current use, many methods exist for maximum likelihood estimation and related analyses, including incorporation of parameter uncertainty, that would work well for many ecological hierarchical models. Gradually these approaches will allow choice of analysis philosophy to be based on scientific needs rather than having it tied by pragmatism to choice of a hierarchical model structure. Bayesian analysis will still be chosen for some important problems. It will be important for more ecologists to understand relationships between analysis methods to reach shared understanding of statistical results, and therefore of the evidence for hypotheses and support for predictions from data.

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Learning hierarchical models: advice for the rest of us

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Cressie et al. (2009) propose that hierarchical modeling can revolutionize ecology, removing constraints that have forced ecologists to oversimplify statistical models and to ignore important distinctions between measurement error, process error, and model uncertainty. Hierarchical models are enormously flexible, allowing ecologists to think about what questions they would like to answer rather than what models their software can fit. However, for ecologists to benefit from the advantages of the hierarchical approach, they will need to give up the safety of procedure-based statistics for a more technically challenging, flexible, and subjective approach to modeling.

Cressie et al. gloss over the huge challenge that this transition poses for most ecologists. Most of my response will address the practical issues that typical ecologists (i.e., those without advanced course work or degrees in statistics) will have to confront if they want to use hierarchical models to understand their systems better.

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BUGS AS A MODELING LANGUAGE

Cressie et al. (2009) briefly describe the various implementations of the BUGS language (WinBUGS, OpenBUGS, JAGS, and so forth) that are available for fitting hierarchical models. Customized code written in lower-level languages is more flexible, and usually much faster, than these tools, but Cressie note that it is “considerably more tedious to implement” (i.e., probably impossible for most ecologists). Ecologists who want to use hierarchical models will usually need to start either by finding existing software designed for a specific class of problems (e.g., Okuyama and Bolker 2005) or by learning to use some dialect of BUGS (Woodworth 2004, McCarthy 2007). While some researchers feel that BUGS is too dangerous for inexperienced users who have “limited understanding of the underlying assumptions” (Clark 2007:456), it is a very good way to get started using Markov chain Monte Carlo (MCMC) methods for simple models. In particular, while McCarthy (2007) touches only lightly on hierarchical models, he provides a gentle introduction to Bayesian statistics and MCMC, after which one can tackle Clark (2007) or Clark et al. (2006). Gelman and Hill (2006) also present an enormous amount of useful knowledge

about hierarchical models, although they focus on problems in social science. Automatic samplers like WinBUGS may be very slow for larger models; after getting the hang of basic models, ecologists should probably follow Clark's advice and graduate to coding their own samplers for more complex problems.

An enormous advantage of the BUGS language is that it separates a statistical model's definition from its implementation. Such ecological realities as nonnormal distributions, nonlinear responses to predictor variables, and multiple levels of error can easily be incorporated in such models, using a straightforward descriptive language. For example, a statistician would describe Ver Hoef and Frost's (2003) example, Poisson-distributed variation in seal counts with random lognormal variation across years, as

$$\begin{aligned}\theta_t &\sim \text{Normal}(\mu, \sigma_t^2), \\ Y_{it} &\sim \text{Poisson}[\exp(\theta_t)].\end{aligned}\quad (1)$$

The first line says that θ_t , the (natural) logarithm of the mean abundance in year t , is drawn from (\sim) a normal distribution with mean μ and variance σ_t^2 ; the second line says that the observed abundance in site i in year t (Y_{it}) is drawn from a Poisson distribution with mean e^{θ_t} . This notation gives us a compact and precise way to describe statistical models, one that is more broadly useful than the decomposition into normally distributed variance components (e.g., $Y_{ij} = \mu + \varepsilon_i + \varepsilon_j$) that ecologists know from ANOVA designs. The BUGS language closely parallels this notation: the statements

$$\begin{aligned}\text{theta}[t] &\sim \text{dnorm}(\mu, \tau[\text{t}]) \\ \text{exptheta}[t] &\leftarrow \exp(\text{theta}[t]) \\ Y[i, t] &\sim \text{dpois}(\text{exptheta}[t])\end{aligned}\quad (2)$$

show the core of the BUGS code for the Ver Hoef and Frost model. The only differences besides basic typography (\sim instead of \sim , \leftarrow for assigning a value to a variable) are that (1) BUGS describes the normal distribution in terms of its inverse variance or precision, $\tau = 1/\sigma^2$, rather than the more familiar description in terms of the variance, and (2) in some dialects of BUGS, the value e^{θ_t} has to be computed in a separate statement.

These notations also solve another challenge raised by hierarchical models. With increasing complexity of statistical models comes decreased replicability. In the old days of simple t tests, ANOVAs, and linear regressions, it was usually easy to understand exactly how authors had analyzed their data. Now, even though raw data are much more likely to be available in electronic form, replicating analyses can be much more difficult. Precise statistical notation, and the lingua franca of the BUGS language, offer a partial solution. The same model run in any dialect of BUGS should give qualitatively similar results. Although the stochastic component of MCMC makes it impossible to replicate results exactly across dialects, within a dialect one can (and should) specify the starting seed for the random

number generator to ensure perfect replicability. Reviewers and editors should continue to hold authors to a high standard of statistical replicability, even (especially) when they present complex hierarchical models.

The recent development of new BUGS dialects like JAGS has opened up the language, allowing cross-validation of the software and driving innovation (much as the development of the open source R language has enhanced the older S-PLUS dialect of the S language). Computational statisticians are also beginning to develop intermediate-level tools (such as the MCMCpack (Martin et al. 2008) and Umacs (Kerman 2007) packages in R, or the HBC tool kit (*available online*),² that will help bridge the gap between the black box of BUGS and the difficulty of coding models from scratch. With these new software tools and the increasing availability of high-performance computer clusters that can run models over days or weeks if necessary, the computational challenges of hierarchical models should diminish greatly over the next few years.

CHALLENGES

Hierarchical models pose a set of challenges distinct from both the research challenges described by Cressie et al. and the computational difficulties I have just described. Hierarchical models and other more general frameworks such as maximum likelihood estimation force researchers to worry about technical statistical details such as whether they can really estimate the parameters of a given model reliably, and how to make inferences from the results. Hierarchical models are much more finicky than classical procedures: ecologists who want to use them will have consider technical details such as choosing starting values, tuning optimization procedures, and figuring out whether a Markov chain sampler has converged.

Some of Cressie et al.'s challenges, such as determining the adequacy of MCMC sampling or assessing convergence, are technical details that can be overcome by increased computer power or better rules of thumb. The much-criticized subjectivity of Bayesian statistics is also, in my opinion, a relatively minor problem. Ecologists are extreme pragmatists, and will tolerate philosophical inconveniences, such as Bayesian subjectivity, or the inferential contortions raised by the use of null hypothesis testing. Reaching reasonably objective conclusions with Bayesian methods is not trivial, but it is no harder than many other technical challenges that ecologists have mastered (Edwards 1996, Berger 2006).

The greatest challenge of hierarchical models is pedagogical: how can ecologists learn to use the power of hierarchical models, and especially of WinBUGS and related tools, without getting themselves in trouble? The WinBUGS manual famously starts by warning the user to "Beware: MCMC sampling can be dangerous!" Even

² (<http://www.cs.utah.edu/~hal/HBC/>)

worse, the previous line of the manual states, "If there is a problem, WinBUGS might just crash, which is not very good, but it might well carry on and produce answers that are wrong, which is even worse." Clark (2007) says that "turning nonstatisticians loose on BUGs is like giving guns to children." These warnings are like Homeland Security threat advisories: they warn of danger, but provide little guidance.

So how can ecologists avoid trouble? Some recommendations:

1) Use common sense. Remember that there are no free lunches: small, noisy data sets (such as many graduate students collect) can only answer simple, well-posed questions. The social and environmental scientists who have driven the development of hierarchical models typically have noisy but large data sets, where one has thousands of data points from which to estimate parameters. (One may be able to use noisy data where there are a small number of samples in any particular sampling unit, but in this case the design must include a large number of sampling units.)

2) Consider identifiability. Cressie et al. point out that incorporating redundant (unidentifiable) parameters in a hierarchical model can cause big problems: "generally speaking, if identifiability problems go undiagnosed, inferences on these model parameters and possibly others can be misleading." For example, they warn that Ver Hoef and Frost's harbor seal data do not provide enough information to estimate both within population variation (as measured by the negative binomial dispersion parameter) and among-population variation. Unfortunately, it is hard to give a general prescription for avoiding weakly unidentifiable parameters, except to stress common sense again. If it is hard to imagine how one could in principle distinguish between two sources of variation—if different combinations of (say) between-year variation and overdispersion would not lead to markedly different patterns—then they may well be unidentifiable.

3) Increase model complexity, and select models, cautiously. Hierarchical models tempt users to include lots of detail. Bayesian MCMC approaches will often give an answer on problems where frequentist models would crash, but the answers may be nonsensical because of convergence problems. Starting chains in different locations and examining graphical and quantitative summaries of chain movement are supposed to identify these problems, but experienced MCMC users know that one can still be fooled by a sampler that gets stuck for many steps. Bayesian statisticians tend to be less concerned with simplifying models than frequentists, in large part because they recognize that small effects are never really zero, and perhaps because they have traditionally worked in data-rich areas such as the social sciences. However, they still recognize the importance of parsimony: too-complex models will predict future observations poorly, because the model

has been forced to fit the noise in the system as well as the underlying regularities.

Model selection tools are similarly tempting. Thoughtless, automated model selection rules always lead to trouble: newer approaches such as AIC are a big improvement over older stepwise techniques (Whittingham et al. 2006), but are still subject to abuse (Guthery et al. 2005). Bayesians have developed some tools, such as DIC (Spiegelhalter et al. 2002) or posterior predictive loss (Gelfand and Ghosh 1998), to estimate appropriate model complexity, but because of problems with convergence and identifiability, it is much better to use self-discipline to limit model complexity to a level that one can expect to fit from data. (I predict that ecologists will rapidly begin to misuse deviance information criterion (DIC), since it is computed automatically by WinBUGS and is the easiest method of Bayesian hierarchical model selection.)

4) Calibrate expectations. Without using model selection tools, how can one know how much model complexity one can expect to fit from a given data set? Some classic rules of thumb, such as needing on the order of 10 points per experimental unit (Gotelli and Ellison 2004), or 10–20 points per estimated parameter (Harrell 2001, Jackson 2003), or needing at least five to six units to estimate variances, can be helpful. Reading peer-reviewed papers, and paying careful attention to the size of the data sets, their noisiness, and the complexity of the models, is also useful. If all the examples you can find that use the kinds of models you want to fit are working with much larger data sets than yours, watch out! McCarthy (2007) gives a variety of examples using MCMC and Bayesian methods for ecological inference on small, noisy data sets, but his models are very simple and many of them use strongly informative priors to fill in holes in the data.

5) Use simulated data to test models and develop intuition. Perhaps the best way to determine whether a model is appropriately complex for the data is to simulate the model with known parameter values and reasonable (even optimistic) sample sizes, and then to try to fit the model to the simulated "data." Simulated data are a best-case scenario: we know in this case that the data match the model exactly; we know whether our fitted parameters are close to the true values; and we can simulate arbitrarily large data sets, or arbitrarily many smaller data sets, to assess the variability of the estimates (or the statistical power for rejecting a null hypothesis, or the validity of our confidence intervals) and determine whether the model could work given a large enough data set. Software bugs are common in complex hierarchical models; data simulation is a way to avoid the intense frustration caused by attempting to debug a model and estimate parameters at the same time. Simulating data is also a great way to gain general understanding and intuition about a model. Simulating data may seem daunting, but in fact a well-defined statistical model is very easy to simulate. Defining the

statistical model specifies how to simulate it. For example, to simulate a single value from the Ver Hoef and Frost seal model, one could run the BUGS model above with specified parameter values, or in the R language, one could use the commands

```
theta[t] <- rnorm(n=1, mean=mu, sd=sigma)
Y[i, t] <- rpois(n=1, exp(theta[t])).
```

(3)

These commands are similar to the original statistical description (Eq. 1) and the BUGS model (Eq. 2). (The parameterization of the normal distribution has changed yet again, with variability expressed in terms of the standard deviation rather than the variance or the inverse variance, and we use the R commands `rnorm` and `rpois` to generate normal and Poisson random deviates rather than `dnorm` and `dpois` as in BUGS.)

BENDING RULES

Expert statisticians often bend statistical rules. For example, Cressie et al. spend a whole section describing the need to think carefully about experimental design, but they then admit that Ver Hoef and Frost's seal study was not randomized due to logistical constraints. How does one decide that this nonrandom sampling design is acceptable? (Since Ver Hoef and Frost's goal is assess trends only within this one metapopulation, they are at least not making the mistake of extrapolating to a larger population, but how do we know that this "convenience sample" is not biased?) They say that one should try fitting the model with a series of different prior distributions to compare inferences: if the prior represents previous knowledge, how can one play with the prior in this way? How did Ver Hoef and Frost decide which factors to incorporate in their model and which (such as spatial or temporal autocorrelation) to leave out? Other such examples abound. For example, Hilborn and Mangel (1997) use AIC to conclude that a simple model provides the best fit to a set of fisheries data, but they proceed with a more complex model because they feel that the simple model underestimates the variability in the system.

While researchers have developed non-Bayesian approaches to hierarchical models (de Valpine 2003, Ionides et al. 2006, Lele et al. 2007), these tools are typically either experimental or much harder to implement than Bayesian hierarchical models, and so the vast majority of hierarchical models are Bayesian. Despite Dennis's (1996) claims, Bayesians are not as a whole sloppy relativists; however, they do in general see the world more in shades of gray than frequentists. Rather than rejecting or failing to reject null hypotheses, they compute posterior probabilities. Rather than use formal tests to assess the validity of model assumptions and goodness of fit, they look at graphical summaries (Gelman and Hill [2006]; even frequentist statisticians would prefer a good graphical summary to a thoughtless

test of a null hypothesis). Other, non-philosophical reasons that Bayesians, and hierarchical modelers in general, tend to be more flexible, are first that they have often come from areas like environmental and social sciences where huge (albeit noisy) data sets are available, and hence they have had to worry a bit less about P values (everything is significant with a large enough data set) and strict model selection criteria; and second, they have traditionally been more statistically sophisticated than average users of statistics (and hence less likely to cling to black-and-white rules).

My point here is not to say that any of these practices is wrong, but rather to point out that despite many ecologists' desire for a completely objective way to make inferences from data, the new world of hierarchical models will require a lot of judgment calls. The pendulum swings continually between researchers who call for greater rigor (such as Hurlbert's [1984] classic condemnation of pseudoreplication) and those who point out that undue rigor, or rigidity, runs the risk of answering the wrong questions with high precision (Oksanen 2001). Since hierarchical models are so flexible, ecologists will have to make a priori decisions about which parameters and processes to exclude from their models. Giving up the illusion of the complete objectivity of procedure-based statistics and dealing with the complexities of modern statistics will be at least as hard as learning the nuts and bolts of hierarchical modeling.

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Preaching to the unconverted

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Rapid advances in computing in the past 20 years have lead to an explosion in the development and adoption of new statistical modeling tools (Gelman and Hill 2006, Clark 2007, Bolker 2008, Cressie et al. 2009). These innovations have occurred in parallel with a tremendous increase in the availability of ecological data. The latter has been fueled both by new tools that have facilitated data collection and management efforts (e.g., remote sensing, database management software, and so on) and by increased ease of data sharing through computers and the World Wide Web. The impending implementation of the National Ecological Observatory Network (NEON) will further boost data availability. These rapid advances in the ability of ecologists to collect data have not been matched by application of modern statistical tools. Given the critical questions ecology is facing (e.g., climate change, species extinctions, spread of invasives, irreversible losses of ecosystem services) and the benefits that can be gained

from connecting existing data to models in a sophisticated inferential framework (Clark et al. 2001, Pielke and Connant 2003), it is important to understand why this mismatch exists. Such an understanding would point to the issues that must be addressed if ecologists are to make useful inferences from these new data and tools and contribute in substantial ways to management and decision making.

Encouraging the adoption of modern statistical methods such as hierarchical Bayesian (HB) models requires that we consider three distinct questions: (1) What are the benefits of using these methods relative to existing, widely used approaches? (2) What are the barriers to their adoption? (3) What approaches would be most effective in promoting their use? The first question has to do with motivation, that is, why does one build a complex statistical model? Like Cressie et al. (2009) we argue that while the goal of a model may be estimation, prediction, forecasting, explanation, or simplification, the purpose of modeling is the synthesis of information. However, HB methods are not the only tools available for synthesis (Hobbs and Hilborn 2006). So the question needs to be refined to address the specific benefits to be derived from HB models relative

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to more traditional statistical approaches vis-a-vis specific user goals. The second question deals primarily with education, which we believe to be the main barrier to the widespread adoption of these methods. Lastly, answers to the third question build on the answers of questions 1 and 2 to propose a series of actions that would lead to a wider use of HB methods in ecology.

1. *What are the benefits to be derived from HB models relative to other statistical tools?*—Statistical modeling in general and HB modeling in particular, are powerful means to synthesize diverse sources of information. With respect to other statistical means of synthesis, hierarchical models have the advantage of allowing us to coherently model processes at multiple levels. Consider, for example, how we might answer the question of the extent to which 10 species growth rates differ and whether differences between tree species in growth rates are correlated to some species trait, ST. One option might be to first fit separate models using growth data for each individual species together with important covariates (e.g., individual level measurements), and then use the results to fit a regression of the mean growth of each species versus their mean ST values. Another option might be to fit all the data at once and include the ST repeated for all individuals in the plot. Although each of these approaches might work adequately, consider now that you have 100 species with unequal sample sizes. With hierarchical models we could include predictors at both the species and individual levels and allow for partial pooling to improve inferences on rarer species in a way that does not ignore the initial uncertainty in the species growth estimates when estimating the effect of ST across species.

Although the above statistical model could be fit using non-Bayesian hierarchical models, HB becomes a superior choice as we try to incorporate more of our understanding of a process into a model. Returning to the example above, consider the case in which there is spatial autocorrelation between individuals sampled in the same area and we realized that growth was measured with error. Both are real concerns that we might typically ignore or deal with in some ad hoc way; however in a HB framework these sources of error could easily be included an estimated as long as we had an adequate data set.

In addition to their value for synthesis, and of far more pragmatic significance, is the value of HB as a tool for inference, particularly through the process of model checking. The majority of ecologists seek to use data to infer which processes are key in structuring populations, communities and ecosystems. Inference is at the heart of our discipline and therefore attaining the statistical literacy necessary to use HB models can be extremely rewarding, since such models allow us to incorporate the complex variance structures inherent in most biological systems. By working with simulated data derived from HB models, rather than simple point estimates (with associated confidence intervals), we can capture infer-

ential uncertainty and propagate it into predictions in a straightforward manner (Gelman and Hill 2006). The ability to not only make predictions from models but also to quantify the uncertainty in our predictions, is imperative for providing sound scientific advice for management and policy decision makers.

For biologists interested solely in basic, rather than applied questions, prediction serves as an important tool for inference. If we approach a problem with an open mind and the understanding that models are always an approximation of reality, then comparison of the actual data to replicate observations drawn from the posterior predictive distribution (i.e., simulated observations based on our model) becomes a learning exercise rather than an effort to formalize what we already know or believe. Although Cressie et al. (2009) argue that model checking is necessary, but tedious, we see it not only as the key to inference but also as one of the strongest selling points of HB models. Prediction using traditional statistical tools is limited, allowing only for a very limited representation of the true complexity of ecological data. In this context, model checking is an opportunity to truly understand what the models are saying, learn which parts of reality are not captured adequately and suggest future steps. In particular, if simulated data sets do not match the original data sets adequately it leads directly to further model development, reexamination of our interpretation of prior studies, or alterations in experimental design for collection of additional data (Fig. 1).

That model development typically follows model checking illustrates that actual modeling of complex data sets is typically an iterative process. Multiple simpler models are fitted before attempts at the full hierarchical model that we may have had in mind all along or that may have evolved as we critically evaluate the process we are trying to model and better understand the data. Published studies typically emphasized final models but understanding the iterative process of model checking and model development is a key to demystifying modeling to an audience of beginners, who are often supplied only with unfamiliar technical descriptions of models in the methods and little discussion of model fit or misfit. Although standard statistical models caution against extensive model checking because it can lead to overfitting (data dredging), in a simulation framework checks are means of understanding the limits of the models' applicability in realistic replications rather than a reason for accepting or rejecting a model.

From a conceptual perspective, HB models offer a consistent framework that allows the user to apply a large, flexible number of models with complex variance structures (e.g., repeated-measures models, time series analysis, simultaneous consideration of observation and process error, and so on). This is important not only because we can tackle more complex problems but also because it offers a way to educate students and practitioners in a more self-consistent and coherent

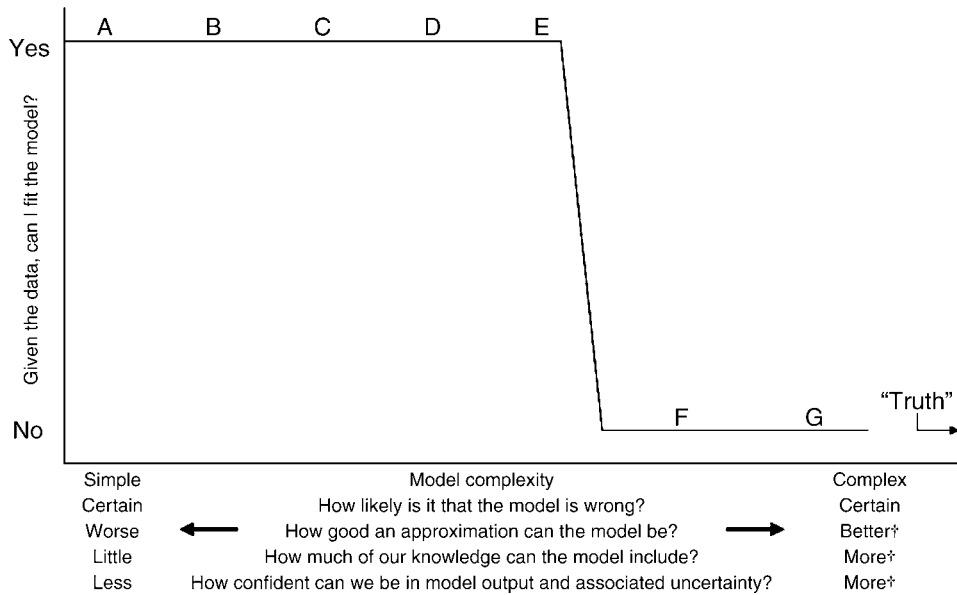


FIG. 1. The model fitting process often consists of fitting progressively more complex models (e.g., A, then B) and/or trying and failing at fitting more complex models (e.g., G, then F) and working backward until one finds a more simplified model that can be fit with the data available (e.g., E). The exact location of the cutoff between E and F will depend on the nature of the data at hand. Knowing which part of reality to allow back into the model by relaxing assumptions or partitioning uncertainty is dependent both on an understanding of the ecological question, the data, and one's statistical literacy. As model complexity increases, one can more closely approximate reality, include more substantial outside (prior) knowledge/intuition, and gain more confidence in the model output and associated uncertainty; however, added complexity only helps if ecological understanding is properly translated into the model structure (the daggers in the figure indicate this caveat).

In the example, Cressie et al. (2009) address a number of models of differing complexity. Model A might correspond to a simple linear regression of numbers vs. time. Such unrealistically simplified models could potentially lead to estimates with tight confidence intervals and low P values, but unreliable inference. Model B might correspond to a generalized linear model with Poisson distributed errors, whereas model C might correspond to the simplest model considered by Cressie et al. (2009), a generalized linear mixed model with multiple explanatory variables. In this context, model C has the advantage that it is no longer assumed that all sites are the same, something we know is false. Partitioning uncertainty into all its potential components and adding site-specific parameters may lead to a model F that cannot be fit with the data at hand, while adding in the assumption that site parameters are related and come from a distribution may result in model D.

approach to statistical analysis that gets away from what has termed a "field-key" approach to statistics, where students collect statistical tools and techniques but fail to see any connections among them at a deep level (Clark 2005, Hobbs and Hilborn 2006).

2. *What are the main barriers to the adoption of HB methods?*—Using HB methods is not easy. There are considerable conceptual and computational barriers to overcome. Conceptually, students must move from a descriptive, test-based statistical framework to an inferential, estimation-based, complex one. Learning to use HB methods requires a larger initial investment to gain a holistic understanding of statistical inference, as opposed to the short term solutions of finding a test for the question at hand or restricting oneself to questions that can be answered with the tests we already know. HB methods may not always be the best tool for answering a particular question, and often simpler methods may be adequate. Nonetheless, learning HB opens up the possibility of addressing a range of previously intractable questions that more accurately encompass the complexity of biological systems. As

ecologists accrue larger datasets, much of it based on remotely gathered data with multiple sources of error, the potential benefits of adopting more complex models increase, moving the curve in Fig. 1 further to the right. Often, students will not see the need for the initial investment in learning HB methods because they lack an understanding of its potential benefits and they perceive modeling as a skill rather than as a tool that anyone can pick up. Thus, ignorance begets indifference, or worst, fear. If they see a paper in say, *Ecological Applications* exhorting the benefits of HB models, they are likely to turn the page and dismiss it as just another modeling paper or simply over their heads. Even if a student or practitioner is interested, the barriers may seem insurmountable without at least some knowledge of either programming or advanced statistical methods.

Indeed, such knowledge is a prerequisite for learning HB methods. One way to acquire these skills is through formal graduate-level courses. Curricula that connect models and quantitative thinking to important questions in ecology have proven to both ignite students' interest in modeling and to convey the relevance and usefulness

of models. However, many ecology and evolution programs still rely on statistics departments to train their students and only a few offer advanced statistical methods courses within their department. Farming out ecology students to be trained in statistics departments is far from ideal because courses are likely to be developed to address the needs of statistics students rather than those of other areas of science. If students fail to see the relevance of the methods to their own discipline, motivation will decline.

Although there are a number of open, short-term courses available (Duke University summer course in ecological forecasting, one-day workshop in Bayesian methods at the Ecological Society of America annual meetings), these offerings are limited, unpredictable, and costly. Moreover, short courses education in HB models often requires not only some programming skills but a complete conceptual overhaul of the students' existing conceptual statistical framework. Although short courses may offer an entry into HB models, the tension between a focus on tools (e.g., WinBUGS) and concepts is very real when time is limited.

A second way to learn HB is through self-teaching. Although a few books have appeared in the last couple of years that make self-teaching possible (Woodworth 2004, Gelman and Hill 2006, Clark 2007, McCarthy 2007), it is still a daunting task to learn these methods on your own without a support network. Fortunately, cyber-communities are becoming an increasingly important form of scientific exchange, and considerable progress can be made in this way (e.g., contributions and exchanges around the development and use of R and WinBUGS Statistical freeware). Auto-didactic approaches are powerful means to learn but they often leave behind major lacunas in knowledge because they tend to focus on the mechanics of carrying out complex statistical analysis with little attention paid to the foundations of underlying statistical inference (e.g., Taper and Lele 2004).

Another barrier to the adoption of HB is the lack of consensus in many of the details of implementation. HB methods are relatively new and there seems to be a lack of consensus on what are the best non-informative priors to use, how best to assess convergence, the utility of deviance information criterion (DIC), etc. This is a major barrier to biologists who are trying to learn and implement these methods, since there is often no clear path to follow. Many ecologists will choose those methods that they know well despite their shortcomings.

3. *What approaches would be most effective in promoting their use?*—Although there are a small number of graduate ecology programs that train some students in modern statistics including HB methods, an impediment to widespread training teaching in these methods is the availability of ecology faculty with statistical background sufficient to offer such courses. Faculty members need efficient and relevant ways to get training in modern statistical modeling and the neces-

sary tools and materials to teach them effectively. Given the time demands placed on faculty, self-education approaches may be unrealistic. One potential solution is to offer one-semester sabbatical leaves that interested faculty could use to attend existing courses at universities where such courses are offered. Better yet, these leaves could be structured around the development of intensive courses that brought together a small group of expert teachers and student-faculty. The advantages of this approach are threefold. First, the burden of teaching could be shared among a small group of experts. Second, the students would be exposed to a variety of viewpoints. Third, participating faculty would gain not only technical and conceptual skills but also a support network to carry the newly acquired skills back to their home institutions. This approach would probably work best with faculty who are already teaching statistics or use modeling in their research, or with postdoctoral researchers who have the time and motivation to learn and use the methods. Costs could be shared by interested institutions and funding agencies.

In institutions that lack faculty trained in modern statistical methods, ecology departments could also work with faculty in the statistics department to develop advanced courses or at least to discuss statistical issues and problems as they arise. The advantage of this approach is that students would be exposed to both the rigor of statistics and disciplinary applications. The shortcomings are generating faculty interest and the considerable investments required to develop a course with multiple instructors from different disciplines and departments. Existing or new collaborations between statisticians and ecologists within the same institution could be leveraged to this end. Educators in ecology and other fields that depend on statistics departments for introductory courses could also initiate a dialog with their statistical colleagues about restructuring "service" courses to cover basic concepts that are at the heart of modern statistical methods such as distributional theory. University administrators could also be approached to offer faculty incentives for the development of courses that cross disciplinary boundaries.

Students can also act as catalysts in the adoption of modern statistics in ecology. Although we caution against the perils of unabashedly using graduate students as a means to improve existing programs, both students and faculty have much to gain from judicious small-scale efforts. Graduate students are often looking for teaching opportunities that give them some experience in curriculum development and allow flexible didactic approaches. At the same time, faculty members are also searching for means to increase students' engagement. One way to address the goals of these two groups is to allow graduate students to structure parts of existing course or to have them offer workshops that provide an introduction to the tools and techniques that will facilitate self-teaching for other students. For instance, a short course in R, or structuring labs in

existing statistics courses in R software rather than a commercial package, will provide students with some familiarity with programming and open the door to a large cyber community with which they can engage. This approach would require some thought on the part of the faculty and students but could potentially be very powerful because students readily accept new knowledge and methods from their peers.

Cyber courses can also be a means to bring statistical literacy to ecologists. This approach could make a number of existing graduate courses in modern statistical methods accessible to ecologists. These courses include among others *Ecological Models and Data* at the University of Florida, *Ecological Theory and Data* at Duke University, *Modeling for Conservation of Populations* at the University of Washington, and *Systems Ecology* at Colorado State University. With relatively minor investments, these courses could be broadcasted to other graduate program in the United States and abroad. Although interactions between students and teaching faculty would be limited, this approach would provide students with a foundation to pursue further education in statistics either through self-teaching or collaboration with statistics faculty at their home institutions. To encourage use and discussion, the cyber courses could be structured around student-faculty groups at the receiving institutions.

Ultimately the widespread adoption of modern statistical methods will require a mix of approaches. What makes sense for individual institutions will depend on the availability of faculty and on motivations to develop offerings in this area. Funding agencies can help

by providing incentives to institutions and individual faculty. To the degree that faculty and students are interested and willing, statistical literacy can be developed.

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