A TAXONOMY AND TREATMENT OF UNCERTAINTY FOR ECOLOGY AND CONSERVATION BIOLOGY

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Abstract. Uncertainty is pervasive in ecology where the difficulties of dealing with sources of uncertainty are exacerbated by variation in the system itself. Attempts at classifying uncertainty in ecology have, for the most part, focused exclusively on epistemic uncertainty. In this paper we classify uncertainty into two main categories: epistemic uncertainty (uncertainty in determinate facts) and linguistic uncertainty (uncertainty in language). We provide a classification of sources of uncertainty under the two main categories and demonstrate how each impacts on applications in ecology and conservation biology. In particular, we demonstrate the importance of recognizing the effect of linguistic uncertainty, in addition to epistemic uncertainty, in ecological applications. The significance to ecology and conservation biology of developing a clear understanding of the various types of uncertainty, how they arise and how they might best be dealt with is highlighted. Finally, we discuss the various general strategies for dealing with each type of uncertainty and offer suggestions for treating compounding uncertainty from a range of sources.

Key words: epistemic uncertainty; linguistic uncertainty; uncertainty; vagueness.

INTRODUCTION

Uncertainty pervades all our attempts to ascertain the truth about the natural and physical environment. It comes in two main flavors: epistemic and linguistic. Epistemic uncertainty is uncertainty associated with knowledge of the state of a system and it includes uncertainty due to limitations of measurement devices, insufficient data, extrapolations and interpolations, and variability over time or space. Linguistic uncertainty, on the other hand, arises because much of our natural language, including a great deal of our scientific vocabulary, is underspecific, ambiguous, vague, context dependent, or exhibits theoretical indeterminacies. To see how linguistic uncertainty may impact on ecology, consider estimating the number of endangered species in a region. Even if all species in the region are known, this estimate may be uncertain because some species are apparently neither endangered nor not endangered and it is not clear whether to count such species or not. In cases such as these, the uncertainty arises because, it is argued, there is no fact of the matter about what constitutes an endangered species. This differs from cases in which there is a fact of the matter but we do not know what it is. Before we can even attempt to count the number of endangered species, it is necessary to decide what we mean by the term ''endangered species.''

There have been a few attempts at the general problem of classifying different types of uncertainty including Kahneman and Tversky (1982), Sorensen (1989), Morgan and Henrion (1990), Kwan et al. (1997), and Smets (1998*a, b*). Some have confused the sources of epistemic and linguistic uncertainty by assigning categories that are too broad, or they have introduced redundant categories. In ecology, Chesson (1978) suggested a scheme that included only epistemic sources of uncertainty. Shaffer (1981, 1987) likewise considered only epistemic uncertainty when he classified phenotypic variation, demographic variation, environmental variation, and catastrophes. His taxonomy (or close relatives like that of Hilborn [1987]) has come to dominate thinking in applied ecology and conservation biology (Boyce 1992, Burgman et al. 1993). Other taxonomies have been suggested, motivated by contexts such as model-building for ecological risk assessment (Ferson and Ginzburg 1996) and management imperatives (Shrader-Frechette 1996).

Specific aspects of the effects of the sources of epistemic uncertainty have attracted attention in ecology mainly for their impacts on decision-making (Taylor 1995, McCarthy et al. 1996, Pascual et al. 1997). In some cases, consideration of even a subset of the full spectrum of uncertainty has been considered to be debilitating (Beissinger and Westphal 1998). But there has been no comprehensive evaluation of the importance of the full spectrum of uncertainties on decision-making processes. Although linguistic uncertainty is common in conservation biology where policy and decision-making play important roles, it is often ignored and only epistemic uncertainty is considered. A clear

understanding of the multifaceted nature of uncertainty will facilitate the implementation of appropriate methods for the treatment of uncertainty in ecology and conservation biology.

EPISTEMIC UNCERTAINTY

Epistemic uncertainty can be classified into six main types: measurement error; systematic error; natural variation; inherent randomness; model uncertainty; and subjective judgment. Each arises in different ways. Since most of these types of uncertainty are well known to working scientists, we treat them only briefly here.

Measurement error

Measurement error results from imperfections in measuring equipment and observational techniques and includes operator error and instrument error. Uncertainty due to measurement error manifests itself as (apparently) random variation in the measurement of a quantity. (It is not truly random—more on this later.) Repeated measurements will vary statistically about a mean. In the absence of all other uncertainty, the relationship between the true quantity and the measured quantity is dependent upon the number of measurements taken, the variation among measurements, the accuracy of the equipment used to take the measurement, and the training and skill of the observer. For example, Taylor and Wade (2000) note that blue whales are conspicuous because of their physical size and the size of their blows. Beaked whales are smaller, surface quickly and erratically, and have no conspicuous blow. They estimate ranges for population sizes from typical surveys to be 600–1600 whales for the former, and 200–3000 whales for the latter, given equal underlying population sizes.

This type of uncertainty is dealt with by applying statistical techniques to multiple measurements or by reporting the measurement with bounds (via confidence intervals or physical constraints of the equipment used).

Systematic error

Systematic error occurs as the result of bias in the measuring equipment or the sampling procedure. It is formally defined as the difference between the true value of the quantity of interest and the value to which the mean of the measurements converges as sample sizes increase. Unlike measurement error, it is not (apparently) random and, therefore, measurements subject to systematic error alone do not vary about a true value. Systematic error can result from the deliberate judgment of a scientist to exclude (or include) data that ought not be excluded (or included), or it can result from unintentional error such as the erroneous calibration of measuring equipment or consistent incorrect recording of measurements. For example, estimates of population sizes based on line transects are sometimes biased because they assume that all animals in the path of the observer (or the ship or plane) are seen. This assumption is false for species that are cryptic, or dive, or otherwise might go unnoticed even in the direct path of a survey (Taylor and Wade 2000). Population sizes will be underestimated unless the violations of this assumption are corrected.

Systematic error can also be introduced due to reference class problems. When deriving statistical results using relative frequencies, choosing the appropriate reference class is crucial. There has been a great deal of recent debate about this issue in the foundations of statistics literature (Hájek 2002, and many papers in Kyburg and Thalos 2002). This issue also has serious consequences in all areas where statistics are used (see, for example, Colyvan et al. 2001). Although there is no known general solution to the reference-class problem, the fact remains that statistics derived by using an inappropriate reference class will seriously bias results. Reference-class problems arise in ecology and conservation biology whenever there are issues of scale. For instance, Hamer and Hill (2000) found that estimates of species richness of butterflies in modified habitat depend on the scale at which surveys are conducted. In other words, the extent of the effects of habitat disturbance depends on the reference class on which the results are based, in this case small or large scales (see also May 1994 on issues of scale).

Some examples of systematic error arise because of the theory ladeness of observation. This alludes to certain biases that exist because observations are tainted, to some extent, by our theories (Chalmers 1999); we observe, in effect, what our theory instructs us to observe. For example, opportunistic records of species often contribute to estimates of species ranges and conservation status (IUCN 1994). But species are the product of scientific interpretation by taxonomists whose species concepts differ, and who have access to different sets of information. Frequently, taxonomic revisions result in the elevation of races or subspecies to the status of a species, and those species may be assessed to be threatened. Such species sometimes appear to increase their ranges through time because the revision and change in conservation status increases interest in the species. This leads in turn to an increase in recorded sightings and creates an illusion of a distributional change that is driven by observational bias. This source of error contributed to biased statistical results for estimates of extinction likelihoods for *Acacia* species in Western Australia that were discounted by independent data (Burgman et al. 2000).

The only way to deal with systematic error is to recognize a bias in the experimental procedure and remove it. Systematic error, however, is notoriously difficult to recognize, except on theoretical grounds. Corrections may only be applied when the magnitude and direction of the bias are known. Such corrections underlie the application of double-sampling methods in environmental science (Gilbert 1987, Philip 1994). Dil-

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igent inspection of the experimental procedure, comparison of estimates with scientific theory and independent studies, and careful attention to detail may be the only tools we have to identify and correct incidences of systematic error in measurements.

Natural variation

Natural variation occurs in systems that change (with respect to time, space, or other variables) in ways that are difficult to predict. Some taxonomies of uncertainty distinguish between the temporal and spatial components of natural variation (e.g., Chesson 1978). An important application of this concept in ecology is the observation that populations are subject to natural variation because individuals die while others are recruited into the population, at rates that may depend on factors such as food availability, weather conditions, fluctuations in predators, disease spread and so on. Natural variation is not a source of epistemic uncertainty per se; it is just that the true value of the parameter in question changes as a result of changes in independent variables. It is often regarded as a source of uncertainty because the true value of the quantity of interest is usually extraordinarily difficult to measure or predict across the full range of temporal and spatial values (or other related variables). A variety of well-known statistical methods are available for the treatment of this kind of uncertainty (Sokal and Rohlf 1981).

Inherent randomness

Inherent randomness in a system occurs not because of our limited understanding of the driving processes and patterns, but because the system is, in principle, irreducible to a deterministic one (the most well-known case is described by Heisenberg's uncertainty principle in quantum mechanics, Hughes 1989). Although many systems are said to be inherently random, genuine examples of this kind of uncertainty are hard to find. Even classic cases of random experiments like coin tosses and the throwing of dice are deterministic; it is just that we do not have enough information about the dynamic processes and initial conditions to make any sensible estimates about the outcomes. Such processes are for all intents and purposes inherently random, but they are not genuinely inherently random. For similar reasons complex systems such as ecosystems and weather patterns are very unlikely to be inherently random. Similarly, chaotic systems are entirely deterministic. They are unpredictable because the deterministic processes generating them and the relevant initial conditions are hard to fully specify (see Stewart 1989, Sugihara et al. 1990). Even though it is extremely unlikely that any biological system is inherently random, this type of uncertainty is mentioned here to distinguish between processes that appear random because of incomplete information and those that are inherently random. We believe the former, rather than the latter, applies in ecology and conservation biology.

Model uncertainty

Model uncertainty occurs as a result of our representations of physical and biological systems. Models may be based on diagrams, flow charts, mathematical representations, computer simulations, and many others. Here, we focus on mathematical and computer models since they are used extensively in applications such as wildlife and natural resource management for predicting future events or for answering questions about a system under specified scenarios (e.g., Possingham et al. 1993, Punt and Smith 1999). The others are more important as conceptual tools, to assist in the understanding of the structure of the system in question.

Model uncertainty arises in two main ways. First, usually only variables and processes that are regarded as relevant and prominent for the purpose at hand are featured in the model. Texts in ecology that describe model building advise that models should be a compromise between the level of understanding of the system, and the kinds of questions it is necessary to answer (e.g., Levins 1966, Burgman et al. 1993). For instance, unstructured, deterministic Malthusian growth models that predict the abundance of populations do not explicitly include parameters that describe rainfall or other weather events because it is thought that although weather patterns may have some indirect effect on reproduction and mortality of the species, they are not sufficiently important in understanding or evaluating the problems at hand that they warrant being explicitly incorporated in the model (Eberhardt 1987).

The second way model uncertainty arises is in the way constructs are used to represent observed processes. The use of the first-order derivative to describe how populations change in time (such as in the logistic growth equation) is a mathematical construct based on an underlying theory about growth rates. Nevertheless, it is still a representation of a natural process; individuals die, others reproduce, they eat available food, encounter predators, sleep, and so forth. None of these activities are mathematical in nature and yet they do have an impact on the population abundance, and may be represented in a variety of mathematical forms. Another abstraction is employed when continuous equations are used to describe discrete processes. These are examples of different views of the correct interpretation of observations and theories. Ginzburg (1986) presented two different ways of interpreting rate-based equations, one in terms of first-order derivatives of population size with respect to time, and the other in terms of second-order derivatives. Which is appropriate depends on whether one views the growth rate or the change in growth rate as driving the population dynamics. Such interpretation and representation of physical systems always leads to model uncertainty. We also note that the uncertainty arising from curve fitting (including interpolation and extrapolation) is a kind of

model uncertainty; the aim is to provide a mathematical expression to describe how variables are related given empirical data points.

Model uncertainty is notoriously difficult to quantify and impossible to eliminate. Morgan and Henrion (1990) offer some solutions for providing the ''best'' available model for particular purposes and scenarios. However, this does not reduce the uncertainty of any particular model. The only reliable way of determining how appropriate a model is for prediction is to perform validation studies. Of course, these are often unfeasible. But when it is feasible to validate aspects of a model, this can be a useful way to determine if it gives the right sorts of outcomes within an acceptable margin of error (see Brook et al. [2000] for one such validation study).

The uncertainty that arises from approximation of established models also fits into the category of model uncertainty. For instance, when a system of continuous differential equations is adopted to represent complicated population dynamics, it is often necessary to employ a numerical algorithm to solve the equations for the quantity of interest. In such cases, a model, or rather a meta-model, is constructed to represent the original model. The uncertainty associated with the meta-model can be viewed as higher order model uncertainty. In some treatments, this type of uncertainty is categorized as uncertainty due to approximation. Approximation of this kind fits quite naturally into the category of model uncertainty; the meta-model is a representation of the original model, constructed in order to make predictions and answer questions about the original model. Treatments of uncertainty in these kinds of meta-models have been well-studied in numerical analysis (see Iserles [1996] and references therein). Many expressions exist for calculating the order of the error associated with particular strategies for numerically solving continuous systems of equations. In this way, higher order model uncertainty is better understood and easier to quantify than its first-order counterpart.

Subjective judgment

Uncertainty due to subjective judgment occurs as a result of interpretation of data. This is especially the case when data are scarce and error prone. There is a vast body of work on scientific reasoning and the philosophical background of the formation of judgments based on empirical data (see, for example, Horwich 1982, Skyrms 1986, Kyburg and Smokler 1964, and Reichenbach 1949). Our aim here is not to summarize the various points of view, but rather to acknowledge that an element of subjective judgment exists in estimates of parameters in the biological sciences, and to highlight the ways it can be dealt with.

Often, there is insufficient empirical data to make reliable statements about parameter values. In such cases, when there is an imperative to proceed with some course of action, the judgment of an expert is used in place of empirical data. Of course, the expert's judgment will be based on observations and experience, both of which constitute empirical data. In all such assessments there is an element of uncertainty.

The standard way of dealing with this type of uncertainty is to assign a degree of belief about an event in the form of a subjective probability. For instance, an expert might assign a probability of 0.7 to the event ''population size of the species is >500 individuals.'' Note that such an assignment might be based on frequency data; one would expect that an expert's judgment would coincide with the results of data if they were available for incorporation into the expert's belief system (Kyburg 1974, Lewis 1986). Degrees of belief, however, are rarely precise. It seems much more reasonable to assign a range of values to represent an expert's degree of belief. Imprecise probabilities can be assigned in the form of interval probabilities, where lower and upper bounds are assigned on the range of beliefs about a particular event. This treatment of uncertainty due to subjective judgment is well known in the literature and includes the imprecise probabilities of Walley (1991) and Dempster-Shafer belief functions (Shafer 1976) and other non-Kolmogorov belief functions such as in Field (2000).

There is a great deal of controversy over the correct interpretation of the probability calculus. In particular, there is an often heated debate between Bayesians, who countenance a subjective interpretation (or degrees of belief) and frequentists, who see probabilities as relative frequencies of one form or another. We do not wish to enter into the debate in any significant way. But since we have raised the issue of a subjective interpretation of probability, we ought to at least rehearse a few of the features of subjective probabilities that are of interest here. The first, we have alluded to already: subjective probabilities can be updated (via Bayes' theorem) when new data comes to hand (where the latter includes frequency data). Second, there are some well-known convergence theorems in Bayesian statistics that tell us that, in most cases of interest, repeated application of Bayes' theorem results in the subjective probabilities converging on the objective chance. (See Howson [1998] for a survey.) The third point is that there are objective ways to arrive at our subjective probabilities. Ramsey (1964) and DeFinetti (1964) showed how to use betting behavior to do this. (See Carnap [1945], Earman [1992], Hájek [1997] and von Mises [1957] for more on the correct interpretation of the probability calculus; see Anderson [1998], Carpenter et al. [1999], Janssen and Carpenter [1999] and Wade [2000] for application of Bayesian methods to conservation biology.)

LINGUISTIC UNCERTAINTY

Linguistic uncertainty can be classified into five distinct types: vagueness, context dependence, ambiguity, indeterminacy of theoretical terms, and underspecif-

icity. All of these uncertainties arise in natural and scientific language, and can impact on biological applications. Of these, vagueness is the most important for practical purposes.

Vagueness

Vagueness arises because our natural language, including much of our scientific vocabulary, permits borderline cases. To reiterate the example given in the introduction, the term ''endangered'' is vague because some species are neither endangered nor not endangered; there are borderline cases. It is generally thought that there is no fact of the matter about whether some borderline case is threatened or not (although, see Williamson [1994] for disagreement on this). This is because there are no facts about our language that determine the extension of the term ''endangered.'' (We should mention that some authors use the term ''fuzziness'' to describe what we are calling ''vagueness.'' We follow Sorensen [1989], Williamson [1994], Read [1995], and others and use the term ''vagueness'' because, unlike ''fuzziness,'' it does not prejudice the question of what is the best method for dealing with the phenomenon in question.)

Vagueness leads to many problems ranging from outright paradox, the so-called Sorites Paradox (Sainsbury 1995), to a particularly resilient kind of uncertainty that can lead to serious problems in management decisions about assigning resources (Regan et al. 2000). For example, the vagueness of the word ''endangered'' ensures that there is no straightforward answer to the question of how many endangered species there are. To be sure, there is no shortage of definitions in the literature for terms such as ''endangered'' (e.g., Millsap et al. 1990, Master 1991, IUCN 1994, Lunney et al. 1996, Nicholopoulos 1999), but the fact remains that terms such as these are vague, and attempts at providing definitions (precise or otherwise) amount to replacing the natural-language word with a technical term. Take, for example, the IUCN treatment of the phrase ''critically endangered.'' Here the IUCN attempts to replace the intuitive meaning with a sharply defined one, the latter given by the relevant IUCN criteria. The strategy is one of eliminating vague terms in favor of sharp ones. So by criterion D (IUCN 1994), for example, critically endangered is redefined to mean ''<50 mature individuals.''

There are many problems with this approach (Williamson 1994). First, a taxon with 50 individuals is classified very differently to a taxon with 49 individuals. This is at odds with the meaning of the original term ''critically endangered'' in which a taxon would not receive a different classification on the basis of a difference of one individual. Perhaps the most significant problem with this elimination strategy, though, is that it is extremely difficult, if not impossible, to implement. Vagueness permeates far too much of our language to hold any serious hope for its elimination. By

way of illustration, consider the U.S. Federal Register's (Vol. 65, Number 218, §219.36) definition of ''species viability'' as:

> A species consisting of self sustaining and interacting populations that are well distributed through the species' range. Self-sustaining populations are those that are sufficiently abundant and have sufficient diversity to display the array of life history strategies and forms to provide for their long-term persistence and adaptability over time.

The number of vague terms employed in the definition gives us some insight into how widespread vagueness is in scientific language and how difficult it would be to eliminate (note, however, that some terms in the definition above may also be subject to the additional sources of linguistic uncertainty described below).

Fortunately, there are other, better ways to deal with uncertainty associated with vagueness than attempting to eliminate it. These include supervaluations (Fine 1975), fuzzy logic and fuzzy set theory (Zadeh 1965, Zimmerman 1996), intuitionistic logic (Putnam 1983), three-valued logic (Körner 1955), paraconsistent logic (Hyde 1997), modal logic (Williamson 1994:270–275), and rough sets (Pawlak 1991, Read 1995). Of these, it is fair to say, that the supervaluational approach is the front runner in philosophical and logical circles, while fuzzy approaches have the edge in computing and engineering circles. The fuzzy set approach uses degrees of membership in a set to deal with borderline cases. For instance, we might decide that under criterion D of the IUCN categories that a species with a population size of 55 will have partial membership (say 0.3 on a scale of 0 to 1) in the set of critically endangered species (Regan et al. 2000). Species with lower population sizes will have a higher degree of membership in the set of critically endangered species. In the supervaluational approach there is no unique sharpening of a vague term. All acceptable sharpenings of the vague concept are used to delineate the borderline region in which the concept neither truly applies nor truly does not apply. For criterion D of the IUCN categories this might result in a range, say population sizes of 50–60 individuals, where a species is considered to be neither critically endangered nor not critically endangered. The supervaluational approach thus recognizes the existence of the borderline region, provides a way of determining the extent of the borderline region, and allows us to treat this region in a natural and intuitive way. In answer to questions about how many objects there are in a particular vague category, the supervaluational approach leads very naturally to an answer in terms of upper and lower bounds.

In the literature on vagueness the usual examples employ predicates like ''tall,'' ''affluent,'' ''mature,'' and the like. All of these admit a very natural, numerical ordering: we can order tallness by height in

meters; we can order affluence by savings (or income) in dollars, and we can order maturity by age in years. It turns out that having this natural ordering is crucial to most of the treatments of vagueness (including the supervaluational approach, fuzzy methods, and even the regimentation approach). Unfortunately many vague terms have a nonnumerical character and so do not readily lend themselves to standard treatments. In fact, many crucial terms in conservation biology are vague in this nonnumerical way. We have in mind here vague predicates such as "threatened," "critically endangered," "optimal habitat," "viable population," and so on. There is no single measure of endangerment, for instance. Instead, we must construct multidimensional measures involving measures of population size, growth/decline rates, extent of habitat decline, and so on (IUCN 1994, see also Burgman et al. 2001 for a treatment of the vague predicate "habitat suitability"). Once such multidimensional measures have been put in place, one of the various numerical treatments can be brought to bear on the problem. It seems to us that approaches such as these to nonnumerical vagueness are theoretically well motivated and are the best way to treat the problems arising from nonnumerical vagueness.

Context dependence

Context dependence is uncertainty arising from a failure to specify the context in which a proposition is to be understood. For example, suppose that it is said that the population size of an unspecified taxon is small. Without specifying the context, the audience is left wondering whether the population size of the taxon in question is small for a vertebrate species, small for a plant species, or small in some other unspecified context. Note that "small" is also vague but that vagueness and context dependence are quite separate issues. The vagueness persists after the context has been fixed. That is, even after we are told the context of the predicate in question, e.g., "small-for-a-plant-species," there are still borderline cases for this. Clearly the way to deal with context dependence is to specify context. But while the solution is clear, this kind of uncertainty is no trivial matter; issues of context dependence arise in classification of threatened species. For instance, much of the IUCN classification scheme applies to terrestrial vertebrate species. So, under the IUCN criteria, a species is classified as endangered in the context of "endangered-for-a-terrestrial-vertebrate-species." Alternative classification criteria have been proposed for plant and butterfly species so they can be considered in the context of relevant threats and demographics of plants and butterflies, using sharp boundaries for vague terms that make sense for these taxa (van Swaay et al. 1997, Keith 1998, van Swaay and Warren 1999).

Ambiguity

Ambiguity is uncertainty arising from the fact that a word can have more than one meaning and it is not clear which meaning is intended. For example, the word 'cover' is used routinely to describe vegetation structural composition. The word is ambiguous between projective foliage cover (the proportion of the ground covered by a vertical projection of the aerial parts of plants e.g., Kershaw 1964:15), and crown cover (the area encompassed by a vertical projection of tree or shrub crown perimeters, e.g., Philip 1994:132). The former definition excludes gaps within crowns from its estimate of cover, whereas the latter definition includes them, relying on the polygon formed by the outer edges of the crown to measure cover. Ambiguity is often confused with vagueness. However, the two types of uncertainty are quite distinct. The ambiguity in the word "cover" does not give rise to borderline cases in the way "endangered" does; there is nothing that is borderline between projective foliage cover and crown cover. Thus tools such as fuzzy logic, which allow for the treatment of borderline cases, are generally of little use in dealing with ambiguity. Ambiguity is best dealt with by making clear which sense of the ambiguous word in question is intended. Though, in practice, this is often easier said than done.

Underspecificity

Underspecificity occurs when there is unwanted generality: the statement in question does not provide the degree of specificity we desire. For example, the statement that there will be rainy days ahead is underspecific because we are left wondering: which days will be rainy?; how many of them will be rainy?; and so on. The statement: "the chance the Tasmanian tiger is extinct is between 0 and 1.0 (inclusive)" is also underspecific. While it is true, it does not indicate that there is a greater chance of the species being extinct than not or vice versa. Underspecificity also arises in situations where data could have been obtained but are no longer available. For example, in fauna and flora surveys it was once sufficient to provide very imprecise locations such as "inland Australia" or "north of Sydney," or to provide no location information at all. Today, most locations are recorded with Global Positioning Systems accurate to a few meters. Opportunistic observations are used to assess temporal trends in species distributions. Records made in the 1800s are especially valuable as signals of past distributions, but underspecification of location renders many of them unusable.

The best we can do with respect to underspecificity is to provide the narrowest possible bounds on estimates given the data, and to make available all the information behind such statements. Unfortunately the word "vague" is commonly used for both underspecificity and borderline cases. We follow Sorensen (1989) here and suggest that the term "vagueness" be reserved for the borderline-case sense.

Indeterminacy of theoretical terms

There is a rather subtle kind of uncertainty that arises from indeterminacies in our theoretical terms. The problem is that the future usage of theoretical terms is not completely fixed by past usage. This means that some of our theoretical terms although not ambiguous now, have the potential for ambiguity. Or, if you prefer, they are ambiguous but such ambiguities are not always recognized when a term first comes into use. (This is sometimes called the open texture of language.) Uncertainty arising from this source is quite different from and more insidious than ambiguity. When we encounter a case of ambiguity we can always use other words to disambiguate. But in the case of theoretical indeterminacy, this can only be done after the fact when new information or usage of the word comes into effect.

An example of this kind of uncertainty is seen in the application of the species concept. (The concept of ''species'' is also vague, but the theoretical indeterminacy associated with the term is quite distinct from its vagueness.) Taxonomic revisions of *Acacia browniana* in 1995 reclassified the taxon into *Acacia browniana*, *A. grisea*, *A. lateriticola*, *A. luteola*, *A. newbeyi*, and *A. subracemosa*. Prior to 1995, taxonomists did not even know that there was an ambiguity in the term *Acacia browniana* and would certainly not have the taxonomic machinery nor the scientific vocabulary to disambiguate. Theoretical indeterminacy might thus be thought of as the potential for ambiguity. Theoretical indeterminacy is also different from vagueness: there are no borderline cases.

Theoretical indeterminacy is dealt with by making conscious decisions about the future usage of theoretical terms when the need presents itself. This is a highly nontrivial matter though. The future usage must be consistent with the past usage and it must be theoretically well motivated and fruitful. The fact that this kind of uncertainty cannot be dealt with now, has ramifications, for instance, for museums and herbariums. It means that there must be trade-offs between acquiring new collections, and allocating resources to superficially redundant collections that may become important, if a taxon is revised.

There is another source of linguistic uncertainty in ecology and conservation biology that defies straightforward classification. This is the uncertainty associated with terms such as ''biodiversity'' and ''biocomplexity'' where not only is there no concise statement or accepted definition, but the very meanings are in dispute. Such terms may well exemplify all sources of linguistic uncertainty, though we believe that the problem here is best thought of as a radical kind of theoretical indeterminacy. The problem is that the relevant theory is so recently developed that the meanings of many of the theory's terms are yet to be settled.

If this is correct, the solution is to develop the relevant theory and allow it to fix the meanings in ways that are fruitful and in keeping with the intuitive themes the words initially evoke. It may turn out that some of these terms are discarded because either they are not fruitful to further theoretical development, or because they are found to describe nothing, but even this is progress. More commonly, suitable meanings are found and agreed upon. In the meantime, the terms are more like placeholders for theoretical terms to which meanings will later be attributed. The focus should thus be on the development of the theory (which, of course, always includes development of the right set of linguistic tools), not on unproductive arguments over what such terms *really* mean. (See Lewis [1983] for more on how to define theoretical terms.)

CONCLUSION

Uncertainty has many different sources. In any application, uncertainties from different sources will compound, including uncertainties from epistemic and linguistic sources (e.g., Regan et al. 2001). It is also important to point out that we do not claim that all uncertainty can be neatly and easily classified into one and only one of the categories we have presented or that the categories presented here are the only ones possible. It may well be that some of our categories are redundant and perhaps some uncertainties seem to fit more than one category. There may even be borderline cases between categories. But the framework above is relatively complete and unambiguous, providing a starting point to think about these often slippery issues.

We have also discussed the different methods required to best deal with the different sources of uncertainty. These appear in Table 1. A very interesting and important question now arises: is there one method capable of dealing with all sources of uncertainty? A good reason to be skeptical that there is such a unified treatment is that the methods outlined above to treat epistemic and linguistic uncertainty are very different. For instance, none of the methods to deal with linguistic uncertainty are probabilistic, while many strategies for treating epistemic uncertainty are. One of the present authors has argued elsewhere that probabilities cannot deal with all sources of uncertainty (Colyvan 2001).

While it is preferable to use the most appropriate method for each type of uncertainty, intervals may be able to cope with all types of numerical uncertainty (i.e., the uncertainty about a parameter value) simultaneously. For instance, uncertainty in the number of endangered species in a region that arises due to vagueness, measurement and systematic error, natural variation, and subjective judgment, can be subsumed within upper and lower bounds. One of the costs of using intervals is that they do not use all of the available information about a number. Using an interval to bound a frequency probability distribution loses information about the central tendency, standard deviation, sample

TABLE 1.   The various sources of epistemic and linguistic uncertainty with their most appropriate general treatments (refer to relevant section for references related to the suggested treatment).

Source of uncertainty	General treatments
Epistemic uncertainty	
Measurement error	statistical techniques; intervals
Systematic error	recognize and remove bias
Natural variation	probability distributions; intervals
Inherent randomness	probability distributions
Model uncertainty	validation; revision of theory based on observation; analytic error estimation (for meta-models)
Subjective judgment	degrees of belief; imprecise probabilities
Linguistic uncertainty	
Numerical vagueness	sharp delineation; supervaluations; fuzzy sets; intuitionistic, three-valued, fuzzy, paraconsistent and modal logics; rough sets
Nonnumerical vagueness	construct multidimensional measures then treat as for numerical vagueness
Context dependence	specify context
Ambiguity	clarify meaning
Indeterminacy in theoretical terms	make decision about future usage of term when need arises
Underspecificity	provide narrowest bounds; specify all available data

size, distribution shape, and so forth. Furthermore, the application of intervals to deal with compounding uncertainty may introduce underspecificity where none existed before. This is perhaps the cost of pursuing a universal treatment. And intervals are only appropriate for numerical uncertainty. Most instances of linguistic uncertainty are not numerical and should be treated in the most appropriate manner for their subcategory.

It may be that the best treatment of compounded uncertainty is a numerical method that incorporates a combination of all the best treatments of the separate sources. Some methods already exist that combine probabilistic and fuzzy set-theoretic methods to treat the combination of vagueness and some types of epistemic uncertainty. In such applications, the probability of a vague event is quantified (Zimmerman 1996, Gabbay and Smets 1998). We should note that in such a treatment the sources of uncertainty are treated separately; probabilistic methods are adopted for epistemic uncertainty and fuzzy set methods for vagueness. This is different from an interval-based method where all the uncertainty is combined. Other methods that integrate probabilistic and fuzzy methods are the hybrid numbers of Ferson and Ginzburg (1995). These attempts to combine methods for dealing with two very different types of numerical uncertainty fall short of providing a unified treatment of all uncertainty. This complaint may not be so serious, since vagueness may well be the dominant source of linguistic uncertainty, and it would seem that probabilities and intervals can deal with all epistemic uncertainty (see Ferson and Ginzburg [1996] and Ferson et al. [1999] for a discussion on the use of intervals and probabilities in risk assessment).

Treatments of uncertainty in ecology and conservation biology are nothing new, and while epistemic uncertainty has largely been the focus, some studies have acknowledged and dealt with both types of uncertainty simultaneously. One notable example is the IUCN categories and criteria for the classification of threatened species. The IUCN categories explicitly deal with nonnumerical vagueness (in the terms vulnerable, endangered, and critically endangered) and natural variation in population sizes (via the probability of extinction, Criterion E). Furthermore, a formal method, based on intervals, exists to deal with the various types of uncertainty in each of the parameters in the criteria (Akçakaya and Ferson 1999, Akçakaya et al. 2000), as well as a method to deal with numerical vagueness in the categories (Regan et al. 2000). This recognition and treatment of the numerous sources of uncertainty in conservation biology results in reliable assessments of threat, given the available data. However, such treatment of both epistemic and linguistic uncertainty is rare.

A comprehensive and systematic treatment of uncertainty in the biological sciences is of considerable importance. In this paper we have made some tentative steps toward that goal by identifying the main sources of uncertainty, including several that, to date, have not been fully appreciated. We have also made recommendations as to the most appropriate methods for dealing with each kind of uncertainty. The issue of whether there is a single method capable of dealing with all uncertainty remains open. There is little doubt, though, that the identification and treatment of uncertainty in the biological sciences is a matter that deserves a great deal of further investigation, and that many of the meth-

ods employed routinely in ecology underestimate the true extent of uncertainty.

Literature Cited

Akçakaya, H. R., and S. Ferson. 1999. RAMAS red list: threatened species classification under uncertainty. User manual for Version 1.0. Applied Biomathematics, Setauket, New York, USA.

Akçakaya, H. R., S. Ferson, M. A. Burgman, D. A. Keith, G. M. Mace, and C. R. Todd. 2000. Making consistent IUCN classifications under uncertainty. Conservation Biology 14:1001–1013.

Anderson, J. L. 1998. Embracing uncertainty: the interface of Bayesian statistics and cognitive psychology. Conservation Ecology 2(1):2. [Online: ⟨http://www.consecol.org/vol2/iss1/art2⟩.]

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821–841.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481–506.

Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387.

Burgman, M. A., D. R. Breininger, B. W. Duncan, and S. Ferson. 2001. Setting reliability bounds on habitat suitability indices. Ecological Applications 11:70–78.

Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London, UK.

Burgman, M. A., B. R. Maslin, D. Andrewartha, M. R. Keatley, C. Boek, and M. McCarthy. 2000. Inferring threat from scientific collections: power tests and an application to Western Australian Acacia species. Pages 7–26 in S. Ferson and M. Burgman, editors. Quantitative methods for conservation biology. Springer-Verlag, New York, New York, USA.

Carnap, R. 1945. The two concepts of probability. Philosophy and Phenomenological Research 5:513–532.

Carpenter, S., W. Brock, and P. Hanson. 1999. Ecological and social dynamics in simple models of ecosystem management. Conservation Ecology 3(2):4. [Online: ⟨http://www.consecol.org/vol3/iss2/art4⟩.]

Chalmers, A. 1999. What is this thing called science? Third edition. University of Queensland Press, Brisbane, Queensland, Australia.

Chesson, P. 1978. Predator–prey theory and variability. Annual Review of Ecology and Systematics 9:323–347.

Colyvan, M. 2001. Is probability the only coherent approach to uncertainty? Risk Analysis, in press.

Colyvan, M., H. M. Regan, and S. Ferson. 2001. Is it a crime to belong to a reference class? Journal of Political Philosophy 9:168–181.

DeFinetti, B. 1964. Foresight: its logical laws, its subjective sources. Reprinted in H. E. Kyburg and H. Smokler, editors. Studies in subjective probability. Wiley, New York, New York, USA.

Earman, J. 1992. Bayes or bust: a critical examination of Bayesian confirmation theory. MIT Press, Cambridge, Massachusetts, USA.

Eberhardt, L. L. 1987. Population predictions from simple models. Journal of Applied Ecology 24:103–118.

Ferson, S., and L. R. Ginzburg. 1995. Hybrid arithmetic. Pages 619–623 in Proceedings of the 1995 Joint ISUMA/NAFIPS Symposium on Uncertainty Modeling and Analysis. IEEE Computer Society Press, Los Alamitos, California.

Ferson, S., and L. R. Ginzburg. 1996. Different methods are needed to propagate ignorance and variability. Reliability Engineering and Systems Safety 54:133–144.

Ferson, S., W. Root, and R. Kuhn. 1999. RAMAS Risk Calc: risk assessment with uncertain numbers. Applied Biomathematics, Setauket, New York, USA.

Field, H. 2000. Indeterminacy, excluded middle and degrees of belief. Noûs 34:1–34.

Fine, K. 1975. Vagueness truth and logic. Synthese 30:265–300.

Gabbay, D. M., and P. Smets, editors. 1998. Handbook of defeasible reasoning and uncertainty management systems. Volume 3. Kluwer, Dordrecht, The Netherlands.

Gilbert, R. O. 1987. Statistical methods for environmental pollution monitoring. Van Nostrand Reinhold, New York, New York, USA.

Ginzburg, L. R. 1986. The theory of population dynamics: I. Back to first principles. Journal of Theoretical Biology 122:385–399.

Hájek, A. 1997. ''Mises redux''—redux: fifteen arguments against finite frequentism. Erkenntnis 45:209–227.

Hájek, A. 2002. Conditional probability is the guide to life. In H. E. Kyburg and M. Thalos, editors. Probability is the very guide of life. Open Court, Chicago, Illinois, USA, in press.

Hamer, K. C., and J. K. Hill. 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. Conservation Biology 14:1435–1440.

Hilborn, R. 1987. Living with uncertainty in resource management. North American Journal of Fisheries Management 7:1–5.

Horwich, P. 1982. Probability and evidence. Cambridge University Press, Cambridge, UK.

Howson, C. 1998. The Bayesian approach. Pages 111–134 in P. Smets, editor. Quantified representation of uncertainty. Volume 1 of D. M. Gabbay and P. Smets, editors. Handbook of defeasible reasoning and uncertainty management systems. Kluwer, Dordrecht, The Netherlands.

Hughes, R. I. G. 1989. The structure and interpretation of quantum mechanics. Harvard University Press, Cambridge, Massachusetts, USA.

Hyde, D. 1997. From heaps and gaps to heaps of gluts. Mind 106:641–660.

Iserles, A. 1996. A first course in the numerical analysis of differential equations. Cambridge Texts in Applied Mathematics. Cambridge University Press, Cambridge, UK.

IUCN. 1994. IUCN red list of threatened animals. International Union for the Conservation of Nature, Gland, Switzerland.

Janssen, M. A., and S. R. Carpenter. 1999. Managing the resilience of lakes: a multi-agent modeling approach. Conservation Ecology 3(2):15. [Online: ⟨http://www.consecol.org/vol3/iss2/art15⟩.]

Kahneman, D., and A. Tversky. 1982. Variants of uncertainty. Pages 509–520 reprinted *in* D. Kahneman, P. Slovic, and A. Tversky, editors. Judgements under uncertainty: heuristics and biases. Cambridge University Press, Cambridge, UK.

Keith, D. A. 1998. An evaluation and modification of World Conservation Union Red List Criteria for classification of extinction risk in vascular plants. Conservation Biology **12**:1076–1090.

Kershaw, K. A. 1964. Quantitative and dynamic ecology. Edward Arnold, London, UK.

Körner, S. 1955. Conceptual thinking. Cambridge University Press, Cambridge, UK.

Kwan, S., F. Olken, and D. Rotem. 1997. Uncertain, incomplete, and inconsistent data in scientific and statistical databases. Pages 127–153 *in* A. Motro and P. Smets, editors. Uncertainty management in information systems: from needs to solutions. Kluwer, Boston, Massachusetts, USA.

Kyburg, H. E. 1974. The logical foundations of statistical inference. Reidel, Dordrecht, The Netherlands.

Kyburg, H. E., and H. Smokler, editors. 1964. Studies in subjective probability. Wiley, New York, New York, USA.

Kyburg, H. E., and M. Thalos, editors. 2002. Probability is the very guide of life. Open Court, Chicago, Illinois, USA, *in press*.

Levins, R. 1966. The strategy of model building in population biology. American Scientist **54**:421–431.

Lewis, D. 1983. How to define theoretical terms. Pages 78–95 reprinted *in* D. Lewis. Philosophical papers. Volume I. Oxford University Press, Oxford, UK.

Lewis, D. 1986. A subjectivist's guide to objective chance. Pages 83–113 reprinted *in* D. Lewis. Philosophical papers. Volume II. Oxford University Press, Oxford, UK.

Lunney, D., A. Curtin, D. Ayers, H. G. Cogger, and C. R. Dickman. 1996. An ecological approach to identifying the endangered fauna of New South Wales. Pacific Conservation Biology **2**:212–231.

Master, L. L. 1991. Assessing threats and setting priorities for conservation. Conservation Biology **5**:559–563.

May, R. M. 1994. The effects of spatial scale on ecological questions and answers. Pages 1–17 *in* P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Science, Oxford, UK.

McCarthy, M. A., M. A. Burgman, and S. Ferson. 1996. Logistic sensitivity and bounds for extinction risks. Ecological Modelling **86**:297–303.

Millsap, B. A., J. A. Gore, D. E. Runde, and S. I. Cerulean. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. Wildlife Monographs **111**:1–57.

Morgan, M. G., and M. Henrion. 1990. Uncertainty: a guide to dealing with uncertainty in quantitative risk and policy analysis. Cambridge University Press, Cambridge, UK.

Nicholopoulos, J. 1999. The endangered species listing program. Endangered Species Bulletin **24**:6–9.

Pascual, M. A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology **11**:966–976.

Pawlak, Z. 1991. Rough sets: theoretical aspects of reasoning about data. Kluwer, Dordrecht, The Netherlands.

Philip, M. S. 1994. Measuring trees and forests. C.A.B., International, Wallingford, UK.

Possingham, H. P., D. B. Lindenmayer, and T. W. Norton. 1993. A framework for the improved management of threatened species based on population viability analysis. Pacific Conservation Biology **1**:39–45.

Punt, A. E., and A. D. M. Smith. 1999. Management of long-lived marine resources: a comparison of feedback-control management procedures. American Fisheries Society Symposium **23**:243–265.

Putnam, H. 1983. Vagueness and alternative logic. Pages 271–286 reprinted *in* H. Putnam. Realism and reason. Cambridge University Press, Cambridge, UK.

Ramsey, F. 1964. Truth and probability. Pages 61–92 reprinted *in* H. Kyburg and H. Smokler, editors. Studies in subjective probability. Wiley, New York, New York, USA.

Read, S. 1995. Thinking about logic: an introduction to the philosophy of logic. Oxford University Press, Oxford, UK.

Regan, H. M., M. Colyvan, and M. A. Burgman. 2000. A proposal for fuzzy IUCN categories and criteria. Biological Conservation **92**:101–108.

Regan, H. M., R. Lupia, A. N. Drinnan, and M. A. Burgman. 2001. The currency and tempo of extinction. American Naturalist **157**:1–10.

Reichenbach, H. 1949. The theory of probability: an inquiry into the logical and mathematical foundations of the calculus of probability. University of California Press, Berkeley, California, USA.

Sainsbury, R. M. 1995. Paradoxes. Second edition. Cambridge University Press, Cambridge, UK.

Shafer, G. 1976. A mathematical theory of evidence. Princeton University Press, Princeton, New Jersey, USA.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. Bioscience **31**:131–134.

Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 59–68 *in* M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Shrader-Frechette, K. 1996. Methodological rules for four classes of scientific uncertainty. Pages 12–39 *in* J. Lemons, editor. Scientific uncertainty and environmental problem solving. Blackwell, Cambridge, Massachusetts, USA.

Skyrms, B. 1986. Choice and chance: an introduction to inductive logic. Third edition. Wadsworth, Belmont, California, USA.

Smets, P. 1998*a*. Numerical representation of uncertainty. Pages 265–309 *in* D. Dubois and H. Prade, editors. Belief change. Volume 3 of D. M. Gabbay and P. Smets, editors. Handbook of defeasible reasoning and uncertainty management systems. Kluwer, Dordrecht, The Netherlands.

Smets, P. 1998*b*. Probability, possibility, belief: which and where? Pages 1–24 *in* P. Smets, editor. Quantified representation of uncertainty. Volume 1 of D. M. Gabbay and P. Smets, editors. Handbook of defeasible reasoning and uncertainty management systems. Kluwer, Dordrecht, The Netherlands.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York, USA.

Sorensen, R. A. 1989. The ambiguity of vagueness and precision. Pacific Philosophical Quarterly **70**:174–183.

Stewart, I. 1989. Does God play dice?: the mathematics of chaos. Penguin, London, UK.

Sugihara, G., B. Grenfell, and R. M. May. 1990. Distinguishing error from chaos in ecological time. Philosophical Transactions of the Royal Society London, Series **B 330**:235–251.

Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. Conservation Biology **9**:551–558.

Taylor, B. L., and P. R. Wade. 2000. 'Best' abundance estimates and best management: why they are not the same. Pages 96–108 *in* S. Ferson and M. Burgman, editors. Quantitative methods for conservation biology. Springer-Verlag, New York, New York, USA.

van Swaay, C. A. M., and M. S. Warren. 1999. Red Data Book of European butterflies (*Rhopalocera*). Nature and Environment, No. 99. Council of Europe Publishing, Strasbourg, France.

van Swaay, C. A. M., M. S. Warren, and A. Grill. 1997. Threatened butterflies in Europe—provisional report. Die Vlinderstichting (Dutch Butterfly Conservation); Wageningen, The Netherlands, report number VS 97.25 and British Butterfly Conservation, Wareham, UK.

von Mises, R. 1957. Probability statistics and truth. George Allen and Unwin, London, UK.

Wade, P. R. 2000. Bayesian methods in conservation biology. Conservation Biology **14**:1308–1316.

Walley, P. 1991. Statistical reasoning with imprecise probabilities. Chapman and Hall, London, UK.

Williamson, T. 1994. Vagueness. Routledge, London, UK.

Zadeh, L. A. 1965. Fuzzy sets. Information and Control **8**: 338–335.

Zimmerman, H.-J. 1996. Fuzzy set theory—and its applications. Third edition. Kluwer Academic, Boston, Massachusetts, USA.