

Opinion

Recommendations for quantitative uncertainty consideration in ecology and evolution

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Ecological and evolutionary studies are currently failing to achieve complete and consistent reporting of model-related uncertainty. We identify three key barriers a focus on parameter-related uncertainty, obscure uncertainty metrics, and limited recognition of uncertainty propagation – which have led to gaps in uncertainty consideration. However, these gaps can be closed. We propose that uncertainty reporting in ecology and evolution can be improved through wider application of existing statistical solutions and by adopting good practice from other scientific fields. Our recommendations include greater consideration of input data and model structure uncertainties, field-specific uncertainty standards for methods and reporting, and increased uncertainty propagation through the use of hierarchical models.

Uncertainty quantification is important but incomplete

Society increasingly relies on ecological and evolutionary models to tackle grand challenges such as conservation [1], public health [2], and climate change [3]. Growing reliance on models allows high levels of rigour, but requires that modelling follows best practices. Ecological and evolutionary modelling approaches are developing rapidly to use novel data sources, but the resulting abundance and complexity of the data create new challenges for identifying sources of uncertainty. Although these models are designed to explain natural variability, they must also distinguish it from uncertainty, which researchers aim to minimise. Despite a good literature base covering uncertainty, we have shown that ecology and evolution still fail to report all quantitative uncertainties associated with their models, and this negatively affects the validity of results [4]. Failure to fully report quantitative uncertainty can have far-reaching consequences when models are used to inform action. For example, Regan et al. [5] found that a lack of uncertainty consideration may have led to a suboptimal conservation decision for a population of the critically endangered Sumatran rhino Dicerorhinus sumatrensis. Secondary consequences come in the form of erosion of public trust in science (Box 1). When results communicated to interested parties are overconfident and incongruent with their perception of uncertainties, support for conservation measures can be reduced [6]. The consequences of omitted quantitative uncertainty (our focus) could be amplified by qualitatively different uncertainty types such as semantic uncertainty [7], but these impacts are beyond our scope.

Despite detrimental consequences, it is still common to omit uncertainties when modelling. The reasons behind these omissions are multifaceted. A growing body of research confirms that clear communication of technical (epistemic) uncertainty can have positive or null impacts on public trust [7–9] and interpretation [10,11], and can even aid decision making [11]. However, persistent apprehension remains concerning how uncertainties will be interpreted. Communication of uncertainty can be perceived by researchers to have a negative impact on public trust [12,13].

Highlights

Correct quantification and reporting of model uncertainties are fundamental to reliable science.

Failing to fully account for uncertainty in scientific work leads to overconfidence and potentially adverse actions. Despite these consequences, many scientific fields do not achieve consistent quantification of all model-related uncertainties.

The factors that drive uncertainty omission are complex, but span methodological challenges to reporting culture and trepidation about uncertainty interpretation.

As ecological and evolutionary models have an increasingly prominent role in informing policy and action, correct uncertainty accounting becomes more vital.

We have many of the tools necessary to close quantitative uncertainty gaps in ecology and evolution. To achieve complete uncertainty consideration, these tools need to be applied more broadly and should be supported by reporting standards.

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This can lead to uncertainty being omitted by researchers to preserve their core message at the expense of transparency.

The rapid rise of novel modelling approaches without accompanying scrutiny, education of users, clear documentation, or coherence across output types has created barriers for quantifying uncertainty [14,15]. We identify three specific barriers that we believe are currently holding back uncertainty quantification in ecology and evolution: a focus on parameter-related uncertainty (see Glossary), obscure uncertainty metrics, and limited recognition of uncertainty propagation (Figure 1). We believe that these issues act as obstacles to complete uncertainty quantification in our fields. However, there are solutions which can be implemented. We discuss each barrier and its role in hindering uncertainty consideration. We then highlight potential solutions to overcome the obstacles supported by examples of good practice (Box 2). Synthesizing these barriers with best practices from our modelling toolkit and insights gathered at an interdisciplinary workshop convened by the study authors [4], we propose concrete recommendations to close uncertainty reporting gaps in ecology and evolution.

Focus on parameter-related uncertainty

Barrier

Ecological and evolutionary studies often overlook uncertainties related to input data and model structure [4]. These sources can add non-trivial uncertainty to model results [16-21] and are

Box 1. Implications of uncertainty omission

Omission of uncertainty can have far-reaching consequences beyond the study of interest. Failure to quantify, acknowledge, or report all uncertainties associated with modelling work has been shown to negatively impact on trust [6,7,57], action [6,58], and even on the scientific process [59]. We present a theoretical example in Figure I to illustrate how uncertainty omission can negatively impact on each of these areas.

Trust

In Figure I, the orange point indicates a possible observation of population growth rate. It is located at a similar distance from both predicted model lines, but the interpretations are very different. Model 1 would seem to be incorrect based on this observation, decreasing trust in the model performance [13,57]. By contrast, for model 2 the observation lies within the plausible range of population growth rates and is therefore consistent with the model findings, maintaining trust in the performance of the model.

Action

Our example shows two dimensions of how uncertainty communication can improve action taken. The first is accuracy. In Figure I model 1 is less accurate than model 2 as a direct result of the lack of consideration of observation uncertainty in model 1. Following model 1 could lead to erroneous action: for example, no action is taken in view of the increasing trend in model 1, whereas in reality the population is declining.

The second is precision. For example, if action is informed by model 2, but ignores the credible interval (parameter uncertainty), then the population would appear to be stable. However, the credible intervals demonstrate that substantial population declines are plausible for this population. Therefore, action to prevent further declines would be needed immediately. To achieve correct action, the uncertainty implications would also need to be discussed clearly.

Scientific process

Omission of uncertainty can also hinder the use and accumulation of scientific evidence because it is more difficult to compare results across studies or to reuse them, for example in meta-analyses [41]. Such studies are becoming more important in ecology and evolution, especially because we need to synthesise their results to inform policy [1]. Obscure uncertainty metrics (e.g., if the credible interval in Figure I is not labelled or discussed) also hinder interpretation, reuse, and comparison.

Omission of uncertainty, explicit or implicit, can also contribute to the reproducibility crisis in ecology and evolution [59,60]. This is because results are more difficult to fully compare in the absence of comprehensively quantified uncertainty. Results can also appear to be more different than they are when only point estimates or mean model predictions are compared. ⁶Observatorio Marino de Asturias (OMA), Departamento de Biología de Organismos y Sistemas, University of Oviedo, 33071 Oviedo, Spain ⁷GOAL, Colonia Castaño Sur, Casa 1901, Calle Paseo Virgilio Zelaya Rubí, Tegucigalpa, Honduras, CA, USA ⁸Department of Mathematics and Statistics, University of Strathclyde, Glasgow G1 1XH, UK ⁹Department of Natural History, Norwegian University of Science and Technology, Trondheim, Trøndelag 7491, ¹⁰Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada ¹¹Organismal and Evolutionary Biology Research Programme, University of Helsinki, Helsinki 00014, Finland

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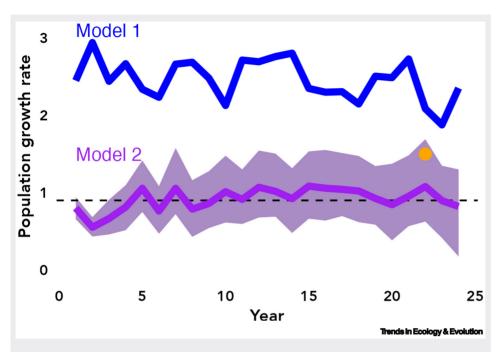


Figure I. Estimated population growth rate for a theoretical population, following the example from [31]. This example shows the results from two exponential models of population growth (blue and purple lines). Model 1 includes no uncertainty, whereas model 2 includes both parameter and input data uncertainty through observation and process equations. Both models were fitted in a Bayesian framework using Markov chain Monte Carlo (MCMC) and R-Nimble (https://zenodo.org/records/8047617). The broken line is the 'true' mean population growth rate, which is the same for both models. The purple shaded area is the 95% credible interval for model 2. The orange point is an illustrative observation (made up).

increasingly relevant as we embrace new data sources such as participatory data collection [22] and increasingly complex computational tools [15].

Uncertainty in input data is common in ecology and evolution, and arises from imperfect mapping between the variable of interest and the observed data [16,20,23]. We often have imperfect data, including observation errors [24,25], measurement errors [26], missing data [20,21], and temporal mismatches [27]. We also use outputs from other models as input data in our studies, such as interpolated weather data [28]. All these characteristics contribute to uncertainty in our model outputs.

Identifying uncertainty in input data requires sufficient knowledge to estimate the observation process accurately [29]. Many standard methods that deal with measurement errors require knowledge of the error mechanism [16]. However, for ecological and evolutionary data we often do not fully know the process that is causing uncertainty in the measured data [16]. Sometimes we may not even know that uncertainties exist. Even when input data uncertainty can be identified, understanding how to account for it can be challenging. Many methods, such as linear models, assume no error or uncertainty in independent variables and therefore cannot incorporate uncertainty in input variables, leading to potential biases in model estimates [23].

Similarly to input data uncertainty, model structure uncertainty is rarely reported [4]. It arises because we need to make assumptions about the factors that are driving the processes under study, for example in choosing the probability function that best captures biological variability.

Glossarv

Implicit omission: when uncertainty is calculated (and sometimes even presented) but its clarity is insufficient for it to be interpreted by a user or reader. Therefore the uncertainty is not omitted but its impacts are the same as if it had been

Measurement errors: discrepancy between the actual value of the target quantity of a measurement and the value observed. This can arise from equipment imprecision or observer effects

Observation errors: as measurement errors, but this category is broader and includes all observations even if they are

Observation process: the process of defining how observations/ measurements map onto the true values of the target quantity.

Parameter-related uncertainty: a metric that represents the uncertainty generated from the estimation of unknown parameters. It gives a plausible range of values for the unknown parameters: examples are standard errors, credible intervals, or confidence intervals.

Participatory data collection: collection of data by non-professionals, often through voluntary contributions from members of the public.

Uncertainty propagation: the process through which uncertainty from a lower-level or initial modelling step is fed through subsequent modelling steps to the model output. This ensures that uncertainty in inputs and estimation processes impact on the distribution of



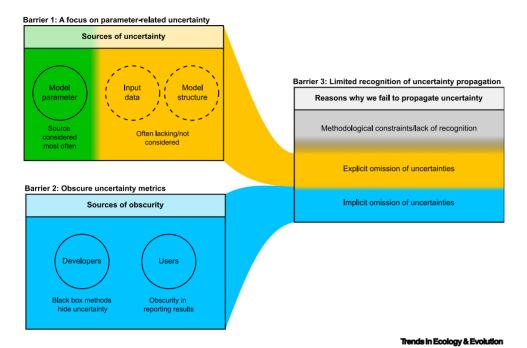


Figure 1. Connections between our three identified barriers. Sources of each barrier are detailed within the boxes. The consequences of each barrier are indicated by flows to other boxes.

Box 2. Case studies examples of good practice

The Box provides examples of good practice that can be used to overcome each key barrier.

Overcoming a focus on parameter uncertainty

- (i) Input data: data uncertainty was quantified in a study of European bats by accounting for detection differences between different bat species [61]. In this work an observation process was modelled explicitly and detection probabilities were estimated for each species. Within the same model, occupancy probability was also estimated while accounting for species-specific probability of detection and its uncertainty (Table 1 in [61]).
- (ii) Model structure: an ensemble of species distribution models of eucalypt tree species was built using the biomod2 package [62] to account for uncertainty in model structure [63]. The ensemble used eight different statistical models and took the mean or weighted average of the estimates of the models. Despite accounting for uncertainty in model structure, and although it was possible to calculate confidence intervals, no such metrics were reported. This demonstrates that even good performance in relation to one barrier is not sufficient for full reporting.

Overcoming obscure uncertainty metrics

- (i) Clarity in method development: the 'ape' R package [64] explicitly mentions the uncertainty associated with the estimates it generates in the associated package manual. Taking the ancestral character estimation ace() function as an example, there is extensive documentation on the estimation procedures which helps to clarify how uncertainty is calculated and what it represents. This package is further supported by a GitHub repository (https://github.com/emmanuelparadis/ape) and a webpage (https://emmanuelparadis.github.io/index.html) that allow dialogue with the developers. Clarity in the package has led to good presentation in papers using this package (e.g., Figure 1 in [65]).
- (ii) Clarity in presentation: a study looking at demographic buffering in Svalbard reindeer (Rangifer tarandus platyrhynchus) [66] clearly details how uncertainty was estimated in the Bayesian analysis in their methodology ('Model for vital rates' section). The uncertainties were then presented clearly, both numerically and visually and with a description (Table 1 in [66] with an associated 'Notes' section, also Figure 1 in [66]).

Overcoming limited recognition of uncertainty propagation

(i) An integrated population model of American Woodcock (Scolopax minor) [67] (a form of Bayesian hierarchical model: Figure 1C in [67]) was used to jointly model three different datasets. By using a single underlying process and three observation process sub-models all within a single framework, it was possible to estimate and propagate uncertainty from input data right through to the final outputs (Figure 2 in [67]).



Although we make informed decisions about model structures based on our best understanding, alternative formulations could also be plausible, generating uncertainty [17]. This is exacerbated in ecology and evolution as we model highly complex biological processes [18] across interacting spatial and temporal scales. Instead of accounting for this source of uncertainty, model selection techniques are typically used to find a single 'best' model to use for inference [17,18,30]. This procedure treats model structure as being fixed, and assesses all other uncertainties conditional on the final structure. This disregards uncertainties introduced during the model selection process which can significantly impact on predictions [17,30].

A major barrier to fully considering model structure uncertainty is that it cannot be quantified exhaustively, and there are infinite ways to model biological processes. Model structure uncertainty can be quantified to an extent by considering a defined subset of structures based on our best knowledge of a system [17], but this is not yet common in ecology and evolution [4]. Most of our standard modelling tools cannot quantify uncertainty across multiple models. This practical constraint and our culture of selecting a single 'best' model have hindered advances in this area.

Solutions

Although quantifying input data uncertainty is challenging, it is becoming feasible because of methodological advances and growing recognition of imperfect data [16,20,31,32]. We now have tools to quantify input data uncertainty through explicit modelling of observation processes or error simulation [16,33,34]. Some methods can even be used when the observation process is unknown [16,35]. We are also starting to leverage data integration tools to use multiple data sources and account for uncertainties in each dataset while broadening spatiotemporal coverage [32,33,36]. By combining datasets that inform on the same underlying process, it can be easier to quantify the uncertainty in each individual dataset [33,36].

Tools are available to account for model structure uncertainty in ecology and evolution, for example model averaging. These tools are gaining popularity, such as the MuMIN package (https://cran.rproject.org/package=MuMIn) (ranked among the top 10 most cited R packages in ecological studies [37]), but are not yet ubiquitous. Learning from fields such as climate science, which embrace model structure uncertainty (including scenario uncertainty) through multi-model ensembles [38], can help to advance our uncertainty consideration. We already have tools to implement model ensembles [39,40], although these are mainly restricted to species distribution models. Wider implementation of these methods would expand our consideration of model structure uncertainty.

Obscure uncertainty metrics

Barrier

Obscure presentation or inadequate discussion of uncertainty equates to its **implicit omission**, leading to overconfidence in the results, misinterpretation [10], and even bias [23]. This obscurity also hinders uncertainty propagation through a modelling pipeline or use in subsequent analyses [41]. In ecology and evolution, obscurity in uncertainty quantification occurs at two points in the scientific process: during modelling and during reporting.

During modelling, both users and developers contribute to obscuring uncertainty. The software used in ecology and evolution often requires no direct engagement with the underlying method to produce results. This can lead users to treat methods as black boxes. Developers can exacerbate user disengagement by inadequately detailing uncertainty metric calculations and assumptions, by insufficiently discussing uncertainty implications, or by failing to consider downstream applications. These implicit omissions can hinder the applied utility of methods by preventing assessment of methods that are fit for a particular purpose such as decision making. For instance, few R packages,



even among the top 10 most cited in ecology [37], adequately document and discuss their uncertainty metrics (Table S1 in the supplemental information online). Lack of explicit details can cause ambiguity, misinterpretation, or uncertainty omission, especially for non-experts. Newer complex tools such as machine learning can appear to be opaque to novice users [42] and could magnify these issues.

During reporting, obscure uncertainty quantification arises from a lack of standardisation. None of the top five journals in ecology and evolution [https://research.com/journals-rankings/ecologyand-evolution] have any specific criteria for how to report model results and uncertainty. This contrasts with other fields, such as political science and health science, which have established reporting standards [43,44]. Our lack of guidelines makes it difficult to interpret (leading to frequent omission of the discussion of uncertainty in relation to results [4]), compare, or use model results (Box 1). It also leads to confusion over reporting expectations and can cause implicit omission, such as presenting an interval on a graph but without indicating the uncertainty metric displayed.

Solutions

Some software packages provide comprehensive documentation and clear uncertainty metrics (Box 2). The rise of additional documentation, such as R vignettes, offers broader informational support for various tools and audiences [45]. We can enhance the presentation of other methodological tools by learning from these examples and establishing minimum documentation standards aimed not only at being able to use a method but also at understanding it. Recently, a shift toward more quantitative education in ecology and evolution has improved user engagement with methods [46]. Although reporting inconsistency remains, clear uncertainty reporting examples (Box 2) can guide effective communication. Implementing such guidelines, akin to the minimum reporting standards in the health sciences [44], would substantially enhance the clarity and accessibility of our published work.

Limited recognition of uncertainty propagation

Transparent, complete scientific results would require uncertainty propagation through all modelling steps. However, full propagation is challenging for complex models [47] and impossible to do exhaustively. Despite these difficulties, we should not refrain from attempting propagation and transparent accounting of uncertainty. Ecological and evolutionary models frequently investigate processes across a range of scales that are linked through several modelling steps. For example, an evolutionary study estimating allele frequency needs to account for uncertainties in individuals' genotype, in sampling of individuals at each location, and in sampling of populations. Limiting uncertainty to the top level (populations) would lead to overconfidence in our understanding of the process being modelled. Despite the central importance of uncertainty propagation, it is inconsistently implemented in ecology and evolution. We found that 20% of ecology papers and 67% of evolutionary papers that generate predictions fail to report predictive uncertainty [4]. This suggests that a lack of consistent uncertainty propagation is leading to omitted uncertainty. We propose that this gap is probably driven by a lack of awareness and practical constraints.

Lack of awareness of uncertainty propagation leads to explicit and implicit uncertainty omission. Explicit omission arises when uncertainty is accounted for in an early modelling step, for example when uncertainty is estimated for parameters in a predictive model [48] but is not conveyed to later steps [48]. Such omission is pertinent for models relying on other studies or outputs (e.g., meta-analyses, comparative studies [41], or those with explanatory variables from



model outputs [28]). If original research omits the necessary uncertainty, it cannot be propagated into subsequent modelling steps. Propagation is also hindered by our modelling toolkit. Several standard tools in ecology and evolution lack the ability to include previously estimated uncertainties, thus preventing propagation of uncertainty. Finally, implicit uncertainty omission occurs when software does propagate uncertainty, but users fail to report it clearly, such as in the use of STRUCTURE (a popular genetic clustering algorithm) [49,50]. Few studies using this algorithm have included estimates of uncertainty, even though these are easily available (e.g., [51]).

Practical constraints further hinder uncertainty propagation. As the complexity of research questions and models increases, so does the challenge of uncertainty propagation because tradeoffs exist between model complexity and ease of uncertainty quantification [47]. Given the sparsity of specific software for propagating uncertainty for many ecological or evolutionary modelling questions, it falls upon users to write their own custom code. Many ecologists and evolutionary biologists are not modelling or statistical experts. As a result, the requirement to construct complex custom models with non-trivial distributions and equations can make uncertainty propagation seem intractable, leading to it being omitted.

Solutions

Hierarchical models are the tidiest way to deal with propagation because all modelling steps are explicitly linked, thus allowing uncertainty to flow through to final estimates. Conceptually, the easiest approach is to use Bayesian models, where the parameters and data can be represented as probability distributions, making propagation a matter of applying probability theory. These models are common [33,36], but could be more widely adopted, particularly accompanied by tools that make them more accessible to non-expert users. Non-Bayesian methods such as bootstrapping [52] and multiple imputation [20] are also possible. These methods are readily available in R (e.g., [53]) and can be more conceptually accessible to non-statisticians. All these methods simulate data or parameters that are then passed on to another model, either in a separate step or in the same model-fitting procedure.

Concluding remarks

Clear quantifying and reporting of the uncertainties associated with our work is a key part of the scientific process [4] and can even be used as a basis for reducing uncertainty (see Outstanding questions). Despite gaps caused partly by our identified barriers, ecology and evolution are in a strong position to progress their consideration of uncertainty. Based on our proposed solutions, we provide the following concrete recommendations to close current gaps and drive improvements in our community:

To overcome the focus on parameter-related uncertainty

- (i) Use checklists, which give details of potential sources of model-related uncertainty, to identify and account for all relevant uncertainty sources [4] (users).
- (ii) Consider input data and model structure uncertainty when developing methods and modelselection tools, and create functionality to include them (developers).
- (iii) Explicitly consider uncertainties in the input data. Quantify uncertainty if possible (e.g., through observation models), record it if it is from a secondary source, and explore its likely importance through sensitivity analysis or simulation (users).
- (iv) Explore more than a single 'best' model; in particular, consider model averaging and ensembles (users).

Outstanding questions

How do we ensure consistent and complete uncertainty reporting in ecology and evolution in the future? For example, how will the recommendations be followed up or enforced?

How has uncertainty omission in ecology and evolution impacted on results? If studies with omitted uncertainty were reanalysed, how would this change the conclusions they drew?

How can we overcome uncertainty aversion or apprehension in ecology and evolution?

How do we move uncertainty acceptance beyond academia and into publishing, politics, and the general public? Publications, politicians, and to some extent the general public, all often want certainty from scientific results and hard-hitting, exciting results. However, we should also strive for methodological rigour and



To overcome obscure uncertainty metrics

- (i) Generate standardised guidelines for uncertainty quantification (such as those used in health sciences [44]) to facilitate clear, consistent, and accessible presentation, including discussion of uncertainty in relation to results. Guidelines could be created and published by journals, professional societies, and funding agencies (community).
- (ii) When documenting methods, include explicit uncertainty sections which discuss the implications of uncertainty for interpretation. Ensure that sufficient detail is given to allow use in downstream applications and decision making (developers).
- (iii) Read and engage with the uncertainty sections of method documentation (users).

To overcome limited recognition of uncertainty propagation

- (i) Use more hierarchical models (e.g., integrated population models [32], Aster models [54], Bayesian measurement error models [55]). This can be achieved by developing clearly documented software and packages aimed at non-expert users, as well as increased training and education for modellers (developers, users).
- (ii) Propagate necessary uncertainties, wherever possible. Consider the whole model pipeline, including providing all the information necessary for propagating uncertainty beyond the focal study (e.g., in decision-making or meta-analyses) (users).
- (iii) When full propagation is not feasible, use sensitivity analyses to explore the impact of omitted uncertainty [56] and discuss the implications qualitatively (users).

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Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

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