



Inferring extinctions I: A structured method using information on threats



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ABSTRACT

Extinctions are important indicators of biodiversity status. When they are detected, they may trigger the re-direction of conservation resources to save other species. Yet declaring extinctions is inherently uncertain. Relevant evidence for consideration includes information on threats, the time series of species records and the effort employed to search for remaining individuals. Quantitative tools have been developed to infer extinctions from data on the timing of records. In contrast, inference of extinction from threats relies on expert judgement and is susceptible to subjective influences. To use qualitative information on threats, we suggest experts should construct an argument map to identify reasons, evidence and sources in support of a claim that a species has gone extinct, as well as objections, evidence and sources as to why the claim may not be true. The reasons must explicitly address: i) whether identified threats are sufficiently severe and prolonged to cause local extinction; and ii) whether such threats are sufficiently extensive to eliminate all occurrences. Transparent mapping of reasons and objections enables experts to estimate subjective probabilities that each alternative claim is true, allowing an overall probability of extinction to be calculated. We provide examples illustrating how typical evidence may be evaluated. To deal with uncertainties, we suggest bounded estimates of subjective probabilities are obtained from multiple experts in a structured elicitation. The method requires no detailed mathematical analysis, but relies on structured reasoning. The subjective estimates of probabilities must be based on the severity and pervasiveness of threats alone, to allow comparison with estimates derived independently from other sources of information such as time series of records.

1. Introduction

Determining whether a species or other taxon (hereafter taxon) is extinct is an uncertain process. The International Union for the Conservation of Nature (IUCN) Red List of Threatened Species criteria permit a taxon to be listed as Extinct when there is no reasonable doubt that the last individual has died (IUCN, 2001; IUCN Standards and Petitions Subcommittee, 2016). The phrase “no reasonable doubt” implies a very small degree of uncertainty that the last individual has indeed died. A false classification can have serious negative implications (Akçakaya et al., 2017-in this issue), especially in jurisdictions in which protective measures and resourcing lapse when the legal status of

a taxon changes from threatened to extinct (e.g. *U.S. Endangered Species Act 1973*; *Australian Environmental Protection and Biodiversity Conservation Act 1999*).

False Extinct classifications arise for two reasons. First, if assessors apply a low threshold for the probability of extinction, above which a taxon is deemed to be extinct, many taxa will be incorrectly classified as extinct by chance, even given error-free data (Regan et al., 2000; Akçakaya et al., 2017-in this issue). Second, the likelihood of extinction may be estimated incorrectly, even if the assessor has a highly conservative attitude to risk and applies a high threshold for the probability of extinction. Although adopting high thresholds will help to reduce false Extinct classifications, one disadvantage of doing so is likely

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under-reporting of extinctions, so that the status of biodiversity is estimated to be better than it actually is. Given the trade-offs and consequences of errors, it is important to employ methods that maximise use of available evidence in a systematic and deductive manner to ensure repeatable and well-justified decisions on extinct listings.

Three main sources of information should be considered in assessing the likelihood that a species has gone extinct: (1) the intensity, extent and timing of threats and the likely susceptibility of the species to these; (2) the time-series of records of the species (sightings, specimen collections, etc.), and the likelihood that each of these are valid; and (3) the timing, extensiveness and adequacy of surveys and searches for the species (Harrison and Stiasny, 1999; Butchart et al., 2006). Inferences drawn from knowledge about threats and species' susceptibility (source 1) rely heavily on expert knowledge and are therefore predisposed to frailties of subjective judgement (Burgman, 2015). Consequently, they have been omitted from most quantitative methods for estimating the probability that a taxon has gone extinct. Most approaches are based exclusively on time series of records alone or include limited analysis of search effort (Solow, 1993, 2005; McCarthy, 1998; Collen et al., 2010). However, assessing probability of extinction based on records alone ignores relevant evidence about threats, their impacts and search effort (Solow, 2005; Collen et al., 2010; Thompson et al., 2017-in this issue). The few studies that have considered all three sources of information do so in a relatively unstructured way (Butchart et al., 2006). A more systematic synthesis of these contrasting sources of information, particularly by producing estimates of the same quantity – the probability that a species has gone extinct – from independent lines of evidence, will support more robust diagnoses of extinction. In this paper, the first in a trilogy, we develop a systematic approach to estimating the likelihood that a species is extinct based only on information about threats. The second paper (Thompson et al., 2017-in this issue) presents a new method for the same task based a time series of records and dedicated surveys, taking into account species detectability and the reliability of surveys. The third paper (Akçakaya et al., 2017-in this issue) focuses on how the likelihood that a species is extinct, as estimated by the previous two papers, is used in conservation assessments, reviews the trade-offs in declaring an extinction when evidence is uncertain, and recommends a decision threshold for assigning species to the Extinct category in IUCN Red Lists.

Qualitative information on threats is particularly important when occurrence records are insufficient or inadequate to estimate extinction probability reliably from time series. For example, 28 Critically Endangered or Data Deficient bird species are known only from the type specimen/series or one additional record. In such cases, information on threats (often with inferences about life history and ecology) may be the only evidence on which to base an assessment. How can this qualitative information be used to produce a quantitative estimate of an extinction probability that is comparable to estimates that can be calculated from quantitative observation data?

We approach this problem by outlining a structured way of inferring a probability that a taxon has gone extinct, using information on threats and species' susceptibility to them. The method requires experts to evaluate the proposition that a taxon has gone extinct by using biological understanding to outline all the plausible reasons why the proposition could be true (supporting reasons) or false (objections). This allows experts to construct an argument map of their reasoning (Walton, 2013), providing a clear and unambiguous platform for quantifying the probability that the taxon has gone extinct, based on the reasons, objections and their weights of evidence. We embed this within elicitation methods that reduce arbitrary and semantic uncertainties. We illustrate the approach by applying it to case studies that result in a probabilistic diagnosis of extinction.

2. A simple threat-based model for diagnosing extinction

The subject of this paper is calculation of the probability that global

extinction has occurred, $P(E)$, which comprises two components: a local extinction component $P(local)$, the probability that the combination of threats affecting the species occurred for a sufficient duration and were sufficiently severe that they caused local extinction; and a spatial scale component $P(spatial)$. The latter is the probability that the threats occurred over the entire species range. We assume that if threats caused local extinction, and they occurred over the entire range, then global extinction has occurred. Thus, $P(spatial)$ is actually the conditional probability $P(E | local)$, so that by definition

$$P(E) = P(local) \times P(spatial) \quad (1)$$

In practical terms, these represent the proportion of like taxa (ecologically similar or phylogenetically related) that would go extinct when subject to the specified severity, duration and extent of threats. This conceptually generic logical treatment of threats is also applied, for example, to the “severity” and “extent” components within criteria C and D for the Red List of Ecosystems (Keith et al., 2013).

Estimation of $P(local)$ requires assessors to draw on the history of the impacts of threats on populations of the target taxon. A relevant historical observation, for example, would be that the taxon disappeared from an area shortly after the introduction of an invasive alien predator. It may also draw on examples where the threats have caused extirpation of ecologically similar or phylogenetically related taxa. Inferences about which taxa are ‘ecologically similar or related’ may be based on life history (e.g. life cycle structure, dependence on hosts, body size, diet), habitat ecology (e.g. microhabitat type, breeding sites) and/or phylogeny.

Estimating $P(spatial)$ requires assessors to evaluate two components: i) the likelihood that the threats (with sufficient severity and duration to have caused local extinction) operated throughout the entire range of the taxon (i.e. distribution of habitat and/or individuals, as appropriate); and ii) the certainty with which the range limits are known. Relevant considerations for the first component include whether the threats operated in such a pattern as to have caused extinction throughout the taxon's range. This may be influenced by the spatial occurrence of different threats, dispersal dynamics, migration patterns and patch dynamics, as well as species life-history traits and cultural factors that influence species susceptibility to threats (see Discussion section). Relevant factors to consider for the second component (range limits) include taxonomic uncertainty, reliability of records and whether potential habitat outside the confirmed range has been adequately searched. These uncertainties can be incorporated into estimates of $P(spatial)$ by setting upper and lower bounds taking into account plausible maximum and minimum extents of the species range (see Section 4 below).

Our generic method should cover a wide range of cases, but some specific cases warrant variations in the model. Firstly, for species that are known only to occur in a small number of discrete areas (e.g. islands), $P(E)$ can simply be estimated from the product of local extinction probabilities, taking into account the specific threats in each area. As all local populations are included, $P(spatial)$ can be dropped from the equation. For a species with three populations

$$P(E) = P(pop_1) \times P(pop_2) \times P(pop_3) \quad (2)$$

where $P(pop_n)$ is the probability that threats affecting population n are sufficiently severe and prolonged to cause its local extinction. We stress that Eq. (2) is only appropriate when there is a negligible chance that unknown populations exist within the species range, and when the three probabilities are independent.

Secondly, in more complex scenarios Eq. (1) could be extended to include multiple values of $P(local)$ for different parts of the species range where a different unique combination of threats contributed to extinction risk. For a species in which three different parts of the range were each affected by different and independent combinations of threats

$$P(E) = P(local_1) \times P(local_2) \times P(local_3) \times P(spatial). \quad (3)$$

$P(spatial)$ in this case is the probability that all (three) combinations of threats in total affect the entire range of the species and are all sufficiently severe and prolonged to cause local extinctions. Eq. (3) should be useful in cases, for example, where habitat loss is a severe threat to a taxon in one country and poaching is a severe threat to the same taxon in another.

When $P(local)$ and $P(spatial)$ equal unity, extinction is guaranteed. For completeness, environmental and demographic stochasticity are regarded as threats in small populations, a result of random events. Thus, all possible causes of extinction, including stochastic events, are treated as threats.

3. Estimating threat parameters

Estimation of $P(local)$ and $P(spatial)$ will often rely on qualitative information viewed through a lens of expert judgement. In such cases, a structured method is needed to minimise subjective bias, inconsistencies, vagueness, expert fatigue and other reducible sources of uncertainty (Burgman, 2005, 2015). One way to arrange ideas about a posited extinction is to use an argument map to represent the reasoning behind an estimate, based on qualitative information. Argument maps hinge on a claim, such as, ‘the species is extinct’. For example, the reasons for thinking the small forb *Gentiana wingecarribiensis* is extinct are outlined in the argument map in Fig. 1. The species has only ever been recorded from around the margins of two, or possibly three mesotrophic valley bogs within a small geographic range in southeastern Australia. It is threatened by hydrological change, competition from dense overgrowth and trampling by domestic or invasive herbivores (Kodola et al., 1994; NSW Scientific Committee, 2008). These threats vary in severity and extent within the species range. The species and its habitat are well known to specialists, but it is difficult to detect due to its small stature and cryptic annual life history. Note that a time series of occurrence records is available since the discovery of the species in the early 1960s until the most recent published record in 2001 (NSW Scientific Committee, 2008), but this information is excluded from the argument map to ensure an independent probability of extinction is based only on information about threats and their effects.

A claim is supported by reasons, evidence and sources (Okada et al.,

2008). With respect to species extinction, for example, the analyst believes the species is extinct because the threats to the species have been severe and persistent over long periods, the species is susceptible to them, and the threats have affected all of the habitat. These reasons are supported by evidence, which should be traced to a source. In the example, the evidence of threats includes changed hydrological regimes, cattle farming, feral pig activity and weed incursions. The species is susceptible to these threats because it is a small forb that is out-competed by tussock grasses and shrubs that have invaded the habitat patches, it is intolerant of dry compacted soils, and it has a very restricted geographic range. Collectively, the threats affect all known sites. Typically, each branch of evidence represented in the argument map is also supported by a source, although the sources have been omitted from Fig. 1 for the sake of readability. Sources may include published data and analyses, informal observations and expert opinion. In this case they include historic portion plans, forestry records, personal observations (DAK), location records and scientific literature (Kodola et al., 1994; NSW Scientific Committee, 2008).

Representing reasoning in this way leads naturally to positing counterfactuals, that is, lines of reasoning that lead to the opposite claim (i.e., that the species is in fact extant). These are usually represented in an argument map as ‘objections’. Three such objections in this example are that the species has a persistent soil bank (and hence might be present but undetectable), its intolerance of changed hydrological conditions was inferred rather than observed or tested, and some potential habitat has never been searched, so that the species may persist in an isolated patch, perhaps one that has not been subjected to the same severity of impacts. Each objection links to particular pieces of evidence or to the reasons themselves.

More generally, to estimate the threat parameters for a taxon that is a candidate for Extinct listing, an assessor must first identify plausible past and recent threats. A plausible threat is a process that is likely to have played a role in the decline and potential extinction of the taxon. How likely it is to have played such a role is a product of the probabilities for the two parameters described above (Eq. (1)). We stress the importance of estimating these parameters as probabilities, rather than as an index on some arbitrary scale. $P(local)$, for example, should be viewed as the proportion of like taxa that will go extinct when subjected to the particular threat regime under consideration.

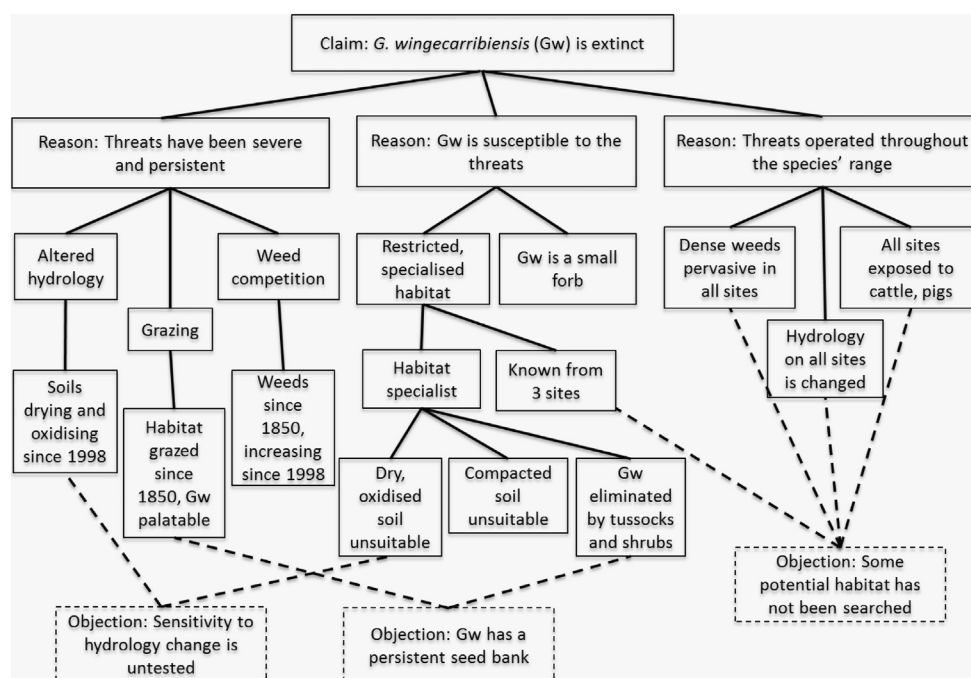


Fig. 1. Argument map for the claim that *Gentiana wingecarribiensis* (abbreviated Gw) is extinct. The claim appears in the uppermost box. The claim is based on severe, persistent threats that affect all of the species' habitat, and to which it is susceptible. Each reason is supported by evidence. Usually, an argument map shows sources supporting each piece of evidence, but these have been omitted for simplicity. Objections to the evidence and by inference, the reasons, are shown as boxes with dotted outlines.

Table 1

Expert estimates of threat parameters and resulting probabilities of extinction for selected birds, plants and fish. $P(\text{local})$ and $P(\text{spatial})$ are as defined above. Numbers in square brackets for $P(\text{local})$ and $P(\text{spatial})$ are the expert opinion on the lower and upper bounds (first and last values in brackets); and best estimate (middle value in the brackets). $P(E)$ is calculated from Eq. (1) (except *Gentiana wingecarribiensis*, Eq. (3)), using interval arithmetic to calculate the bounds. Nomenclature and taxonomy follow BirdLife International (2014) for birds, Harden (1990–2002) for plants, Eschmeyer and Fricke (2015) for fishes.

Species	$P(\text{local})$	$P(\text{spatial})$	$P(E)$	Justification for parameter estimation
Birds				
<i>Tachybaptus rufolavatus</i> Alaotra Grebe	[0.95, 0.97, 0.99]	[0.90, 0.925, 0.95]	[0.86, 0.90, 0.94]	Threats to this Madagascan waterbird during recent decades in which it declined and apparently disappeared were multiple and intense: the introduction of the carnivorous fish <i>Micropterus</i> and <i>Ophiocephalus</i> is likely to have driven rapid declines; soil erosion from deforested hillsides, agriculture and sedimentation lowered water quality; introduced exotic plants, mammals and fish, especially Tilapia, probably depleted essential food; habitat has been lost through the conversion of marsh areas to rice farms; hybridisation with the recently colonising African Little Grebe <i>T. ruficollis</i> probably reduced the number of pure-bred birds; poaching occurred at high levels; and monofilament nylon gill-nets now cover a large part of Lake Alaotra and kill many diving waterbirds, but possibly only proliferated after the grebe had already been greatly reduced in numbers or had disappeared. Together, these threats (and their known impacts on other waterbirds at Lake Alaotra and on related species elsewhere) are very severe, prolonged and highly likely to affect the entire species range.
<i>Sporophila melanops</i> Hooded Seed eater	[0.10, 0.30, 0.50]	[0.01, 0.50, 0.99]	[0.001, 0.15, 0.5]	Threats to this Brazilian bird are poorly understood, as it is known only from a single nineteenth century specimen collected from a lake in Goiás state, central Brazil. The only plausible threat is from habitat destruction driven by agricultural conversion, but this may not have a severe impact on the bird. Hence $P(\text{local})$ is set to be low, and with a broad interval. The distributional limits are highly uncertain (although likely to be restricted), so $P(\text{spatial})$ is also highly uncertain.
<i>Pterodroma caribbaea</i> Jamaica Petrel	[0.95, 0.97, 0.99]	[0.75, 0.85, 0.95]	[0.71, 0.82, 0.94]	This seabird is likely to have faced severe threats from predation by introduced rats (which took eggs) and mongooses (capable of taking incubating adults). Introduced pigs may also have been an important factor, and the species was hunted for food until the middle of the 19th century. It is likely that these drove at least local extinction, so $P(\text{local})$ is high. These threats likely operated throughout the Jamaican breeding range, but it is conceivable that it occurred on Dominica and Guadeloupe, where there is more uncertainty over the threats. Therefore $P(\text{spatial})$ is moderately high, but with fairly broad limits.
Plants				
<i>Haloragodendron lucassii</i>	[0.99, 0.99, 1.00]	[0.25, 0.50, 0.65]	[0.25, 0.50, 0.65]	A forest shrub from a restricted area that is now within the urbanised area of northern Sydney, Australia. The principal threat is habitat destruction during the expansion of suburban Sydney, which began slowly in the early 19th century and accelerated during the 20th century. Although the rate of habitat destruction had slowed by the late 20th century, the remnants continue to be degraded by eutrophication and alien plant invasions. This makes the habitat unsuitable for persistence of many native plant taxa. The threats are sufficiently severe and occurred over a time interval sufficient to eliminate a local population $P(\text{local})$, even where individuals may have evaded habitat destruction, they are very likely to succumb to habitat degradation based on observed elimination of many other native plant taxa by eutrophication of habitats and the superior stature of woody alien plants. Whether the threats have affected the entire distribution of <i>H. lucassii</i> $P(\text{spatial})$ is less certain due to existence of suitable habitats in less accessible terrain. [Note that <i>H. lucassii</i> was presumed extinct since its last collection in 1926 until rediscovered in 1986 – this assessment was done for 1985]
<i>Persoonia laxa</i>	[0.99, 0.99, 1.00]	[0.70, 0.85, 0.95]	[0.69, 0.84, 0.95]	A shrub of oligotrophic sclerophyll vegetation, found in northeast Sydney. Its habitat and threats are similar to those described for <i>H. lucassii</i> , but its distribution is more coastal, further within the urban limits of the city and encompasses less remnant habitat. Furthermore, the genus <i>Persoonia</i> includes a considerable number of taxa with restricted distributions, including the sister species, which persists in vegetation remnants in western Sydney. The severity and duration/timing of threats to <i>P. laxa</i> , and hence $P(\text{local})$, is similar to that estimated for <i>H. lucassii</i> , but it is more likely that the threats have affected its entire range $P(\text{spatial})$.
<i>Gentiana wingecarribiensis</i>	[0.90, 0.95, 1.00] [0.85, 0.90, 1.00]	[0.50, 0.70, 0.90]	[0.38, 0.60, 0.90] (based on Eq. (3))	An ephemeral forb restricted to margins of two or three temperate mesotrophic mires of the Robertson plateau in southeast Australia. Main threats are hydrological change from sedimentation, peat mining, peat oxidation, pine plantations, trampling by cattle and feral pigs and weed invasion (Kodela et al., 1994, NSW Scientific Committee, 2008). These threats are associated with local disappearances of the species, hence $P(\text{local})$ is set high, but the potential existence of a soil seed bank suggests some propensity for persistence through unfavourable periods of unknown duration. The range is unlikely to be much larger than previously known, but there are also some swamps in the west of the distribution that have not been thoroughly searched, and its small size and cryptic annual life cycle suggests a possibility that some populations remain undiscovered. Hence $P(\text{spatial})$ has large bounds. One confirmed and one uncertain location are modified by intensive agriculture with associated livestock and weeds, including one site severely impacted by mining. The third site is exposed to sedimentation associated with forestry with feral pig activity and cattle grazing, apparently transformed to a lesser degree than the other sites. Hence, a slightly lower $P(\text{local})$ value is set for this site than the others.
Fishes				
<i>Irvineia voltae</i> Butterfish	[0.10, 0.20, 0.49]	[0.4, 0.65, 0.75]	[0.04, 0.13, 0.38]	Noted as possibly extinct by Harrison and Stiasny (1999: 313), this west African species of catfish may have been impacted by the construction of the Volta Dam on the lower Volta River. The construction of this dam may have changed the available habitat to this species (Tyson Roberts, pers. comm.). The habitat is also declining due to bad agricultural practices (Entsua-Mensah and Lalèyè, 2010). However, the extent to which these habitat changes affect <i>I. voltae</i> across its range is not known, therefore $P(\text{local})$ is set relatively low, and with a broad range. The species is currently known only from the lower River Volta, and this entire region is likely

(continued on next page)

Table 1 (continued)

Species	<i>P(local)</i>	<i>P(spatial)</i>	<i>P(E)</i>	Justification for parameter estimation
<i>Rhizosomichthys totae</i>	[0.25, 0.50, 0.60]	[0.5, 0.6, 0.75]	[0.1, 0.30, 0.45]	to be impacted by the presence of the dam. There is some possibility that the species is found in nearby tributaries, though this is not confirmed. Thus <i>P(spatial)</i> is given a mid- to high range score. Several threats may impact this species of catfish, known from only a few unusual specimens found in lake Tota of the Colombian Andes (Mojica et al., 2012). Tectonic instability in the region where the fish is found causes earthquakes and possible landslides that may eliminate populations, and introduction of trout to the lake may bring competition with the fish, or predation on them, or even possibly the introduction of disease. However, the severity of these threats to the aquatic fauna is uncertain. Evidence of geologic events is not based on direct accounts, and there has not been a thorough study of the impacts of trout in the species' home lake. Thus <i>P(local)</i> is set with relatively broad bounds around a mid-value. The single lake from which the few specimens are known, is relatively well isolated high in the Andes (with one affluent stream and one effluent stream). However, local experts suggest it is possible that the species may be found in one of these connecting streams.
<i>Barbodes pachycheilus</i>	[0.80, 0.90, 0.95]	[0.4, 0.5, 0.6]	[0.32, 0.45, 0.57]	According to Kornfield and Carpenter (1984) the decline of the Lake Lanao cyprinids could primarily be due to introduction of the goby <i>Glossogobius giuris</i> around 1963 and the eleotrid <i>Hypseleotris agilis</i> (around 1975–1980), but might also be the consequence of habitat alteration and overfishing. Therefore, <i>P(local)</i> can be set relatively high. A single collection of <i>Barbodes pachycheilus</i> has been made from Lake Lanao, in 1921 (Herre, 1924). Thus, the full distribution of the species, and the impacts of the threats across this range, are less well known. <i>P(spatial)</i> is given a mid-range value.
<i>Cyprinodon inmemoriam</i> Charco Azul pupfish	[0.90, 0.95, 0.99]	[0.90, 0.95, 0.99]	[0.81, 0.90, 0.98]	Contreras-Balderas and de (1996) state that Ojo La Trinidad, Mexico, (a spring where <i>Cyprinodon inmemoriam</i> is endemic) was reduced from an area of 10,000 m ² to an area of “murky brown and stinky” water less than 1000 m ² in area, with no fishes; they note that the spring dried completely thereafter, flowing only once during a rainy season. According to Contreras-Balderas and de (1996) the falling water levels are due to water extraction from local aquifers for use in agricultural irrigation. Therefore, <i>P(local)</i> was estimated to be high. The species is very likely endemic to the pools of Ojo La Trinidad. The possibility that this species might be present in neighbouring pools cannot be discounted, but high localised endemism is a common feature of many cyprinodontids. <i>P(spatial)</i> is also given a high value.
<i>Haplochromis boops</i>	[0.80, 0.90, 0.94]	[0.40, 0.7, 0.80]	[0.32, 0.63, 0.75]	Several threats have quite clearly impacted the numbers of Lake Victoria cichlids, including the introduction of Nile perch, <i>Lates niloticus</i> , and the eutrophication of lake Victorian waters caused by increased lakeside agriculture, urbanization, and deforestation. Introduction of the water hyacinth, <i>Eichhornia crassipes</i> , has reduced light intensities in the waters and caused further stagnation. The increased use of fish poison in shallow waters has also threatened the cichlids (Harrison and Stiassny, 1999). Therefore, <i>P(local)</i> was set relatively high. However, most analyses of the ecology of the Lake Victoria cichlids and the impacts of the threats have been focused on the southern parts of the lake; the distribution of the species through the entire lake, and the extent of impacts throughout the lakewide range are less well known. Thus <i>P(spatial)</i> is given a mid-range score with broad bounds.

If there is more than one plausible threat, the assessor needs to take into account the combined effects of their occurrence, severity, timing, duration and geographic scope, their effect on population persistence and any plausible interactions between them. For example, for a taxon threatened by habitat loss and overharvesting, it may be plausible to infer that the relative intensity of harvest increases as the area of available habitat contracts.

There is no formal way of assigning a weight to each of the reasons, lines of evidence, or objections that contribute to an overall assessment. Assessors must form a subjective opinion on the likelihood that the species is extinct, based on the weight of evidence in support of all reasons and objections.

This task is complicated by the fact that multiple threats do not necessarily have to occur synchronously throughout the range of a taxon to cause extinction. Different threats may affect different parts of the range at different times, although this may be tempered by dispersal and the dynamics of suitable habitat patches within the landscape (see examples in Table 1). Use of Eq. (3) (see *Gentiana wingecarribiensis* in Table 1) may help to resolve some of this complexity. Nonetheless, to estimate $P(\text{spatial})$ assessors need to consider the cumulative spatio-temporal pattern of threats (van Teeffelen et al., 2012). One approach to this is to first consider the proportion of the range affected by the most pervasive threat(s), and then consider the degree to which the other identified threats affect the remainder of the range. In both cases, the effect needs to be of sufficient severity and duration to cause local extinction. For threats that act episodically or otherwise for a short duration, the assessor also needs to consider whether taxon movement reduces its likelihood of going extinct. The estimates of $P(\text{local})$ and $P(\text{spatial})$ for *Gentiana wingecarribiensis* and other taxa in Table 1 reflect these considerations.

4. Dealing with uncertainty

Experts are susceptible to a range of subjective influences. They tend to rely heavily on earlier judgements, and are affected by context, framing and recent, easily recalled events (Burgman, 2015). Language-based misunderstandings also introduce unwanted, arbitrary variation in expert judgements (Regan et al., 2002). Many of these issues can be anticipated and mitigated by employing simple, structured procedures to question experts and combine their judgements. We suggest using a procedure for estimating the probability that a species is extinct, based on three parameters (upper and lower bounds, and the best estimate), in a setting in which people make an initial private estimate (Burgman, 2015). They then discuss the issue and any differences of opinion with other experts, and lastly, make a second, private estimate (McBride et al., 2012). These estimates may be combined in a variety of ways, depending on the needs of the elicitation process (Martin et al., 2012).

To illustrate how single experts can deal with their uncertainties, we estimated threat parameters and calculated extinction probabilities for representative taxa of birds, mammals, fishes and vascular plants (Table 1). For each parameter, experts provided a bounded best estimate of subjective probabilities that threats were of sufficient severity and geographic scope to have caused extinction. Their confidence in the best guess is summarised by the width of the bounds of their estimates. The justification for these parameter estimates shows the kinds of qualitative information, assumptions and inferences that experts have used in quantifying their opinion. We provide general guidance in Table 2 to assist experts to assign values for probabilities.

5. Discussion

Our structured method for diagnosing extinctions should balance risks of errors (Akçakaya et al., 2017-in this issue) more effectively than current practices for listing extinct taxa, which tend to ignore uncertainty and rely on unstructured expert intuition. Moreover, our approach should enhance new methods of inference by generating

relatively reliable probabilities of extinction that can be compared with those derived from independent time series of occurrence records and search effort (Scott et al., 2008; Thompson et al., 2017-in this issue). In some cases it might be possible to use threat-based estimates of $P(E)$ as initial values that could be updated in a model of a time series of records (Thompson et al., 2017-in this issue). This would only be valid if i) a threat-based $P(E)$ could be estimated based on knowledge of antecedent threats at those respective times; and ii) the estimate draws only on information about the likely impact and pervasiveness of threats and not on the time series of records or search effort. The requirement for independence ensures that statistical inferences avoid circularity in calculating probabilities of extinction (McCarthy, 2007). Where time series of records and information on unsuccessful surveys are lacking or the assumptions of statistical models are not met (Collen et al., 2010; Boakes et al., 2015), subjective estimates based on threats will be the primary means of estimating extinction probability.

Argument maps and structured elicitation methods should substantially improve the consistency and accuracy of expert opinion about extinctions by obliging experts to be more explicit about different components contributing to extinction probability. This, and bounded estimates of subjective probabilities, will provide a basis for discussing uncertainty and resolving differences of opinion about whether a species has gone extinct. Furthermore, the method is simple and can be applied by biologists even when very little is known about the taxon under consideration. Experts may draw inferences from knowledge about similar or related taxa that they may consider relevant to the likelihood of persistence of the candidate taxon (Table 1). By itself, the method requires no detailed mathematical analysis, but may complement such methods when sufficient data are available to apply them.

Information about candidate taxa may be limited, for example, to anecdotal information about the effects of threats within a small part of the range or information about the effects of similar threats on similar or related taxa. In these cases, inferences can draw on understanding about the susceptibility of related taxa to particular threats and on threats operating in the area of concern and affecting syntopic taxa. Species life-history traits may also inform the estimation of $P(E)$ by highlighting vulnerabilities to particular threats. In plants of fire-prone habitats, for example, the trait combination of obligate-seeding, long generation time and serotiny is one that predisposes populations to a high risk of local extinction under high frequency fire regimes (Keith, 1996; Enright et al., 2015). Similarly, there is considerable evidence that flightlessness, long generation time and insularity predispose birds to the impacts of invasive alien predators. Hence the presence of introduced rats, for example, can often be inferred to threaten population persistence (BirdLife International, 2013). In grouper fishes (Epinephelidae), longevity and late sexual maturation are compounded by aggregation spawning to make them vulnerable to fisheries operations (Sadovy de Mitcheson et al., 2013). For fishes generally, the relationship between extinction risk and body size is not straightforward, particularly in freshwaters, emphasizing the need to consider coevolving complexes of multiple traits when assessing extinction risk (Olden et al., 2007). Cultural and economic factors can be relevant to estimating $P(E)$, particularly for species exposed to harvest or hunting.

Phylogenetic relationships may also be a means of inferring susceptibility to particular threat. For example, disease carried by introduced mosquitoes is believed to have been an important factor in the extinction of the Hawaiian bird species Kamao *Myadestes myadestinus* and Amaui *Myadestes woahensis*. It may be inferred that the same disease is a threat to congeneric Olomao *Myadestes lanaiensis*, which is also suspected to be extinct in Hawaii.

Expert judgements are routinely beset with overconfidence and submerged bias (McBride et al., 2012; Burgman, 2015). To reduce effects of overconfidence and bias on their estimates of $P(\text{local})$ and $P(\text{spatial})$, experts should be asked to provide three quantities for each, namely, a credible lower and upper bound and a best guess (McBride et al., 2012). The width of the interval captures the expert's confidence

Table 2

Guidance for estimating subjective probabilities that threats are sufficiently severe $P(local)$ and of sufficient geographic scope $P(spatial)$ to have caused extinction of a taxon under consideration. The nominal thresholds in the left-hand column are for illustrative purposes and are not intended to be prescriptive for experts estimating subjective probabilities.

Range of probabilities	Severity of threat(s) – $P(local)$	Geographic scope of threat(s) – $P(spatial)$
0.99–1.00	The severity and duration/timing of threats are virtually certain to have caused local extinction, i.e. would cause 99 of 100 species similar to the target to go extinct.	It is virtually certain that the threats affect or affected the entire range of the taxon, given any possibility that the taxon occurs or occurred outside its known range. There is a less than a one in a hundred chance that the taxon persists within its known range or at an undiscovered location outside the known range.
0.95–0.98	The severity and duration/timing of threats are very highly certain to have caused local extinction, i.e. would cause 49 of 50 to 19 of 20 similar species to go extinct. There is a one in a fifty to one in twenty chance that the taxon may persist despite the threats.	It is very highly certain that the threats affect or affected the entire range of the taxon, given any possibility that the taxon occurs or occurred outside its known range. There is a one in a hundred to one in twenty chance that the taxon persists within its known range or at an undiscovered location outside the known range.
0.75–0.94	The severity and duration/timing of threats are quite likely to have caused local extinction, i.e. would cause 19 of 20 to three in four similar species to go extinct. There is a one in twenty to one in four chance that the taxon may persist despite the threats.	It is quite likely that the threats affect or affected the entire range of the taxon, given any possibility that the taxon occurs or occurred outside its known range. There is a one in twenty to one in four chance that the taxon persists within its known range or at an undiscovered location outside the known range.
0.50–0.74	The severity and duration/timing of threats are more likely than not to have caused local extinction, i.e. would cause half to three-quarters of similar species to go extinct. There is a one in four to 50:50 chance that the taxon may persist despite the threats.	It is more likely than not that the threats affect or affected the entire range of the taxon, given any possibility that the taxon occurs or occurred outside its known range. There is a one in four to 50:50 chance that the taxon persists within its known range or at an undiscovered location outside the known range.
0.25–0.49	The severity and duration/timing of threats are quite possible but unlikely to have caused local extinction, i.e. would cause one quarter to one half of similar species to go extinct. There is more than a 50:50 and up to a 3 in 4 chance that the taxon may persist despite the threats.	It is quite possible but unlikely that the threats affect or affected the entire range of the taxon, given any possibility that the taxon occurs or occurred outside its known range. There is more than a 50:50, but not more than 75% chance that the taxon persists within its known range or at an undiscovered location outside the known range.
0.10–0.24	The severity and duration/timing of threats are quite unlikely to have caused local extinction, i.e. would cause one tenth to one quarter of similar species to go extinct. There is a 3 in 4 to 9 in 10 chance that the taxon may persist despite the threats.	It is quite unlikely that the threats affect or affected the entire range of the taxon, given any possibility that the taxon occurs or occurred outside its known range. There is a more than 75%, but not more than 90% chance that the taxon persists within its known range and/or at an undiscovered location outside the known range.
0–0.09	The severity and duration/timing of threats are very unlikely to have caused local extinction, i.e. would cause up to one tenth of similar species to go extinct. There is more than a 9 in 10 chance that the taxon may persist despite the threats.	It is very unlikely that the threats affect or affected the entire range of the taxon, given any possibility that the taxon occurs or occurred outside its known range. There is more than a 90% chance that the taxon persists within its known range and/or at an undiscovered location outside the known range.

in their best guess.

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