



Statistical inference for extinction rates based on last sightings



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HIGHLIGHTS

- Past and present extinction rates are generally assumed as constant.
- Marine extinctions are expected to rapidly increase in the future.
- We developed a model based on last sightings for estimating extinction rates.
- Recent marine extirpations are increasing but at an uncertain rate.
- A constant rate of modern extinctions in the sea is statistically plausible.

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ABSTRACT

Rates of extinction can be estimated from sighting records and are assumed to be implicitly constant by many data analysis methods. However, historical sightings are scarce. Frequently, the only information available for inferring extinction is the date of the last sighting. In this study, we developed a probabilistic model and a corresponding statistical inference procedure based on last sightings. We applied this procedure to data on recent marine extirpations and extinctions, seeking to test the null hypothesis of a constant extinction rate. We found that over the past 500 years extirpations in the ocean have been increasing but at an uncertain rate, whereas a constant rate of global marine extinctions is statistically plausible. The small sample sizes of marine extinction records generate such high uncertainty that different combinations of model inputs can yield different outputs that fit the observed data equally well. Thus, current marine extinction trends may be idiosyncratic.

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1. Introduction

Extinction is the ultimate fate of all species; in fact, 99.9% of all evolutionary lines that once existed on Earth have vanished (Jablonski, 2004). For some authors, such as Mayr (1942, 1970, 2001), Valentine (1973) and Futuyma (2009), the concept has been broadened to address population losses, also known as extirpations. In this study, we adopt this approach and include recent documented extirpations and extinctions in the marine realm

(from 1500 onwards; see MacPhee and Flemming (1999) for the sake of a more complete analysis).

Although extinction is a recurrent evolutionary phenomenon, it does not proceed at the same pace at all times. Whilst a relatively low number of species usually become extinct during any given time span (background extinctions), there are periods during which a large proportion of the biota is exterminated in a very short time on a geological timescale (mass extinctions (Mayr, 2001)). These two different extinction rates have been considered as a reference point for contextualising the current state of the global biological diversity (Pimm and Jenkins, 2010).

1.1. The analysis of extinction

In terrestrial groups, estimates of recent extinction rates are between 100 and 1000 times higher than the long-term global average derived from the geological record (May et al., 1995).

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This phenomenon has been interpreted as evidence of the 6th mass extinction period in the Earth's history (Barnosky et al., 2011).

No similar estimation exists for marine groups, but the increasing concern that human development may be acting as a major driver of current and future marine extinctions and biodiversity loss (Myers and Worm, 2003; Worm et al., 2006; Dulvy et al., 2009; Millennium Ecosystem Assessment, 2005; Rogers and Laffoley, 2011), is propelling formal attempts to estimate the number of species that have recently disappeared from the oceans (Smith and Solow, 2012), incorporating probabilistic methods.

Over the past 500 years there have been 21 documented extinctions in the sea (Dulvy et al., 2003; del Monte-Luna et al., 2007), which corresponds to an average constant rate of 0.04 species per year (1 species every 25 years). This value is lower than the fossil background rate, estimated as 1 species per year (May et al., 1995). Another way to measure extinction rates is as a function of the extant biota per unit of time; i.e., the number of extinct species per million species per year. If there are 21 documented cases of contemporary global marine deletions, and considering an estimate of 1.4 to 2.2 million extant species in the ocean (Bouchet, 2006; Mora et al., 2011), then the current marine extinction rate would be ~ 0.03 to ~ 0.02 species per million species per year. Using this metric, historical background extinction rates stand between 0.1 and 1 species per million species per year or less (Primm et al., 1995; Pimm and Brooks, 2000).

However, as noted by Regan et al. (2001), there are important issues to be considered when comparing present and past extinction rates, including the disparity of temporal scales, the amount of effort applied to detect modern extinctions and the uncertainty associated to the estimation of the total biodiversity. Thus, valid comparisons of this type demand more accurate information about modern extinction trends in the ocean. In the present contribution we show that it may be possible to infer extinction rates of a group of species when only the time of the most recent sighting is available, and independently of the total number of species on Earth.

The exact time of extinction is unknown in most cases, therefore the time of last sighting or the last few sightings of a species are frequently used as indirect proxies for the true extinction date; however, this practice is highly controversial since there are numerous cases of species that have been sighted long after being declared extinct (Wignall and Benton, 1999).

Many statistical methodologies for estimating extinction dates assume that a representative record of historical sightings precedes the time of last sighting (Roberts et al., 2010; Rivadeneira et al., 2009). In reality, however, the observational basis for inferring extinctions is very weak (Smith and Solow, 2012). Specifically, historical sighting records are difficult to secure and last sightings are often the only realistic data available (Dulvy et al., 2003, 2009).

We explore a probabilistic approach to determine how recent marine extinction rates have changed over the past 500 years by: (1) proposing a mathematical description of the relationship between extinction, sampling effort, and time of last sighting; (2) describing how statistical inference may be conducted if the only reliable data point is the time of last sighting; and (3) applying the proposed method to datasets on recent marine extirpations and extinctions.

We acknowledge that this study is based on the marine extirpations and extinctions that have been documented over the past 500 years, which may not coincide with the number of populations and species that have been lost without being recorded.

2. Models and inference for extinctions based on last sightings

In formal statistical analysis, data are regarded as random observations that can be described through a probability density. This density depends on unknown parameters that become the items of interest in scientific studies (Spratt, 2000). In this section, we derive a probability density for the time of last sighting by conceptualising the data acquisition process.

The time of last sighting results from the combination of the biological species itself, which is the entity subject to extinction, and the human observers, who record what is being sighted. These processes occur in time and, with rare exceptions (Turvey et al., 2007), they can be considered unpredictable. We begin by characterising probabilistically these two processes observed over a given time interval $[0, \tau]$.

2.1. Modelling extinction, extinction rates, and sampling effort

For describing the biological extinction of a given species, let us denote by E its random time to extinction, measured from time $t = 0$. Assuming that we have observed over the interval $[0, \tau]$, then $E > \tau$ means that the species did not become extinct within that lapse and $E \leq \tau$ indicates that the species became extinct during the observed time frame, even if we do not know the exact value of E . For a general description of the probabilistic behaviour of E , we can use a continuous probability density $g(t)$ over the domain of the positive real numbers. A cumulative probability distribution function is then implicitly defined as

$$G(t) = \int_0^t g(u) du$$

(or equivalently $g(t) = (d/dt)G(t)$).

Answering questions regarding extinction rates will be essential in our discussion. A complementary probabilistic concept, adopted from the survival analysis and reliability theory (Lawless, 2003), will be useful for that purpose: the *hazard function* (sometimes called *failure rate*), which for E is defined as

$$h(t) = \frac{g(t)}{1-G(t)}.$$

It has the interpretation of being an “instantaneous rate of extinction” in the following sense:

$$h(t) = \lim_{\Delta t \rightarrow 0} \frac{P(t \leq E < t + \Delta t | E > t)}{\Delta t}.$$

For small Δt , $h(t)\Delta t$ is approximately the probability that the species will become extinct within the next Δt units of time given that it has not yet become extinct by time t . An important special case is a constant hazard, $h(t) = c$, which can be seen to correspond to an exponential density, $g(t) = c \exp(-ct)$. However, as the hazard function describes variation in the risk of extinction as a function of time, we may also refer to decreasing or increasing extinction rates.

Addressing extinction rates via a hazard function appears to be a novel concept. Average measures of extinction rates of the form

$$\frac{\# \text{extinctions}}{\# \text{species}} \times \frac{10^6}{t_2 - t_1}$$

or similar, are the norm in the biological literature (Regan et al., 2001). In this particular metric, the number of extinctions is calculated between years t_1 and t_2 and standardised to one million years. Such estimates assume that the extinction rate is constant, yet our interest is in investigating whether such rates vary over time. The hazard function, in contrast, is an instantaneous rate (an analogy is the rate shown by an automobile speedometer at any time vs. a mean rate given as the total distance travelled divided by the total time for a given trip).

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