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Opinion

# Population abundance estimates in conservation and biodiversity research

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**Measuring and tracking biodiversity from local to global scales is challenging due to its multifaceted nature and the range of metrics used to describe spatial and temporal patterns. Abundance can be used to describe how a population changes across space and time, but it can be measured in different ways, with consequences for the interpretation and communication of spatiotemporal patterns. We differentiate between relative and absolute abundance, and discuss the advantages and disadvantages of each for biodiversity monitoring, conservation, and ecological research. We highlight when absolute abundance can be advantageous and should be prioritized in biodiversity monitoring and research, and conclude by providing avenues for future research directions to better assess the necessity of absolute abundance in biodiversity monitoring.**

## Highlights

Abundance can be used to describe how a population changes across space and time, but it can be measured in different ways, with consequences for the interpretation and communication of spatiotemporal patterns.

There are many reasons why absolute abundance can benefit biodiversity research, including monitoring, conservation, and ecology.

Protocols to measure absolute and relative abundance can differ in data collection and/or analysis, with the key difference being if, and to what extent, the probability of detection is accounted for.

As we attempt to 'bend the curve' of biodiversity loss in the Anthropocene, it is important to continuously (re)consider how biodiversity is measured.

## Assessing biodiversity change in the Anthropocene

Anthropogenic changes have profound effects on the distribution and abundance of species worldwide [1], with potential widespread negative consequences [2,3]. Extinction rates are currently orders of magnitude higher than background levels [4], leading to international targets for increasing 'abundance of native wild species … to healthy and resilient levels' (Goal A of the recent Kunming–Montreal Global Biodiversity Framework, https://www.cbd.int/gbf/). Biodiversity monitoring is required at multiple scales to track progress towards such targets and to identify drivers of change to inform conservation actions [5]. However, quantifying and tracking biodiversity change is not straightforward, partly due to the multifaceted nature of biodiversity and associated variety of metrics that are used to describe spatial and temporal patterns [6,7]. Such ambiguity has led to challenges in comparing, interpreting, and communicating estimated biodiversity change, for example, highlighted by different interpretations of the Living Planet Index and its change across time [8–11].

As an Essential Biodiversity Variable, abundance can be used to describe how a population changes across space and time [12] and is critical to predicting population collapse [13] and measuring recovery [14]. Abundance estimates and trends often provide the backbone of regional and global conservation assessments [e.g., the International Union for Conservation of Nature (IUCN) Red List], as well as policies for conserving particular species (e.g., the Endangered Species Act). These estimates are often aggregated into multispecies indicators (e.g., the Farmland Bird Index [15]), which are used to provide a representative picture of biodiversity change across many species simultaneously. Single- and multispecies abundance indicators are also used to compare abundance change across guilds and ecosystems, aiming to compare rates of change or identify putative drivers of change.

Often overlooked, however, is that abundance can itself be measured in different ways, which affects how the data can be modeled, and how analytical outputs can be interpreted and communicated. Estimates of abundance broadly fall into two categories, namely **absolute**

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**abundance** (see Glossary), and **relative abundance**, with the latter being especially common (Figure 1). Probably because of its dominance in empirical studies, relative abundance data are often just referred to as 'abundance' in many scientific studies, sometimes without clarification that they can only be interpreted in relative terms. In this article, we aim to highlight the value of absolute abundance estimates for biodiversity monitoring, conservation, and research.

## Distinguishing between relative and absolute abundance

Absolute abundance refers to the total number of individuals in an area, which can be obtained by estimating abundance for a given area directly or by estimating the density (i.e., the number per unit of area) for an area. Absolute abundance intends, as far as possible, to estimate the 'true' total population size of a species. Regardless of the approach taken to collect and analyze the data, these estimates will generally be measured with some error (excluding the case of a total perfect **census**), with the degree of uncertainty depending on species attributes (e.g., rarity and **detectability**) as well as survey attributes (e.g., sampling intensity). Relative abundance, also sometimes known as abundance indices, by contrast, does not explicitly attempt to measure the 'true' size of the total population but rather aims to be a proxy of it. For instance, relative abundance could represent the number of birds detected along a fixed transect length or the number of rodents trapped within a unit of time. Relative abundance is usually used to compare the differences in abundance along a gradient of interest, usually time or space, in relative terms; for instance, they can show where and/or when species are more or less abundant [16]. Relative abundance is also often assumed to

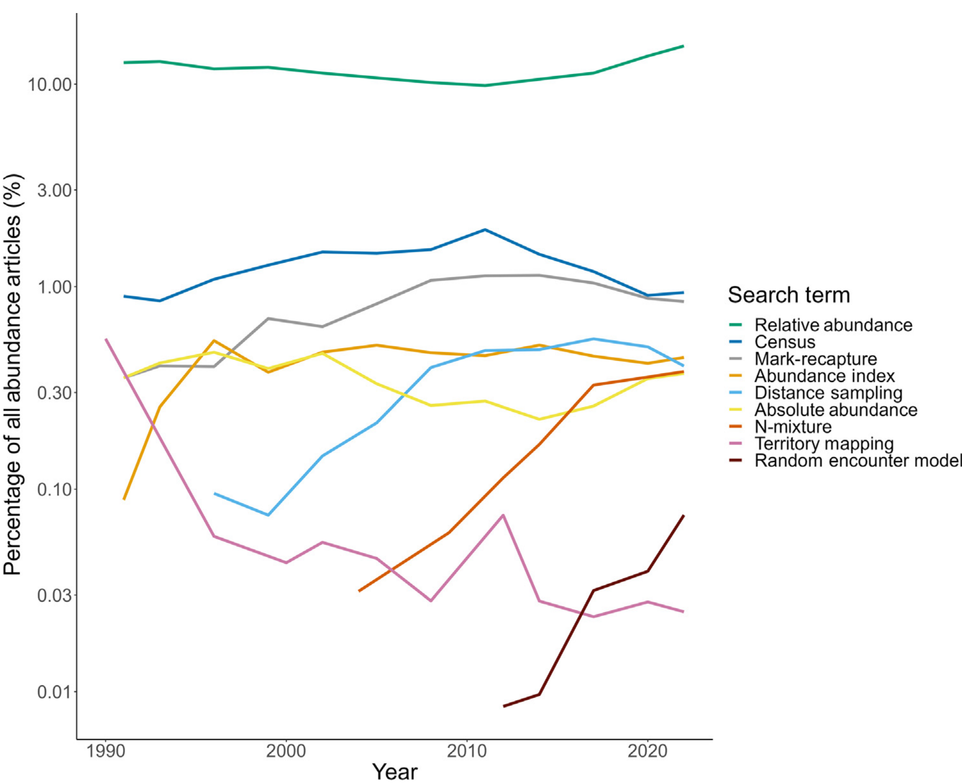


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Figure 1. Trends in publishing of abundance-related terms. The number of search hits from Web of Science for the different search terms represented as the proportion of all 'abundance' hits used to control for the increasing number of publications. We included 'AND (species or biodiversity)' in all searches to represent ecological studies. The majority of the hits are from relative abundance (green line) compared with absolute abundance (light blue line).

## Glossary

**Absolute abundance:** the total number of individuals in an area.
**Detectability:** the likelihood or probability of observing or detecting a particular species or individual during a survey, study, or observation.
**Census:** the systematic and comprehensive counting or estimation of the entire population of a species within a specific area.
**Distance-sampling:** collecting data on the distances between observers and individual organisms or objects of interest during field surveys. This method is particularly useful for estimating the abundance or density of populations in situations where a direct full census is challenging or impractical.
**eDNA:** the genetic material (DNA) shed by organisms into their surrounding environment, such as the water, soil, or air. This can be collected and analyzed to identify the presence of specific species in an ecosystem without directly observing the organisms themselves.
**iDNA:** a subset of eDNA where vertebrate species can be identified by the DNA that has been ingested by various invertebrate taxa, including leeches, ticks, and mosquitoes.
**N-mixture models:** a statistical approach to estimate the abundance or population size of a species by accounting for both observed and unobserved individuals in a population.
**Random encounter model:** a statistical method to estimate the abundance or density of animal populations through the analysis of camera trap data. It utilizes the concept that the probability of an individual encountering a camera trap is random and not influenced by its abundance.
**Relative abundance:** a proxy for the true total population size of a species.
**Territory mapping:** identifying and delineating the specific areas that individual animals or groups of animals defend and occupy as their own. These territories are then used to provide an estimate of absolute abundance (e.g., the number of pairs).

show the relative differences among species (i.e., to indicate whether, and by how much, one species is more or less common than another species) [17]. To make such interpretations, individuals are assumed to have similar probabilities of detection across the gradient of interest, so that the relative abundance is linearly related to the absolute abundance, though this is rarely explicitly stated or justified.

Similar data collection protocols can be used for both absolute and relative abundance, with the key difference being if, and to what extent, detection probability is taken into account (Figure 2). Relative abundance data can be collected via simple point or line-transect counts. For example, the protocol of the North American Breeding Bird Survey involves counting birds seen or heard for 3 min at designated points along a survey route [18]. Indeed, one strength of relative abundance collection protocols is the ease of regular surveys leading to long-term time series. The simplicity of protocols for relative abundance estimates has likely aided the growing contribution of citizen science in monitoring. By contrast, protocols for collecting, handling, and modeling absolute abundance data are varied but are typically more complex and demanding in terms of both time and expertise. Traditional survey methods used to estimate absolute abundance involve intense field surveying (e.g., census surveys or **territory mapping** that aim to be sufficiently intensive to detect all individuals living in an area) [19] or marking individuals (e.g., capture–recapture). A range of newer methods statistically predict the absolute abundance without marked individuals, by estimating and accounting for the varying detectability of individuals within the study area. For example, **distance-sampling** protocols involve recording the distances at which detected individuals are observed, and then estimating the fraction of the survey area that was effectively surveyed and the number of individuals that were likely to have been missed [20–22]. Alternatively, data from repeated surveys within the same season at the same sites can be used to estimate detection probabilities and therefore the total population size (e.g., **N-mixture models** [23]). These methods can explicitly account for variation in detection probability that may arise along spatial (e.g., due to habitat differences affecting visibility) or temporal (e.g., due to changes in methodology or catch efficiency) gradients, as well as differences among species (e.g., due to body size or behavior affecting the probability to detect) (Figure 2). Some of the traditional methods, such as territory mapping, have become less popular over time, while newer, more statistics-driven approaches, such as N-mixture models and the **random encounter model** used with camera trap data [21], have grown (Figure 1). Additionally, recent advancements in DNA sampling, such as the use of scat, hair, invertebrate-derived (**i)DNA**, or environmental (**e)DNA**, have introduced novel methods for monitoring populations [24], facilitating the tracking of individuals and the estimation of abundance through noninvasive mark–recapture methods.

## Why we need absolute abundance for biodiversity monitoring and ecological research

The relative utility of different sampling protocols has been extensively debated in the past [25,26]. For questions about long-term trends in abundance, relative abundance indices are often justifiable when data are collected by standardized sampling protocols. This is because standardization should limit the variation in detection probabilities and mean that trends in relative abundance reflect the trends in absolute abundance (Figure 2 and Table 1) ([27–29], but see [30]). Only absolute abundance estimates, however, provide information on the actual population size of a species [29]. Because of this, there are many reasons why absolute abundance can benefit biodiversity research, including monitoring, conservation, and ecology. However, as highlighted in [13], other indices such as changes in habitat or body condition can also be critical, providing early warning signals of future population changes. Box 1 provides a nonexhaustive list of potential contexts where absolute abundance may be particularly beneficial.

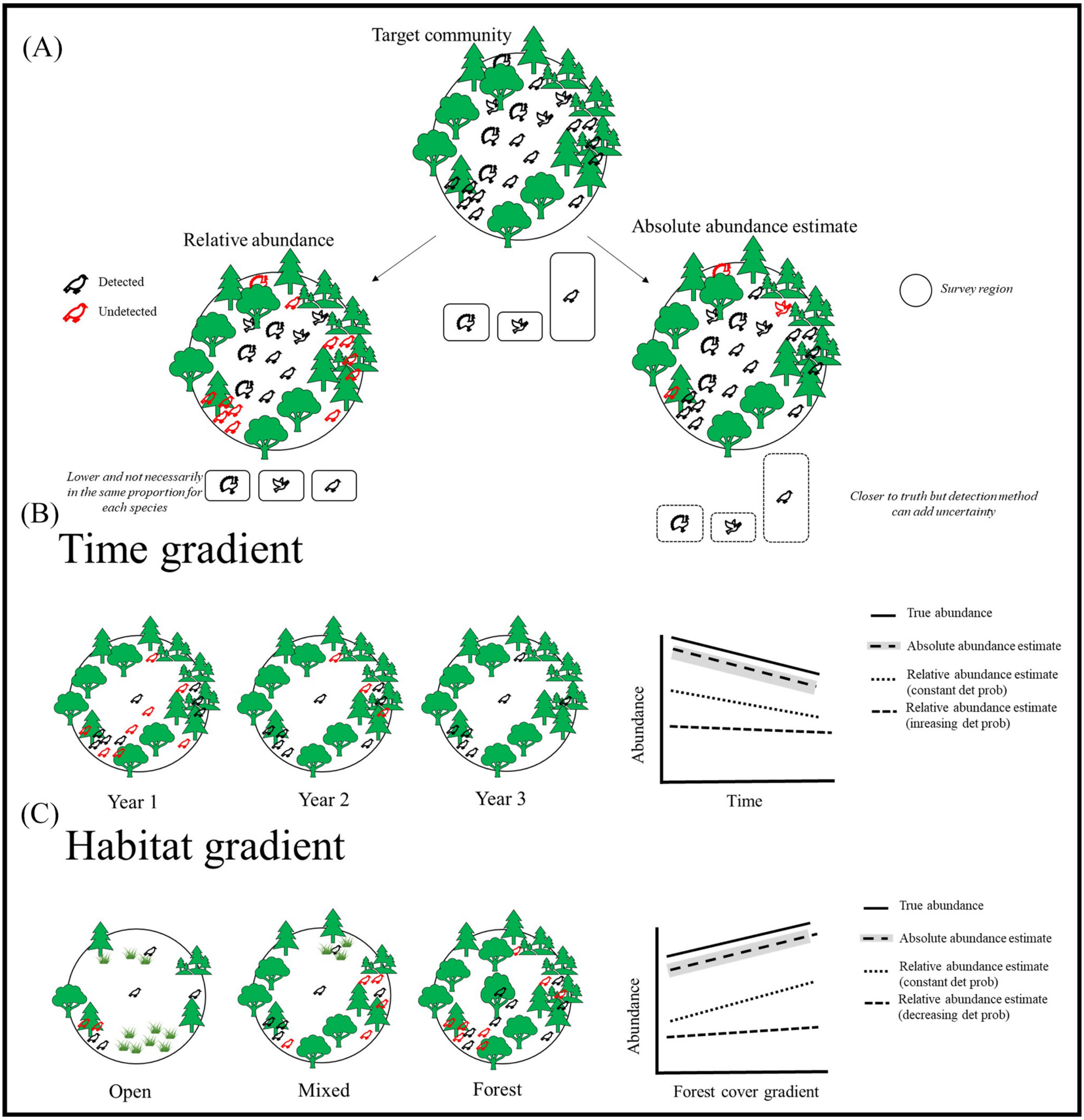


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Figure 2. Differences in relative and absolute abundance. (A) A schematic representation illustrating the differences in absolute and relative abundance and how they can differ from the 'true target community', where the size of the box under each schematic is a representation of the population size of that species. Differences in detection probability (det prob) among species can hamper the reliability of both measurements, but more so for relative abundance. (B,C) A theoretical representation of how values and trends in absolute abundance can differ from those for relative abundance over time (B) or along a spatial gradient (C), such as a forest cover gradient, where each circle represents a different location along the gradient. Estimates of absolute abundance could aim to account for the changing probabilities of detection. By contrast, a study using only relative abundance data could conclude that the true abundance changes, when only the detection of probability has changed instead. In (B), we contrast scenarios where the probability of detection is constant or increases through time (e.g., due to learning by the surveyors). In (C), we contrast scenarios where the probability of detection is constant or decreases with increasing forest cover (e.g., if species become harder to spot during visual surveys). In (B) and (C), the red 'undetected' individuals are for the changing detection probability scenario.

Table 1. An overview of the advantages and disadvantages of relative and absolute abundance[a]

| | Relative abundance | | Absolute abundance | |
|---|---|---|---|---|
| | Advantages | Disadvantages | Advantages | Disadvantages |
| Measurement | Can be cheaper and less time-consuming, enabling repeat surveys in time series<br><br>Easier for mass participation from citizen science | Need to be collected with standard protocol if the aim is to compare across time/space | Can quantify the certainty in the estimate | Costly and more time-consuming<br>May be particularly limited by sample size sampling intensity |
| Modeling | Statistically simpler to analyze and explore variation among sites and times | Comparability compromised when data are collected under different ecological conditions or with different methods that affect detection probabilities | Comparable across species and ecological conditions even when detection probabilities vary | Some methods rely on statistical assumptions (e.g., the independence of individual detections) |
| Interpretation | Can be used to estimate the percentage of population change, which can inform Red List assessments (criterion A in Red List assessments) | Differences in baselines can make comparisons of relative abundance challenging | Can be used to measure the achievement of conservation targets aimed at persistence<br><br>Can inform about distance from local extinction (e.g., crit. C and D in Red List assessments, and underpin estimates for crit. E), demographic, or genetic stochasticity, and Allee effects | Sampling method and important key parameters (e.g., extent of the study area) must be taken into consideration<br>Uncertainty and varying levels of bias in a series of estimates may cause mis-leading or unclear indica-tions of population trends |
| Communication | Expressing changes as percentages may be impactful for communication | Spatiotemporal change in multispecies indices is difficult to communicate<br><br>The index can be harder to communicate to scientists, policymakers, and practitioners, and is prone to misinterpretation | Provides tangible numbers<br><br>Can be compared with targets or biologically meaningful reference conditions<br><br>Provides values that people may be more readily able to relate to | Prone to misinterpretation if lacking reference values |

[a]This table is not meant to be exhaustive but is rather an overview of the advantages and disadvantages.

## Challenges and limitations to absolute abundance

For both the individual researcher and monitoring program designer, many factors still affect the choices concerning the methods of data collection, analysis, and reporting of abundance data (Table 1). Estimates of absolute abundance are more commonly attempted for taxa with relatively low densities, such as birds and mammals, and for sessile organisms, such as trees. The reasons vary; for example, an estimate of absolute abundance may be deemed to be more relevant for species of high conservation concern or for setting hunting quotas (e.g., game species), while sessile organisms are easy to count and therefore the absolute abundance can be commonly calculated. For species with typically high densities, absolute estimates are usually only feasible at very small scales (but see [31] for an attempt to estimate the global number of ants). However, absolute abundances have been collected for butterflies using distance-sampling protocols [32] and soil organisms, such as earthworms, in terms of the density of individuals [33].

Species mobility and spatial scale can affect the interpretation of absolute abundance, since the number of individuals within the study area may vary during the sampling period. Methods such as classical mark–recapture, for example, define the study area on the basis of assumptions about animal movement (e.g., using half the maximum distance moved vs. the maximum distance moved). Similarly, aerial censuses of mammals must account for the fact that detected individuals might have home ranges extending beyond the study area. One tool that attempts to overcome some of these challenges is the use of spatially explicit capture–recapture models that are used

Box 1. Examples of research areas where absolute abundance may be particularly beneficial over relative abundance

**Absolute abundance can help establish the risk of extinction**

Absolute abundance provides the best evidence of how close a population currently is to extinction, alerting the need for immediate conservation actions, even when only a single survey has been undertaken. By contrast, trends in relative abundance can only be used to project the risk of extinction [53]. Nevertheless, the IUCN Red List classifies a species as critically endangered if it has declined by 80% or more over three generations, regardless of whether this is based on population estimates, indices, or area of occupancy data.

**Managing sustainable yields**

Absolute abundance data are valuable for setting and revising harvest limits for hunted populations, ensuring a sustainable harvest strategy, which can also be informed by monitoring demographic rates.

Absolute abundance is required to effectively monitor and track the successful achievement of conservation targets. Current narratives about 'bending the curve' focus only on trends but not where (i.e., what population abundance) the curve should plateau for a given species. While trend targets are important, additional targets of abundance goals would better reflect the variation in conservation goals (i.e., desired population sizes) of different species [54], something that is only possible if reasonable estimates of absolute abundance can be derived from the monitoring data.

**Estimate ecosystem services and disservices**

With absolute abundance estimates, it becomes possible to quantify the total contribution of species to ecosystem functioning and ecosystem services, such as those based on estimates of biomass (e.g., [31,55,56]). Absolute abundance can also help quantify the transmission of diseases or parasites (e.g., the abundance of mosquitos [57]), which is relevant for public health impacts or the impact of pest species (e.g., feral cats [58]).

**Energy flows, resource requirements, and species' interactions**

Energy fluxes between trophic levels and the frequency of species interactions are strongly influenced by their absolute abundance or density, which affect the encounter rates of different species [59,60]. Absolute abundance allows the inference of food webs and interactions [61]. The ability to disentangle whether the frequency of interactions between organisms are dependent on the absolute abundance or real preferences for such interactions [62].

to model movement processes when estimating density [34]. Moreover, extrapolation of abundance estimates beyond the sampled region adds further uncertainty [35], but statistical weighting approaches can help account for sampling biases [36].

Large-scale syntheses have become a popular approach to assess patterns in biodiversity change across the world [37–39]. These syntheses often collate relative abundance data for a range of taxa, collected via a range of sampling methods, and so the values of abundance are only comparable within studies (as within-study trends). To facilitate the comparison of within-study trends across studies, these trends in abundance are typically expressed as proportionate changes (e.g., as log ratios, percentage differences, or as regression slopes on a logarithmic scale) [10,40]. This may be useful for making comparisons of abundance trends between taxa with 'baseline' abundances that vary by orders of magnitude (e.g., beetles and birds). However, the choice of the scale used to measure trends, whether arithmetic or proportionate differences in abundance, can yield very different conclusions about the direction and magnitude of driver impacts such as climate and land use intensity [10,41].

## Avenues for future research

Many approaches and tools are needed to truly understand the differences in absolute abundance among species and regions to provide a comprehensive picture of biodiversity change. Here, we present what we see as four key areas of future research regarding the use of absolute abundance in biodiversity monitoring.

### Improve understanding of when variation in detection probability does and does not matter

Detection probabilities do not need to be constant for relative abundance to be useful. As noted [26], with enough surveys over an extended period, fluctuating detection probabilities may introduce noise rather than bias, and be sufficiently small that trends in true abundance are revealed. Understanding when there is systematic variation in detection probability that will influence inferred biodiversity patterns is critical. Detection probability can refer to the probability of detecting a species or the probability of detecting an individual of a species. For abundance estimates, it is typically the probability of detecting an individual that is important. Detection probabilities can vary greatly across space, for instance, among habitats that vary in vegetation structure or other attributes that affect how well visual or acoustic signals are transmitted. Detection probabilities can also change over time. For example, although the study methodology (i.e., the method of the survey or census) might not vary, detection probability can change seasonally due to changes in species behavior (e.g., during the breeding season or due to food availability), annually due to climate variations or disturbances that affect visibility or audibility, or over the longer term due to changes in observer abilities [42]. Detection probabilities can also vary among species, potentially affecting the shape of species abundance distributions within communities. However, attempts to account for such variation in detection probabilities and derive 'absolute' estimates can also introduce uncertainty. Studies should continue to compare methods to reveal the usefulness of different approaches (e.g., [43]). Understanding the limitations of each method is key to choosing the right metric for a given context.

### Integrate multiple data streams to estimate absolute abundance and spatiotemporal patterns

Occupancy (i.e., presence or absence) has also been used to describe spatial and/or temporal species' patterns. Occupancy is potentially easier to estimate than abundance and can be related to abundance at some spatial scales [44], but trends in occupancy can also differ from trends in abundance (e.g., [45]). A better understanding of the coupling between occupancy and abundance at different spatial scales can help us understand when occupancy is an appropriate surrogate. Integration of the data is an increasingly popular statistical approach to take advantage of multiple data streams, such as occupancy and abundance, and exploit the relative advantages of each one. Integrating absolute abundance data, such as those from distance sampling point counts, together with occupancy or relative abundance data derived from less complex data collection methods [46], could mitigate a disadvantage of absolute abundance: the high cost and effort. This approach could decrease the amount of absolute abundance data that are required. Citizen science data represent one potential means of leveraging diverse data sources covering large taxonomic, temporal, and spatial scales [47]. To effectively use these integrated methods, guidelines for approaches to integration and model validation need to be established [48]. By strategically planning the collection of abundance data with an eye towards integration with other available data (e.g., occupancy data [46]), assessments of absolute abundance at large scales could be possible.

### Focus on openness and reproducibility to push the field

Data syntheses have yielded important insights about large-scale biodiversity change, but most have presented analyses of relative abundance change so far. Potential synthesis of absolute abundance data would rely on open data and detailed metadata, but absolute abundance estimates that might not be deemed interesting enough to share via publication when assessed at a small spatial scale and are only comparable when the study area is known. Absolute population estimates should be presented with the extent of the study area, the exact sampling and estimation method, the dates of data collection, and error measures (if raw data are not shared). Standards for reporting absolute abundance data should continue to be refined to encourage researchers to share data in useful formats for reuse [49].

### Improve understanding of how absolute numbers resonate with members of the public

Societal support is needed for transformative change and to impede biodiversity loss. Framing plays a key role in how people engage with and respond to conservation messages [50]. We are unaware of any research that explicitly investigates the interpretability of 'indices' versus absolute abundance by the public. Anecdotally, absolute abundance can resonate with members of the public. As an example, [51] estimated that about three billion birds have been lost since the 1970s, and this message is now well known beyond the academic community. At the same time, large numbers can be hard to grasp. We speculate that some members of the public seek a broader perspective, such as national or global population figures, rather than data from a localized study area. However, other members of the public might relate more to the number of individuals in their local nature reserve. Moreover, the public is probably often more influenced by alarming rates of decline or conservation success stories than by specific population figures, underscoring the need for effective communication strategies that balance detailed information on abundance with compelling narratives of change. Interdisciplinary research on the communication and visualization of changes in absolute and relative abundance can help us to better understand how analyses of changes in biodiversity can impact policy.

## Concluding remarks

As we attempt to 'bend the curve' of biodiversity loss in the Anthropocene [52], it is important to continuously (re)consider how biodiversity is measured. The differences between relative abundance and absolute abundance are sometimes nuanced but can also lead to differences in interpretation, extrapolation, and prediction, all of which are necessary for an integrated strategy to combat biodiversity loss. Furthering our understanding of and ability to estimate abundance is essential for biodiversity research and conservation (see Outstanding questions). Here, we highlighted some of the benefits of considering absolute abundance and density in future biodiversity research and monitoring. We do not intend to negate the importance and utility of relative abundance, as there is room for both. However, the advantages of absolute abundance are many and, as a field, it should continue to be considered as the end-goal for advancing our understanding of ecology and biodiversity.

### Outstanding questions

How do relative and absolute abundance differ in their role in monitoring biodiversity and research?

What are the optimal methods and future opportunities to integrate diverse types of data to estimate absolute abundance?

Are there advantages of absolute abundance in the way the public interprets this information?

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### Declaration of interests

The authors have no interests to declare.

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