A tradable metric of local biodiversity impact linked to the Living Planet Index and global biodiversity conservation

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November 1, 2022

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Abstract

Difficulties identifying appropriate biodiversity impact metrics remain a major barrier to inclusion of biodiversity considerations in environmentally responsible investment. We show that changes in this metric quantify changes in the mean long-term global survival probability of species. We propose and analyse a simple science-based local metric: the sum of the proportions that all local populations contribute to their global species abundances, with a correction for species close to extinction. It links mathematically to a widely used global biodiversity indicator, the Living Planet Index, for which we propose an improved formula that directly addresses the known problem of singularities caused by extinctions. We show that, in an ideal market, trade in our metric would lead to near-optimal conservation resource allocation, emphasising support of extinction-threatened species. We further show that the metric is closely related to several other metrics and indices already in use. Barriers to adoption are therefore low. Used in conjunction with metrics addressing ecosystem functioning and services, potential areas of application include biodiversity related financial disclosures and voluntary or legislated no net biodiversity loss policies.

1 Introduction

The rapid recent growth of markets for responsible investments considering Environmental, Social and Governance (ESG) concerns (Diab and Adams, 2021), and the growing attention biodiversity receives in this context (Addison et al., 2019; Nauman, 2020), highlight the need for metrics of biodiversity impacts appropriate for use by businesses and in financial markets (Addison et al., 2019; Smith et al., 2020; TNFD, 2021).

Requirements on such metrics include most of the desiderata for metrics in the ecosystem management and scientific context, listed, e.g., in the author guidelines of Ecological Indicators: simplicity, relevance, sci-
entific justifiability, cost-efficiency, reliable quantification, among others. The business community, however, emphasises other needs, some summarised in Table I. These derive from aspects of the business world not encountered as such in traditional conservation, including continuous innovation, risk taking, hierarchical structures of ownership and accountability, transactions under private law, and decision making in a fluid, complex socioeconomic context. We address these needs in our work (Table I).

Additionally, it is important to understand how markets will respond when biodiversity impacts are quantified by a particular metric and in particular whether this may create unintentional, perverse incentives. We study this question here as well.

It is widely acknowledged that a range of different metrics is needed to capture all relevant aspects of biodiversity. Our study focuses on metrics related to what is called the “intrinsic value” of biodiversity ([TNFD 2022](#)), i.e. the proposition that species should be protected irrespective of their immediate utility to society. To guide these considerations, however, we invoke a utilitarian argument as follows: Even when there is no utility to us of a particular species, future generations of our descendants, with needs and priorities potentially very different from what we can conceive, may yet find this species valuable and suffer from its loss if we do not protect it now.

Considering that the time between speciations of higher organisms is measured in millions of years ([Sepkoski 1998](#) [McPeek and Brown 2007](#)), any attempt to anticipate how and why a currently extant species might become important to future generations would be preposterous. The argument therefore naturally leads into the widely accepted conclusion that we should reduce extinction rates across all biota to near-natural levels (for example, the draft post-2020 Biodiversity Framework states a target: “the rate of extinctions has been reduced at least tenfold”). Importantly, since the time scales in question are long compared to those between human migration events, the question where on Earth a particular species lives is irrelevant by this argument.

Regardless of whether the ‘intrinsic value’ of species is invoked as a metaphor to capture these considerations or as an ethical axiom, quantification of the long-term extinction risk of species is a natural starting
point for the construction of a pertinent science-based metric.

Before we proceed, however, we stress that, as a matter of intergenerational justice, the metric we develop here must be complemented by one or several targeted metrics quantifying the ability of nature to provide ecosystem services to current generations. The Mean Species Abundances (MSA) metric, originally called the Biodiversity Intactness Index (Scholes and Biggs 2005), is a well-established metric suitable for this role (Mace 2005). (MSA is defined as the average over all native species in the area of interest and over space of the ratio of a species’ population to what it would be in an undisturbed ecosystem, capped to be \( \leq 1 \).) We propose to use both kinds of metrics in conjunction by aiming to optimise ecosystem service provision while remaining below or reverting to an upper bound on extinction risk (Rossberg et al. 2017).

The two closely related metrics derived here, which we call Biodiversity Impact Credits (BIC) and Biodiversity Stewardship Credits (BSC), are aligned through approximate mathematical relations to several other widely used and cited metrics that are already in use for similar purposes. We show below that: i) BIC quantify impacts on the Living Planet Index (LPI) (WWF 2020; McRae et al. 2017), one of the most widely cited global biodiversity indicators currently in use (4,710 publications identified by Google Scholar in July 2022); ii) BIC are strongly correlated with the Species Threat Abatement and Recovery (STAR, 21 publications) metric (Mair et al. 2021), a spatially resolved variant of the IUCN’s Red List Index (Butchart et al. 2007, 2010; 2,490 publications); iii) BIC are approximated by life-cycle impact assessments scores based on the Potentially Disappeared Fraction (PDF) of species (De Schryver et al. 2009; 1,680 publications); and iv) BIC are closely related to Range-Size Rarity (RSR; Williams et al. 1996; 307 publications), a metric used in conservation ecology to identify sites for protected areas. Thus, BIC unify several existing approaches to quantifying biodiversity impacts and support the established intuitive motivations of these approaches with a strong theoretical rationale.

In Material and Methods below we will first establish the theoretical basis for BIC and demonstrate the metric’s linkage to the LPI. In doing so, we derive a solution to a long-standing conceptual problem arising with use and interpretation of the LPI when populations of species entering the LPI approach zero.
In the Theory section we begin by deriving BIC as a measure of local impact on global species extinction risk and show how BIC can indeed predict regional-scale species losses in a mechanistic metacommunity model. Then we study the incentive structure generated by BIC in an ideal market to satisfy ourselves that BIC are well-aligned with the species conservation objective. As a final point, we again use simulations to explore the non-localised impacts of interventions designed to generate positive BIC.

In the Calculation section, we first derive approximate relations between BIC, BSC, the the STAR metric, RSR, PDF-based impact assessments, large-scale species density. We also present examples of practical calculations of BIC in particular contexts. The Discussion section puts emphasis on uses of BSC and BIC in the business context.

2 Materials and Methods

This methods section develops conceptual, theoretical, and methodological background that we shall rely on when defining and interpreting our biodiversity impact metric below. We first establish, in several steps, a relationship between the Living Planet Index and the mean long-term extinction risk of species. Then we describe briefly a metacommunity model that we will use to study some aspects of the proposed metric in complex, dynamics metacommunities.

2.1 Estimating the long-term extinction risk of species

As a first step in developing a science-based metric of biodiversity change, we consider a simple mathematical model that allows us to analytically link the populations sizes of species to their long-term survival. For a given taxonomic or functional group of species (below ‘group of species’ or similar), denote for each species \( i \) in that group by \( N_i \) the global population size of that species. Population sizes can be measured by the number of mature individuals or population biomass, in some cases even by the number of colonies,
Table 1: Desiderata for biodiversity metrics voiced by the business community, and how Biodiversity Stewardship Credits (BSC) address these.

| The needs we address                                                                 | How we achieve this                                                                                     |
|-------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------|
| Scientifically robust ([TNFD](2022))                                                | BSC are mathematically linked to long-term species extinction risk.                                      |
| Can assess both negative and positive impacts                                       | BSC naturally quantify both positive and negative impacts.                                              |
| Can be used to assess biodiversity risks, opportunities ([TNFD](2022))             | BSC are linked to long-term extinction risk; (up)predictability of future BSC can be understood in terms of uncertainty in data, population dynamics and market competitor behaviour. |
| Comparable across sectors and providing insights to inform corporate and financial institution decision making, including at aggregated portfolio levels for financial institution ([TNFD](2022)) | BSC measure biodiversity impact in a single currency based on a simple formula and can be aggregated from site to portfolio level. Decision making based on BSC pricing aligns with conservation objective. |
| Can be used at scale and at different levels ([TNFD](2022))                        | We show how BSC impacts can be estimated at site, product, or corporate level using existing metrics and tools. |
| Can be used for corporate target setting ([TNFD](2022))                            | Corporations can use BSC to set and demonstrably achieving net-zero or net-positive biodiversity targets. |
| Aligned with broader national and global public policy goals for reversing nature loss ([TNFD](2022)) | BSC are aligned with widely used geometric mean abundance indices such as the global Living Planet Index (LPI) ([WWF](2020)) or UK’s Wild-Bird Indicator ([gov.uk](2021)). |
| Marketability                                                                       | BSC are additive, so total BSC do not change through paper transactions.                              |
whichever approximates total reproductive value (Rossberg and Farnsworth, 2011) well.

It has been shown on long-term time series data, e.g., for trees (Kalyuzhny et al., 2014; Kessler et al., 2015), fish (Kessler et al., 2015), herbaceous plants (Kessler et al., 2015), and birds (Kalyuzhny et al., 2014) that the populations of most species exhibit random walks on the log($N$) axis with mean-squared increments that are largely independent of $N$, a phenomenon known as ‘environmental stochasticity’ (caused by variability in both the abiotic environment and the abundances of other, co-occurring species). For a given population, we denote the mean square of this increment during a time interval of length $\Delta t$, divided by $\Delta t$, by $v_e$. Since the same studies reveal little if any detectable drift towards smaller population sizes or any preferred value, we disregard such drift here.

On top of environmental stochasticity, the discrete nature of life-history events (e.g. birth, germination, death etc.) generates additional variability in population sizes, known as ‘demographic stochasticity’, for which mean-squared increments in $N$ over a given time interval $\Delta t$ scale proportionally to $N$. We denote the corresponding proportionality constant, divided by $\Delta t$, by $v_d$. As a driver of fluctuations in species abundance, demographic stochasticity is widely understood to be negligible compared to environmental stochasticity, except the case of small populations (Melbourne, 2012). The ratio $N^* = v_d/v_e$ specifies the population size below which demographic stochasticity dominates over environmental stochasticity.

In Box 1 we show for populations driven by environmental and demographic stochasticity that the quantity

$$L_{\text{reg}} = \sum_i^S \log (1 + N_i/N_i^*)$$

is, for a given group of $S$ species, proportional to the expected number of surviving species after a long time $T$. Larger values of $L_{\text{reg}}$ imply that less species will go extinct. Next, we establish a relation between this result and the LPI.
We show that with a small modification the LPI can be understood as quantifying long-term extinction risk. We model the change in the population size of a species over a time interval $\Delta t$ as

$$N(t + \Delta t) = \exp \left[ \xi(t)\sqrt{v_d \Delta t} \right] N(t) + \xi'(t)\sqrt{v_d \Delta t}N(t),$$

where $\xi(t)$ and $\xi'(t)$ denote independent standard normal random numbers. Parameters $v_d$ and $v_l$ represent the strengths of environmental and demographic stochasticity, respectively. Formally taking the limit $\Delta t \to 0$, standard procedures lead to an approximation of this process by the Ito stochastic differential equation

$$dN = \frac{v_e}{2} N dt + \sqrt{v_d N + v_e N^2} dW_t,$$

where $W_t$ represents a Wiener process (Brownian motion). The first term on the right-hand-side describes drift to larger values. It goes back to the fact that the expectation value of the log-normal distribution $\exp[\xi(t)\sqrt{v_d \Delta t}]]$ in Eq. (1) is $\exp(v_d \Delta t/2)$. If one were to formulate this process in terms of $\log(N)$ rather than $N$, this term would disappear. However, demographic stochasticity would then generate another drift term instead. To eliminate drift altogether, we express population sizes in terms of $x = \log(1 + N/N^*)$, where $N^* = v_d/v_e$ is the population size at which environmental and demographic stochasticity have the same strength (see Eq. (2)). Note that $x$ becomes zero when a species goes extinct ($N = 0$). Applying Ito’s lemma, this change of variables simplifies Eq. (2) to

$$dx = \sqrt{(1 - e^{-x})v_e}dW_t.$$

That is, $x$ performs a Brownian motion, represented by $dx = \sqrt{v_e}dW_t$.

except when $x$ is of the order of one or smaller.

For $x$ approaching zero from above, the factor $1 - e^{-x}$ reduces the magnitude of fluctuations in $x$, slowing down the random walk. As a result, $x$ can get trapped in the region of low $x$, and the vicinity of 0 acts similar to an absorbing boundary (Pechenik and Levine, 1999; Dornic et al., 2005). This effect is reinforced by the breakdown of the diffusion approximation underlying Eqs. (2) and (3) for small $x$ (Kessler et al., 1998). In reality $N$ and so $x$ reach zero eventually, implying global extinction of that species. We therefore approximate the dynamics of $x$ by simple Brownian motion with an absorbing boundary at $x = 0$ (Pande et al., 2021).

Now consider the probability that a species starting from $x = x_0$ will still exist after a time $T$, i.e., the probability for $x$ to never reach 0 before $T$. Textbook methods evaluate this to $\text{erf}(x_0/\sqrt{2Tv_e})$ (Gardiner, 1990), where $\text{erf}$ denotes the error function (Abramowitz and Stegun, 1972). For $T$ not too near in the future ($T \gg v_e x_0^2$), this simplifies to

$$\text{(probability of survival until } T) = \sqrt{\frac{2}{\pi Tv_e}} x_0.$$

That is, for any sufficiently large, fixed observation time $T$, the current value of $x_0 = x = \log(1 + N/N^*)$ is directly proportional to the probability of species survival. In Supplementary Information (A) we demonstrate validity of Eq. (4) for a model with discrete population sizes $N$.

Data suggest that $v_e$ does not usually vary strongly within taxonomic groups (Kalyuzhny et al., 2014; Kessler et al., 2019). When this is so, $\sum_{i}^{S} \log (1 + N_i/N_i^*)$ is, for a given group of $S$ species, proportional to the expected number of species surviving after a long time $T$.

2.2 The Living Planet Index

The global Living Planet Index (LPI) is designed to track average “species population trends” (WWF, 2020) for a given taxonomic or functional group of species. In defining the LPI, one needs to distinguish the quantity it aims to represent conceptually and how it is being computed in practice.
2.2.1 Definition of the Living Planet Index

Conceptually, LPI represents the geometric mean\(^1\) of the global abundances of all species in the group considered, normalised to a fixed baseline year. Geometric mean abundance biodiversity indices of this type stand out by their combined simplicity, favourable statistical properties (Santini et al., 2017), intuitive accessibility and ecological plausibility (Santini et al., 2017).

Mathematically, if\( S \) is the total number of species in the group and\( N_i \) the global population size of the\( i \)-th species in this group, one can compute the sum of the natural logarithms (symbol: log) of population sizes as

\[
\mathcal{L} = \sum_i^S \log N_i, \quad (6)
\]

and from this

\[
\text{LPI} = \exp \left( \frac{\mathcal{L} - \mathcal{L}_0}{S} \right), \quad (7)
\]

where\( \mathcal{L}_0 \) is the value of\( \mathcal{L} \) in the baseline year.

2.2.2 Computation of the Living Planet Index

The global LPI for vertebrate species is regularly published by the WWF (WWF, 2020). The baseline year is 1970. Its value is estimated from a large database of population time series using a methodology developed by the Zoological Society of London (Collen et al., 2009). The current methodology compensates for incomplete and uneven temporal, taxonomic and geographic coverage by the database (McRae et al., 2017). It also takes into account that many times series in the database refer to local or regional rather than global populations.

\(^1\)The geometric mean of\( N \) numbers\( x_1, \ldots, x_N \) is defined as\( \sqrt[N]{x_1 \cdot \ldots \cdot x_N} \).
Figure 1: Comparison of the global Living Planet Index for two methods to estimate global abundances trends of species from limited local abundance data. Shaded areas indicate confidence intervals. The ‘Standard’ method represents the global abundance trends by the trend of the geometric mean of local abundances, the ‘Modified’ method, described in Sec. 2.2.2, estimates the trend from the sum of the available local population time series.

To address the last issue, the methodology estimates the trend in the global abundance of a recorded species by the trend in the geometric mean of all population time series available for that species. One therefore might argue that the published LPI does not actually estimate changes in the geometric mean of global population sizes, but the geometric mean of the sizes of local populations, which is different, especially in cases of local species extinctions. However, we found that if one changes this methodology such as to use a more appropriate method to estimate global abundance trends of species from the limited available data, the resulting estimate of global LPI changes only little.

Specifically, we used the following alternative method to estimate the global population trend of each species entering the empirical LPI. After the smoothing and interpolation of all population time series data for a given species following the established methodology (McRae et al., 2017), we standardised all these time series to attain the same maximum value. This was done to account for ignorance of the absolute

\[ n_1 = 100 \text{ and } n_2 = 100 \text{ in 1980, while } n_1 = 100 \text{ and } n_2 = 0 \text{ in 1990. Then geometric mean local population size has declined from 100 to 0 during this decade. As an estimate of global population trend, this would imply species extinction. In fact, the species' global population declined only by a factor } 1/2. \]
population size that each time series effectively represents. For each pair of subsequent years \( y, y + 1 \), we then first determined the set of those time series for that species that were available in both years (time series are considered available over the time interval over which data have been recorded). Then we computed for both \( y \) and \( y + 1 \) the sums over all these population times series and from the ratio of these two sums the estimated change in \( \log_{10} \) global abundance from \( y \) to \( y + 1 \). These estimated increments in \( \log_{10} \) global abundance were the averaged over species and regions following the established methodology to compute yearly changes in \( \log_{10} \) LPI (McRae et al., 2017).

As we show in Fig. 1, the impact of this conceptual refinement of methodology on calculated LPI time series is minimal. One can therefore safely interpret the published global LPI as estimating trends in global population sizes of species, as given by Equations (6) and (7). Our analysis relies on this interpretation.

### 2.2.3 Regularisation of the Living Plant Index and its link to extinction risk

If one of the \( S \) species entering the LPI goes extinct \( (N_i = 0) \) at some time after the baseline year, the quantity \( \mathcal{L} \) defined by Eq. (6) attains a value of negative infinity for that year and LPI becomes zero by Eq. (7), irrespective of all other species. Practical calculations of the LPI avoid this mathematical singularity by introducing ad hoc rules to handle rare or extinct species or populations (Collen et al., 2009). A barrier to conceptually satisfactory resolution of this issue has been that the interpretation of geometric mean abundance metrics in terms of ecological first principles has remained incomplete.

Here we propose to resolve this issue by making use of the intuitive interpretation of \( \mathcal{L}_{\text{reg}} \), as defined by Eq. (5), as quantifying long-term species survival. Using \( \mathcal{L}_{\text{reg}} \) in place of \( \mathcal{L} \) and correspondingly defining the regularised Living Planet Index as

\[
\text{LPI}_{\text{reg}} = \exp\left(\frac{\mathcal{L}_{\text{reg}} - \mathcal{L}_{\text{reg},0}}{S}\right),
\]

with \( \mathcal{L}_{\text{reg},0} \) denoting the value of \( \mathcal{L}_{\text{reg}} \) at the baseline year, the singularities occurring when species go extinct
disappear. Instead, the corresponding entry in the sum in Eq. (5) becomes zero [since \( \log(1 + N_i/N^*_i) = 0 \) when \( N_i = 0 \)]. Consistent with intuition, an extinct species is thus treated the same way as a non-existent species in calculating its contribution to the regularised LPI.

Otherwise, when all species populations \( N_i \) are much larger than the corresponding \( N^*_i \), LPI and LPI\(_{\text{reg}}\) are nearly identical. Both are then strictly increasing functions of the mean long-term species survival probability in our approximation.

### 2.3 The Lotka-Volterra Metacommunity Model

While many of the properties of the metric we propose can be elucidated analytically, it can also be informative to study its more complex aspects using numerical simulations. To this end we adopt a simulation approach previously found to reproduce a variety of fundamental macroecological patterns (O’Sullivan et al., 2019, 2021a). Recently, we employed this model to explore the long-term impacts of local perturbation on regional-scale biodiversity (O’Sullivan et al., 2021b) and here we adapt these results to demonstrate the usefulness of the biodiversity metric we propose.

The basic structure of the model was as follows. *Abiotic filtering:* The abiotic environment was modelled by assigning to each site of the metacommunity a random variable sampled from a spatially correlated Gaussian random field (Adler, 2010). Each species in the metacommunity was randomly allocated an environmental optimum and local intrinsic growth rates were defined by a simple quadratic function, taking as a parameter the difference between the value of the environmental variable at the local site and the species’ environmental optimum. *Biotic filtering:* Local ecological interactions were described by a simple Lotka-Volterra competition model with interspecific interaction coefficients randomly sampled; intraspecific coefficients were set to 1 by convention. *Dispersal:* The locations of and connections between sites, were modelled as a random planar graph. The exchange of biomass between adjacent sites was modelled using an exponential function of site separation. *Metacommunity assembly:* Model metacommunities were as-
sembled by iteratively introducing species to the landscape at low biomass. Metapopulation distributions then emerged as a result of abiotic and biotic filtering and mass effects driving local colonisation-extinction dynamics. Species which dropped below a numerical threshold in all sites of the metacommunity were considered regionally extinct and removed from the model. In this way we assembled model metacommunities with self-organised macroecology previously found to correspond well to empirical observation.

In addition to the randomly sampled, species specific parameters, each model included two metacommunity scale parameters, set equivalently for all species and used to defined differing ecological regimes. These were the width of the quadratic environmental response function in environment space and a parameter which moderates the rate of decay of mass effect pressure with spatial separation.

2.4 Population modelling using GLOBIO

We based our calculations on the 2015 land-use and cover map created by Jung et al. (2020), which we resampled to a spatial resolution of 10 arc-seconds (∼ 300 m) using the majority rule in order to match the resolution used in GLOBIO-Species. To create the restoration scenario, we changed all arable land, pastureland, plantations, rural gardens and subtropical/tropical heavily degraded former forest within the (hypothetical) restoration area to the potential natural vegetation (Hengl et al., 2018) occurring at that cell (scenario ‘Restored to PNV’). We then used GLOBIO-Species to calculate, per scenario (i.e., baseline and ‘Restored to PNV’), for each of 130 Malagasy mammals and each grid cell the population size of a species. From that we derived the BIC values per species by calculating the fraction of the difference between the population size after restoration at the restoration site compared to the total potential population size after restoration of that species. In GLOBIO-Species, the total potential population size is derived by multiplying the density of a species (based on the TetraDENSITY database; Santini et al., 2018) with the range size of a species excluding cells that consist of unsuitable natural land cover or are outside of species’ elevation preferences. The population size of a species for each scenario is then derived by including the impacts
of land use, infrastructure and habitat fragmentation on the distribution and abundance of the species within the area encompassing the total initial population size (see [www.globio.info](http://www.globio.info) for more information). Through restoration, the impacts of these anthropogenic pressures can be offset which results in higher population sizes for the species.

3 Theory

We now propose our biodiversity impact metric and report some of its key characteristics, especially in the context of a biodiversity credit market.

3.1 Quantifying local biodiversity impact

Since $L_{reg}$ is proportional to the expected number of surviving species in our approximation, we can quantify the impact of any human intervention on long-term species extinction risk by the resulting change $\Delta L_{reg}$ in this metric. If the changes in population sizes $\Delta N_i$ resulting from this impact are just small fractions of population sizes $N_i$, as will often be the case, $\Delta L_{reg}$ is well approximated to linear order in $\Delta N_i$, i.e., as

$$\Delta L_{reg} \approx \sum_i S \frac{\partial L}{\partial N_i} \Delta N_i = \sum_i S \frac{\Delta N_i}{N_i^* + N_i}.$$  \hspace{1cm} (9)

From Eq. (9) it is clear that $\Delta L_{reg}$ weights impacts on globally rare species higher than impacts on common species, thus plausibly providing an appropriate measure of pressure on ($\Delta L_{reg} < 0$), or relief to ($\Delta L_{reg} > 0$) global biodiversity.

3.2 The Biodiversity Impact Credit metric

In view of above result, we define the Biodiversity Impact Credits associated with a site $\alpha$ as
\[
\text{BIC}_\alpha = \sum_i^S \frac{\Delta n_{\alpha,i}}{N_{i}^* + N_i},
\]

with \(N_i\) denoting the current global abundance and \(\Delta n_{\alpha,i}\) denoting the difference between current local abundances and a baseline abundances documented at some time in the past. The \(\Delta n_{\alpha,i}\) do not need to be small compared to \(N_i\) and can be negative.

Compared to values of \(N_i\) larger than about 100-1000, \(N_{i}^*\) is generally sufficiently small that it can be disregarded in the evaluation of Eq. (10) [Melbourne, 2012; Kalyuzhny et al., 2014]. The \(N_{i}^*\) hence play a role of regularisation constants that are relevant only when dealing with species close to global extinction. Where required, \(N^*\) values can be computed as \(N^* = v_d/v_e\), with \(v_d\) and \(v_e\) estimated from population time series data as used in calculations of the global LPI [Kalyuzhny et al., 2014; Kessler et al., 2015], life-history data [Sæther et al., 2004; Engen et al., 2009; Sæther et al., 2013], or combinations thereof [Sæther et al., 2009].

We designed BIC for use in a biodiversity credit markets. In order to avoid undesired artefacts in such markets, we propose a set of rules for the setting of baseline abundances:

1. Tradable gains can be claimed only against empirically determined published baseline abundances.

2. When publishing baseline abundances to determine BIC for a site, values for all species within the group considered must be published at the same time. For species that are empirically absent from a site, baseline abundance is zero.

3. Baseline abundances can be amended when more accurate data become available but not to get a ‘fresh start’ after a population decline.

In particular, these rules forbid the banking of BIC, that is, market participants cannot claim BIC for past gains that have since been reversed.
Two desirable properties of BIC follow directly from Eq. (10): First, BIC are additive, that is, the BIC of a combination of non-overlapping areas is simply the sum of their BIC. Additivity is a crucial property for a tradable credit metric. If violated, credits can appear or disappear by simply merging or splitting the areas of site in paper transactions without any actual ecological change—an undesirable outcome. We note that measurement of biodiversity gain (or loss) in terms of the exact effects local populations gains (or losses) $\Delta n_{\alpha,i}$ have on $L_{\text{reg}}$, i.e.

$$\Delta L_{\text{reg}} = \sum_i S \sum_\alpha \log \left[ 1 + \frac{N_i}{N_i^*} \right] - \log \left[ 1 + \frac{(N_i - \Delta n_{\alpha,i})}{N_i^*} \right] = \sum_i S \sum_\alpha \log \left[ \frac{N_i(\Delta N_i)^{\text{off}} + N_i}{N_i^* + N_i - \Delta n_{\alpha,i}} \right],$$  

(11)

is not additive in this sense. This is why, in the context of marketisation, the approximate measure of impact on species extinction risk provided by BIC is preferable over the exact measure $\Delta L_{\text{reg}}$.

Second, BIC represent a strictly finite resources. The total population sizes $N_i$ of each species $i$ can never be smaller than the sum of all population increments over all sites $\sum_\alpha \Delta n_{\alpha,i}$. The sum of all BIC

$$\sum_\alpha \text{BIC}_\alpha = \sum_\alpha \sum_i S \frac{\Delta n_{\alpha,i}}{N_i^* + N_i} = \sum_i S \frac{\sum_\alpha \Delta n_{\alpha,i}}{N_i^* + N_i},$$

(12)

is therefore always less than $S$. For ecosystem types whose extent is strongly depleted on Earth, restoration of this type over areas representing a multiple of the current extent can lead to values of $\sum_\alpha n_{\alpha,i}$ close to $N_i$, such that the terms in the sum over $i$ attain values close to 1 and the sum of BIC$\alpha$ over sites representing this ecosystem type attains a value close to $S$. Numerical BIC values can therefore be interpreted by comparison to global species richness $S$, that is, BIC have units of ‘species’.

3.3 Incentive structure generated by BICs

What would the overall effect a trade in BICs be? Could it create perverse incentives running contrary to the original objective of reducing extinction rates? We study these question in the following, assuming a
perfect market.

Let \( p \) be the price of one BIC and \( C_\alpha = C_\alpha(n_{\alpha,1}, \ldots, n_{\alpha,S}) \) the net present value of the costs of sustaining local population sizes \( n_{\alpha,1}, \ldots, n_{\alpha,S} \geq 0 \) in areas of land held by market participant \( \alpha \), including costs related to lost opportunities for other uses, minus the net present value of the resulting ecosystem services. Denote by \( n_{\alpha,i,0} \) the baseline abundances for species \( i \) over all sites held by market participant \( \alpha \), so that \( \Delta n_{\alpha,i} = n_{\alpha,i} - n_{\alpha,i,0} \) are the increments entering Eq. (10). The total value of that area is then \( V_\alpha = -C_\alpha(n_{\alpha,1}, \ldots, n_{\alpha,S}) + p \text{BIC}_\alpha \), plus value unrelated to \( n_{\alpha,1}, \ldots, n_{\alpha,S} \).

In a perfect market, market participant \( \alpha \) will take measures to maximise \( V_\alpha \), at which point

\[
0 = \frac{\partial V_\alpha}{\partial n_{\alpha,i}} = -\frac{\partial C_\alpha}{\partial n_{\alpha,i}} + \frac{p}{N_i^* + N_i} \left( \text{or } n_{\alpha,i} = 0 \right) \tag{13}
\]

for all species \( 1 \leq i \leq S \). The last term in Eq. (13) results because \( n_{\alpha,i} \) contributes to total population size \( N_i \) (so \( \partial N_i / \partial n_{\alpha,i} = 1 \)). The \( n_{\alpha,i} = 0 \) case arises when there are no net benefits at all in sustaining species \( i \). In such a case one typically finds that even small populations of \( n_{\alpha,i} > 0 \) do not add value, implying that \( \partial C_\alpha / \partial n_{\alpha,i} > p/(N_i^* + N_i) + p n_{\alpha,i,0} / (N_i^* + N_i)^2 \) at \( n_{\alpha,i} = 0 \), which in turn implies that \( \partial C_\alpha / \partial n_{\alpha,i} > p/(N_i^* + N_i) \).

Now, consider the problem of minimising the global costs of sustaining \( \mathcal{L}_{\text{reg}} \) at a given level by appropriately choosing the population sizes \( n_{\alpha,i} \geq 0 \) sustained by each land holder \( \alpha \). The solution of this constrained non-linear optimisation problem satisfied the Karush–Kuhn–Tucker conditions \((\text{Chiang and Wainwright}, 2005)\) derived from the Lagrangian

\[
\sum_\alpha C_\alpha - \sum_{\alpha,i} \mu_{\alpha,i} n_{\alpha,i} - \lambda \mathcal{L}_{\text{reg}}, \tag{14}
\]

where \( \mu_{\alpha,i} \) and \( \lambda \) are the Karush-Kuhn-Tucker multipliers. These condition require that
\[- \frac{\partial C_\alpha}{\partial n_{\alpha,i}} - \mu_{\alpha,i} + \frac{\lambda}{N_i^* + N_i} = 0 \] (15)

for all \( \alpha \) and \( i \), where either \( \mu_{\alpha,i} = 0 \) and \( n_{\alpha,i} \geq 0 \) or \( \mu_{\alpha,i} > 0 \) and \( n_{\alpha,i} = 0 \). Comparison of Eqs. (13) and (15) and of the considerations for \( n_{\alpha,i} = 0 \) shows that with \( p = \lambda \) the two conditions are identical, except for effects of the term \( p \Delta n_{\alpha,i}/(N_i^* + N_i)^2 \) in Eq. (13). However, this term makes a sizeable contribution compared to the term \( p/(N_i^* + N_i) \) only when \( \alpha \) has changed the abundance of a species \( i \) by an amount that is comparable to or larger than the current global abundance \( N_i \) (so \( \Delta n_{\alpha,i} \) and \( N_i \) are of comparable size). Absent such dominant market participants, an ideal BIC market leads to near optimal allocation of resources to sustain \( L_{\text{reg}} \), and so \( \text{LPI}_{\text{reg}} \), at a given level. Larger \( \text{LPI}_{\text{reg}} \) correspond to higher BIC prices \( p \).

To study the case of dominant market participants, we first consider the case of negative \( \Delta n_{\alpha,i} \). In this case, Eq. (13) can be read as implying that the marginal cost \( \partial C_\alpha/\partial n_{\alpha,i} \) that \( \alpha \) is willing to incur to maintain the abundance of species \( i \) is by a factor \( 1 + |\Delta n_{\alpha,i}|/(N_i^* + N_i) \) larger than the price of BIC. This additional conservation effort will not usually be detrimental.

The opposite case, positive \( \Delta n_{\alpha,i} \) that are of similar magnitude as \( N_i \), can arise only when most of the population of species \( i \) is held by \( \alpha \). To address situations with such dominant market participants, we now show the following: Firstly, even when a species is dominantly held by a single market participants, BIC still incentivise protection this species and growing its populations. Secondly, BIC dis incentivise dominance.

Consider first a market participant \( \alpha \) whose land is home to the entire global population of some species \( i \). Suppressing the indices \( i \) and \( \alpha \), assume that this market participant has grown this population from an initial size of \( n_0 \), so that \( \Delta n = N - n_0 \), implying \( N = n_0 + \Delta n \). The participant’s BIC associated with species \( i \) are then

\[
\text{bic} = \frac{\Delta n}{N^* + n_0 + \Delta n}. \] (16)
Figure 2: Accumulation of BIC when rebuilding a species as a dominant market participant. The solid line gives the BIC associated with this species, Eq. (16). As illustrated by the dashed lines, BIC gained by increasing the species’ population by a single individual are largest when it is closest to its baseline population \( n_0 \). However, to achieve full BIC, the species’ population must be lifted well above \( N^\ast + n_0 \).

A population gain of \( \Delta n = N^\ast + n_0 \), for example, earns this market participant BIC worth 0.5 species (Fig. 2). For a species that originally was close to extinction, so that \( n_0 \) is of similar magnitude as \( N^\ast \), maintaining the population at this or even higher levels can be well worth while, even when, by Eq. (13), the effective value of BIC for this species is for \( \alpha \) discounted by a factor \( 1 - \Delta n/(N^\ast + n_0 + \Delta n) = (N^\ast + n_0)/(N^\ast + n_0 + \Delta n) \).

Importantly, market incentives to rebuild the species’ population are highest at the lowest population size (Fig. 2).

To see that BIC disintencvise market dominance, note that market participants that achieved a smaller population gain of a species \( i \) on their land benefit more from increasing this population than those who have achieved larger gains. The reason is that increasing a population not only generates further BIC gains through the numerator in Eq. (10), but also penalises the value of previous gains by increasing global species abundance in the denominator, and this penalty is larger for those who have achieved larger
previous gains. Hence BIC disincentivise dominant holdings of population gains. With several market participants and several rare species, market dynamics favour instead a situation where, all else equal and to the degree permitted by species interactions and environmental conditions, all market participants sustain ecological communities containing all species. We therefore expect that market misalignment due to the difference between conditions Eq. (13) and (15) will be harmless in most cases, implying near-optimal resource allocation as explained above.

3.4 Compensation of off-site impacts

For most business activities, impacts on biodiversity are not constrained to sites the businesses hold. Often, these off-site impacts will be spread out widely, e.g., along complex supply chains or because they result from widely dispersing pollutants. It can then be impractical for a business to avoid the biodiversity impacts generated by the production of their supplies or to make arrangements to directly avoid BIC losses in all areas affected by pollution.

In order not to endanger, despite this, attainment of the societal goal of reducing species extinction risk, a business (or a similar organisations) can compensate the non-local increase in mean long-term species extinction risk resulting from its activity by the generation of BIC at its site or by purchasing BIC that other organisations generate for this purpose.

Specifically, denote by $\Delta N_{\text{off},i}$ the diffuse off-site changes in species abundances generated by the activity of a business compared to the baseline, and define

$$BIC_{\text{off}} = \sum_i S \frac{\Delta N_{\text{off},i}}{N_i^* + N_i},$$

with $N_i$ again denoting current species abundances. Since the $\Delta N_{\text{off},i}$ will usually be negative, so will $BIC_{\text{off}}$. However, we can show that when
the resulting change in $L_{\text{reg}}$ is always positive. This result holds for both small and large $\text{BIC}_\alpha$ and $\text{BIC}_{\text{off}}$ without invoking any approximation. Since a positive change $\Delta L_{\text{reg}}$ implies a positive overall impact on mean long-term species survival, one can identify Eq. (18) as a condition for a business to be biodiversity positive in with respect to protection of species.

The proof of above result starts with the analogue of Eq. (11), taking both on-site and off-site changes in abundances into account, and then makes use of the fact that $\log(1 + x) \leq x$ for any $x > -1$ (so that $-\log(1 + x) \geq -x$) and Eq. (18) to demonstrate an increase in $L_{\text{reg}}$:

$$\Delta L_{\text{reg}} = \sum_i S \log \left[ 1 + \frac{N_i}{N_i^*} \right] - \log \left[ 1 + \frac{(N_i - \Delta n_{\alpha,i} - \Delta N_{\text{off},i})}{N_i^*} \right]$$

$$= \sum_i S \log \left[ 1 + \frac{N_i}{N_i^*} \right] - \log \left[ \left(1 + \frac{N_i}{N_i^*} \right) \left(1 - \frac{(\Delta n_{\alpha,i} + \Delta N_{\text{off},i})}{1 + \frac{N_i}{N_i^*}} \right) \right]$$

$$= \sum_i -\log \left[ 1 - \frac{(\Delta n_{\alpha,i} + \Delta N_{\text{off},i})}{N_i^* + N_i} \right]$$

$$\geq \sum_i \frac{\Delta n_{\alpha,i} + \Delta N_{\text{off},i}}{N_i^* + N_i}$$

$$= \sum_i \frac{\Delta n_{\alpha,i}}{N_i^* + N_i} + \sum_i \frac{\Delta N_{\text{off},i}}{N_i^* + N_i}$$

$$= \text{BIC}_\alpha + \text{BIC}_{\text{off}} > 0$$

It is worth noting that a positive $\Delta L_{\text{reg}}$ can result even when for some species $i$ the change in abundance $\Delta n_{\alpha,i} + \Delta N_{\text{off},i}$ is negative.
3.5 The Biodiversity Stewardship Credit metric

A special case of the BIC metric arises when the baseline abundances of all species are zero. Such a situation might occur, e.g. when rewilding barren land or intensively used agricultural land. From the abstract standpoint that all land and water on Earth was originally lifeless, one can argue that zero is the natural value for all baseline abundances, and that the current holders of any site are entitled to credits for sustaining, to the present day, the biodiversity on this site that were pass on to them by their predecessors. Such credits are therefore awarded not for changes in biodiversity but for exercising stewardship over existing biodiversity. We therefore call the variant of BIC where the baseline abundances are set to zero Biodiversity Stewardship Credits (BSC). The explicit formula for this metric is

\[
\text{BSC}_\alpha = \sum_{i}^{S} \frac{n_{\alpha,i}}{N_r^i + N_i},
\]

with \(n_{\alpha,i}\) denoting the sustained abundance of species \(i\) at site \(\alpha\).

BSC share with BIC all the properties derived above. While BSC have the advantage over BIC of being conceptually simpler, BSC are not immediately suitable for a trade in biodiversity impacts. Global BSC are overabundant, and trading them off against negative impacts could theoretically bring Earth back to its lifeless primordial state.

BSC have their own role to play when biodiversity stewardship itself is of interest rather than the balancing of impacts. Organisations can, for example, include accounts of the total BSC they hold in yearly reports to demonstrate their biodiversity credentials.

In addition, there is a second important role for BSC. It arises because BIC can in many practical cases be approximated by the change in BSC between baseline year and present:

\[
\text{BIC} \approx \Delta \text{BSC}. \tag{21}
\]
This approximation breaks down only when the global abundances $N_i$ of the species present at a site have changed substantially since the baseline year. This would be the case, for example, when a site holder rebuilds a species’ population from the verge of extinction. In such cases care should be taken to use BIC rather than BSC to avoid undesirable artefacts. Often, however, this is not required and site holders can track changes in the BSC they hold to estimate their BIC. Site holders should, however, keep records of baseline abundances $n_{\alpha,i,0}$ so BIC can accurately be computed using Eq. (10) if required.

### 3.6 BIC and BSC density

Since BIC and BSC are additive across sites, one can define a corresponding $BIC$ density and $BSC$ density by dividing BIC and BSC, respectively, by site area, thus making metric values more comparable across sites of different size. Below we will provide some empirical values of this density in units of species km$^{-2}$.

### 3.7 Local vs regional impacts on species populations

Both BIC and BSC are defined in terms of the local population sizes of species at at sites, disregarding the effects local changes in these populations might have at regional level. Such regional responses might take time to unfold (Tilman et al. 1994; Jackson and Sax 2010; Essl et al. 2015) and can be difficult to predict. This might raise concerns that the long-term ecological reverberations of local impacts are yet to unfold after they registered in BIC or BSC, and so be missed by these metrics.

Indeed, we demonstrated such complex, far-reaching long-term effects of perturbations in recent simulation of a species-rich metacommunity model (O’Sullivan et al. 2021b). Remarkably, however, these simulations also revealed that, at least in the case of complete eradication of all species on a site (as when building a warehouse on a meadow), that the average long-term change in the total population of each species across the metacommunity is nearly identical to the size of the local population removed by the intervention (Fig. [3]). This suggests that biodiversity impacts quantified by local, short term changes in population sizes
Figure 3: Long-term, regional-scale impacts of localised perturbations in simulated meta-communities. In each simulation, we removed a single patch from a model metacommunity compared the initial population biomasses of each species in that patch with the resulting long-term impact on the regional biomass of that species. While there is variation in the long-term biomass change, in some case larger than removed biomass, on average biomass removed is a good predictor of long-term regional biomass loss. Axes are equally scaled. The grey dotted line represents a linear regression (O'Sullivan et al., 2021b).
provides good estimate of the expectation value of the long-term impact, even when ecological complexity makes the actual long-term impacts less predictable.

3.8 Rewilding

The perhaps simplest approach to gaining BIC is to permit the natural rewilding of a barren area. We used model simulations to get a first idea of how BIC in such areas increase over time as rewilding progresses. For this, first we kept all biomass at zero in a given site in our metacommunity model and allowed the surrounding metacommunity to relax to a new equilibrium or steady state. Then we allowed recolonisation of the barren site to occur, recording the associated BIC, where we used as the ‘global’ abundances of species their metacommunity-level population biomasses. As shown in Fig. 4, BIC are rapidly accumulated over the first 10 unit times. Since the intrinsic growth rates of local populations in absence of competitors are $O(1)$ in our model, these results suggest that BIC tend to recover on a similar time scale as community biomass. The fluctuations in BIC on longer time scales seen in Fig. 4 are due to intrinsically driven community turnover O’Sullivan et al. (2021a), where globally rare species can replace globally abundant species, leading to an increase in BIC, and vice versa. Such slow fluctuations can similarly be expected on real sites where community turnover occurs.

4 Calculating BICs and BSCs

BICs and BSCs can be determined by a variety of methods. Here we discuss both direct approaches based on bespoke and public survey data, and indirect approaches where closely related other metrics are converted into BICs. The latter methods provide more than just useful shortcuts to computing BICs. They also highlight a unifying threads running through various approaches of quantifying biodiversity impacts, and, given the fact that BICs are directly derived from analysis of extinction risk, lend additional scientific rigour to established tools.
Figure 4: **Accrueeum of BIC during local site rewilding.** Each line corresponds to a different simulation of ‘rewilding’ a single site as detailed in the text. After verifying that the precise value of $B^*$ has little effect on metric values, we set $B^*$ to one $10^{th}$ of the local single-species carrying capacity. Note the logarithmic time axis. Accrueeum tends to be fast but can be followed by ongoing slow fluctuations.
The choice of method/approximation will depend on the spatial resolution required, the accuracy sought and the type/quality of the available data. When simplified methods yield inconsistent results, it is likely that one of the underlying simplifying assumptions linking them to BIC has been violated in an essential way. Since these assumptions are spelled out in the derivation of the rules to convert between related metrics below, research can seek to refine existing tools where these assumptions are violated to align better with the objective of quantifying impact on extinction risk.

We begin by addressing the task of computing BIC directly based on Eq. (10), which is most suitable for small sites with good data availability.

4.1 Direct determination of BICs and BSCs

4.1.1 From bespoke survey data and global population estimates

Both BIC and BSC metric can be determined directly by evaluating Eq. (20) for survey data. As a pilot test on commercial property, we obtained permission from the owner of a grouse moor estate in Yorkshire, UK, to determine BSCs on their estate. Grouse moors are managed to provide optimal growth conditions for populations of game birds for recreational shooting. For an in-depth discussion of this practice, see, e.g. Grouse Moor Management Review Group (2019). Many grouse moors are run as businesses, and BSCs might provide opportunities and incentives to create additional value through biodiversity protection.

A commercial biodiversity survey provider (Ecology Services Ltd) was commissioned to conduct bird surveys on a representative area (1.6km$^2$ size) within the estate. One-hour surveys were conducted on four days in the spring of 2022 (9, 21 April and 13, 26 May). To conduct the surveys, the area was divided into 5 sections along clearly visible boundaries and consecutively for each section the birds present in it at one moment were counted by observation from an adjacent road.

BSC were determined for each day, inserting observed population sizes as $n_i$ in the BSC definition, Eq. (20). Chicks were included where visible, but did not affect the counts in a relevant way. For the global
population sizes $N_i$ in Eq. (20) we used the central estimates of Callaghan et al. (2021) (see also Robinson et al. 2022, Callaghan et al. 2022). The globally rarest observed species was the stock dove ($Columba oenas$) with an estimated global abundance of 5 million individuals. For comparison, typical estimates for the regularisation constants $N^* = v_d/v_e$ for birds are in the range of 2.6–60 individuals (Sæther et al., 2004; Engen et al., 2009; Sæther et al., 2013), i.e., much smaller. We therefore disregarded the regularisation constants here and, by the same reasoning, in all subsequent calculations.

Averaging over the four days, we calculated a bird BSC density of $2.36 \pm 0.21 \times 10^{-6}$ species km$^{-2}$. Just 14 species contributed over 99% to this score – a pattern reflecting the known high skews of local and global species abundance distributions (Enquist et al., 2019; Callaghan et al., 2021) and expected to be typical for BSC. Here, the metric was dominated by black-headed gull ($Chroicocephalus ridibundus$), which contributed 33%, willow ptarmigan ($Lagopus lagopus$) contributing 23%, and Eurasian curlew ($Numenius arquata$) contributing 18%. While Eurasian curlew is listed as Near Threatened on the IUCN Red List (REF), the reason is not a low population ($\sim 26$ million) but a rather high rate of population decline. The next largest contributions came from European golden plover ($Pluvialis apricaria$, 7%) and stock dove (5%). The latter was represented by only 4 of a total of 705 observations (0.6%) but contributed disproportionately due its low global abundance. This finding might indicate a potential to increase BSC at the site by creating conditions somewhat more suitable for this comparatively rare species.

4.1.2 Using the GLOBIO global population model

As an alternative to direct surveys, BSCs and BICs can be computed from model-based predictions of population sizes. We illustrate this here by a prediction of BIC gains resulting from hypothetical habitat restoration in Madagascar using the GLOBIO-Species model.

We delineated a hypothetical restoration area (dashed rectangle in Fig. 5) and assumed that all anthropogenic land use types except for urban areas would be restored to potential natural vegetation. We then used GLOBIO-Species to calculate the BIC metric based on the distributions and population sizes of
130 mammal species endemic to Madagascar before and after restoration. That is, for each species $i$ we computed the quantities $\Delta n_i$ and $N_i$ entering Eq. (10) directly from the model. Non-native mammals were excluded, as we would expect their contributions to be negligible in view of large global population sizes $N_i$.

The density of BIC gained was positive throughout the restoration area (Fig. 5), reflecting that restoration was predicted to increase the populations of all 57 mammals native to this area. In most of the area BIC density was relatively low (but comparable to the BSC density computed above) because of small population increases compared to total population size. The highest BIC values were found along the eastern edge of the restoration area, where most of the Malagasy mammals occur.

The model predicts an overall BIC gain of 7.4 species. As for the grouse moor, this score was dominated by just a few species. Leading where the contributions from the Betsileo short-tailed rat (*Brachyuromys betsileoensis*), contributing 0.91 species and the lesser long-tailed shrew tenrec (*Microgale longicaudata*) with 0.81 species.
4.2 Indirect computation from established metrics

4.2.1 From Range Size Rarity

For practical reasons, conservation ecologists often work with presence/absence data of species at lattice elements. Population density is disregarded. A biodiversity metric that is often computed from such data is Range Size Rarity [Howard (1991); Williams et al. (1994)].

Do derive the approximate relation between Range Size Rarity and BSC (and to avoid the notational complexities of integral calculus), we assume Earth’s surface to be covered by a lattice of $E$ non-overlapping surface elements of equal area $\Delta A$ and, to the degree possible, approximate square shape. We denote by $n_{i,e}$ the number of individuals of species $i$ in lattice element $e$ and by $\Delta n_{i,e}$ changes in these numbers. Summing over all lattice elements, $N_i = \sum_e E n_{i,e}$.

Denote by $C_i$ the index set of the lattice elements occupied by species $i$ and by $S_e$ the set of (the indices of) the species present at $e$, so that $i \in S_e$ if and only if $e \in C_i$. We shall write $|\cdot|$ to denote the number of elements of a set. So $|C_i|$ is the number lattice elements in which species $i$ is present—a measure of range size. The Range Size Rarity (RSR) at a given lattice element $e$ is then defined as (Williams et al., 1994)

$$\text{RSR}_e = \sum_{i \in S_e} \frac{1}{|C_i|}. \quad (22)$$

RSR is therefore interpreted as a measure of local species richness where species are weighted by inverse range size (REF).

The Range-Size Rarity metric and variants thereof (Moilanen et al., 2022) are often considered in conservation ecology, especially in the selection of protected areas for species conservation. In the simplest case, one would place protected areas in the subset of lattice elements with the highest Range-Size Rarity, with the size of this subset depending on conservation effort.

To emulate presence/absence (rather than abundance) data in our analysis, assume that each species
\( i \) has, wherever it is present, a constant density \( \rho_i \). That is, either \( n_{i,e} = \rho_i \Delta A \) or \( n_{i,e} = 0 \). In this approximation, \( N_i = \rho_i |C_i| \Delta A \).

For the following demonstration of the close relation between RSR, BIC and BSC, we consider only the case where the changes in the abundances of species resulting from the impact of a business activity are small compared to their global abundances, such that \( \text{BIC}_\alpha = \Delta \text{BSC}_\alpha \) and in the definitions of \( \text{BIC}_\alpha \), \( \text{BIC}_{\text{off}} \), and \( \text{BSC}_\alpha \) we do not need to distinguish between the values of \( N_i \) before and after the impact occurred. To handle larger impacts one would need to make sure that that occurrences of \( N_i \) and \( |C_i| \) in the denominators of expressions below refer to abundances and range sizes after impact.

To compute BIC using RSR, Eq. \([10]\), we further assume that the site \( \alpha \) is given by one or more lattice elements and write \( e \in \alpha \) to express that an element \( e \) is contained in \( \alpha \). We introduce indicator variables \( x_{i,e} \) such that \( x_{i,e} = 1 \) if the impact leads to extirpation of species \( i \) in element \( e \) and \( x_{i,e} = 0 \) otherwise, so that \( \Delta n_{i,e} = -\rho_i x_{i,e} \Delta A \). Thus \( \Delta n_{\alpha,i} = \sum_{e \in \alpha} \Delta n_{i,e} = -\sum_{e \in \alpha} \rho_i x_{i,e} \Delta A \). The above assumption that changes in the \( N_i \) are small implies that most \( x_{i,e} \) are zero. Disregarding the regularisation constants \( N^*_i \), we can then write

\[
\text{BIC}_\alpha \approx \sum_i \frac{\Delta n_{\alpha,i}}{N_i} \approx -\sum_i \frac{\sum_{e \in \alpha} \rho_i x_{i,e} \Delta A}{\rho_i |C_i| \Delta A} = -\sum_{e \in \alpha} \sum_i \frac{\rho_i x_{i,e} \Delta A}{\rho_i |C_i| \Delta A} = -\sum_{e \in \alpha} \frac{\sum_i x_{i,e}}{|C_i|} \tag{23}
\]

Analogously,

\[
\text{BIC}_{\text{off}} \approx -\sum_{e \notin \alpha} \frac{\sum_i x_{i,e}}{|C_i|} \tag{24}
\]

The crucial observation at this step is that each species’ density \( \rho_i \) and the size of lattice elements \( \Delta A \) cancel out.

As a simple example, consider the case where site \( \alpha \) becomes uninhabitable to all species in the group of interest (e.g. due to conversion of natural land to intensively farmed land). All species present at \( \alpha \)
disappear from that site, implying that \( x_{i,e} = 1 \) for all \( e \in \alpha \) and all species \( i \in S_e \), and otherwise \( x_{i,e} = 0 \). Then we get from Eqs. (23), applying Eq. (22),

\[
\text{BIC}_\alpha \approx -\sum_{e \in \alpha} \sum_{i \in S_e} \frac{1}{|C_i|} = -\sum_{e \in \alpha} \text{RSR}_e .
\] (25)

The simple case of rewilding can be handled analogously. In more complicated situations, however, more detailed calculations as demonstrated in Sec. 4.1.2 are recommended.

By the interpretation of the BIC as a predictor of species survival, this implies that selection of protected areas based on Range-Size Rarity is the strategy that minimises long-term global species extinction risks if range maps are the only data available. This result substantiates intuitive arguments conservation ecologists have invoked since Howard (1991) to justify use of Range-Size Rarity in conservation decisions.

A simple way to understand Eq. (25) is to notice the analogy between BSCs and RSR: while BSCs are given by the sum of the proportions that the focal area contributes to the global populations of species, RSR are defined as the sum of the proportions that the area contribute to the total ranges of species. In the approximation that species are evenly distributed over ranges, the BSC of a lattice element equal its RSR.

In reality, however, the populations of species are not as evenly distributed and their ranges not as sharply defined as assumed above; and whether a species is detected as present or absent in a given lattice element depends on the sampling effort. In Fig. 6 we address the question at what sampling effort the expected correlation between BSC and RSR is optimised. The result, based on LVMCM model data, suggest to sample randomly, in each lattice element, individuals of the species group considered until around 5 times more samples have been collected than species observed, and to determine RSR from this to obtain a good approximation of BSC.
Figure 6: Optimised sampling and the correlation between BSC and RSR. A: The correlation between BSC and RSR generated by random sampling as a function of the number of individuals sampled (sampling effort) normalised by the average local richness and fitted with a LOESS model. B: As A, except sampling effort normalised by regional diversity. C: BSC plotted against average RSR of 100 random samples with optimised sampling effort. For each site in a metacommunity model at equilibrium (or steady state) we generated a random sample of species observations (integer numbers of individuals) taking the actual biomass distribution at a given time point, normalised to sum to 1, as the multinormal probabilities of each species’ observation in a given site. In this way, we generated 100 random species-by-site abundance tables, converted these to binary presence-absence tables, and computed the correlation between local site BSC and RSR associated with a given random sample.

Figure 7: Comparison of Range-Size Rarity (RSR) and Species Threat Abatement and Recovery (START) metrics for amphibians, birds and mammals. Spearman’s rank correlation of the two global data sets is 0.80. Logarithmic major axis regression yields $\text{START} \propto (\text{RSR})^{1.51}$. The START data was published in Ref. 32, the RSR data was provided by IUCN (https://www.iucnredlist.org/resources/other-spatial-downloads).
4.2.2 From the STAR metric

The Species Threat Abatement and Recovery (STAR) metric \cite{Mair2021} is a weighted variant of Range-Size Rarity. The threat-related STAR (summed over all threats), for example, is given by

\[
\text{STAR}_{T,e} = \sum_{e \in C_i} \frac{W_i}{|C_i|},
\]

with the weighing factors \(W_i\) quantifying the IUCN Red-List category of species \(i\) by an integer ranging from 0 (Least Concern) to 4 (Critically Endangered).

IUCN's threat-level categories are determined based not only by population size, but also by observations that make future population decline more likely, such as past or current population decline. Population size itself enters the \(\text{STAR}_T\) metric twice. As an important determinant of threat level \(W_i\) and in the form of range size \(|C_i|\). Indeed, \(W_i\) and logarithmic range size are strongly correlated\(^3\). Because \(|C_i|\)-values vary over many orders of magnitude, most of the variation in \(\text{STAR}_T\) is due to \(|C_i|\) rather than \(W_i\). As a result, the global patterns of variation in \(\text{STAR}_{T,e}\) and RSR, and so in BIC/BSC, are very similar (Fig. \(\overline{7}\)).

Unfortunately, the published global data sets of RSR and \(\text{STAR}_{T,e}\) available to us have been generated using incompatible methodologies. We therefore could not determine a valid statistical relationship that would permit numerical conversion between the two metrics, but hope that future work will close this gap.

4.2.3 From Range Size Rarity and the Potentially Disappeared Fraction of species

As explained above, the off-site biodiversity impacts of business activity can spread out widely across the world. Even when impacts at any given location are small, the accumulated global impact may not be. This is the kind of problem often considered in life-cycle assessments. In this context, the concept of the Potentially Disappeared Fraction of species (PDF) has been introduced to quantify diffuse impacts of

\(^3\)See Extended Data Figure 4b in the original publication \cite{Mair2021}.
products on the environment (Müller-Wenk, 1998). The metric is defined as the proportion of locally extant species that get extirpated (i.e. ‘disappear’) as a result of exposure to a pressure such as environmental pollution. The local ‘disappearance’ of species quantified by PDF is considered reversible once the pressure has ceased.

Denote by PDF\(_e\) the potentially disappeared fraction of species at lattice element \(e\). Now, recall that if a species \(i\) locally disappears (i.e. is extirpated), then \(x_{i,e}\) in Equation (23) is one, and otherwise it is zero. We therefore have on average

\[
PDF_e = \frac{1}{|S_e|} \sum_{i \in S_e} x_{i,e}. \tag{27}
\]

PDF and RSR together can be used to compute to approximate BIC\(_{off}\). This approximation depends on the assumption that disappearance of species at a site where it is present is uncorrelated with its inverse range size, that is we can approximate the mean of \(x_{i,e}|C_i|^{-1}\) at \(e\) by the product of the means of the two factors (at least on the global average). With \(|S_e|\) denoting local species richness, we can then write

\[
\frac{\sum_{i \in S_e} x_{i,e}|C_i|^{-1}}{|S_e|} \approx \frac{\sum_{i \in S_e} x_{i,e} \sum_{i \in S_e} |C_i|^{-1}}{|S_e|}. \tag{28}
\]

This assumption is justified, e.g., when, as resent results suggest (O’Sullivan et al., 2021a, 2022), population and range sizes of species are controlled by complex ecological interaction networks rather than by the species’ own traits.

Equations (28), (27) and (22) allow us to evaluate Eq. (24) as

\[
BIC_{off} \approx -\sum_{e \notin \alpha} E \sum_{i} \frac{x_{i,e}}{|C_i|} - \sum_{e \in \alpha} \sum_{i \in S_e} \frac{x_{i,e}}{|C_i|} \approx -\sum_{e \notin \alpha} \sum_{i \in S_e} \frac{1}{|C_i|} \approx -\sum_{e \notin \alpha} PDF_e RSR_e. \tag{29}
\]
4.2.4 From species density and PDF

Range-Size Rarity is closely related to species density. To demonstrate this, compute the sum of RSR\(_e\) over a hypothetical large area in which all species are endemic. We denote the set of lattice elements forming this area by \(\Omega\) and the set of endemic species by \(S_\Omega\). Then

\[
\sum_{e \in \Omega} \text{RSR}_e = \sum_{e \in \Omega} \sum_{i \in S_e} \frac{1}{|C_i|} = \sum_{i \in S_\Omega} \sum_{e \in C_i} \frac{1}{|C_i|} = \sum_{i \in S_\Omega} \frac{1}{|C_i|} \sum_{e \in C_i} 1 = \sum_{i \in S_\Omega} 1 = |S_\Omega|.
\]  

(30)

Dividing both the first and the last expression by the size of the area \(A = |\Omega| \Delta A\), we see that species density \(|S_\Omega|/A\) equals the average of RSR\(_e\) over \(\Omega\) divided by \(\Delta A\).

In the more general case where the ranges a few species extend beyond the area considered, Eq. (30) holds only approximately. At a minimum the global sum of Range Size Rarity, RSR\(_e\), equals global species richness \(S\).

For pollutants that spread globally before they decay, we may assume that PDF\(_e\) is constant or at least uncorrelated with RSR\(_e\). Disregarding the exclusion of the (usually small) site area \(\alpha\) in Eq. (29), we can then replace PDF\(_e\) by its global average PDF to obtain, using Eq. (30),

\[
\text{BIC}_{\text{off}} \approx -E \sum_{e} \text{PDF}_e \text{RSR}_e \approx -E PDF \sum_{e} \text{RSR}_e = -PDF \sum_{e} \text{RSR}_e = -SPDF.
\]  

(31)

When PDF\(_e\) and species density are correlated, e.g., on continental scale, expressions such as the right-hand-side of Eq. (31) should be evaluated for each continent separately and then added up.

An alternative formulation of Eq. (31) expresses species richness \(S\) in terms of global species density SD = \(S/(E \Delta A)\), recalling that \(E\) is the total number of lattice elements covering Earth’s surface:

\[
\text{BIC}_{\text{off}} \approx -SPDF = -SD E \Delta A \frac{\sum_{e} \text{PDF}_e}{E} = -SD \sum_{e} \text{PDF}_e \Delta A.
\]  

(32)
In practical calculations care must be taken to average and sum only over land surfaces, only over water surfaces, or consistently over both.

4.2.5 From PDF-based metrics in species×year units

Tool such as ReCiPe 2016 (Huijbregts et al., 2019), which have their roots in life-cycle impact assessment, allow users to compute a measure of the ecosystem damage (ED) resulting from a single unit of business activity. Such a unit may be the production, sale and use of a single product, emission of one unit of pollutant, or one year of business activity. Since the environmental impact of one such unit will eventually, if slowly, decline as pollutants decay and mineralise and ecosystems recover, ecosystem damage is not measured as static value (such as mean global PDF) but in terms of the integral of a dynamically declining impacts over time. As a result, units of impact generally contain a factor ‘year’.

ED, for example, is computed by a formula analogous to the right-hand-side of Eq. (32), where in place of PDF$_e$ one finds a sum of impacts along different pathways (e.g. different pollutants). While the right-hand-side of Eq. (32) has units of species, ED is, due to the time integration, expressed in units of species×year.

The simplest way to convert time-integrated metrics into metrics of static impact is the multiply them with the rate $r$ at which units of business activity are produced (when the unit is all activity over one year, then $r = 1\,\text{year}^{-1}$), which yields the long-term impact that would result if the business activity would progress indefinitely at a constant rate. We can then approximate BIC$_{off}$ in terms of ED as

$$BIC_{off} \approx -SD \sum_e PDF_e \Delta A = ED \, r.$$  \hspace{1cm} (33)

More detailed calculations would take the time scales of accumulation and decline of various pressures on biodiversity into account, e.g. according to the models underlying ReCiPe 2016.
Change in expected long-term species survival

Box 1

\[ \Delta \mathcal{L}_{\text{reg}} \]
\[ \Delta N_i \ll N_i \]

only BIC\(_\alpha\)

\[ \sum_i \frac{\Delta n_{i,\alpha}}{N_i^* + N_i} \] (as BIC\(_\alpha\) and/or BIC\(_{\text{off}}\))

\[ \sum_i \frac{\Delta N_i}{N_i^*} \ll N_i \]

\[ \sum_i \Delta n_{i,e} \]

rasterization

constant pop. density

total eradication in \(\alpha\)

\[ \sum_{e \in \alpha} RSR_e \]

extirpations uncorrelated with \(|C_i|^{-1}\)

\[ \sum_{e \in \alpha} RSR_e \text{ PDF}_e \]

RSR\(_e\) and PDF\(_e\) uncorrelated

\[ \sum_{e \in \alpha} \text{STAR}_T,e \]

constant production rate \(r\)

\[ -\sum_{e \in \alpha} \text{SD} \sum_e \text{PDF}_e \Delta A \]

\[ -ED \, r \]

Figure 8: Approximations underlying the relations discussed in this section. Annotations of arrows indicate the underlying simplifying assumptions. Where these assumptions are inadequate corresponding approximations can be omitted.
5 Discussion

5.1 BIC in a nutshell

The use of BICs by business is based on two simple messages: (1) When $\text{BIC}_\alpha + \text{BIC}_{\text{off}} > 0$ the mean long-term survival probability of species increases as a result of the business’s activities. Businesses that are biodiversity positive in the sense that $\text{BIC}_\alpha + \text{BIC}_{\text{off}} > 0$ contribute to overcoming the global extinction crises rather than being part of the problem. (2) The value of LPI (as fundamentally defined; not necessarily empirical estimates of its value from population time series) increases as a result of the business’s activities by a proportion

$$\frac{\Delta \text{LPI}}{\text{LPI}} \approx \frac{\text{BIC}_\alpha + \text{BIC}_{\text{off}}}{S},$$

(34)

where $S$ is the total number of species in the group considered. Businesses that are biodiversity positive in the sense that $\text{BIC}_\alpha + \text{BIC}_{\text{off}} > 0$ therefore increase the value of this widely cited measure of biodiversity loss.

The majority of businesses will have negative off-site impacts BIC$_{\text{off}}$. Many will also have negative on-site impacts. To the extent that these cannot be avoided, businesses will need to be compensated them by positive on-site impacts, which they either generate themselves or, more likely, acquire from partners. An internal market for BICs will emerge as a result, stimulating entrepreneurial thinking to find cost efficient ways to protect species in the context of other needs, such as ecosystem services.

5.2 A worked example

Let’s consider an example. In a recent self-assessment using the ReCiPe 2016 tool, University of Oxford reported to be generating an ecosystem damage (ED) of 1.6 species × year in the academic year 2019-20 (Bull et al. 2022). As this quantifies the summed impact for one year of activity, we can estimate the
corresponding steady-state impact by setting \( r = \text{year}^{-1} \) in Eq. (33), giving an estimated offsite impact of \( \text{BIC}_{\text{off}} \approx -1.6 \) species.

To compensate this increase in species extinction risk, University of Oxford could acquire BICs from a conservation NGO such as the Tree Conservation Fund. With funding from University of Oxford, the Fund and its partners would, say, acquire an area of land suitable for the reintroduction of Chinese watermelon trees (\textit{Artocarpus nanchuanensis}), which are critically endangered, with perhaps only 100 individuals remaining in the wild. They might plant 1000 saplings of \textit{A. nanchuanensis} in this area. Let us assume that, when the trees mature after about five years, over 200 saplings survive, increasing the tree’s population on the land held by the fund or its partners by \( \Delta n = 200 \) and bringing the total global population to about \( N = 300 \). Assume further a regularisation constant of \( N^* \approx 100 \) for this species. The resulting BICs would then evaluate by Eq. (10) to

\[
\text{BIC} \approx \frac{\Delta n}{N^* + N} \approx \frac{200}{100 + 300} = 0.5, \tag{35}
\]

where we disregarded all other biodiversity impacts as these would likely be dwarfed by the \textit{A. nanchuanensis} contribution. The Tree Conservation Fund can provide this contribution to species conservation at an estimated cost of just around USD 250,000 (Tree Conservation Fund, 2021).

Supporting four projects of this kind, University of Oxford might be able to obtain BSC\(_\alpha\) = 2 species at a cost of around USD 1,000,000 after five years, thus having turned from a negative to a positive impact to the long-term survival of species, quantified by BIC as \( \text{BIC}_{\text{off}} + \text{BSC}_{\alpha} \approx 0.4 \) species, with some margin of error.

The range of taxa considered in \textit{ReCiPe 2016} is very broad, covering \( S = 1.85 \times 10^6 \) species (Goedkoop et al., 2013). For an LPI computed for this large group of species, the effect of above measures would be small, amounting, by Eq. (34) to an proportional increase of just \( 0.4 \) species/\( S \approx 2 \times 10^{-7} \).

In view of the convertibility between metrics we demonstrated here, an important goal of future metric
development might be to align the groups of species used by various tools to compute metrics.

5.3 A dynamic economy of biodiversity

By being mathematically linked to an internationally agreed objective and to a global metric of biodiversity status, the scheme described above has the potential to strengthen ongoing efforts by the international community to reverse the trends of fast biodiversity loss.

To meet the needs of the business community, the BIC metric has deliberately been designed to be simple and widely applicable, and to rely as little as possible on expert input. Rather than attempting to incorporate the complexities and uncertainties of ecological and social systems in the metric’s definition, the decision how best to deal with these it is intentionally left to businesses and other players using the metric.

There will, for example, always be some uncertainty as to whether restoration measures will generate the anticipated gains in BIC. Rather than awarding credits to plans to restore populations and ecosystems and the resulting projected gains, BIC and BSC are strictly linked to the documented current state. This does not stop business partners from agreeing on restoration plans and making commitments for gains in BIC, the associated uncertainty is just not part of the metric’s definition. Instead, allocation of risks and opportunities amongst business partners should be part of contractual agreements. To stimulate entrepreneurial spirit, an agreement might, for example, permit an organisation growing BIC for a client to sell BICs grown beyond the contractual agreement to third parties, while also leaving it responsible to compensate the client for underachievement. Alternatively, BIC growers might act as a service providers, leaving any risks to the commissioning clients, while the latter might hedge these risk by investing into a diverse portfolio of BIC-growing projects.

This flexibility arises because the BIC metric measures a variety of positive and negative impacts in the same, convertible currency, thus providing the foundations of a wide BIC market capable of absorbing unexpected gains and losses. Critics might argue that this flexibility constitute a weakness of the metric:
how can rebuilding one species’ population in Malaysia compensate the decline of another species’ population in Guatemala? Doesn’t the metric’s proposed use as a commodity imply that species are substitutable with each other, while in fact the irreplaceable of each species provides the moral underpinning of biodiversity conservation at the species level?

Such arguments, however, derive from one or more misunderstanding. The first potential misunderstanding might be that our scheme aims fundamentally at the maintenance of species populations. This is not the case. The scheme aims fundamentally to reduce the risk of species extinctions; keeping species populations large is a means to this end.

Once this point is clarified, a second potential misunderstanding might be that BICs directly trade off gains in one population against losses in another. This would indeed be inadequate for species conservation, especially if the species experiencing losses is the rarer one of the two. However, this is not what BIC does. Rare species enter BIC with a higher weight, which intrinsically encourages the rebuilding of the populations of rare species.

Finally, should above critical argument relates to the situation where both the Malaysian and the Guatemalan species are rare and at similarly high risk of extinction, its fallacy lies in the assumption that sufficient funding to protect these two species and all other species with a similar status is available. Global resources for conservation are insufficient and inadequately allocated (Deutz et al., 2020; Rodríguez et al., 2022) and so choices need to be made about how much effort to invest into protection of which species. We invoked a substitutability argument at this point only insofar as we assumed the extinction of one species (within the group considered) to be just as undesirable as the extinction of any other. Resources should therefore be allocated such as to maximising overall expected long-term species survival, even if this means leaving some species at a high risk of extinction. In the face of limited resources, portfolio strategies that distribute effort over several conservation projects with some risk of failure can be more effective in achieving this goal than strategies aiming at near certain success for a smaller number of projects. By being closely related to a measure of species survival probability, BICs are particularly suited to guide optimisation of
such probabilistic portfolio strategies.

Intuitively, the above example of rebuilding the *A. nanchuanensis* population might strike readers as somewhat artificial and barely generates any of the benefits we are used to associate with the restoration of nature. Readers may also wonder how a tree restoration project in China can compensate for damage to the environment done by an institution in England. Believe that such concerns arise from confounding species conservation with the conservation of ecosystems and ecosystem services. Indeed, service provision tends to require complex ecosystems and is often not substitutable over large geographic distances. For species conservation, neither must be an immediate constraint. Yet, linkages between BICs, complex ecosystems, and ecosystem services naturally arise.

In terms of species conservation, it currently makes sense to focus investments on those species that are at highest risk of extinction, and BICs provide the market signal to do this wherever feasible. After these low-hanging fruit of species conservation have been picked, more intricate schemes, where populations of several species are rebuilt as natural parts of ecosystems, are likely to become increasingly attractive for BIC generation. This shift in species conservation efforts from the population- to the ecosystem level would be reinforced by the property of BICs, discussed above, of disincentivising dominant holdings for population gains.

Linkages to ecosystem services arise when organisations develop “nature-based solutions” that combine generation of BIC with the provision of ecosystem services (e.g. food, clean water, tourism, carbon sequestration, etc.). The market price of BIC and the expected benefits from ecosystem service provision (which depend on the local conditions) will signal to these organisations how best to allocate their resources and where the highest potential for effective synergies might lie. Thus, our focus on species protection in the design of BICs does not deny the importance of ecosystem services. We just consider that a clean conceptual separation of the two is conducive to the efficient conservation of both.
Conclusion

We have demonstrated that Biodiversity Impact Credits have properties suitable for use in biodiversity-related disclosures in business and financial contexts. The metric can also support voluntary or legislated no-net-loss policies. In all cases, we recommend its use in conjunction with metrics for ecosystem services or natural capital. Many of the attractive properties of BIC reflect that this metric is strictly science based, mathematically linked to the LPI and the species conservation objective. Data requirements of BIC are similar to those of existing comparable metrics. Pilot studies are now underway to test the application of BIC in practice.
Appendices

A Numerical test of our model for extinction risk

Here we demonstrate that Eq. (4) provides a good estimate of mean species lifetime despite making use of the diffusion (continuum) approximation and disregarding the decline of the strength of fluctuations near $x = 0$.

For this we simulated an asexual population with non-overlapping generations as

$$\lambda(t) \sim \exp\left(\frac{v_e^2}{2} \xi(t)\right),$$  \hspace{1cm} (A.1a)

$$N(t + 1) \sim \text{Poisson}(\lambda(t) N(t)),$$  \hspace{1cm} (A.1b)

with $\xi(t)$ denoting a standard normal random number and Poisson($\mu$) a Poisson-distributed random number with mean $\mu$. The model implies $v_d = 1$.

We set $v_e = (0.15)^2$ and evaluated 26 values for the initial population size $N(0) = N_0$, spaced equally on the log axis from 1 to $10^5$, except for rounding to the nearest integer. For each $N_0$, the probability of species survival ($N(T) > 0$) until time $T = 10^4$ was estimated from $10^4$ replicates.

As shown in Fig. A.1a, extinction probability increases linearly with $\log(N_0)$ only for large $N_0$. By contrast, $x_0 = \log(1 + N_0/N^*)$, with $N^* = v_e/v_e = 44.4$, is linearly related to extinction probability for all $N_0$ considered (because probabilities are $\leq 1$ by definition, the relationship would break down for even larger $N_0$). The slope of the relation is as predicted by Eq. (4).
Figure A.1: **Demonstration that** $x_0$ **predicts expected species lifetime better than** $\log(N_0)$. Points are simulation results for the individual-based model Eq. (A.1) with $v_e = (0.15)^2$ over $T = 10^4$ time steps. The dashed line is the probability of survival as approximated by Eq. (4). Panels (a) and (b) represent the same data on different horizontal scales.
Data availability statement  No new data were recorded for this manuscript though simulated data generated for previous studies was re-analysed in light of the proposed metric.

Code availability statement  For review purposes, the R code underlying Appendix A has been deposited at http://axel.rossberg.net/pExt.R. The simulation model used to elucidate some properties of the BIC/BSC is available at http://github/jacobosullivan/LVMCM_src.

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