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Linking indices for biodiversity monitoring to extinction risk theory

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Abstract

Biodiversity indices often combine data from different species when used in monitoring programs. Heuristic properties can suggest preferred indices, but we lack objective ways to discriminate between indices with similar heuristics. Biodiversity indices can be evaluated by determining how well they reflect management objectives that a monitoring program aims to support. For example, the Convention on Biological Diversity (CBD) requires reporting about extinction rates, so simple indices that reflect extinction risk would be valuable. Here we develop three biodiversity indices based on simple models of population viability that relate extinction risk to abundance. The first index is based on the geometric mean abundance of species. A second uses a more general power mean. A third integrates both the geometric mean abundance and trend. These indices require the same data as previous indices, but they also relate directly to extinction risk. Field data for butterflies and woodland plants, and experimental studies of protozoan communities show that the indices correlate with local extinction rates. Applying the index based on the geometric mean to global data on changes in avian abundance suggests that the average extinction probability of birds has increased approximately 1% from 1970 to 2009.

Keywords: biodiversity index, biodiversity measure, extinction risk, geometric mean.

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INTRODUCTION

The importance of biodiversity for a healthy and equitable society has been acknowledged by over 190 countries who ratified the Convention on Biological Diversity (CBD). The convention has a specific target to reduce the extinction risk of species (Secretariat of the CBD 2010), so monitoring of species extinction is important. Reporting actual extinctions, while potentially informative, is retrospective, whereas the convention and many other biodiversity programs seek to reduce future extinctions. Further, retrospective assessments are subject to error because the fate of species is known imprecisely (Collar 1998; Keith & Burgman 2004; Rout et al. 2010). Hence, biodiversity monitoring programs would be more valuable if they can be interpreted in terms of extinction risk.

Changes in the assessed risk to species can contribute to biodiversity monitoring. For example, the IUCN Red List is used to calculate the Red List Index (RLI, Butchart et al. 2007), one of four global indicators of biodiversity status and trends approved by the CBD (Jones et al. 2011). The relationships of the other three indicators (extent of forest; protected-area coverage; and the Living Planet Index, LPI, Jones et al. 2011) to extinction risk are not explicit.

Buckland et al. (2005) identified three aspects of species diversity that are of primary interest when monitoring changes over time: number of species, overall abundance and species evenness, from which they derived six desirable criteria for an index of biodiversity based on abundance data. On evaluating several proposed indices against these criteria, the geometric mean of relative abundances was one of only two that met all six criteria. van Strien et al. (2012) lend further support to the geometric mean.

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While we agree with the heuristic properties used to assess different indices of biodiversity, a good index should also be clearly related to particular management objectives or biodiversity outcomes. For example, where extinction risk is the management concern, understanding how the index reflects changes in this risk would be desirable. In the absence of a single measurable definition of biodiversity (Secretariat of the Convention on Biological Diversity 2010; Jones et al. 2011), we aim to examine how abundance data might be used to monitor extinction rates of species for the purposes of reporting under the CBD and other biodiversity programs.

Here, we use simple models of population viability to develop three indices of extinction risk based on abundance data. These indices are designed to have the same data requirements as those considered by Buckland et al. (2005), but with the additional benefit of being directly related to extinction risk. We evaluate the indices using simulation, field data on local extinctions of butterflies and woodland plants, and experimental data on protozoan communities. Finally, we interpret changes in the LPI in terms of changes in the average probability of extinction of species.

Methods

The indices are derived from simple models of population viability, using clearly articulated assumptions that can be tested. First, consider the case when the long-term average population growth of each species is negative. If we assume that each species is experiencing deterministic exponential decline, then

$$x(t) = x(0)\lambda^t,$$

where $x(t)$ is population abundance at time t, and λ is the growth parameter ($\lambda < 1$ for a declining population). It is then straightforward to calculate that extinction (such

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that $x(t) = 1$) occurs at time $T = -\ln[x(0)]/\ln[\lambda]$. If the long-run growth rate is negative, then for stochastic population models the mean extinction time is also approximately logarithmically dependent on initial population size (Lande 1993).

With the simplifying assumption that the rate of decline is the same for each species (we address this particular assumption later), the mean expected time to extinction, averaging over n species, is proportional to the mean of the logarithm of population abundance. As we show below, the mean expected time to extinction is proportional to the logarithm of the geometric mean of population abundances (M_0);

$$\bar{T} \propto \overline{\ln(x)} = \frac{1}{n}\sum_{i=1}^{n}\ln(x_i)$$

$$= \ln\left(\left[\prod_{i=1}^{n} x_i\right]^{1/n}\right)$$

$$= \ln(M_0). \qquad (1)$$

Equation 1 relates the mean time to extinction to the geometric mean abundance. However, it would be helpful to determine how this index might relate to the proportion of species going extinct. We approximate this by assuming that times to extinction have an exponential distribution. The proportion of species going extinct within time t is then $1 - \exp(-t/\bar{T})$. When this proportion is ≤ 0.2, it can be approximated by $t/\bar{T}$, leading to:

$$I_g = \frac{1}{\ln(M_0)}. \qquad (2)$$

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This index should correlate linearly with the proportion of species going extinct under the assumptions stated above.

We develop a second index based on a different set of assumptions. We consider a stochastic population model in which the logarithm of the population growth rate has a normal distribution with a mean of zero and variance σ^2. For this model, the risk of extinction within a given time period t is (Ginzburg et al. 1982; Dennis et al. 1991; McCarthy & Thompson 2001):

$$q_i(x_0) = 2\varphi(-v) \ .$$

where $\varphi()$ is the standard normal cumulative distribution function, $v = -\ln(1/x_0)/(\sigma\sqrt{t})$ and x_0 is the initial population size. This functional form could be used as an index, but it does not provide a simple numerical solution. Instead, we approximated this equation by a function of the form, $A\, x^{-B/(\sigma\sqrt{t})}$, with the values of A and B depending on the value of the extinction risk. For small extinction risks, $q_i <\approx 0.15$, $A = 2.2$ and $B = 1.87$ provide a good approximation. When the extinction risk is close to one, a better approximation is $A = 1$ and $B = 0.798$. Regardless, the probability of extinction scales approximately with abundance in proportion to x^{-b}, with $b = B/(\sigma\sqrt{t})$. Thus, averaged across n species, we would expect the proportion of species going extinct to be

$$L = \sum_{i=1}^{n} q_i / n = k \sum_{i=1}^{n} x_i^{-b} / n = k(M_{-b})^{-b}, \qquad (3)$$

where k is a constant of proportionality and M_{-b} is a power mean of abundance with power $p = -b$,

$$M_{-b} = \left(\frac{1}{n}\sum_{i=1}^{n} x_i^{-b}\right)^{-1/b} .$$

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Consequently, our second index is based on a power mean of abundance:

$$I_b = (M_{-b})^{-b}. \tag{4}$$

The value of b depends on the time horizon over which risks are assessed. If we consider a time horizon of T=100 years and a standard deviation of σ= 0.1 (Dennis et al. 1991), the extinction risk of each species is likely to be relatively small (recall, zero mean growth rate), and b would be of the order 1.8 ≈ 2. The value of b will be larger for shorter time horizons.

A third index can be derived from the deterministic model that accounts for the population growth rate, in addition to population size. Noting again that the mean time to extinction under deterministic decline is $-\ln[x(0)]/\ln[\lambda]$, then the proportion of species going extinct can be approximated by $-\ln[\lambda]/\ln(M_0)$, allowing communities with different population growth rates of species to be compared. Using the mean of the logarithmic population growth rate of species within a community, μ_r, as the estimate of $\ln[\lambda]$ leads to the index:

$$I_{\mathrm{t}} = \frac{-\mu_r}{\ln(M_0)}. \tag{5}$$

This index requires extra data, being the population growth rates of species within the community. Such data might be uncommonly available, but are necessary to compare risks among communities where the species are declining at different rates.

Simulations for evaluating indices

Stochastic simulations of species within communities were used to evaluate how well the different indices correlated with the proportion of species going extinct. Each

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community consisted of 500 species, and there were 100 different communities. For each species j in community i, we simulated the population dynamics over 20 time steps using the exponential growth model such that the population size in time t+1 is given by:

$$x_{ijt+1} = \lambda_{ijt} x_{ijt}.$$

Parameter values for the 100 different communities were chosen such that the proportion of species going extinct spanned a wide range (in our case between 0.02 and 0.64). Within each community, the initial population size $\ln x_{ij0}$ was drawn from a lognormal distribution with mean μ_N and coefficient of variation c_N, and the logarithmic growth rate $\ln \lambda_{ijt}$ was drawn from a normal distribution with mean μ_r and standard deviation σ_r. The proportion of 500 species that fell to or below one individual measured the average extinction risk of the community.

To ensure that each community had different initial population sizes and different trends in abundance (and hence different average extinction risks), the mean and coefficient of variation of the population size (μ_N and c_N) and the mean and standard deviation of population growth rate (μ_r and σ_r) of each was varied among communities. The coefficient of variation c_N was drawn from a uniform distribution on the interval [0.5, 3.0]. The mean population size was equal to $1.2^d 100$, where d was drawn from a uniform distribution on the interval [0, 20], so mean population size varied among communities over the interval [100, 3834]. The mean population growth rate (μ_r) was drawn from a uniform distribution on the interval [–0.3, –0.1], and the standard deviation (σ_r) was drawn from a uniform distribution on the interval [0.05, 0.4]. To test how differences in abundance, rather than population trend,

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influence the performance of the indices, data were also simulated with μ_r set to –0.2 for all communities.

The three indices of extinction risk (I_g, I_b and I_t) were calculated for the simulated communities and the correlations between these and the proportion of species going extinct was examined. The performance of the arithmetic mean abundance and the modified Shannon diversity index of Buckland et al. (2005), other putative biodiversity measures, were also examined for the simulated data. For these two cases, we multiplied the indices by −1 so that the indices would be expected to be positively correlated with extinction risk.

Data for evaluating indices

The correlation between the indices and local extinction risk was evaluated using field data on Lepidopetera (Krauss et al. 2003) and woodland plants (Sutton and Morgan 2009). Because data on differences in population trend among sites and species were unavailable, only eqns 2 and 4 were evaluated. We evaluated all three indices with data from experimental protozoa communities (Clements et al. 2013). The original publications detail the data and its collection; some information is provided here for context.

The abundances of butterfly species in 31 patches of habitat were estimated in both 1996 and 2000 (Kruass et al. 2003). Data were restricted to those species present in at least 24 of the 31 patches so that extinction risk was assessed for a pool of species that were relatively similar at all sites. Thus, differences among sites tended to reflect differences in abundance rather than inherent differences among species. For all these species, probabilities of detection given presence, based on occupancy/detection

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models (Stauffer et al. 2002) using data on detections in sets of 5-minute intervals, were estimated to be >95% in the surveys. In each patch, between 13 and 16 of the species being considered were observed in the first instance. For each index, we plotted the mean extinction risk (calculated as the proportion of species that went extinct) against the index. For this case study, the time horizon is relatively short, T = 8 (assuming two generations per year). For the second index, this results in $b \approx 6.6$ assuming $\sigma = 0.1$. Greater variability in the population dynamics (i.e., $\sigma > 0.1$) would lead to smaller values for b. The data were also analysed when the data were restricted to species that were genuine grassland specialists, but as the results were qualitatively the same, only results with the larger number of species are reported.

The composition and abundance of all native plant species of ten grassy woodland patches in western Victoria, Australia were surveyed in 2006 (Sutton and Morgan 2009). These data were compared to the species composition and population abundance of the same patches observed in 1975 to determine patch extinction rates. To reduce false absences, sites were surveyed on three occasions, with the time spent searching being proportional to each site's size and heterogeneity. To further minimize chances of missed detections, we restricted our analyses to perennial species. Finally, we limit variation in extinction risk due to idiosyncratic differences among species by considering only species that were present in at least eight of the ten patches in the analysis.

Abundances of the plants was estimated in 1975 using a four-point scale: "Very Rare" (less than two dozen individuals seen across the site), "Rare" (appearing in dozens), "Common" (appearing in hundreds), "Very Common" (appearing in thousands). The discretised and censored data meant we were unable to calculate the indices directly.

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Instead, we fitted a Pareto distribution to the abundance data, using maximum likelihood methods, and calculated the indices from the parameters of the estimated distribution. To fit the Pareto distribution, we assumed that the four abundance class were distinguished by threshold values of 24, 100 and 1000 (*i.e.*, "Very Rare" was assumed to be <24 individuals, "Rare" was 24-100, etc).

We chose to fit a Pareto distribution since, for the deterministic model with negative growth rate, if the mean time to extinction (T) is exponentially distributed with parameter θ, abundance ($x = \exp[T/k]$) is a Pareto random variable with scale parameter $x_m = 1$, and shape parameter $\alpha = k\theta$ (Krishnamorrthy 2006). We also fitted a log-normal distribution instead of a Pareto distribution. The results obtained were very similar in both cases, so we only present results for the Pareto. Assuming σ=0.1 and T=30 leads to b = 3.4 in the power mean index I_b.

Experimental protozoan communities were assembled with 4 ciliate species, at 2 temperatures (15 °C and 20 °C), and sampled for abundance data 3 times a week for 163 days (Clements et al. 2013). Four 3-species communities and one 4-species community were replicated at each temperature giving a total of 10 communities (a "community" in this case being a particular combination of species and temperatures). Extinction events were driven by either competitive exclusion or starvation. Population trends between days 5 and 9, abundance at day 9, and the proportion of species extinct by day 163, were calculated and averaged across replicates. Day 9 was chosen as the initial date because this day occurred prior to all but one extinction event, and effects of initial conditions on the community dynamics had attenuated. Each community was replicated 5 times each, except for one community in which a replicate was excluded when a species went extinct prior to day 9. The indices for

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each of the 10 communities were then compared to the proportion of species extinct by day 163. Given the ecological time frame of this experiment (≈200 protozoan generations; Clements et al. 2013), the extinctions observed indicate possible long-term extinction trends. The parameter b in the index based on the power mean was approximately 1.3, assuming $\sigma = 0.1$.

Relating I_g to the Living Planet Index

The LPI is the geometric mean abundance of vertebrate species in a particular year divided by the geometric mean in 1970 (Loh et al. 2005, Collen et al. 2009). Therefore, the index based on the geometric mean can be related to the LPI simply as $I_g = 1/\ln(c\ \mathrm{LPI})$, where c is the geometric mean abundance in 1970. If I_g is proportional to the probability of extinction, as assumed in its derivation, LPI values can be converted to proportional changes in the probability of extinction of species, which will equal $-\ln(\mathrm{LPI}) / [\ln(c) + \ln(\mathrm{LPI})]$. We calculated this quantity for the world's birds based on published avian LPI values (Baille et al. 2010).

These proportional changes depend on c, which is not well known. The arithmetic mean abundance of birds is thought to be approximately 10 million individuals per species but, because species abundance distributions are heavily right-skewed, the geometric mean will be substantially less (Gaston and Blackburn 2003). We estimated the global species abundance distribution of birds, and hence the geometric mean, by fitting a log-normal distribution to data on reported population size for the global list of 1253 threatened species on BirdLife International's website (http://www.birdlife.org/datazone/species/search; accessed 20 December 2011) and assuming an arithmetic mean of 10 million birds per species. We assumed that abundances of the remaining 8663 non-threatened species were greater than 1000. In

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this case, and in cases where the data on threatened species were provided as ranges, we fitted the model assuming censored data. When an upper limit was not provided, we set the upper limit of 10 billion individuals for each species, which is greater than the reported abundance of passenger pigeons, the world's most abundant bird prior to its extinction. The geometric mean of the resulting log-normal probability distribution was then calculated. The sensitivity of the results to the calculated value of c was examine by varying c by one order of magnitude and re-calculating the proportional changes in the probability of extinction.

Results

For the simulated communities with variation in mean growth rate among communities, the index based on the power mean (I_b) and the index based on the geometric mean (I_g) were positively correlated with the proportion of species going extinct (Pearson product moment correlations $r = 0.39$ and $r = 0.50$, respectively). Spearman rank correlations were similar ($r_S = 0.34$ and 0.49 respectively). Variation in mean growth rates among communities explained much of the imperfect correlations; correlations for the index that is based on population trend were high ($r = 0.96$; $r_S = 0.99$ for I_t), and were similarly high for the geometric mean index (I_g) when all communities had the same mean rate of decline ($r = 0.97$ when $\mu_r = -0.2$ for all communities).

The index based on the geometric mean (I_g) and the index that considers population trend (I_t) were more strongly correlated with the proportion of species going extinct than either index based on the arithmetic mean or the Shannon diversity ($r = 0.44$ in both cases when μ_r varied on the interval [–0.3,–0.1], and $r = 0.94$ and 0.91 respectively when μ_r was –0.2). The index based on the power mean (I_b) was the least

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strongly correlated with the proportion of species going extinct (r = 0.39 when the mean population growth rate varied among communities, r = 0.66 when it was consistent); this might be expected given the strong influence of the population trend on the simulated extinction risks, whereas the index I_b assumed no trend.

The index based on the geometric mean abundance was positively correlated with the proportion of Lepidopetera and woodland plant species that went extinct (r = 0.67 and 0.66 respectively; fig. 1a,b). The correlation was –0.32 for the protozoan community (fig. 1c), although abundances were similar for most communities, so the index spanned a narrow range. Thus, the data had little power to indentify a relationship. The correlation was positive when differences in population trends in the protozoan community were accommodated by using the index I_t (r=0.33; fig. 2).

The correlations between the proportion of species going extinct and the index based on the power mean were r = 0.25 for the butterfly data, r = 0.40 for the woodland plants, and r = –0.20 for the protozoan community (fig. 3). Again, the narrow range of abundances for the protozoan community limited the ability of this dataset to reveal the nature of the relationship between the index and the proportion of species going extinct, especially given the large influence of population trends on extinction in these data.

The geometric mean abundance (c) of birds was estimated to be approximately 100,000 individuals per species. Assuming that the index based on the geometric mean is proportional to the extinction risk of species at the global scale, the reported decline in the LPI for birds from 1970 to 2009 of 13% (Baille et al. 2010) reflects a proportional increase in the probability of extinction of approximately 1% for values of c between 10,000 and 1,000,000 (Fig. 4). Smaller values of c imply larger changes

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in the risk of extinction for a given change in LPI, although the results are relatively insensitive to the choice of *c* (Fig. 4).

Discussion

We derived indices that can be interpreted in terms of changes in extinction risk. By deriving the indices from theoretical population models, the merits of possible alternative indices can be assessed to determine which indices are best supported by data. Our analysis shows that the indices are positively correlated with the proportion of species going extinct in small patches, despite highly simplified assumptions used to build the indices.

In addition to the heuristic properties that Buckland et al. (2005) and van Strien et al. (2012) used to assess different indices of biodiversity, a good index should also be clearly related to particular management objectives. For example, we have shown that the geometric mean abundance of species, which has good heuristic properties (Buckland et al. 2005; van Strien et al. 2012), can be related to the proportion of species within an area that are likely to become extinct. This lends much greater support to this index as a biodiversity metric.

The geometric mean abundance of species is used increasingly, including in North American and European bird monitoring (Gregory and van Strien 2010; Butchart et al. 2010) and for planning fire management (Di Stefano et al. 2013). The LPI for reporting the state of species is the geometric mean abundance in each period, divided by the geometric mean abundance in the first time period (Loh et al. 2005; Collen et al. 2009). The LPI is based on the notion that changes in species abundance are important, but was not derived directly from ecological theory. We do not intend this as a particular criticism of the LPI, which has more support than some alternative

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indices, but we argue that ecological indices should have sound theoretical foundations. A theoretical foundation helps make the meaning and scope of the index clearer and more easily justified. For example, the derivation of the index based on the geometric mean implies that reductions in the LPI can be interpreted in terms of an increased average probability of extinction of the species. We estimate that the reduction of the global avian LPI of approximately 13% between 1970 and 2009 corresponds to approximately a 1% increase in the probability of extinction (Fig. 6). This is less than the increased risk of 7% implied by the Red List Index (RLI) of birds for the period 1988 to 2004 (Butchart et al. 2004), which is the only CBD index that is related directly to extinction. The larger increase in extinction risk implied by the RLI compared with I_g might be expected given the RLI's focus on threatened species.

Using a theoretical foundation to develop indices suggests ways in which the indices can be evaluated and improved, and assumptions underlying the indices are clear. The clear assumptions can be tested individually to determine whether they are violated in particular circumstances and the consequences of those errors. Further, the overall properties of an index can be assessed against data if it approximates an explicit quantity. In our case, we sought an index that would be linearly correlated with the proportion of species becoming extinct such that a change in the index would reflect a particular change in the proportion of species going extinct. The clear assumptions help highlight how the indices could be modified.

As an example of modification, trends in population size are likely to influence extinction risks. The index that incorporates trend (I_t) shows how abundance and trend might be incorporated into a single index if the assumption of a consistent trend among communities is not supported. In the case of the experimental protozoan

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community, an assumption of an equal trend is clearly not supported. Of the four protozoan species, one went extinct in all 40 experimental replicates, and one persisted in all replicates. Thus, the proportion of species in each community that went extinct was influenced substantially by the identity of the species, which had different trends not just different population sizes.

Biodiversity indices, such as those developed here, will be sensitive to the choice of species that are included. For example, species included in the LPI calculations are not a random sample of all possible species, with biases likely. Unless the scheme used to select the sample of species used in the index is considered carefully, it will be unclear how the selected species will represent the broader suite of biodiversity.

Factors other than those included in the indices are likely to influence extinction. The Lepidoptera species will be differentially susceptible to apparent local extinction because of different dispersal and abilities to persist outside the focal habitat patches. Other species will occur only ephemerally in the patches, reducing the influence of abundance on local extinction. However, the results were qualitatively identical when analysing only strict grassland specialists, so we reported only the results for the larger collection of species.

Our indices were based on models of exponential decline of single populations, thereby ignoring spatial aspects and density-dependence. Other indices based on metapopulation dynamics, for example, could be developed to account for spatial effects. Indeed, metapopulation capacity, which r colonisation and extinction dynamics of habitat patches (Day and Possingham 1995; Hanski & Ovaskainen 2000), can be viewed as an index of metapopulation persistence (Moilanen and Nieminen 2002). Density-dependence might be less important for populations that are declining

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deterministically, although accounting for non-exponential decline might be important because temporal patterns of decline influence risk (Di Fonzo et al. 2013).

Imprecise estimation of abundance (particularly in the woodland case study), some residual uncertainty about the local extinction of species due to imperfect detection, and the false assumption of equivalent dynamics of all species would all weaken the correlation between the indices and the observed extinction rate. Despite this, the predicted and observed extinction risks were correlated (Figures 1-3). This implies that using the indices to aggregate data across species is reasonable. However, further tests of the indices to predict local extinction would be valuable, as would evaluating extinction risk over regions larger than just single patches (e.g., based on spatial population dynamics).

The index based on the power mean is sensitive to the choice of the parameter b, and estimating it via estimates the standard deviation of the population growth rate (σ) might be difficult. Thus, the indices based on the geometric mean (I_g and I_t) might be more appealing because a freely-varying parameter does not require estimation. Further, extinctions might be dominated by deterministic declines rather than random fluctuation around a zero mean growth rate. If true, the indices based on the geometric mean might be preferred over that based on the power mean.

The SAFE index (Clement et al 2011; see also Akçakaya et al. 2011, Beissinger et al. 2011 and McCarthy et al. 2011) is essentially equal to the logarithm of population size. Our analysis shows, therefore, that the SAFE index will be proportional to the expected time to quasi-extinction (time to reaching a given threshold). But it also shows that the SAFE index will be comparable among species as a measure of threat only if trends in population size of those species are similar. Where trends differ

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among species, an index based on $-\ln[x(0)]/\ln[\lambda]$ is likely to better reflect threat. Further, prioritization of management, which apparently motivated the SAFE index, should not be based on extinction risk, but on the ability to change risks (McCarthy et al. 2011). This might be assessed, for example, by the relative cost of changing $x(0)$ or λ and their influence on $-\ln[\lambda]/\ln[x(0)]$ (Baxter et al. 2006).

An index developed without theory does not mean it will have poor properties. As we have seen, the geometric mean was developed without theory but appears to have useful properties (Buckland et al. 2005; van Strien et al. 2012). The demonstrated relationship to extinction risk lends further support to the geometric mean. Our analysis also indicates how the geometric mean might incorporate population trends. We suggest that biodiversity indices should be developed more frequently from theoretical foundations to provide more explicit links between the index, the data underlying the index, and the meaning of changes in the index. Such indices will inevitably exclude factors that might be important; this is a feature of any model. However, stronger theoretical foundations for biodiversity indices would clarify the features that are considered and those that are ignored, and would allow the indices to be more easily evaluated and improved.

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Figure 1. Relationship between the index based the geometric mean, I_g, and the proportion of species going locally extinct for the three case studies: a, Lepidopetera (r = 0.67); b, woodland plants (r = 0.66); and c, protozoan communities (r = –0.32). Each point represents a patch for the field studies (a, b) or the average of each type of community for the protozoans (c). The lines are linear regressions.

Figure 2. Relationship between the index based the population trend, I_t, and the proportion of species in protozoan communities going locally extinct (r = 0.43). Each point represents the average of each type of community for the protozoans. The line is a linear regression.

Figure 3. Relationship between the index based the power mean, I_b, and the proportion of species going locally extinct for the three case studies: a, Lepidopetera (r = 0.40); b, woodland plants (r = 0.66); and c, protozoan communities (r = –0.20). Each point represents a patch for the field studies (a, b) or the average of each type of community for the protozoans (c). In (a) there are multiple data points near the origin, and in (c) there are three data points at the coordinate (0.33, 0.67). The lines are linear regressions.

Figure 4. Proportional changes in the probability of extinction from levels in 1970 based on changes in the Living Planet Index for birds (Baille et al. 2010) assuming values for the geometric mean abundance in 1970 of 10,000, 100,000 or 1,000,000 individuals.

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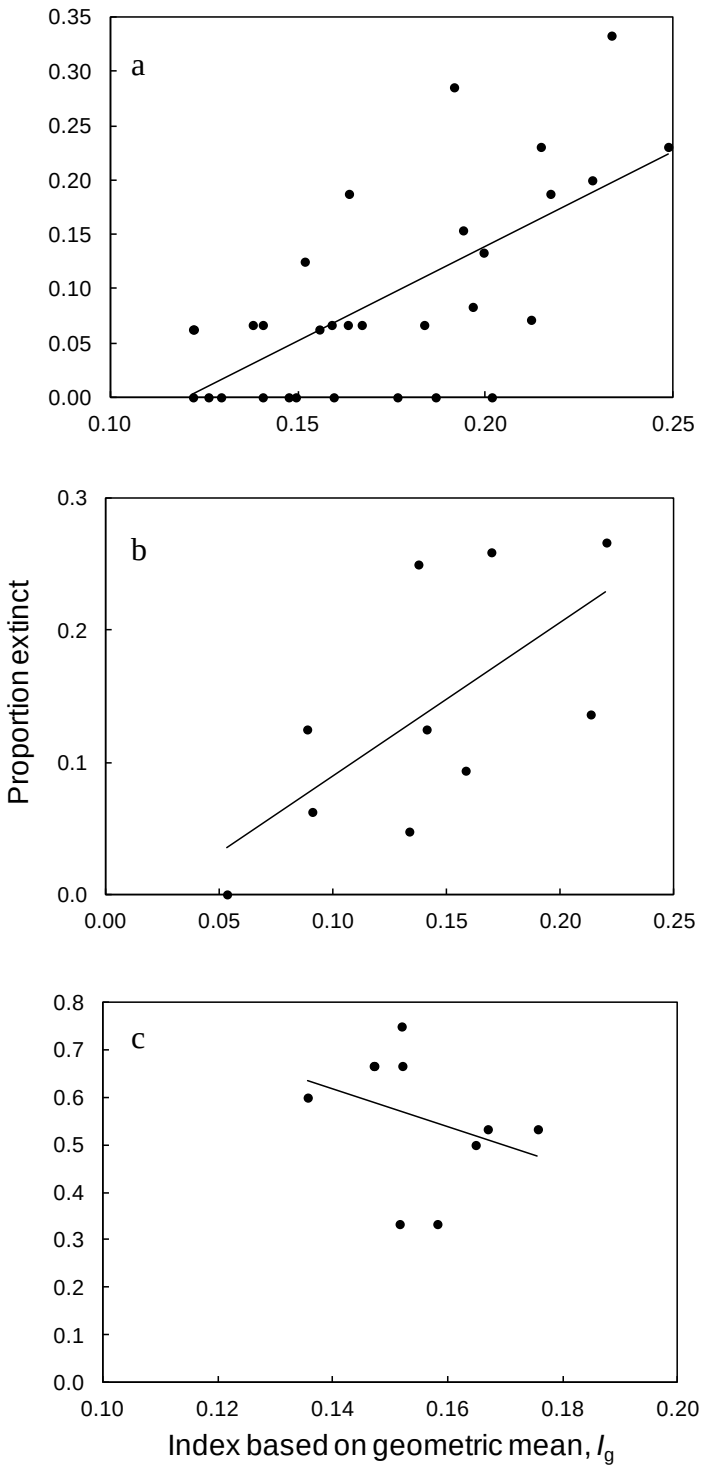

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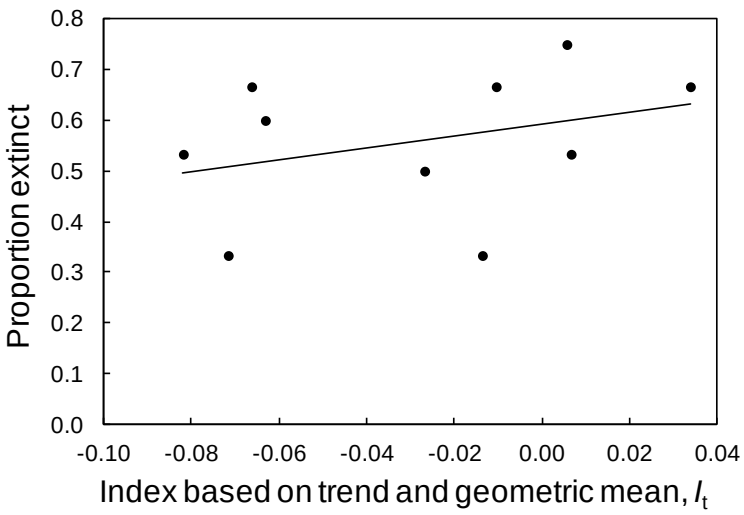

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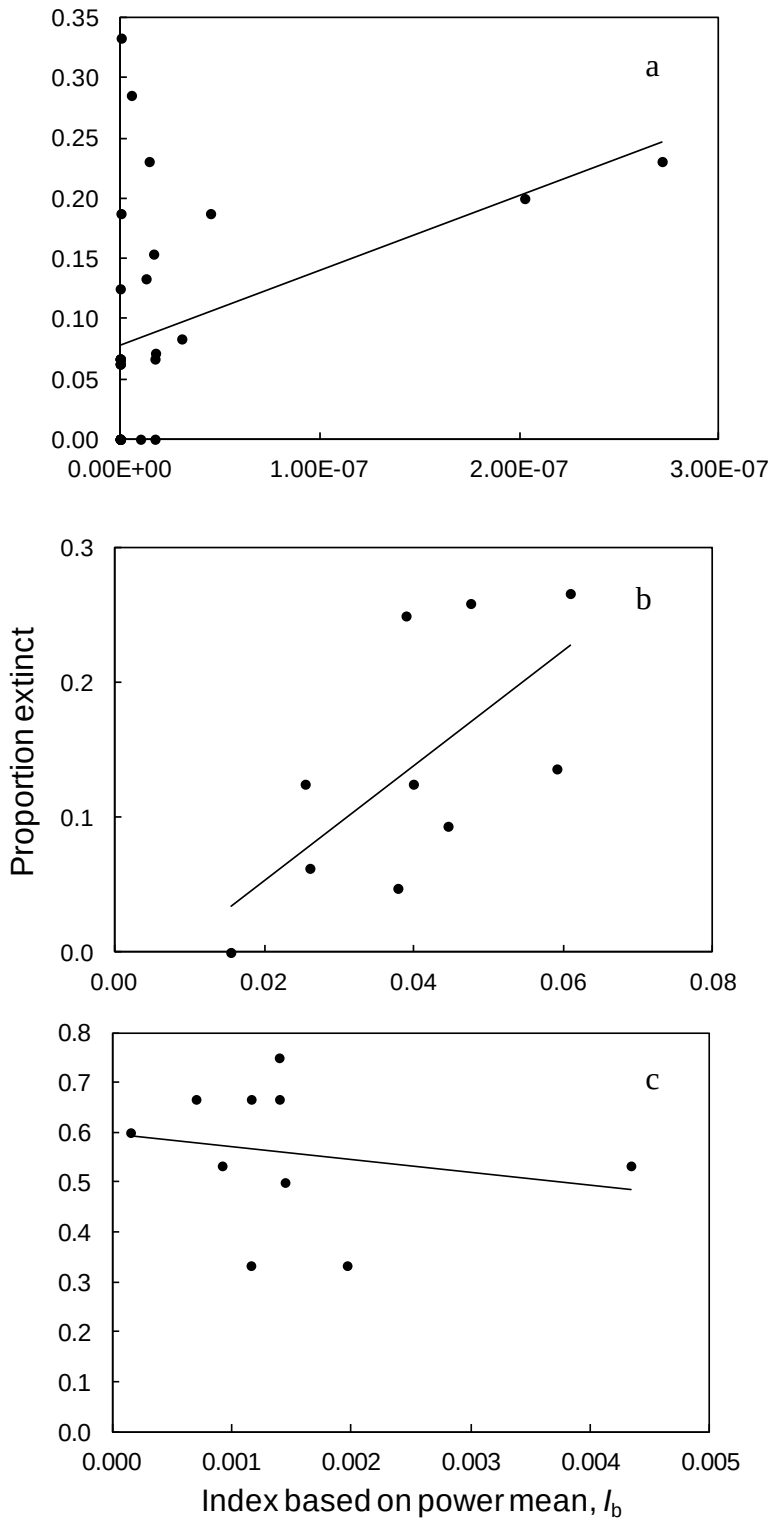
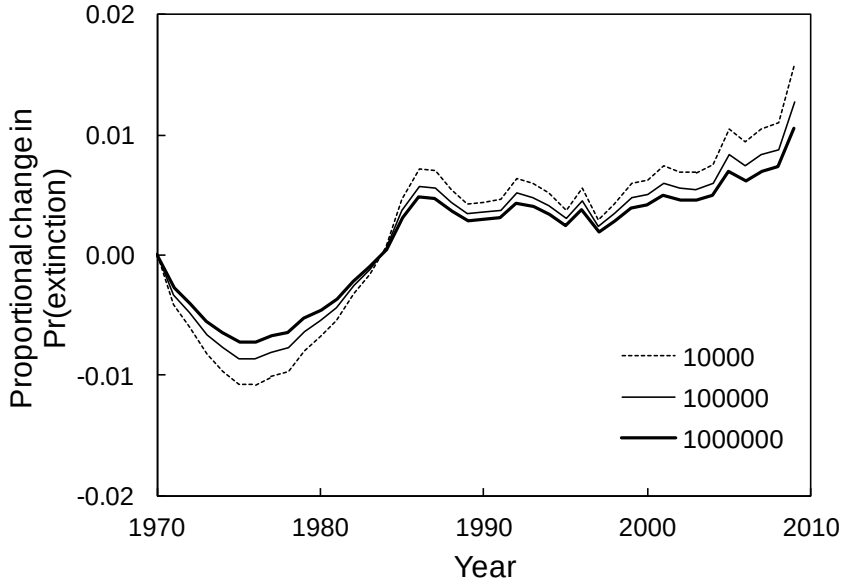
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