

1 **Linking indices for biodiversity monitoring to extinction risk**

2 **theory**

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11

12 **Abstract**

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

29

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

31

32 **INTRODUCTION**

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

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

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

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

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

71 **Methods**

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

$$76 \quad x(t) = x(0)\lambda^t,$$

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

79 that $x(t) = 1$ occurs at time $T = -\ln[x(0)]/\ln[\lambda]$. If the long-run growth rate is
80 negative, then for stochastic population models the mean extinction time is also
81 approximately logarithmically dependent on initial population size (Lande 1993).
82 With the simplifying assumption that the rate of decline is the same for each species
83 (we address this particular assumption later), the mean expected time to extinction,
84 averaging over n species, is proportional to the mean of the logarithm of population
85 abundance. As we show below, the mean expected time to extinction is proportional
86 to the logarithm of the geometric mean of population abundances (M_0);

$$\begin{aligned} 87 \quad \bar{T} &\propto \overline{\ln(x)} = \frac{1}{n} \sum_{i=1}^n \ln(x_i) \\ 88 \quad &= \ln \left(\left[\prod_{i=1}^n x_i \right]^{1/n} \right) \\ 89 \quad &= \ln(M_0). \end{aligned} \tag{1}$$

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

$$96 \quad I_g = \frac{1}{\ln(M_0)}. \tag{2}$$

97 This index should correlate linearly with the proportion of species going extinct under
98 the assumptions stated above. The approximation of $1 - \exp(-t/\bar{T})$ by t/\bar{T} will tend to
99 lead to non-linearity (but a monotonic relationship) for higher risks.

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

$$105 \quad q_i(x_0) = 2\varphi(-\nu) .$$

106 where $\varphi()$ is the standard normal cumulative distribution function, $\nu = -\ln(1/x_0)/(\sigma\sqrt{t})$
107 and x_0 is the initial population size. This functional form could be used as an index,
108 but it does not provide a simple numerical solution. Instead, we approximated this
109 equation by a function of the form $A x^{-B/(\sigma\sqrt{t})}$ (by approximating $\log(q_i(x_0))$ as a linear
110 function of $\log(x)$) with the values of A and B depending on the value of the extinction
111 risk. For small extinction risks, $q_i < \approx 0.15$, $A = 2.2$ and $B = 1.87$ provide a good
112 approximation. When the extinction risk is close to one, a better approximation is A
113 $= 1$ and $B = 0.798$. Regardless, the probability of extinction scales approximately with
114 abundance in proportion to x^{-b} , with $b = B/(\sigma\sqrt{t})$. Thus, averaged across n species, we
115 would expect the proportion of species going extinct to be

$$116 \quad L = \sum_{i=1}^n q_i / n = k \sum_{i=1}^n x_i^{-b} / n = k(M_{-b})^{-b}, \quad (3)$$

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

119
$$M_{-b} = \left(\frac{1}{n} \sum_{i=1}^n x_i^{-b} \right)^{-1/b}.$$

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

121
$$I_b = (M_{-b})^{-b}. \quad (4)$$

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

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

134
$$I_t = \frac{-\mu_r}{\ln(M_0)}. \quad (5)$$

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

138 **Simulations for evaluating indices**

139 We simulated stochastic species dynamics within communities to evaluate the
140 correlation between the different indices and the proportion of species going extinct.
141 Each community consisted of 500 species, and there were 100 different communities.
142 For each species j in community i , we simulated the population dynamics over 20
143 time steps using the exponential growth model such that the population size in time
144 $t+1$ is given by:

$$145 \quad x_{ijt+1} = \lambda_{ijt} x_{ijt}.$$

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

153 To ensure that each community had different initial population sizes and different
154 trends in abundance (and hence different average extinction risks), the mean and
155 coefficient of variation of the population size (μ_N and c_N) and the mean and standard
156 deviation of population growth rate (μ_r and σ_r) of each was varied among
157 communities. The coefficient of variation c_N was drawn from a uniform distribution
158 on the interval [0.5, 3.0]. The mean population size was equal to $1.2^d 100$, where d was
159 drawn from a uniform distribution on the interval [0, 20], so mean population size
160 varied among communities over the interval [100, 3834]. The mean population
161 growth rate (μ_r) was drawn from a uniform distribution on the interval [-0.3, -0.1],

162 and the standard deviation (σ_r) was drawn from a uniform distribution on the interval
163 [0.05, 0.4]. To test how differences in abundance, rather than population trend,
164 influence the performance of the indices, data were also simulated with μ_r set to -0.2
165 for all communities.

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

173 **Data for evaluating indices**

174 The correlation between the indices and local extinction risk was evaluated using field
175 data on Lepidoptera (Krauss et al. 2003) and woodland plants (Sutton & Morgan
176 2009). Because data on population trends were unavailable for these datasets, only
177 eqns 2 and 4 were evaluated. We evaluated all three indices with data from
178 experimental protozoan communities (Clements et al. 2013). The original publications
179 detail the data and its collection; some information is provided here for context (see
180 also Supporting Information). The data sets we examined reported both extinctions of
181 multiple species and information on initial abundances.

182 Each dataset included information on the abundance of each of the species in replicate
183 local communities at a particular point in time, and data on the proportion of those
184 species that went extinction over a subsequent period of time. For the protozoan

185 community, estimates of abundance were available at multiple points in time prior to
186 the period over which extinctions were assessed. For each dataset, we calculated the
187 indices using the abundance data (and the trend data in the case of the index I_t for the
188 protozoan dataset).

189 For each dataset, we calculated the correlation (with 95% confidence interval based
190 on a z -transformation; Sokal & Rohlf 1981) between the value of each index and the
191 proportion of species in each community going extinct. We also determined, via
192 simulation, the correlations that would be expected if each index were perfectly
193 correlated with extinction of species, while accounting for the finite number of
194 species in each community (Supporting Information). This allowed us to determine
195 whether the observer correlations were substantially different from what would be
196 expected given the limitations of the datasets.

197 **Relating I_g to the Living Planet Index**

198 The LPI is the geometric mean abundance of vertebrate species in a particular year
199 divided by the geometric mean in 1970 (Loh et al. 2005; Collen et al. 2009).

200 Therefore, the index based on the geometric mean can be related to the LPI simply as
201 $I_g = 1/\ln(c \text{ LPI})$, where c is the geometric mean abundance in 1970. If I_g is
202 proportional to the probability of extinction, as assumed in its derivation, LPI values
203 can be converted to proportional changes in the probability of extinction of species,
204 which will equal $-\ln(\text{LPI}) / [\ln(c) + \ln(\text{LPI})]$. We calculated this quantity for the
205 world's birds based on published avian LPI values (Baille et al. 2010).

206 These proportional changes depend on c , which is not well known. The arithmetic
207 mean abundance of birds is thought to be approximately 10 million individuals per
208 species but, because species abundance distributions are heavily right-skewed, the

209 geometric mean will be substantially less (Gaston & Blackburn 2003). We estimated
210 the global species abundance distribution of birds, and hence the geometric mean, by
211 fitting a log-normal distribution to data on reported population size for the global list
212 of 1253 threatened species on BirdLife International's website
213 (<http://www.birdlife.org/datazone/species/search>; accessed 20 December 2011) and
214 assuming an arithmetic mean of 10 million birds per species. We assumed that
215 abundances of the remaining 8663 non-threatened species were greater than 1000. In
216 this case, and in cases where the data on threatened species were provided as ranges,
217 we fitted the model assuming censored data. When an upper limit was not provided,
218 we set the upper limit of 10 billion individuals for each species, which is greater than
219 the reported abundance of passenger pigeons, the world's most abundant bird prior to
220 its extinction. The geometric mean of the resulting log-normal probability distribution
221 was then calculated. The sensitivity of the results to the calculated value of c was
222 examine by varying c by one order of magnitude and re-calculating the proportional
223 changes in the probability of extinction.

224 **Results**

225 For the simulated communities with variation in mean growth rate among
226 communities, the index based on the power mean (I_b) and the index based on the
227 geometric mean (I_g) were positively correlated with the proportion of species going
228 extinct (Pearson product moment correlations $r = 0.39$ and $r = 0.50$, respectively).
229 Spearman rank correlations were similar ($r_s = 0.34$ and 0.49 respectively). Variation
230 in mean growth rates among communities explained much of the imperfect
231 correlations; correlations for the index that is based on population trend were high ($r =$
232 0.96 ; $r_s = 0.99$ for I_t), and were similarly high for the geometric mean index (I_g) when

233 all communities had the same mean rate of decline ($r = 0.97$ when $\mu_r = -0.2$ for all
234 communities).

235 The index based on the geometric mean (I_g) and the index that considers population
236 trend (I_t) were more strongly correlated with the proportion of species going extinct
237 than either index based on the arithmetic mean or the Shannon diversity ($r = 0.44$ in
238 both cases when $\mu_{r,i}$ varied on the interval $[-0.3, -0.1]$, and $r = 0.94$ and 0.91
239 respectively when $\mu_{r,i}$ was -0.2 for all communities). The index based on the power
240 mean (I_b) was the least strongly correlated with the proportion of species going extinct
241 ($r = 0.39$ when the mean population growth rate varied among communities, $r = 0.66$
242 when it was consistent); this might be expected given the strong influence of the
243 population trend on the simulated extinction risks, whereas the index I_b assumed no
244 trend. Note, the derivation of I_g included a trend, but it dropped out of the calculation
245 of the index as a proportionality constant by assuming the same trend for all
246 communities.

247 For the real communities, the index based on the geometric mean abundance (I_g) and
248 the index based on the power mean (I_b) were positively correlated with the proportion
249 of Lepidoptera and woodland plant species that went extinct (Fig. 1a,c; Fig. 2). The
250 95% confidence intervals for these correlation coefficients did not encompass zero. In
251 contrast, the correlations for these indices were negative for the protozoan dataset
252 (Fig. 1e,f), although the correlation for the index that included population trends was
253 positive ($r=0.33$; Fig. 1g, Fig. 2). In this dataset, abundances were similar for most
254 communities, so the indices spanned a narrow range of values. The 95% confidence
255 intervals for the correlation coefficient were wide (Fig. 2), so the strength of the
256 relationship could not be determined reliably for the protozoan dataset.

257 There was only one case (the index based on the power mean for the protozoan
258 dataset) that the observed correlation coefficient was both not significantly different
259 from zero (Fig. 2) and substantially less than the correlation coefficient that might be
260 expected even if the indices were perfectly correlated with the proportion of species
261 going extinct (Fig. S1). In the other cases, either the 95% confidence intervals of the
262 observed correlations were greater than zero (Fig. 2), or the observed correlations
263 were consistent with the range of values that might be expected (Fig S1).

264 The geometric mean abundance (c) of birds was estimated to be approximately
265 100,000 individuals per species. Assuming that the index based on the geometric
266 mean is proportional to the extinction risk of species at the global scale, the reported
267 decline in the LPI for birds from 1970 to 2009 of 13% (Baillie et al. 2010) reflects a
268 proportional increase in the probability of extinction of approximately 1% for values
269 of c between 10,000 and 1,000,000 (Fig. 3). Smaller values of c imply larger changes
270 in the risk of extinction for a given change in LPI, although the results are relatively
271 insensitive to the choice of c (Fig. 3), and are primarily driven by the LPI values (Fig.
272 S2).

273 **Discussion**

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

280 In addition to the heuristic properties that Buckland et al. (2005) and van Strien et al.
281 (2012) used to assess different indices of biodiversity, a good index should also be
282 clearly related to particular management objectives. For example, we have shown that
283 the geometric mean abundance of species, which has good heuristic properties
284 (Buckland et al. 2005; van Strien et al. 2012), can be related to the proportion of
285 species within an area that are likely to become extinct. This lends much greater
286 support to this index as a biodiversity metric.

287 The geometric mean abundance of species is used increasingly, including in North
288 American and European bird monitoring (Gregory & van Strien 2010; Butchart et al.
289 2010) and for planning fire management (Di Stefano et al. 2013). The LPI for
290 reporting the state of species is the geometric mean abundance in each period, divided
291 by the geometric mean abundance in the first time period (Loh et al. 2005; Collen et
292 al. 2009). The LPI is based on the notion that changes in species abundance are
293 important, but was not derived directly from ecological theory. We do not intend this
294 as a particular criticism of the LPI, which has more support than some alternative
295 indices, but we argue that ecological indices should have sound theoretical
296 foundations. A theoretical foundation helps make the meaning and scope of the index
297 clearer and more easily justified. For example, the derivation of the index based on
298 the geometric mean implies that reductions in the LPI can be interpreted in terms of
299 an increased average probability of extinction of the species. We estimate that the
300 reduction of the global avian LPI of approximately 13% between 1970 and 2009
301 corresponds to approximately a 1% increase in the probability of extinction (Fig. 6).
302 This is less than the increased risk of 7% implied by the Red List Index (RLI) of birds
303 for the period 1988 to 2004 (Butchart et al. 2004), which is the only CBD index that is

304 related directly to extinction. The larger increase in extinction risk implied by the RLI
305 compared with I_g might be expected given the RLI's focus on threatened species.

306 The indices based on the power mean (I_b) and geometric mean (I_g) have the same data
307 requirements as those considered by Buckland et al. (2005). That is, they require
308 information on the abundance of a suite of species at a particular point in time. The
309 index that accounts for different trends among communities, (I_t) requires additional
310 information (the average trend of the species in the community). Such data will tend
311 to be available for only a subset of species, and this subset is likely to be a biased
312 sample of relevant species in a community. Any bias will be common to all indices,
313 with the consequence that they might not broadly represent all possible species of
314 interest.

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

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

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

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

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

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

352 populations that are declining deterministically, although accounting for non-
353 exponential decline might be important because temporal patterns of decline influence
354 risk (Di Fonzo et al. 2013).

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

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

371 The SAFE index (Clement et al 2011; see also Akçakaya et al. 2011; Beissinger et al.
372 2011; McCarthy et al. 2011) is essentially equal to the logarithm of population size.
373 Our analysis shows, therefore, that the SAFE index will be proportional to the
374 expected time to quasi-extinction (time to reaching a given threshold). But it also
375 shows that the SAFE index will be comparable among species as a measure of threat

376 only if trends in population size of those species are similar. Where trends differ
377 among species, an index based on $-\ln[x(0)]/\ln[\lambda]$ is likely to better reflect threat.
378 Further, prioritization of management, which apparently motivated the SAFE index,
379 should not be based on extinction risk, but on the ability to change risks (McCarthy et
380 al. 2011). This might be assessed, for example, by the relative cost of changing $x(0)$ or
381 λ and their influence on $-\ln[\lambda]/\ln[x(0)]$ (Baxter et al. 2006).

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

394 **Acknowledgments**

395 This research was supported by an Australian Research Council (ARC) Future
396 Fellowship to M.A.M. (FT100100923), and the ARC Centre of Excellence for
397 Environmental Decisions. We thank J. Baumgartner for help with collating the data
398 on bird abundances, B. Collen for providing values for the Living Planet Index of

399 birds, and J. Moore, R. Gregory, R. Camp and two anonymous reviewers for
400 comments on a draft manuscript.

401 **Supporting Information**

402 Further details on the datasets used (Appendix S1), details on calculating the expected
403 correlation (Appendix S2), and Figs S1 and S2 are available online. The authors are
404 solely responsible for the content and functionality of these materials. Queries (other
405 than absence of the material) should be directed to the corresponding author.

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497 Figure 1. Relationship between the three different indices (I_g , I_b , I_t) and the proportion
498 of species going locally extinct for the three case studies: (a-b) for Lepidoptera; (c-d)
499 for woodland plants; and (e-g) for protozoan communities. Each point represents a
500 patch for the field studies (Lepidoptera and woodland plants) or the average of each
501 type of community for the protozoan. The lines are linear regressions. Correlation
502 coefficients with 95% confidence intervals are given in Fig. 2.

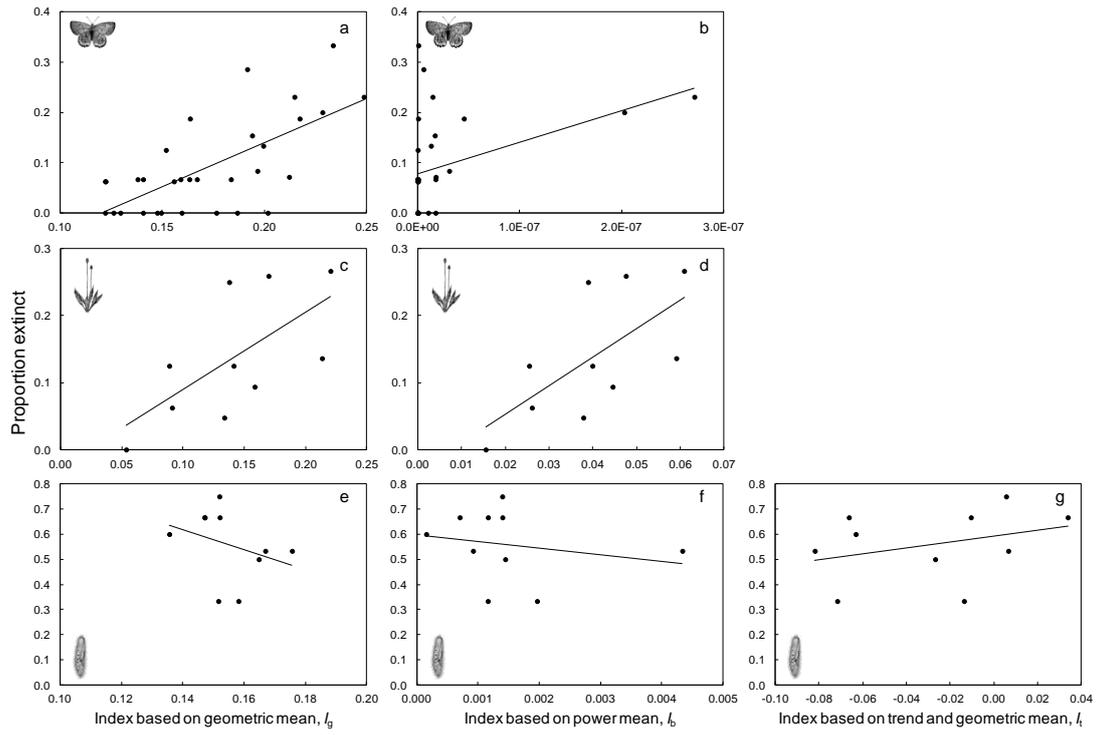
503 Figure. 2. Observed correlation between the three indices (I_g based on the geometric
504 mean; I_b based on the power mean; and I_t based on the geometric mean and trend) and
505 the proportion of species going extinct from a community. Results are shown for each
506 of the three different datasets (butterflies, plants, protozoa). The circles are the
507 observed correlation coefficients and the bars are 95% confidence intervals.

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509 Figure 3. Proportional changes in the probability of extinction from levels in 1970
510 based on changes in the Living Planet Index for birds (Baille et al. 2010) assuming
511 values for the geometric mean abundance in 1970 of 10,000, 100,000 or 1,000,000
512 individuals.

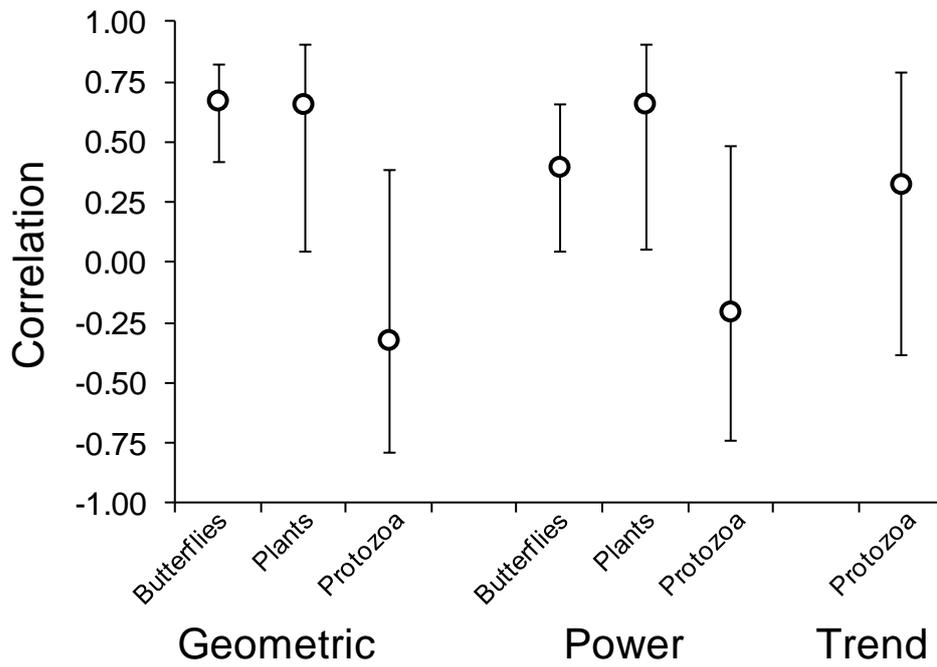
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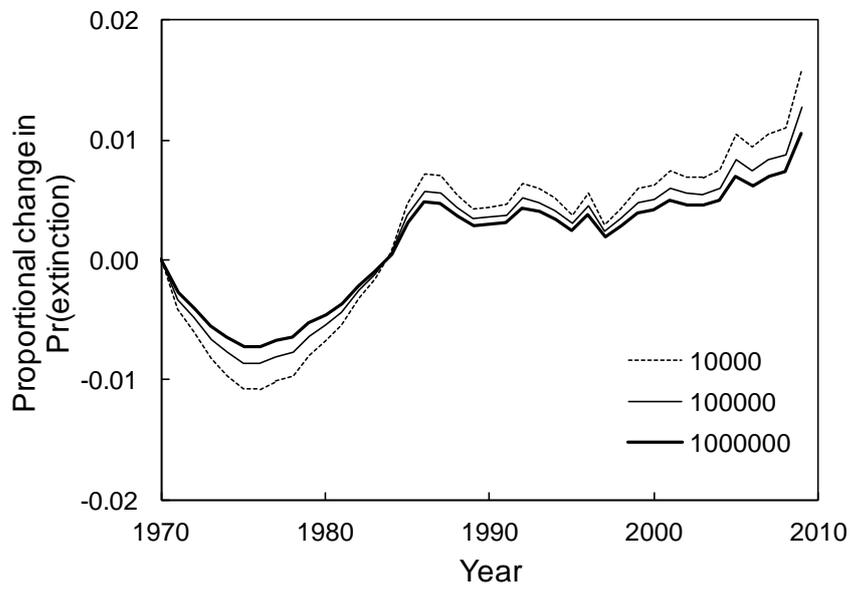
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