

Ecological prophets: quantifying metapopulation portfolio effects

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Summary

1. A financial portfolio metaphor is often used to describe how population diversity can increase temporal stability of a group of populations. The portfolio effect (PE) refers to the stabilizing effect from a population acting as a group or ‘portfolio’ of diverse subpopulations instead of a single homogeneous population or ‘asset’. A widely used measure of the PE (the average-CV PE) implicitly assumes that the slope (z) of a log–log plot of mean temporal abundance and variance (Taylor’s power law) equals two.

2. Existing theory suggests an additional unexplored empirical PE that accounts for z , the mean–variance PE. We use a theoretical and empirical approach to explore the strength and drivers of the PE for metapopulations when we account for Taylor’s power law compared with when we do not. Our empirical comparison uses data from 51 metapopulations and 1070 subpopulations across salmon, moths and reef fishes.

3. Ignoring Taylor’s power law may overestimate the stabilizing effect of population diversity for metapopulations. The disparity between the metrics is greatest at low z values where the average-CV PE indicates a strong PE. Compared with the mean–variance method, the average-CV PE estimated a stronger PE in 84% of metapopulations by up to sevenfold. The divergence between the methods was strongest for reef fishes ($1.0 < z < 1.7$) followed by moths ($1.5 < z < 1.9$). The PEs were comparable for salmon where $z \approx 2$.

4. We outline practical recommendations for estimating ecological PEs based on research questions, study systems and available data. Because most PEs were stabilizing and diversity can be slow to restore, our meta-analysis of metapopulations suggests that the safest management approach is to conserve biological complexity.

Key-words: Allee effect, biocomplexity, Great Barrier Reef, Moran effect, population diversity, response diversity, stability, synchrony

Introduction

Biological complexity is increasingly recognized as a critical factor underpinning the stability of ecological systems (e.g. Hilborn *et al.* 2003; Ives & Carpenter 2007; Schindler *et al.* 2010). While the diversity–stability relationship for ecosystem properties is generally held to be true, what is not known is the relative increase in benefit from each additional element of biodiversity for stability and persistence (Cardinale *et al.* 2012). For example, Schindler *et al.* (2010) found that sockeye salmon populations in Bristol Bay were twice as stable as a homogeneous population, and management should focus on retaining biological diversity to ensure a tenfold reduction in the frequency of fishery closures. The stabilizing benefit of such population diversity is clearly a critical and undervalued component of ecological systems for resource management to conserve, yet there are few ways to quantify its benefit.

The empirical portfolio effect (PE) is a rapidly popularized metric (e.g. Schindler *et al.* 2010; Carlson & Satterthwaite 2011; IMCC 2011) derived from theory introduced a decade

earlier (Doak *et al.* 1998; Tilman, Lehman & Bristow 1998; Tilman 1999) that aims to measure the increase in stability due to subpopulation diversity within a metapopulation (or greater species diversity within a community). For example, we can think of salmon from individual streams as assets (subpopulations) within a portfolio (metapopulation) that comprises the watershed. If subpopulations react differently to environmental variability, then the metapopulation may experience a reduced risk of collapse or decline. Similarly, financial managers choose portfolios of diverse financial assets to reduce their risk of financial losses.

Financial managers estimate the benefit of diversifying a financial portfolio by comparing the variability in returns from investing in a single asset to the variability from investing in a diversified portfolio (Markowitz 1959). In ecology, the empirical PE has been calculated by comparing the temporal coefficient of variation (CV) of metapopulation abundance (the diversified portfolio; Fig. 1a) with the average-CV of subpopulation abundances (the single assets; Fig. 1b) (Secor, Kerr & Cadrin 2009; Schindler *et al.* 2010; Carlson & Satterthwaite 2011). We refer to this approach as the average-CV PE (Fig. 1c). But, ecological and financial systems differ; it is

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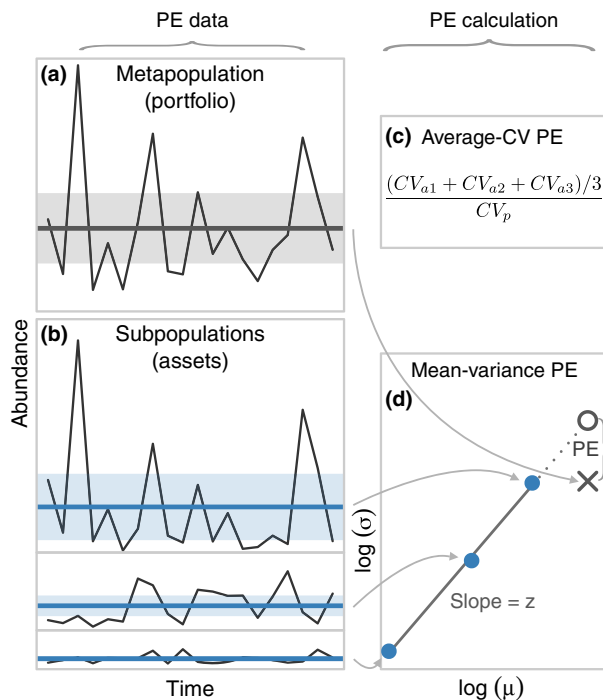


Fig. 1. Estimating the two PEs from empirical data. (a, b) Example metapopulation (portfolio) and subpopulation (asset) abundance time series. Horizontal lines represent the time-series' means, and the shaded regions represent variability. (c) We calculated the average-CV PE by dividing the average-CV of the subpopulations (CV_a) by the CV of the metapopulation (CV_p). (d) We calculated the mean-variance PE by (i) plotting the mean and variance of each subpopulation on log-log axes, (ii) extrapolating the subpopulation mean-variance relationship to the metapopulation mean (open grey circle) and (iii) comparing the predicted (open grey circle) and observed (grey cross) metapopulation variability. Both methods will estimate the same PE if the slope of the log-log plot (z) equals two.

timely to consider whether we can apply the same approach to ecological systems.

One crucial difference between financial and ecological portfolios is how asset variability scales with investment. For a financial asset, the standard deviation of an investor's returns increases linearly with investment because investing in a financial stock does not meaningfully affect the stock's properties. Therefore, as mean financial investment increases, we expect the variance in returns to increase by a power of two. This is not true in ecological systems. As abundance of a subpopulation grows (i.e. as investment in the single asset grows), the standard deviation usually increases nonlinearly according to Taylor's power law: the slope (z) of a log-log plot of the variance and mean of subpopulation abundance is typically less than two (Taylor & Woiod 1980, 1982). This means that larger populations may be less variable than expected if we applied the financial metaphor. The CV is not necessarily a size-independent metric of variability (McArdle, Gaston & Lawton 1990).

The theoretical work of Tilman, Lehman & Bristow (1998) implies an alternative way to measure the empirical PE that accounts for the mean-variance relationship. Rather than

assuming we can represent the variability of the theoretical homogeneous metapopulation (the single asset) by the average subpopulation CV, we can estimate the variance of the homogeneous metapopulation by extrapolating the mean-variance relationship to the observed metapopulation size (Fig. 1d). We can then compare this expected homogeneous population variability with the observed metapopulation variability to get what we call the mean-variance PE. This mean-variance PE asks: If the mean-variance relationship continued to scale as we observed for larger and larger subpopulations, how much more variable would we expect the metapopulation to be if it was identically sized but acted with the same dynamics as any one subpopulation? Therefore, although both the mean-variance PE and the average-CV PE get at the benefit of splitting one large population into many subpopulations, only the mean-variance PE accounts for the observed mean-variance scaling relationship – the average-CV PE assumes that $z = 2$. Given this theoretical advantage of the mean-variance PE, what happens when we apply the average-CV PE to empirical data where z is typically less than two, as recent literature has done (Secor, Kerr & Cadrin 2009; Schindler *et al.* 2010; Carlson & Satterthwaite 2011)?

Here, we conducted the first large-scale cross-taxa evaluation of the average-CV PE compared with the mean-variance PE for metapopulations, specifically addressing three main questions: (i) How does the average-CV PE differ compared with the mean-variance PE when applied to theoretical systems with varying z values? (ii) How prevalent and strong is this difference across 51 metapopulations and 1070 subpopulations of salmon, moths and reef fishes? (iii) Despite its stronger theoretical foundations, is the mean-variance PE a reliable empirical metric of how subpopulation diversity benefits stability? We conclude with a guide to measuring ecological PEs based on question, study system and data type.

Materials and methods

DEFINING THE METAPOPOPULATION PORTFOLIO

In our finance-ecology metaphor, we represent portfolio value as metapopulation abundance and financial asset value as subpopulation abundance. We define metapopulations as groups of subpopulations that behave largely independently but are linked by dispersal of individuals among subpopulations (Levins 1969). Although our data represent subpopulations in the spatial metapopulation sense, the methods in this study could be applied more broadly. For example, future studies could consider different age classes, different life-history variants or populations with different thermal tolerances as subpopulations. Although the PE has also been applied to multiple species within a community (e.g. Doak *et al.* 1998; Tilman, Lehman & Bristow 1998; Karp *et al.* 2011), and elements of our analysis are applicable to community portfolio effects, the analysis of PEs in communities is complicated by trophic interactions, changes in mean abundance with increasing diversity (the overyielding effect) and differing mean-variance scaling relationships across species (e.g. Loreau 2010; Thibaut & Connolly 2013).

When discussing the properties of metapopulation portfolios, we use three terms (stability, diversity and homogeneous population),

which we define here. We define *stability* in terms of the variability (CV) of population trajectories through time. We define *population diversity* as the asynchrony (lack of correlation) between the groups defined as subpopulations. Because our metrics are phenomenological, they do not specify the mechanism generating asynchrony, but a central candidate would be diversity of response to environmental fluctuations (e.g. Elmqvist *et al.* 2003; Loreau & de Mazancourt 2008; Thibaut, Connolly & Sweatman 2012). We define a *homogeneous population* as a theoretical population the same size as the existing 'diverse' population but lacking whatever subpopulation diversity we are measuring. For metapopulations, we can think of this in one of two ways: (i) a population the same size as the metapopulation that behaves like the average subpopulation or (ii) a metapopulation with synchronized subpopulation dynamics.

THEORETICAL EVALUATION OF PORTFOLIO EFFECTS

We defined the PE as the ratio of the CV of a theoretical system composed of a single subpopulation or asset (CV_a) to the observed metapopulation or portfolio CV (CV_p). A PE of two, for example, would indicate that a metapopulation is two times less variable than if it were comprised of a single homogeneous population. For uncorrelated subpopulations and $\sigma^2 = c\mu^z$ (where σ^2 is the temporal variance, μ is the temporal mean, and c is a constant that doesn't affect the PE and is hereafter ignored for simplicity), both interpretations of the PE define CV_p for subpopulations i 1 through n as

$$CV_p = \frac{\sqrt{\mu_1^2 + \mu_2^2 + \dots + \mu_n^2}}{\mu_1 + \mu_2 + \dots + \mu_n}. \quad \text{eqn 1}$$

The average-CV PE defines CV_a as

$$CA_a = \frac{\frac{\sqrt{\mu_1^2}}{\mu_1} + \frac{\sqrt{\mu_2^2}}{\mu_2} + \dots + \frac{\sqrt{\mu_n^2}}{\mu_n}}{n}, \quad \text{eqn 2}$$

whereas the mean-variance PE defines CV_a as

$$CV_a = \frac{\sqrt{(\mu_1 + \mu_2 + \dots + \mu_n)^z}}{\mu_1 + \mu_2 + \dots + \mu_n}. \quad \text{eqn 3}$$

Equations 2 and 3 are equal if $z = 2$.

To extend the theoretical PE calculations to metapopulations with ρ correlation between subpopulations, we can calculate the metapopulation or portfolio variance σ_p^2 as

$$\sigma_p^2 = \sum_{i=1}^n \sigma_i^2 + \sum_{i=1}^n \sum_{j=1, j \neq i}^n \rho \sqrt{\sigma_i^2 \sigma_j^2}. \quad \text{eqn 4}$$

We explored the implications of the two PE definitions across four statistical properties that are ecologically meaningful and have precedence in the PE literature (Tilman 1999; Cottingham, Brown & Lennon 2001; Loreau 2010; Thibaut & Connolly 2013): the correlation between subpopulations, the temporal mean-variance scaling relationship (z), the number of subpopulations and the evenness of subpopulation mean abundance. The expected effect of these properties on stability has been addressed in the literature cited above. Our focus, instead, is to understand the performance of the average-CV method compared with the mean-variance PE across these four ecological attributes. We show that differences between these PE metrics arise in real-world metapopulations, and for each taxon, we diagnose the ecological reasons why the differences arise.

EMPIRICAL EVALUATION OF PORTFOLIO EFFECTS

Data sources

To test the real-world strength of the average-CV and mean-variance PEs, we collected metapopulation time-series data for salmon, moths and reef fishes (Table S1; Figs S1 and S2). We obtained salmon returns from the primary literature, in particular Dorner, Peterman & Haeseker (2008), and government research documents (Table S1). We obtained moth abundance trends from the Rothamsted Insect Survey (Conrad *et al.* 2004). These data represent univoltine moths captured by light traps. We obtained reef visual census fish counts from the Australian Institute of Marine Science Long-term Monitoring Program (Sweatman *et al.* 2008). See Tables S2 and S3 for the subpopulation site locations of the moth and reef fish populations, respectively. Details on our data sources are available in the Supporting Information.

We defined data inclusion criteria to ensure adequate estimation of temporal mean-variance relationships. For salmon and moths, we excluded populations with less than four subpopulations or 10 years of data and where the largest subpopulation temporal mean was less than three times the size of the smallest temporal mean. To reduce the number of reef fish populations to an approximately comparable number, we used the metapopulations used by Mellin *et al.* (2010). Their main inclusion criteria were five subpopulations, 15 years of data and two orders of magnitude difference in subpopulation means.

Average-CV PE

We calculated the empirical average-CV PE as the ratio of the mean subpopulation CV to the observed metapopulation CV (Fig. 1c). We estimated confidence intervals by bootstrap; we sampled the subpopulations within each metapopulation 500 times, with replacement, and recalculated the PE. We then used the adjusted bootstrap percentile (BCa) 95% confidence intervals (Canty & Ripley 2012).

Mean-variance PE

To calculate the empirical mean-variance PE, we estimated z as the slope of a linear regression of the subpopulations' (i) interannual log (σ^2) and $\log(\mu)$,

$$\log(\sigma_i^2) = \beta_0 + z \cdot \log(\mu_i) + \varepsilon_i \quad \text{eqn 5}$$

where ε_i represents independent and identically distributed residual error with mean zero and an estimated variance. We used this model to predict the variance given the mean of the metapopulation abundance ($\hat{\sigma}^2$; Fig. 1d). The $\hat{\sigma}^2$ reflects the variance we would expect if the portfolio was composed of a homogeneous population. We then calculated the mean-variance PE as the ratio of observed σ^2 to predicted $\hat{\sigma}^2$. The mean-variance PE is therefore equivalent to the average subpopulation CV adjusted for the observed subpopulation CV mean-variance scaling relationship. We obtained confidence intervals on the mean-variance PE by recalculating the PE using the 95% confidence intervals on the predicted metapopulation variance.

Our empirical mean-variance PE calculation assumes the intersubpopulation mean-variance relationship can be used as a proxy for the intrasubpopulation relationship. To test this, we estimated the intrasubpopulation mean-variance relationship between the first and second halves of the subpopulation time series for the time series in which one half was at least two times greater. We compared these intrasubpopulation z values with the intersubpopulation z values used in our analysis.

ALTERNATIVE WAYS OF EXTRAPOLATING THE MEAN-VARIANCE PE

Quadratic extrapolations

In our main analysis, we estimated Taylor's power law z values by linear regression of the time-series' log-transformed mean and variance values. In some cases, a quadratic fit may be more appropriate (Routledge & Swartz 1991; Perry & Woiwod 1992). We fit a quadratic model,

$$\log(\sigma_i^2) = \beta_0 + \beta_1 \log(\mu_i) + \beta_2 \log(\mu_i)^2 + \varepsilon_i, \quad \beta_2 \geq 0. \quad \text{eqn 6}$$

Perry & Woiwod (1992) suggest limiting the lower value of β_2 to 0 because a negative β_2 would imply that at some value of μ , the σ^2 would decrease with increasing μ and eventually become negative. We used the *R* package *nls* (R Core Team 2012) with the *port* algorithm to fit the quadratic model and bound the lower value of β_2 to 0. If $\beta_2 = 0$, the quadratic model simplifies to the linear model.

Model averaging

Whereas the quadratic version of Taylor's power law can only provide a closer fit to the data than the linear version due to the added coefficient, it does so at the expense of greater model complexity and potentially poorer predictive capacity. We also examined predictions averaged across the linear and quadratic models with the predictions weighted by the Akaike weights of their respective models (Burnham & Anderson 2002). We fit an AICc model-averaged version of the linear and quadratic Taylor's power law fits using the *R* package *MuMIn* (Barton 2012).

ACCOUNTING FOR NONSTATIONARY TIME SERIES

Long-term trends in data can upwardly bias variability metrics such as the CV. We therefore conducted two alternative analyses in which we detrended the data before estimating the PEs. We used the residuals from (i) a fitted linear model and (ii) a fitted loess smoother (*loess* function; R Core Team 2012) with a smoothing span of 75% of the data. For both the subpopulations and metapopulations, we calculated the mean abundance before detrending. We estimated the variance of each subpopulation using the detrended time series. We estimated the variance of the metapopulations using the detrended version of the original metapopulation abundance time series. A more thorough analysis of

PEs for nonstationary time series might consider the distribution of means, variances and CVs within each subpopulation, but was beyond the scope of our analysis.

THE ECOFOLIO R PACKAGE

We provide an *R* package *ecofolio* to estimate the PEs described in this study (see the Supporting Information). In addition to the average-CV and mean-variance PEs, our package includes options to fit quadratic mean-variance scaling models, average across mean-variance model predictions and detrend nonstationary time series.

Results

THEORETICAL EVALUATION OF PORTFOLIO EFFECTS

By assuming $z = 2$, the average-CV method can misrepresent the effect of changes in subpopulation number, correlation and evenness on the PE (Fig. 2). The average-CV PE universally becomes more stabilizing (higher PE) as subpopulation number increases regardless of z , whereas when we account for the mean-variance relationship, the PE can become destabilizing with more subpopulations at small z values (Fig. 2a). The PE becomes less stabilizing as correlation increases regardless of the method, although accounting for the mean-variance relationship shifts the PE uniformly (assuming even subpopulation sizes) across all correlation values (Fig. 2b). The average-CV PE can erroneously become more stabilizing as subpopulations become uneven; the mean-variance PE indicates that the PE would become less stabilizing at high z values or remain relatively constant at low z values (Fig. 2c).

EMPIRICAL EVALUATION OF PORTFOLIO EFFECTS

The key assumption that ecological systems have the same mean-variance relationship as financial systems ($z = 2$) does not hold across taxa. Whereas z was not significantly different from two for 17/20 of the salmon metapopulations, there was infrequent overlap between the 95% CI and two for the moth metapopulations (3/20) and no overlap for reef fish

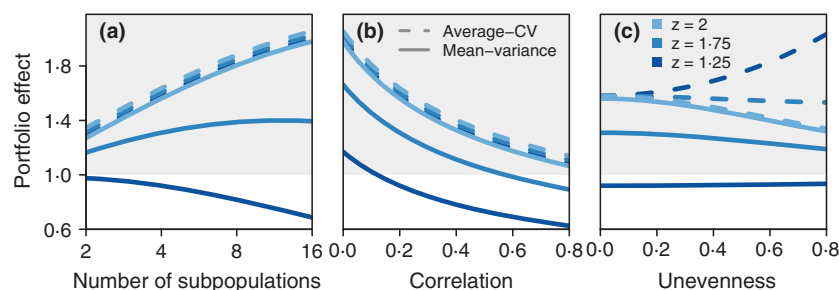


Fig. 2. The ecological factors driving the PE in theoretical systems. A PE of two, for example, would indicate a twofold increase in stability for the portfolio compared with what we would expect in a single homogeneous population of the same size. We show the mean-variance PE and average-CV PE for three z values across (a) number of subpopulations, (b) correlation between subpopulation time series and (c) unevenness of mean subpopulation abundance. We generated uneven mean subpopulation abundances by drawing four values at quantiles of 0.2, 0.4, 0.6 and 0.8 from a log-normal distribution with log mean μ ($\mu = 2$) and log standard deviation of the unevenness value (the x -axis) times μ . We fixed correlation at 0.2 and subpopulation number at four in all panels where these parameters were not varying. The grey shading indicates stabilizing PEs. Both PE definitions are equal across all scenarios at $z = 2$. In panels (a) and (b), the average-CV PE is the same regardless of z .

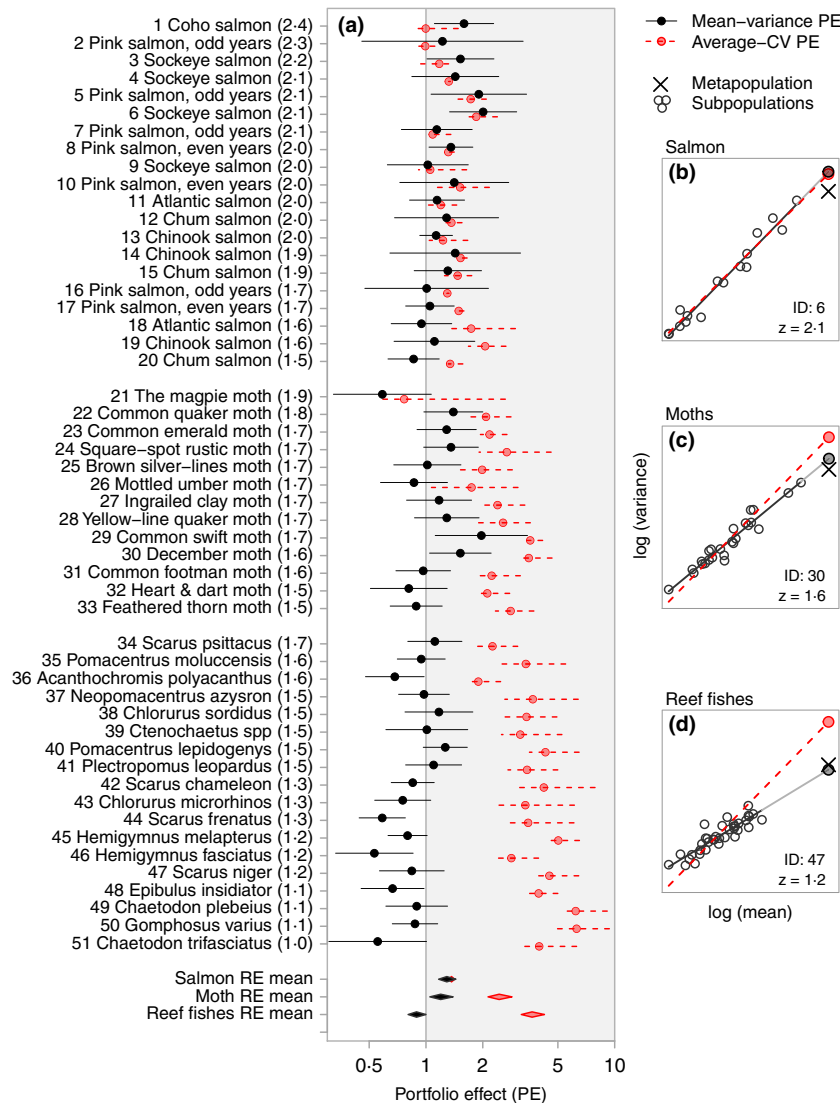


Fig. 3. PEs across 51 metapopulations. (a) Empirical PEs (circles) and 95% CIs (lines) for the mean-variance method and the average-CV PE method. We ordered metapopulations within taxonomic groups by Taylor's law z values (indicated in brackets beside each metapopulation name). Diamonds represent inverse-variance-weighted random effect (RE) meta-analytic means and 95% CIs. Numbers before population names represent population IDs (see Table S1). PEs > 1 (grey shading) represent stabilizing effects; note the log-distributed x -axis. (b, c, d) Examples of using Taylor's power law to calculate the mean-variance PE. The solid black regression line projects the subpopulation mean-variance relationship to the metapopulation mean abundance (shaded grey circle). The \times denotes the observed metapopulation mean and variance. The ratio of the observed to predicted variance represents the mean-variance PE. The red circle denotes the variance predicted by the average-CV PE, and the dashed red line the mean-variance relationship under the assumption that $z = 2$, as the average-CV PE assumes.

metapopulations (Figs S3 and S4). The intersubpopulation mean-variance relationship was a reasonably unbiased proxy for the intrasubpopulation mean-variance relationship. The slope of a regression of median intra- and intersubpopulation z was 1.04 (95% CI: 0.51–1.57) although there was a high degree of scatter ($R^2 = 0.25$; Fig. S5).

In our empirical meta-analysis, the PEs varied strongly between, but also within, taxonomic groups due to the mean-variance scaling (Fig. 3). The mean-variance PE ranged from 0.5 to 2.0 and the average-CV PE from 0.8 to 6.3. Hence, at best, the mean-variance PE suggests that the metapopulation portfolio is twice as stable as the homogeneous single asset. In comparison, the average-CV PE suggests that the metapopula-

tion portfolio could be up to six times more stable. The z values varied by taxonomic group, with the highest observed for salmon populations and the lowest for reef fishes. As z decreased (reading from top to bottom), the average-CV PE indicated increasingly stabilizing PEs compared with the mean-variance PE (Fig. 3a). For salmon, where the z values tended to be near two, the PE metrics were largely in agreement (Fig. 3a,b). By contrast, for reef fishes, where the z values were small (mean = 1.3, range = 1.0–1.7), the meta-analytic average-CV PE indicated a substantially more stabilizing PE (mean = 3.6, 3.2–4.3 95% CI) than the mean-variance PE (mean = 0.9, 0.8–1.0 95% CI) (Fig. 3a,d). The dashed red lines in Fig. 3b–d illustrate the mean-variance fit if z is assumed to

equal two as in the average-CV PE. Whereas the mean–variance relationship assumed by the average-CV appears reasonable for salmon (Fig. 3b), it deviates strongly from the observed relationship for some moth and reef fish metapopulations (Fig. 3c,d).

The mean–variance PE was highly sensitive to the estimation method (Fig. 4). In particular, 13/18 reef fish metapopulations

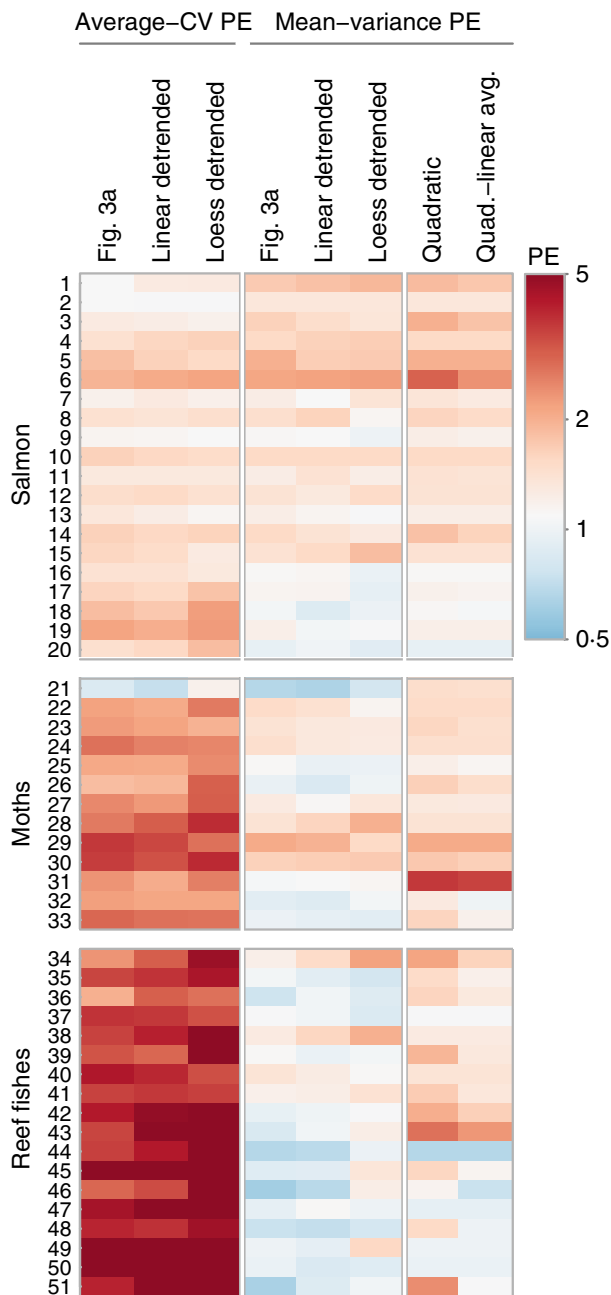


Fig. 4. The sensitivity of PE metrics across two detrending (linear and loess) methods (columns 2–3 and 5–6) and three mean–variance model fits (columns 4, 7–8). Columns 1 and 4 represent the same PEs as shown in Fig. 3, but with colour indicating the strength of stabilizing effect. Red indicates a stabilizing PE, blue indicates a destabilizing PE, and white indicates a neutral PE. The y-axis shows the same metapopulation IDs as Fig. 3.

switched from destabilizing to stabilizing PEs with quadratic (Fig. S6) or quadratic-linear averaged (Fig. S7) models. The AICc of the quadratic models was lower in 11/51 metapopulations and at least two units lower in 8/51, indicating increased support despite the added model complexity. Linear detrending generally created a similar mean–variance PE pattern to the original mean–variance PEs (Figs 4 and S8). Loess detrending increased the mean–variance PE in 34/51 cases and the average-CV PE in 34/51, lowering it in the others (Figs 4 and S9). None of the detrending options or alternative mean–variance extrapolations resulted in a similar pattern for both the mean–variance and average-CV PE.

DIAGNOSING THE ECOLOGICAL PROPERTIES OF EMPIRICAL PORTFOLIO EFFECTS

Plotting the empirical metapopulations in the theoretical PE parameter space revealed five key findings (Fig. 5). (i) By viewing the coloured shading of the panels from left to right, we can see that the average-CV PE responds inversely to z compared with the mean–variance PE, and this issue is prevalent for the parameter space observed in real ecological systems. (ii) The empirical PEs were strongly grouped by taxonomy (see also Fig. S10). (iii) We did not observe metapopulations that were both highly uneven and highly correlated (lower right panels of Fig. 5). (iv) The PE surface surrounding the observed metapopulations (the colour shading) was highly sensitive to changes in z for the mean–variance method when correlation was low (e.g. Fig. 5b), but the corresponding surface of the average-CV PE for the same metapopulations was insensitive to changes in z (e.g. Fig. 5k). (v) The average-CV method, however, considerably overestimated the PE compared with the mean–variance PE for uneven metapopulations with small values of z (Fig. 5c versus 5l).

Predicting the PE using these four properties alone (binned as shown in Fig. 5) explained 84% of the variability in the average-CV PE and 53% of the mean–variance PE (R^2 from a regression of log theoretical PE and log empirical PE; Fig. S11). The factors driving the PE co-varied; in particular, we observed high correlation of subpopulations associated with high variability (CV) and few subpopulations (Fig. S12b,c). High z values occurred when there were few moderately to highly correlated subpopulations (Fig. S12e,f).

Discussion

We conclude that the empirical average-CV PE is incompatible with Taylor's power law and, due to the parameter space in which most ecological populations exist, will tend to estimate a stronger benefit of population diversity than the mean–variance PE. In this discussion, we begin by considering the influence of mean–variance scaling on subpopulation and metapopulation stability and the possible mechanisms behind stabilizing portfolio effects. We then review limitations of these phenomenological metrics and discuss the potential of mechanistic models. We conclude

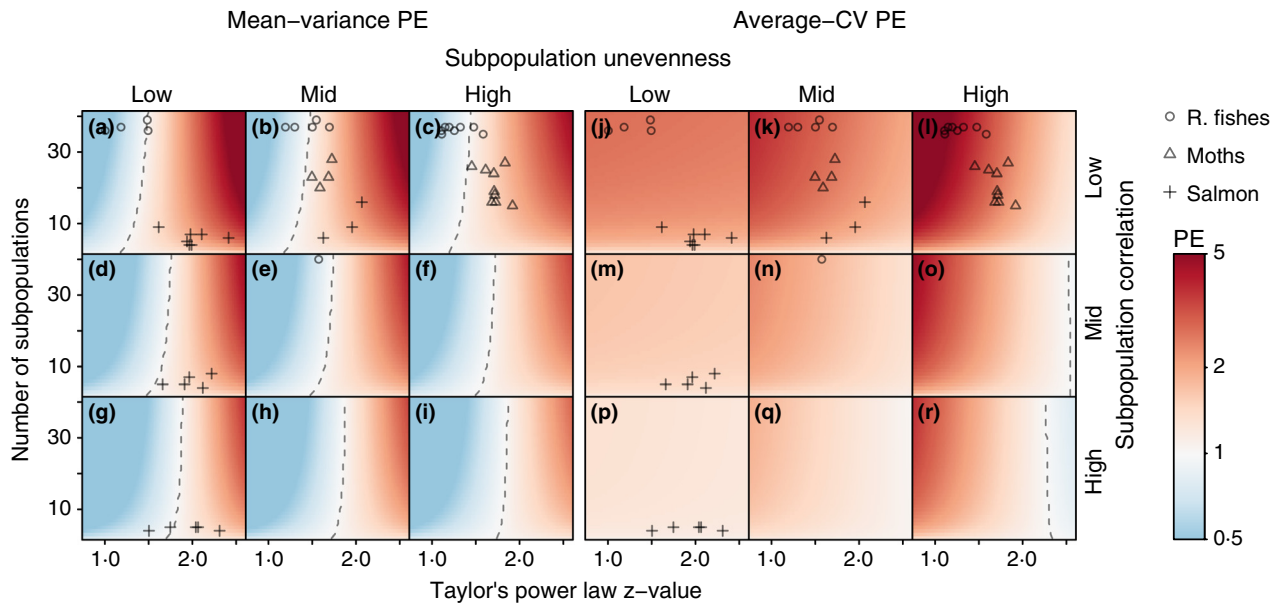


Fig. 5. Empirical ecological PEs (points) overlaid in theoretical PE parameter space (colour shading). The colour shading indicates the stabilizing effect of the theoretical mean-variance PEs (a–i) and average-CV PEs (j–r): red indicates a stabilizing effect, and blue indicates a destabilizing effect. The dashed lines indicate neutral PEs. Columns from left to right show systems with increasingly uneven subpopulation sizes, and rows from top to bottom show systems with increasingly strong mean correlation between subpopulation (see the Supporting Information).

by synthesizing our results into practical recommendations for quantifying ecological PEs.

THE INFLUENCE OF MEAN-VARIANCE SCALING

The primary difference between the mean-variance and average-CV PEs is how they depend on z . The mean-variance PE becomes more stabilizing with increasing z . The average-CV PE does the opposite (or remains constant) because the theory assumes $z = 2$ and the measures increasingly diverge as empirical populations deviate from this value. An increased z value (with all else being equal) means that all subpopulations are more variable (Mellin *et al.* 2010), but it also increases the benefit of a portfolio structure (Tilman, Lehman & Bristow 1998; Tilman 1999; Cottingham, Brown & Lennon 2001). This subtlety highlights a potential source of confusion: the PE is a relative measure comparing two sources of variability. It does not reflect the absolute stability of the portfolio or of the theoretical homogeneous portfolio. The stability of these components could decline while the PE increases. In some scenarios, we can think of the mean-variance PE as a consolation prize for a higher z value – the subpopulations become less stable and the metapopulation becomes less stable, but the stabilizing effect of diversity increases.

Why is z usually less than two? Explanations tend to fall into one of three categories. First, the most common explanation is demographic stochasticity. Demographic stochasticity has been implicated via simple stochastic population growth models (e.g. Anderson *et al.* 1982; Ballantyne 2005) and may be a particularly strong driver when density dependence generates chaotic dynamics (Perry 1994). In simplified theoretical systems, z will tend towards two under conditions that increase population synchrony (such as strong environmental forcing)

and tend towards one under conditions that decrease synchrony (such as strong demographic stochasticity) (Loreau 2010). Secondly, competitive species interactions can affect z values (Kilpatrick & Ives 2003). For example, if competition with other species impacts larger populations less than smaller populations, then z will be less than two. Thirdly, measurement error in abundance estimates (Perry 1981), and particularly rounding at low abundance (Taylor & Woivod 1982), can create artificially low z values. However, it remains unclear which of these three explanations, under what conditions, are responsible for observed z values across real ecological systems. Further, z can depend on the spatial and temporal scale of analysis (Lepš 1993) and most existing theories do not explain why z could be greater than two as we observed in 8/51 of our metapopulations and other experimental and observational studies have observed (e.g. Valone & Hoffman 2003).

In financial systems, analysts use the equivalent of the average-CV PE to calculate the benefit of diversifying a financial portfolio. For such systems, the approach makes sense because the standard deviation of investment value should scale directly with investment ($z = 2$). For example, if a financial investor triples investment in an asset, the investor can expect the standard deviation of the returns from that investment to triple. Similarly, the average-CV PE may be an appropriate method if applied to analogous questions about natural resource extraction. For example, we can ask how stable a fisher's catches would be if the fisher targeted a diverse portfolio of stocks instead of a single stock. Here, the analogy is more straightforward: the fisher (the investor) invests time, effort and resources into fishing a fish stock (the asset) or multiple fish stocks (the portfolio) and catches are returned. Given moderate levels of fishing and ignoring issues related to efficiency, any one fisher will not change the mean-variance

properties of the fish stock, and hence, the average-CV PE will be appropriate.

The PE metrics in this study compare the observed metapopulation variability with the theoretical variability of a single homogeneous population. This homogeneous population reference point is the most direct interpretation of the financial portfolio analogy – a financial investor can invest all her money in a single asset (our reference point) or in a diversified portfolio (our comparison). This homogeneous population reference point is loosely equivalent to the monoculture reference point often used in community PE analyses (e.g. Equation 7 in Thibaut & Connolly 2013). However, other reference points may be more relevant to ecology and easier to test experimentally. For example, researchers might instead choose as a reference point metapopulation variance under a harvesting regime that tends to synchronize subpopulations or metapopulation variance if habitat loss eliminated certain subpopulations.

MECHANISMS DRIVING METAPOPOPULATION PORTFOLIO EFFECTS

Two major mechanisms may generate stabilizing metapopulation PEs. First, diversity of phenotypes across subpopulations can cause subpopulations to react differently to the same environmental forces (response diversity; Elmqvist *et al.* 2003). Secondly, because metapopulations can exist over a large area, subpopulations may experience a greater diversity of environmental conditions than an individual population (i.e. Moran effect). In contrast, nonsystematic sources of variability such as demographic stochasticity should not generate stabilizing PEs (Loreau & de Mazancourt 2008). Our results suggest a research agenda that seeks to understand the relative contribution of these mechanisms across taxa and geography and the ecological management approaches that can promote stabilizing PEs.

We observed a number of PEs less than one. These PEs indicate the metapopulations would theoretically be less variable as one large homogeneous population than as the product of many small subpopulations. These have been referred to as inverse PEs (Thibaut & Connolly 2013) and documented in other observational studies (DeClerck, Barbour & Sawyer 2006). One explanation for these inverse PEs could be increased demographic stochasticity at low population densities resulting in an Allee effect (Allee 1931). Further, Minto, Myers & Blanchard (2008) demonstrated an increase in the variability of fish offspring survival at low population densities. The same-sized metapopulation split into fewer subpopulations might avoid these effects. A second explanation for these apparent inverse PEs could involve hidden diversity. Other elements of diversity, such as size and age structure, can be reduced at low population densities (e.g. Hutchings & Myers 1993). Therefore, inverse PEs could arise if the diversity we are measuring (subpopulation number) increases, but the unmeasured diversity within the subpopulations decreases. This hidden diversity may be more relevant to stability.

LIMITATIONS OF PHENOMENOLOGICAL PORTFOLIO EFFECTS

Beyond tending to overestimate the benefit of diversity if $z < 2$, there are potential consequences to applying the average-CV as an ecosystem index. First, the average-CV PE could fail to prioritize conservation of populations most in need. For example, if we consider two otherwise similar metapopulations, the average-CV PE will always be the same or stronger for metapopulations divided into more subpopulations. However, the mean–variance PE indicates that there is a threshold at which subdivision no longer benefits metapopulation stability (Figs 2a, 5a–i and S13). Secondly, used as an ecosystem index through time, the average-CV PE could fail to warn us of critical change or create the false impression of recovery. For example, if a reef fish metapopulation with a low z value and moderate evenness (circles in Fig. 5k) became more uneven in mean subpopulation size (see Fig. 5l), the average-CV PE would become up to about five times more stabilizing. The mean–variance PE informs us, however, that a change in evenness has little influence on the portfolio effect in this parameter space (Fig. 5b cf. c).

Despite its stronger theoretical foundations, we emphasize caution when interpreting empirical mean–variance PE values for reasons related to model, biological and measurement uncertainty. *Model uncertainty*: Is a log–log mean–variance linear model always best supported by the data? We often observed nonlinearities in the relationship, and studies have suggested numerous other mean–variance models (e.g. quadratic models, Routledge & Swartz (1991), or models with a break point at low population abundance, Perry & Woiwod (1992)). *Biological uncertainty*: Even if we knew the mean–variance model precisely, will the same dynamics persist when extrapolating outside the range of observed data? *Measurement uncertainty*: There may be biases in the estimated z values because of observation error (Perry 1981; Taylor & Woiwod 1982), and estimates of z can depend on how time series are aggregated (here, what we define as a subpopulation) (Fronczak & Fronczak 2010). Conclusions drawn from any phenomenological mean–variance relationships should be tempered with caveats such as these.

The PE metrics measured in this study are limited by the observational data to which they are typically applied. Recent mechanistic stability–diversity models that explicitly account for asynchrony of response to environmental conditions exist (e.g. Ives *et al.* 2003; Loreau & de Mazancourt 2008; Loreau 2010; Thibaut, Connolly & Sweatman 2012; de Mazancourt *et al.* 2013) but are still largely unexplored beyond theory. However, mechanistic stability–diversity models have at least two major problems. First, they must assume a functional form to a mechanism and their results may be sensitive to this decision. For example, does the environment affect productivity and does productivity impact population growth rate through a Ricker or logistic growth function? Secondly, the number of estimated parameters may exceed the power of most ecological data sets (Thibaut, Connolly & Sweatman

2012). Therefore, there remains a need for phenomenological metrics.

PRACTICAL RECOMMENDATIONS FOR QUANTIFYING ECOLOGICAL PORTFOLIO EFFECTS

Given the need for phenomenological PE metrics, which metric should you chose? The answer depends on the research question and the scope of the ecological system and data

(Fig. 6). *Research question:* The PE metrics discussed in this study ask specifically how much more stable the observed portfolio is than a theoretically homogeneous portfolio. These metrics do not address the benefit of increases in portfolio size (e.g. metapopulation size) itself. In financial portfolio terms, these PE metrics address the expected variability of a portfolio without addressing the expected rate of return. *Scope:* The average-CV or mean–variance PEs are relevant to any portfolio-like aggregation in which the stability of the overall portfolio

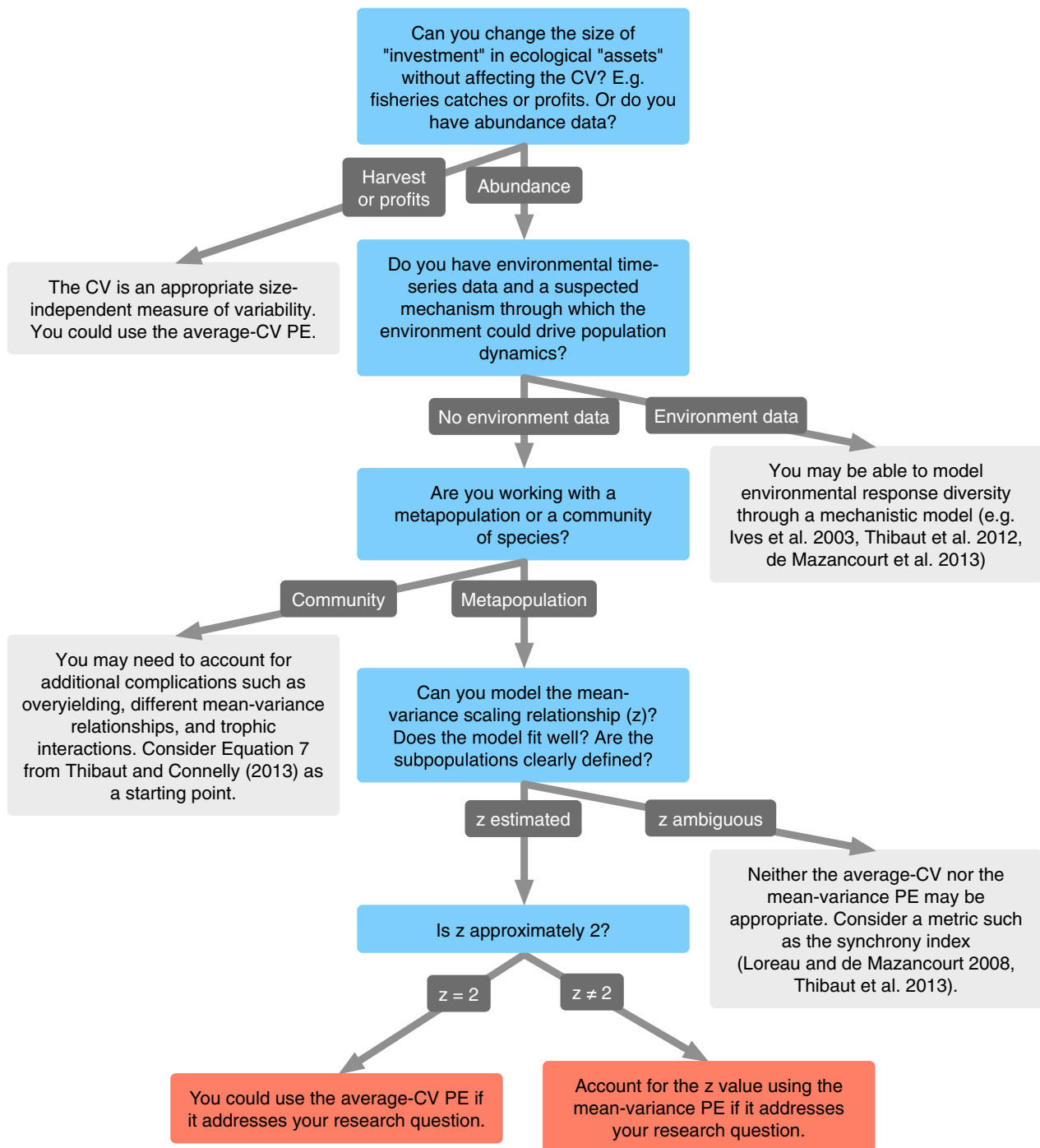


Fig. 6. Decision tree showing options for quantifying ecological portfolios. Blue boxes in the middle column show questions to ask of the study system and available data. The orange boxes at the bottom represent the methods demonstrated in this study. The light grey boxes along the sides show other options to quantify ecological portfolios given different research questions, study systems and available data.

'value' is of interest and the interaction between 'assets' is minimal. As demonstrated in this study, metapopulation abundance or biomass data can fall into this scope. Other examples include fishers harvesting a portfolio of fish stocks or a predator hunting a portfolio of species. These PE metrics are not necessarily appropriate for a community of species where complications such as multiple mean–variance relationships and trophic interactions may require different phenomenological models (Thibaut & Connolly 2013).

Assuming the research question, ecological system and data are appropriate for the methods shown in this study, we recommend the following when choosing between the average-CV and mean–variance PEs (Fig. 6). First, consider whether the mean–variance scaling relationship can be estimated. Does a power law fit the data well? Are the subpopulations clearly defined? Is there minimal observation error?

- If the answer to any of these questions is no, then mean–variance scaling (z) is not well defined and you may need to ask a different question with a different metric. For example, you could quantify the synchrony of the populations using the synchrony index (Loreau & de Mazancourt 2008; Thibaut & Connolly 2013).
- If $z \approx 2$, then use the average-CV PE, which amounts to the same metric as the mean–variance PE at $z \approx 2$ and is simpler to estimate, conceptualize and communicate.
- If z is well defined but different than two, then account for the mean–variance scaling relationship using the mean–variance PE.

The financial metaphor is an engaging and accessible way to convey the importance of biological diversity to the public and provides a framework to guide stability–diversity research (Figge 2004; Koellner & Schmitz 2006). However, our results indicate that the metaphor should be used with caution. By ignoring a fundamental ecological property – the mean–variance scaling relationship – the commonly applied average-CV PE method will tend to overestimate the benefit of subpopulation diversity in real-world systems and may respond in nonintuitive ways to ecosystem change. Conversely, mechanistic stability–diversity models offer the gold standard of PE metrics but are challenging to apply in practice, and so, we still need phenomenological PE metrics. Our results highlight the importance of ground-truthing these metrics and acknowledging their limitations. Based on these results, our study outlines practical recommendations for estimating ecological PEs for metapopulations and similarly structured ecological systems. Irrespective of the challenges of finding a suitable metric to describe the ecological PE, given the tendency for stabilizing PEs and the challenges of restoring lost population diversity, it is clear that we need to find ways of understanding, prioritizing and conserving the processes that give rise to ecological stability.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

ecofolio R package. Tools to quantify metapopulation portfolio effects.

Table S1. Metapopulations used in the empirical PE analyses. ID column numbers correspond to ID numbers in the figures.

Table S2. Moth sites used from the Rothamsted Insect Survey database.

Table S3. Reef locations used from the AIMS LTMP Great Barrier Reef database.

Figure S1. Subpopulation time series.

Figure S2. Map of included metapopulations.

Figure S3. Calculation of the mean-variance PE using Taylor's power law.

Figure S4. Taylor's power law z values across metapopulations.

Figure S5. Intra- vs. inter-subpopulation mean-variance scaling relationship (Taylor's power law z -value).

Figure S6. PEs with the mean-variance PEs estimated from a quadratic model.

Figure S7. PEs with the mean-variance PEs estimated from a linear-quadratic averaged model.

Figure S8. PEs from linear detrended time series.

Figure S9. PEs from loess detrended time series.

Figure S10. Empirical ecological PEs (points) overlaid in theoretical PE parameter space (colour shading) with empirical PE values shown beside the points.

Figure S11. Predicted vs. observed mean-variance (a) and average-CV PEs (b). Predicted PEs correspond to the colour underlying the metapopulations displayed in Fig. 5; observed PEs to the values calculated directly from the empirical data and shown in Fig. 3.

Figure S12. Relationship between the drivers of the PE in empirical systems for moths (red), reef fishes (purple), and salmon (blue).

Figure S13. The PE used as an index of ecosystem change.