

Ecological prophets: quantifying metapopulation portfolio effects

Sean C. Anderson^{1*}, Andrew B. Cooper² and Nicholas K. Dulvy¹

¹Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada; and ²School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada

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

*Correspondence author. E-mail: sean_anderson@sfu.ca

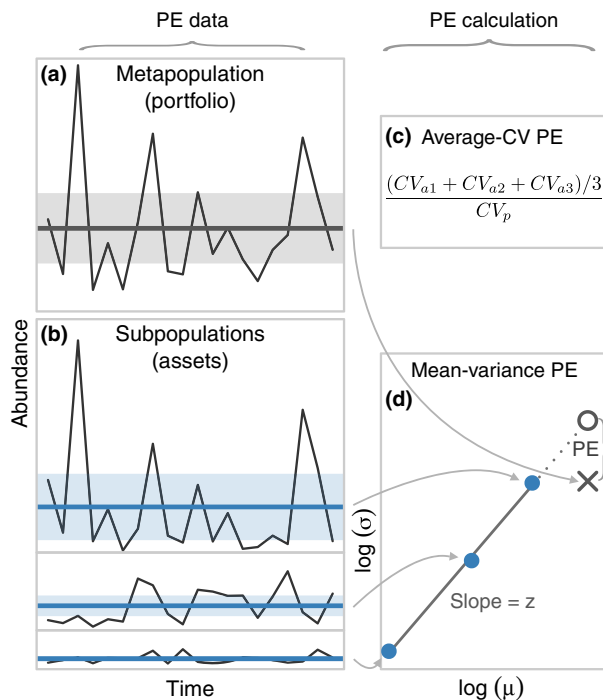


Fig. 1. Estimating the two PEs from empirical data. (a, b) Example metapopulation (portfolio) and subpopulation (asset) abundance time series. Horizontal lines represent the time-series' means, and the shaded regions represent variability. (c) We calculated the average-CV PE by dividing the average-CV 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

$$CV_p = \frac{\sqrt{\mu_i^2 + \mu_{i+1}^2 + \dots + \mu_n^2}}{\mu_i + \mu_{i+1} + \dots + \mu_n}. \quad \text{eqn 1}$$

The average-CV PE defines CV_a as

$$CA_a = \frac{\frac{\sqrt{\mu_i^2}}{\mu_i} + \frac{\sqrt{\mu_{i+1}^2}}{\mu_{i+1}} + \dots + \frac{\sqrt{\mu_n^2}}{\mu_n}}{n}, \quad \text{eqn 2}$$

whereas the mean–variance PE defines CV_a as

$$CV_a = \frac{\sqrt{(\mu_i + \mu_{i+1} + \dots + \mu_n)^z}}{\mu_i + \mu_{i+1} + \dots + \mu_n}. \quad \text{eqn 3}$$

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

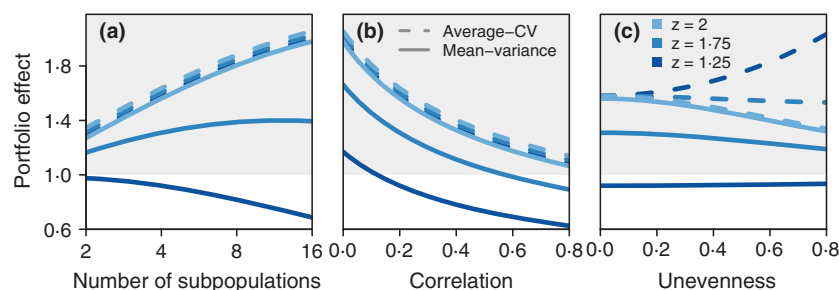


Fig. 2. The ecological factors driving the PE in theoretical systems. A PE of two, for example, would indicate a twofold increase in stability for the portfolio compared with what we would expect in a single homogeneous population of the same size. We show the mean–variance PE and average-CV PE for three 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 .

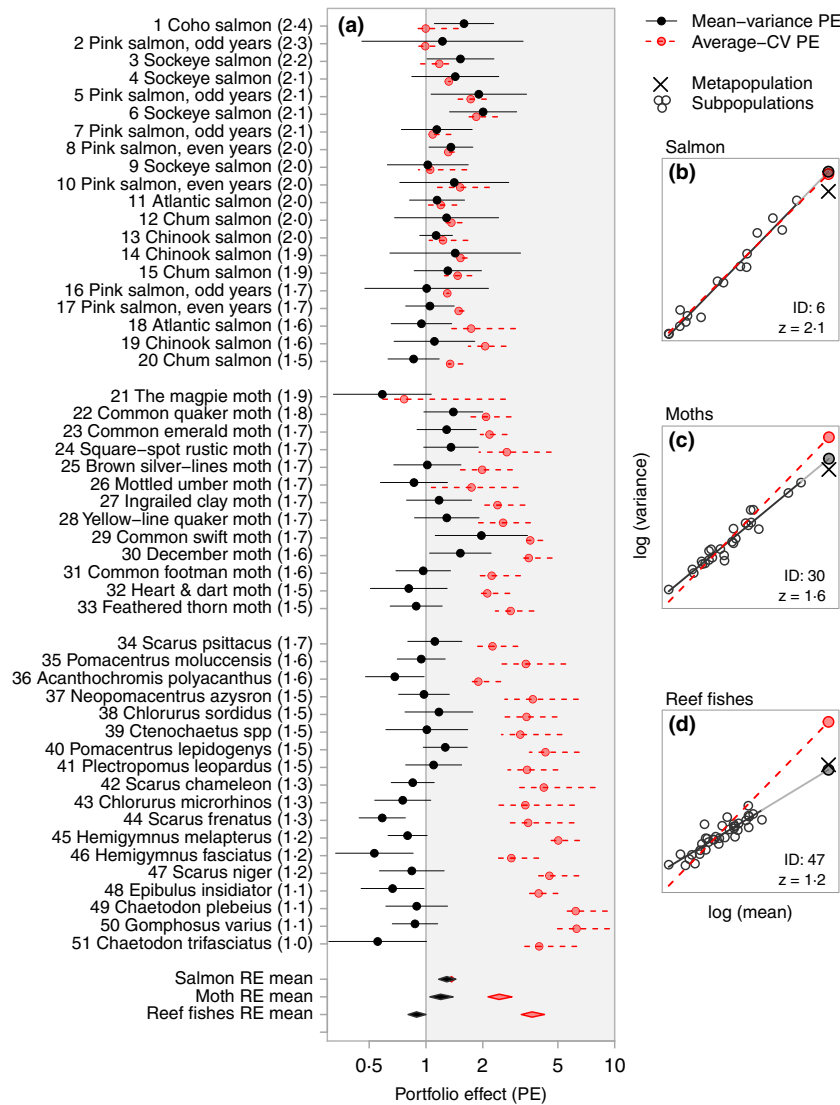


Fig. 3. PEs across 51 metapopulations. (a) Empirical PEs (circles) and 95% CIs (lines) for the mean-variance method and the average-CV PE method. We ordered metapopulations within taxonomic groups by Taylor's law z values (indicated in brackets beside each metapopulation name). Diamonds represent inverse-variance-weighted 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 metapopu-

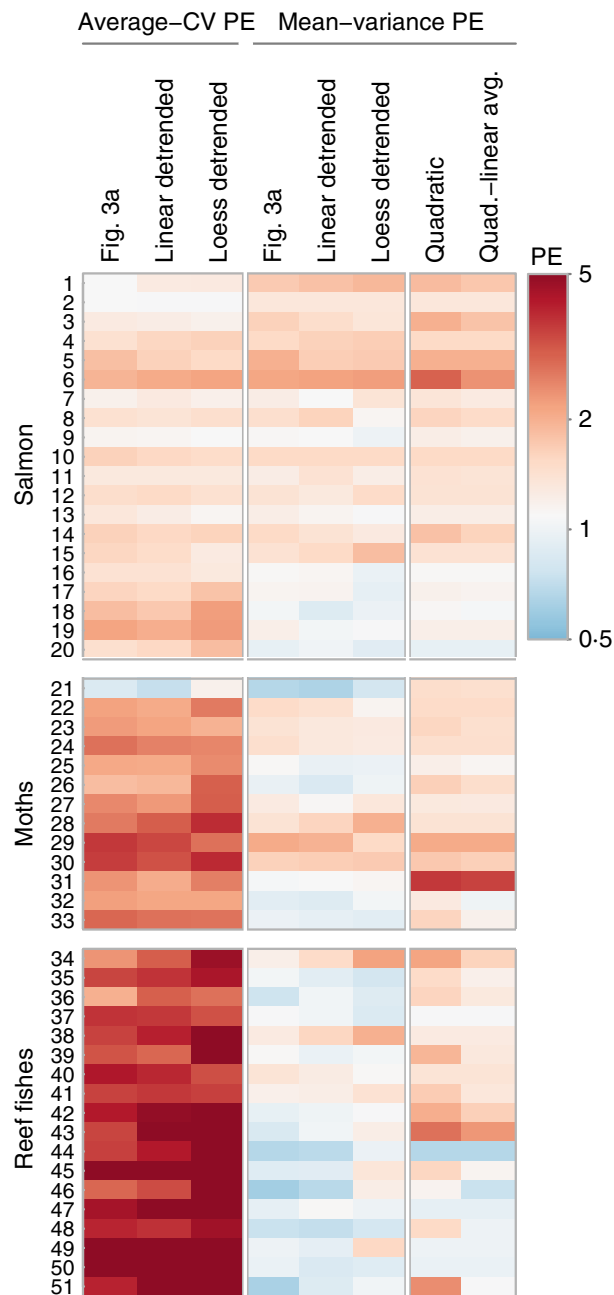


Fig. 4. The sensitivity of PE metrics across two detrending (linear and loess) methods (columns 2–3 and 5–6) and three mean–variance model fits (columns 4, 7–8). Columns 1 and 4 represent the same PEs as shown in Fig. 3, but with colour indicating the strength of stabilizing effect. Red indicates a stabilizing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

lations 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

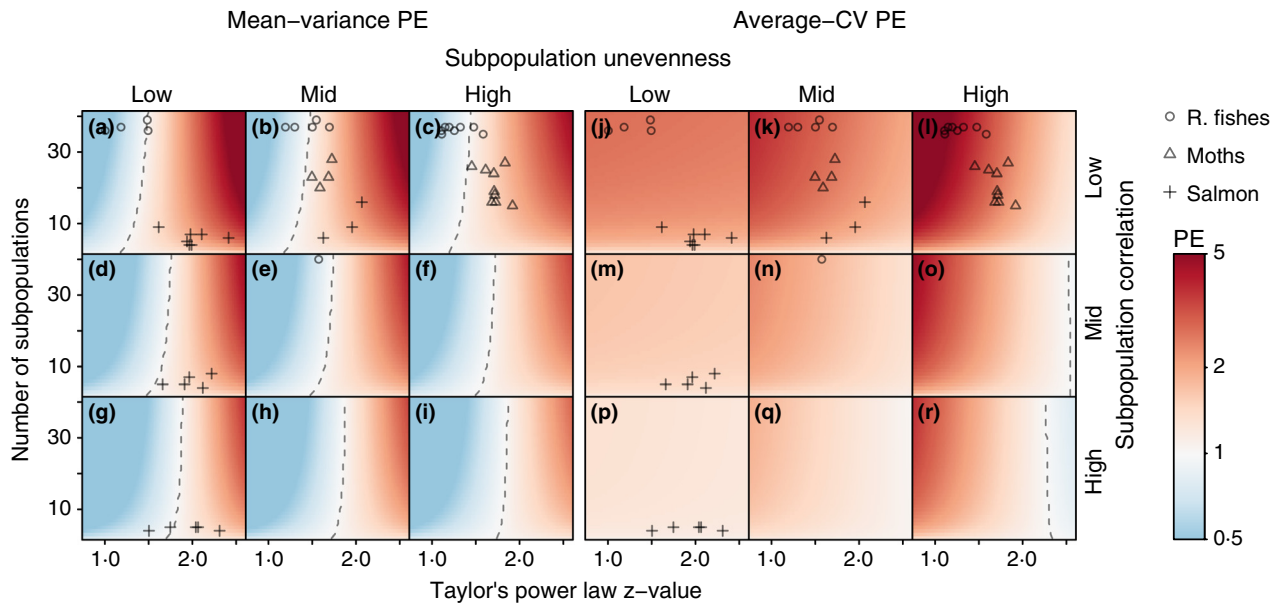


Fig. 5. Empirical ecological PEs (points) overlaid in theoretical PE parameter space (colour shading). The colour shading indicates the stabilizing effect of the theoretical mean-variance PEs (a–i) and average-CV PEs (j–r): red indicates a stabilizing effect, and blue indicates a destabilizing effect. 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 & Woivod (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 & Woivod 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

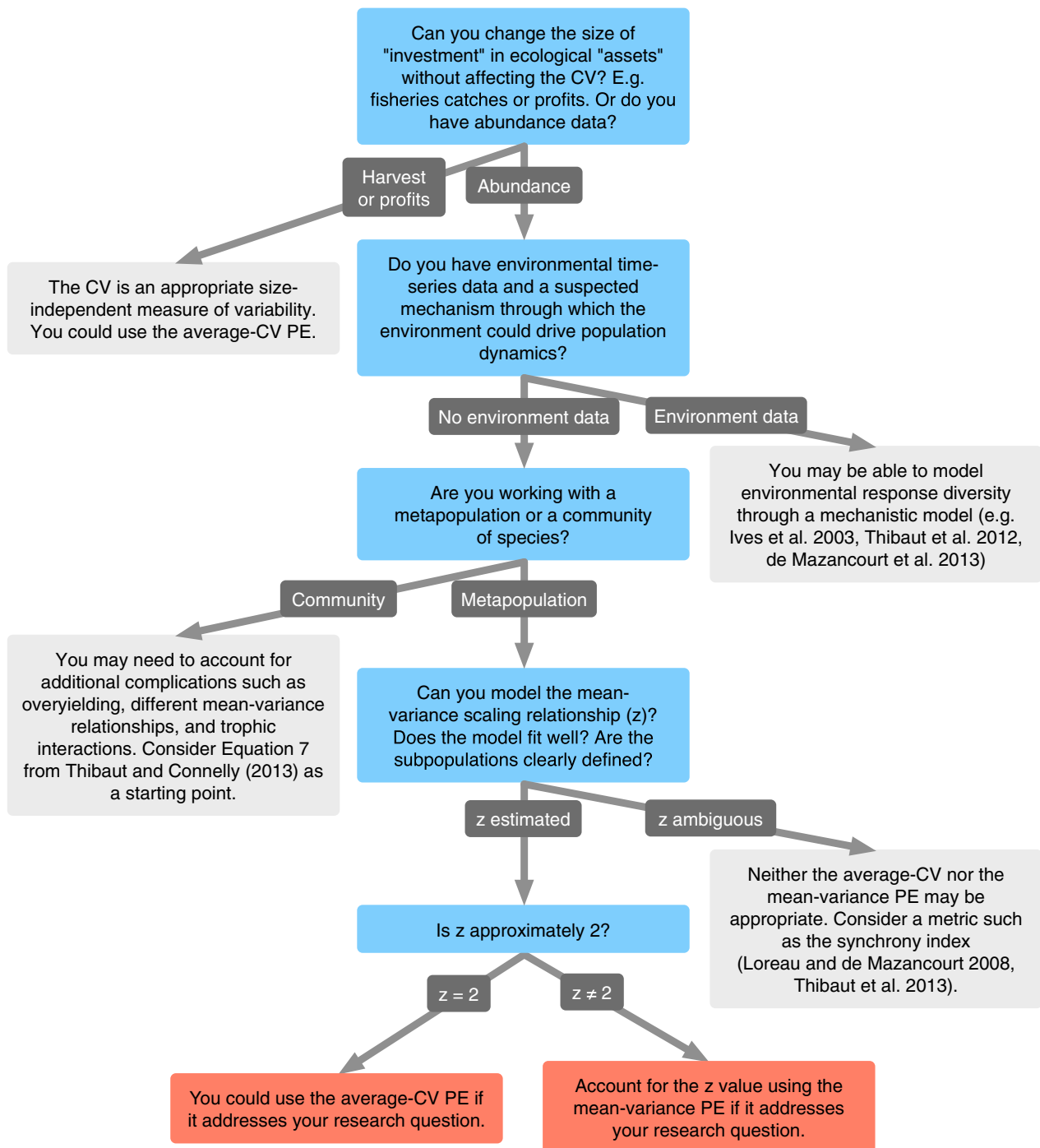


Fig. 6. Decision tree showing options for quantifying ecological portfolios. Blue boxes in the middle column show questions to ask of the study system and available data. The orange boxes at the bottom represent the methods demonstrated in this study. The light grey boxes along the sides show other options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

Acknowledgements

We thank R.M. Peterman, R. Harrington and P. Verrier (Rothamsted Insect Survey, a UK BBSRC-supported National Capability) and H. Sweatman (Australian Institute of Marine Science Long-term Monitoring Program) for providing data. We thank J.W. Moore, R. Harrington and H. Sweatman, and four

anonymous reviewers for comments that greatly improved this manuscript. We are grateful to M.P. Beakes, T.A. Branch, M. Loreau, C. Monnahan and S.M. O'Regan for helpful discussions. Funding was provided by NSERC, the Canada Research Chairs Program, Simon Fraser University and Fulbright Canada.

References

- Allee, W.C. (1931) *Animal Aggregations: A Study in General Sociology*. The University of Chicago Press for The American Society of Naturalists, Chicago.
- Anderson, R.M., Gordon, D.M., Crawley, M.J. & Hassell, M.P. (1982) Variability in the abundance of animal and plant species. *Nature*, **296**, 245–248.
- Ballantyne, F. IV (2005) The upper limit for the exponent of Taylor's power law is a consequence of deterministic population growth. *Evolutionary Ecology Research*, **7**, 1213–1220.
- Bartoń, K. (2012) MuMin: multi-model inference. R package version 1.7.7.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.
- Canty, A. & Ripley, B. (2012) Boot: Bootstrap R (S-Plus) functions. R package version 1.3-7.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.
- Carlson, S.M. & Satterthwaite, W.H. (2011) Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1579–1589.
- Conrad, K.F., Woiod, I.P., Parsons, M., Fox, R. & Warren, M.S. (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119–136.
- Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, **4**, 72–85.
- DeClerck, F.A.J., Barbour, M.G. & Sawyer, J.O. (2006) Species richness and stand stability in conifer forests of the Sierra Nevada. *Ecology*, **87**, 2787–2799.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998) The statistical inevitability of stability–diversity relationships in community ecology. *American Naturalist*, **151**, 264–276.
- Dorner, B., Peterman, R.M. & Haeseker, S.L. (2008) Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed by using a Kalman filter. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1842–1866.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488–494.
- Figge, F. (2004) Bio-folio: applying portfolio theory to biodiversity. *Biodiversity and Conservation*, **13**, 827–849.
- Fronczak, A. & Fronczak, P. (2010) Origins of Taylor's power law for fluctuation scaling in complex systems. *Physical Review E*, **81**, 066112.
- Hilborn, R.W., Quinn, T., Schindler, D. & Rogers, D. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 6564–6568.
- Hutchings, J.A. & Myers, R.A. (1993) The effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2468–2474.
- IMCC (2011) Portfolio effect in fisheries. Symposium 25. 2nd International Marine Conservation Congress. Victoria, BC, Canada.
- Ives, A.R. & Carpenter, S.R. (2007) Stability and diversity of ecosystems. *Science*, **317**, 58–62.
- Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003) Estimating community stability and ecological interactions from time-series data. *Ecological Monographs*, **73**, 301–330.
- Karp, D.S., Ziv, G., Zook, J., Ehrlich, P.R. & Daily, G.C. (2011) Resilience and stability in bird guilds across tropical countryside. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 21134–21139.
- Kilpatrick, A.M. & Ives, A.R. (2003) Species interactions can explain Taylor's power law for ecological time series. *Nature*, **422**, 65–68.
- Koellner, T. & Schmitz, O.J. (2006) Biodiversity, ecosystem function, and investment risk. *BioScience*, **56**, 977–985.
- Lepš, J. (1993) Taylor's power law and the measurement of variation in the size of populations in space and time. *Oikos*, **68**, 349–356.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.
- Loreau, M. (2010) *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*. Princeton University Press, Princeton, New Jersey.

- Loreau, M. & de Mazancourt, C. (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist*, **172**, E48–E66.
- Markowitz, H.M. (1959) *Portfolio Selection: Efficient Diversification of Investments*. Wiley & Sons, New York.
- de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J.B. *et al.* (2013) Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters*, **16**, 617–625.
- McArdle, B.H., Gaston, K.J. & Lawton, J.H. (1990) Variation in the size of animal populations: patterns, problems and artefacts. *Journal of Animal Ecology*, **59**, 439–454.
- Mellin, C., Huchery, C., Caley, M.J., Meekan, M.G. & Bradshaw, C.J.A. (2010) Reef size and isolation determine the temporal stability of coral reef fish populations. *Ecology*, **91**, 3138–3145.
- Minto, C., Myers, R.A. & Blanchard, W. (2008) Survival variability and population density in fish populations. *Nature*, **452**, 344–347.
- Perry, J.N. (1981) Taylor's power law for dependence of variance on mean in animal populations. *Journal of the Royal Statistical Society. Series C (Applied Statistics)*, **30**, 254–263.
- Perry, J.N. (1994) Chaotic dynamics can generate Taylor's power law. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **257**, 221–226.
- Perry, J.N. & Woivod, I.P. (1992) Fitting Taylor's power law. *Oikos*, **65**, 538–542.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org> [accessed 10 August 2012].
- Routledge, R.D. & Swartz, T.B. (1991) Taylor's power law re-examined. *Oikos*, **60**, 107–112.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A. & Webster, M.S. (2010) Population diversity and the portfolio effect in an exploited species. *Nature*, **465**, 609–612.
- Secor, D.H., Kerr, L.A. & Cadrin, S.X. (2009) Connectivity effects on productivity, stability, and persistence in a herring metapopulation model. *ICES Journal of Marine Science*, **66**, 1726–1732.
- Sweatman, H., Cheal, A., Coleman, G., Emslie, M., Johns, K., Jonker, M., Miller, I. & Osborne, K. (2008) Long-term monitoring of the Great Barrier Reef. Technical Report Status Report Number 8, Australian Institute of Marine Science, Townsville, Australia.
- Taylor, L.R. & Woivod, I.P. (1980) Temporal stability as a density-dependent species characteristic. *Journal of Animal Ecology*, **49**, 209–224.
- Taylor, L.R. & Woivod, I.P. (1982) Comparative synoptic dynamics. I. Relationships between inter- and intra-specific spatial and temporal variance/mean population parameters. *Journal of Animal Ecology*, **51**, 879–906.
- Thibaut, L.M. & Connolly, S.R. (2013) Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecology Letters*, **16**, 140–150.
- Thibaut, L., Connolly, S.R. & Sweatman, H.P.A. (2012) Diversity and stability of herbivorous fishes on coral reefs. *Ecology*, **93**, 891–901.
- Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455–1474.
- Tilman, D., Lehman, C.L. & Bristow, C.E. (1998) Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist*, **151**, 277–282.
- Valone, T.J. & Hoffman, C.D. (2003) Population stability is higher in more diverse annual plant communities. *Ecology Letters*, **6**, 90–95.

Received 19 May 2013; accepted 2 July 2013

Handling Editor: David Hodgson

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.

Supporting Information for Ecological prophets: Quantifying metapopulation portfolio effects Methods in Ecology and Evolution

Sean C. Anderson^{1*} Andrew B. Cooper² Nicholas K. Dulvy¹

¹Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby BC, V5A 1S6, Canada

²School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada

*Corresponding author: sean_anderson@sfu.ca

R package to estimate metapopulation portfolio effects

In an R console, the `ecofolio` package can be installed either from the included source package (`.tar.gz` file) or via the web (instructions below). First, install dependencies if needed:

```
install.packages(c("plyr", "reshape", "MuMIn", "robustbase"))
```

Then, to install the included package:

```
install.packages("mee312093-sup-0001-Sourcepackage.tar.gz", type = "source")
```

or to install the current version from the web:

```
install.packages("devtools") # if needed  
devtools::install_github("ecofolio", username = "seananderson")
```

Current code and install details are available at
<https://github.com/seananderson/ecofolio>

You can load the package, read the vignette, and access the help pages with:

```
library(ecofolio)
vignette("ecofolio")
help(package = "ecofolio")
```

Data sources for the empirical portfolio effect analysis

We sought to include as many metapopulation time series from as diverse taxonomic groups as possible. However, due to availability, the included data primarily represent metapopulations in North America (salmon), the United Kingdom (moths), and Australia (reef fishes) (Fig. S2). We show a summary of the data included in our analysis of empirical ecological systems in Table S1 and the time series in Fig. S1.

Salmon

We obtained salmon data from a variety of sources, in particular Dorner *et al.* (2008). Most of the salmon populations are from the northwest coast of North America, but also: Kola Peninsula, Russia (Jensen *et al.* 1999), southern New England (Kocik & Sheehan 2006), and Central Valley, California (Carlson & Satterthwaite 2011) (Fig. S2). All data represent annual estimated returns — fisheries catch plus escape-ment to the spawning grounds. We divided pink salmon annual estimated returns into odd- and even-year time series due to their strongly distinct runs that do not interbreed (Quinn 2005). To maintain consistency with previous PE analyses involving sockeye salmon (Schindler *et al.* 2010) and analyses of time series of these data (Dorner *et al.* 2008), and due to the less distinct separate runs (Quinn 2005), we did not divide the sockeye salmon into separate runs.

Subsets of these salmon data have been used in numerous analyses relating diversity with stability. A particular feature of the salmon literature is a focus on the role of “biocomplexity” — a diversity of life-histories and local adaptations to the environment — in producing stability (Hilborn *et al.* 2003) and recent papers have focussed on measuring the portfolio effects we investigate in this paper (Schindler *et al.* 2010; Carlson & Satterthwaite 2011). In studying the mechanisms behind sub-population asynchrony, and hence portfolio effects, studies of Pacific salmon have generally focussed on drivers that fall into two categories: (1) landscape filtering of

the environment so that different subpopulations experience different environmental forces (e.g. local topology affecting stream flow) (e.g. Schindler *et al.* 2008), and (2) biologically-based response diversity to the environment (e.g. genetically-based variation in thermal tolerances) (e.g. Eliason *et al.* 2011). These patterns of asynchrony can play out not just at the decadal scale but also over centuries (Rogers *et al.* 2013).

Moths

We obtained moth abundance time series from the Rothamsted Insect Survey (RIS). L. R. Taylor started the trap network that forms the RIS in the early 1960s; the RIS is now one of the longest-running and largest-scale insect surveys in the world (Conrad *et al.* 2004). Details on the survey are available in Conrad *et al.* (2004) and Taylor (1986). The RIS captures moths by light traps (Williams 1948) placed 1–2 m above ground; these traps catch small but reliable samples of moth populations (Williams 1948; Taylor & French 1974; Conrad *et al.* 2004). Although different species may show different responses to the traps (Miurhead-Thomson 1991; Woiwod & Hanski 1992), we compare across sites within the same species so this should not affect our results.

Our moth data spanned from 1999–2010 for 13 species (Table S1) and 28 sites (Table S2). We included only moths with single broods per year (univoltine moths) and single annual flight episodes since we were aggregating the data annually to maintain consistency with data from other taxonomic groups that were available. We removed site-species combinations where there were eight or more years with zero moths caught in traps to avoid sites where a given species was exceptionally rare and not likely to be consistently censused. This removed 97 subpopulations leaving 280. Further culling of populations according to the criteria in the Methods section left us with 268 subpopulations. All the species included are common within Great Britain, although some have undergone declines in abundance since the RIS began (Conrad *et al.* 2004).

Earlier versions of these moth data featured heavily in the work of Taylor and colleagues on the property now known as Taylor’s power law (Taylor & Taylor 1977; Taylor & Woiwod 1980; Perry 1981). This early work focussed on behavioural properties that might regulate the stability and variance of moth populations (Taylor & Woiwod 1980). Work has continued with these datasets and studies have shown a

number of mechanisms generating stability. For example, authors have shown spatial asynchrony (Gaston 1988), polyphagy (eating different kinds of food) (Redfearn & Pimm 1988), and density dependence to act as stabilizing forces (Hanski & Woiwod 1993).

Reef fishes

We obtained reef visual census fish counts within the Greater Barrier Reef (GBR) from the Australian Institute of Marine Science’s (AIMS) Long-term Monitoring Program (LTMP) (Sweatman *et al.* 2008). The AIMS survey data used here are from fixed transects at selected sites across 46 reefs from 1994–2010 (Table S3). Details of the sampling design are available from Halford & Thompson (1994). Briefly, AIMS surveys reef fish annually within six sectors of the GBR. AIMS identifies inner-, mid-, and outer-shelf positions and three reefs within each shelf position. Within each reef, AIMS chooses three sites of the same habitat and establishes five permanent 50m transects at 6–9m depth 10m apart and parallel to the reef crest. Divers count damselfishes (Pomacentrids) on 1m-wide transects and all other families on 5m-wide transects. AIMS only censuses fish one year or older since recruitment can be highly spatially and temporally variable. AIMS conducts annual standardization exercises to avoid temporal bias in counts within and across divers (Halford & Thompson 1994).

A number of recent studies have used these reef-fish data to investigate stability-diversity relationships, often focusing on functional diversity or reef size and isolation. For example, Thibaut *et al.* (2012) found strong asynchrony of response to the environment between three functional groups of herbivorous reef fishes, which lead to greater stability. Another benefit to this functional diversity may be increased disease resistance (Raymundo *et al.* 2009), presumably enhancing stability. Independent of functional roles, Mellin *et al.* (2010) found that small, isolated reefs have higher population variability and therefore higher probability of local extinction.

Diagnosing the ecological properties of empirical portfolio effects

We overlaid the empirical PEs in their respective theoretical parameter space to investigate the ecological properties of real-world metapopulations (subpopulation correlation, mean-variance scaling, subpopulation number richness, and evenness). Specifically, we matched the empirical linear-regression z values and the number of subpopulations with their theoretical counterparts.

To present our results graphically in Fig. 5, we categorized the mean correlation of the empirical subpopulations ($\bar{\rho}$) into bins of $0 \leq \bar{\rho} < 0.25$, $0.25 \leq \bar{\rho} < 0.5$, and $0.50 \leq \bar{\rho} < 0.75$ and matched these with the theoretical PE estimated at the midpoints of these bins (i.e. 0.125, 0.375, and 0.625). We matched the disparity in subpopulation size by: (1) calculating the CV of the log of the subpopulation time series' means, $CV(\log \mu)$; (2) categorizing the empirical metapopulations into bins of $0 \leq CV(\log \mu) < 0.3$, $0.3 \leq CV(\log \mu) < 0.6$, and $0.6 \leq CV(\log \mu) < 0.9$; (3) estimating the theoretical PE using evenly-spaced values from a log-normal distribution with a mean of two and standard deviation of the midpoints of these bins (i.e. 0.15, 0.45, and 0.75). Here and in Fig. 2, we derived these evenly-spaced values as follows. We drew subpopulation (i) quantiles q_i from the evenly-spaced sequence: a_1, a_2, \dots, a_n , where $a_1 = 1/(n+1)$ and $a_n = 1 - (1/(n+1))$. We then calculated the subpopulation means at each q_i from a log-normal distribution with log-mean of two and a log-standard deviation of the “unevenness value” times the log-mean.

References

- Carlson, S.M. & Satterthwaite, W.H. (2011) Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1579–1589.
- Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R. & Warren, M.S. (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119–136.

- Dorner, B., Peterman, R.M. & Haeseker, S.L. (2008) Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed by using a Kalman filter. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1842–1866.
- Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G. & Farrell, A.P. (2011) Differences in thermal tolerance among sockeye salmon populations. *Science*, **332**, 109–112.
- Fair, L.F., Willette, T.M., Erickson, J.W., Yanusz, R.J. & McKinley, T.R. (2011) Review of salmon escapement goals in Upper Cook Inlet, Alaska, 2011. Fishery Manuscript Series 10–06, Alaska Department of Fish and Game.
- Gaston, K.J. (1988) Patterns in the local and regional dynamics of moth populations. *Oikos*, **53**, 49–57.
- Halford, A.R. & Thompson, A.A. (1994) Long-term monitoring of the great barrier reef. Technical Report Standard Operational Procedure Number 3, Australian Institute of Marine Science, Townsville, Australia.
- Hanski, I. & Woiwod, I.P. (1993) Mean-related stochasticity and population variability. *Oikos*, **67**, 29–39.
- Hilborn, R.W., Quinn, T., Schindler, D. & Rogers, D. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 6564–6568.
- Jensen, A.J., Zubchenko, A.V., Heggberget, T.G., Hvidsten, N.A., Johnsen, B.O., Kuzmin, O., Loenko, A.A., Lund, R.A., Martynov, V.G., Næ sje, T.F., Sharov, A.F. & Økland, F. (1999) Cessation of the Norwegian drift net fishery: changes observed in Norwegian and Russian populations of Atlantic salmon. *ICES Journal of Marine Science*, **56**, 84–95.
- Kocik, J.F. & Sheehan, T.F. (2006) Status of fishery resources off the northeastern US: Atlantic salmon. Technical report, NEFSC Resource Evaluation and Assessment Division.

- Krkošek, M., Connors, B.M., Morton, A., Lewis, M.A., Dill, L.M. & Hilborn, R. (2011) Effects of parasites from salmon farms on productivity of wild salmon. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 14700–14704.
- Mellin, C., Huchery, C., Caley, M.J., Meekan, M.G. & Bradshaw, C.J.A. (2010) Reef size and isolation determine the temporal stability of coral reef fish populations. *Ecology*, **91**, 3138–3145.
- Miurhead-Thomson, R.C. (1991) *Trap Responses of Flying Insects*. Academic Press, London.
- Perry, J.N. (1981) Taylor’s power law for dependence of variance on mean in animal populations. *Journal of the Royal Statistical Society Series B (Statistical Methodology)*, **30**, 254–263.
- Quinn, T.P. (2005) *The Behaviour and Ecology of Pacific Salmon and Trout*. American Fisheries Society, Bethesda, Maryland.
- Raymundo, L.J., Halford, A.R., Maypa, A.P. & Kerr, A.M. (2009) Functionally diverse reef-fish communities ameliorate coral disease. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 17067–17070.
- Redfearn, A. & Pimm, S.L. (1988) Population variability and polyphagy in herbivorous insect communities. *Ecological Monographs*, **58**, 39–55.
- Rogers, L.A., Schindler, D.E., Lisi, P.J., Holtgrieve, G.W., Leavitt, P.R., Bunting, L., Finney, B.P., Selbie, D.T., Chen, G., Gregory-Eaves, I., Lisac, M.J. & Walsh, P.B. (2013) Centennial-scale fluctuations and regional complexity characterize pacific salmon population dynamics over the past five centuries. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 1750–1755.
- Schindler, D.E., Augerot, X., Fleishman, E., Mantua, N.J., Riddell, B., Ruckelshaus, M., Seeb, J. & Webster, M. (2008) Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries*, **33**, 502–506.

- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A. & Webster, M.S. (2010) Population diversity and the portfolio effect in an exploited species. *Nature*, **465**, 609–612.
- StreamNet (2011) Adult return-estimates of spawning population for chinook salmon. URL <http://www.streamnet.org> [accessed on 25 November 2011].
- Sweatman, H., Cheal, A., Coleman, G., Emslie, M., Johns, K., Jonker, M., Miller, I. & Osborne, K. (2008) Long-term monitoring of the Great Barrier Reef. Technical Report Status Report Number 8, Australian Institute of Marine Science, Townsville, Australia.
- Taylor, L.R. (1986) Synoptic dynamics, migration and the rothamsted insect survey: Presidential Address to the British Ecological Society, December 1984. *Journal of Animal Ecology*, **55**, 1–38.
- Taylor, L.R. & French, R.A. (1974) Effects of light-trap design and illumination on samples of moths in an English woodland. *Bulletin of Entomological Research*, **63**, 583–594.
- Taylor, L.R. & Taylor, R.A.J. (1977) Aggregation, migration and population mechanics. *Nature*, **265**, 415–421.
- Taylor, L.R. & Woiwod, I.P. (1980) Temporal stability as a density-dependent species characteristic. *Journal of Animal Ecology*, **49**, 209–224.
- Thibaut, L., Connolly, S.R. & Sweatman, H.P.A. (2012) Diversity and stability of herbivorous fishes on coral reefs. *Ecology*, **93**, 891–901.
- West, F.W. & Fair, L.F. (2006) Abundance, age, sex, and size statistics for Pacific salmon in Bristol Bay, 2003. Fishery Data Series 06–47, Alaska Department of Fish and Game.
- Williams, C.B. (1948) The Rothamsted light trap. *Proceedings of the Royal Entomological Society of London Series A, General Entomology*, **23**, 80–85.
- Woiwod, I.P. & Hanski, I. (1992) Patterns of density dependence in moths and aphids. *Journal of Animal Ecology*, **61**, 619–629.

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

ID	Species	Common	Location	Subpopulations	Years	Reference
1	<i>Oncorhynchus kisutch</i>	Coho salmon	Broughton archipelago, BC, Canada	6	16	(Krkošek <i>et al.</i> 2011)
2	<i>Oncorhynchus gorbuscha</i>	Pink salmon, odd years	Puget Sound, WA, United States	4	19	(Dorner <i>et al.</i> 2008)
3	<i>Oncorhynchus nerka</i>	Sockeye salmon	Bristol Bay, AK, United States	8	43	(West & Fair 2006)
4	<i>Oncorhynchus nerka</i>	Sockeye salmon	Kodiak, AK, United States	7	24	(Dorner <i>et al.</i> 2008)
5	<i>Oncorhynchus gorbuscha</i>	Pink salmon, odd years	Broughton archipelago, BC, Canada	7	19	(Krkošek <i>et al.</i> 2011)
6	<i>Oncorhynchus nerka</i>	Sockeye salmon	Fraser River, BC, Canada	16	44	(Dorner <i>et al.</i> 2008)
7	<i>Oncorhynchus gorbuscha</i>	Pink salmon, odd years	Kodiak, AK, United States	5	8	(Dorner <i>et al.</i> 2008)
8	<i>Oncorhynchus gorbuscha</i>	Pink salmon, even years	Chignik, AK, United States	5	16	(Dorner <i>et al.</i> 2008)
9	<i>Oncorhynchus nerka</i>	Sockeye salmon	Upper Cook Inlet, AK, United States	4	29	(Fair <i>et al.</i> 2011)
10	<i>Oncorhynchus gorbuscha</i>	Pink salmon, even years	Broughton archipelago, BC, Canada	7	19	(Krkošek <i>et al.</i> 2011)
11	<i>Salmo salar</i>	Atlantic salmon	Kola Peninsula, Russia	4	15	(Jensen <i>et al.</i> 1999)
12	<i>Oncorhynchus keta</i>	Chum salmon	Puget Sound, WA, United States	7	26	(Dorner <i>et al.</i> 2008)
13	<i>Oncorhynchus tshawytscha</i>	Chinook salmon	Columbia Estuary, OR/WA, United States	9	23	(StreamNet 2011)
14	<i>Oncorhynchus tshawytscha</i>	Chinook salmon	Elochoman River, WA, United States	5	27	(StreamNet 2011)
15	<i>Oncorhynchus keta</i>	Chum salmon	Arctic, Yukon, Kuskokwim, US and Canada	5	18	(Dorner <i>et al.</i> 2008)
16	<i>Oncorhynchus gorbuscha</i>	Pink salmon, odd years	Chignik, AK, United States	5	15	(Dorner <i>et al.</i> 2008)
17	<i>Oncorhynchus gorbuscha</i>	Pink salmon, even years	Kodiak, AK, United States	5	9	(Dorner <i>et al.</i> 2008)
18	<i>Salmo salar</i>	Atlantic salmon	Southern New England, United States	6	39	(Kocik & Sheehan 2006)
19	<i>Oncorhynchus tshawytscha</i>	Chinook salmon	Central Valley, California	9	54	(Carlson & Satterthwaite 2011)
20	<i>Oncorhynchus keta</i>	Chum salmon	Alaska Peninsula, AK, United States	4	32	(Dorner <i>et al.</i> 2008)
21	<i>Aburax grossulariata</i>	The magpie moth	UK	15	12	(Conrad <i>et al.</i> 2004)
22	<i>Orthosia cerasi</i>	Common quaker moth	UK	27	12	(Conrad <i>et al.</i> 2004)
23	<i>Hemithea aestivaria</i>	Common emerald moth	UK	16	12	(Conrad <i>et al.</i> 2004)
24	<i>Xestia xanthographa</i>	Square-spot rustic moth	UK	28	12	(Conrad <i>et al.</i> 2004)
25	<i>Pterophora chlorosata</i>	Brown silver-lines moth	UK	18	12	(Conrad <i>et al.</i> 2004)
26	<i>Erannia defoliaria</i>	Mottled umber moth	UK	19	12	(Conrad <i>et al.</i> 2004)
27	<i>Diarsia mendica</i>	Ingrailed clay moth	UK	24	12	(Conrad <i>et al.</i> 2004)
28	<i>Agrochola (Leptologia) macilenta</i>	Yellow-line quaker moth	UK	23	12	(Conrad <i>et al.</i> 2004)
29	<i>Pharmacis lupulina</i>	Common swift moth	UK	16	12	(Conrad <i>et al.</i> 2004)
30	<i>Poecilocampa populi</i>	December moth	UK	25	12	(Conrad <i>et al.</i> 2004)
31	<i>Eilema lurideola</i>	Common footman moth	UK	20	12	(Conrad <i>et al.</i> 2004)
32	<i>Agrotis exclamationis</i>	Heart and dart moth	UK	23	12	(Conrad <i>et al.</i> 2004)
33	<i>Colotois pennaria</i>	Feathered thorn moth	UK	26	12	(Conrad <i>et al.</i> 2004)
34	<i>Scarus psittacus</i>	Scarus psittacus	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
35	<i>Pomacentrus moluccensis</i>	Pomacentrus moluccensis	GBR, Australia	35	14	(Sweatman <i>et al.</i> 2008)
36	<i>Acanthochromis polyacanthus</i>	Acanthochromis polyacanthus	GBR, Australia	40	14	(Sweatman <i>et al.</i> 2008)
37	<i>Neopomacentrus azysron</i>	Neopomacentrus azysron	GBR, Australia	39	14	(Sweatman <i>et al.</i> 2008)
38	<i>Chlorurus sordidus</i>	Chlorurus sordidus	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
39	<i>Ctenochaetus spp</i>	Ctenochaetus spp	GBR, Australia	36	14	(Sweatman <i>et al.</i> 2008)
40	<i>Pomacentrus lepidogenys</i>	Pomacentrus lepidogenys	GBR, Australia	39	14	(Sweatman <i>et al.</i> 2008)
41	<i>Plectropomus leopardus</i>	Plectropomus leopardus	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
42	<i>Scarus chameleon</i>	Scarus chameleon	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
43	<i>Chlorurus microrhinos</i>	Chlorurus microrhinos	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
44	<i>Scarus frenatus</i>	Scarus frenatus	GBR, Australia	36	14	(Sweatman <i>et al.</i> 2008)
45	<i>Hemigymmus melapterus</i>	Hemigymmus melapterus	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
46	<i>Hemigymmus fasciatus</i>	Hemigymmus fasciatus	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
47	<i>Scarus niger</i>	Scarus niger	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
48	<i>Epibulus insidiator</i>	Epibulus insidiator	GBR, Australia	37	14	(Sweatman <i>et al.</i> 2008)
49	<i>Chaetodon plebeius</i>	Chaetodon plebeius	GBR, Australia	35	14	(Sweatman <i>et al.</i> 2008)
50	<i>Gomphosus varius</i>	Gomphosus varius	GBR, Australia	36	14	(Sweatman <i>et al.</i> 2008)
51	<i>Chaetodon trifasciatus</i>	Chaetodon trifasciatus	GBR, Australia	36	14	(Sweatman <i>et al.</i> 2008)

Table S2. Moth sites used from the Rothamsted Insect Survey database. Sites are ordered from north to south. County refers to the British County. “Number of spp.” refers to the number of moth species remaining that matched our inclusion criteria.

Site name	County	Northing	Easting	Altitude (m)	Number of spp.
Starcross	South Devon	821	2972	9	12
Denny Lodge	South Hampshire	1056	4333	30	10
Bentley Wood	South Wiltshire	1324	4253	130	12
Winkworth	Surrey	1412	4991	130	12
Alice Holt	North Hampshire	1428	4803	122	12
Perry Wood	East Kent	1565	6040	80	13
Wisley II	Surrey	1579	5065	40	10
Westonbirt	West Gloucestershire	1898	3847	46	13
Geescroft I	Hertfordshire	2128	5132	130	12
Allotments	Hertfordshire	2134	5134	130	7
Barnfield	Hertfordshire	2135	5132	130	10
Hereford	Herefordshire	2476	3564	91	10
Cockayne Hatley	Bedfordshire	2494	5253	76	11
Llysdinam	Breconshire	2586	3009	197	11
Tregaron	Cardiganshire	2618	2687	198	10
Broom’s Barn	West Suffolk	2656	5752	73	9
Compton Park	Staffordshire	2988	3889	105	9
Preston Montford II	Shropshire	3143	3433	61	13
Malham Tarn	Mid-west Yorkshire	4672	3894	396	8
Shildon	County Durham	5262	4239	150	9
Forest-in-Teesdale	North-west Yorkshire	5306	3853	381	5
Castle Eden Dene I	County Durham	5394	4428	91	10
Auchincruive II	Ayrshire	6233	2377	52	10
Brodick	Clyde Islands	6380	2014	50	8
Rowardennan	Stirlingshire	6960	2378	15	8
Kindrogan	East Perthshire	7630	3055	259	7
Beinn Eighe I	West Ross & Cromarty	8629	2024	25	9
Cromarty	East Ross & Cromarty	8672	2785	30	10

Table S3. Reef locations used from the AIMS LTMP Great Barrier Reef database. Reefs are ordered from north to south. “Number of spp.” refers to the number of fish species remaining that matched our inclusion criteria.

Reef	Latitude (deg south)	Longitude (deg east)	Number of spp.
Carter Reef	14.52	145.58	17
Yonge Reef	14.57	145.62	16
No Name Reef	14.62	145.64	18
Macgillivray Reef	14.64	145.49	18
Lizard Island	14.69	145.46	18
North Direction Reef	14.74	145.51	18
Martin Reef(14123)	14.75	145.37	18
Linnet Reef	14.79	145.35	18
Agincourt Reefs (no 1)	16.04	145.87	17
St Crispin Reef	16.07	145.84	18
Opal (2)	16.20	145.90	18
Low Islands Reef	16.38	145.57	17
Hastings Reef	16.49	146.02	17
Michaelmas Reef	16.55	146.05	18
Green Island Reef	16.77	145.97	18
Fitzroy Island Reef	16.92	145.99	18
Myrmidon Reef	18.25	147.38	18
Dip Reef	18.39	147.45	17
Rib Reef	18.47	146.88	18
John Brewer Reef	18.62	147.08	18
Chicken Reef	18.66	147.72	18
Davies Reef	18.80	147.66	18
Pandora Reef	18.81	146.43	3
Slate Reef	19.66	149.91	18
Hyde Reef	19.73	150.09	18
19131s	19.77	149.38	18
Rebe Reef	19.80	150.16	18
19138s	19.80	149.43	18
Hayman Island Reef	20.05	148.89	4
Langford-bird Reef	20.07	148.87	4
Border Island Reef (no 1)	20.18	149.03	13
East Cay Reef	21.46	152.56	18
Turner Reef	21.70	152.56	18
21529s	21.87	152.18	18
Gannett Cay Reef	21.98	152.47	18
Horseshoe	22.02	152.62	18
Snake (22088)	22.02	152.19	18
Broomfield Reef	23.24	151.94	18
One Tree Reef	23.48	152.09	18
Lady Musgrave Reef	23.88	152.42	18

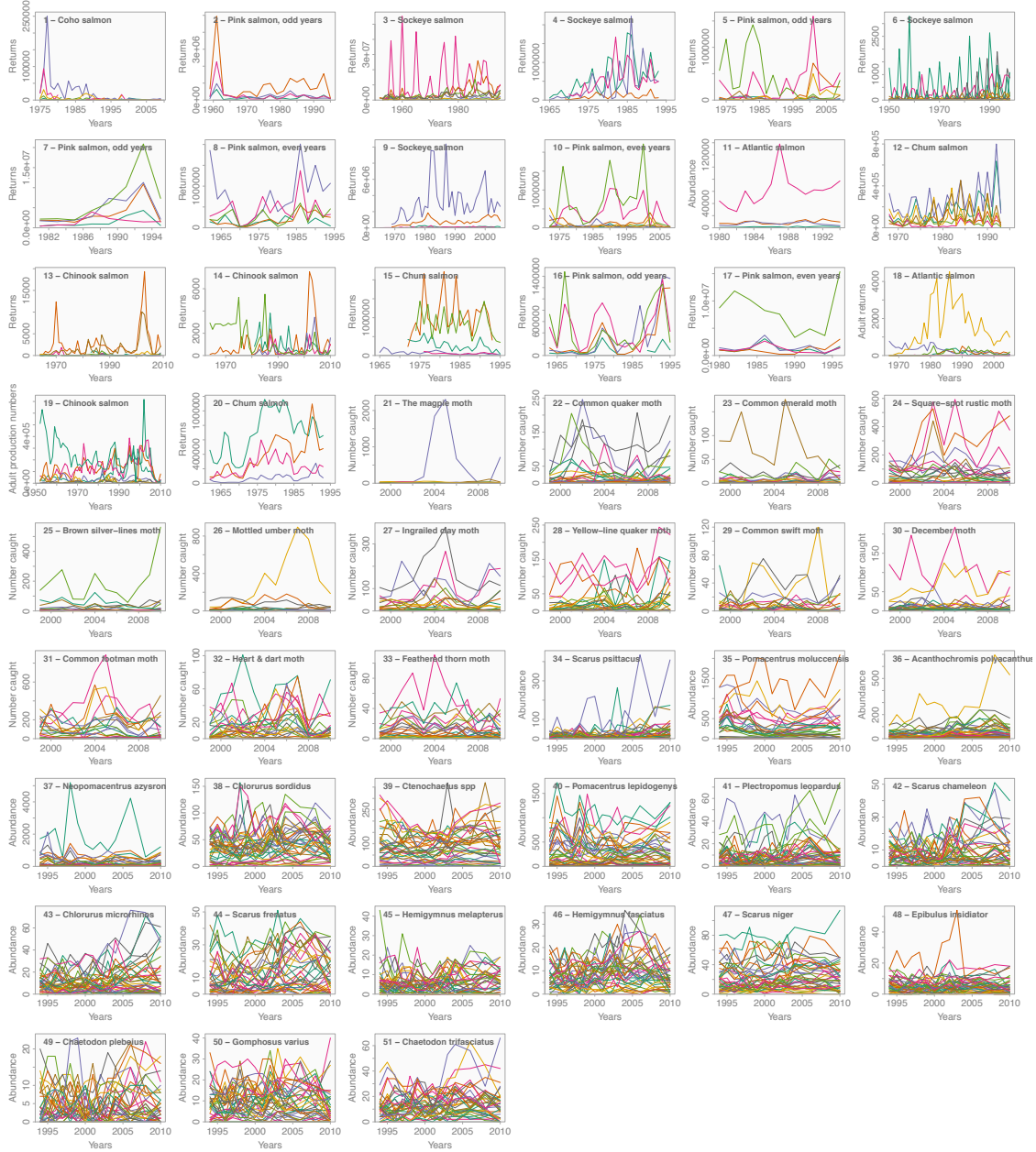


Fig. S1. Subpopulation time series. Each panel contains one metapopulation. Colours were randomly assigned to distinguish subpopulations. Numbers in top-left corners refer to metapopulation IDs (see Table S1).

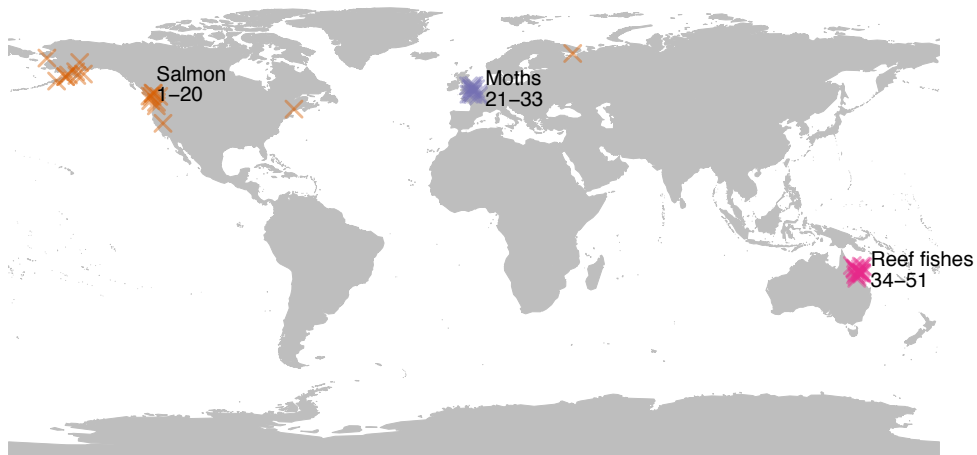


Fig. S2. Map of included metapopulations. We represented salmon metapopulations with orange symbols, moths with purple, and reef fishes with pink. Numbers refer to metapopulation IDs (Table S1). Points are jittered slightly for visual clarity.

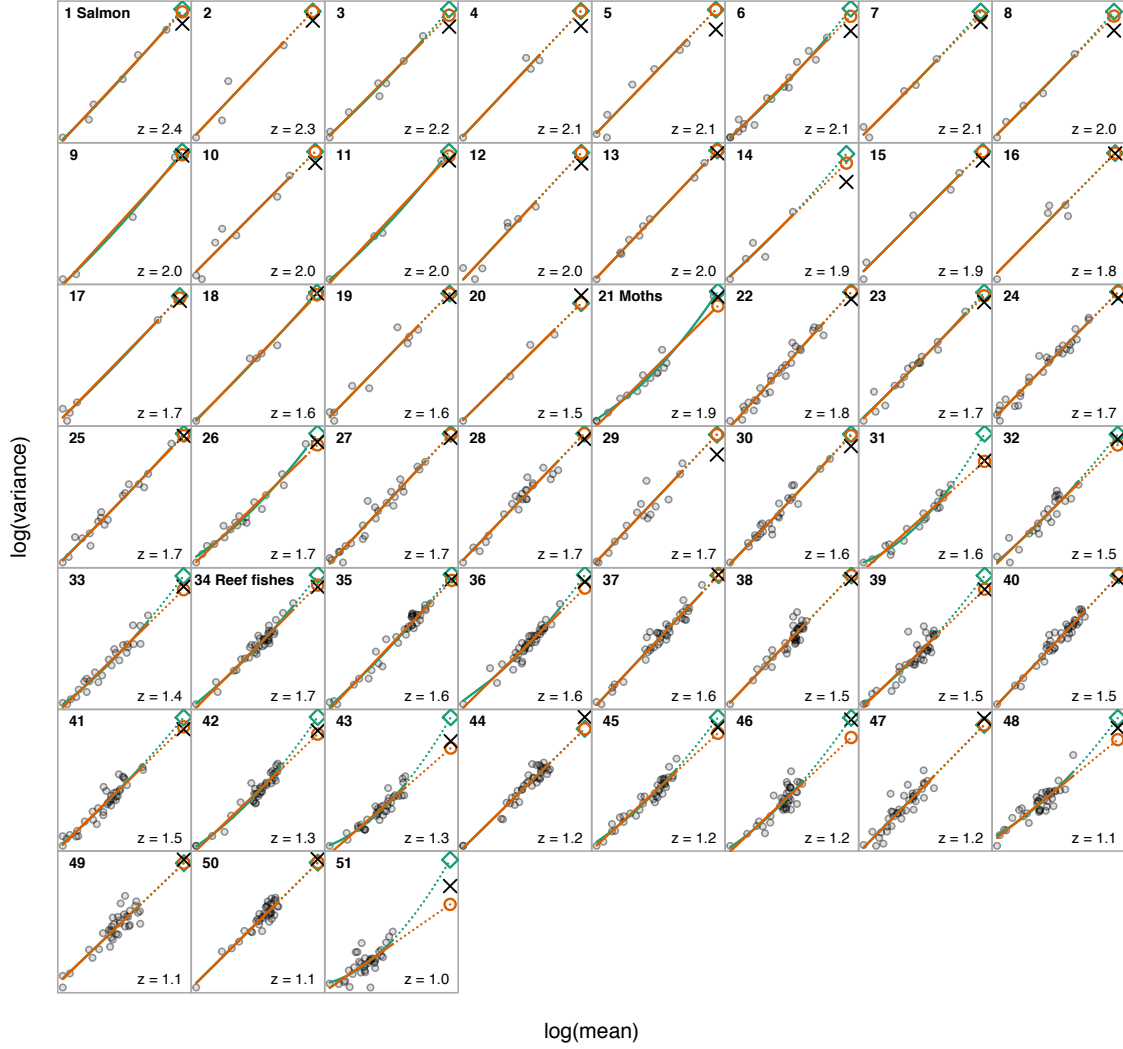


Fig. S3. Calculation of the mean-variance PE using Taylor's power law. Each dark-grey circle represents the $\log(\mu)$ and $\log(\sigma^2)$ of an individual subpopulation timeseries. The orange lines represent fitted linear regressions. The green lines represent fitted quadratic regressions. Black x symbols represent the observed meta-population or portfolio mean and variance. Dashed lines indicate the extrapolation of the model fit to the observed meta-population or portfolio mean and variance. Open-orange circles represent the predicted variance under the linear-fit assumption. Open-green diamonds represent the predicted variance under the quadratic-fit assumption. Metapopulations in which the predicted variance is greater than the observed variance represent variance-reducing PEs. We ordered the panels by decreasing Taylor's power law z -value (slope of the linear regression) within taxonomic groupings. Numbers in upper left of panels refer to metapopulation IDs (Supplementary Table 1)

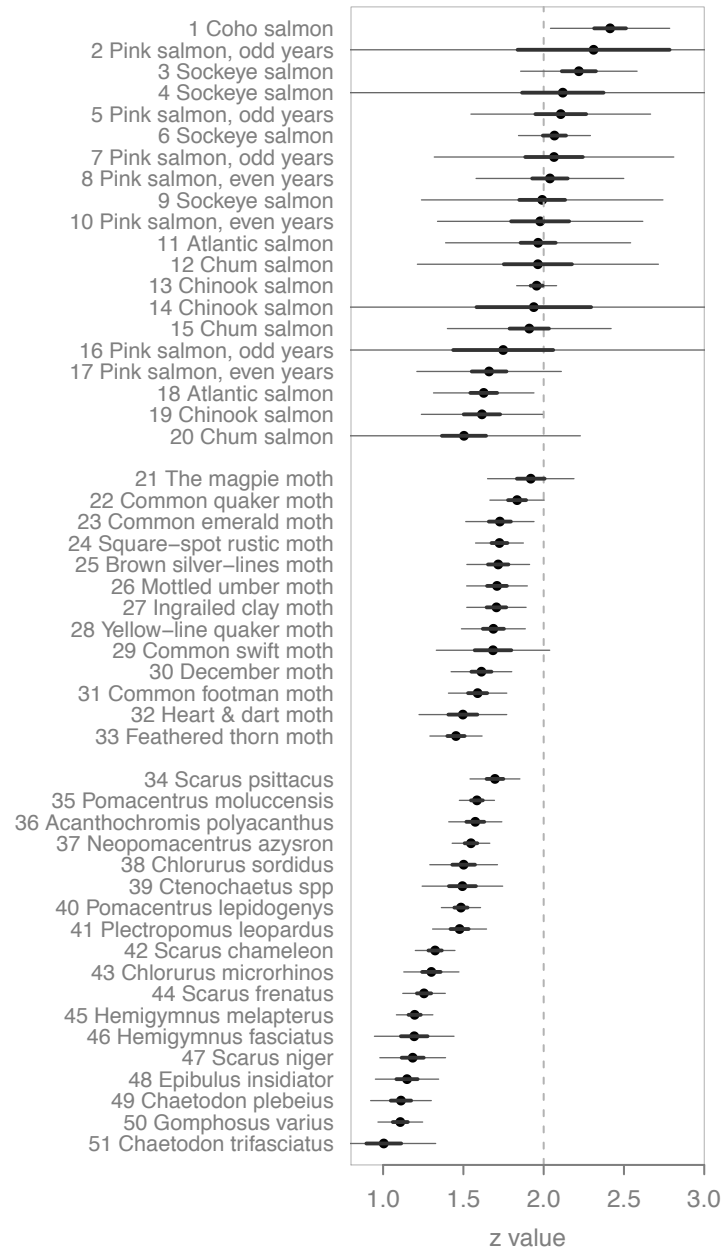


Fig. S4. Taylor's power law z values across metapopulations. Points represent maximum likelihood estimates, thick line segments represent 50% confidence intervals, and thin line segments represent 95% confidence intervals. The vertical dashed line at $z = 2$ represents the value assumed by the average-CV PE method.

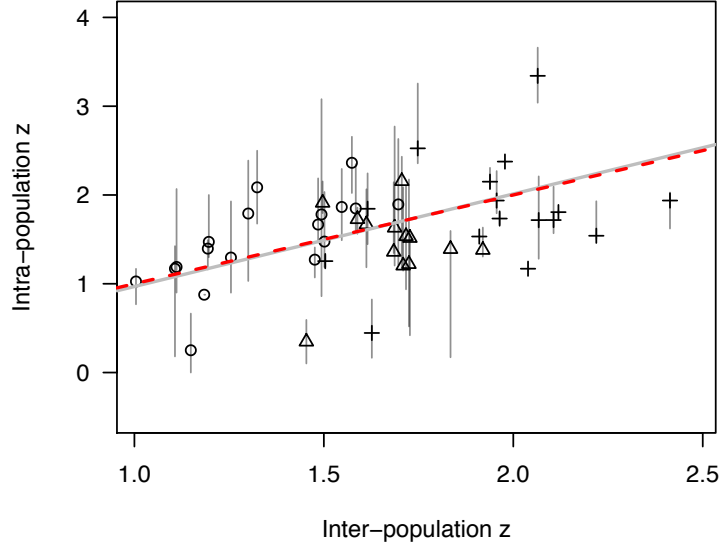


Fig. S5. Intra- vs. inter-subpopulation mean-variance scaling relationship (Taylor’s power law z -value). Our estimation of the empirical mean-variance PE assumes that the inter-subpopulation z -value can approximate the intra-subpopulation z -value. We use the inter-subpopulation z -value throughout our paper. Here, we have also calculated the intra-subpopulation z -value for subpopulation time series in which the mean abundance in the 1st or 2nd half of the time series is twice the magnitude of the other half. Points represent median intra-subpopulation z -values within each metapopulation and vertical line segments represent 1st and 3rd quartile values. The dashed-red line represents a one-to-one relationship and the solid-grey line (under the one-to-one line) represents a linear regression of the median intra-subpopulation z -values with inter-subpopulation z -values. Symbols represent salmon (crosses), moths (triangles), and reef fishes (circles).

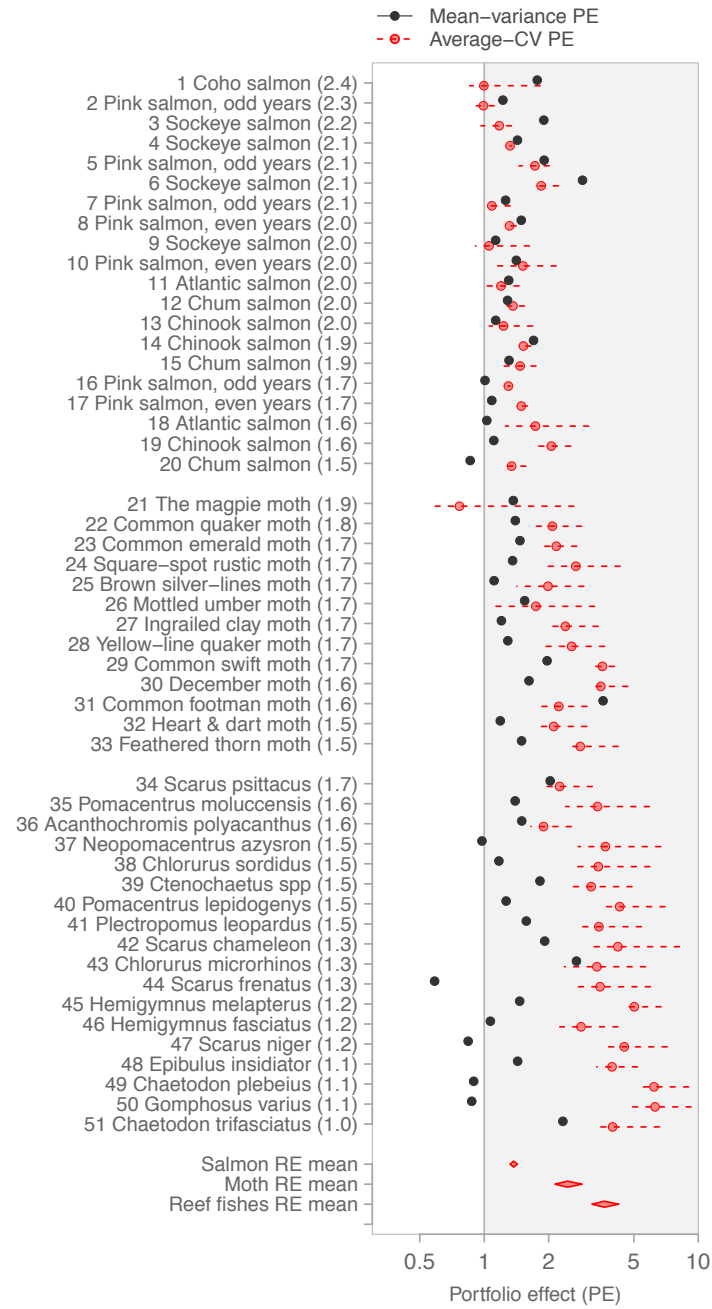


Fig. S6. PEs with the **mean-variance PEs** estimated from a quadratic model. See Fig. 3 for details.

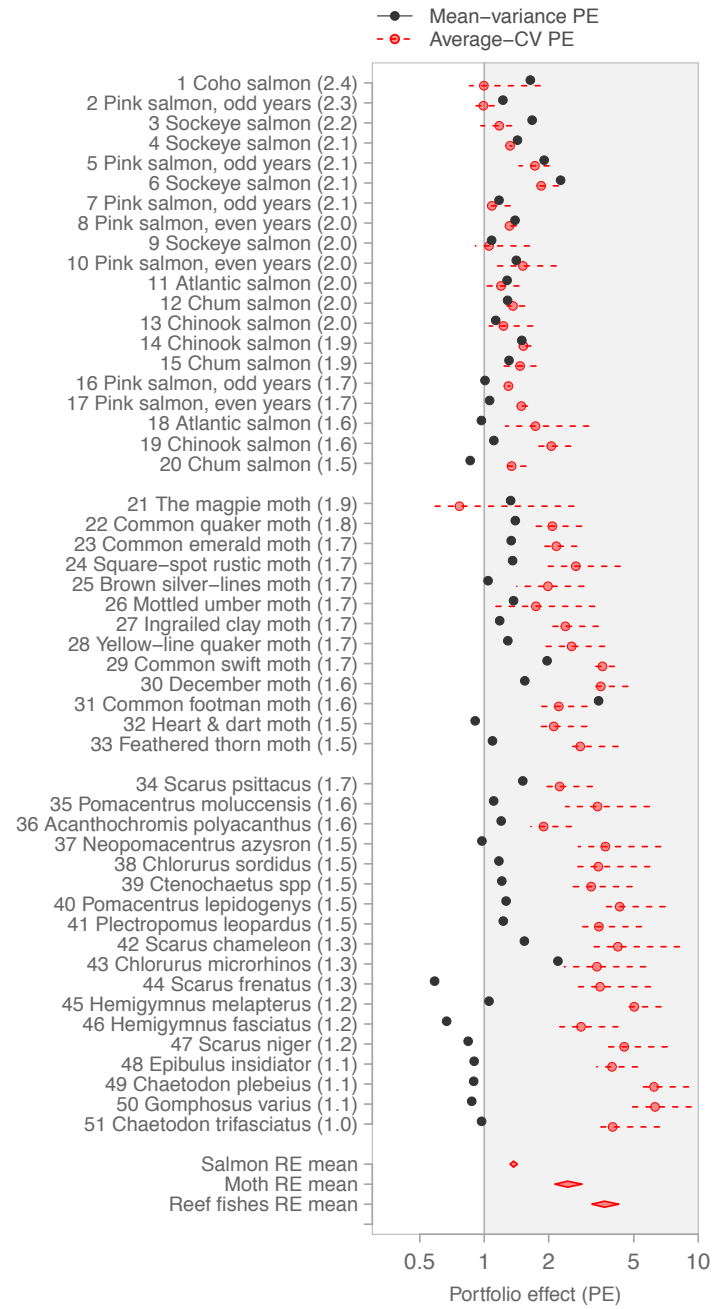


Fig. S7. PEs with the **mean-variance PEs** estimated from a linear-quadratic averaged model. See Fig. 3 for details.

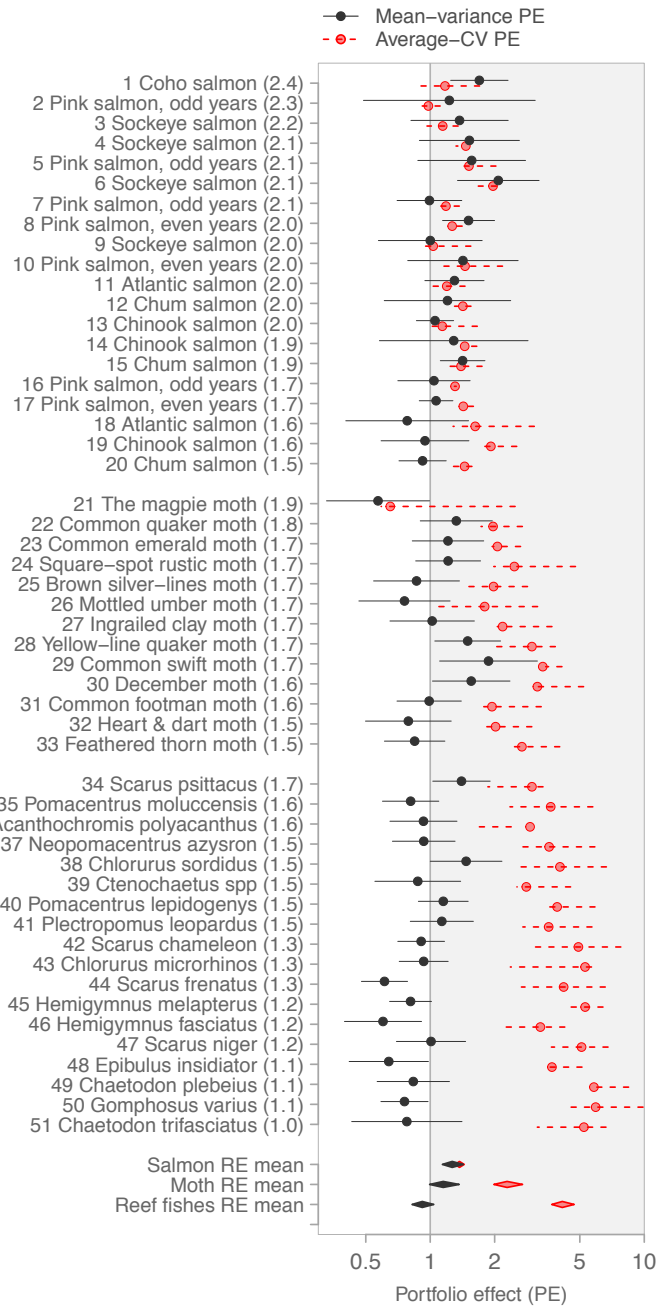


Fig. S8. PEs from **linear detrended** time series. See Fig. 3 for details.

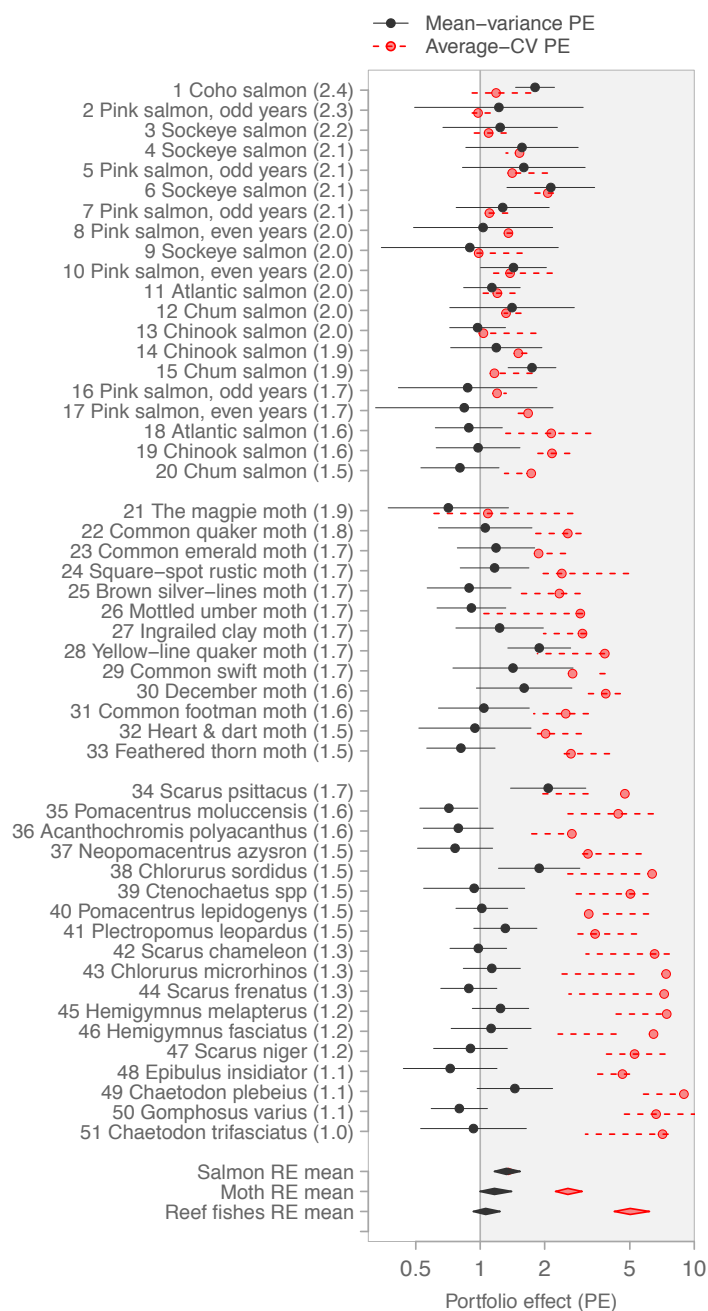


Fig. S9. PEs from **loess detrended** time series. See Fig. 3 for details.

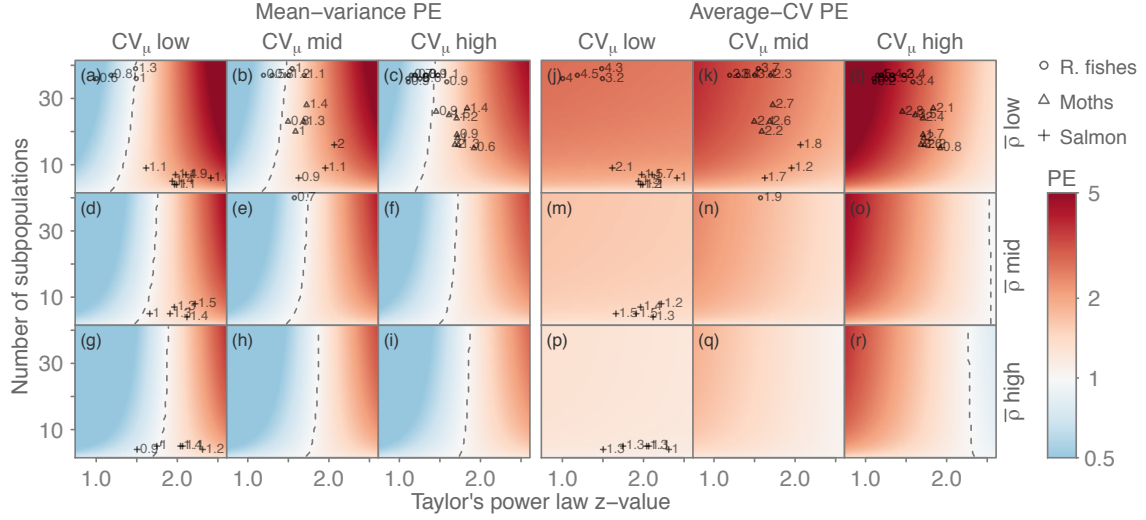


Fig. S10. Empirical ecological PEs (points) overlaid in theoretical PE parameter space (colour shading). **This is the same as Fig. 5 except that here we indicate the empirical PE values beside the points.** The colour shading indicates the stabilizing-effect of the theoretical mean-variance PEs (a–i) 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

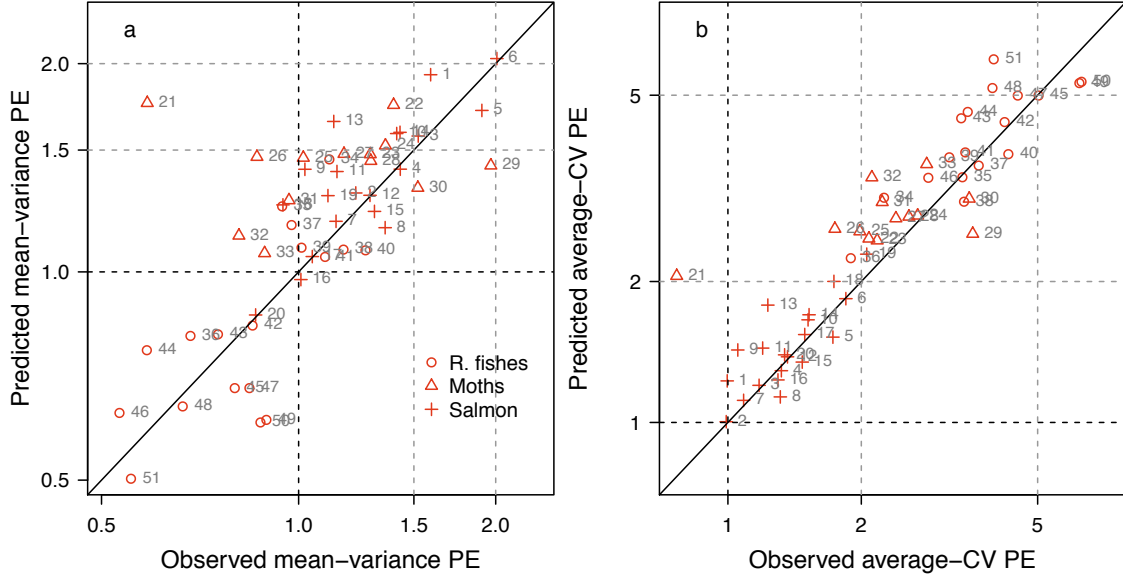


Fig. S11. Predicted vs. observed mean-variance (a) and average-CV PEs (b). Predicted PEs correspond to the colour underlying the metapopulations displayed in Fig. 5; observed PEs to the values calculated directly from the empirical data and shown in Fig. 3. The predicted PEs are approximate due to other statistical properties of the data beyond the four examined in Fig. 5, and due to grouping the CV_{mu} and correlation values from the metapopulations to match the displayed theoretical values in the bins. Numbers indicate the metapopulation IDs used throughout the paper (Table S1). The solid sloped lines indicate one-to-one relationships. Note that all axes have been log transformed and the two panels have separate axis limits.

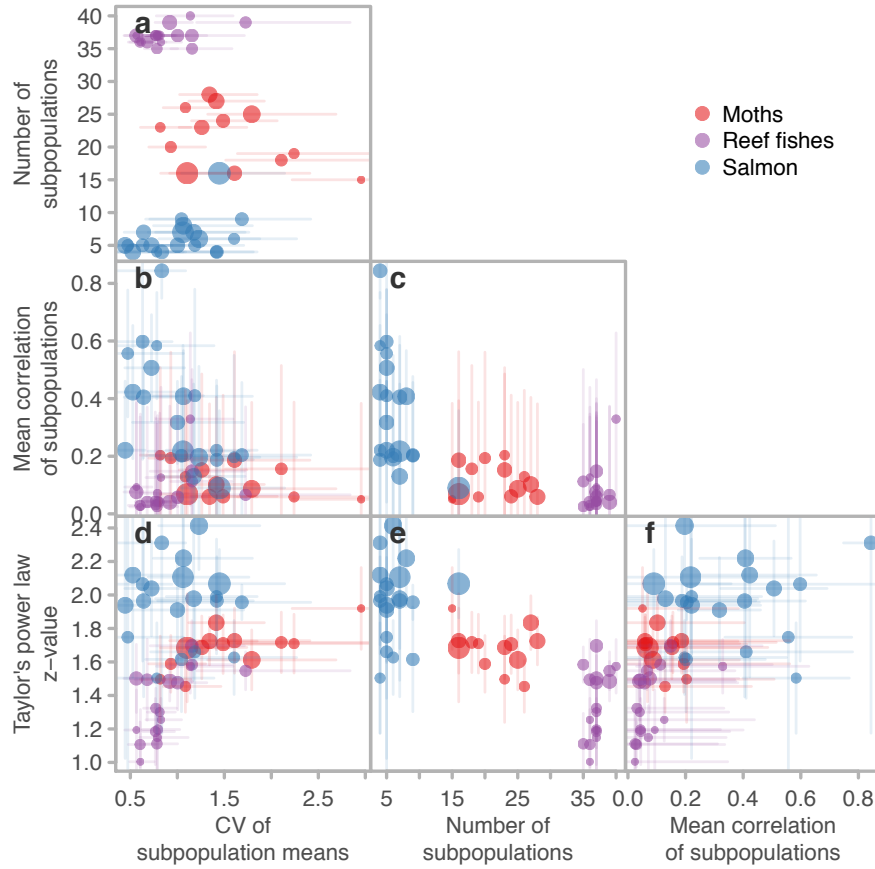


Fig. S12. Relationship between the drivers of the PE in empirical systems for moths (red), reef fishes (purple), and salmon (blue). The area of the filled circles corresponds to the strength of the mean-variance PE with larger circles corresponding to more stabilizing PEs. Line segments indicate 95% confidence intervals.

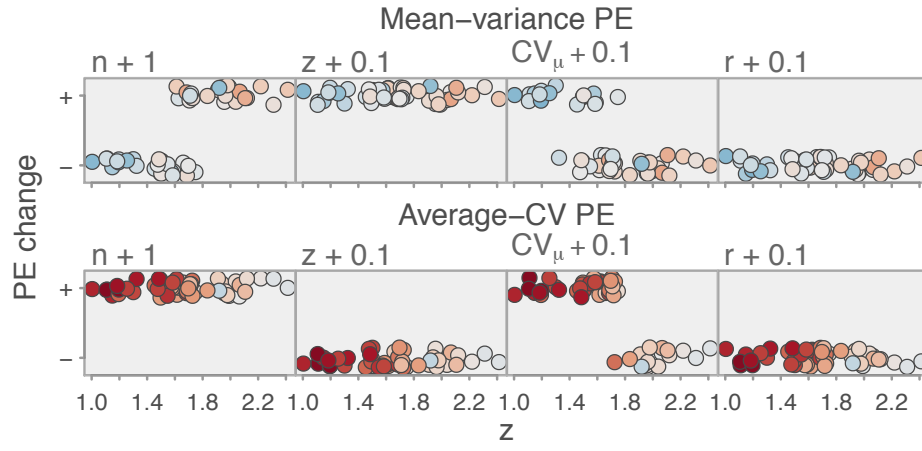


Fig. S13. The PE used as an index of ecosystem change. The upper panel shows the mean-variance PE and the lower panel the average-CV PE. The horizontal axis shows Taylor's power law z -value. The vertical axis shows the change in the PE (more stabilizing = +, less stabilizing = -). The panels from left to right indicate an increase in the number of subpopulations ($n+1$), Taylor's power law z -value ($z+1$), subpopulation unevenness ($CV_\mu+0.1$), or the correlation between subpopulations ($r+0.1$). The quantities added are arbitrary and the results would look the same for any quantity added greater than zero. Each dot represents an empirical metapopulation and the colour indicates the observed empirical PE using the same colour scale as Figs. 4 and 5. The dots are jittered vertically slightly for visual clarity.