Ecological prophets:
Quantifying metapopulation portfolio effects

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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 to 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 to the mean-variance method, the average-CV PE estimated a stronger PE in 84% of metapopulations by up to seven-fold. 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. Since most PEs were stabilizing and diversity can be slow to restore, our meta-analysis of metapopulations suggests the safest management approach is to conserve biological complexity.

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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 ten-fold 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 *et al.* 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) to the average CV of subpopulation abundances (the single assets; Fig. 1b) (Secor *et al.* 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 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 doesn't 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 & Woiwod 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 *et al.* 1990).

The theoretical work of Tilman *et al.* (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 to 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

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— 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 *et al.* 2009; Schindler *et al.* 2010; Carlson & Satterthwaite 2011)?

Here, we conducted the first large-scale cross-taxa evaluation of the average-CV PE compared to the mean-variance PE for metapopulations, specifically addressing three main questions: (1) How does the average-CV PE differ compared to the mean-variance PE when applied to theoretical systems with varying z values? (2) How prevalent and strong is this difference across 51 metapopulations and 1070 subpopulations of salmon, moths, and reef fishes? (3) 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 metapopulation PEs based on question, study system, and data type.

Materials and methods

Defining the metapopulation 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 paper 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 *et al.* 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 in-

teractions, changes in mean abundance with increasing diversity (the over-yielding
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 *subpopulation diversity* as the asynchrony (lack of correlation) between
the groups defined as subpopulations. Since our metrics are phenomenological, they
don't 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 *et al.* 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: (1) a population the same size as the
metapopulation that behaves like the average subpopulation or (2) 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

$$CV_p = \frac{\sqrt{\mu_i{}^z + \mu_{i+1}{}^z + \ldots + \mu_n{}^z}}{\mu_i + \mu_{i+1} + \ldots + \mu_n}. \tag{1}$$

The average-CV PE defines CV_a as

$$\text{CV}_a = \frac{\dfrac{\sqrt{\mu_i}^z}{\mu_i} + \dfrac{\sqrt{\mu_{i+1}}^z}{\mu_{i+1}} + \ldots + \dfrac{\sqrt{\mu_n}^z}{\mu_n}}{n},\tag{2}$$

whereas the mean-variance PE defines CV_a as

$$\text{CV}_a = \frac{\sqrt{(\mu_i + \mu_{i+1} + \ldots + \mu_n)^z}}{\mu_i + \mu_{i+1} + \ldots + \mu_n}.\tag{3}$$

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

$$\sigma_p^2 = \sum_{i=1}^{n} \sigma_i^2 + \sum_{i=1}^{n} \sum_{\substack{j=1 \\ j \neq i}}^{n} \rho \sqrt{\sigma_i^2 \sigma_j^2}.\tag{4}$$

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 *et al.* 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 to 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.

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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 **??**; Figs **??**, **??**). We obtained salmon returns from the primary literature, in particular Dorner *et al.* (2008), and government research documents (Table **??**). 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 **??** and **??** 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 ten 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

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

$$log(\sigma_i^2) = \beta_0 + z \cdot log(\mu_i) + \epsilon_i \qquad (5)$$

4 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

6 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

8 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

10 for the observed subpopulation CV mean-variance scaling relationship. We obtained confidence intervals on the mean-variance PE by re-calculating the PE using the 95%

12 confidence intervals on the predicted metapopulation variance.

Our empirical mean-variance PE calculation assumes the inter-subpopulation

14 mean-variance relationship can be used as a proxy for the intra-subpopulation relationship. To test this we estimated the intra-subpopulation mean-variance rela-

16 tionship 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

18 intra-subpopulation z values with the inter-subpopulation z values used in our analysis.

20 # Alternative ways of extrapolating the mean-variance PE

Quadratic extrapolations: In our main analysis, we estimated Taylor's power law

22 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

24 1991; Perry & Woiwod 1992). We fit a quadratic model,

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

Perry & Woiwod (1992) suggest limiting the lower value of β_2 to 0 since 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` (Bartoń 2012).

Accounting for non-stationary 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 (1) a fitted linear model and (2) 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 non-stationary 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 paper (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 non-stationary 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 metapopulations (Figs **??**, **??**). The inter-

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

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 0.5–2.0 and the average-CV PE from 0.8–6.3. Hence, at best the mean-variance PE suggests the metapopulation portfolio is twice as stable as the homogeneous single asset. In comparison, the average-CV PE suggests the metapopulation 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 to 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 switched from destabilizing to stabilizing PEs with quadratic (Fig. ??) or quadratic-linear averaged (Fig. ??) 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, ??). Loess detrending increased the mean-variance

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PE in 34/51 cases and the average-CV PE in 34/51, lowering it in the others (Figs 4, **??**). 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). (1) 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 to the mean-variance PE, and this issue is prevalent for the parameter space observed in real ecological systems. (2) The empirical PEs were strongly grouped by taxonomy (see also Fig. **??**). (3) We did not observe metapopulations that were both highly uneven and highly correlated (lower-right panels of Fig. 5). (4) 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). (5) The average-CV method, however, considerably overestimated the PE compared to 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. **??**). The factors driving the PE co-varied; in particular, we observed high correlation of subpopulations associated with high variability (CV) and few subpopulations (Fig. **??**b, c). High z values occurred when there were few moderately-to-highly correlated subpopulations (Fig. **??**e, f).

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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 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 *et al.* 1998; Tilman 1999; Cottingham *et al.* 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

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models (e.g. Anderson *et al.* 1982; Ballantyne IV 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 stochastic-

ity) (Loreau 2010). Second, 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. Third,

measurement error in abundance estimates (Perry 1981), and particularly rounding

at low abundance (Taylor & Woiwod 1982), can create artificially low z values. How-

ever, 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 since 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

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appropriate.

2   The PE metrics in this paper compare the observed metapopulation variability to 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 metapopulation portfolio effects

14 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). Second, since 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, non-systematic 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.

24   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

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studies (DeClerck *et al.* 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 *et al.* (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, **??**). Second, 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 inter-

preting 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 non-linearities 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 ex-
trapolating 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 ag-
gregated (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 paper 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 *et al.*
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? Second, the number of estimated parameters may exceed the power of
most ecological data sets (Thibaut *et al.* 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 paper 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 expect 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 "value" is of interest and the interaction between "assets" is minimal. As demonstrated in this paper, 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 paper, 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).

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- If $z \approx 2$ then use the average-CV PE, which amounts to the same metric as the mean-variance PE at $z = 2$ 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 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 non-intuitive 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 paper 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 we need to find ways of understanding, prioritizing, and conserving the processes that give rise to ecological stability.

Acknowledgements

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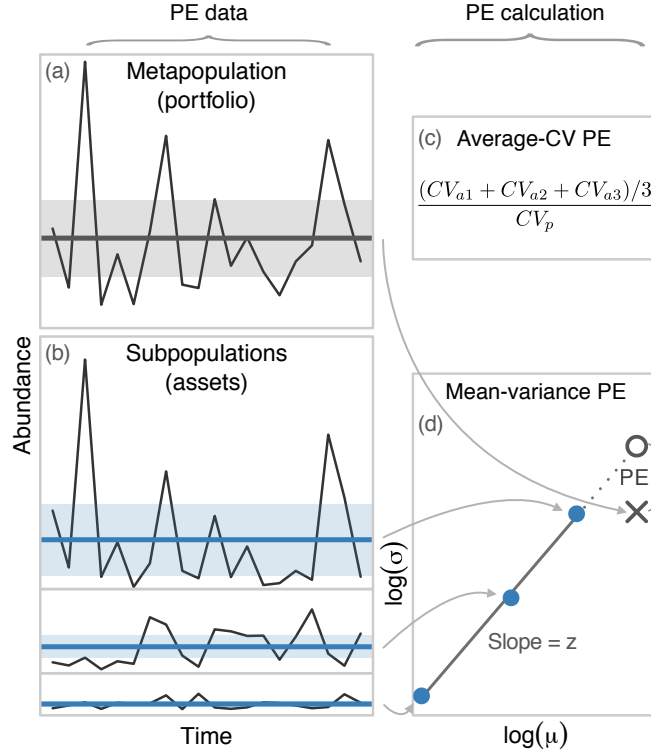
Figure 1: Estimating the two PEs from empirical data. (a, b) Example metapopulation (portfolio) and subpopulation (asset) abundance time-series. Horizontal lines represent the time-series' means and the shaded regions represent variability. (c) We calculated the average-CV PE by dividing the average CV of the subpopulations (CV_a) by the CV of the metapopulation (CV_p). (d) We calculated the mean-variance PE by (1) plotting the mean and variance of each subpopulation on log-log axes, (2) extrapolating the subpopulation mean-variance relationship to the metapopulation mean (open-grey circle), and (3) 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.
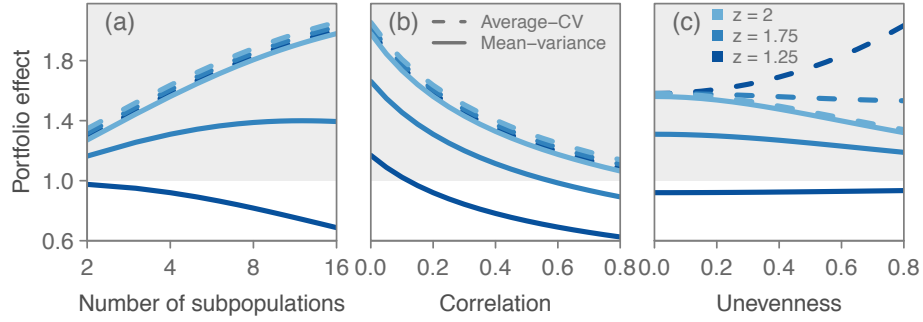
Figure 2: The ecological factors driving the PE in theoretical systems. A PE of two, for example, would indicate a two-fold increase in stability for the portfolio compared to what we would expect in a single homogeneous population of the same size. We show the mean-variance PE and average-CV PE for 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 weren't 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.
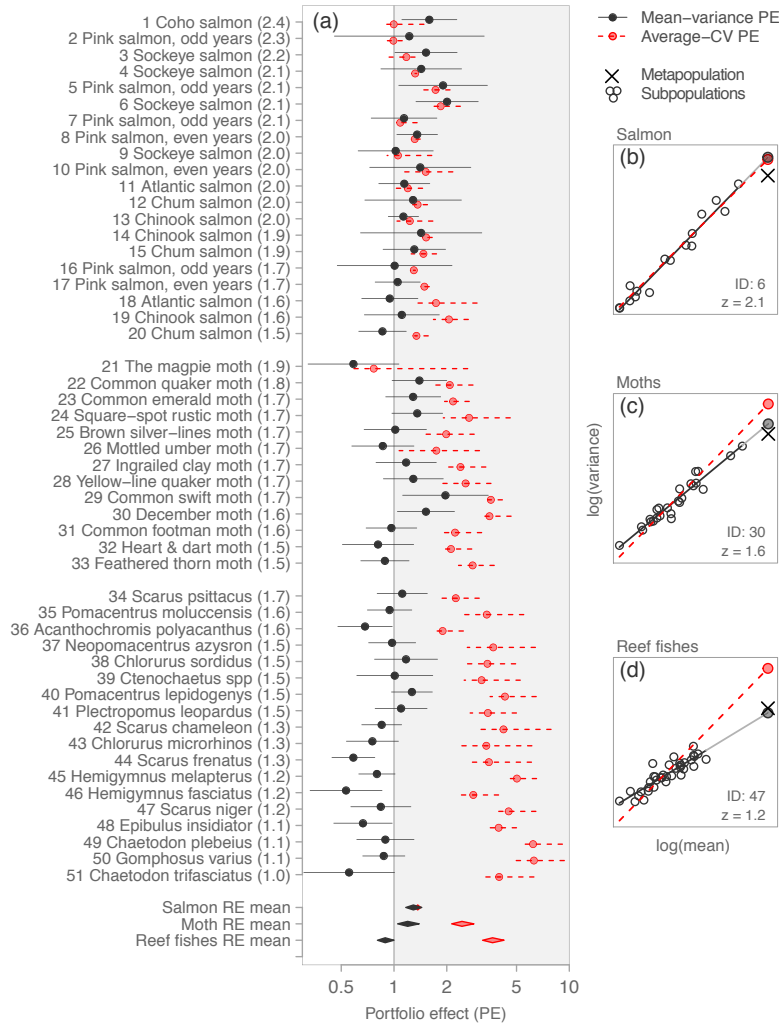
Figure 3: PEs across 51 metapopulations. (a) Empirical PEs (circles) and 95% CIs (lines) for the mean-variance method and the average-CV PE method. We ordered metapopulations within taxonomic groups by Taylor's law z values (indicated in brackets beside each metapopulation name). Diamonds represent inverse-variance weighted random-effect (RE) meta-analytic means and 95% CIs. Numbers before population names represent population IDs (see Supplementary Table 1). 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 × 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 average-CV PE and the dashed-red line the mean-variance relationship under the assumption that z = 2, as the average-CV PE assumes.
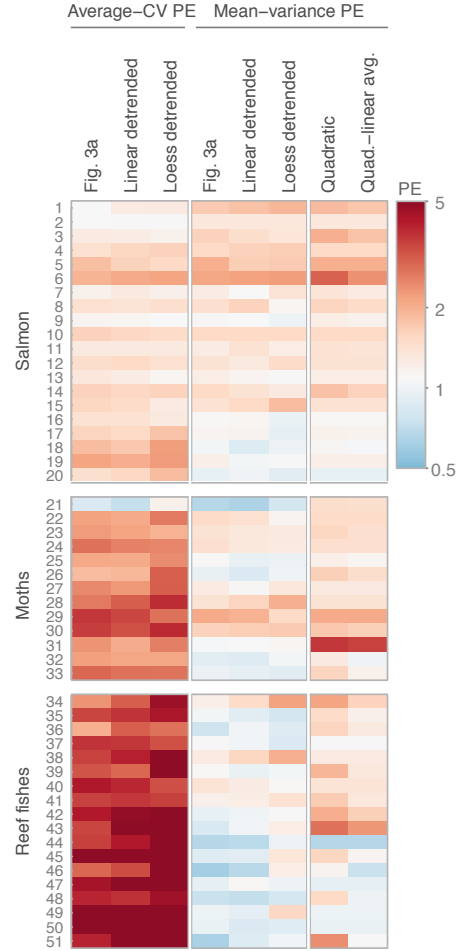
29

Figure 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
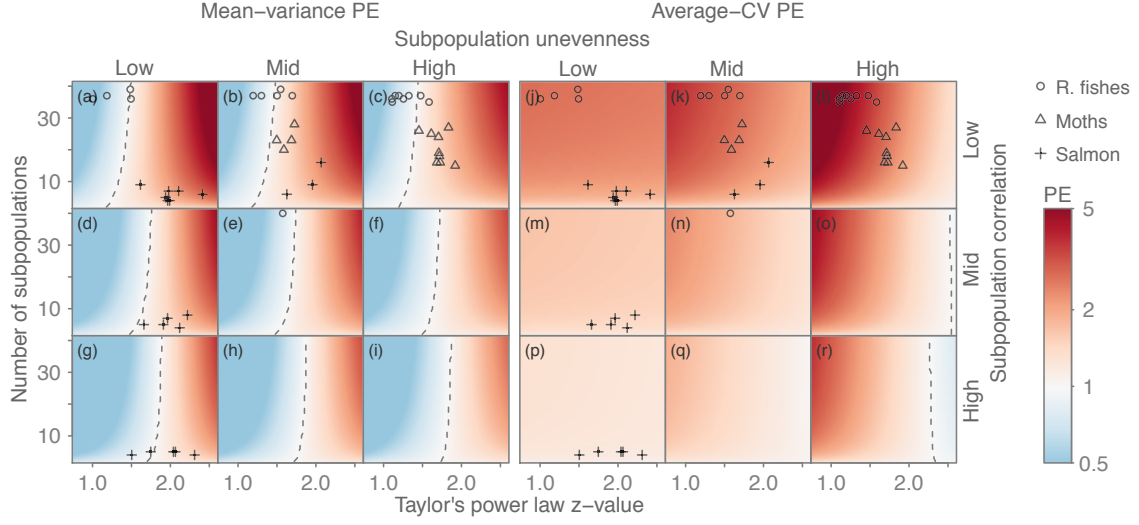
Figure 5: Empirical ecological PEs (points) overlaid in theoretical PE parameter space (colour shading). The colour shading indicates the stabilizing-effect of the theoretical mean-variance PEs (a–i) and average-CV PEs (j–r): red indicates a stabilizing effect and blue indicates a destabilizing effect. 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).
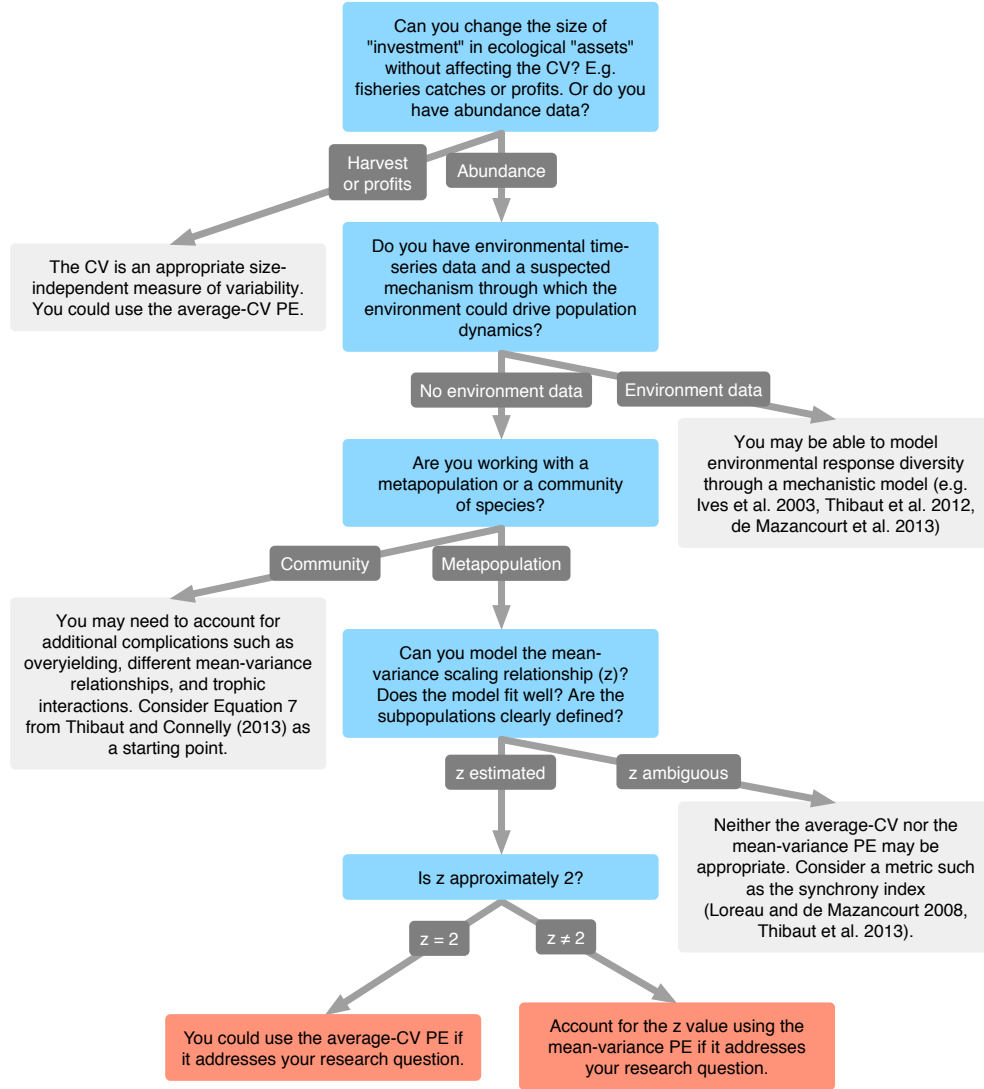
Figure 6: Decision tree showing options for quantifying ecological portfolios. Blue boxes in the middle column show questions to ask of the study system and available data. The orange boxes at the bottom represent the methods demonstrated in this paper. The light-grey boxes along the sides show other options to quantify ecological portfolios given different research questions, study systems, and available data.

Ecological prophets: Quantifying metapopulation portfolio effects

Sean C. Anderson, Andrew B. Cooper, Nicholas K. Dulvy

Supporting Information

R package to estimate metapopulation portfolio effects

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

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

Then, to install the included package:

```
install.packages("ecofolio_0.1.tar.gz", type = "source")
```

or to install the current version from the web:

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

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

2 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

4 metapopulations in North America (salmon), the United Kingdom (moths), and Australia (reef fishes) (Fig. **??**). We show a summary of the data included in our

6 analysis of empirical ecological systems in Table S1 and the time series in Fig. **??**.

Salmon

8 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

10 also: Kola Peninsula, Russia (Jensen *et al.* 1999), southern New England (Kocik & Sheehan 2006), and Central Valley, California (Carlson & Satterthwaite 2011)

12 (Fig. **??**). All data represent annual estimated returns — fisheries catch plus escapement to the spawning grounds. We divided pink salmon annual estimated returns

14 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 involv-

16 ing 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

18 not divide the sockeye salmon into separate runs.

Subsets of these salmon data have been used in numerous analyses relating di-

20 versity 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

22 environment — in producing stability (Hilborn *et al.* 2003) and recent papers have focussed on measuring the portfolio effects we investigate in this paper (Schindler

24 *et al.* 2010; Carlson & Satterthwaite 2011). In studying the mechanisms behind subpopulation asynchrony, and hence portfolio effects, studies of Pacific salmon have

26 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 **??**). 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

3

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 **??**). 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 $0.50 \leq \bar{\rho} < 75$ 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, $\mathrm{CV}(\log \mu)$; (2) categorizing the empirical metapopulations into bins of $0 \leq \mathrm{CV}(\log \mu) < 0.3$, $0.3 \leq \mathrm{CV}(\log \mu) < 0.6$, and $0.6 \leq \mathrm{CV}(\log \mu) < 0.9$; (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: $a_1, a_2, \ldots, a_n$, 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.

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

ID	Species	Common	Subpopulations	Years	Location	Reference
1	Oncorhynchus kisutch	Coho salmon	6	16	Broughton archipelago, BC, Canada	(Krkošek et al. 2011)
2	Oncorhynchus gorbuscha	Pink salmon, odd years	4	19	Puget Sound, WA, United States	(Dorner et al. 2008)
3	Oncorhynchus nerka	Sockeye salmon	8	43	Bristol Bay, AK, United States	(West & Fair 2006)
4	Oncorhynchus nerka	Sockeye salmon	4	24	Kodiak, AK, United States	(Dorner et al. 2008)
5	Oncorhynchus gorbuscha	Pink salmon, odd years	7	19	Broughton archipelago, BC, Canada	(Krkošek et al. 2011)
6	Oncorhynchus nerka	Sockeye salmon	16	44	Fraser River, BC, Canada	(Dorner et al. 2008)
7	Oncorhynchus gorbuscha	Pink salmon, odd years	5	8	Kodiak, AK, United States	(Dorner et al. 2008)
8	Oncorhynchus gorbuscha	Pink salmon, even years	5	16	Chignik, AK, United States	(Dorner et al. 2008)
9	Oncorhynchus nerka	Sockeye salmon	4	29	Upper Cook Inlet, AK, United States	(Fair et al. 2011)
10	Oncorhynchus gorbuscha	Pink salmon, even years	7	19	Broughton archipelago, BC, Canada	(Krkošek et al. 2011)
11	Salmo salar	Atlantic salmon	4	15	Kola Peninsula, Russia	(Jensen et al. 1999)
12	Oncorhynchus keta	Chum salmon	7	26	Puget Sound, WA, United States	(Dorner et al. 2008)
13	Oncorhynchus tshawytscha	Chinook salmon	9	23	Columbia Estuary, OR/WA, United States	(StreamNet 2011)
14	Oncorhynchus tshawytscha	Chinook salmon	5	27	Elochoman River, WA, United States	(StreamNet 2011)
15	Oncorhynchus keta	Chum salmon	5	18	Arctic, Yukon, Kuskokwim, US and Canada	(Dorner et al. 2008)
16	Oncorhynchus gorbuscha	Pink salmon, odd years	5	15	Chignik, AK, United States	(Dorner et al. 2008)
17	Oncorhynchus gorbuscha	Pink salmon, even years	5	9	Kodiak, AK, United States	(Dorner et al. 2008)
18	Salmo salar	Atlantic salmon	6	39	Southern New England, United States	(Kocik & Sheehan 2006)
19	Oncorhynchus tshawytscha	Chinook salmon	9	54	Central Valley, California	(Carlson & Satterthwaite 2011)
20	Oncorhynchus keta	Chum salmon	4	32	Alaska Peninsula, AK, United States	(Dorner et al. 2008)
21	Abraxas grossulariata	The magpie moth	15	12	UK	(Conrad et al. 2004)
22	Orthosia cerasi	Common quaker moth	27	12	UK	(Conrad et al. 2004)
23	Hemithea aestivaria	Common emerald moth	16	12	UK	(Conrad et al. 2004)
24	Xestia xanthographa	Square-spot rustic moth	28	12	UK	(Conrad et al. 2004)
25	Petrophora chlorosata	Brown silver-lines moth	18	12	UK	(Conrad et al. 2004)
26	Erannis defoliaria	Mottled umber moth	19	12	UK	(Conrad et al. 2004)
27	Diarsia mendica	Ingrailed clay moth	24	12	UK	(Conrad et al. 2004)
28	Agrochola (Leptologia) macilenta	Yellow-line quaker moth	23	12	UK	(Conrad et al. 2004)
29	Pharmacis lupulina	Common swift moth	16	12	UK	(Conrad et al. 2004)
30	Poecilocampa populi	December moth	25	12	UK	(Conrad et al. 2004)
31	Eilema lurideola	Common footman moth	20	12	UK	(Conrad et al. 2004)
32	Agrotis exclamationis	Heart and dart moth	23	12	UK	(Conrad et al. 2004)
33	Colotois pennaria	Feathered thorn moth	26	12	UK	(Conrad et al. 2004)
34	Scarus psittacus	Scarus psittacus	37	14	GBR, Australia	(Sweatman et al. 2008)
35	Pomacentrus moluccensis	Pomacentrus moluccensis	35	14	GBR, Australia	(Sweatman et al. 2008)
36	Acanthochromis polyacanthus	Acanthochromis polyacanthus	40	14	GBR, Australia	(Sweatman et al. 2008)
37	Neopomacentrus azysron	Neopomacentrus azysron	39	14	GBR, Australia	(Sweatman et al. 2008)
38	Chlorurus sordidus	Chlorurus sordidus	37	14	GBR, Australia	(Sweatman et al. 2008)
39	Ctenochaetus spp	Ctenochaetus spp	36	14	GBR, Australia	(Sweatman et al. 2008)
40	Pomacentrus lepidogenys	Pomacentrus lepidogenys	39	14	GBR, Australia	(Sweatman et al. 2008)
41	Plectropomus leopardus	Plectropomus leopardus	37	14	GBR, Australia	(Sweatman et al. 2008)
42	Scarus chameleon	Scarus chameleon	37	14	GBR, Australia	(Sweatman et al. 2008)
43	Chlorurus microrhinos	Chlorurus microrhinos	37	14	GBR, Australia	(Sweatman et al. 2008)
44	Scarus frenatus	Scarus frenatus	36	14	GBR, Australia	(Sweatman et al. 2008)
45	Hemigymnus melapterus	Hemigymnus melapterus	37	14	GBR, Australia	(Sweatman et al. 2008)
46	Hemigymnus fasciatus	Hemigymnus fasciatus	37	14	GBR, Australia	(Sweatman et al. 2008)
47	Scarus niger	Scarus niger	37	14	GBR, Australia	(Sweatman et al. 2008)
48	Epibulus insidiator	Epibulus insidiator	37	14	GBR, Australia	(Sweatman et al. 2008)
49	Chaetodon plebeius	Chaetodon plebeius	35	14	GBR, Australia	(Sweatman et al. 2008)
50	Gomphosus varius	Gomphosus varius	36	14	GBR, Australia	(Sweatman et al. 2008)
51	Chaetodon trifasciatus	Chaetodon trifasciatus	36	14	GBR, Australia	(Sweatman et al. 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 l	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 dataset. 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
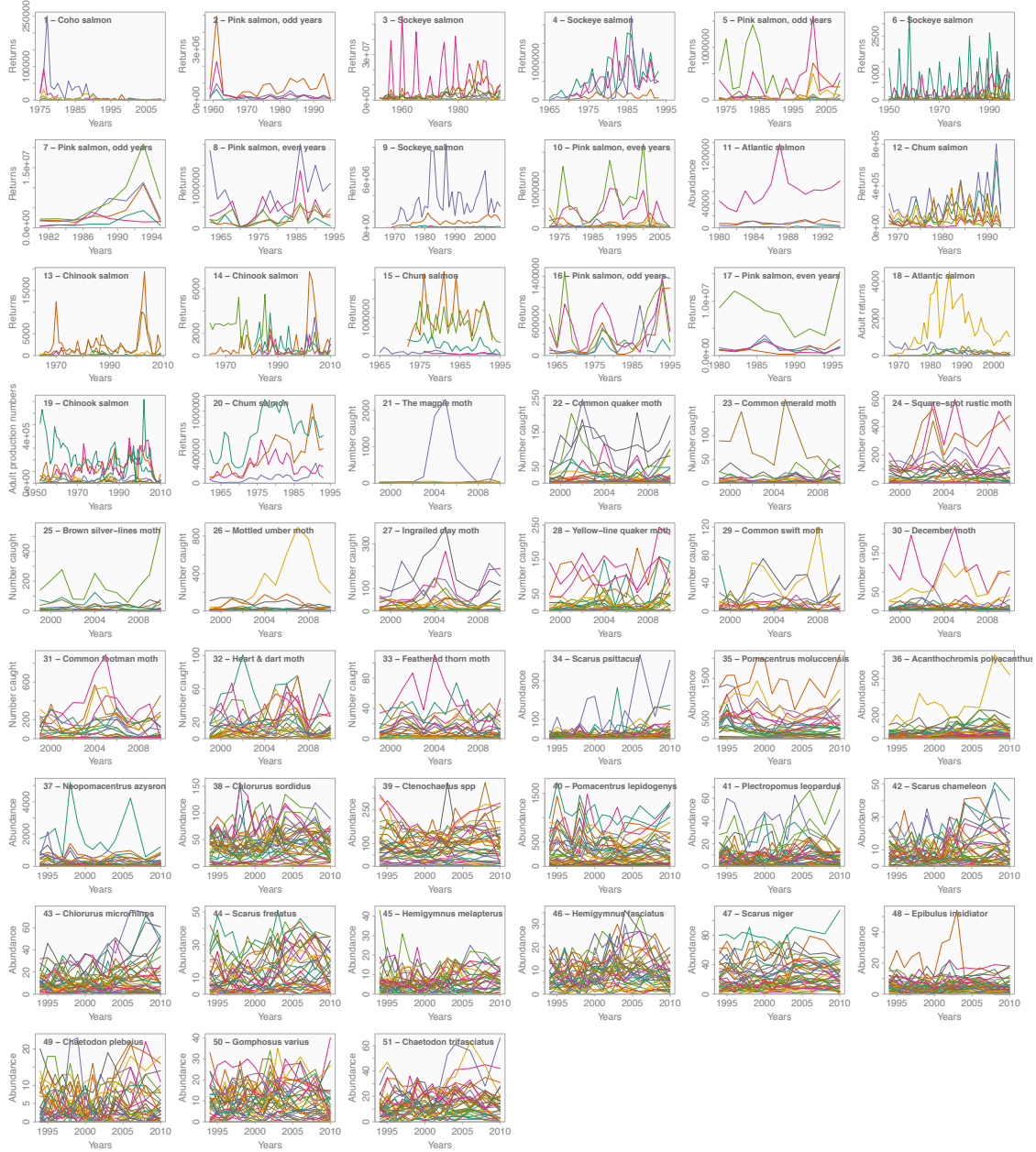
Fig. S1. Subpopulation time series. Each panel contains one metapopulation. Colours were randomly assigned to distinguish subpopulations. Numbers in top-left corners refer to metapopulation IDs (see Table S1).
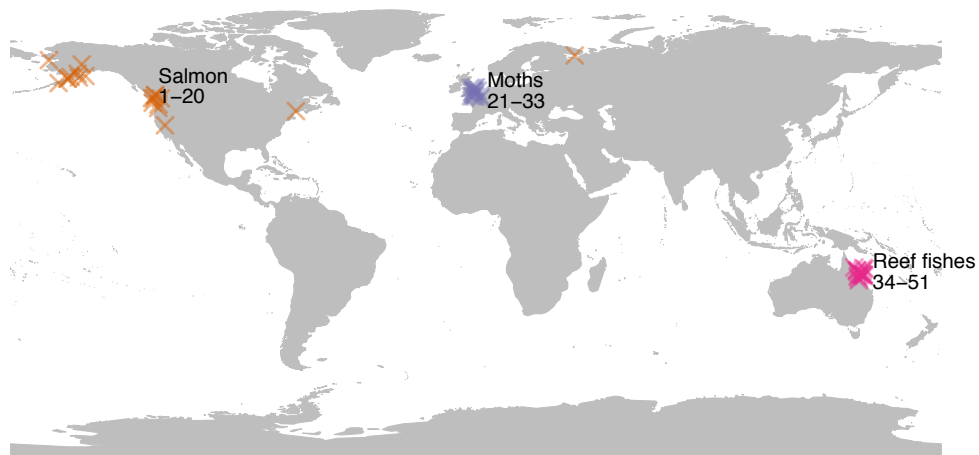
Fig. S2. Map of included metapopulations. We represented salmon metapopulations with orange symbols, moths with purple, and reef fishes with pink. Numbers refer to metapopulation IDs (Table S1). Points are jittered slightly for visual clarity.
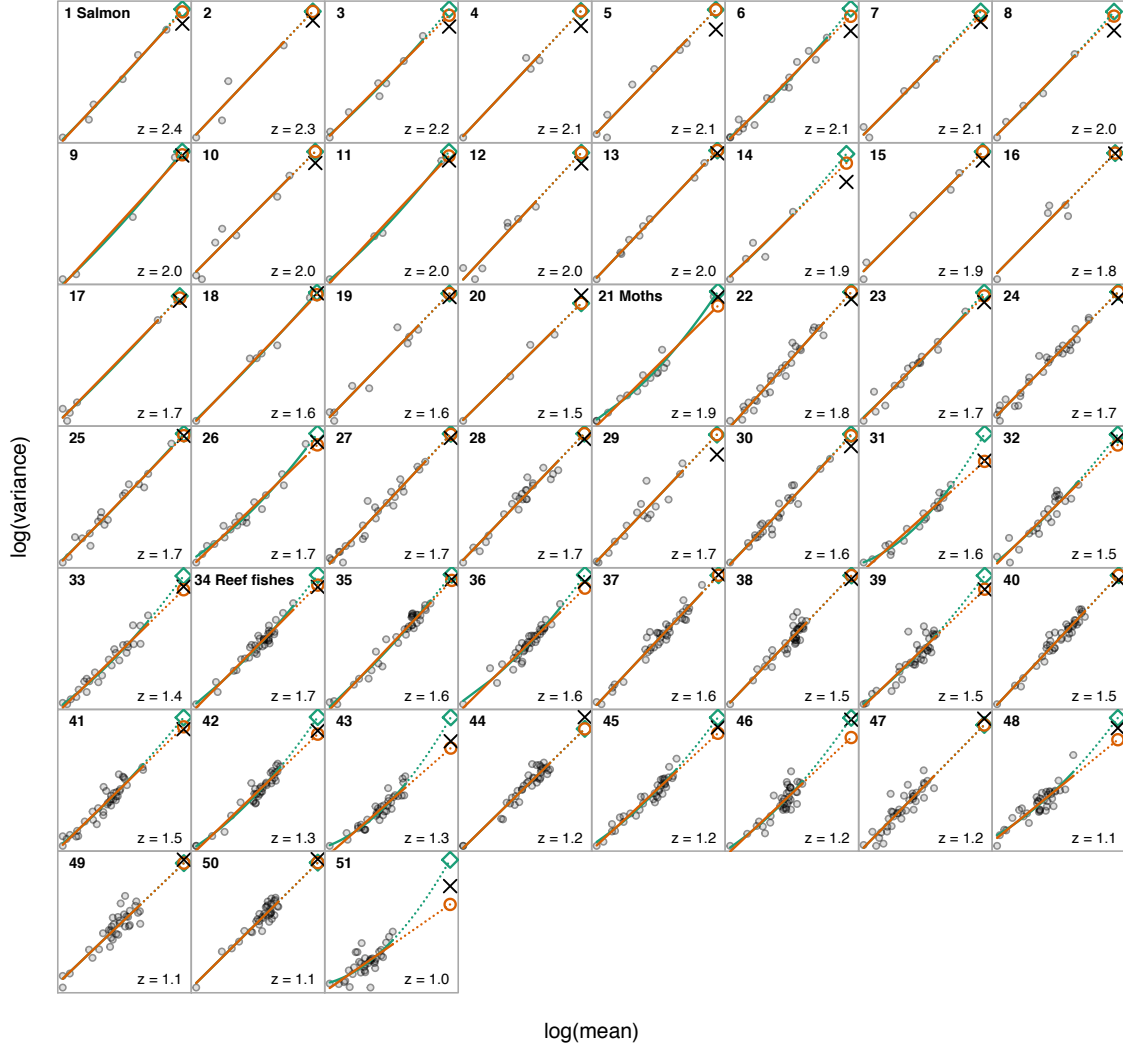
Fig. S3. Calculation of the mean-variance PE using Taylor's power law. Each dark-grey circle represents the $\log(\mu)$ and $\log(\sigma^2)$ of an individual subpopulation timeseries. The orange lines represent fitted linear regressions. The green lines represent fitted quadratic regressions. Black x symbols represent the observed meta-population or portfolio mean and variance. Dashed lines indicate the extrapolation of the model fit to the observed metapopulation 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)

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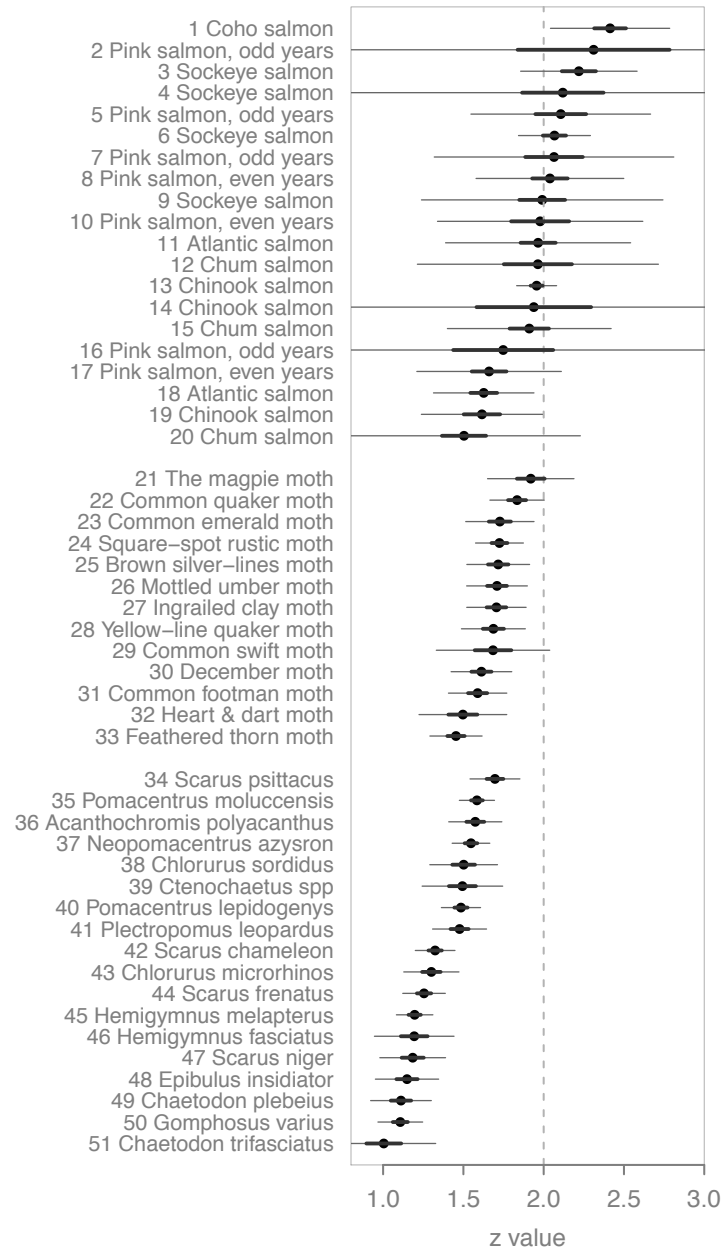
Fig. S4. Taylor's power law z values across metapopulations. Points represent maximum likelihood estimates, thick line segments represent 50% confidence intervals, and thin line segments represent 95% confidence intervals. The vertical dashed line at z = 2 represents the value assumed by the average-CV PE method.
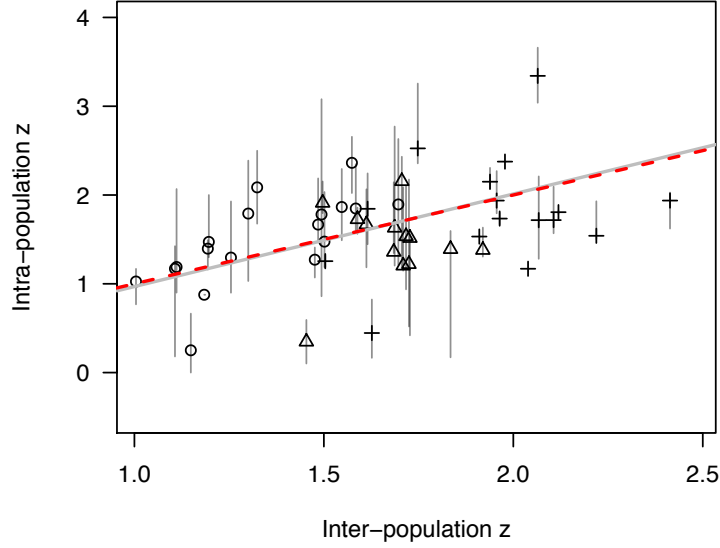
Fig. S5. Intra- vs. inter-subpopulation mean-variance scaling relationship (Taylor's power law z-value). Our estimation of the empirical mean-variance PE assumes that the inter-subpopulation z-value can approximate the intra-subpopulation z-value. We use the inter-subpopulation z-value throughout our 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).
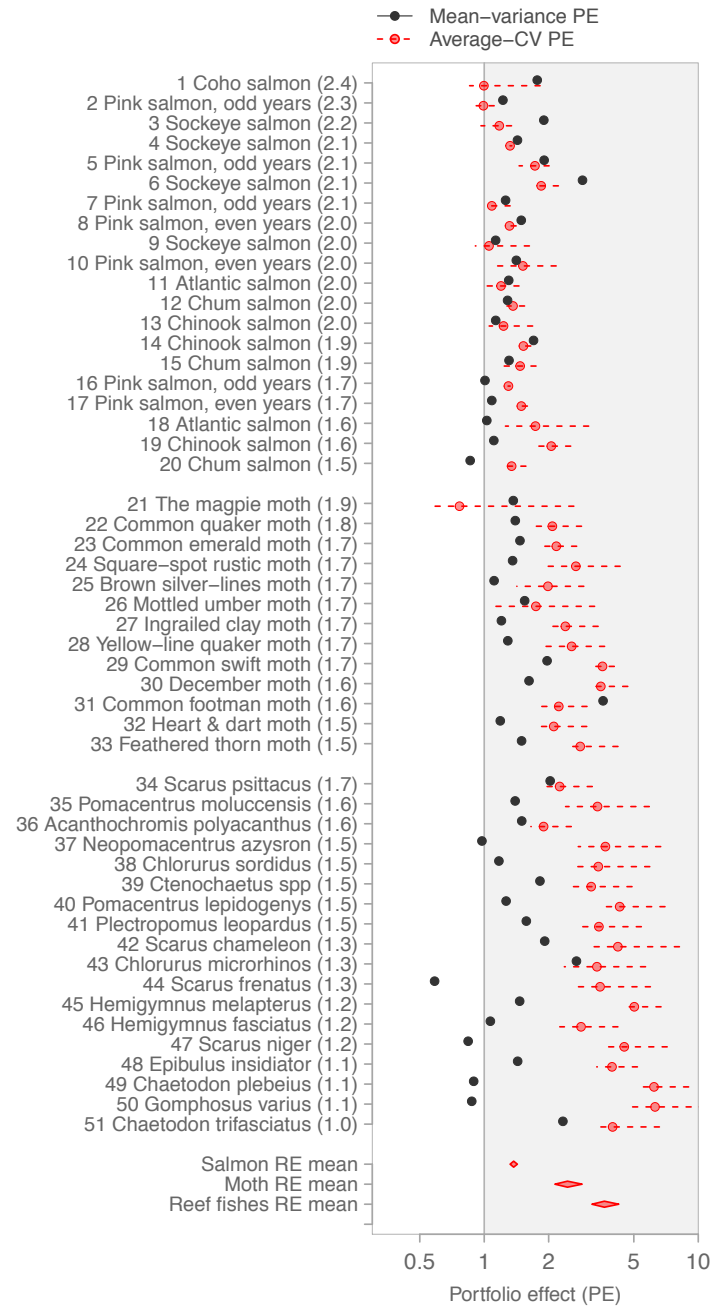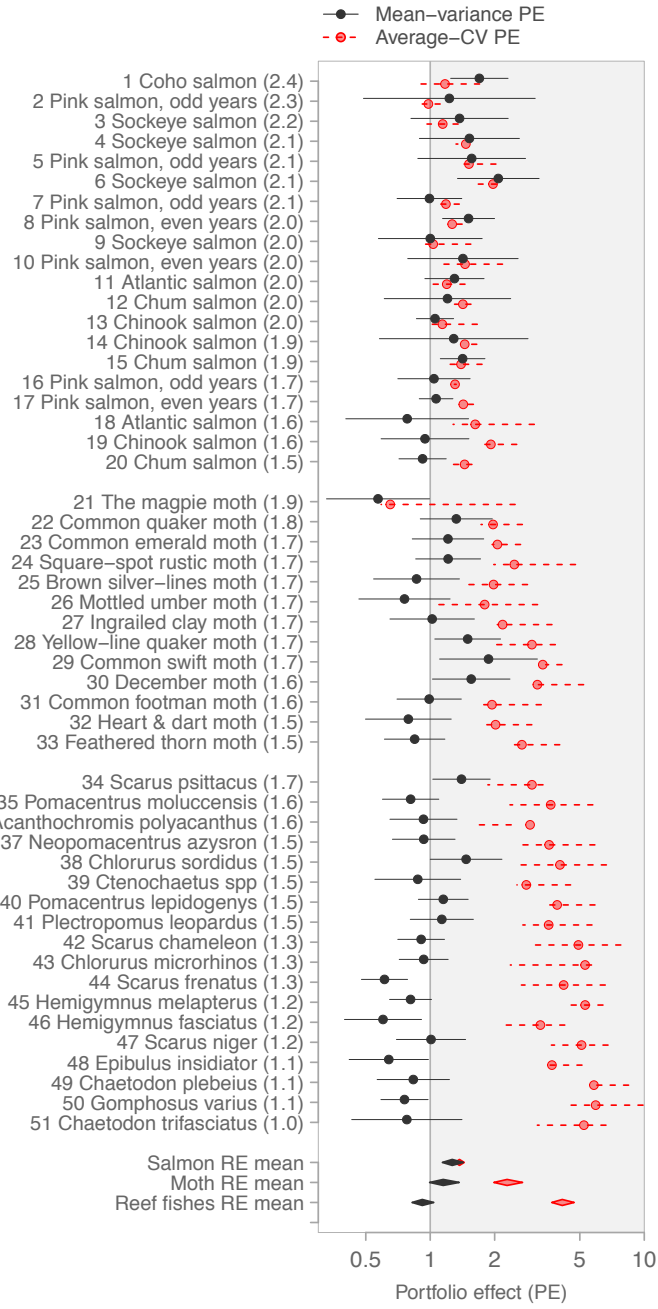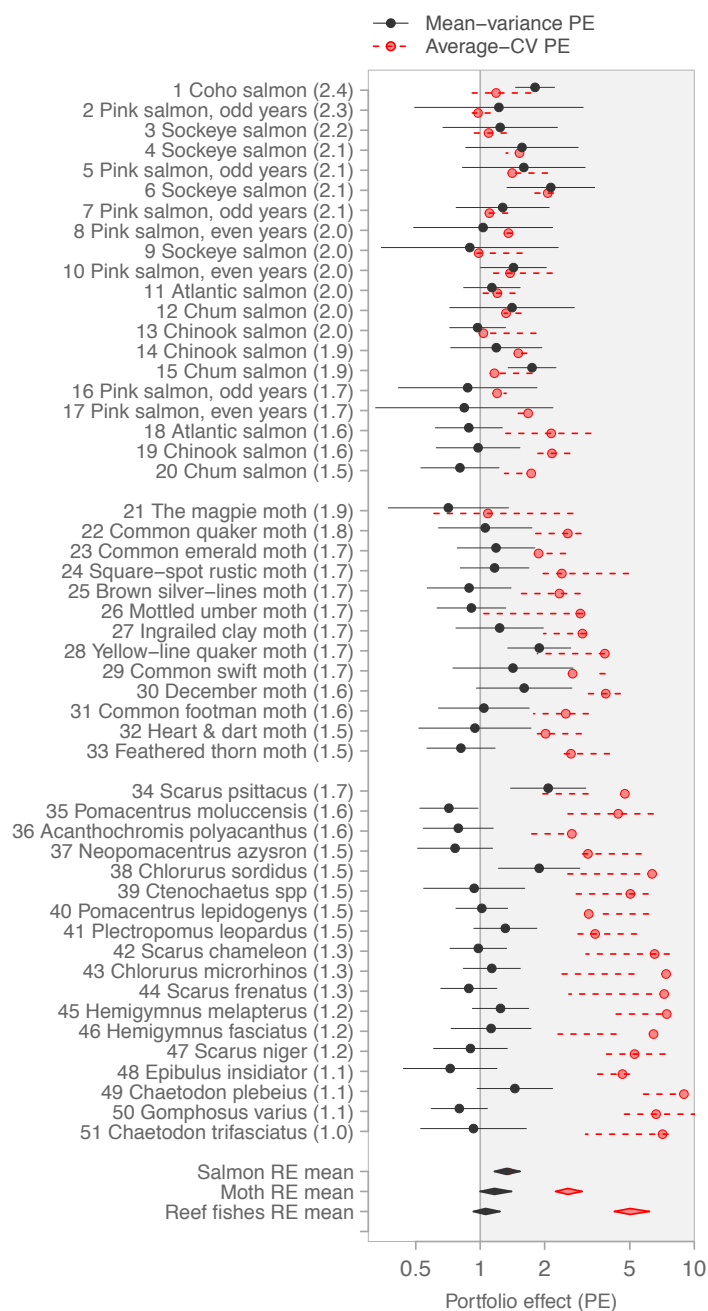
Fig. S6. PEs with the **mean-variance PEs estimated from a quadratic model**. See Fig. 3 for details.
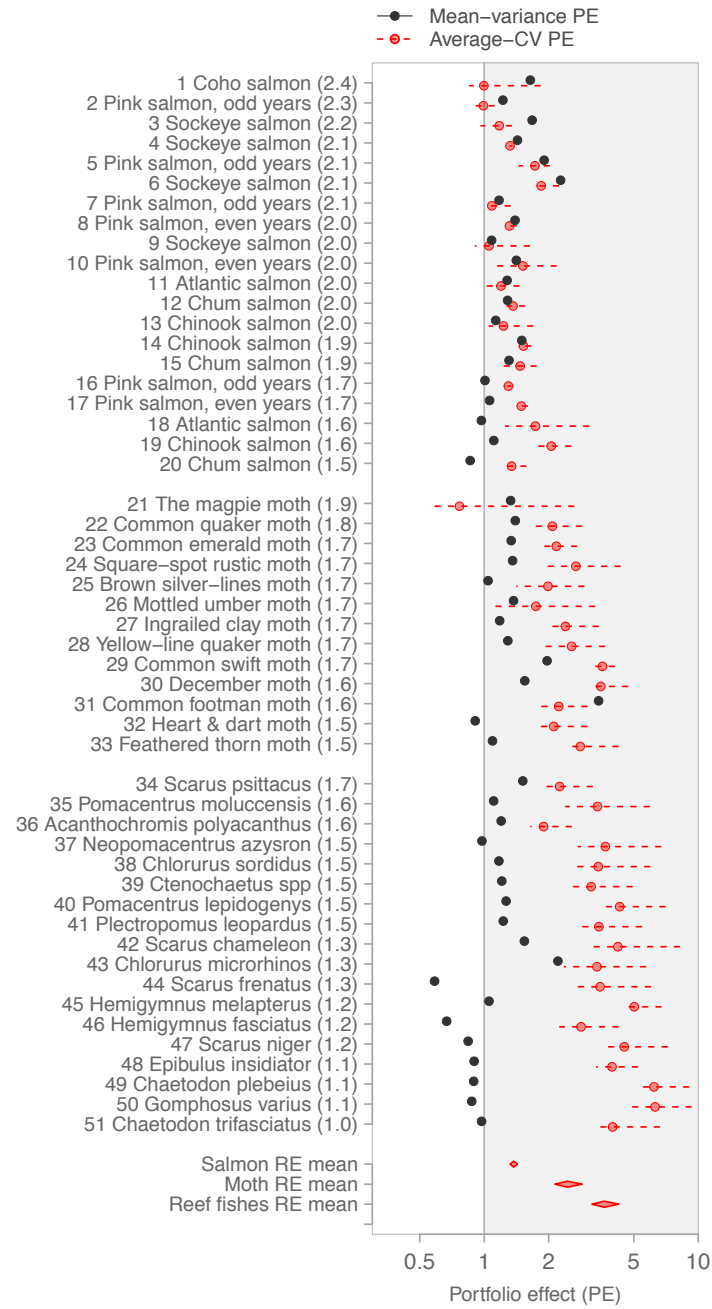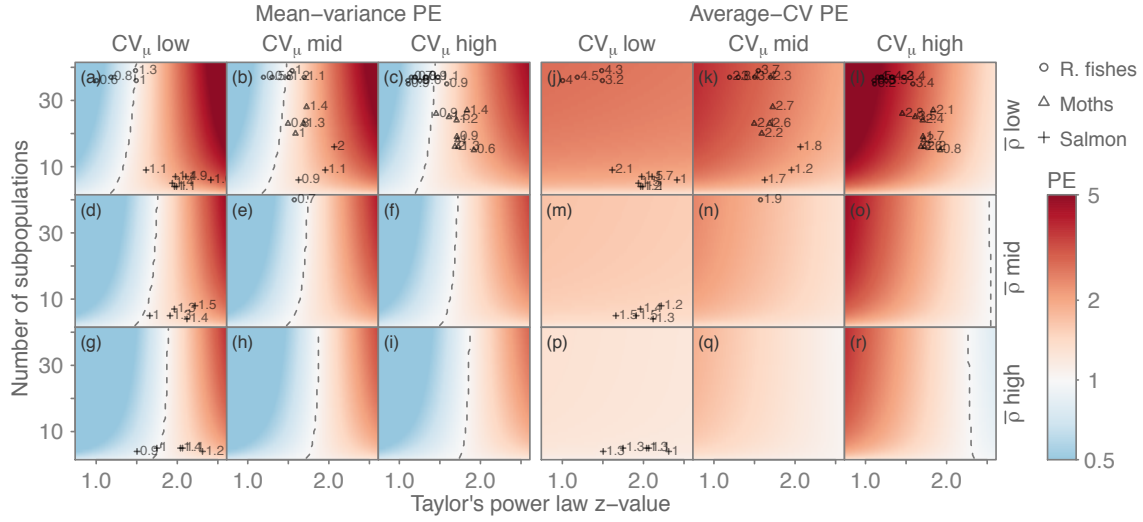
Fig. S7. PEs with the **mean-variance PEs estimated from a linear-quadratic averaged model**. See Fig. 3 for details.

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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.

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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
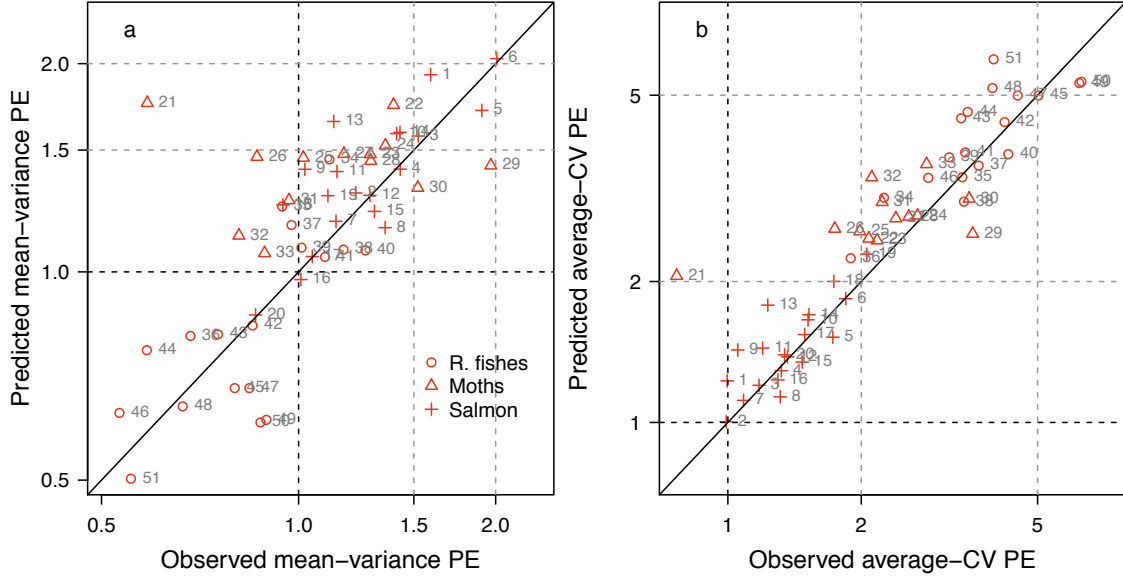
Fig. S11. Predicted vs. observed mean-variance (**a**) and average-CV PEs (**b**). Predicted PEs correspond to the colour underlying the metapopulations displayed in Fig. 5; observed PEs to the values calculated directly from the empirical data and shown in Fig. 3. The predicted PEs are approximate due 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.
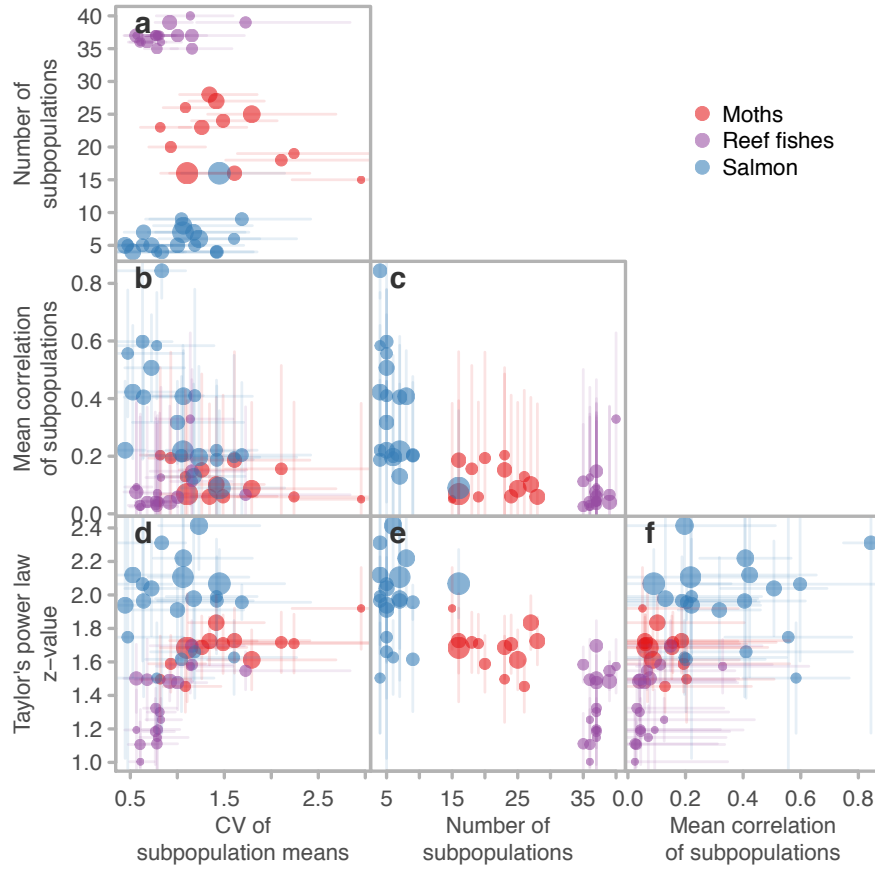
Fig. S12. Relationship between the drivers of the PE in empirical systems for moths (red), salmon (blue), and other taxa (green). The area of the filled circles corresponds to the strength of the mean-variance PE with larger circles corresponding to more stabilizing PEs. Line segments indicate 95% confidence intervals.
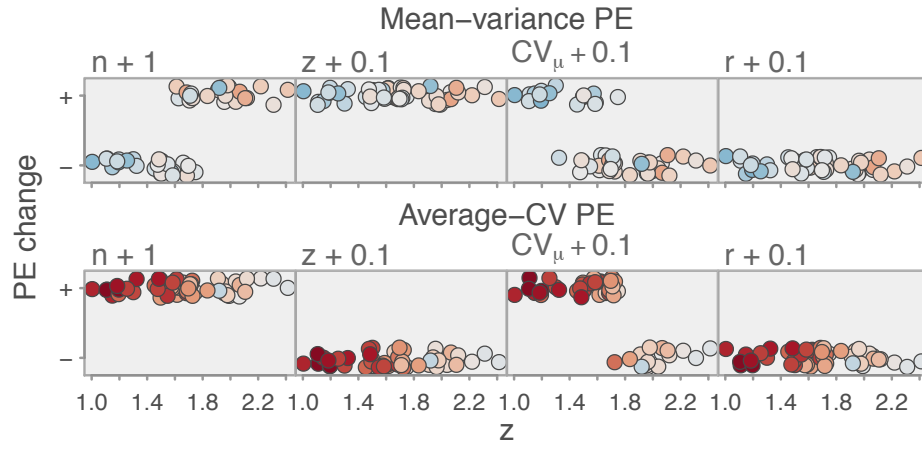
Fig. S13. The PE used as an index of ecosystem change. The upper panel shows the mean-variance PE and the lower panel the average-CV PE. The horizontal axis shows Taylor's power law z-value. The vertical axis shows the change in the PE (more stabilizing $= +$, less stabilizing $= -$). The panels from 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.