

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.

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

Introduction

2 Biological complexity is increasingly recognized as a critical factor underpinning
the stability of ecological systems (e.g. Hilborn *et al.* 2003; Ives & Carpenter 2007;
4 Schindler *et al.* 2010). While the diversity-stability relationship for ecosystem proper-
ties is generally held to be true, what is not known is the relative increase in benefit
6 from each additional element of biodiversity for stability and persistence (Cardi-
nale *et al.* 2012). For example, Schindler *et al.* (2010) found that sockeye salmon
8 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 reduc-
10 tion in the frequency of fishery closures. The stabilizing benefit of such population
diversity is clearly a critical and undervalued component of ecological systems for
12 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
14 *et al.* 2010; Carlson & Satterthwaite 2011; IMCC 2011) derived from theory intro-
duced a decade earlier (Doak *et al.* 1998; Tilman *et al.* 1998; Tilman 1999) that
16 aims to measure the increase in stability due to subpopulation diversity within a
metapopulation (or greater species diversity within a community). For example,
18 we can think of salmon from individual streams as assets (subpopulations) within
a portfolio (metapopulation) that comprises the watershed. If subpopulations react
20 differently to environmental variability, then the metapopulation may experience a
reduced risk of collapse or decline. Similarly, financial managers choose portfolios of
22 diverse financial assets to reduce their risk of financial losses.

Financial managers estimate the benefit of diversifying a financial portfolio by
24 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
26 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
28 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
& 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 *et al.* 1990).

The theoretical work of Tilman *et al.* (1998) implies an alternative way to mea-
sure the empirical PE that accounts for the mean-variance relationship. Rather than
assuming we can represent the variability of the theoretical homogeneous metapop-
ulation (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 subpop-
ulation? 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
2 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.*
4 2009; Schindler *et al.* 2010; Carlson & Satterthwaite 2011)?

Here, we conducted the first large-scale cross-taxa evaluation of the average-CV
6 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-
8 variance PE when applied to theoretical systems with varying z values? (2) How
prevalent and strong is this difference across 51 metapopulations and 1070 subpop-
10 ulations of salmon, moths, and reef fishes? (3) Despite its stronger theoretical foun-
dations, is the mean-variance PE a reliable empirical metric of how subpopulation
12 diversity benefits stability? We conclude with a guide to measuring metapopulation
PEs based on question, study system, and data type.

14 **Materials and methods**

Defining the metapopulation portfolio

16 In our finance-ecology metaphor we represent portfolio value as metapopulation
abundance and financial-asset value as subpopulation abundance. We define meta-
18 populations as groups of subpopulations that behave largely independently but are
linked by dispersal of individuals among subpopulations (Levins 1969). Although
20 our data represent subpopulations in the spatial-metapopulation sense, the meth-
ods in this paper could be applied more broadly. For example, future studies could
22 consider different age classes, different life-history variants, or populations with dif-
ferent thermal-tolerances as subpopulations. Although the PE has also been ap-
24 plied 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
26 portfolio effects, the analysis of PEs in communities is complicated by trophic in-

teractions, changes in mean abundance with increasing diversity (the over-yielding
 2 effect), and differing mean-variance scaling relationships across species (e.g. Loreau
 2010; Thibaut & Connolly 2013).

4 When discussing the properties of metapopulation portfolios we use three terms
 (stability, diversity, and homogeneous population), which we define here. We define
 6 *stability* in terms of the variability (CV) of population trajectories through time.
 We define *subpopulation diversity* as the asynchrony (lack of correlation) between
 8 the groups defined as subpopulations. Since our metrics are phenomenological, they
 don't specify the mechanism generating asynchrony, but a central candidate would be
 10 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*
 12 as a theoretical population the same size as the existing "diverse" population but
 lacking whatever subpopulation diversity we are measuring. For metapopulations
 14 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
 16 with synchronized subpopulation dynamics.

Theoretical evaluation of portfolio effects

18 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
 20 (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.
 22 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
 24 ignored for simplicity), both interpretations of the PE define CV_p for subpopulations
i 1 through *n* as

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

The average-CV PE defines CV_a as

$$CV_a = \frac{\frac{\sqrt{\mu_i^z}}{\mu_i} + \frac{\sqrt{\mu_{i+1}^z}}{\mu_{i+1}} + \dots + \frac{\sqrt{\mu_n^z}}{\mu_n}}{n}, \quad (2)$$

2 whereas the mean-variance PE defines CV_a as

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

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

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

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

We explored the implications of the two PE definitions across four statistical
8 properties that are ecologically meaningful and have precedence in the PE literature
(Tilman 1999; Cottingham *et al.* 2001; Loreau 2010; Thibaut & Connolly 2013): the
10 correlation between subpopulations, the temporal mean-variance scaling relationship
(z), the number of subpopulations, and the evenness of subpopulation mean abun-
12 dance. 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
14 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
16 metapopulations, and for each taxon we diagnose the ecological reasons why the
differences arise.

Empirical evaluation of portfolio effects

2 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, S2). We obtained salmon returns from the primary literature, in particular Dorner *et al.* (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 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 $\log(\mu)$,

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

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 relationship between the first and second halves of the subpopulation time series for the
16 time-series in which one half was at least two-times greater. We compared these 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,

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

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

2 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,
4 our package includes options to fit quadratic mean-variance scaling models, average
across mean-variance model predictions, and detrend non-stationary time-series.

6 Results

Theoretical evaluation of portfolio effects

8 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-
10 CV PE universally becomes more stabilizing (higher PE) as subpopulation number
increases regardless of z , whereas when we account for the mean-variance relation-
12 ship, 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
14 method, although accounting for the mean-variance relationship shifts the PE uni-
formly (assuming even subpopulation sizes) across all correlation values (Fig. 2b).
16 The average-CV PE can erroneously become more stabilizing as subpopulations be-
come uneven; the mean-variance PE indicates that the PE would become less stabi-
18 lizing at high z values or remain relatively constant at low z values (Fig. 2c).

Empirical evaluation of portfolio effects

20 The key assumption that ecological systems have the same mean-variance relation-
ship as financial systems ($z = 2$) does not hold across taxa. Whereas z was not
22 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
24 (3/20), and no overlap for reef fish metapopulations (Figs S3, S4). The inter-

subpopulation mean-variance relationship was a reasonably unbiased proxy for the
2 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
4 high degree of scatter ($R^2 = 0.25$; Fig. S5).

In our empirical meta-analysis, the PEs varied strongly between, but also within,
6 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
8 mean-variance PE suggests the metapopulation portfolio is twice as stable as the
homogeneous single asset. In comparison, the average-CV PE suggests the meta-
10 population 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
12 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).
14 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
16 (mean = 1.3, range = 1.0–1.7), the meta-analytic average-CV PE indicated a sub-
stantially more stabilizing PE (mean = 3.6, 3.2–4.3 95% CI) than the mean-variance
18 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
20 PE. Whereas the mean-variance relationship assumed by the average-CV appears
reasonable for salmon (Fig. 3b), it deviates strongly from the observed relationship
22 for some moth and reef fish metapopulations (Fig. 3c, d).

The mean-variance PE was highly sensitive to the estimation method (Fig. 4). In
24 particular, 13/18 reef fish metapopulations switched from destabilizing to stabilizing
PEs with quadratic (Fig. S6) or quadratic-linear averaged (Fig. S7) models. The
26 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.
28 Linear detrending generally created a similar mean-variance PE pattern to the orig-
inal mean-variance PEs (Figs 4, 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,
2 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.

4 **Diagnosing the ecological properties of empirical portfolio ef- fects**

6 Plotting the empirical metapopulations in the theoretical PE parameter space re-
vealed five key findings (Fig. 5). (1) By viewing the coloured shading of the panels
8 from left to right, we can see that the average-CV PE responds inversely to z com-
pared to the mean-variance PE, and this issue is prevalent for the parameter space
10 observed in real ecological systems. (2) The empirical PEs were strongly grouped
by taxonomy (see also Fig. S10). (3) We did not observe metapopulations that were
12 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
14 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 metapop-
16 ulations 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
18 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)
20 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
22 factors driving the PE co-varied; in particular, we observed high correlation of sub-
populations associated with high variability (CV) and few subpopulations (Fig. S12b,
24 c). High z values occurred when there were few moderately-to-highly correlated sub-
populations (Fig. S12e, f).

26 Discussion

We conclude that the empirical average-CV PE is incompatible with Taylor’s power
2 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
4 PE. In this discussion, we begin by considering the influence of mean-variance scaling
on subpopulation and metapopulation stability and the possible mechanisms behind
6 stabilizing portfolio effects. We then review limitations of these phenomenological
metrics and discuss the potential of mechanistic models. We conclude by synthesizing
8 our results into practical recommendations for quantifying ecological PEs.

The influence of mean-variance scaling

10 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
12 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
14 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
16 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
18 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
20 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
22 and the metapopulation becomes less stable, but the stabilizing effect of diversity
increases.

24 Why is z usually less than two? Explanations tend to fall into one of three
categories. First, the most common explanation is demographic stochasticity. De-
26 mographic stochasticity has been implicated via simple stochastic population growth

models (e.g. Anderson *et al.* 1982; Ballantyne IV 2005) and may be a particularly
 2 strong driver when density dependence generates chaotic dynamics (Perry 1994). In
 simplified theoretical systems, z will tend towards two under conditions that increase
 4 population synchrony (such as strong environmental forcing) and tend towards one
 under conditions that decrease synchrony (such as strong demographic stochastic-
 6 ity) (Loreau 2010). Second, competitive species interactions can affect z values.
 (Kilpatrick & Ives 2003). For example, if competition with other species impacts
 8 larger populations less than smaller populations, then z will be less than two. Third,
 measurement error in abundance estimates (Perry 1981), and particularly rounding
 10 at low abundance (Taylor & Woiod 1982), can create artificially low z values. How-
 ever, it remains unclear which of these three explanations, under what conditions,
 12 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
 14 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
 16 (e.g. Valone & Hoffman 2003).

In financial systems, analysts use the equivalent of the average-CV PE to calculate
 18 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
 20 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
 22 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
 24 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
 26 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
 28 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.

2 The PE metrics in this paper compare the observed metapopulation variability to
the theoretical variability of a single homogeneous population. This homogeneous-
4 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
6 point) or in a diversified portfolio (our comparison). This homogeneous-population
reference point is loosely equivalent to the monoculture reference point often used in
8 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 experimen-
10 tally. For example, researchers might instead choose as a reference point metapop-
ulation variance under a harvesting regime that tends to synchronize subpopulations
12 or metapopulation variance if habitat loss eliminated certain subpopulations.

Mechanisms driving metapopulation portfolio effects

14 Two major mechanisms may generate stabilizing metapopulation PEs. First, di-
versity of phenotypes across subpopulations can cause subpopulations to react dif-
16 ferently to the same environmental forces (response diversity; Elmqvist *et al.* 2003).
Second, since metapopulations can exist over a large area, subpopulations may expe-
18 rience a greater diversity of environmental conditions than an individual population
(i.e. Moran effect). In contrast, non-systematic sources of variability such as demo-
20 graphic stochasticity should not generate stabilizing PEs (Loreau & de Mazancourt
2008). Our results suggest a research agenda that seeks to understand the rela-
22 tive 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 metapop-
ulations would theoretically be less variable as one large homogeneous population
26 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 *et al.* 2006). One explanation for these inverse PEs could be in-
 2 creased demographic stochasticity at low population densities resulting in an Allee
 effect (Allee 1931). Further, Minto *et al.* (2008) demonstrated an increase in the
 4 variability of fish offspring survival at low population densities. The same sized
 metapopulation split into fewer subpopulations might avoid these effects. A second
 6 explanation for these apparent inverse PEs could involve hidden diversity. Other el-
 ements of diversity, such as size and age structure, can be reduced at low population
 8 densities (e.g. Hutchings & Myers 1993). Therefore, inverse PEs could arise if the
 diversity we are measuring (subpopulation number) increases but the unmeasured
 10 diversity within the subpopulations decreases. This hidden diversity may be more
 relevant to stability.

12 **Limitations of phenomenological portfolio effects**

Beyond tending to overestimate the benefit of diversity if $z < 2$, there are potential
 14 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,
 16 if we consider two otherwise similar metapopulations, the average-CV PE will always
 be the same or stronger for metapopulations divided into more subpopulations. How-
 18 ever, the mean-variance PE indicates that there is a threshold at which subdivision
 no longer benefits metapopulation stability (Figs 2a, 5a–i, S13). Second, used as an
 20 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 metapop-
 22 ulation 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
 24 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
 26 space (Fig. 5b cf. c).

Despite its stronger theoretical foundations, we emphasize caution when inter-

2 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
 4 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
 6 population abundance, Perry & Woiod 1992). *Biological uncertainty*: Even if we
 knew the mean-variance model precisely, will the same dynamics persist when ex-
 8 trapolating outside the range of observed data? *Measurement uncertainty*: There
 may be biases in the estimated z values because of observation error (Perry 1981;
 10 Taylor & Woiod 1982), and estimates of z can depend on how time-series are ag-
 gregated (here, what we define as a subpopulation) (Fronczak & Fronczak 2010).
 12 Conclusions drawn from any phenomenological mean-variance relationships should
 be tempered with caveats such as these.

14 The PE metrics measured in this paper are limited by the observational data
 to which they are typically applied. Recent mechanistic stability-diversity models
 16 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.*
 18 2012; de Mazancourt *et al.* 2013) but are still largely unexplored beyond theory.
 However, mechanistic stability-diversity models have at least two major problems.
 20 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
 22 does productivity impact population growth rate through a Ricker or logistic growth
 function? Second, the number of estimated parameters may exceed the power of
 24 most ecological data sets (Thibaut *et al.* 2012). Therefore, there remains a need for
 phenomenological metrics.

26 Practical recommendations for quantifying ecological portfolio effects

2 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 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 “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).

18 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).

- 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.

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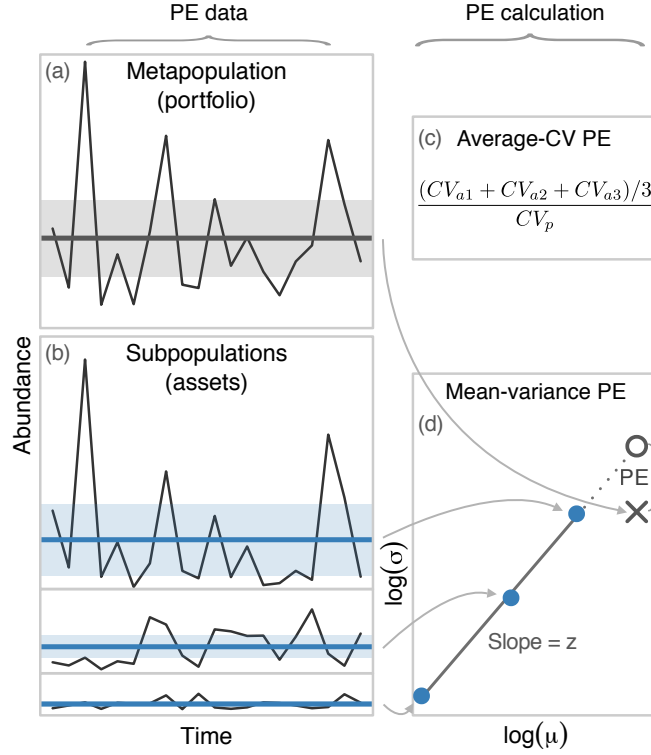


Figure 1: Estimating the two PEs from empirical data. (a, b) Example metapopulation (portfolio) and subpopulation (asset) abundance time-series. Horizontal lines represent the time-series' means and the shaded regions represent variability. (c) We calculated the average-CV PE by dividing the average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

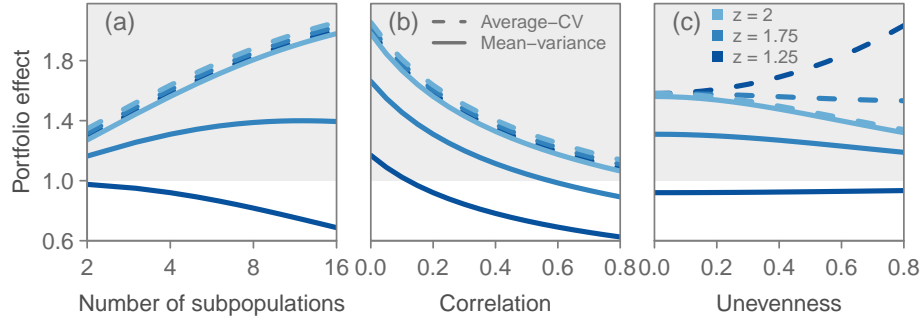


Figure 2: The ecological factors driving the PE in theoretical systems. A PE of two, for example, would indicate a two-fold increase in stability for the portfolio compared to what we would expect in a single homogeneous population of the same size. We show the mean-variance PE and average-CV PE for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

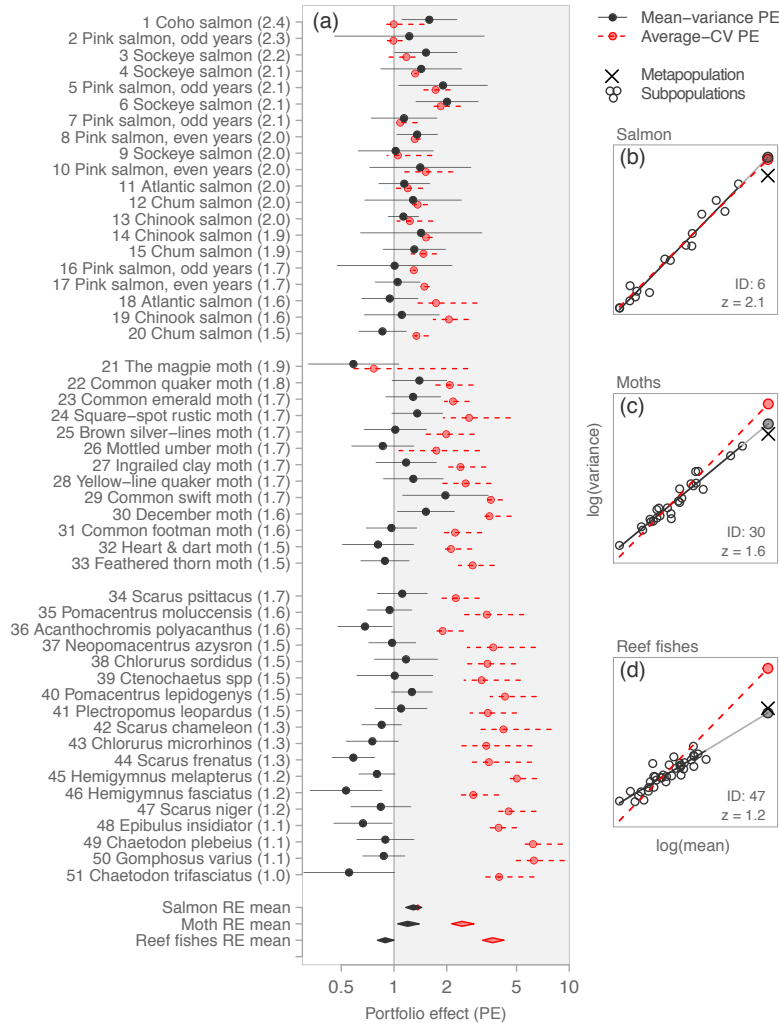


Figure 3: PEs across 51 metapopulations. (a) Empirical PEs (circles) and 95% CIs (lines) for the mean-variance method and the average-CV PE method. We ordered metapopulations within taxonomic groups by Taylor's law z values (indicated in brackets beside each metapopulation name). Diamonds represent inverse-variance 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 \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 average-CV PE and the dashed-red line the mean-variance relationship under the assumption that $z = 2$, as the average-CV PE assumes.

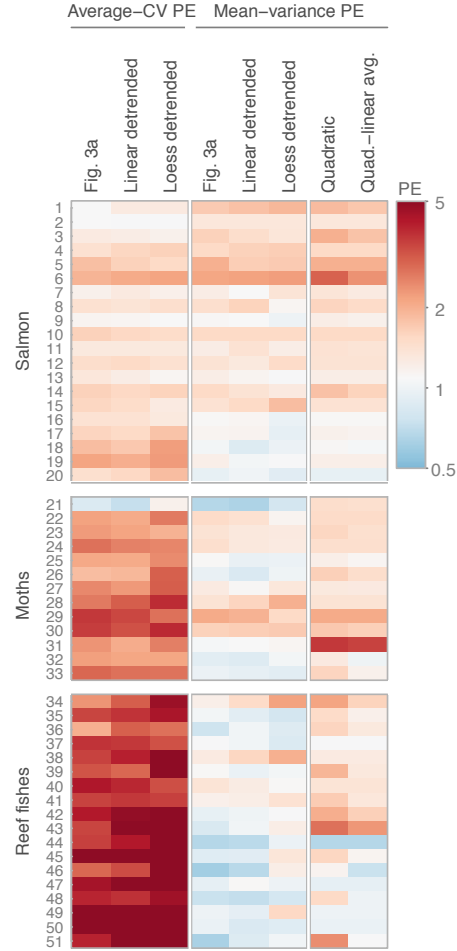


Figure 4: The sensitivity of PE metrics across two detrending (linear and loess) methods (columns 2–3 and 5–6) and three mean-variance model fits (columns 4, 7–8). Columns 1 and 4 represent the same PEs as shown in Fig. 3, but with colour indicating the strength of stabilizing effect. Red indicates a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

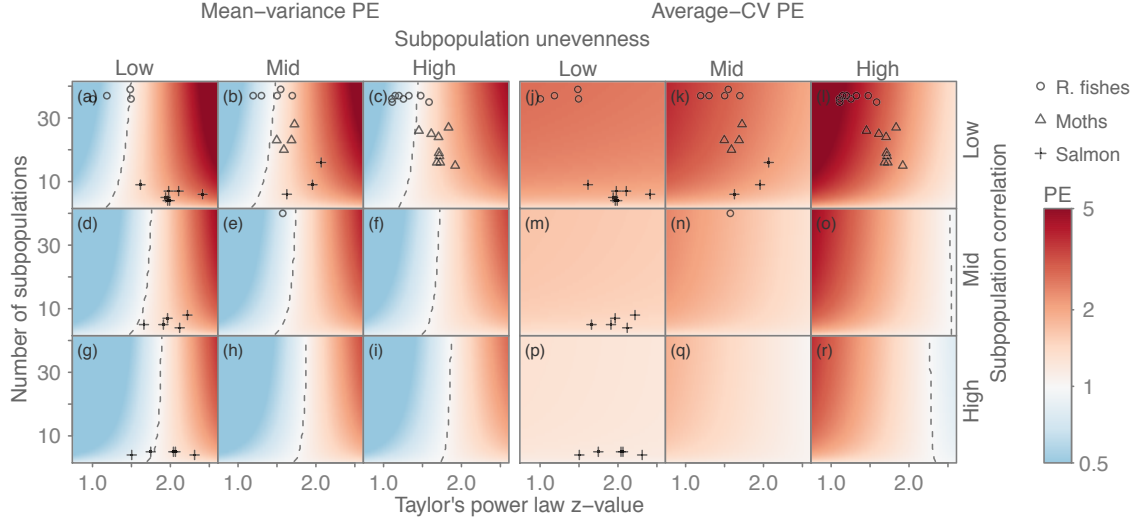


Figure 5: Empirical ecological PEs (points) overlaid in theoretical PE parameter space (colour shading). The colour shading indicates the stabilizing-effect of the theoretical mean-variance PEs (a–i) and average-CV PEs (j–r): red indicates a stabilizing effect and blue indicates a destabilizing effect.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

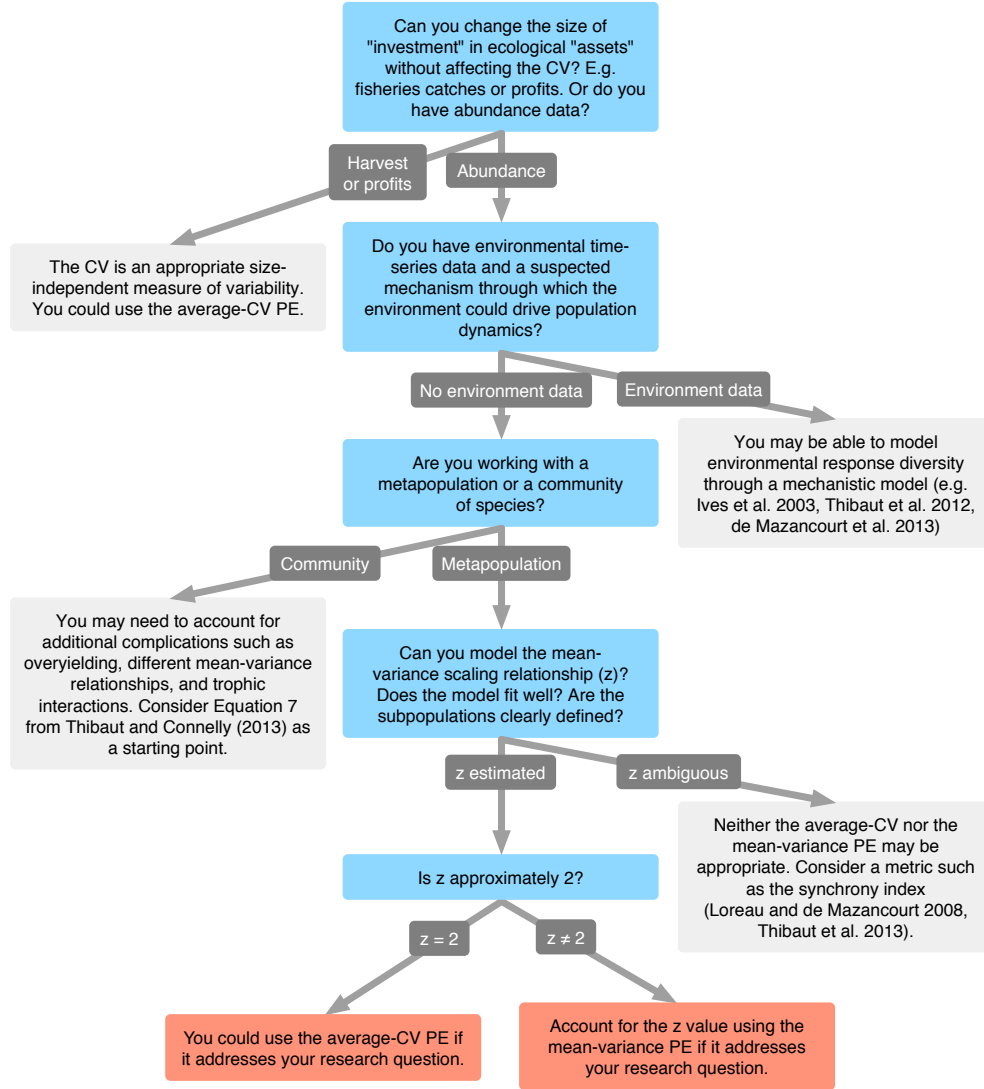


Figure 6: Decision tree showing options for quantifying ecological portfolios. Blue boxes in the middle column show questions to ask of the study system and available data. The orange boxes at the bottom represent the methods demonstrated in this paper. The light-grey boxes along the sides show other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

Ecological prophets: Quantifying metapopulation

2 portfolio effects

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

4 Supporting Information

R package to estimate metapopulation portfolio effects

6 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:

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

Then, to install the included package:

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

or to install the current version from the web:

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

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

```
library(ecofolio)  
16 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. S2). 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. S1.

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. S2). All data represent annual estimated returns — fisheries catch plus escape-
ment 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 sub-
population 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)
2 biologically-based response diversity to the environment (e.g. genetically-based vari-
ation in thermal tolerances) (e.g. Eliason *et al.* 2011). These patterns of asynchrony
4 can play out not just at the decadal scale but also over centuries (Rogers *et al.* 2013).

Moths

6 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
8 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
10 (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
12 1948; Taylor & French 1974; Conrad *et al.* 2004). Although different species may
show different responses to the traps (Miurhead-Thomson 1991; Woiwod & Hanski
14 1992), we compare across sites within the same species so this should not affect our
results.

16 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)
18 and single annual flight episodes since we were aggregating the data annually to
maintain consistency with data from other taxonomic groups that were available.
20 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
22 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
24 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
26 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;
2 Taylor & Woiwod 1980; Perry 1981). This early work focussed on behavioural prop-
erties that might regulate the stability and variance of moth populations (Taylor &
4 Woiwod 1980). Work has continued with these datasets and studies have shown a
number of mechanisms generating stability. For example, authors have shown spatial
6 asynchrony (Gaston 1988), polyphagy (eating different kinds of food) (Redfearn &
Pimm 1988), and density dependence to act as stabilizing forces (Hanski & Woiwod
8 1993).

Reef fishes

10 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
12 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
14 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-,
16 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
18 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
20 transects. AIMS only censuses fish one year or older since recruitment can be highly
spatially and temporally variable. AIMS conducts annual standardization exercises
22 to avoid temporal bias in counts within and across divers (Halford & Thompson
1994).

24 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 isola-
26 tion. 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
 2 disease resistance (Raymundo *et al.* 2009), presumably enhancing stability. Inde-
 pendent of functional roles, Mellin *et al.* (2010) found that small, isolated reefs have
 4 higher population variability and therefore higher probability of local extinction.

Diagnosing the ecological properties of empirical portfolio ef- 6 fects

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

12 To present our results graphically in Fig. 5, we categorized the mean correlation
 of the empirical subpopulations ($\bar{\rho}$) into bins of $0 \leq \bar{\rho} < 0.25$, $0.25 \leq \bar{\rho} < 0.5$,
 14 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
 16 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
 18 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
 20 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
 22 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
 24 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
 26 log-mean.

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