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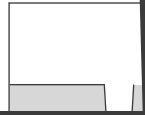
that undergoes an sudden shift, due to some abrupt environmental change, but subsequently remains stable at a new carrying capacity of 10 for the next 50 years. Following this, it then returns to the old carrying

value of abundance relative to every other value of abundance, similar to metrics like Kendall's test for trend, we consider all possible combinations of abundance (C) which can be calculated from the number of time steps n in the time series as:

$$C = \frac{n(n-1)!}{2} \tag{1}$$

We can then define z as the list of these possible pairwise comparisons; therefore $z = 1 \ldots C$). Each z therefore represents a pair of time steps z_i and z_j to be compared by the difference function D(z). This function simply calculates proportional difference between each z pair of abundances:

$$D(z) = \begin{cases} 0 & \text{if } z_i = z_j \\ \dfrac{ABS(z_i - z_j)}{MAX(z_i, z_j)} & \text{if } z_i \neq z_j \end{cases} \tag{2}$$

Using absolute value of the difference between z_i and z_j divided by the larger number simply ensures the proportion is the same even if we switch the values of z_i and z_j. That is, if $z_i = 10$ and $z_j = 100$, $D(z) = 90/100 = 90\%$, and likewise if $z_i = 100$ and $z_j = 10$, $D(z)$ is still $90/100 = 90\%$ (and not e.g. $90/10 = 900\%$). It is established that comparisons of absolute values, such as mean absolute deviation, provide more robust estimators (Press 1989). PV similarly uses absolute comparisons of abundance, however instead of standardizing using deviation from the mean, Eq. 2 standardizes by calculating the proportional difference between each value of abundance, i.e. the difference over the maximum. In fact, although Eq. 2 represents the framework in which PV was developed, it can be algebraically transformed to:

$$D(z) = 1 - \frac{\min(z_i, z_j)}{\max(z_i, z_j)} \tag{3}$$

indicating that it is based on a ratio comparison of each value in the time series. In this manner, abundance at every time step is compared with that at every other time step, yielding a distribution of proportional differences D(z). While it may be interesting to investigate frequency distributions of D(z) scores, most often an average will provide an adequate summary of population variability PV:

$$PV = \frac{\sum\limits^{z} D(z)}{C} \tag{4}$$

We can therefore calculate variability based on a simple but thorough comparison of all abundances in a time series. Equation 2 calculates proportional difference, so the domain of D(z) and PV is [0, 1] in contrast with SDL and CV, which, at least in theory, is [0, ∞). A score of zero represents complete stability among years (i.e. 1/PV measures stability), while a value of 1 is approached as differences in population size approach infinity.

Like SDL and CV, the chronology of abundances is irrelevant and in fact, the PV approach quantifies differences across all time-lags. As chronology is irrelevant, autocorrelation structure will not influence the value of PV; the same time series could be randomly reorganized and lead to the same value of PV. However, it is noteworthy that sorting time series by abundance, rather than by time, can provide some insight into the behaviour of the different variability metrics. In this manner, trends in the ranked abundances can reflect underlying variability; for example, if sorted abundances exhibit no trend (constant abundance), then PV is equal to zero. In contrast, if the sorted abundances progress geometrically, then PV will approach 1. Intermediate between these extremes, PV will approach 0.5 when the sorted abundances approach an arithmetic progression, where the common difference of the progression and the lowest abundance have the same value. This can be understood by realizing that, in such cases, the frequency distribution of pair-wise propor-

measure of variability precludes direct testing of any metric, making example analyses using real or population model data a relatively uninformative exercise. For this very reason, it is useful to have several different metrics in our toolbox which allow us to characterize different things about a time series, and a comparative approach can provide significant insight. As an important first step, it is desirable that PV behave similarly to CV and SDL for 'well behaved' Gaussian time series. PV, CV and SDL were calculated for 100 time series simulated with random mean [100,1000] and standard deviation [0,100] over 100 time steps. Correlation coefficients were calculated to evaluate concordance between PV, CV and SDL. This entire process was repeated 1000 times. PV was strongly correlated with both CV (mean $r = 0.997 \pm 0.001$ SD) and SDL (mean $r = 0.967 \pm 0.012$ SD). Therefore, PV behaves the same as CV and SDL for 'normal' (Gaussian) populations, as desired and expected. However, the necessity for an additional approach and a major advantage of PV is it's robustness to non-Gaussian behaviour. I herein discuss how PV addresses and resolves several issues of non-Gaussian behaviour associated with CV and SDL.

The effect of zeros

The presence of zero counts in biological time series is a major issue, and prevents using SDL as (Log 0) is undefined (Taylor 1961, McArdle et al. 1990). A first step is to consider the appropriateness of including zeros. Including data when the population is absent is uninformative if variability of the population is of interest but rather indicates variation of animals at a site (McArdle and Gaston 1993). In meta-population contexts, including local extinctions in sub-population variability could be important, particularly when evaluating local demographic differences (e.g. source-sink dynamics; Howe et al. 1991). When including zeros is important, often an arbitrary constant a is added (i.e. $SD[Log(N+a)]$), however this means variability is no longer on a proportional scale and is severely biassed at low abundances (Gaston and McArdle 1994). PV calculates proportional differences using Eq. 2 which keeps $D(z)$ defined when either z_i or z_j equals zero. Such comparison between 'extant' and 'extinct' years is the only situation where $D(z) = 1$; otherwise $D(z)$ approaches 1 as the difference approaches infinity. The if condition ensures $D(z) = 0$ whenever $z_i = z_j$ including $z_i = z_j = 0$. If including zeros is important to the research question, then $z_i = z_j = 0$ can be biologically defined as "stabily extinct". It is important to note that I have been discussing true zeros: zeros due to sampling error will require careful consideration (McArdle and Gaston 1993, Gaston and McArdle 1994, McArdle and Gaston 1995).

Independence of average deviation from the mean

As mentioned in section 1, even though statistical measures of variability based on deviation from the mean can be calculated independent of the mean (i.e. by using the mean sum of squared differences), the proof of the equivalence of these approaches indicates that average deviation from the mean still underlies these metrics, regardless of how they are calculated. While no such proof exists for PV, simulations can be used to determine if PV is correlated with average deviation from the mean (ADM). Of course, given it has been demonstrated that PV behaves similar to CV and SDL for 'normal' populations, we would expect it to be correlated to ADM for Gaussian data, even though, unlike SDL and CV, it is not fundamentally based on deviation from the mean. However, for very non-Gaussian data, such as the heavy tailed Cauchy distribution, PV should not be correlated with ADM unless ADM somehow some how underlies PV. (Note that, although the mean and ADM can be calculated for any set of numbers/abundances, the mean is actually undefined for the Cauchy distribution). 100 time series of 100 units were generated to fit the normal distribution (mean $[1000-4000]$, SD $[10-90]$) and the heavy-tailed Cauchy distribution) location $[1000, 5000]$, scalar $[10, 100]$). For each time series, PV, CV and SDL were calculated, and correlation with ADM was determined across the 100 time series. This entire process was repeated 2000 times for each distribution. Figure 3 indicates, that as expected, each metric is correlated with average deviation from the mean for the normal distribution. However, unlike SDL and particularly CV, PV is not correlated with average deviation from the mean for the very non-Gaussian Cauchy distribution. While indirect, and not as elegant as a mathematical proof, this result indicates that average deviation from the mean is not an underlying feature of PV. As discussed previously, this is desirable for considering 'rare' events and comparing populations undergoing different dynamics, including those exhibiting non-Gaussian patterns of abundance.

Rareness and the 'extreme-event' issue

Extreme sensitivity of SDL and CV to rare events has been recognized as a serious issue (for example, see Pimm's (1991) analysis of song thrush populations which crashed following an extreme winter). While it may be tempting to exclude such 'outliers', this is undesirable as both rare and common events are expected to be important in ecology (Halley 1996). The remainder of this section and the next deal with devising a quantitative way to illustrate that PV is a more 'robust' measure than CV or SDL, in that it

Correlation coefficent

Normal
Distribution

functions more appropriately across time scales, and is not over-sensitive to rare events, but rather handles them in a fair and desirable manner.

An exciting recent line of research is focussed on investigating coupling between environmental and biological variation with important implications for understanding responses to environmental change. Many physical processes show scaling relationships with time, exhibiting more variation as time scale increases (Steele 1985; this has been termed spectral 'reddening', with analogy to visible light, to reflect the dominant importance of low frequency processes; Schneider 1994, Halley 1996). It has therefore been of interest to ask if reddened physical processes can force more time−more variation effects in ecological systems, in contrast to common assumption that ecological stochasticity follows a white-noise model (equal contribution across frequencies).

More time−more variation (reddening) of population abundances has been observed across a wide variety of taxa (Pimm and Redfearn 1988, Arino and Pimm 1995, Cyr 1997, Inchausti and Halley 2002) often using SDL or CV to measure variability. However, rare events can produce reddening in otherwise stationary time series (Mandelbrot 1999, Inchausti and Halley 2002). Spectral analysis more accurately evaluates reddening and therefore provides a gold standard against which to compare and evaluate the robustness of SDL, CV and PV. Therefore, time series of stable populations undergoing rare events were generated for 100 time steps. Abundance at each time step was randomly selected from normal distributions of known mean and standard deviation. Rare-crashes (stable at 100 ± 5, crashed to 10 ± 5) were simulated for 1000 time series, and rare-outbursts (stable at 10 ± 5, outburst to 100 ± 5) for an additional 1000 time series. Rare events were set to occur at a frequency of 0.02, 0.05 and 0.1. An additional 2000 time series were simulated to fit the heavy tailed Cauchy distribution (random location parameter [1000,5000]; random scale parameter [10,100]). For each randomization (8000 time series), variability was measured over all time scales from 3 to 100 time steps using variance growth exponents after Inchausti and Halley (2002), with each of SDL, CV and PV as metrics. Variance exponents γ measure increase in variability over time quantified as regression slope of log variability against log time scale $\gamma = 0$ indicates white noise; $0 < \gamma < 1$ indicates decelerated increasing variance; $\gamma = 1$ indicates a random walk; $\gamma > 1$ indicates accelerating increasing variance; see Inchausti and Halley 2002 for details). Spectral exponents (SE; zero indicates white-noise, greater values indicate reddening) were calculated as (negative) regression slope of log spectral density versus log frequency from spectral analysis (Inchausti and Halley 2002). SE therefore provided a standard to confirm simulated

time series met white noise criteria (SE < $|\pm 0.1|$), and

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