





The consecutive disparity index, D : a measure of temporal variability in ecological studies

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Abstract. Temporal variability in ecological processes has attracted the attention of many disciplines in ecology, which has resulted in the development of several quantitative indices. The coefficient of variation ($CV = \text{standard deviation} \times \text{mean}^{-1}$) is still one of the most commonly used indices to assess temporal variability, despite being known to present several problems on its assessment (e.g., mean dependence or high sensitivity to rare events). The proportional variability (PV) index was developed to solve some of the CV's drawbacks, but, so far, no variability index takes into account the chronological order of the values in time series. In this paper, we introduce the consecutive disparity index (D), a temporal variability index that takes into account the chronological order of the values, assessing the average rate of change between consecutive values. We used computer simulations and empirical data for fruit production in trees, bird counts, and rodent captures to compare the behavior of D , PV, and CV under different scenarios. D was sensitive to changes in temporal autocorrelation in the negative autocorrelation range, and CV and PV were sensitive in the positive autocorrelation range despite not considering the chronological order of the values. The CV, however, was highly dependent on the mean of the time series, while D and PV were not. Our results demonstrate that, like PV, D solves many of the problems of the CV index while taking into account the chronological order of values in time series. The mathematical and statistical features of D make it a suitable index for analyzing temporal variability in a wide range of ecological studies.

Key words: coefficient of variation; disparity; proportional variability; temporal dynamics.

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INTRODUCTION

Knowing how and why systems fluctuate with time is of paramount importance for a better understanding of how they work. The study of temporal variability has, therefore, attracted the attention of a wide variety of empirical and theoretical ecologists. Temporal variability have been

studied in various systems and using very different approaches among subdisciplines, such as resource pulse ecology (Yang et al. 2008), the study of temporal variability in ecosystem productivity (Knapp and Smith 2001), the study of chaotic fluctuations of ecosystems (Hastings et al. 1993), studies of masting (Norton and Kelly 1988), or the study of population abundances

(Heath 2006). Obtaining reliable measures of temporal variability is, therefore, of major importance in these fields of ecology.

Temporal variability in population abundances, such as bird counts, has been extensively discussed (McArdle et al. 1990, McArdle and Gaston 1995, Leirs et al. 1997, Heath 2006) because of its implications in evolutionary ecology, population dynamics, the transmission of infectious diseases to humans, and the evaluation of extinction risks (Heath 2006). Temporal variability in the field of population dynamics has been mostly assessed using the coefficient of variation (CV) or the standard deviation (SD) of log-transformed time series (i.e., $SD[\log(N_t + 1)]$; Inchausti and Halley 2002, Heath 2006; where $N_t + 1$ are the values of the time series plus a unit to avoid zero values). A mean fluctuation of 100 individuals represents low variability in a mean population of one million but huge variability in a population of 200. This is why the CV has been used more often than the SD when comparing variability among groups with very different means. Mast seeding studies are also very dependent on the correct assessment of variability. Masting is a reproductive phenomenon that mainly consists in erratic and extremely variable production of fruits, combining years with very large fruit crops and years with very low fruit production, occurring synchronously among individuals (Kelly and Sork 2002, Koenig and Knops 2005, Fernández-Martínez et al. 2016b). So far, masting behavior has been numerically described mostly using the indices of the coefficient of variation ($CV = SD \times \text{mean}^{-1}$) and temporal autocorrelation (AR, i.e., correlation with previous values at different lags; Kelly and Sork 2002, Fernández-Martínez et al. 2015).

The CV, though, has some limitations describing temporal variability, despite being the most common index for assessing variability (Martín-Vide 1986, McArdle et al. 1990). First, the CV is, by definition, inversely proportional to the mean of the time series. However, because SD also increases with the mean, dividing SD by the mean allows an easier comparison between datasets. Nonetheless, comparing several time series with very different means, especially when some mean values are between 0 and 1, may thus lead to biases in temporal variability. This makes differences in variability to be confounded with differences in means. Second, the CV is very

sensitive to rare events, and therefore, analyzing non-Gaussian data (e.g., data with highly skewed distributions) with CV may lead to misleading conclusions. Third, the estimation of variability with CV increases with increasing length of the time series (despite those being detrended; Heath 2006). And fourth, and despite not being a formal drawback, CV is insensitive to the chronological order of time series. Therefore, autocorrelation structure should not influence the value of CV and the reorganization of a time series should lead to the same value of CV.

To solve some of the abovementioned problems of CV, Heath (2006) defined the proportional variability index (PV). The PV index assesses variability by calculating the average proportional variability among all possible combinations of values in a time series as follows:

$$PV = \frac{2 \sum z}{n(n-1)} \quad (1)$$

where z is calculated as

$$z = 1 - \frac{\min(z_i, z_j)}{\max(z_i, z_j)} \quad (2)$$

where n represents the number of values in a variable, and z represents the list of individual values from which to calculate the pairwise comparisons (e.g., observation z_i vs. observation z_j). Eq. 1 differs from the original one written in Heath (2006) because there was a mistake calculating the number of combinations (an unnecessary factorial), further corrected in Rouyer et al. (2010) and Heath and Borowski (2013). It is, therefore, an index restricted to values between 0 (minimum) and 1 (maximum variability, only achieved when time series are of length 2 and one of its values is 0). Notice, though, that estimates of variability in time series containing both positive and negative values will lead to misleading results (Eq. 2). Contrarily to CV, the estimation of variability with PV does not increase with increasing length of the time series and it has been proven robust assessing variability of non-Gaussian data as well (Heath 2006). Additionally, the way PV estimates variability solves the dependency of variability values on the mean of time series. However, despite PV was meant to be used for assessing temporal variability, it does not take into account the chronological order of

values in time series despite being, in fact, an indispensable feature of time series.

Two time series with identical means and SDs can have completely different temporal behaviors and hence completely different biological consequences. In Fig. 1a and 1b, both time series have the same CV and PV but completely opposite temporal behaviors. The first time series is stable during the first half and shifts to a second state of stability, but the second time series fluctuates every year. Instead, in Fig. 1c, both time series present similar temporal autocorrelation but different variability and, therefore, different

CV and PV indices. Hence, it is warranted that the assessment of temporal variability takes into account the chronological order of time series, not only because different autocorrelation structure can lead to very different biological scenarios but also because the order of values is what defines the concept of time itself. To the best of our knowledge, there is no state of the art index sensitive to variability and autocorrelation at the same time. This insensitivity of the CV to temporal autocorrelation was the main motivation for the development of the consecutive disparity index, D . D assesses the consecutive variations in

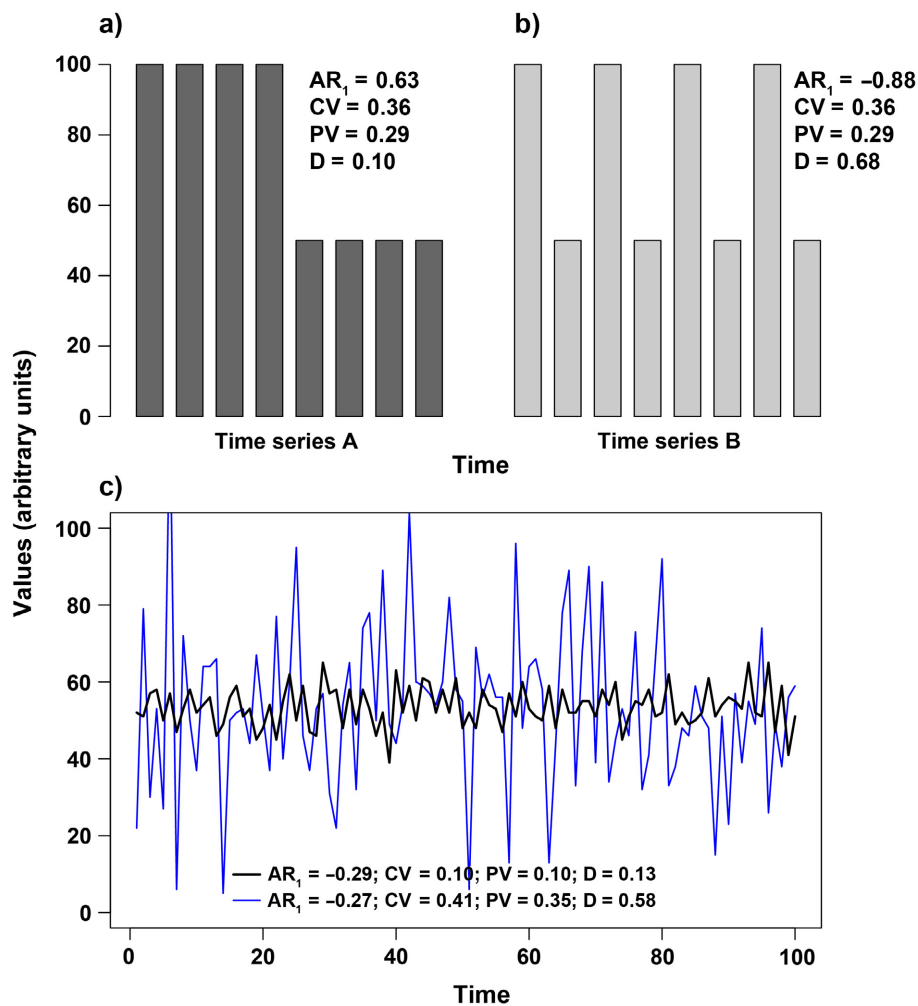


Fig. 1. Panels (a) and (b) show the comparison of two time series with equal means and standard deviations but different autocorrelation structures, and panel (c) shows comparison of two time series with similar AR_1 but different variability. Acronyms: AR_1 , autocorrelation coefficient for lag 1; CV, coefficient of variation (standard deviation \times mean⁻¹); PV, proportional variability; and D , disparity index (see Eqs. 3 and 4).

a time series, and therefore, it is sensitive to real time-step to time-step variations, leading to different values for the different time series presented in Fig. 1a and 1b. In layman’s terms, it assesses the average rate of change between consecutive values. A summary of the main features of CV, PV, and D can be found in Table 1.

D was used in climate research to better assess interannual variability in the highly irregular precipitation time series of the Iberian Peninsula (Martín-Vide 1986, 2002, Lana and Burgueño 2000, Lana et al. 2004, Meseguer-ruiz et al. 2014, Meseguer-Ruiz et al. 2016) and only recently introduced in the field of ecology to study masting behavior (Fernández-Martínez et al. 2016a). D is calculated as

$$D = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1}}{p_i} \right| \quad (3)$$

where p_i is the series value at time i , and n is the series length.

To avoid numerical indetermination (division by 0 or negative values) when a time series contains zeros, a constant (k , usually a unit) can be added to all values of the entire time series as

$$D = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1} + k}{p_i + k} \right|, \quad (4)$$

Including a constant to avoid zero values has been suggested to bias variability estimation at low values (Gaston and McArdle 1994). Also,

because the core of D lies in the assessment of temporal variability by taking into account the consecutive changes in a time series (see Eqs. 3 and 4), removing any time step would entail misleading results. Therefore, when comparing D of different time series, a different constant should be used for each dataset, yet all constants should represent a similar proportion from each dataset’s mean (e.g., 1% of the mean of the time series) in order to apply the same bias in variability estimation. The constant, though, must be chosen carefully; applying a constant of 1% or less of the value of the mean of the time series will change D by 1% or less (Appendix S1: Fig. S1), which is acceptable given the fact that very few ecological variables can be measured with such high accuracy.

Hence, from the formulation of D we can deduce that the estimations of D will be, like PV, independent of the mean of the time series, since it calculates the natural logarithm of the proportion of consecutive values. Therefore, it is expected to be also robust against non-Gaussian data and the length of time series. Additionally, because D is sensitive to the chronology of time series, estimation of variability will be lowest when a time series is chronologically sorted in an ascending or descending way. Hence, assessment of variability with D in non-stationary time series can lead to misleading conclusions. This means that de-trending time series is recommended as mentioned before.

Table 1. Summary of the main mathematical properties of the variability indices used.

| Feature | CV | PV | D |
|---|---------------------------------------|---|---|
| Range | 0–∞† | 0–1 | 0–∞ |
| Minimum | 0 when $X_i = X_{i+1}$, for all i | 0 when $X_i = X_{i+1}$, for all i | 0 when $X_i = X_{i+1}$, for all i |
| Maximum | – | When $n = 2$, $X_1 = 0$ and $X_2 \neq 0$ | – |
| Chronological order matters | No | No | Yes |
| Approach | Overall assessment of the time series | All pairwise proportional comparisons | Log-proportional comparison of consecutive values |
| Sensitivity to mean‡ | High | Low | Low |
| Sensitivity to temporal autocorrelation | Low | Low | High |
| Sensitivity to length of time series | High | Low | Very low |

Note: En dash indicates no theoretical maximum.

† Negative values are only possible when the mean of a time series is negative. In that case, the absolute value of the CV can be used.

‡ Sensitivities based on the results presented in this study and references herein.

The aim of this study was to compare the assessment of temporal variability of D , PV , and CV for capturing temporal variability in different computer simulations and real ecological time series. We first performed computer simulations to demonstrate the different behaviors of the D , PV , and CV indices relative to different distributions and temporal autocorrelation. We then continued exploring the behavior of D , PV , and CV indices using time series of annual fruit production in forests, annual bird counts, and a monthly time series of rodent captures.

MATERIALS AND METHODS

Simulations

We compared the behavior of D and PV , despite the fact that PV does not take into account the chronology of the time series, because PV was defined to assess temporal variation in population abundances (Heath 2006). Hence, D and PV were both defined for the same purpose, to assess variability in temporal datasets. To study the responses of the PV , CV , and D indices to different distributions and temporal autocorrelations of the time series, we simulated 1000 time series for eight different scenarios being: (1) a Gaussian distribution of mean = 100 and standard deviation $SD = 5$; (2) a Gaussian distribution of mean = 100 and $SD = 25$; (3) same as (2) with an autoregressive structure or ARMA [$p = 1, q = 0$] (autoregressive structure for lags until [p] and moving average for lags until [q]) and a temporal autocorrelation coefficient for lag 1 (AR1, a measure of correlation between all pairs of consecutive points in a time series) of $AR1 = -0.1$. To simulate these time series, we used the `arima.sim` function in R (R Core Team 2015) and removed the first 100 simulated values to stabilize the time series; (4) same as (3) with $AR1 = 0.5$; (5) same as (2) including a probability of 0.05 of having a rare event (of doubling the value or reducing it to one-fourth); (6) same as v but with a probability of 0.1 of having a rare event; (7) a negative binomial distribution of mean $\mu = 100$ and a size (or inverse of the dispersion) of 4; and (8) same as (7) but with size = 2. This test will provide information on how the three indices vary when estimating variability from time series with different statistical distributions, allowing a direct comparison among them.

We also studied whether PV , CV , and D increase their estimates of variability when lengthening the time series. To do so, we calculated their variance exponents (γ , regression estimates of the natural logarithm of variability with natural logarithm of time window [k], being: $3 \leq k \leq n$ where n is the length of the time series) as described in Inchausti and Halley (2002). Variance exponents for D , PV , and CV were calculated for six different scenarios of 1000 time series of 100 randomly generated values. Five of them were generated using a Gaussian distribution of mean = 100 and $SD = 5$. One of them did not include any other calculation, two of them had temporal autocorrelation ($AR1 = -0.5$ and 0.5), and two of them presented rare events with a probability of 0.05 and 0.1. The last of them was a negative binomial distribution of $\mu = 100$ and a size = 1. $\gamma = 0$ indicates the time series follows a white noise process, while $0 < \gamma < 1$ indicates decelerated increasing variance. $\gamma \geq 1$ would indicate accelerated increase in variance with the lengthening of the time series. For each simulation, we used t -test to check whether the mean of the distributions of the variance exponents differed from 0. Robust estimates of variability should not increase with lengthening of the time series and, therefore, should present variance exponents close to 0.

Data for fruit productions, bird counts, and rodent captures

To further study the behavior of the D , PV , and CV indices with $AR1$, we downloaded litterfall data from the ICP Forests database (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forest, operated under the UNECE Convention on Long-range Transboundary Air Pollution, <http://icp-forest.net/>), containing data for fruit production for several forest tree species in Europe. The database contained data from 210 plots, for which only 113 were used in models (only plots with at least five consecutive years of data were used). Fruit production was summarized per plot and year in $\text{g C m}^{-2} \text{ yr}^{-1}$. We calculated the variability (D , PV , and CV) and the temporal autocorrelation coefficient at lag 1 ($AR1$, `acf` function in R) indices and the average value of the time series for each plot.

We also used data from the North American Breeding Bird Survey Dataset 1966–2014 (Pardieck

et al. 2015, www.pwrc.usgs.gov/BBS/RawData). Bird-count data per year and species were downloaded for Quebec (Canada) for 242 species. Similar to the fruit-production data, we calculated the variability and autocorrelation indices and the average counts for each species.

Finally, we obtained rodent data from a long-term (1978–2002) monitoring and experimental manipulation study in the Chihuahuan Desert ecosystem (Morgan Ernest et al. 2009) and calculated monthly captures and annual mean monthly captures. We then calculated the annual variability and autocorrelation (AR1) indices using the average of the 12 months as an example of an assessment of intra-annual variability or seasonality.

Overall, we used 355 time series of different nature with which we tested D , PV, and CV variability indices. The fact that the time series comprised almost the whole spectrum from negative to positive AR1 makes the election of these datasets a good approach to understand the differences in behavior of the three variability indices used.

Statistical analyses

We performed linear regressions using ordinary least squares to correlate the D , PV, and CV metrics to AR1 for the data for fruit production and bird counts. We also constructed models in which D , PV, and CV were to be predicted by AR1, the log-transformed mean of the time series, and the CV (to predict D and PV) or PV (to predict CV) metrics. These analyses were performed to evaluate which proportion of the variance in the estimates of variability provided by the different indices of variability (D , PV, and CV) can be explained by (1) the stochastic variability itself (using CV or PV indices), (2) temporal autocorrelation at lag 1, and (3) the mean of the time series. These analyses thus show which indices are more robust estimating variability, given that robust estimates should be independent of the mean of the time series. They also provide insights into how temporal autocorrelation can affect estimates of variability. In order to assess the variance explained by the predictors, we used the proportional marginal variance decomposition (PMVD metric; Grömping 2006, 2007). We used the relaimpo package to perform this analysis in R.

RESULTS

Our simulations showed that CV, PV, and D indices behave very similarly for normally distributed time series (Fig. 2). However, D experienced a strong increase with respect to CV and PV indices for the negatively autocorrelated Gaussian time series, which demonstrates its sensitivity to the chronological order of time series. On the contrary, D was very similar to CV and PV indices for positively autocorrelated time series (Fig. 2). This difference in behavior of D for positively and negatively autocorrelated time series lies in the fact that, given the same variability, consecutive variability is lower in positively autocorrelated than in negatively autocorrelated time series (see Fig. 1a and b). For non-Gaussian distributions (Fig. 2, negative binomial plots), D was higher than CV and PV in almost all simulations. Also, D increased more than CV and PV with increasing variance in the simulated distributions.

CV had a clear tendency to increase variability with increasing timescale for all simulations ($\gamma > 0$), especially for non-Gaussian distributions (Fig. 3). On the other hand, variance exponents of PV were close to zero for all simulations except for those with autocorrelated time series. For negatively autocorrelated time series, PV tended to show decreasing variance with timescale ($\gamma < 0$), while for positively autocorrelated time series, PV tended to show increasing variance with timescale ($\gamma > 0$). Instead, variance exponents of D were close to zero for all the simulations, indicating that variance in D did not tend to increase or decrease with increasing timescales (Fig. 3).

The fruit-production data were mostly negatively autocorrelated (Fig. 4a) and indicated that D had a negative logarithmic association with AR1 ($R^2 = 0.27$, $P < 0.001$), while PV and CV were not ($P > 0.05$; Fig. 4a). Linear models relating D for the fruit-production data to CV and AR1 metrics and the log-transformed mean of the time series explained 63% of the variance in D . AR1 and CV were negatively and positively correlated with D and accounted for 21 and 34% of the variance in D , respectively, and the mean was positively correlated with D and explained only 8% of the variance (Table 2). The model fitting PV as a function of CV and AR1 showed that only CV was a statistically significant predictor

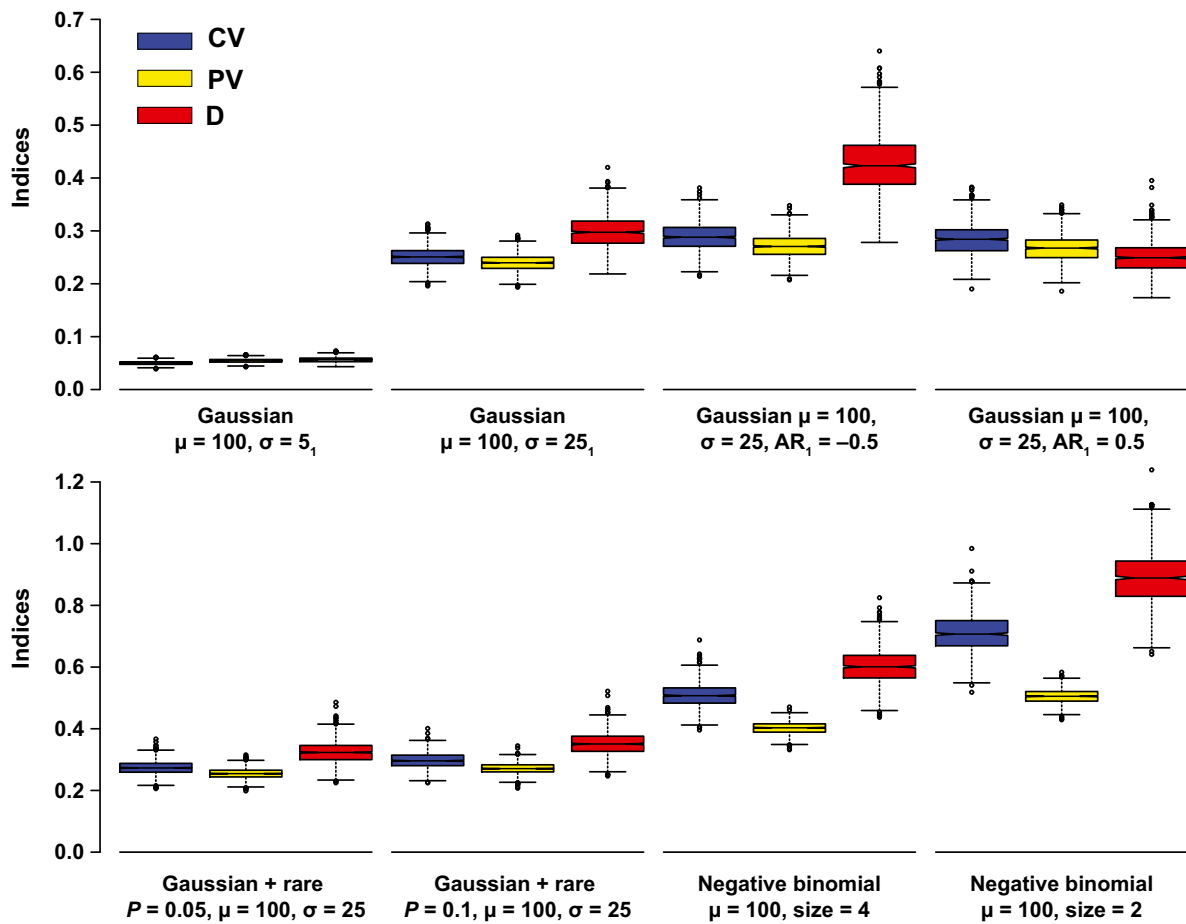


Fig. 2. Boxplots with notch showing the comparison of CV, PV, and *D* indices for eight different simulated distributions (four Gaussian with equal mean but different variance, two Gaussian with rare events occurring with different probability, and two negative binomial with equal mean but different size). In each case, 1000 time series of 100 values were simulated. See *Materials and Methods* and *Simulations* for further details on the simulations.

of PV, accounting for 47% of the variance in PV (Table 2). The model correlating the fruit-production CV with AR1, PV, and the mean accounted for 81% of the variance in the CV. AR1 explained only 1% of the variance in the CV, and PV accounted for 70% of the variance, being positively correlated to CV, and the mean, which was negatively correlated with CV, explained 10% of the variance in the CV (Table 2).

In contrast to the fruit-production data, the bird-count data were mostly positively autocorrelated (Fig. 4b), which is related to the fact that some time series presented temporal trends. *D* was not significantly associated with AR1. Instead, PV and CV were, respectively, positively and negatively correlated to AR1 (PV: $R^2 = 0.19$,

$P < 0.001$; CV: $R^2 = 0.47$, $P < 0.001$, Fig. 4b). The relationship found in PV and CV with positive AR1 is a consequence of the temporal trend of the time series, while *D* is insensitive to that. PV increases its value when increasing AR1 because of the different average of the initial and final parts of the time series (therefore increasing proportional variability when comparing initial to final parts). Conversely, CV decreases when increasing AR1 because of the underlying relationship between the mean and the SD of time series in which mean increases (or decreases) faster than SD; that is, the slope of the relationship $SD \sim \text{mean}$ in our fruit-production dataset was 0.66 ± 0.06 ($R^2 = 0.54$, $P < 0.001$) and in our bird-count dataset was 0.37 ± 0.02 ($R^2 = 0.63$,

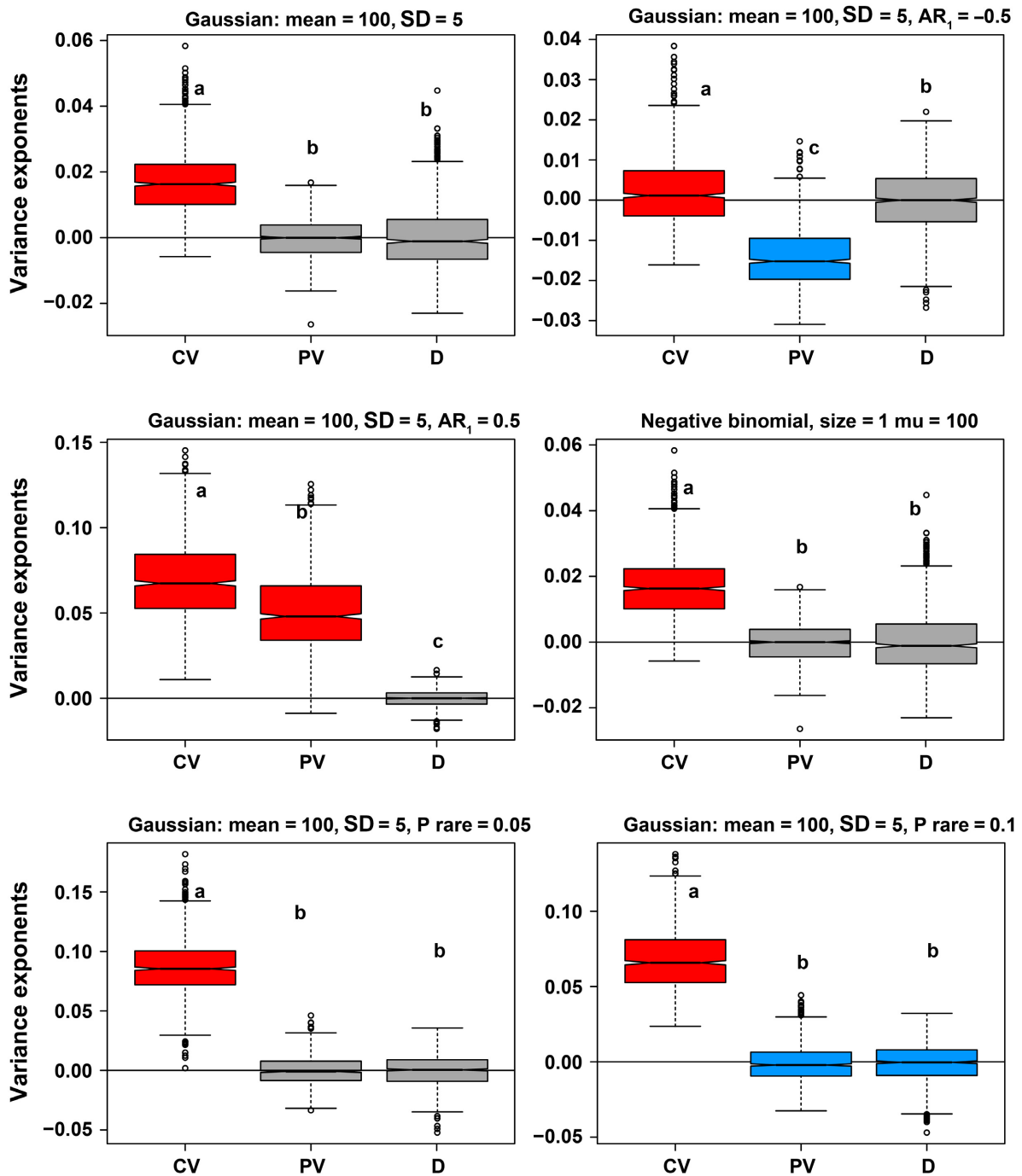


Fig. 3. Boxplots with notch showing the variance exponents for CV, PV, and *D* indices using six different simulated distributions (three Gaussian, one with negative, one with positive, and one with no temporal autocorrelation; one negative binomial; and two Gaussian with rare events occurring with different probability). In each case, 1000 time series of 100 values were simulated. Blue (negative) and red (positive) boxplots indicate that the mean of the distribution differed from zero at the 0.05 level using a *t*-test, while gray boxplots presented a mean distribution that could not be distinguished from 0. See *Materials and Methods* and *Simulations* for further details on the simulations.

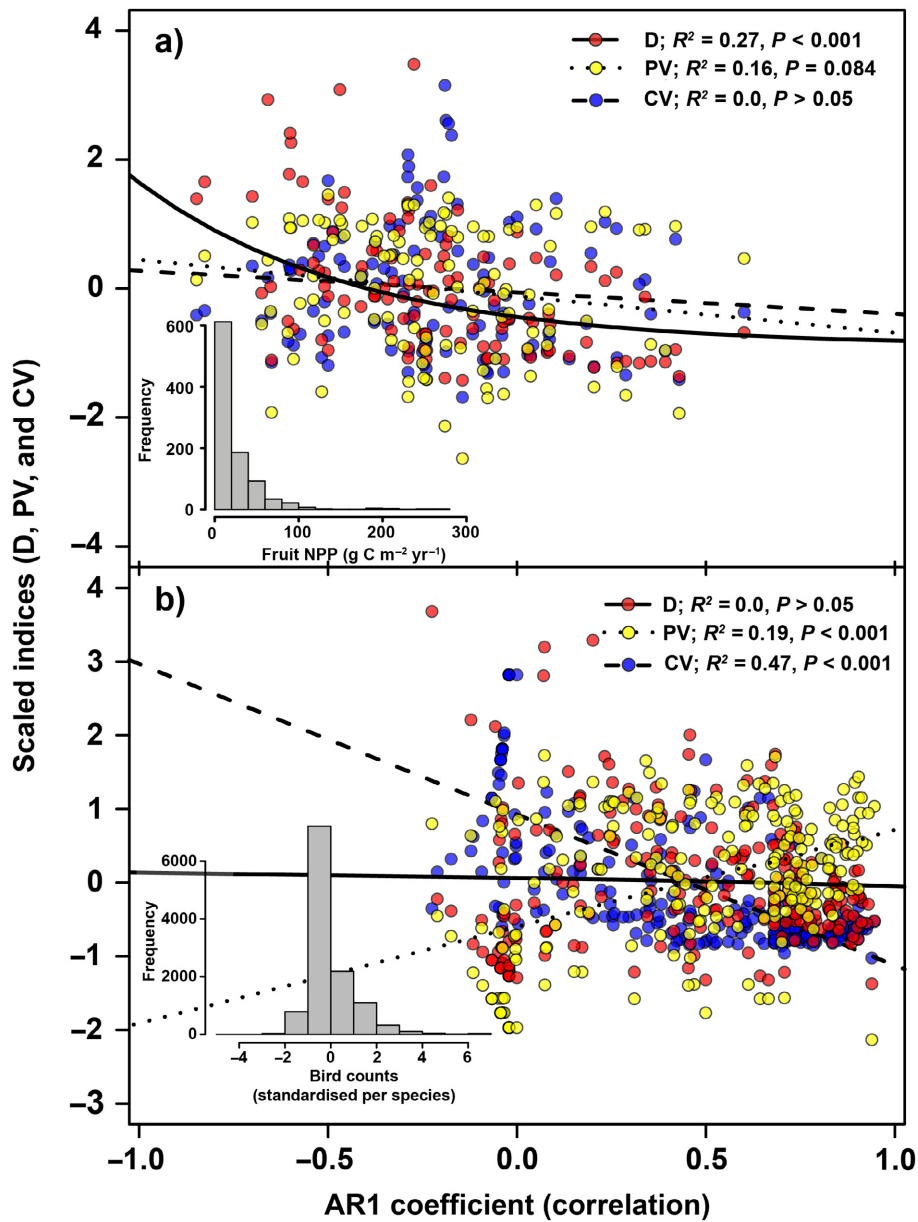


Fig. 4. Relationships between AR1 and the *D*, PV, and CV indices for (a) fruit-production data and (b) bird-count data. The insets show the distribution of the fruit-production data (a) and the bird-count data. NPP indicates net primary production.

$P < 0.001$). Time series with trends will then have larger changes in their means than in their SD, thereby affecting CV.

Linear models predicting *D* for the bird-count data explained 46% of the variance in *D*. Both AR1 and CV were negatively correlated with *D* and accounted for 10 and 33% of the variance in

D, respectively. The mean of the time series was positively correlated with *D* and explained 7% of the variance (Table 2). The same model predicting PV did only find CV to be significantly negatively correlated to PV, explaining 61% of the variance in PV. The model correlating the fruit-production CV with AR1, PV, and the mean

Table 2. Summary of models using fruit-production and bird-count data correlating the *D*, *PV*, and *CV* indices with *AR1*, *PV*, or *CV*, and the natural logarithm of the mean of the time series.

| Index | $\beta \pm SE$ | R^2 |
|------------------|------------------------|-------|
| Fruit production | | |
| Ln <i>D</i> | | |
| <i>AR1</i> | $-0.40 \pm 0.06^{***}$ | 0.21 |
| <i>CV</i> | $0.71 \pm 0.07^{***}$ | 0.34 |
| Mean | $0.34 \pm 0.07^{***}$ | 0.08 |
| Ln <i>PV</i> | | |
| <i>AR1</i> | -0.06 ± 0.07 | 0.00 |
| <i>CV</i> | $0.34 \pm 0.08^{***}$ | 0.47 |
| Mean | 0.12 ± 0.08 | 0.01 |
| Ln <i>CV</i> | | |
| <i>AR1</i> | $-0.09 \pm 0.04^*$ | 0.01 |
| <i>PV</i> | $0.75 \pm 0.04^{***}$ | 0.70 |
| Mean | $-0.31 \pm 0.04^{***}$ | 0.10 |
| Bird counts | | |
| Ln <i>D</i> | | |
| <i>AR1</i> | $-0.58 \pm 0.08^{***}$ | 0.10 |
| <i>CV</i> | $-0.77 \pm 0.08^{***}$ | 0.33 |
| Mean | $0.23 \pm 0.09^*$ | 0.03 |
| Ln <i>PV</i> | | |
| <i>AR1</i> | -0.06 ± 0.06 | 0.00 |
| <i>CV</i> | $-0.91 \pm 0.07^{***}$ | 0.61 |
| Mean | -0.11 ± 0.08 | 0.01 |
| Ln <i>CV</i> | | |
| <i>AR1</i> | $-0.17 \pm 0.05^{**}$ | 0.04 |
| <i>PV</i> | -0.04 ± 0.04 | 0.00 |
| Mean | $-0.70 \pm 0.05^{***}$ | 0.70 |

Notes: The regression coefficients are beta weights (β , standardized coefficients) \pm standard error (SE). The proportional marginal variance decomposition (PMVD) metric (Grömping 2007) is also shown as a measure of the explained variance (R^2). Ln indicates the variables were transformed to the natural logarithm.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

accounted for 74% of the variance in the *CV*, and *AR1*, *PV*, and the mean explained 4, 0, and 70% of the variance, respectively, and all were negatively correlated with the *CV* (Table 2). These results indicate that the *CV* is highly dependent on the mean of the time series, while *PV* and *D* are weakly dependent on the mean.

All three indices can also be used to assess intra-annual variability (Fig. 5), as a measure of seasonality. All indices behaved similarly (for all comparisons $R > 0.75$; $P < 0.001$) when assessing intra-annual variability using the monthly rodent data (Fig. 5a). The intra-annual index values, however, can be quite similar or dissimilar, even independently of the *AR1* index, depending on

the behavior of the captures within a year (Fig. 5b, c). Both indices provided the same value for captures in 1978, which peaked twice during the year (Fig. 5b). Rodent captures in 1990 mostly declined from January to September and then increased until December (Fig. 5c). The progressive evolution of rodent captures led to higher *CV* and *PV* than *D* values, compared to year 1978. These results highlight again the different behaviors of the *CV*, *PV*, and *D* indices with the chronological order of the values within a time series.

DISCUSSION

The analyses of the fruit-production and bird-count datasets, combined to those of our simulations, suggest that *D* is more sensitive than *PV* and *CV* to changes in time series with negative temporal autocorrelations (Figs. 2 and 4). In datasets with positive autocorrelation structure, *PV* and *CV* increase their estimation of variability because of temporal trends in the data. This opposite behavior is because *D* calculates temporal variability within each time step (see Eqs. 3 and 4) and is thus sensitive to the chronological order of the time series, whereas *PV* and *CV* are blind to the order, but if the average increases or decreases (e.g., non-stationary time series), their estimation of variability changes as well. Additionally, our simulations showed that *D* did not increase the estimate of variability with increasing timescale of the calculation (Fig. 3), even when using non-Gaussian distributions or temporally autocorrelated time series. Our results also confirmed the higher dependence on the mean of the *CV* compared to *PV* and *D*, which carries important implications for the correct assessment of temporal variability. In light of these results, the application of *D* in the field of ecology is justified.

Possible applications of *D* in ecology

A broad range of ecological subdisciplines involves temporal variability, such as resource pulse ecology (Yang et al. 2008), population ecology (Heath 2006), or the study of non-linear dynamics in ecosystems (Hastings et al. 1993). Any field needing to evaluate temporal variability can thus potentially benefit from the use of *D*, as shown by our analyses. Masting studies have

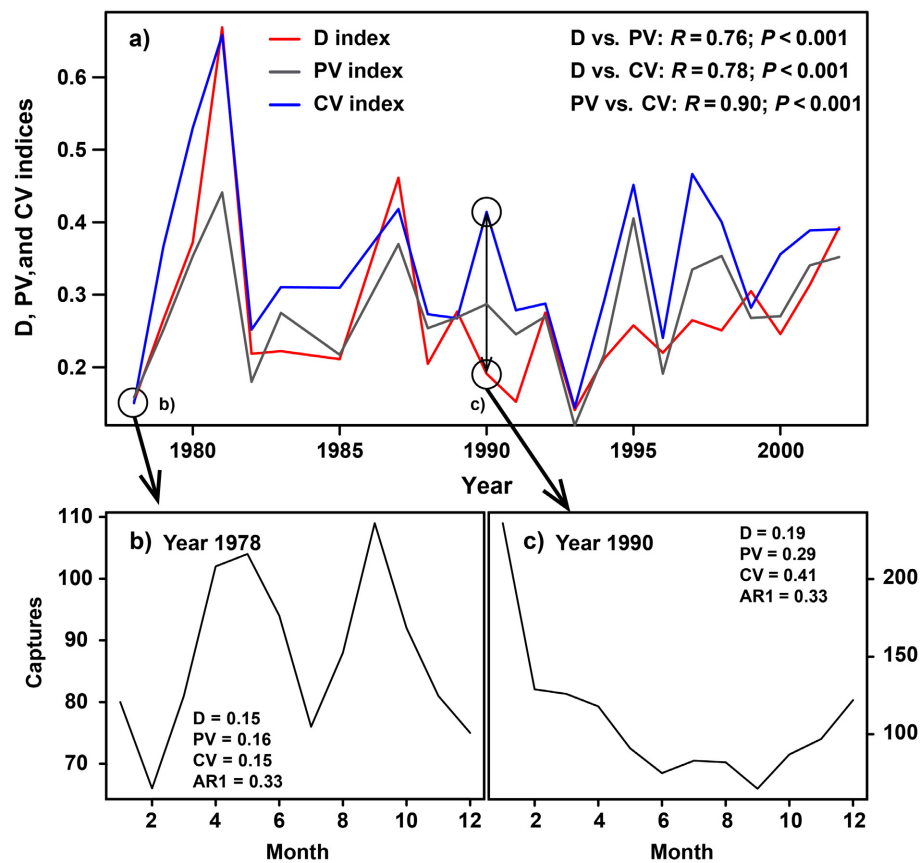


Fig. 5. (a) Intra-annual variability of rodent captures measured with the D , PV, and CV indices. The years with the minimum and maximum differences between the D and the CV indices are marked with a circle (1978 and 1990, respectively). Panels (b) and (c) show the monthly captures for 1978 and 1990.

particularly often relied on describing the behavior of fruit production using CVs and temporal autocorrelation (Sork et al. 1993, Herrera et al. 1998, Kelly and Sork 2002). D may represent an opportunity to explore masting with an aggregated index combining the information of both variability (CV or PV) and temporal autocorrelation (AR1), which would help to better characterize the interannual variability in fruit production (i.e., the higher the D index, the stronger the masting behavior). Nonetheless, the most interesting advantage of D and PV compared to the CV may be their much reduced dependence on the mean (Table 2). Large differences in the mean of fruit production might occur when comparing the reproductive behavior of different species or populations, which might result in underestimates of temporal variability in species with large means, given the negative relationship between

the mean and the CV (Table 2), which could lead to erroneous biological conclusions. This potential bias applies also to population ecology (e.g., bird counts). Comparing the CV for species or populations with very different means could lead to erroneous conclusions, because the variance explained by the mean of the time series can be as high as 70% (Table 2). We therefore recommend that these types of studies support their analyses with other indices whose values do not strongly rely on the mean of the time series. In that case, PV and D would be both a good choice for avoiding this drawback of the CV. Nonetheless, D is the only index that takes into account the chronological order of time series.

D could be useful in the study of resource ecology to characterize different temporal patterns of resource pulses. Biologically, it has different implications if a population, a species, or a

community produces pulses of resources with low or high disparity (time series A and B in Fig. 1). In time series A with low D (Fig. 1a), the system shifts from one state with large resource availability to another with fewer resources to which populations of fruit consumers must adapt, but only once during the time series. In time series B with high D (Fig. 1b), the pulses of resources are intermittent, so the population of consumers will fluctuate with the pulses with a time delay (Clotfelter et al. 2007). The biological strategies and evolutionary or behavioral adaptations of organisms living under these two regimes of resource pulses would necessarily differ (Owen-Smith 2008, Yang et al. 2008). D combined with the PV or CV might then be used to assess the kind of behavior of the system and allow comparisons among systems.

CONCLUSIONS

Our results indicate that D can be more suitable than the PV and the CV indices for assessing temporal variability in cases where taking into account the chronology of time series is important. D is more suitable when time series are negatively autocorrelated, and it does not increase its estimation of variability when increasing the length of time series. D varies not only with temporal variability but also with the degree of autocorrelation, so using only one index (D) would allow the capture of both variability and temporal autocorrelation in similar proportions. D , as well as PV, is more suitable than CV when comparing temporal variability in time series with very different means or when assessing the evolution of the temporal variability of a time series. We recommend introducing D in ecological studies with temporal variation, at least, as a support for PV or CV in those cases in which the chronological order of the time series is important.

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